Fuelling ecology and migratory strategies: a study of two *Acrocephalus* Warblers

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Declaration:

I declare that this thesis has not been submitted, either in the same or different form, to this or any other University for a degree. All the work described in this thesis was carried out by myself in the School of Biological Sciences at the University of Sussex. Where other sources are referred to this is indicated.

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SUMMARY

Migratory journeys by birds are divided into fuelling phases and flight phases. Fuelling behaviour may influence not only flight length but also the time-course and organisation of migration. I investigated fuelling behaviour using two long distance migrants, Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *A. schoenobaenus*, as models.

Two key components of fuelling behaviour are: the fuel deposition rate (FDR) and the fuelling duration (FD). Using ringing data on Reed Warblers collected at four sites during the autumn (England & Portugal) and spring (Senegal & Spain) migration seasons, I found that FDRs and FDs varied considerably in space and time. This correlational study suggested that food availability, metabolic constraints, moult, time, and ecological barriers all influenced Reed Warbler fuelling. Fuelling behaviour therefore seemed to respond flexibly to the conditions experienced at a site and the demands of the journey ahead.

Recent models have assumed that fuelling behaviour is optimised such that time spent, energy costs or predation risk (or some combination), are minimised during migration. I performed feeding experiments to test the model predictions and found that Reed and Sedge Warbler behaviour was consistent with time-minimisation. However, early-migrating Reed Warblers were minimising both time and predation risk. I conclude that region-specific fixed FDs, selected to minimise time within the range of FDRs typically experienced, are a key way in which time-minimisation is achieved. Indeed, Sedge Warbler FDs had even been optimised by an expectation that FDRs increase at future sites. FDRs are simply maximised and are therefore only constrained by food availability and metabolic capacity (which appears flexible).

Reed Warblers appeared to avoid departing in adverse weather: therefore departure decisions were not determined by FD alone. However, Reed Warblers did not wait for optimal conditions. FDRs and time-selected FDs may therefore be primary influences on the time-course and organisation of migration.
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LIST OF ABBREVIATIONS

FDR = Fuel deposition rate
MD predation risk = Mass-dependent predation risk
FID predation risk = Foraging-intensity dependent predation risk
CHAPTER 1

SCIENTIFIC CONTEXT AND BACKGROUND

1.1 GENERAL INTRODUCTION

Of all life-history traits, migration is one of the most fascinating and one that generates some of the most impressive spectacles on Earth. No one can deny the sheer beauty of thousands of Monarch butterflies *Danaus plexippus* migrating down the Mississippi river in North America or the drama of Wildebeest *Connochaetes taurinus* negotiating swollen, crocodile-filled rivers in their quest to follow the cycle of rains across Africa. In the world of ornithology, there are equally impressive spectacles, like the sight of thousands of White Storks *Ciconia ciconia* gliding serenely across the narrow Bosphorus Strait or the immense coastal ‘falls’ where every tree, bush, and piece of open turf can be hopping with birds (Elkins 1988, Alerstam 1990). Often it is the feat of migration that people marvel at. How does a turtle find its way back to the same beach to breed each year through the featureless deep ocean? How does an Arctic Tern *Sterna paradisaea* cope with the immense physical exertion required to fly from one pole to the other?

Whilst many animals undergo migrations, the prevalence of migration within the bird class (Aves) is well recognised. It is the power of flight that makes birds, like bats and insects, well adapted to taking advantage of seasonally and spatially fluctuating resources, and to escape resource-limiting conditions (Alerstam 1990). Numerous families of birds have at least one member that is considered migratory, from Grebes (Podicipedidae) and Finches (Fringillidae) to Falcons (Falconidae) and Hummingbirds (Trochilidae). The diversity of migratory journeys is equally impressive. Some birds travel less than 100 km, moving from highland to lowland habitats, whilst others travel 3000 km or more, moving from the Northern to the Southern Hemisphere (Alerstam 1990).

In northern Europe almost all species have migratory tendencies in at least part of their range. Birds such as the Wren *Troglodytes troglodytes* migrate in parts of their range, even making long sea crossings (Alerstam 1990); though most people observing
one in their back garden might doubt their ability to cross even the smallest stretch of water. Many European songbirds (Passerines) are characterised by long distance migrations that take them south through Europe, across the Mediterranean Sea and the Sahara desert, and into Africa, thus escaping the Northern Hemisphere winter. Indeed, every autumn approximately four billion birds belonging to some 200 species leave the Palaearctic region and head for Africa (Moreau 1972). Whilst many of these species spend the winter north of the equator, many continue south even reaching the southern coast of Africa. It is the ability of ‘trans-Saharan’ migrant passerines to complete such an incredible journey that is the main focus of this study.

1.2 THE MIGRATORY JOURNEY AND FUELLING BEHAVIOUR

How does a migratory passerine, that may be little more than 10 cm in length, complete a 4500 km journey from northern Europe to Africa? To fly anywhere, a bird requires energy in order to drive its flight muscles. The energy must be derived from food, or from energy stores that are built up when the energy obtained from food is surplus to metabolic requirements. As many passerines migrate by night, they are unable to attain food whilst on the wing and are therefore reliant on stored energy (Alerstam 1990). Consequently, the migration of a typical passerine is characterised by fuelling phases when energy stores are accumulated and flight phases when the stored energy is expended to power flight. As there are few cases in which energy stores are sufficient to complete a long distance migration in one go, almost all journeys require a number of fuelling and flight phases (Lindström & Alerstam 1990). The time taken to burn fuel during flight is typically less than the time taken to accumulate it, therefore the greatest investment of time, and probably energy, during a migratory journey is expected to occur during fuelling phases (Hedenström & Alerstam 1997). Many authors have therefore argued that behaviour during fuelling phases is critical to determining the organisation and time course of migration (see Alerstam & Hedenström 1998 for a review).

The majority of migratory journeys involve complications beyond simply attaining enough fuel to fly the distance. For example, there are large areas between northern Europe and Africa in which fuelling is not possible. These areas are classed as barriers and the Mediterranean Sea and the Sahara desert are the two largest barriers a
typical trans-Saharan migrant will face (Alerstam 1990). In some cases this may become one barrier if the North African coast does not provide suitable fuelling opportunities. In order to cross such large barriers, migrants must typically accumulate large energy reserves (Schaub & Jenni 2000b): the mass of these reserves can be equivalent to the fuel free mass of a bird.

**Regulation of Fuelling Behaviour**

The autumn migration of passerines from northern Europe to Africa begins for adults and juveniles at the breeding site. Before leaving breeding sites or areas nearby, the birds undergo pre-migratory fuelling. The timing and initiation of this period of fuelling may depend on a number of factors. Adults do not usually commence fuelling until breeding activities have been completed, although I found evidence that suggests that active fuelling sometimes begins before parental duties cease (section 2.3.1). For juveniles, fuelling may commence once independence is achieved although in a number of species a post-juvenile moult must first be at least partly completed (Schaub & Jenni 2000a). Genetic factors also determine the initiation of fuelling: the onset of fuelling and the phenomenon of ‘migratory restlessness’ have been linked to an endogenous time program in a number of species (for review see Gwinner 1990). There is also evidence that the timing of fuelling has been shaped such that species, which would otherwise experience inter-specific competition due to niche similarities, fuel at different times (Howlett et al. 2000). However, most of the cases highlighted by Howlett et al. could be explained by differences in the length of the journey ahead, as long distance migrants must typically commence their journey earlier than short distance migrants.

The extent of pre-migratory fuelling, and fuelling during ‘stopovers’ between flight phases, might be determined by a number of factors. These may include food availability and quality, competition, predation risk and innate behavioural programs (Alerstam 1990, Bairlein 1998, Houston 1998, Berthold 1999). The observation that fuel loads are typically below their physiological maxima suggests that any one, or a combination, of these factors actually constrain fuel loads. Indeed the benefits of fuel storage are offset by costs associated with accumulating, maintaining and transporting stores (Witter & Cuthill 1993, Klaassen 1996, Fransson & Weber 1997).
Food availability and quality is widely believed to be an important determinant of the fuel load accumulated (Alerstam 1990, Fransson 1998a). Most fuel is stored in the form of fat (Odum et al. 1965, Blem 1976), although recent work suggests that protein, despite yielding less energy per gram, is also stored to fuel flight (Piersma 1990, Lindström & Piersma 1993). The amount of fat stored will depend not only on the amount of food consumed but also on the percentage of that food that can be converted to fat. To aid the deposition of fat, migrants typically increase their intake rate, becoming hyperphagic, whilst some species even alter their diet to increase their intake of ‘fatty’ foods. For example, a number of warbler species in the genus Sylvia show a dramatic shift from a largely insectivorous diet to one of fruit prior to migration (Herrera 1984, Alerstam 1990). Bairlein (1998) demonstrated that Garden Warblers Sylvia borin, given a choice of foods of equal energy content, actively choose the food with the higher lipid content.

Whilst some species switch to frugivory, other species have evolved to take advantage of abundant food sources. The Sedge Warbler Acrocephalus schoenobaenus has been shown to seek out reedbeds with a superabundance of Plum-reed aphids Hyalopterus pruni, on which they gorge themselves (Bibby et al. 1976, Bibby & Green 1981). Sedge Warblers feeding on a good crop of aphids have been known to accumulate fuel loads that weigh more than their lean body mass (mass of a bird carrying no fuel), thereby more than doubling in weight (Bibby et al. 1976). Many other migratory species do not show any particular diet shift but will actively seek out habitats with abundant resources and show behavioural adaptations like hyperphagia (Alerstam 1990). Despite the adaptations to increase food intake, food availability is likely to be an important constraint on fuelling behaviour.

Even when food availability is high, other factors could constrain the fuelling rate. Competition with individuals of the same or other species, especially if either species is territorial, can reduce fuelling rates, as aggressive defence and alertness to intruders will reduce feeding time. Work on Wilson’s Warblers Wilsonia pusilla, a New World Warbler, suggests that mass gain (equivalent to fuel gain) is density dependent (Kelly et al. 2002) and Lindström & Alerstam (1992) noted aggression between Bluethroats Luscinia svecica attending an artificial food source. Competition may even shape the timing of migration within species; a common trend is for adults to commence migration before juveniles, which greatly outnumber adults on autumn migration.
Predation risk has often been cited as an important factor constraining fuel loads (Witter & Cuthill 1993, Gosler et al. 1995, Weber, Ens & Houston 1998). Flight comes at a high premium as weight must be kept to a minimum, and any increase in body mass will reduce the power output of the flight muscles and impair flight ability. This impairment can lead to reduced escape performance and an increase in predation risk (Witter et al. 1994, Metcalfe & Ure 1995, Kullberg et al. 1996, Kullberg 1998, Kullberg et al. 2000, Lind et al. 1999). This mass dependent predation risk has been shown to lead to reductions in body mass if risk is increased (Gosler et al. 1995, Krams 2000, Lilliendahl 2000, Gentle & Gosler 2001). Fuelling migrants regularly increase their body mass by 50% and thus greatly increase their predation risk. The extent to which predation risk constrains fuel loads is unknown but Fransson & Weber (1997) tried to answer this question. By exposing caged Blackcaps *Sylvia atricapilla* to different predator regimes, they found that birds experiencing the greatest predation risk fuelled faster and showed heightened levels of migratory restlessness before birds at lower risk. Although this response may not represent the situation in the field, it suggests that birds may not alter their fuel load in response to predators but instead reduce the amount of time at which they are at risk. Conversely, Houston (1998) hypothesised that birds may reduce, not increase, their feeding rate, so that predator awareness is not diminished.

Further, Kullberg et al. (2000) argued that higher fuel loads in Sedge Warblers, relative to Reed Warblers *Acrocephalus scirpaceus*, may be responsible for differential predation rates on these two species by Eleonora’s Falcons *Falco eleonorae* on Crete. Despite Reed Warblers being the commoner species, Sedge Warbler remains make up the majority of *Acrocephalus* warbler remains in the nests of Falcons, highlighting the peril of large fuel loads.

The cost of transporting fuel reserves, described by the relationship between fuel load and flight range, is a further constraint on fuel loads. As mass increases, the increase in flight range per unit of fuel added decreases, due to increasing transport costs and drag (Pennycuick 1989). Therefore, for a bird trying to complete its migration as quickly as possible, there will come a point during fuelling when the benefits of increased flight range are outweighed by the time taken to accumulate the additional fuel (Lindström & Alerstam 1990). Maintenance of a fuel load may also incur a metabolic cost and therefore loads should be further constrained by the increasing metabolic costs associated with larger loads (Witter & Cuthill 1993, Klaassen 1996, Klaassen & Lindström 1996).
The level of fuel stored is therefore under the control of a complex web of factors, which may promote or constrain reserves depending on the trade off between the costs and benefits of accumulating, maintaining and transporting fuel reserves. The interplay of these factors will also be affected by the journey ahead. For example, a bird facing a short journey is unlikely to increase its predation risk in order to save time, whilst a bird with a longer journey might. The physiological and ecological factors outlined above may be important determinants of energy reserves, but a large body of theoretical work, aimed at identifying optimal strategies, points to innate behaviours having a greater role.

1.3 OPTIMAL MIGRATION

Evolution by natural selection is a process of optimisation in the mathematical sense (Alexander 1982). Theoretical work on ‘optimal migration’ has introduced a whole new framework in which to examine the journeys of migratory birds (Alerstam & Hedenström 1998). Starting with Alerstam & Lindström (1990), numerous models have been developed to demonstrate how fuelling behaviour may be optimised. An important premise behind these models is that the time course and organisation of migration is strongly influenced by the fuelling behaviour exhibited during pre-migratory fuelling and on stopover. Therefore fuel loads and fuelling rates are expected to hold adaptive significance.

Models of Fuelling Behaviour

Lindström & Alerstam (1990) first introduced the idea that fuelling decisions may be governed by an overall migration strategy. Hedenström & Alerstam (1997) later modelled three strategies that could apply to migrants under different circumstances. For each of the strategies, selection is theorised to have favoured birds that minimised one of three currencies: time, total energy spent on migration, and the energy cost of transport. Further models have included predation risk as a currency (Houston 1998). Any of these strategies may be adopted depending on circumstance. For example, every spring the race to reach breeding grounds and secure a territory can be intense (Kokko 1999, Currie et al. 2000), so selection for minimising the total time spent migrating may have shaped the fuelling behaviour of spring migrants (Hedenström & Alerstam 1997).
During autumn migration, it can be argued that time is not an overriding constraint and thus energy may be the currency under selection. For each currency, the models generate unique and testable predictions concerning the relationship between the fuel deposition rate (FDR) and the fuel load at departure (departure load), and also between the FDR and the time spent fuelling (section 4.1).

Empirical data on FDRs and departure loads have only been gathered in the field in four studies (Carpenter et al. 1983, Lindström & Alerstam 1992, Fransson 1998a, Danhardt & Lindström 2001). From the relationship between FDR and departure load, three of the studies concluded that the study species were time-minimising, although not all the data agreed with that outcome. In the fourth study by Danhardt & Lindström (2001), the results were largely inconclusive, although there was some support for the energy cost of transport model. Without more empirical tests, the key selective pressures shaping fuelling behaviour cannot be identified nor can the models be improved and refined. Therefore, further studies are crucial if the relationship between fuelling rates and departure loads and its adaptive significance are to be understood. I aim to provide two further tests of these models in this thesis (Chapters 4 & 5).

Models Incorporating Departure Decisions and Weather

A number of other models have been generated that give more emphasis to the flight stage of a migratory journey. Weber, Alerstam & Hedenström (1998) were the first to argue that optimising the decision to depart could have a greater impact on the course of the migratory journey than decisions made during the fuelling phase. Calculations of flight ranges based on real day-to-day weather data support this argument: Liechti & Bruderer (1998) demonstrated that failure to take wind conditions into account could halve the potential flight range of a bird with a moderate fuel load. Conversely, a bird actively selecting tailwinds can greatly increase its flight range and thus increase its speed of migration relative to a bird optimising its departure load alone.

Studies to date indicate that in some cases birds are highly sensitive to weather conditions whilst in others the decision to depart is only affected by particularly adverse conditions (Fransson 1998b, Åkesson & Hedenström 2000, Danhardt & Lindström 2001). Radio tracking experiments on migrants showed a strong association between the presence of tailwinds and departure in some species but not in others (Åkesson & Hedenström 2000, Åkesson et al. 2002). Regardless of when and where a bird pays
attention to conditions aloft, the key point is that taking weather conditions into account may alter the predictions of the models of fuelling behaviour outlined above (Weber, Alerstam & Hedenström 1998). A bird that reaches its optimal departure load but chooses not to leave due to unfavourable flight conditions may continue to fuel until suitable conditions arise. Therefore, at a site where favourable conditions are uncommon, one would expect to see inflated departure loads, a situation that has been noted in the datasets discussed earlier (Lindström & Alerstam 1992, Fransson 1998a). However, no cases of delayed departure concurrent with an inflated departure load have been identified to date. In Chapter 6, I aim to discover the extent to which the departure decisions of Reed Warblers are influenced by weather conditions.

**An Alternative Model**

The models of fuelling behaviour driven by time- or energy-minimisation, which underlie even the theoretical investigations into wind influence, assume that migrants possess behavioural programs that calculate the optimal departure load, or the optimal time to spend fuelling, given a certain fuel deposition rate. They also assume that a migrant can measure its own FDR to a fairly high degree of accuracy. The validity of both these assumptions must be considered doubtful given the complexity of the behavioural rules and the calculations involved. Many behavioural traits are governed by simple rules and one would expect that the same might be true of migratory behaviour.

A recent theoretical study by Erni et al. (2002) demonstrated that a simple rule could indeed lead to time-minimising behaviour closely resembling that generated by the complex rules of optimal migration models. In fact, this simple rule so closely mimics optimal behaviour that future studies must seek to test any unique predictions arising from it. The rule states that a bird should adhere to a ‘constant stopover duration’ (CSD), regardless of its FDR, and depart when that period is over. Empirical evidence for such a rule is lacking at present. However, an examination of stopover durations by Schaub & Jenni (2001) and experimental work by Gwinner (1986), both indicated fairly constant durations, and a lack of the variation in duration predicted by more complex rules. Discovering that migrants use a CSD rule would be an important step in understanding the control of fuelling behaviour and I aim to test for the existence of such a rule in this thesis.
Crossing Barriers

One problem that all the models of fuelling behaviour must address is the question of barriers. Using any of the models described above, a fuel deposition rate of less than 0.04 (fraction of the lean body mass accumulated per day) will result in a fuel load equivalent to less than 50% of lean body mass. For a bird attempting to cross a barrier as large as the Sahara, such a fuel load would theoretically be insufficient (Biebach 1992). Further, Schaub and Jenni (2000a) measured the FDRs of three migratory warblers at sites throughout Europe and found that their mean FDR rarely exceeded 0.04, and at many sites, including those in southern Europe, rarely exceeded 0.03. Thus on the basis of this evidence, behavioural programs must be modified in response to an appropriate cue as barriers are approached, such that migrants remain at fuelling sites longer and accumulate greater fuel loads. Fransson et al. (2001) may have found one of those cues. By exposing Thrush Nightingales Luscinia luscinia to different magnetic regimes, corresponding to southern Sweden and northern Egypt, they showed that birds fuelled for longer and attained larger fuel loads under the latter regime.

The ease with which behavioural programs can be modified, to allow the successful crossing of barriers, depends on the complexity of the rules underlying the program. If birds simply fuel for fixed periods of time (CSD rule), then this period could easily be increased in response to a magnetic cue for example. A more complex program in which the time spent fuelling is a function of the FDR, may be much more difficult to modify.

Summary

The adaptive significance of fuel loads, fuelling durations and fuelling rates, and the currencies governing them are currently poorly understood, as is the influence of departure decisions on the migratory journey as a whole. For long distance migrants, I would have expected time-minimisation to be a key selection pressure shaping fuelling behaviour, however, the empirical support for any currency at present is weak. Therefore, discovering the main selective pressure(s) shaping fuelling behaviour, is one of the key questions of this thesis. The decision to depart from a fuelling site may be influenced either by weather conditions or by the time taken for a bird to optimise its fuel load, which in turn may affect the migratory strategy a bird adopts. The degree to which these two factors influence departure decisions is also a key question for this
thesis. Whilst a currency such as time may have shaped both fuelling behaviour and departure decisions, a number of other factors are likely to impact on fuelling behaviour. Therefore, a number of subsidiary questions arise that I shall attempt to answer in this thesis. The most important of these, are how food availability, ecological barriers, predation risk and an expectation of future fuelling conditions affect fuelling strategies.

1.4 MIGRATORY STRATEGIES – DIVERSITY, AND FLEXIBILITY IN THE FACE OF CHANGE

Migration strategies show great variation between species. The strategies of Reed and Sedge Warblers illustrate this clearly, as both species favour reedbeds and show considerable morphological and ecological similarities (Leisler et al. 1989). Bibby & Green (1981) argued that Sedge Warblers from northwest Europe are using a ‘long hop’ strategy in which they complete the journey from northwest Europe to sub-Saharan Africa without refuelling. Conversely, Reed Warblers were argued to adopt a ‘short hop’ strategy in which they take 3-4 steps to travel from northwest Europe to the Iberian Peninsula, where they fuel extensively in order to cross the Sahara. Whilst most species are believed to cross the Sahara in one non-stop flight (Biebach et al. 2000), the Spotted Flycatcher is thought to make a gradual crossing, feeding along the way (Schaub & Jenni 2000b). Aerial feeders such as Barn Swallows Hirundo rustica, and other members of the Hirundine family, may also feed along the way.

Whether the diversity of migratory strategies can be explained simply by differences in FDRs is unclear but seems unlikely. In some cases it is evident that the choice between long and short hops is governed by habitat availability: this is particularly true of waders (Alerstam 1990, Farmer & Wiens 1998, 1999). The advantage of one strategy over another will depend on the physiological, morphological and ecological constraints a given species faces. The constraints on a migrant are likely to change both on a geographical scale and in time, particularly with respect to ecological constraints. As humans continue to alter the environment, and the large-scale changes associated with global warming seem inevitable, the habitats and fuelling sites that birds currently rely on are likely to change.

The adaptability and flexibility of migratory strategies faced with such changes is unclear, although a landmark study by Berthold et al. (1992) showed that the genetic
basis underlying certain migratory behaviours could change surprisingly rapidly. The big question as to whether migrants will be able to cope with continuing change has yet to be addressed, although migrants have clearly adapted to large-scale changes in the past (Sutherland 1988). However, many would favour the approach of assessing the needs of migrants and acting to conserve them, rather than learning from the consequences of destroying them. Migrants may be particularly vulnerable because their survival is dependent not just on their breeding habitat but also on their wintering habitat and all the stopover habitats in between (Bairlein 2000).

The destruction or degradation of stopover habitats could have a strong impact on the migratory journey of any species. The impact is likely to be greatest on those species that rely on just a few key staging areas and for this reason it is critical that we identify and conserve these staging areas at an early stage (Bairlein 2000, Wernham et al. 2002). However, habitat degradation on a large scale, due to processes such as global warming, can also threaten survival. Regardless of which model of optimal migration is closest to the truth, the consequences of decreased habitat quality are the same; FDR will decrease and the migratory journey will take longer to complete. Given that the limited testing of optimality models to date indicates that long-distance migrants have been selected to minimise time (section 1.3), this must have fitness/survival consequences. Therefore it is crucial that we gain a greater understanding of the various migratory strategies, as it is a prerequisite for sound conservation strategies and action plans (Bairlein 2000, Wernham et al. 2002).

1.5 THE EURASIAN REED WARBLER ACROCEPHALUS SCIRPACEUS

Numerous authors have studied Reed Warblers, leading to a wealth of information on their breeding biology (e.g. Bibby 1978, Cramp 1992), habitat preferences and aspects of their migratory behaviour (Wernham et al. 2002). This information provided an invaluable background for the design and interpretation of the work carried out in this thesis. Much of the data on Reed Warblers has come from ‘ringing’ which typically involves catching birds in mist nets and fitting them with uniquely marked rings whilst also taking data on size, body mass and condition. Birds caught repeatedly at the same site (retraps) have provided data on the FDRs of Reed Warblers and allowed some of the variables influencing fuelling behaviour to be
identified (e.g. Schaub & Jenni 2000a). Ringed birds may also be caught at other sites and are termed as ‘recoveries’ whilst a bird caught at one site that was ringed at another, is termed a ‘control’. Controls and recoveries have been used to identify key fuelling areas and the migratory routes taken by Reed Warblers (e.g. Wernham et al. 2002). To date, the studies based on ringing data, have largely described fuelling rates and durations but have not identified many variables influencing fuelling behaviour or analysed the data within the framework of ‘optimal migration’ (section 1.3). There have been no experimental studies on Reed Warblers aimed at specifically testing models of optimal migration. I aim to build on the current knowledge of Reed Warbler fuelling behaviour using both ringing data and experimental data.

Classification

The Reed Warbler belongs to the order Passeriformes and is a member of the Old World warbler family, the Sylviidae. Many of the 54 Sylviidae breeding in the Western Palearctic are migratory, indeed 25 species are trans-Saharan migrants (Snow & Perrins 1998). The Reed Warbler is part of the genus Acrocephalus, which also includes the Sedge Warbler and the Great Reed Warbler A. arundinaceus. Of the seven Acrocephalus warblers breeding in Europe, only one regularly winters in Europe whilst five winter in Africa and one in Asia. Two races of Reed Warbler are currently recognised: ssp. scirpaceus breeds in Europe and North Africa (race of birds in this thesis), and ssp. fuscus breeds in southeast Russia, southwest Siberia, the Kazakh and Kirghiz steps, Central Asia, Asia Minor and the north Near East (Svensson 1992).

Plumage Appearance and Moult

The Reed Warbler (ssp. scirpaceus) is approximately 13 cm in length, has a wing-span of 17-21 cm and is described as a medium sized, compact, robust and skulking warbler (Snow & Perrins 1998). Adults typically have brown-olive upperparts and warm white underparts, with a suffusion of pale buff on the side of the breast and flanks. The head has a distinct dull cream eye-ring and supercilium, and dark lores. Juveniles are altogether brighter and rustier than adults (Cramp 1992, see Plate 2). Overall, the Reed Warbler is a fairly non-descript warbler that can be confused with similar species in the same genus. In particular, the largely sympatric Marsh Warbler A.
*palustris* can be very difficult to separate. Fortunately, Marsh Warblers were very rare at all my study sites.

The plumage is brightest after a complete moult, in which all feathers are replaced. Adults have a complete post-breeding moult that typically commences at breeding sites in July/August but is interrupted before any flight feathers are replaced. The moult is suspended until the wintering grounds are reached. The exact timing of the moult in Africa varies between populations and wintering areas, with the majority of birds completing their moult between October and December. Birds that moult early often partially moult their body feathers in early spring. Juveniles undergo a post-juvenile moult involving head and body feathers, and the lesser and median upper wing-coverts (Jenni & Winkler 1994). The moult starts at the age of 6-7 weeks and is completed 3-4 weeks later. Like adults, juveniles undergo a complete moult in their winter quarters and some birds may partially moult before departing north in spring (Cramp 1992).

**Distribution and Breeding Ecology**

Reed Warblers breed throughout much of Europe but have a patchy distribution due to their reliance on wetland habitats that are typically situated in lowland areas (Fig. 1.1). Range expansions have been made in parts of northern Europe: in particular, a dramatic northward expansion occurred in Scandinavia, the Baltic states and northwest Russia during the 20th Century and is still ongoing (Snow & Perrins 1998). In Belgium, Luxembourg, Greece, Albania, Ukraine and Moldova, slight decreases in distribution have been noted. There have also been moderate expansions in Britain (Mead 2000). Birds from west and north Europe appear to winter north of the equator in West Africa (Wernham *et al.* 2002) whilst populations from south-central Europe and from the eastern part of the range, winter in East Africa both north and south of the equator (Pearson & Lack 1992). Reed Warbler breeding populations appear to be relatively stable throughout much of their range and increases have largely been associated with range expansions.

Breeding habitats are strongly tied to the presence of mature beds of reed *Phragmites* with strong stems taller than one metre (Cramp 1992). Although Reed Warblers nest almost exclusively in reeds, patches of reeds do not have to be extensive.
FIGURE 1.1: Breeding distribution of the Eurasian Reed Warbler *Acrocephalus scirpaceus* within Europe (green).
In wintering areas, most habitats used are associated with water but drier habitats such as tall grass and thickets are also adopted. Whilst reeds are favoured in some parts of the wintering range, they appear to be shunned in others (Cramp 1992). In both breeding and wintering habitats, Reed Warblers have been shown to be territorial (Cramp 1992).

Breeding commences in May in western and central Europe, with the first eggs being laid from mid-May. Most birds have one or two broods with each clutch containing an average of 3-5 eggs (Bibby 1978). Incubation takes 9-12 days and chicks usually fledge after a further 10-12 days (Cramp 1992). Chicks are fed a predominantly insectivorous diet, mirroring the diet of Reed Warblers at all stages in their lifecycle.

Migration

Autumn migration begins towards the end of the breeding season across much of the range. In north and west Europe passage begins in late July and continues until the end of September, with a few stragglers in October and even into November (Bibby & Green 1981, Omerod 1990). Peak passage at many northern sites occurs at the end of August, although adults peak earlier in numbers than juveniles at all sites (Wernham et al. 2002). At more southerly sites, passage is conspicuous in September and October (Bibby & Green 1981) whilst below the Sahara the first birds appear in mid-September and passage continues into early November. Further south still, the first birds in Nigeria and Ivory Coast do not arrive until early October (Cramp 1992). Birds in East Africa show a delayed arrival, with the main arrival in Kenya and Uganda occurring between November and January, suggesting that birds pause further north for several weeks before continuing south (Pearson & Lack 1992).

Spring migration in sub-Saharan Africa occurs chiefly between March and the end of April. In North Africa, the first arrivals are in March but the peak is often not until the end of April or early May. Throughout much of Europe the first arrivals occur in April but the bulk of birds do not arrive until May, whilst arrival at the most northerly of sites may not be until late May/early June (Cramp 1992).

Reed Warblers from much of Western Europe migrate in a southwest in autumn, passing through Iberia before crossing the Sahara in order to reach wintering areas in West Africa (Wernham et al. 2002). Birds in the eastern part of the range, particularly of the race fuscus, migrate round the eastern end of the Mediterranean in order to reach east Africa (Cramp 1992).
During migration, the habitats used for fuelling include reedbeds but fields of beans, gardens, flooded shrubland, woodland clearings and dry scrub may be utilised in parts of Europe. However, a preference for wet habitats seems to determine habitat choice in the majority of birds. The extent to which fuelling birds are territorial is unclear, although Bibby & Green (1981) noted that birds defended temporary territories at fuelling sites in Portugal.

FDRs have been measured at sites across Europe in autumn and they indicate a general pattern in which rates are low at more northerly sites and increase towards southern Europe. Bibby & Green (1981) first highlighted this pattern in a study that looked at sites in Britain, western France and Portugal and further support was provided by an examination of 12 widely separated sites in Europe by Schaub & Jenni (2000a). Studies restricted to single sites and data on fuel loads across Europe also support this trend (Bibby & Green 1981, Omerod 1990, Garcia Piero 1995, Chernetsov 1998, Merom et al. 2000). Bibby & Green (1981) proposed that adult Reed Warblers migrating from Britain, fly to Portugal in one flight and then fuel up extensively in Portugal in order to fuel the flight across the Sahara. Juvenile Reed Warblers were expected to make a number of stops in France before reaching Portugal. Evidence from other parts of Europe suggests a similar strategy, although some birds are capable of longer flights (Cramp 1992).

Few studies have looked at the fuelling behaviour of spring migrating Reed Warblers. Early studies in sub-Saharan Africa suggest fairly high FDRs and fuel loads (e.g. Fry et al. 1970, Aidley & Wilkinson 1987). Cramp (1992) noted that passage in southern Europe is limited, and ringing data from north-east Spain showed that a high percentage of birds had moderate fuel loads (Robson et al. 2001). A number of authors have therefore argued that Reed Warblers fuel extensively in North Africa before making a long flight to their breeding grounds (Alerstam 1990, Cramp 1992, Robson et al. 2001).

Much of the work on the migration of Reed Warblers has concentrated on defining routes and site use, and showing how FDRs and fuel loads vary across Europe. The next step is to investigate spring fuelling behaviour further, and to understand the adaptive significance and control of fuelling behaviour. I aim to answer these questions in this thesis.
1.6 CONCLUSION AND GENERAL AIMS

Migratory fuelling is a complex behaviour that may be controlled, promoted or constrained by a combination of environmental, physiological and endogenous factors. The interplay of these factors may not only influence fuelling behaviour but also the organisation of the migratory journey as a whole. Therefore, the time taken to reach the migratory goal, the sites used along the way, and the number of fuelling stops made, are all likely to be dependent on the rate and duration of fuelling at stopover sites, which together determine the fuel available for flight stages. Decisions made during flight stages may also influence the progress of a migratory journey. The relative contribution of behaviour during flight versus fuelling stages to the organisation of a migratory journey is at present unknown.

The general aim of this thesis was to use data collected primarily from Reed Warblers, but also from Sedge Warblers, to examine fuelling behaviour and to identify the key variables that influence its outcome and understand how it is controlled. The conclusions drawn from these two species are expected to be applicable to long distance migratory passerines in particular, but also to a wider range of migratory birds. Further, I aimed to use this understanding to examine the flexibility of fuelling behaviour, and therefore migratory strategies (Chapter 3). Using this increased understanding of fuelling behaviour, I set out to make predictions about the migratory strategy of the Reed Warbler and identify the pressures that may be placed on this species in future and the measures that could be taken to ensure its continued success on migration (section 7.2). This thesis does not only concentrate on fuelling behaviour, but also on how weather can influence departure decisions, and therefore the extent to which behaviour on flight phases can determine the time-course and organisation of the migratory journey (Chapter 6).

Specific Aims

Two types of data are included in this thesis: (1) historical datasets: ringing data collected over the last 15 years largely by other persons, (2) experimental data collected by myself. I therefore discuss the aims of collecting and analysing each type of data first, and then the aims of using a combination of the two.
Historical Datasets (Chapter 2)

Using historical datasets collected at four different sites, I aimed to describe the fuelling behaviour of Reed Warblers in terms of the timing of fuelling, fuelling rates, fuelling durations and the fuel loads birds accumulated (Chapter 2). Each of these aspects of fuelling behaviour were examined to see whether they were affected by variables such as time of year, competition, moult and age. The four datasets were separated not only by geographic location but also by the time of year they were collected. I aimed to see whether these temporal and geographic differences lead to differences in fuelling behaviour between sites and discuss the selective pressures that could give rise to differences (section 2.5).

One of the ringing datasets was collected in autumn in Portugal whilst another was collected in Senegal in spring (section 2.2). At both these sites, birds are theoretically preparing to cross the barrier/s formed by the Mediterranean Sea and the Sahara desert. These datasets were compared to the those collected from sites that were not in close proximity to a barrier, to test whether proximity to a barrier causes a change in fuelling behaviour and if it does, how behaviour is modified in order to accumulate fuel loads sufficient for crossing such significant barriers.

Experimental Datasets (Chapters 3-6)

The extent to which food availability affects fuelling behaviour and therefore how flexible fuelling behaviour is in response to food availability is little known (section 1.4). By providing three species of migratory warblers - the Reed Warbler, Sedge Warbler and Great Reed Warbler - with an additional food source, I tried to discover the extent of flexibility and constraint in their fuelling strategies (Chapter 3).

A number of optimal migration models have generated testable predictions regarding the relationship between fuel deposition rates and either departure loads or fuelling durations, for migrants that have been selected to minimise one of a number of currencies during their migration (section 1.3). These currencies include time, total energy expenditure, transport costs and predation risk. The models have only been formally tested on four occasions and due to small sample sizes the conclusions drawn have been tentative (section 4.1). Using larger sample sizes, I set out to test these models with data on the fuelling durations, fuel deposition rates and departure loads of Reed Warblers (Chapter 4) and Sedge Warblers (Chapter 5). I also tried to discover how
minimisation of a currency is achieved behaviourally, i.e., whether it is by complex rules or a simpler rule such as the CSD (section 1.3).

Theoretical models also predict that migrants should reduce or increase their fuel loads if they expect fuelling conditions at future sites to be better or worse respectively. Further, FDRs are predicted to decrease, if metabolic costs increase in line with fuel loads. I set out to test both these predictions using data on fuelling Reed (Chapter 4) and Sedge Warblers (Chapter 5).

The extent to which weather influences departure decisions and therefore fuelling behaviour is poorly understood (section 1.3). By examining the departure decisions of Reed Warblers, and to a lesser degree Sedge Warblers, I aimed to determine the extent to which weather influences these decisions and discover the impact this might have on fuelling behaviour (Chapter 6).

**Combining the results of Historical and Experimental Datasets (Chapter 7)**

By drawing all the results of this thesis together, I aimed to show how my work has increased our knowledge of fuelling behaviour and how it may be applicable to other species (section 7.1). I also intended to use the results from this thesis to present an overview of what is known about the migratory strategy of Reed Warblers in north and west Europe and discuss how habitat destruction and degradation may impact on the success of Reed Warbler migration (section 7.2).
CHAPTER 2

SEASONAL AND GEOGRAPHIC VARIATION IN THE FUELLING BEHAVIOUR OF REED WARBLERS

2.1 INTRODUCTION

2.1.1 AUTUMN MIGRATION

Leaving the Breeding Site

The majority of migratory species show some degree of pre-migratory fuelling at breeding sites (Alerstam 1990), although some species have been shown to disperse short distances before commencing fuelling (Baker 1978, Insley & Boswell 1978). There is no clear pattern as to which species make these movements, although aerial feeders rarely remain at breeding sites for long (Wernham et al. 2002). The energy accumulated during pre-migratory fuelling is rarely sufficient to fuel a non-stop flight to the wintering grounds, especially for trans-Saharan migrants breeding in N Europe (Alerstam & Lindstrom 1990). Therefore the amount of fuel accumulated will be influenced by factors other than the distance to be covered. Indeed, environmental variables, innate behavioural programs and even metabolic capacity may influence the magnitude of the final energy store (Alerstam & Hedenström 1998, Schaub & Jenni 2000a). The fuel load a migrant has at the end of pre-migratory fuelling will influence the distance that can be covered on the first flight phase and therefore where it will stop to refuel. Indeed, the rate and duration of fuelling, and the fuel load accumulated are expected to be crucial determinants of the spatial and temporal organisation of migration (section 1.2).

The initiation of pre-migratory fuelling is generally believed to be under the control of an internal time program, which may respond to seasonal factors such as decreasing day length (Gwinner 1990, 1996). How the time program responds to factors expected to delay the onset of migration is unclear. For instance, adults would be expected to complete breeding duties before commencing fuelling and thus birds whose breeding attempt is delayed by weather must override their time program. A number of
authors have highlighted post-breeding and post-juvenile moults as constraints on fuelling (Lindström et al. 1994, Schaub & Jenni 2000a). Whilst some migrant passerines undertake such moults, many do not (Jenni & Winkler 1994): differences in migratory strategy have been noted between these two groups (Schaub & Jenni 2000a). The energy cost associated with feather replacement is expected to suppress fuelling rates to the extent that fuelling is delayed until moult is completed (Lindström et al. 1993). Reed Warblers, however, migrate whilst still moulting, albeit with small fuel loads (Herremans 1990, Schaub & Jenni 2000a).

Once fuelling has commenced, several variables may either promote or constrain fuelling. A key variable, which has been shown to increase fuel deposition rates (FDRs), is food availability (section 1.2). Several experimental studies have demonstrated higher FDRs within species in response to increased food availability (Lindström & Alerstam 1992, Fransson 1998, Danhardt & Lindström 2001). However, FDRs will not increase indefinitely as food availability increases, as migrants will be limited by their maximum rate of intake or their metabolic capacity (McWilliams & Karasov 2001). Further, even if food availability is high, factors such as predation risk (Houston 1998) and competition are expected to reduce the rate of intake (see section 1.2). Whilst no studies have found a link between predator abundance and FDRs (Dierschke & Delingat 2001, Dierschke et al. 2003), the case for competition is stronger (see section 1.2). A trend commonly noted in datasets of retrapped birds, is an increase in FDR with date (Schaub & Jenni 2000a). Whilst this increase may be due to an increasing time pressure, it may be due to reduced competition levels at the end of the migratory period.

The final fuel load of a migrant will depend not just on its FDR but also on the time spent fuelling. The mechanism by which the length of pre-migratory fuelling or fuelling on stopovers is controlled is unclear. Whilst durations may be expected to vary greatly depending on the FDR (Alerstam & Lindström 1990), Schaub & Jenni (2001) noted that the stopover durations of three migrant passerines were surprisingly constant across a range of sites and therefore stopover durations may be of set length.

Few studies have concentrated specifically on pre-migratory fuelling, as many have focused on stopover decisions. Further, we have little knowledge of the impact either predation risk or competition have on FDRs and therefore the fuelling behaviour of migratory birds. In section 2.3.1, I investigate the fuelling behaviour of Reed Warblers at a breeding site in southern England. Using ringing data collected at the site,
I examined the effects of moult, competition, time of year and other factors on the FDR and body mass of Reed Warblers.

**Flying South**

In southern Europe most trans-Saharan passerines are on active migration and typical migrants are either stopping at sites to rest after nocturnal flights or to replenish their fuel reserves after a series of nocturnal flights. Ringing recoveries from sites across Europe suggest that many passerines orientate either southwest towards the Iberian peninsula or southeast towards the Balkans and the eastern Mediterranean (Alerstam 1990, Wernham *et al.* 2002). The selection pressure for both strategies appears to be the reduced distance of flights across the Mediterranean Sea and the Sahara desert and the distribution of suitable habitats both north and south of the Sahara (Alerstam 1990). Whilst these strategies increase the overall migratory distance, theoretical work suggests that such detours still have a selective advantage due to reduced overall energy expenditure (Alerstam 2001).

Whilst many of the factors expected to influence pre-migratory fuelling will affect fuelling behaviour at southerly stopover sites, the proximity of the ecological barriers represented by the Mediterranean Sea and the Sahara desert, should cause changes in fuelling behaviour (section 1.3). These constitute the largest barriers a trans-Saharan migrant will face on its autumn migration, indeed a number of species routinely attempt to cross both barriers at once without refuelling. Therefore fuel loads at sites shortly before this barrier/s are expected to be greater than anywhere else in Europe (Schaub & Jenni 2000b). Whilst, this may be true of most species, there is evidence that some species perform extremely long flights from as far north as southern England (e.g. the Sedge Warbler in northwest Europe, Bibby & Green 1981), accumulating enormous fuel loads in order to do so (strategy 3 in Fig. 2.2.1).

For migrants that stop at sites close to the edge of the Mediterranean Sea and/or the Sahara desert before crossing, a sufficient fuel load may be accumulated in two ways. A bird can either fuel extensively at a site close to the edge (Fig. 2.1.1, strategy 1) or the total fuel load can be built up gradually at a number of sites on the journey south (Fig. 2.1.1, strategy 2). Both of these strategies have been observed in different species of migratory bird (Schaub & Jenni 2000a), therefore the strategy adopted may depend on the fuelling constraints each species faces. Finally, there are a few notable exceptions
FIGURE 2.1.1: Fuelling strategies for crossing the Mediterranean Sea and the Sahara Desert.
1 – Birds do not begin to accumulate fuel for the crossing until reaching sites close to the edge of the Mediterranean.
2 – Birds show a gradual increase in the base level of their fuel stores, such that the fuel required to cross the barrier is accumulated in a series of fuelling stops.
3 – Fuel for both the journey across much of Europe and across the Mediterranean and the Sahara is accumulated some distance from the desert edge. Consequently, birds can reach sub-Saharan Africa from northern Europe without the need to refuel.
where birds can find sufficient food whilst crossing the Sahara desert for it not to be considered a barrier (e.g. the Spotted Flycatcher, Schaub & Jenni 2000b; this alternative strategy is not illustrated in Fig. 2.1.1).

How birds adopting strategy 1 (Fig. 2.1.1) alter their fuelling behaviour in order to accumulate larger fuel loads has not been thoroughly investigated. One mechanism is to increase FDRs and this appears to be true of some but not all species (Schaub & Jenni 2000a): in a number of species FDRs did not change with latitude across Europe. A second mechanism is to increase fuelling durations. An experimental study on Thrush Nightingales, *Luscinia luscinia*, supported this mechanism (Fransson et al. 2001), however, an investigation of stopover durations in three migratory passerines at sites across Europe revealed no tendency for an increase in duration (Schaub & Jenni 2001). Finally, migrants could increase both their FDR and fuelling duration. Whether a species adopts either mechanism or both may depend on food availability and therefore whether it is possible to increase FDRs at all.

To test how fuelling behaviour alters prior to a barrier, I compare and contrast the fuelling behaviour of Reed Warblers at a breeding site in England, with birds on stopover in Portugal. The site in Portugal was close to the Mediterranean Sea and within a regular staging area for Reed Warblers migrating from Britain (Bibby & Green 1981, Wernham et al. 2002). Therefore, I expected the birds at this site to already have or to accumulate large fuel loads. Using ringing data from each site, I aimed to discover which strategy Reed Warblers use to cross the Mediterranean and Sahara (see Fig. 2.1.1) and how fuelling behaviour is modified to achieve the large fuel loads required to do so.

### 2.1.2 SPRING MIGRATION

During spring migration the pressure for migrants to complete their migration in as short a time as possible is hypothesised to be stronger than in autumn (Weber & Houston 1997, Kokko 1999). The most important selective force for faster migrations is expected to be the competition for territories and mates on the breeding grounds (Sandberg 1996, Weber & Houston 1997, Fransson & Jakobsson 1998, Kokko 1999). A number of studies have demonstrated that territory possession in migrants is not directly related to competitive superiority but is determined on a first come first served basis (Møller 1994, Lozano *et al.* 1996, Currie *et al.* 2000, Forstmeier 2002). Thus the first
males to arrive on the breeding grounds will secure the best territories, and enjoy the greatest breeding success. The same pressure applies to female migrants, as the first to arrive will be able to choose the male with best territory. As early arrival may come at a high price, mates on better territories may be of higher phenotypic quality (Møller 1994).

Unlike in autumn, when climatic conditions and resource levels deteriorate gradually, certain resources may increase rapidly and almost simultaneously across much of Europe. For example, the timing of emergence of folivorous caterpillars on trees is sufficiently similar that the mean egg laying date of Blue Tits *Parus caeruleus*, whose chicks are dependent on the caterpillars, differs by little more than 10 days across Europe (Visser *et al.* 2002). The almost simultaneous increase in resources may mean that migrants cannot gradually creep up Europe but must make a headlong dash from staging areas in North Africa or southern Europe as soon as conditions become favourable, further increasing the time pressure.

Consequently, one would expect migrants to alter their fuelling behaviour between seasons. Theoretical work suggests that time-selected migrants should accumulate larger fuel loads than birds minimising either energy costs or predation risk (Weber & Houston 1997, Houston 1998). Thus higher body masses in spring migrating birds relative to autumn migrants may be a signature of time-selection, especially if their FDRs are not significantly different. Possible mechanisms for maximising the speed of migration are likely to involve behavioural and metabolic adaptations that increase FDRs. For example a bird might increase its feeding intensity by reducing predator awareness, a factor that would normally constrain feeding rates (Weber, Ens & Houston 1998). Hypertrophy of the metabolic organs could maximise the efficiency and speed of digestion, and thus elevate FDRs. Indeed, theoretical modelling has suggested that time-selected migrants should always maximise their metabolic machinery during migration, despite additional energetic costs (Weber & Hedenström 2001).

Few studies have concentrated on migratory behaviour in spring and the strategies adopted at this time of year are little known. A number of ringing studies carried out south of the Sahara in spring, have shown that many migrants accumulate large fuel loads (e.g. Alerstam 1990, Loske 1990, Ottosson *et al.* 2001), but this comes as no surprise given the need to cross the Sahara. Once migrants have crossed the Sahara, there are very few studies describing fuelling behaviour. In a study of Reed Warblers in north-east Spain, Robson *et al.* (2001) argued that birds were making short
stops, i.e. lasting 1 or 2 days, but accumulating enough fuel during these short periods for onward flight. A similar situation was found for a number of North American passerines that had just crossed the Gulf of Mexico in spring (Moore & Kelinger 1987, Yong & Moore 1997). Such short stopovers have been ruled out previously, as migrants are expected to pay a ‘stopover cost’ when arriving at a new site (Lindström & Alerstam 1990, Hedenström & Alerstam 1997). This cost, incurred as a result of search and settling behaviour or metabolic constraints after migratory flights, is expected to prevent migrants increasing their fuel reserves for one or two days. The behaviour of these spring migrants suggests they are not paying a stopover cost and can therefore adopt a time saving strategy of short but effective fuelling bouts.

In order to increase out understanding of fuelling behaviour and strategies on spring migration, I have analysed two ringing datasets on Reed Warblers: one from a site south of the Sahara in Senegal and one from north of the Sahara in Spain. I also used the Senegalese data to investigate the strategy Reed Warblers use to cross the Sahara in spring.

2.1.3 SUMMARY AND MAIN OBJECTIVES

The fuelling behaviour of migrants at sites separated geographically and by season is expected to vary if environmental variables and/or the selection pressures acting on birds differ between sites. Variation may arise from differences in the time pressure experienced by birds separated by season or by differences in the journey birds face. I aimed to discover whether selection had shaped fuelling behaviours at different sites and between seasons, according to the pressures experienced at each site using four ringing datasets on Reed Warblers. I hoped to highlight the degree of flexibility within fuelling behaviour with respect to the various challenges that are faced on a migratory journey. The main aspects of fuelling behaviour that I examined were FDRs, fuelling durations and the magnitude of mass (equivalent to fuel) increases.

In this chapter, I also intend to use the ringing datasets to provide vital background information on the migratory behaviour of Reed Warblers that will form an invaluable reference point not only for discussion in this chapter but throughout this thesis. This background information for each site includes data on:

- The phenology of migration.
• The proportion of birds that actually use each site to fuel, relative to those that simply rest at the sites between nocturnal flights (these birds are termed transients).

• The body mass (fuel load) distribution of birds, which can be used to predict the flight range of birds and therefore where birds will stop to refuel.

2.2 METHODS

Study Sites

• Icklesham, southeast England (N50°54´, E0°41´)

Icklesham was situated on a privately owned farm where conservation measures had been taken in order to create the Pannel Valley Reserve. The Reserve was owned and managed by the Wetland Trust. The reserve consisted of a 23 ha mosaic of Phragmites reedbed, sallow scrub and open water, surrounded by mixed farmland and grazing marshes, 1.7km from the southern coast of Britain. The reserve was part of the working farm up until 1985, and the areas that became the reserve were largely used for grazing and cereals. At different stages between 1985 and 1994, the key features and habitats of the reserve were created. The reserve typically holds around 150-200 pairs of Reed Warblers (Papazoglou 1997).

Bird ringing had been carried out at Icklesham on a regular basis from at least 1988, and since 1989 ringing has been carried out every autumn, typically between July and November. The data in this study were collected between 1997-2002, during which period ringing took place daily during August and September given suitable conditions, and most days in July. Tape lures were used in all years, although recordings of Reed Warblers were not played between 1997-2002. However, Reed Warblers may be attracted to the calls of other warblers. I assisted in ringing operations in the years 2000-2002, personally ringing over 3000 Reed Warblers.

• Quinta da Rocha, south-west Portugal (N37°8´, W8°43.5´)

Quinta da Rocha was an area of scrub and mixed woodland, including citrus, olive, almond and fig, surrounded by mixed farmland and scrub. The site was on the
southern coast of Portugal approximately 1 km from the sea. Reed warblers were captured at the site using mist nets from 1986 to 2002, both in the spring and autumn. The trapping effort was rather variable, in some years trapping was almost daily during September and October whilst in others it was more erratic. Tape lures were used in some years, including the songs of Reed Warblers. Reed Warblers did not breed at the site, but were known to breed at sites within 20km.

• Djoudj, northwest Senegal (N16°25´, W16°18´)

Parc National des Oiseaux du Djoudj was situated in the Senegal River delta in northwest Senegal. The park was approximately 60 km from the coast and was bordered to the north by the Senegal River (Ottosson et al. 2001). The national park was part of a larger area that represented one of the most northerly, heavily vegetated sites south of the Sahara desert. There were few suitable fuelling habitats north of this site. Habitat within the park comprised of seasonally flooded waterways, extensive areas of open water, reedbeds consisting of both Phragmites and Typha, low sedge-beds of Carex spp., and areas of scrub formed largely by a tamarisk Tamarix senegalensis. There were also smaller areas of trees and even sandy plains with limited vegetation.

Ringing had been carried out at the park between 1987 and 1996. Between 1990-1993, an international ornithological expedition organised by the Wetland Trust visited the park and carried out regular ringing between October and May. In this study I have concentrated on the data collected in the years 1991-1993. Activity varied between these years, with ringing taking place on 176 days in 1991, 191 day in 1992 and 114 days in 1993 (Ottosson et al. 2001). In all three years, ringing was carried out daily between February and the end of April if conditions allowed. Birds were caught in mist nets and tape lures were used to attract birds to the netting area. Unfortunately, I have been unable to discover which species vocalisations were used.

• Aiguamolls de L’Emporda, northeast Spain (N42°13´,W3°8´)

Aiguamolls de L’Emporda Naturel Parc was situated in northeast Catalonia, approximately 30 km south of the French border. The park was bordered by the Mediterranean Sea to the east and a small mountain range that stretched down to the coast lay to the north, whilst the Pyrenees lay to the west. To the south was a coastal
plain. The park consisted of two main blocks, separated by human settlements and farmland. Habitat within these blocks included open water, freshwater marshes, extensive salt marsh, farmland, and areas of both reedbed and scrub.

Different sites within the park have been used for ringing by the Catalan ringing group (Grup Catala d’Anellement). Between the 15th April and the 15th May, 1993-1997, Reed Warblers were rung as part of the Progetto Piccole Isole (Spina et al. 1993). In the years 1999-2002, ringing was carried out in a different part of the park from 2nd March to 30th May. I aided data collection at this site in 2002 and 2003. Data from 1999-2002 has been used in this study. The ringing area, known as El Cortalet, was a mixture of open grassland, scrub and Phragmites reedbed, criss-crossed by tamarisk Tamarix gallica lined, water filled ditches, approximately 1 km from the sea. Ringing was carried out between dawn and midday and before sunset. Tape lures were not used at this site.

**Collection of Historical Ringing Data**

At all the study sites, the date, time of capture, species and age of all birds caught was recorded. In addition, wing length, body mass and fat score were recorded for the majority of birds. Data on moult status was collected for a large number (>2000) of juvenile Reed Warblers by myself at Icklesham in 2002. The above data measures have all been used in this chapter and are described below.

- **Time of Capture:** Birds at Icklesham and Djoudj were assigned an hour of capture which corresponded to the hour in which the bird was extracted from the mist net. Birds at Aiguamolls de l’Empordà and Quinta da Roche were assigned a time to the nearest half hour of the net round in which they were extracted.

- **Species:** Determined using the criteria described in Svensson (1992).

- **Age:** Determined using the criteria described in Svensson (1992). The classes used included 3 (juvenile) and 4 (adult).

- **Wing Length:** Measured to the nearest 0.5mm at all sites using the maximum chord method (Svensson 1992).

- **Body Mass:** Measured to the nearest 0.1g using Pesola spring balances or electronic balances at all sites.
• Fat Score: Fat in the tracheal pit and on the abdomen was scored on a 9 point scale which ranged between 0-8 at Icklesham and Aiguamolls (Kaiser 1993). At Quinta da Roche, a 6 point scale ranging between 0-6 was used between 1988-1994 and the 9 point scale between 1995-2001. At Djoudj a 6 point scale was also used (Busse & Kania 1970).

• Body Moult Intensity: This variable was only recorded for juvenile Reed Warblers at Icklesham in 2002 by myself. Scoring of intensity was on a three point scale: 0 – no body feathers growing, 1 – one to 20 body feathers growing, 2 – more than 20 body feathers growing.

**Body Mass as a Measure of Fuel Load**

Body mass is used as a measure of the fuel load throughout this study. Whilst not all increases above the lean body mass will be due to fat deposition (water and protein may account for some of the increase), the body mass still provides a useful guide to fuel mass. At all sites in this study there is a positive relationship between body mass and fat score (see Table 2.2.1).

**Time of Day Effect on Body Mass**

Body mass and fat stores follow a strong rhythm during the course of the day (Lehikoinen 1987, Schaub & Jenni 2000b) and therefore for accurate fuelling rates to be calculated, a time correction is required. Linear regression models for body mass against time were calculated for all data sets and body mass was corrected to the modal time of capture for each data set.

**Lean Body Mass (LBM)**

Lean body mass is the estimated value for a bird that carrying no stored fuel/fat. As body mass may vary due to factors other than the mass of energy stores e.g. water content and protein mass, there will always be error in estimating the LBM. Throughout this thesis, lean body mass is largely used as a scaling factor for body size and thus has no effect on the conclusions drawn. The only case where the actual value of the LBM becomes important is in the calculation of flight ranges (see section 7.2). However, as
TABLE 2.2.1: Regression analyses of body mass on fat score for the four sites examined in this chapter. The scale used for fat score is noted in the second column. The increase per fat score was derived from the regression equation. Sample sizes can be calculated from the degrees of freedom. These analyses are presented to demonstrate that there was positive relationship between fat score and body mass. Whilst the relationship may not be linear, the shape is not of consequence in this thesis. DF = degrees of freedom.

<table>
<thead>
<tr>
<th>Site</th>
<th>Scale</th>
<th>Increase per Fat Score</th>
<th>F</th>
<th>DF</th>
<th>P</th>
<th>Adjusted R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Icklesham</td>
<td>9 point</td>
<td>0.55g</td>
<td>26,852</td>
<td>13,676</td>
<td>&lt;0.001</td>
<td>66.3%</td>
</tr>
<tr>
<td>Quinta da Roche</td>
<td>6 point</td>
<td>0.99g</td>
<td>1,915.5</td>
<td>1721</td>
<td>&lt;0.001</td>
<td>52.7%</td>
</tr>
<tr>
<td></td>
<td>9 point</td>
<td>0.76g</td>
<td>428.5</td>
<td>201</td>
<td>&lt;0.001</td>
<td>68.0%</td>
</tr>
<tr>
<td>Djoudj</td>
<td>6 point</td>
<td>0.55g</td>
<td>6,726.2</td>
<td>12,356</td>
<td>&lt;0.001</td>
<td>35.2%</td>
</tr>
<tr>
<td>Aiguamolls</td>
<td>9 point</td>
<td>0.59g</td>
<td>1,704.3</td>
<td>2401</td>
<td>&lt;0.001</td>
<td>41.5%</td>
</tr>
</tbody>
</table>

TABLE 2.2.2 – Lean body mass estimates for birds at Djoudj, Icklesham and for a modified Icklesham data set (explained in text). An estimate for LBM in Europe is also given, based on the mean of the Djoudj LBM and the modified Icklesham LBM.

<table>
<thead>
<tr>
<th>WING LENGTH</th>
<th>DJOUDJ LBM (g)</th>
<th>ICKLESHAM LBM (g)</th>
<th>ICKLESHAM 25% LBM (g)</th>
<th>LBM FOR EUROPE (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>60</td>
<td>8.4</td>
<td>10.0</td>
<td>9.3</td>
<td>8.8</td>
</tr>
<tr>
<td>61</td>
<td>8.5</td>
<td>10.1</td>
<td>9.4</td>
<td>9.0</td>
</tr>
<tr>
<td>62</td>
<td>8.7</td>
<td>10.2</td>
<td>9.6</td>
<td>9.1</td>
</tr>
<tr>
<td>63</td>
<td>8.8</td>
<td>10.3</td>
<td>9.7</td>
<td>9.3</td>
</tr>
<tr>
<td>64</td>
<td>9.0</td>
<td>10.4</td>
<td>9.9</td>
<td>9.4</td>
</tr>
<tr>
<td>65</td>
<td>9.1</td>
<td>10.5</td>
<td>10.1</td>
<td>9.6</td>
</tr>
<tr>
<td>66</td>
<td>9.3</td>
<td>10.7</td>
<td>10.2</td>
<td>9.7</td>
</tr>
<tr>
<td>67</td>
<td>9.4</td>
<td>10.8</td>
<td>10.4</td>
<td>9.9</td>
</tr>
<tr>
<td>68</td>
<td>9.6</td>
<td>10.9</td>
<td>10.5</td>
<td>10.0</td>
</tr>
<tr>
<td>69</td>
<td>9.7</td>
<td>11.0</td>
<td>10.7</td>
<td>10.2</td>
</tr>
</tbody>
</table>
the accuracy of flight range calculations is presently un-testable, the error in range estimation is likely to be greater than that caused by inaccurate estimations of LBM. However, in order to reduce any source of error, I have attempted to generate as accurate an estimate of LBM as possible.

The standard method of calculating LBM is to regress body mass on wing length for all birds with a fat score of 0. Using this method I found that estimates for Reed Warblers at Icklesham were higher than estimates for Djoudj (Table 2.2.2). The elevated masses at Icklesham might be explained in a number of ways. Firstly, birds may have hidden energy stores that are essential for survival in northern climes, which are not required in the more homogenous and amenable climate of Africa. Secondly, many of the birds at Icklesham were in moult and a number of studies noted body mass increases during moult, linked to an increase in body water content (Newton 1968, Chilgren 1977). Finally, Weber & Hedenström (2001) argue that the optimal LBM a bird carries may vary with life-stage and predict that migrating birds should carry the maximum possible LBM. Much of the additional mass is expected to be due to hypertrophy of the digestive organs, giving rise to increased digestive capacity and therefore higher FDRs and speed of migration. This could explain the difference between Icklesham where the majority of birds are actively migrating, and Djoudj, where wintering birds formed part of the dataset examined.

In light of the differences in LBM, I have generated two measures of LBM for birds at different sites: one for birds at European sites and one for birds in Senegal. If one refers to Fig. 2.5.2, it will become clearer as to why I have made this distinction. For these calculations, I have only used data from Djoudj and Icklesham as these represent the largest two data sets by an order of magnitude: they also represent the two extremes in LBM found in the four datasets (see Fig. 2.5.2).

For the Senegal estimate of LBM, I took all birds with a fat score of 0 from the Djoudj data set and corrected body mass for time of day using linear regression. Body mass was then regressed on wing length. For the European estimate, I took the lowest 25% of body masses for each wing length from the Icklesham data set (806 of 2964 birds) and calculated the regression equation, after correcting for time of day. By taking only the lowest body masses, I aimed to remove birds that had elevated masses due to variables such as moult status. To calculate the final LBM values for Europe, I took the mean value of the LBM calculated for Djoudj and Icklesham. This final measure (Table 2.2.2) takes into account that European Reed Warblers wintering in West Africa
clearly attain low body masses (mean LBM of 17 British rung Reed Warblers in Senegal = 9.5g) but without conceeding that the entirety of the increase observed in Europe is a consequence of hidden fuel reserves, as this is considered unlikely.

**Calculating Fuel Deposition Rates (FDRs)**

The fuel deposition rate was calculated as the proportion of lean body mass (fat free mass) accumulated per day, using the following equation (Lindström & Alerstam 1992, Fransson 1998a, Danhardt & Lindström 2001):

\[
FDR = \frac{(\text{Body mass at last capture} - \text{Body mass at first capture}) \times \text{Lean Body Mass}^4}{\text{Number of days between captures}}
\]

The calculation of FDRs from the ringing data was possible, as birds were regularly caught more than once at the same site. These individuals are referred to as ‘retraps’. As all masses were corrected to the same time of day, the appropriate values could be entered into the equation. The values for LBM are given in Table 2.2.2.

At Icklesham, retrap data from the years 1997-2002 were used to calculate FDRs, as long as body mass had been recorded on each capture occasion. Data from Djoudj between 1991-1993, from Aiguamolls de L’Emporda between 1999-2002 and from Quinta da Roche between 1988-2001 were also used to calculate FDRs. If birds were retrapped on more than one occasion, the ‘body mass at last capture’ was always the mass on the last recorded capture. The ‘body mass at first capture’ was not always taken as the first capture event, instead the first capture was chosen so that FDR was maximised. FDRs are typically underestimated (Schaub & Jenni 2000a), therefore the maximum is preferred as it provides a better estimate of natural FDRs.

For the majority of FDR data presented in this chapter, only birds retrapped at least two days apart were included. This policy was adopted because we do not know the exact effects of capture, therefore mass changes shortly after capture may be an artefact of being caught and handled. A number of studies have indicated that capture may lead to mass loss (e.g. Gosler 2001). Indeed, it has been shown that capturing Reed Warblers results in mass loss, and that the lost mass may not be regained for a number of days (Schwilch & Jenni 2001). See Chapter 3 for a method of measuring FDRs without this problem.
‘Positive’ Mass Changes and FDRs

At all four sites, mass changes and therefore FDRs of many birds were negative. As these are not representative of fuelling behaviour, a number of tables and figures only include birds with positive mass changes/FDRs above a certain threshold. In all cases, these only include birds that displayed a body mass change greater than 0.45g which is approximately 5% of lean body mass. Mass changes below this value were considered unlikely to represent actual fuelling. Indeed, a large prey item such as a caterpillar can weigh up to 0.15g; if a bird had consumed two such items prior to capture, the increase of 0.3g may be confused with an increase in fuel load. An additional criterion was introduced for some of the statistics presented for Djoudj (section 2.4), due to the long fuelling durations exhibited by birds at this site. As fuelling durations regularly exceeded 30 days, birds present for more than 20 days were excluded if they had gained less than or equal to one gram. This arbitrary cut-off point was chosen as it removes birds that were gaining less than 0.5% of their LBM per day and were therefore unlikely to have been fuelling for the entire 20 days, given that some birds at Djoudj gained up to 5% of LBM per day.

Whilst the selection criteria described above help to remove non-fuelling individuals from the population, they will also inevitably lead to some fuelling individuals being excluded. Further, a small percentage of non-fuelling birds will still be included in the fuelling population. This unavoidable outcome is illustrated in Fig. 2.2.1. This mixing of populations was taken into account when interpreting the distribution of ‘positive’ mass changes and FDRs.

Duration of Fuelling

Whilst complex statistical methods exist for estimating longevity, stopover/fuelling durations, etc, from mark-recapture data (Lebreton et al. 1992, Pradel 1996), the need for accurate estimates of fuelling durations was not deemed necessary in this study. Indeed, the data on durations presented in this study was used to allow direct comparisons between sites, which only requires that the probability of capture is similar between sites or is not a potential cause of any differences. For a detailed look at stopover durations using recent statistical methods, see Schaub et al. (2001) and Schaub & Jenni (2001).
FIGURE 2.2.1: Hypothetical distribution of mass changes for fuelling and non-fuelling populations: the later is skewed to the left because some individuals will encounter problems (e.g. bad weather) whilst fuelling. For some individuals bad weather may even result in mass loss, even when birds are trying to fuel. The cut-off point represents the 0.45g selection criteria outlined above. The yellow area represents fuelling individuals excluded from the fuelling population and the blue area highlights non-fuelling individuals included in the fuelling population.

Table 2.2.3: Capture probabilities at the four sites examined in this chapter. Sample sizes, mean probability and the standard deviation (S.D) are given for each site. Probabilities were calculated by dividing the number of days a bird was known to be present at a site (i.e. the number of days between first and last captures, inclusive of the first and last day) by the number of times a birds was captured during that period.

<table>
<thead>
<tr>
<th>SITE</th>
<th>Icklesham</th>
<th>Quinta Da Roche</th>
<th>Djoudj</th>
<th>Aiguamolls</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>246</td>
<td>59</td>
<td>235</td>
<td>30</td>
</tr>
<tr>
<td>MEAN ± S.D.</td>
<td>0.33 ± 0.22</td>
<td>0.31 ± 0.14</td>
<td>0.18 ± 0.12</td>
<td>0.74 ± 0.23</td>
</tr>
</tbody>
</table>
For the purposes of this study, I have calculated the minimum fuelling duration (see Cherry 1982 and Morris et al. 1996), which is simply the time elapsed between first and last captures. Whilst this method will underestimate durations, the data are still suitable for comparisons between sites. Further, I have concentrated on fuelling durations rather than the total length of stay at a given site (stopover duration) and thus some of the statistical methods employed by Schaub & Jenni (2001) would be inappropriate. In concordance with the methods employed for examining ‘positive’ mass changes and FDRs, fuelling durations were only calculated for those birds that increased by at least 0.45g between captures. Thus for birds only caught on two occasions, the duration was simply the number of days that elapsed between captures (first and last days included). For birds caught on more than two occasions, the fuelling period was considered as the period in which body mass increased between all captures. For example, for a bird caught on four occasions, if body mass remained stable between the first and second capture but increased from the second to the fourth capture, the fuelling duration was the time elapsed between the second and fourth captures.

Whilst the methods outlined above will lead to both overestimates and underestimates of fuelling durations, the differences found in this chapter are large and are therefore unlikely to be a result of the uncertainty involved in the calculation of durations.

**Recapture Probabilities**

The plausibility of comparing the three main variables described above (‘positive’ mass changes, ‘positive’ FDRs and fuelling durations) between sites depends on the probability of recapture at each site. To examine this issue, I calculated the probability of capture on any given day at each of the sites examined. These were calculated by dividing the number of days a bird was known to be present at a site (i.e. the number of days between first and last captures, inclusive of the first and last day) by the number of times a birds was captured during that period. The mean probabilities and standard deviations for each site are presented in Table 2.2.3 (previous page).

Capture probabilities were very similar at Icklesham and Quinta da Roche, therefore no caution is required in direct comparisons of these two sites. However, capture probabilities were lower at Djoudj than all other sites, whilst at Aiguamolls they were notably higher than at all sites. The higher the recapture probability the more accurate estimates of mass changes and fuelling duration will be, as birds are likely to
be caught at both the beginning and end of their fuelling period. At lower recapture probabilities, underestimates of mass changes and fuelling durations are expected to increase with longer fuelling durations, as the final capture is increasingly unlikely to occur at the end of the fuelling period. For the purposes of this thesis I have not attempted to correct for the differences between sites in recapture probability. The main reason for not correcting for recapture probabilities, was that for nine out of ten between site comparisons, the differences found could not have been caused by recapture probabilities, as they were in the opposite direction to that expected if recapture probabilities were acting alone (an examination of Table 2.2.3 and Figure 2.5.1 will demonstrate this). Therefore the recapture probabilities support the key results in this chapter rather than question their validity. In the one case that this was not true (mass changes at Djoudj and Quinta da Roche), I have interpreted the result cautiously.

For estimates of FDR, low recapture probabilities may result in slight underestimates, as the period between captures may include a period in which a bird had not commenced fuelling. Further, if FDRs vary between days, the methods described above for estimating FDRs may lead to overestimates/underestimates of a bird’s overall FDR; if the period between captures is not representative of the entire fuelling period. However, by trying to identify maximum FDRs (see calculating FDRs above), I believe FDRs should be directly comparable between sites without taking recapture probabilities into account.

**Statistical Methods**

The following description of statistical methods covers those employed throughout this thesis. Where departures from the methods described here occur, or where statistical methods specific to a chapter are used, descriptions appear in the relevant methods section or alongside the statistics themselves. The use of transformations has been noted alongside the presentation of the statistics in all cases.

All statistics were calculated using Minitab Release 13.3 for Windows. All analyses involving multiple factors were performed by Analysis of Variance (ANOVA), specifically utilising General Linear Models (GLMs). In all cases, a histogram of residuals, a plot of fitted values versus residuals and a normal plot were generated in order to ensure that the assumptions of a GLM were not broken and that a parametric model was appropriate (Field 2000). If assumptions were violated, appropriate
transformations were used and if assumptions were still broken, an appropriate non-parametric test was employed (Siegal & Castellan 1989). In cases where model selection was required, the simplest and most parsimonious model was chosen in order to avoid the problems associated with a multiplicity of P-values. Regression analysis has been used extensively, and in all cases the data has been checked for compatibility with the assumptions of regression analysis (Field 2000).

For the direct comparison of distributions and means, two-sample t-tests were employed, as long as the data were approximately normally distributed. In cases where data could not be analysed by t-tests, an appropriate non-parametric method was employed. All tests were two-tailed and a significance level of 0.05 was used throughout.

2.3 RESULTS & DISCUSSION – AUTUMN MIGRATION

2.3.1 ICKLESHAM

Phenology of Migration

Assuming that the number of birds caught is a function of the intensity of passage, the main period of passage for juvenile Reed Warblers at Icklesham began in approximately mid July and tailed off by early October (Fig. 2.3.1). Peak passage occurred in August whilst smaller but significant numbers of birds were caught throughout September. Passage for adults was much less protracted, with passage commencing in mid to late July and tailing off by early September. The peak period for adults was fairly restricted, beginning in late July and finishing by mid-late August.

Recapture Probabilities

The probability of a bird caught on any one day being recaptured, is an indication of turnover rate at a site. Low probabilities suggest that the majority of birds are transients and may only be resting at the site between consecutive nocturnal flights. High recapture rates suggest that the majority of birds are staying at the site, and
FIGURE 2.3.1: Capture rates, expressed as a percentage of the total number of birds caught, averaged across the years 1998-2002 for adult (white) and juvenile (dark grey) Reed warblers at Icklesham. The average capture rate for a given day was only calculated if data from three of the five years were available. Capture rates are expected to reflect the phenology of Reed Warbler migration.
Therefore may be: (1) breeding adults or locally born juveniles undergoing post-
juvenile moult and pre-migratory fuelling, (2) refuelling birds. At Icklesham, recapture
probabilities were high (0.45) in early to mid July but rapidly dropped to around 0.1 at
the end of July and the beginning of August, as passage commenced (see Fig. 2.3.1).
Recapture probabilities remained at around 0.1 for the rest of the passage period. The
majority of Reed Warblers at Icklesham therefore appeared to have been transients.

The Timing of Post-Juvenile Moult

Moult is likely to be a constraining factor on pre-migratory fuelling and thus the
timing of moult will have an important influence on the timing and extent of pre-
migratory fuelling. In 2002, juvenile Reed Warblers were scored for body moult
intensity on a scale of 0-2: 2 being a bird in heavy moult, 0 being a bird that had
completed its moult and 1 being in between. The number and percentage of birds at
each moult score is illustrated in Fig. 2.3.2.

In late July almost all birds were in heavy body moult but this dropped to about
50% by late August. Many birds (20-40%) were still in heavy moult towards the end of
the passage period. The percentage of birds that had almost finished their moult (score
of 1), increased significantly with date (Regression, $F_{1,65} = 58.8$, $P<0.001$, adjusted $R^2$
= 46.7%), having shown an initial increase at the onset of passage.

The percentage of juveniles that had completed their moult (moult score 0) did
not increase in number until mid-August and levelled off at between 20-40% percent of
the total birds caught. The percentage of birds scored as zero increased significantly
with both date and the total number of birds caught (ANOVA, Date, $F_{2,64} = 26.6$, $P<
0.001$, Total caught, $F_{2,64} = 26.3$, $P< 0.001$). The increase with the total number of birds
catch, suggests that many transient birds had finished moultling. However, many of
these actively migrating birds must also have been moulting, therefore one would
expect moult to constrain FDRs and the speed of migration in these birds.

Body Mass as an Indicator of Fuel Loads

Body mass is a good indicator of the level of fuel reserves a bird has attained
(see section 2.2). The estimated mean lean body mass of Reed Warblers at Icklesham
was 9.6g (mean wing length = 65mm) and thus increases above this value are
FIGURE 2.3.2:
A) Capture rate for Icklesham 2002 with the proportion of birds at each moult score superimposed. Only days in which ten or more birds were caught were included, whilst days with fewer than 10 points were amalgamated with the next date.

B) Percentage of birds at each moult score against date. A score of 2 = heavy moult, 1 = moult nearly completed, 0 = moult completed.
representative of the mass of stored fuel. The distribution of body masses for juvenile and adult birds at Icklesham shows that the majority of birds only had between 0.5 and 1.5g of fuel (Fig. 2.3.3). These small reserves may only represent emergency reserves rather than fuel for flight. Adult Reed Warblers at Icklesham had higher fuel loads than juveniles (Fig. 2.3.3) and were therefore capable of longer flights (see section 7.2).

Fig. 2.3.4 shows the mass distribution of juvenile Reed warblers at different moult scores. The majority of birds in heavy body moult (moult = 2) had low body masses between 10 and 11g and may not have commenced fuelling. Birds finishing their moult (moult = 1) largely had low body masses but some had higher body masses, indicating fuelling had commenced. Juvenile Reed Warblers that had completed their moult had moderate fuel loads (20-40% of LBM), and their mean body mass was not significantly different from that of adults (mean ± SD: adults, 12.25g ± 1.04; juveniles, 12.22g ± 1.17; t-test, t_{2217} = 0.62, P = 0.538). The intensity of moult had a significant relationship with juvenile body mass in a model that controlled for Date and Date*Date (ANOVA, F_{3,2684} = 598, P<0.001, see also Table 2.3.1).

Taking the mean body mass of all Reed Warblers, captured on a given day, shows how the body mass of the population varies in time. At Icklesham, mean body mass had a cubic relationship with date (ANOVA, F_{2,352} = 79.8, P<0.001), such that body mass increased from mid-July to mid-August, then decreased until early September and finally showed a large increase in late September (Figure 2.3.5). Mean body mass increased significantly with the intensity of passage (Total), indicated by the total number of birds caught each day, and was partly responsible for the cubic relationship between body mass and date (ANOVA, Interaction Date*Total, F_{8,343} = 21.8, P<0.001). Mean body mass also increased with the percentage of adults in the population (ANOVA, Interaction Date*%Adults, F_{8,343} = 15.89, P<0.001).

A second analysis was carried out to test the interactions described above, in which ‘Date’ was divided into three blocks consisting of July, August and September (Table 2.3.2). In July mean body mass increased with both ‘date’ and the ‘percentage of adults’ whilst ‘total’ had no affect. In August, ‘date’ had no effect and most of the variance in body mass could be explained by the ‘intensity of passage’ (total = number of new birds caught per day) and the ‘percentage of adults’ caught. In September, body mass increased steeply with date, whilst intensity of passage and the percentage of adults only explained some of the variance. Referring back to Fig. 2.3.1, it is clear that
FIGURE 2.3.3:
A – Body mass distribution of juvenile Reed Warblers caught at Icklesham between August and September in the years 1998-2002. All birds were caught before 12pm.
B - Body mass distribution of adult Reed Warblers caught at Icklesham between August and September in the years 1998-2002. All birds were caught before 12pm.

TABLE 2.3.1: ANOVA output from an analysis of body mass including the factors Moul, Date and Date². Adj MS = adjusted mean square, Coef = regression equation coefficient.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Adj MS</th>
<th>F</th>
<th>P</th>
<th>Coef</th>
</tr>
</thead>
<tbody>
<tr>
<td>MOULT</td>
<td>2</td>
<td>462</td>
<td>598</td>
<td>&lt;0.001</td>
<td>2 = -0.72,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1 = -0.15, 0</td>
</tr>
<tr>
<td>DATE</td>
<td>1</td>
<td>14.1</td>
<td>18.2</td>
<td>&lt;0.001</td>
<td>-0.0231</td>
</tr>
<tr>
<td>DATE²</td>
<td>1</td>
<td>7.08</td>
<td>9.15</td>
<td>0.003</td>
<td>0.0001</td>
</tr>
<tr>
<td>ERROR</td>
<td>2688</td>
<td>0.77</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>2692</td>
<td>0.77</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
FIGURE 2.3.4: Distribution of body masses by moult class for juvenile Reed Warblers at Icklesham. Body mass was corrected to 7am, the mean time of capture for the data set. The data are from all birds that were scored for moult and weighed in 2002. Moult scores: 2 – bird in mid moult; 1 – bird finishing or in some cases beginning moult; 0 – moult completed or in rare cases, with respect to the data presented here, moult has yet to commence.
FIGURE 2.3.5: Mean body mass of birds captured at Icklesham against date. Includes data from 1998-2002, excluding days on which the body mass (g) of less than 10 birds was recorded. Both adults and juveniles were included in the calculation of mean body mass.

TABLE 2.3.2: Analysis of variance for the mean daily body mass of Reed Warblers caught at Icklesham between 1998-2002. Factors include date, total (number of birds captured), %adults (percentage of adults in catch) and year. The analysis is divided into 3 blocks, July, August and September. DF = degrees of freedom, MS = adjusted mean square, Coef = regression equation coefficient.

<table>
<thead>
<tr>
<th></th>
<th>JULY</th>
<th>AUGUST</th>
<th>SEPTEMBER</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>ms</td>
<td>P-value</td>
</tr>
<tr>
<td>Total</td>
<td>1</td>
<td>0.02</td>
<td>0.582</td>
</tr>
<tr>
<td>%Adult</td>
<td>1</td>
<td>0.46</td>
<td>0.014</td>
</tr>
<tr>
<td>Year</td>
<td>4</td>
<td>0.30</td>
<td>0.005</td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>0.23</td>
<td>0.079</td>
</tr>
<tr>
<td>Date²</td>
<td>1</td>
<td>0.59</td>
<td>0.006</td>
</tr>
<tr>
<td>Error</td>
<td>65</td>
<td>0.07</td>
<td>-</td>
</tr>
<tr>
<td>Total</td>
<td>73</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
neither the intensity of passage or the percentage of adults can explain the large increases in mean body mass at the end of September.

**Analyses of Retraps – Body Mass Changes**

Birds caught more than once at the same site (retraps) provide data on body mass changes and FDRs. The magnitude of body mass change is a reflection of the extent of fuelling in migrant birds. In Table 2.3.3 a set of descriptive statistics for birds at Icklesham with ‘positive’ (see section 2.2) mass changes are displayed: this excludes birds that lost mass between captures and were therefore unlikely to have been fuelling. The mean mass change of 1.06g is approximately equal to 10% of LBM and suggests that birds at Icklesham did not undergo extensive fuelling prior to departing on migration. Whilst this may be an underestimate, the value for the upper quartile (1.19g) still suggests that the majority of birds were not fuelling extensively.

Reed Warblers that lost mass at Icklesham were likely to be moulting juveniles that had yet to commence fuelling. In order to investigate the course of body mass changes in juveniles, a model of mass change was generated using data on retraps from 1997-2002 (see table 2.3.4 for ANOVA output). Only birds that were weighed on first and last capture were included, the mass change being calculated as the difference between the two. Birds trapped on consecutive days were excluded (see section 2.2 for justification). Significant factors in the model included: ‘number of days’ (between captures), ‘start mass’ (body mass on first capture), ‘date’ (on first capture) and ‘year’ (table 2.3.4)

The model suggests that a number of variables had an important influence on body mass changes. In particular, body mass has a distinctive quadratic relationship with the number of days since first capture, such that birds initially lost mass for approximately 10-15 days before gradually gaining mass. The shape of this relationship is dependent on the starting conditions. High initial body masses result in larger decreases and thus ‘start mass’ may partly represent the level of emergency reserves a juvenile has at the time of capture. These reserves may decrease initially because birds are still relatively inexperienced and are learning to forage effectively. Later start dates result in smaller decreases and a more rapid switch to gaining mass, this may reflect the higher probability of birds having completed their moult and commenced fuelling later in the year. This model is only expected to provide a guide to the pattern of mass
TABLE 2.3.3: Descriptive statistics for ‘positive’ mass changes (in grams) of Reed Warblers retrapped at Icklesham. Only birds retrapped 2 or more days after first capture were included.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>MEAN</th>
<th>ST. DEV.</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>236</td>
<td>1.06</td>
<td>0.709</td>
<td>0.046</td>
<td>0.63</td>
<td>1.19</td>
<td>4.89</td>
</tr>
</tbody>
</table>

TABLE 2.3.4: ANOVA output for an analysis of body mass change in juvenile Reed Warblers retrapped at Icklesham. All retraps were included regardless of interval length. DF = degrees of freedom; Adj MS = adjusted mean square; Coef = coefficient from regression equation.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Adj MS</th>
<th>F</th>
<th>P</th>
<th>Coef</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start Mass</td>
<td>1</td>
<td>16.3</td>
<td>32.1</td>
<td>&lt;0.001</td>
<td>-0.242</td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>2.13</td>
<td>4.19</td>
<td>0.041</td>
<td>0.004</td>
</tr>
<tr>
<td>Nº of Days</td>
<td>1</td>
<td>9.79</td>
<td>19.3</td>
<td>&lt;0.001</td>
<td>0.183</td>
</tr>
<tr>
<td>Nº of Days²</td>
<td>1</td>
<td>10.8</td>
<td>21.3</td>
<td>&lt;0.001</td>
<td>0.0016</td>
</tr>
<tr>
<td>Nº of Days* Start Mass</td>
<td>1</td>
<td>16.7</td>
<td>32.9</td>
<td>&lt;0.001</td>
<td>-0.021</td>
</tr>
<tr>
<td>Nº of Days* Date</td>
<td>1</td>
<td>2.37</td>
<td>4.66</td>
<td>0.031</td>
<td>0.0004</td>
</tr>
<tr>
<td>Year</td>
<td>5</td>
<td>1.89</td>
<td>3.72</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>ERROR</td>
<td>921</td>
<td>0.51</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>932</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
change, the actual durations of each phase and the slopes of increases and decreases are only expected to be crude estimates.

**Analyses of Retraps – Fuel Deposition Rates**

Reed Warblers had a range of positive and negative FDRs at Icklesham and the modal FDR was 0 (Fig. 2.3.6). This suggests that many of the Reed Warblers retrapped at Icklesham had yet to commence pre-migratory fuelling. As I was interested in fuelling birds, I have also looked just at juvenile Reed Warblers with ‘positive’ FDRs (for selection criteria see section 2.2). The mean ‘positive’ FDR was 0.018, which for a bird of mean wing length (65mm) is equivalent to a 0.17g increase per day or 1.8% of LBM (Table 2.3.5). Thus for a juvenile bird with an initial mass of 10.5g, it would take approximately 10 days for it to reach the mean body mass for birds which have completed their moult (12.2g). There was no significant difference in the mean ‘positive’ FDR between adult and juvenile birds (t-test, $t_{14} = 0.06$, P = 0.953), although the sample size for adults was very small (N = 14).

FDRs may be influenced by a number of variables. I looked at the effect of interference competition (calculated as the mean daily capture rate during the period when a bird was ‘known’ to be present, on the assumption that the greater the number of individuals present the greater the interference an individual will experience), the number of days between captures, date and year, on the FDRs (‘positive only) of juvenile Reed Warblers using an ANOVA model (table 2.3.6). Birds caught on consecutive days were not included (see section 2.2 for justification).

FDR was found to decrease significantly as the number of days between captures increased (Fig. 2.3.7). This relationship is expected if birds are not fuelling for the entire period between captures and can tell us something about fuelling durations (see following sub-section; see also Fig 2.3.8 in which examples of fuelling curves are given). If one makes the conservative assumption that a Reed Warbler can achieve an average FDR of 0.01 across the fuelling period, then examination of Fig. 2.3.7 suggests that fuelling durations are likely to be eight days in length or less.

FDR increased with date, which may be due to an ecological variable such as competition or a behavioral adaptation to an increasing time pressure (see section 2.1.1). Competition did not have a significant effect on FDR in the model presented in Table 2.3.6, however, when date was removed from the model, competition became
FIGURE 2.3.6: Histogram of fuel deposition rates of all birds retrapped at Icklesham between 1998 and 2002. All birds were trapped more than 1 day apart. The bars for juveniles (dark grey) represent the true number of birds in each class, whilst the values for adults (white) have been multiplied by five in order to make direct comparison easier. FDRs are expressed as the proportion of LBM gained per day.

TABLE 2.3.5: Basic statistics for ‘positive’ FDRs. Includes juvenile Reed Warblers caught in the autumns of 1997-2001 at Icklesham that gained more than 0.45g between captures (236 of 1069 retrap records for juvenile birds). Adults were not included.

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST. DEV.</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
</tr>
</thead>
<tbody>
<tr>
<td>236</td>
<td>0.018</td>
<td>0.014</td>
<td>0.001</td>
<td>0.008</td>
<td>0.024</td>
</tr>
</tbody>
</table>

TABLE 2.3.6: Output from an Analysis of Variance of FDR (log10 transformed). All factors were treated as covariates except Year.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Adj MS</th>
<th>F</th>
<th>P</th>
<th>Coef</th>
</tr>
</thead>
<tbody>
<tr>
<td>Start Mass</td>
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<td>0.026</td>
<td>0.58</td>
<td>0.449</td>
<td>0.016</td>
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<tr>
<td>Date</td>
<td>1</td>
<td>0.49</td>
<td>10.6</td>
<td>0.001</td>
<td>0.003</td>
</tr>
<tr>
<td>Nº of Days</td>
<td>1</td>
<td>4.07</td>
<td>88.7</td>
<td>&lt;0.001</td>
<td>-0.067</td>
</tr>
<tr>
<td>Nº of Days²</td>
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<td>0.96</td>
<td>20.9</td>
<td>&lt;0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Competition</td>
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<td>0.028</td>
<td>0.62</td>
<td>0.433</td>
<td>0.003</td>
</tr>
<tr>
<td>Wing Length</td>
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<td>0.02</td>
<td>0.892</td>
<td>-0.001</td>
</tr>
<tr>
<td>Year</td>
<td>5</td>
<td>0.029</td>
<td>0.64</td>
<td>0.672</td>
<td></td>
</tr>
<tr>
<td>ERROR</td>
<td>212</td>
<td>0.046</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>223</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
FIGURE 2.3.7: Fuel deposition rate against the number of days between captures. The raw data (white symbols) include all juvenile birds with ‘positive’ FDRs at Icklesham. The black curve is the predicted relationship between FDR and number of days between captures generated from the ANOVA model in Table 2.3.6.

![Graph showing fuel deposition rate against number of days between captures.](image)

TABLE 2.3.7: Descriptive statistics for the minimum duration in days spent at the site of birth, Icklesham. The sample is made up of birds either rung as nestlings or as birds aged as 1Js (not fully grown but had left the nest less than 15 days prior to capture).

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST DEV</th>
<th>SE MEAN</th>
<th>Q1</th>
<th>Q2</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>56</td>
<td>30</td>
<td>10.6</td>
<td>1.41</td>
<td>21</td>
<td>38</td>
<td>52</td>
</tr>
</tbody>
</table>

TABLE 2.3.8: Descriptive statistics for the minimum fuelling duration (days) of all Reed Warblers showing ‘positive’ mass changes at Icklesham. See section 2.2 for method of estimation.

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST DEV</th>
<th>SE MEAN</th>
<th>Q1</th>
<th>Q2</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>246</td>
<td>9.9</td>
<td>7.0</td>
<td>0.4</td>
<td>5.0</td>
<td>13.0</td>
<td>41.0</td>
</tr>
</tbody>
</table>
FIGURE 2.3.8: Examples of Reed Warbler fuelling curves at Icklesham (individual points represent captures). This subset of birds was chosen to demonstrate the variation in the slope and shape of fuelling curves. The birds pictured here are all juvenile birds that were caught on four occasions and gained at least 0.45g at some point during their fuelling period. The general shape of these curves suggests that fuelling rates increased towards the point of departure. If this is true of most retrapped birds, then FDRs are likely to have been underestimated, as many birds are unlikely to have been caught close to the point of departure. The most likely explanation for this pattern of increasing FDR, is that the period between captures will often contain days prior to when a bird commenced fuelling. Thus if birds are caught on several occasions, then only the later captures are likely to have occurred during the fuelling period, whilst earlier captures will include a non-fuelling period. A weight gain of 1g over three days may therefore be averaged over six days, thereby reducing the estimated FDR.

The curves also illustrate how birds often lose weight before fuelling commences. This loss is not expected to be associated with a stopover cost, as the period over which it takes place is too long, but is more likely to reflect the period in which juvenile birds are gaining independence and moulting: both of these processes can place an energetic strain on the birds.
significant although the coefficient indicates that the effect size was small (ANOVA, \( F_{6,213} = 4.30, P = 0.039, \text{Coefficient} = -0.006 \)). By examining juvenile Reed Warblers for which moult data were taken 2002, I found that FDR increased as the extent of moult decreased (ANOVA, \( F_{1,180} = 5.55, P= 0.005 \)).

**Moult and Fuelling Durations**

I expected Reed Warblers born at Icklesham to remain at the site until they had at least partly completed their post-juvenile moult and deposited enough fuel to initiate a flight phase. Reed Warblers at Icklesham ringed either as nestlings or aged as 1Js (bird not fully grown but left nest within the last 15 days) were present for a mean of 30 days between first and last capture (Table 2.3.7). This is likely to be an underestimate of the true period, and the values for the upper quartile and the maximum probably provide a more realistic estimate (Table 2.3.7).

The mean fuelling duration for Reed Warblers with ‘positive’ mass gains was 10 days rounded to a whole day (Table 2.3.8). The true fuelling durations of individual birds may have been both over and underestimated. The capture probability at Icklesham was relatively low (0.33) therefore durations may have been underestimated. Conversely, birds may have not been fuelling for the entire period between captures and thus durations will have been overestimated (see previous sub-section). Indeed, Fig. 2.3.7 suggests that durations may be 8 days or less, if it is assumed that Reed Warblers can achieve an average FDR of at least 0.01. The reliability of the estimates in Table 2.3.8 is therefore difficult to determine.

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2.3.2 **QUINTA DA ROCHE, PORTUGAL**

**Phenology of Migration**

Given the southerly location of Quinta da Roche, I expected the timing of passage to be later than at Icklesham (Fig. 2.3.1). The main passage period for adult Reed Warblers was from the end of August and throughout September, with peak passage occurring in mid-September (Fig. 2.3.9). Juvenile Reed Warblers arrived later
than adults, the main period of passage being between mid-September and the end of October (Fig. 2.3.9). At Icklesham the number of juvenile Reed Warblers greatly outnumbered adults (5.3:1), however in Portugal the ratio was considerably lower at 1.2:1.

**Body Mass Distributions**

Reed Warblers in Portugal are approaching the ecological barrier formed by the Mediterranean Sea and the Sahara desert and are therefore expected to have large fuel loads. The modal body mass for birds at Quinta da Roche was 15g (equivalent to a fuel load of 57% of LBM) and was therefore more than double the modal fuel load at Icklesham (approx. 12% LBM). The distribution of body masses for birds at first capture in Portugal was significantly different from a normal distribution (Kolmogorov-smirnov test (Siegal & Castellan 1989), Dmax = 0.085, P<0.01) and had two distinct peaks as indicated by the position of Dmax at 14g which lies between the two (Fig. 2.3.10). The first peak was at 10.5g and was probably due to the arrival of birds at the site before they had fuelled for the Sahara crossing. The larger, second peak at 15g presumably corresponds to birds that had finished fuelling and were only passing through the site. Retraps tended have lower body masses than birds that were not retrapped (Fig. 2.3.10) and suggests that birds at lower weights were more likely stay at the site and initiate a stopover. Indeed, the body mass of retraps was significantly lower than of birds only caught once (t-test, t99 = -9.46, P<0.001). Adults Reed Warblers were heavier than juveniles on first capture (means: adult = 14.6g, juveniles = 13.2g, t1917 = -14.08, P<0.001).

The mean body mass of Reed Warblers at Quinta da Roche did not show a significant relationship with date as it did at Icklesham (ANOVA, F1,1936 = 1.26, P = 0.26).

**Analyses of Retraps – Mass Changes**

The proximity of the Mediterranean Sea and, more importantly, the Sahara Desert to Quinta da Roche, should have selected for large fuel loads; therefore I also expected large mass changes at this site. The mean body mass change at Quinta da Roche was 2.5g whilst the maximum was 8.4g (Table 2.3.9). The mean change
FIGURE 2.3.9: Capture rates, expressed as the percentage of the total autumn catch, of adult and juvenile Reed Warblers at Quinta da Roche, Portugal. Low daily capture rates at the site, meant that the capture rate was calculated as a series of five-day averages. Only data collected between 1992-1994 was used, as catching effort in all other years was erratic. Before the five-day averages were calculated, the average catch on a given date was calculated using data from all three years.
FIGURE 2.3.10:
A – Body mass distribution of Reed Warblers on first capture at Quinta da Roche (N = 1934). The bars represent the percentage of birds at a given body mass. Includes birds caught between August and November in the years 1988-2001.
B – Body mass distribution of birds retrapped at Quinta da Roche, data was selected from the same months and years as above (N = 248).
represents an increase of 26% of LBM whilst 13 percent of birds gained more than 50% of their LBM, suggesting that some birds fuelled extensively. Birds at Quinta da Roche gained more mass than birds at Icklesham (t-test, $t_{66} = 6.35$, $P < 0.001$).

The extent of mass change did not vary significantly between age groups (ANOVA, $F_{1,98} = 1.64$, $P = 0.20$) and showed no relationship with time of year (ANOVA, $F_{1,99} = 0.72$, $P = 0.40$). Body mass change increased significantly with the number of days between captures (ANOVA, $F_{1,99} = 84.0$, $P < 0.001$), as would be expected.

**Analyses of Retraps – Fuel Deposition Rates**

FDRs were largely positive at Quinta da Roche and only a small number of birds had negative FDRs (Fig. 2.3.11). The modal value for FDR of all birds at Quinta da Rocha was 3% of LBM/day whilst it was 0% at Icklesham. To directly compare FDRs between Icklesham and this site, I have only considered ‘positive’ FDRs. The mean ‘positive’ FDR at Quinta da Roche was twice that at Icklesham (Table 2.3.10 & Table 2.3.5), a difference that was found to be significant ($t_{75} = 6.38$, $P < 0.0001$, see also Fig. 2.3.12). Reed Warblers in Portugal also showed a greater range of FDRs at the higher end (Upper Quartile, Portugal = 0.044, Icklesham 0.024).

It was not possible to examine the affect of the number of individuals present at the site on FDRs in Portugal due to the erratic trapping effort at the site. However, neither age ($t_{24} = 1.22$, $P = 0.233$) nor time of year (Regression of FDR on Date, $F_{1,60} = 0.56$, $P = 0.46$, adjusted $R^2 = 0.0\%$) had a significant effect on FDR. Moult was unlikely to have had any affect on FDR in Portugal, as the majority birds had completed their moult. Of 187 birds scored for moult intensity, only 6 birds were still moulting and all six were trapped in August.

FDR decreased with the number of days between captures but the effect was not strong, as indicated by the low value of the adjusted $R^2$ (Regression of FDR on Number of Days between Captures, $F_{1,58} = 6.15$, $P = 0.016$, adjusted $R^2 = 8\%$, Coefficient = -0.0014). The gentle slope of the relationship suggests that FDRs varied little during the fuelling period (Fig. 2.3.13) and therefore birds were probably actively fuelling for the entire period between captures. The slight decrease may be due to increasing metabolic costs as body mass increased. For examples of fuelling curves, see Fig. 2.3.14.
TABLE 2.3.9: Descriptive statistics for birds showing ‘positive’ body mass changes (grams) at Quinta da Roche. Includes Reed Warblers retrapped between the years 1988-2001 that were caught more than one day apart.

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST DEV</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>62</td>
<td>2.52</td>
<td>1.77</td>
<td>0.23</td>
<td>1.28</td>
<td>3.65</td>
<td>8.4</td>
</tr>
</tbody>
</table>

FIGURE 2.3.11: A comparison of the frequency of fuel deposition rates recorded at Quinta da Roche in the years 1988-2001 for adult (N=26) and juvenile (N=66) Reed Warblers. Only birds that were trapped at least one day apart were included. FDR is given as the proportion of LBM accumulated per day.

TABLE 2.3.10: Descriptive statistics for ‘positive’ fuel deposition rates at Quinta da Roche, Portugal. The statistics are calculated from the data on FDRs of both adult and juvenile Reed Warblers, excluding those that were trapped on consecutive days.

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST DEV</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
</tr>
</thead>
<tbody>
<tr>
<td>60</td>
<td>0.036</td>
<td>0.021</td>
<td>0.003</td>
<td>0.024</td>
<td>0.044</td>
</tr>
</tbody>
</table>
FIGURE 2.3.12: A comparison of ‘positive’ Mass Changes and Fuel Deposition Rates of Reed Warblers at Icklesham (black bars) and Quinta da Roche (white bars) during autumn migration. The Y axis values are presented as a percentage of the population due to the differences in sample sizes between sites (England = 236, Portugal 59).

FIGURE 2.3.13: ‘Positive’ FDRs against number of days between captures at Quinta da Roche. Equation of regression line: FDR = 0.0469 - 0.00137* Number of Days.
**Fuelling Duration**

The fuelling durations of Reed Warblers at Quinta da Roche were not significantly different from those at Icklesham (t-test, \( t_{105} = 0.48, P = 0.629 \); see also Table 2.3.11). Capture probabilities did not differ significantly between the two sites either (t-test, \( t_{140} = -0.64, P = 0.523 \)), which supports the lack of a difference found above. However, as argued in the previous paragraph, Reed Warblers probably fuelled for the entire period between captures at Quinta da Roche and therefore fuelling durations are unlikely to have been overestimated. Instead, the low probability of capture at Quinta da Roche (0.31) is likely to have led to underestimates. Therefore durations may be greater than those at Icklesham.

**Summary – Main results from Autumn Sites**

The FDRs and fuel loads of Reed Warblers at Icklesham were low relative to Quinta da Roche, although adults accumulated larger fuel loads than the majority of juveniles. FDRs were therefore likely to have been constrained. Moult was found to be an important constraint on both the FDRs and fuel loads of juvenile birds. Whilst many transient juveniles had completed their moult, it is evident from the occurrence of moultting birds throughout the migration period that many juveniles were actively migrating whilst still moultting. The measure of competition used here (number of individuals caught per day) did not appear to constrain FDRs, however, a number of approaches could be taken to examine the affect of competition which may refute this conclusion. Fuel loads and FDRs both increased with date, which suggests that selection for time-minimisation had promoted FDRs towards the end of the migratory period but not at the beginning. Fuelling durations were difficult to measure accurately at Icklesham but appear to be between 5 and 10 days in length.

The fuel loads of Reed Warblers at Quinta da Roche were larger than at Icklesham: as would be expected given the imminent need to cross both the Mediterranean Sea and Sahara desert. In order to achieve larger fuel loads, Reed Warblers at Quinta da Roche had significantly higher FDRs relative to Icklesham, and fuelling durations may have been slightly longer too. FDRs did not vary with date at Quinta da Roche suggesting that they were maximal throughout.
FIGURE 2.3.14: Examples of fuelling curves from Reed Warblers at Quinta da Roche in Portugal. Includes all retrap records in which birds gained more than 4g between first and last captures. The bird marked by white symbols was originally ringed in Britain before being controlled in Portugal.

TABLE 2.3.11: Descriptive statistics for the minimum fuelling duration (days) of all Reed Warblers showing ‘positive’ mass changes at Quinta da Roche. See section 2.2 for method of estimation.

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST DEV</th>
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<th>UPPER QUARTILE</th>
<th>MAX</th>
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<tbody>
<tr>
<td>59</td>
<td>10.3</td>
<td>5.6</td>
<td>0.7</td>
<td>6.0</td>
<td>15.0</td>
<td>28.0</td>
</tr>
</tbody>
</table>
2.4 RESULTS & DISCUSSION – SPRING MIGRATION

2.4.1 DJOUDJ

Phenology of Migration

Passage appeared to commence in mid-February at Djoudj, after which point passage appears to have been steady, although erratic, until at least the end of April (Fig. 2.4.1). Ringing operations were typically terminated at the end of April at Djoudj and thus it is not possible to determine whether passage continued into May.

Recapture Probabilities

The retrap rate at Djoudj, calculated as the percentage of each daily catch that was later retrapped, showed no trend with date (ANOVA, $F_{3,148} = 0.45$, $P=0.502$). The retrap rate did vary between years (ANOVA, $F_{3,148} = 6.31$, $P=0.002$) and decreased as the magnitude of the daily catch increased (ANOVA, $F_{3,148} = 8.85$, $P=0.003$). Thus the probability of recapture was lowest on days when passage was high. The mean recapture probability was 0.09, and typically varied from 0.05-0.11 between days (lower quartile = 0.045, upper quartile = 0.111).

Body Mass Distributions

The body mass distribution of Reed Warblers on first capture indicated that the majority of birds arrived at Djoudj with minimal fuel reserves and had not yet commenced fuelling for the Sahara crossing (Fig. 2.4.2). The body mass distribution for retrapped birds appeared to have two components (Fig. 2.4.2). The first component was a hump centred around 9g, which may represent birds that had not started fuelling. The second component was a much smaller hump centred around 13.5g and was most likely caused by birds that had undergone extensive fuelling. The body mass distributions suggest that few Reed Warblers fuel extensively at sites south of Djoudj. Unlike Reed Warblers at Quinta da Roche (section 2.3.2), few birds arriving at Djoudj had fuel loads
FIGURE 2.4.1: Daily capture rate of Reed Warblers, expressed as a percentage of the total seasons catch, during spring passage at Djoudj, Senegal. Daily capture rates were based on a three-year average from ringing operations carried out between 1991-1993. Ringing was carried out daily, when weather conditions allowed, from February to the end of April.
sufficient for crossing the Sahara. Therefore, it is difficult to justify a direct comparison of body masses at these sites; however, it is evident from Fig. 2.4.2 and 2.3.10, that birds in Portugal accumulated larger fuel loads.

**Retrap Analyses – Body Mass Changes**

Body mass changes at Djoudj were quite large (max 6.9g, Table 2.4.1), as would be expected given the proximity of the Sahara desert (section 2.1.1). The mean body mass change was significantly greater than that at Icklesham (t-test, $t_{357} = 9.89$, $P<0.001$), but significantly less than Quinta da Roche (t-test, $t_{296} = -2.10$, $P = 0.037$).

The extent of mass change may vary with date and the length of a bird’s stay: I examined the effect of these factors on ‘positive’ mass changes using an ANOVA model (Table 2.4.2). Mass change increased significantly with date, indicating that fuelling typically occurred later in the period examined (Feb-Apr). Mass change had a quadratic relationship with the number of days between captures, such that no more mass was added after a certain point (Fig. 2.4.3). Assuming that birds may not have fuelled for the entire period between captures, and that birds do not remain at the site once they are no longer gaining fuel, then this point can be used to estimate fuelling durations. Therefore the model suggests that durations may be 25-30 days in length whilst the raw data suggest longer durations of 25-35 days (Fig. 2.4.3). Both the relationships described in this paragraph, were still significant after controlling for wing length (wing length varies between populations which may in turn vary in the timing of passage and fuelling behaviour).

In Fig. 2.4.3, apparent bimodality can be seen in the raw data: one set of birds made large increases in mass (1-7g, upper half of graph) whilst the second set increased by little more than one gram, despite being present for up to 50 days (lower half of graph). This probably reflects the difference between fuelling and non-fuelling birds. Real fuelling curves show greater similarities to the first set of birds (Fig. 2.4.4).

**Retrap Analyses – Fuel Deposition Rates**

The majority of Reed Warblers at Djoudj had positive FDRs (65%) whilst a small number of birds had negative FDRs and were thus losing weight (Fig. 2.4.5). The modal FDR was zero, suggesting that many birds did not start fuelling as soon as they
FIGURE 2.4.2: Body mass distributions for birds on first capture (New) and for all retrap records (Retraps). Frequencies of each body mass class are expressed as a percentage of the total number of birds across all classes. Only birds caught in the years 1991-1993 and caught between the 15th February and the 30th April were included.
TABLE 2.4.1: Descriptive statistics for ‘positive’ body mass changes (g) of birds retracted at Djoudj between the 15\textsuperscript{th} February and the 1\textsuperscript{st} May, 1991-1993. Birds caught on consecutive days were excluded. The second row gives statistics for birds selected using stricter criteria in which birds present for more than 20 days and with a mass change of 1g or less were excluded.

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST. DEV.</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
<th>MAX</th>
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</thead>
<tbody>
<tr>
<td>250</td>
<td>1.83</td>
<td>1.34</td>
<td>0.085</td>
<td>0.70</td>
<td>2.70</td>
<td>6.90</td>
</tr>
<tr>
<td>236</td>
<td>2.07</td>
<td>1.40</td>
<td>0.091</td>
<td>0.90</td>
<td>3.00</td>
<td>6.90</td>
</tr>
</tbody>
</table>

TABLE 2.4.2: ANOVA output for the model: ‘Positive’ Mass Change = Wing + Date + Nº of Days + Nº of Days\(^2\). Data entered in to model included all Reed Warblers retracted two days apart at Djoudj that had a ‘positive’ mass change. All variables were treated as covariates.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Adj MS</th>
<th>F</th>
<th>P</th>
<th>Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing</td>
<td>1</td>
<td>12.8</td>
<td>9.14</td>
<td>0.003</td>
<td>0.130</td>
</tr>
<tr>
<td>Date</td>
<td>1</td>
<td>5.33</td>
<td>3.81</td>
<td>0.052</td>
<td>0.010</td>
</tr>
<tr>
<td>Nº of Days</td>
<td>1</td>
<td>59.5</td>
<td>42.5</td>
<td>&lt;0.001</td>
<td>0.129</td>
</tr>
<tr>
<td>Nº of Days(^2)</td>
<td>1</td>
<td>21.9</td>
<td>15.7</td>
<td>&lt;0.001</td>
<td>-0.002</td>
</tr>
<tr>
<td>ERROR</td>
<td>262</td>
<td>1.40</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL</td>
<td>266</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
FIGURE 2.4.3: Raw data for ‘positive mass changes’ against the number of days between captures (Black symbols, N = 267). The white curve was generated using the ANOVA model presented in Table 2.4.2. The mean values for the sample were used such that the value for wing = 65mm and date = 53. Heteroscedacity and apparent bimodality in the raw data gave rise to a poor model fit. The fit should not be taken as an approximation of typical fuelling behaviour.

FIGURE 2.4.4: Examples of natural fuelling curves from Reed Warblers at Djoudj, Senegal. Only birds caught on at least three occasions and with a mass gain greater than 3.5g are pictured.
arrived at the site. The mean ‘positive’ FDR was low, suggesting that FDRs were generally low at Djoudj (Table 2.4.3). The mean ‘positive’ FDR was not significantly different to that at Icklesham (t-test, $t_{470} = -1.53$, $P = 0.126$). The negative t-value even suggests that FDRs were slightly but not significantly lower than at Icklesham. The mean FDR at Djoudj was less than half the mean at Quinta da Roche and was found to be significantly different (t-test, $t_{67} = -7.15$, $P<0.001$).

Reed Warbles at Djoudj were about to cross the Sahara and I would expect that a body mass of at least 14g may be necessary to make the crossing (see section 7.2). If we accept that the mean ‘positive’ FDR is an underestimate and use the value for the upper quartile instead (Table 2.4.3, FDR = 0.021), it would take a bird 23 days to reach 14g if it started at a body mass of 9.5g. Fuelling prior to crossing the Sahara in spring is therefore likely to be a lengthy process.

FDR may vary with a number of factors and at Djoudj, FDR decreased with the number of days between capture events (Table 2.4.4). The slope of the decrease was approximately a third of that at Icklesham (Djoudj –0.022, Icklesham –0.067), suggesting that periods of sustained fuelling were longer at Djoudj than at Icklesham. FDR increased significantly with both wing length and date (Table 2.4.4). The relationship with wing length could be explained if the LBM estimate used for calculating FDRs was inaccurate. However, wing length was still significant after correcting for body size ($P = 0.012$).

The increase in FDR with date mirrors the increase in the proportion of birds with positive FDRs by month (Fig. 2.4.6). The distribution of FDRs by month shows that few birds had commenced fuelling in February (only 30%), whilst this increased to 50% in March and 63% by April. Unfortunately, no data were available for May but I predict that the highest FDRs and proportion of fuelling birds would be observed in May.

**Fuelling Durations**

Fuelling durations at Djoudj were very long and were likely to have been between 20 and 40 days in length (Table 2.4.5). Durations at Djoudj were significantly longer than those at Icklesham (t-test, $t_{382} = 10.17$, $P < 0.001$) and Quinta da Roche (t-test, $t_{192} = 8.09$, $P < 0.001$). This was not because of higher capture probabilities at Djoudj: the probability of capture was significantly lower than at Icklesham or Quinta
FIGURE 2.4.5: Frequency distribution of FDRs for birds caught and retrapped between the 15\(^{th}\) Feb and the 1\(^{st}\) May, 1991-1993, at Djoudj. Only captures more than one day apart were included in the figure (N= 591 of 756 records).

![Frequency distribution of FDRs for birds caught and retrapped between the 15\(^{th}\) Feb and the 1\(^{st}\) May, 1991-1993, at Djoudj. Only captures more than one day apart were included in the figure (N= 591 of 756 records).](image)

TABLE 2.4.3: Descriptive statistics for ‘positive’ fuel deposition rates of birds caught between the 15\(^{th}\) February and the 1\(^{st}\) May at Djoudj. Birds caught on consecutive days were excluded.

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>STDEV</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
</tr>
</thead>
<tbody>
<tr>
<td>250</td>
<td>0.016</td>
<td>0.011</td>
<td>0.001</td>
<td>0.008</td>
<td>0.021</td>
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</table>

TABLE 2.4.4: ANOVA output for the model: LogFDR = Date + Nº of Days\(^2\) + Wing. FDR was log10 transformed and Date was calculated as the mean of the date on first and second captures. All variables were treated as covariates. Data includes all birds with ‘positive’ FDRs caught between the 15\(^{th}\) February and the 1\(^{st}\) May, 1991-1993 at Djoudj.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Adj MS</th>
<th>F</th>
<th>P</th>
<th>Coef</th>
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<tr>
<td>Wing</td>
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<td>6.62</td>
<td>0.011</td>
<td>0.025</td>
</tr>
<tr>
<td>Date</td>
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<td>0.31</td>
<td>4.26</td>
<td>0.040</td>
<td>0.002</td>
</tr>
<tr>
<td>Nº of Days</td>
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<td>2.15</td>
<td>29.6</td>
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<td>-0.024</td>
</tr>
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<td>Nº of Days(^2)</td>
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<td>0.38</td>
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<td>0.023</td>
<td>0.0002</td>
</tr>
<tr>
<td>ERROR</td>
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<td>0.07</td>
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<td></td>
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<tr>
<td>TOTAL</td>
<td>266</td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
FIGURE 2.4.6: The distribution of FDRs by month at Djoudj. Month was assigned using the mid-point of the two captures rather than the first capture or recapture event. All Reed Warblers recaptured during the years 1991-1993 are included, except for those caught on consecutive days.
da Roche (t-tests, \( t_{383} = -8.80, P < 0.001 \), \( t_{82} = -6.55, P < 0.001 \), respectively). Long fuelling durations therefore appear to be the means by which fuel loads sufficient for crossing the Sahara are achieved at Djuodj, rather than having high FDRs: as was the case for Reed Warblers in Portugal (section 2.3.2).

The low probability of capture at Djuodj (mean = 0.18) implies that durations will have been underestimated to a greater extent than at other sites. Thus the values estimated earlier in this section using data on mass changes and FDRs are probably more realistic than the mean value in Table 2.4.5.

| TABLE 2.4.5: Descriptive statistics for the minimum fuelling duration (days) of all Reed Warblers showing ‘positive’ mass changes at Djuodj. |
|---|---|---|---|---|---|---|---|
| N | MEAN | STDEV | SE MEAN | LOWER QUARTILE | UPPER QUARTILE | MAX |
| 235 | 18.8 | 11.5 | 0.75 | 9.0 | 27 | 56 |
2.4.2 AIGUAMOLLS DE L’EMPORDA – NORTH-EAST SPAIN

Phenology of Migration

The first Reed Warblers typically arrived at Aiguamolls by mid-April and passage was steady by late April (Fig. 2.4.7). The majority of birds passed through the site in May, with some of the highest capture rates being recorded in mid-May. Passage probably continued into June, but data were not available after the end of May.

Recapture Probabilities

Retrap rates were low at Aiguamolls, with a mean of 4% and a median of 0%, when only considering days when more than five birds were caught. The rate of recapture showed no trend with date (ANOVA, $F_{1,106} = 0.03$, $P = 0.874$), indicating that birds were no more likely to stopover at the site at any time during the passage period.

Body Mass Distributions

Reed Warblers arriving at Aiguamolls were typically carrying small fuel loads and few birds arrived with large fuel loads: the median value for body mass on first capture was 11.5g and only 12% had body masses above 13g (see Fig. 2.4.8). Reed Warblers arriving at the site may therefore only have had enough fuel for one night of flight and birds with body masses below 10.5g (approx. 24%) might be expected to initiate a refuelling stop either at Aiguamolls or nearby.

The body mass distribution for Reed Warblers retrapped at least one day after initial capture indicated that some of these birds had refuelled (Fig 2.4.8). Many of these refuelling birds only attained small fuel loads (e.g. 11g), however, 43% of birds achieved body masses of 12g or greater, allowing for potential onward flights of 1000-1500km in still air (see section 7.2). Birds present for one day had significantly higher body masses than birds retrapped on subsequent days, after correcting for time of day (means ± S.D: one day, 11.55 ± 1.07; retraps, 11.09± 1.02, $t_{2077} = 3.67$, $P<0.001$).
FIGURE 2.4.7: Daily capture rate, expressed as a percentage of the total seasons capture, during spring passage at Aiguamolls de l’Emporda, north-east Spain. Rates were averaged over the four years (1999-2002) of data obtained from this site.
FIGURE 2.4.8: Body mass distributions for birds on first capture (New) and for all retap records (Retraps) at Aiguamolls de l’Emporda. Frequencies in each mass class are expressed as a percentage of the total number of birds across all classes. The data include all birds caught during April and May in the years 1999-2002 at Aiguamolls.
Retrap Analyses – Mass Changes

Body mass changes in retrapped birds were not large at Aiguamolls but were striking due to the short periods over which they occurred (see Table 2.4.8). It was not unusual for Reed Warblers at Aiguamolls to increase in mass by one gram between captures on the same day (Fig. 2.4.9). Similar data from Icklesham and the other sites (not presented in this thesis), typically show decreases or slight increases on the day of first capture. The decreases observed in these data sets and other published data sets have often been attributed to stopover costs or considered as an artefact of the capture process (section 2.1.2).

Despite some birds decreasing in mass over the course of a day, body mass increased significantly with hour (Regression, $F_{1,138} = 80.7$, $P<0.001$, adjusted $R^2 = 36.4\%$). Body mass changes of Reed Warblers retrapped at least one day after initial capture were also largely positive, only 28% showed negative mass changes. The mean ‘positive’ mass change (Table 2.4.6) was significantly lower than at Quinta da Roche and Djoudj (t-tests, $t_{84} = -6.09$, $P<0.001$ and $t_{75} = -7.50$, $P<0.001$ respectively) and was not significantly different from Icklesham (t-test, $t_{39} = -0.60$, $P=0.549$). The low mean mass change is largely a product of short fuelling durations rather than the quality of the site, as indicated by the rapid rates of mass gain of birds trapped on the same day (Fig. 2.4.9).

Variation in the extent of ‘positive’ mass changes was largely explained by the number of days between captures (ANOVA, $F_{2,27} = 30.77$, $P<0.001$, Coefficient = 0.28), as would be expected. The extent of mass change did not vary significantly with date after controlling for the number of days between captures (ANOVA, $F_{2,27} = 0.01$, $P = 0.906$).

Retrap Analyses – Fuel Deposition Rates

FDRs were high at Aiguamolls (Fig. 2.4.10 & Table 2.4.7) and 70% of all retraps had positive FDRs. Indeed, even 50% of birds that were retrapped on the same day had positive FDRs. The mean ‘positive’ FDR at Aiguamolls (Table 2.4.7) was significantly higher than at all three sites examined in this study (t-tests, Icklesham $t_{33} = 8.57$, $P<0.001$, Portugal $t_{62} = 2.97$, $P = 0.004$, Djoudj $t_{33} = 9.18$, $P < 0.001$) and is
FIGURE 2.4.9: Body mass changes in birds retrapped on the day of initial capture at Aiguamolls. Includes data on all same day retraps from the years 1999-2002.

![Graph showing body mass changes over hours]

TABLE 2.4.6: Descriptive statistics for ‘positive’ body mass changes (grams) of birds retrapped at Aiguamolls. Birds caught on consecutive days or on the same day were not included.

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST. DEV.</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>20</td>
<td>1.17</td>
<td>1.08</td>
<td>0.15</td>
<td>0.75</td>
<td>1.42</td>
<td>3.40</td>
</tr>
</tbody>
</table>
FIGURE 2.4.10: Frequency distribution of the fuel deposition rates of Reed Warblers between the 1\textsuperscript{st} April and the 30\textsuperscript{th} May at Aiguamolls de l’Empordà. Includes all retraps, including those with negative FDRs.

![Frequency distribution of fuel deposition rates](image)

TABLE 2.4.7: Descriptive statistics for ‘positive’ fuel deposition rates at Aiguamolls. Includes 30 of 77 birds, and unlike for the other sites, it includes birds caught on consecutive days but not on the same day.

<table>
<thead>
<tr>
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<th>ST. DEV.</th>
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<th>UPPER QUARTILE</th>
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<tbody>
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<td>30</td>
<td>0.049</td>
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<td>0.004</td>
<td>0.034</td>
<td>0.064</td>
<td>0.09</td>
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</tbody>
</table>

Table 2.4.8: Descriptive statistics for the minimum fuelling duration (days) of all Reed Warblers showing ‘positive’ mass changes at Aiguamolls.

<table>
<thead>
<tr>
<th>N</th>
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<th>ST. DEV.</th>
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<td>57</td>
<td>2.2</td>
<td>1.6</td>
<td>0.22</td>
<td>1.0</td>
<td>2.0</td>
<td>9.0</td>
</tr>
</tbody>
</table>
also higher than other published FDRs from across Europe (Shaub & Jenni 2000a, means > 0.02 were only recorded at 3 out of 13 sites).

In an analysis of factors influencing ‘positive’ FDRs, only the number of days between captures was found to decrease FDRs significantly (ANOVA, $F_{3,26} = 6.35$, $P=0.018$, Coefficient = -0.006). This affect was also observed in the other three data sets examined in this chapter. Neither date or wing length were found to have a significant effect on FDRs ($P=0.812$ and 0.513 respectively).

**Fuelling Durations**

Fuelling durations at Aiguamolls were extremely short (see Table 2.4.8), with most birds only staying at the site between one and three days. Whilst the length of some durations will have been underestimated, the probability of capture was high at this site (mean ± S.D. = 0.74 ± 0.23) and therefore errors in estimation will have been relatively infrequent. Further, a large number of birds (43) that were only retrapped on the same day, showed clear evidence of fuelling (Fig. 2.4.9) but did not gain more than 0.45g and were therefore excluded from Table 2.4.8. If one includes birds that showed any mass gain on the first day of capture, then the mean duration is even lower (means ± S.D. = 1.7 ± 1.4 days, $N=100$). Durations at Aiguamolls were significantly shorter than at Icklesham, Quinta da Roche and Djoudj (t-tests, $P < 0.001$ in all cases).

**Summary – Main results from Spring Migration**

FDRs were low at Djoudj and appear to be constrained relative Quinta da Roche and Aiguamolls. As large fuel loads were required for birds to cross the Sahara, low FDRs were compensated for by long fuelling durations. The distribution of body masses supports the conclusion from Quinta da Roche that Reed Warblers adopt strategy 1 for crossing the Sahara (Fig. 2.1.1). Time-minimisation appears to have selected for higher FDRs as the time available for migration decreased, as was the case at Icklesham.

Reed Warblers at Aiguamolls were typically transients only stopping at the site for one day. Birds that did stop mostly stayed at the site for just two days and fuelled at rapid rates. Indeed, FDRs at Aiguamolls were higher than at any of the other sites (Fig. 2.5.1). The behaviour of Reed Warblers at Aiguamolls suggests that they had been strongly selected to minimise time.
The influences on fuelling rates and durations, and consequent fuel loads may vary in space and time, giving rise to a variety of fuelling strategies both between and within species. Reed Warbler fuelling strategies have been investigated by a number of authors covering a range of sites throughout Europe (Bibby & Green 1981, Omerod 1990, Garcia Piero 1995, Robson et al. 2001, Schaub & Jenni 2000a) and in the Middle East (Merom et al. 2000). Whilst these studies have identified key factors such as moult as constraining factors on fuel deposition (Herremans 1990, Schaub & Jenni 2000a), few other factors influencing fuelling behaviour have been identified. Further, the strategies by which Reed Warblers negotiate the Sahara have not been examined in detail. Fuelling rates and durations can vary on a geographical scale and therefore the factors influencing them are expected to show similar variation. I will therefore discuss the causes and consequence of fuelling behaviours by site before taking an overview of the influences on Reed Warbler fuelling behaviour.

In the discussion that follows, I have not addressed a number of possible queries that could arise about my interpretation of the data, given the manner in which it was collected. Catching birds in mist nets will always lead to inherent biases in the data, as is the case for many sampling methods (Gauthier-Clerc & Le Maho 2001). For example, birds may become either trap-happy or trap-shy and as I have explained already, the action of catching a bird may induce stress and subsequent changes in a bird’s energetic state (section 2.1.2). Further, at three of the sites examined in this chapter, tape lures were used to increase catch rates and there is good evidence that tape lures increase the recruitment of birds that may have otherwise over flown a site (Schaub et al. 1999). Tape luring may also bias age sampling, as adults and juveniles may react differently to such lures. Whilst I have tried to limit the effect of these various factors in the analyses presented here (e.g. removing birds trapped on consecutive days, to try and reduce trapping effects), it is not possible to account for the biases caused by practices such as tape luring. In the following discussion, these potential biases have been born in mind and I have applied caution in all interpretations. However, I believe that the method of data collection could not have been responsible for the key results presented in this chapter.
Autumn – Icklesham, Southern England

Interpretation of the ringing data from Icklesham could potentially have been confounded by behavioural differences between Reed Warblers trapped at the site. Reed Warblers at Icklesham may be placed in three main behavioural classes: (1) juveniles born at the site that had not begun fuelling or migrating; (2) fuelling adults and juveniles; (3) transients that had fuelled at other sites and were only stopping at Icklesham between nocturnal flights. The population of breeding Reed Warblers at Icklesham was large (section 2.2) and many of the juvenile birds trapped had probably been born there. The ringing data will therefore have contained an unknown proportion of fuelling and non-fuelling juveniles. Whilst, I introduced measures to remove non-fuelling individuals from the population (section 2.2), some of these birds may have inadvertently been included and will have given rise to underestimates of FDRs and overestimates of fuelling durations. However, I am confident that the measures I took will give a more accurate picture of fuelling behaviour than has been presented in other studies in which birds that were clearly not fuelling (i.e. they had large negative FDRs) were not removed (e.g. Bibby & Green 1981, Schaub & Jenni 2000a, 2001).

The combination of a high trapping rate and low retrap rate in August and September (Fig. 2.3.1) indicates that transients were common at Icklesham during this period. The number of transient birds stopping at Icklesham may have been augmented by the use of tape lures (although Reed Warbler calls were never played), therefore the prevalence of this behaviour in the population must not be taken at face value. Indeed, tape lures are known to increase trapping rates (Schaub & Jenni 1999) and it is reasonable to assume that many of the transients at Icklesham may have over flown the site if it were not for tape lures. It is also worth noting that birds that stayed at the site for more than one day were unlikely to have done so because of the tape lures. Despite the potentially confounding effects of large numbers of transients within the population, transients were not included in any of the analyses of FDRs and fuelling durations, and were therefore only likely to confound the conclusions drawn on fuel loads.

Fuelling behaviour at Icklesham was characterised by low FDRs and fuelling durations of medium length relative to the other three sites in this chapter (Fig. 2.5.1). This suggests that FDRs were constrained at Icklesham and a number of variables could be responsible, such as food availability, competition, moult and even incompetence. Food availability was unlikely to have been the only constraining factor at Icklesham, as
FIGURE 2.5.1: A comparison of the distribution of ‘mass changes’, FDRs and fuelling durations of Reed Warblers at Icklesham (England), Quinta da Roche (Portugal), Djoudj (Senegal) and Aiguamolls (Spain). The black circles represent the mean value for each population and boxes define the median, inter-quartile range and the range (whiskers). Shading denotes the direction of migration: unshaded = south in autumn, shaded = north in spring. N.B. All data refer to birds with a ‘positive’ mass changes.
FIGURE 2.5.2: Body mass distributions for both adults and juveniles during the main migration seasons at Icklesham, England (Aug-Oct); Quinta da Roche, Portugal (Sept-Nov); Djoudj, Senegal (Feb-May); Aiguamolls, Spain (April-May). All body masses were corrected for time of day.
during the main migration period (August-September) insect abundance is expected to
be high (Alerstam 1990, Speight et al. 1999). Further, FDRs increased with date, in
contrast with the expected trend for insect abundance. The increase in FDR with date is
better explained by decreasing levels of competition, however, I found no evidence for
competition affecting FDRs. Low foraging success as a consequence of incompetence
could explain the low FDRs. Indeed, the majority of FDRs were from juvenile birds that
had been learning to forage for as little as 40 days before they began fuelling. If this was
the main cause though, I would have expected adults to have higher FDRs than
juveniles, as they should be more experienced foragers: this was not the case (although
the sample size for adults was very small and therefore the possibility cannot be ruled
out).

Moulting juvenile Reed Warblers had unusually low FDRs and therefore moult
could be partly responsible for low FDRs at Icklesham. The extent to which moult
suppressed FDRs, will depend on the timing and therefore the prevalence of moult
amongst fuelling birds. Juvenile Reed Warblers were found to be in active moult
throughout the migratory season (July-October); indeed close to 40% of birds were still
in heavy moult at the end of September (Fig. 2.3.2) This implies that Reed Warblers
fuelled and migrated whilst still actively mouling, which is surprising given that moult
is an energetically demanding process (Ginn & Melville 1983, Lindström et al. 1993,
Jenni & Winkler 1994). The cost of moulting and migrating simultaneously appears to
be low FDRs and therefore small fuel loads, and a lower overall speed of migration.
That Reed Warblers can afford to moult at this time of year, suggests that the benefits of
reaching the wintering grounds early or completing their migration quickly are not as
great as in species that do not have a post-juvenile moult prior to/during autumn
migration.

Indeed, that juveniles can afford a post-juvenile moult suggests that Reed
Warblers have not been selected to minimise time at this stage in their migration and
may therefore be minimising another currency (see section 1.3). Whilst selection for
time-minimisation should give rise to maximum FDRs (Lindström & Alerstam 1990),
selection for minimising an alternative currency, such as predation risk, favours non-
maximal FDRs (Houston 1998). Therefore, FDRs at Icklesham may be suppressed
through behavioural means as a result of selection for minimisation of a currency other
than time. Indeed, the trend of increasing FDRs and fuel loads with date (Fig. 2.3.5),
suggests that time-minimisation may become a greater selective pressure later in the
season as the time available to complete migration decreases. Further, this trend cannot be entirely explained by the prevalence of moult within the population, as the proportion of moultng birds did not decrease significantly after approximately mid-August (Fig. 2.3.2).

It is likely that Reed Warbler FDRs were constrained by a combination of factors at Icklesham, including moult, selection for minimising a currency such as predation risk, and maybe foraging incompetence in juveniles. The trend of increasing FDRs with date has been shown in species that do not moult and migrate simultaneously (Fransson 1998a, Schaub & Jenni 2000a) and thus selection for an overall currency other than time may be a common trend amongst migratory passerines in the early stages of their autumn migration.

The large numbers of locally born Reed Warblers trapped at Icklesham, provide information on the timing of pre-migratory fuelling, relative to when birds left the nest, and also provide a guide to the pattern of body mass change during this period. Estimates from the model in Table 2.3.4, indicate that it took birds approximately 40 days to accumulate a moderate fuel load after gaining independence. This is in agreement with the length of time that birds ringed in the nest at Icklesham remained at the site (mean 30 days, max 52 days) and also with estimates of 51-60 days, given for the timing of dispersal by Reed Warblers ringed as nestlings (Wernham et al. 2002).

The pattern of mass change during this period showed an initial decline followed by a gradual increase. The decline, which is probably responsible for the majority of negative FDRs at Icklesham and in other studies (e.g. Bibby & Green 1981, Schaub & Jenni 2000a), was most likely a result of two main factors. Firstly, juveniles must learn how to forage effectively and mass losses are likely until this is achieved. Secondly, the energetic demands of moult, which takes place during this period, will probably result in a negative energy budget and mass loss. The increase in mass was presumably a consequence of pre-migratory fuelling, which started approximately 30 days after birds gained independence. The exact pattern of mass change during this period was dependent on initial body mass and the date. The model suggested that birds born later in the season stabilised their weight faster and gained more mass, a pattern that was likely to be caused by selection for time minimisation as discussed above. The length of time between gaining independence and the start of fuelling suggests that many Reed Warblers delayed fuelling until they had nearly or completely finished moultng.
The low FDRs of Reed Warblers at Icklesham, combined with fuelling durations of medium length, typically resulted in relatively small fuel loads, as indicated by the distribution of body masses (Fig 2.5.2). Therefore, the strategy of Reed Warblers leaving from Icklesham is expected to involve relatively short flights with one or two refuelling stops until they reach key fuelling areas in southern Portugal and southwest Spain (Bibby & Green 1981, see also section 7.2). However, for many juveniles, which had completed their moult, and adults a single flight stage to southern Portugal without refuelling may be possible, especially for birds leaving at the end of September (see Fig. 2.3.5). Indeed, this strategy may be commoner (see section 7.2) than previously thought (Bibby & Green 1981).

**Autumn – Quinta da Roche, Portugal**

Reed Warbler passage at Quinta da Roche occurred later than at Icklesham, as would be expected given its more southerly location. Interestingly, the ratio of juveniles to adults was almost one to one in Portugal, approximately five times lower than at Icklesham. This change in the age structure of the population may be due to differential habitat selection between age classes or a consequence of high juvenile mortality. If this dramatic shift is due to mortality it highlights the inherent risks of migration.

Reed Warblers at Quinta da Roche were almost exclusively transients or birds on stopover, as there were no breeding records within 20 km of the site. As at Icklesham, tape lures may have increased the proportion of transients in the population. Reed Warblers at this site were approaching the Sahara and therefore were expected to accumulate large fuel loads. Body mass data from this site reveals two classes of birds: those that had already fuelled for the Sahara crossing and those that had yet to fuel. Given that the Atlantic Ocean lies directly to the south of Quinta da Roche, I assume that birds that had already fuelled had done so at sites to the north. Reed Warblers that were retrapped at the site had lower body masses than birds that were not, therefore birds that had yet to fuel were more likely to stay at the site for more than a day.

Reed Warblers that stopped and fuelled at Quinta da Roche had high FDRs and increased their body mass more than at any other site (Fig. 2.5.1). The body masses and therefore fuel loads that birds accumulated have been estimated to be sufficient for completing the journey across the Sahara without the need to refuel (Bibby & Green 1981, see also section 7.2). The mean body mass of fuelling birds on first capture of was
11.8g, which suggests that birds had not gradually built up their fuel reserves as they travelled south. Instead, the majority of the fuel required for the Sahara crossing was accumulated at Quinta da Roche. Reed Warblers are therefore likely to be adopting strategy 1 for crossing the Sahara in autumn (Fig. 2.1.1).

The key means by which Reed Warblers accumulate large fuel loads in Portugal appears to be through elevated FDRs. Very few Reed Warblers were moult ing in Portugal and thus with the constraints of moult removed, higher FDRs may have been possible. However, non-moulting adult Reed Warblers at Icklesham did not achieve such high FDRs. Food availability may have been higher in Portugal but there have been no studies of the relative abundance of prey items between fuelling sites in northern versus southern Europe to test this hypothesis. Whilst I could have measured insect abundance at Icklesham, I had neither the funds or the time to do the same in Portugal and was therefore unable to test this important hypothesis myself. Alternatively, behavioural changes may have occurred. These changes might include reducing predator awareness, thereby allowing an increase in the time devoted to foraging (Houston 1998). Larger fuel loads may also have been achieved by increasing fuelling duration. The data I have presented do not directly support this possibility, however, Reed Warblers in Portugal fuelled at a consistent rate for longer than birds at Icklesham (Fig. 2.3.13); fuelling durations may therefore have been longer. Previous studies found no evidence for increasing stopover duration with latitude (Schaub & Jenni 2001).

FDRs, the extent of mass changes and mean body mass did not show any trend with date in Portugal, which suggests that the main pressure shaping final fuel loads was the distance across the Sahara. It is logical to assume that the fuel needed to cross the Sahara will not vary with date, and therefore it is not surprising that there is no sign of an increasing time pressure.

Extensive fuelling at Quinta da Roche, made possible through elevated FDRs and possibly longer fuelling durations, suggests that the majority of reserves required to cross the Sahara are accumulated at sites such as this in southern Europe. This conclusion is supported by evidence from a number of other studies, which have shown similarly higher FDRs and fuel loads in Reed Warblers but not to the same extent as at Quinta da Roche (e.g. Garcia Piero 1995, Merom et al. 2000, Schaub & Jenni 2000b). The conservation of sites such as Quinta da Roche may therefore be particularly important to the success of migration in species like the Reed Warbler.
Spring – Djoudj, Senegal

Reed Warblers wintered at the site described in Senegal (Djoudj) and thus the exact onset of passage was unclear. However, the catch rate appeared to increase midway through February and there was clear evidence of passage until at least the end of April when ringing operations were terminated. This prolonged passage period may be a consequence of the mixing of populations at this site. Reed Warblers controlled at Djoudj had been ringed at sites throughout Western Europe, therefore one would expect some differentiation in site usage by the different populations. Interestingly, Reed Warblers do not pass through southern Spain in any numbers until early May and there are only limited records in the latter half of April and even fewer in the first half of April (Finlayson 1992). Thus birds arriving at Djoudj in mid to late February must presumably remain at the site for some time before crossing the Sahara and heading into Europe.

Many of the birds trapped at Djoudj had surprisingly low body masses and there was little evidence of birds arriving at the site with high body masses (and therefore fuel loads). Like the situation in Europe in autumn, it would appear that Reed Warblers migrating north towards the Sahara do not accumulate sufficient fuel loads to cross this barrier until reaching sites close to its edge. Data on retrapped birds at Djoudj showed that some birds fuelled extensively, presumably in preparation for crossing the Sahara. These fuel loads were attained through lengthy stopover durations, rather than by elevated FDRs, as the FDRs at this site were similar to those observed at Icklesham (Fig. 2.5.1) and other sites in northern Europe (Shaub & Jenni 2000a). Indeed, the fuelling trajectories of birds that attained high fuel loads at Djoudj are gradual and indicate fuelling durations in excess of 30 days (Fig. 2.4.4). This lengthy fuelling period may in part explain why birds arrived at Djoudj long before they start arriving in southern Europe.

Despite Djoudj appearing to be an important fuelling site, few of the birds trapped were later retrapped. This is not to say that the birds did not remain in the general area in order to fuel. There was extensive fuelling habitat around the ringing site and many of the birds may have dispersed into this area. This would explain why the probability of capture was significantly lower at Djoudj than at all the sites examined here. Further, birds that stayed in the ringing area fuelled extensively and were retrapped on a number of occasions. These observations indicate that these birds may
have been holding territories and would therefore have prevented further birds from using the trapping area for fuelling. Reed Warblers have been observed to hold territories at other stopover sites (Bibby & Green 1981).

Both the extent of mass change and the FDR increased as the spring progressed at Djoudj. This may be partly explained by birds that had not commenced fuelling on initial capture, however, as all the birds in these analyses had increased in mass by at least 0.45g, this is unlikely to explain all the variance. Indeed, it seems more likely that an increasing selection pressure for time-minimisation, as seen in birds at Icklesham, may have driven birds to attain higher FDRs and fuel loads. The extent of mass change and FDR also had a positive relationship with wing length. This raises the possibility that longer winged birds, which are normally associated with more northerly and easterly populations (Cramp 1992), may fuel faster and accumulate larger loads as a response to the length of journey ahead of them. Alternatively, it may represent a difference between birds of different age and/or sex. Whilst FDRs and fuel loads are known to differ between species with onward journeys of different length (Moore & Kelinger 1987, Yong & Moore 1997, Berthold 1999), I have only found one study that shows differences between individuals from different populations of a migratory passerine (Dierschke & Delingat 2001).

**Spring – Aiguamolls, North-East Spain**

The passage of Reed Warblers through Aiguamolls began towards the end of April and continued throughout May. The majority of birds trapped at the site were not retrapped, an indication that many birds were transients. Unlike at other sites, tape lures were not used, therefore the proportion of transients within the population is likely to reflect the true number of birds adopting this behaviour.

Birds that were trapped once had higher body masses than birds that were later retrapped and therefore appear to have sufficient reserves to continue their onward journey. Indeed, the mean body mass (11.6g) of birds that were not retrapped indicates that the majority of birds had attained moderate fuel loads at sites to the south. Further, birds with a body mass greater than 12g were probably able to cover the 1000-2000 km to breeding areas without refuelling (see section 7.2 for flight ranges). Reed Warblers that were controlled at Aiguamolls, indicated that many of the birds originated from
Czechoslovakia, Croatia and Slovakia, however, some birds had been ringed in Poland and even Sweden and one would expect these to have to refuel on route (Pers. Obs.).

Birds that remained at the site, often only stayed for two days and the longest duration was nine days. Unlike birds at Icklesham or even in Portugal, the majority of birds did not lose weight during these short stays but instead gained weight at high rates. Therefore Reed Warblers at this site did not appear to be paying a stopover cost, unlike at six sites throughout Europe examined by Schaub & Jenni (2000a). FDRs were higher even than those observed in Portugal (Fig. 2.5.1) and birds regularly gained in excess of one gram during their short stays. Indeed, a conservative regression model for hourly mass gain predicts that a bird feeding at the site for a day of typical length (approx. 14 h) should increase by 0.8g (approx. 10% of LBM). These rapid fuelling bouts have been observed in other spring migrants, including two diverse groups of birds in North America: *Catharus* thrushes (Yong & Moore 1997) and Wood-Warblers, *Parulinae* (Moore & Kelinger 1987). The studies just cited, argued that birds were accumulating sufficient reserves during their short stops to fuel a night’s flying and were therefore minimising the number of nights spent on the ground rather than flying: thereby maximising the time available to them. Moore & Kelinger (1987) also argued that as these birds did not appear to be paying a stopover cost, they were maximising their flight range by not accumulating large loads for which the return in terms of range diminishes as the load increases (Pennycuick 1989). Further, if the mean FDR for birds at Aiguamolls and a stopover cost of 0 are entered into a time-minimising model, the model predicts that birds should only stopover for one or two days (Hedenström & Alerstam 1997). Therefore, birds at Aiguamolls were likely to be minimising the total time they spent migrating.

Passage at Aiguamolls de L’Emporda was characterised by birds with medium fuel reserves making brief stops at the site before continuing their journey. Birds that remained at the site for more than one day fuelled at high rates and rapidly accumulated sufficient reserves for onward flight. The rapid fuelling exhibited by these birds, which appear to be newly arrived, suggests that these birds were not paying a stopover cost and were adopting the behaviour predicted by a time-minimising model of fuelling behaviour.
Overall Discussion – Spring versus Autumn

The four sites in this study, separated both geographically and by the season in which the data was collected, show that stopover and fuelling behaviour is highly variable and apparently flexible within one species. Whilst it is apparent that much of the variability, particularly in fuelling duration, was induced through behavioural means, we have little knowledge as to how this is controlled.

Much of the variation in fuelling strategy was likely to have arisen from considerable differences in the position of birds relative to their migratory goal and in the quality and availability of fuelling sites on the route to this migratory goal. Whilst the geographical separation of the sites prevented direct comparison, two of the sites had one overriding factor in common. Reed Warblers fuelling at the Portuguese site and the Senegalese site must both cross the Sahara Desert; an inhospitable barrier for which birds require extensive fuel loads. Whilst other factors may influence the fuelling behaviour of Reed Warblers either side of this barrier, the main factor influencing behaviour was likely to have been the need to accumulate sufficient fuel for the crossing. There are a number of possible strategies for overcoming a barrier such as the Sahara and Reed Warblers appeared to adopt strategy 1 (Fig. 2.1.1), in which fuel reserves are accumulated at one site close to the Sahara’s edge. The advantages of this strategy over a strategy in which fuel reserves are gradually built up at several sites (strategy 2, Fig. 2.1.1) are likely to be the reduced costs in terms of carrying and maintaining the fuel load. Carrying an increasing fuel load between sites is energetically expensive and will also increase a migrant’s predation risk as its escape ability is compromised by the additional body mass (see section 1.2). However, the most striking aspect of this strategy was the marked difference in the way in which it was achieved in Portugal and Senegal.

Reed Warblers in Portugal achieved high fuel loads through elevated FDRs and possibly through a slight increase in fuelling duration relative to Icklesham (Fig. 2.5.1). Conversely, Reed Warblers in Senegal did not increase their FDR but had notably extended fuelling durations (Fig. 2.5.1). The pressures shaping these two rather different strategies are unclear. An important factor must be the elevated FDRs at the Portuguese site. It is unknown as to whether the increased rate was due to an abundance of food at this site or to changes in the metabolism and feeding behaviour of the Reed Warblers present. Regardless of the cause, the elevated FDRs allowed Reed Warblers in Portugal
to rapidly attain large fuel loads. Migrants are hypothesised to be under a heightened time pressure during spring migration and thus it is surprising that birds in Senegal had such extensive fuelling durations. However, it is apparent that many Reed Warblers arrived at the site long before they were expected to cross the Sahara and thus their strategy may incorporate a lengthy stop.

Whilst time may allow for a lengthy fuelling period in Senegal, other factors would be expected to promote relatively rapid fuelling. Increasing predation risk has been shown to actively select for lower body masses in Great Tits *Parus major* (Gosler *et al.* 1995), and it is apparent from the magnitude of these reductions that relatively small increases in body mass can lead to a heightened predation risk. Consequently, fuelling birds are expected to minimise the time spent at high body masses by fuelling as rapidly as possible (Weber, Ens, & Houston 1998). It seems unreasonable to suggest that predation risk is low in Senegal where I would expect a more diverse assemblage of predators than within Europe. It is possible that increases in flight muscle mass compensate for some of the power loss associated with increased total body mass, thereby keeping predation risk low. Indeed, plasticity of the flight muscles has now been recognised as an adaptive phenomena in situations where increased efficiency of the flight muscles is favoured (Dietz *et al.* 1999, Lindström *et al.* 2000). However, it is apparent that the FDRs of Reed Warblers in Senegal must be severely constrained, as increases in muscle mass could not compensate entirely for the predation risk associated with increasing body mass.

The most likely and plausible explanation for the FDRs observed in Senegal, is that food availability was very low. The erratic rainy season in Senegal occurred between June and October and thus during March and April much of Senegal had become very arid and as a consequence, insect abundance was likely to have been very low. Therefore, the long fuelling durations were probably only selected for because FDRs were constrained by food availability, and a fuel load for crossing the Sahara could not be accumulated any faster. This suggests that any deterioration in conditions, at sites like Djoudj, might be disastrous. Whilst I was unable to visit and measure food abundance at Djoudj due to funding limitations, this is clearly an important avenue for future work.

The body masses and therefore fuel loads that birds accumulated in Senegal and Portugal were also different (Fig. 2.5.2). Whilst Reed Warblers at both sites were preparing to cross the Sahara, I hypothesise that the birds were facing flights of different
lengths and thus required fuel loads of different magnitude. Reed Warblers in Portugal, which had the largest fuel loads, had to overfly part of the Atlantic Ocean and non-arid areas of North Africa before they commenced their journey across the Sahara. The reason for this extended flight may lie in the aridity of North Africa during the late autumn period. Whereas in spring, North Africa receives heavy rainfall and provides suitable fuelling conditions, the same area is very dry in autumn following a hot summer with minimal rainfall (Alerstam 1990). Thus whilst spring migrants only had to cross the Sahara in order to find suitable stopover habitat, autumn migrants were forced to make much longer flights and had to accumulate larger loads.

The low FDRs of Reed Warblers in Senegal during spring migration were not mirrored by birds at the second spring site in north-east Spain. Indeed, birds in northeast Spain had very short stopover durations and elevated FDRs, relative to birds in Senegal (Fig. 2.5.1). Spring migrants are expected to be under a considerable time pressure and the fuelling behaviour of Reed Warblers at Aiguamolls fitted the predictions of a time-minimising model (Hedenström & Alerstam 1997). The time saving short stops and rapid fuelling bouts observed at Aiguamolls appeared to be facilitated by high FDRs. This raises a question that is also relevant to the elevated FDRs found in Portugal as well. Are elevated FDRs a consequence of high food availability or of behavioural and metabolic adaptations? There is no a priori reason why prey abundance should be higher at sites either in Portugal or Spain, relative to a variety of European sites previously studied (Schaub & Jenni 2000a) or to Icklesham, England (this study). Further, FDRs have not always been found to be highest in southern Europe: the highest mean FDR for Reed Warblers at 13 European sites was found in central Europe and two sites examined in Spain had low to medium FDRs relative to the other sites (Schaub & Jenni 2000a).

Behavioural and physiological mechanisms for increasing FDRs are little known at present but a number of possibilities present themselves. Behaviourally, a bird can simply increase the intensity at which it feeds, thereby increasing the rate of intake. Feeding intensities may typically be constrained in a trade-off against predator awareness (Weber, Ens & Houston 1998). However, the reduction in fuelling duration and consequent reduction in mass-dependent predation risk (less time spent at high masses) associated with a higher foraging rate, may outweigh the costs of decreased vigilance (Weber, Ens & Houston 1998). Physiologically, increasing the size and therefore capacity of the digestive organs could increase the FDR (McWilliams &
Karasov 2001). Whilst such increases are likely to incur energetic costs, these may be outweighed by the time saved on fuelling. There is also a growing body of evidence demonstrating remarkable structural plasticity in the digestive organs of migrant birds (Jehl 1997, Piersma & Lindström 1997, Biebach 1998, Piersma 1998). Indeed, theoretical work has predicted that lean body mass, increased through organ hypertrophy, should always be at its maximum during the migration of birds that have been selected to minimise time whilst migrating (Weber & Hedenström 2001).

Lean body mass varied between sites in my study (Fig. 2.5.3) and during migration periods LBMs were higher than in wintering birds in Africa (Jan-Feb), except for birds beginning their spring migration in Senegal (March-April). Further, birds in Portugal and Spain, which had the highest FDRs, also had the highest LBMs. However, birds in England had the highest LBMs but did not have high FDRs. So whilst hypertrophy of digestive organs could explain the correlation between high LBM and heightened FDRs in Spain and Portugal, it does not explain the anomaly observed in England. One explanation does present itself though; moultng birds are known to have a higher water body content (Newton 1968, Chilgren 1977), and a large percentage (typically >50%) of juvenile birds at Icklesham were in active post-juvenile moult. It can also be argued that birds moultng and fuelling simultaneously, face the greatest energetic strain and would benefit considerably from organ hypertrophy. Therefore, the high lean body masses observed at Icklesham may represent both increases in the mass of the digestive organs and in the mass of body water. The low FDRs observed in Senegal also show a clear correlation with the low LBM exhibited by Reed Warblers at the site in March and April (Fig. 2.5.3)

**Summary**

The detailed look at four sites differentiated by geographical location and season in this study, has highlighted considerable variation in fuelling strategies within a typical migratory passerine, the Reed Warbler. It is clear therefore that fuelling is not a uniform behaviour but is a flexible response to the conditions typically experienced at a site and the demands of the journey ahead. Whilst different selective pressures can explain some of the variation between sites, such as the constraint placed on fuelling by moult at Icklesham and the apparent constraint of food availability in Senegal, it is clear that fuelling behaviour is determined by a complex web of factors that may act on both
FIGURE 2.5.3: Lean body mass distributions of Reed Warblers at different times of year and at sites from England to Senegal. Lean body masses were only calculated for birds with a fat score of 0 and masses in grams were corrected for wing length and time of capture. The boxplots define the inter-quartile range, the median and the range (whiskers).
a geographical and temporal scale. It is evident that time-minimisation can have an
important selective input on overall migratory strategies, but Reed Warblers at
Icklesham highlight the fact that migrants may be selected to minimise time on a
continuous scale rather than as an all or nothing response.

Future work must concentrate on the relative costs and benefits of different
FDRs in terms of predation risk and time minimisation, and investigate how FDRs can
be increased through behavioural means. Further tests of hypotheses invoking organ
hypertrophy are also important and require more analyses of carcasses obtained by
ethical means or the improvement of ultrasound techniques for measuring organ size
(Starck & Buram 1998).
PLATE 1: Feeder set up used in all experiments described in Chapters 3, 4, 5 & 6. Mealworms were placed in the pot within the Perspex box, which prevented birds from accessing the mealworms without using the perch. When data were not being recorded, the Perspex box was removed, making access to the mealworms easier. The perch was attached to the electronic balance through the hole in the top of the box. A Great Reed Warbler is pictured just before it sits on the perch to feed on the mealworms.
PLATE 2: A juvenile Reed Warbler being weighed whilst consuming a mealworm at an *ad lib* feeder at Icklesham. The body mass of the bird can be read to two decimal places from the balance display (16.59g).
PLATE 3: A juvenile Sedge Warbler being weighed whilst attending an *ad lib* feeder at Icklesham. The body mass of the bird can be read to two decimal places from the balance display (15.99g). A thinner Sedge Warbler of lower body mass can also be seen waiting its turn at the feeder.
CHAPTER 3

VARIABILITY, FLEXIBILITY AND CONSTRAINT IN THE MIGRATORY STRATEGIES OF TRANS-SAHRAN MIGRANTS

3.1 INTRODUCTION

Species of migratory birds vary considerably in the distance they travel, the routes they take between breeding and wintering grounds, the timing of their journey and their behaviour during fuelling and flight phases (Alerstam 1990). However, the causes and consequences of this variation, and its adaptive significance remain largely unexplored. This variation even exists between species that share similar breeding and wintering ranges and take the same route between the two (e.g. Bibby & Green 1981, Schaub & Jenni 2000b). For example, Pied Flycatchers *Ficedula hypoleuca* and Spotted Flycatchers *Muscicapa striata* both breed in northern Europe and winter in sub-Saharan Africa. Whilst both species take several stages to reach the Sahara’s northern edge, Pied Flycatchers are believed to gradually build up fuel reserves whilst travelling to the desert edge, enabling them to cross the Sahara without refuelling. Conversely, Spotted Flycatchers rarely accumulate large reserves and are thought to cross the Sahara in several stages feeding along the way (Schaub & Jenni 2000b).

These contrasting strategies are thought to reflect the outcome of a set of trade-offs, in which the costs and benefits of certain behaviours differ between species (section 1.2). Many of these costs and benefits are expected to be associated with fuelling behaviour and may be key to determining the amount of fuel available for migratory flights (Lindstrom & Alerstam 1990). Whilst there are clear benefits to storing fuel in terms of increased flight range, these are offset by costs of fuel storage that act to keep fuel loads below their maximum (Witter & Cuthill 1993). The fuel load a bird has available for flight, determines the distance that can be covered in each flight phase, and therefore the strategy adopted e.g. short stages (‘hopping’) or long stages (long haul migration).
Strategy Diversity

The combination of factors that promote and constrain fuelling can result in markedly different strategies between closely related species. For example, the Reed Warbler has a diverse diet whilst fuelling in North-West Europe, feeding on a range of low-density prey (Bibby & Green 1981). As a result Reed Warblers have a low capture rate, typically only achieve low FDRs and depart with relatively small fuel loads (10-30% of lean body mass). Consequently, Bibby & Green (1981) proposed that Reed Warblers migrating from NW Europe to the Iberian Peninsula do so in a number of flight stages, refuelling between each. Extensive fuelling in southern Iberia then allows these birds to make the long journey across the Sahara, to wintering areas in West Africa.

In contrast the closely related Sedge Warbler, which shares both morphological similarities and habitat preferences with the Reed Warbler during autumn migration (Leisler et al. 1989), adopts a very different strategy. Sedge Warblers fuelling in NW Europe have a specialised diet, relying largely on dense populations of insects (particularly the Plum-Reed Aphid Hyalopterus pruni and Mayflies, order Ephemeroptera), which can be superabundant in reedbeds in late summer (Bibby & Green 1981, Cramp 1992). This dietary specialisation leads to higher intake rates and faster rates of fuel deposition, and can result in extremely large fuel loads (100% of LBM or more). Sedge Warblers are therefore believed to be capable of departing from NW Europe and completing their migratory journey (of about 4000 km) in a single flight phase, over-flying Iberia, the Mediterranean, North Africa and the Sahara (Bibby & Green 1981, Wernham et al. 2002). In some circumstances (e.g. unfavourable weather conditions) birds may be forced to pause and refuel in Iberia (Bibby & Green 1981). Bibby & Green (1981) argued that the difference in diet and hence ‘food availability’ were largely responsible for the extreme contrast in strategies between these two congeners. However, it is possible that Sedge Warblers have a greater digestive capacity than Reed Warblers, brought about through an increase in the size of the digestive organs (McWilliams & Karasov 2001). Organ hypertrophy may therefore facilitate higher FDRs in Sedge Warblers.
Coping with Change

Whilst migratory strategies are expected to have evolved as the best solution to the problem of getting from A to B (there are obvious exceptions to optimality, see Sutherland 1998), it is unclear how strategies cope with change in the environment whether it be through natural processes or those driven by man. Detailed genetic studies have demonstrated that evolutionary responses to environmental change can be remarkably rapid (Berthold & Terrill 1988, Berthold et al. 1992), but evolutionary change is not quick enough to adjust to between-year variation in a variable such as food availability or to track rapid environmental changes. Therefore one might expect flexibility in fuelling behaviour to have evolved in order to cope with rapid change, as fuelling site quality and availability are expected to be key variables affecting the success of a migratory journey (Weber, Houston & Ens 1999).

Whilst between-species variation in fuelling behaviour is well known (Bibby & Green 1981, Schaub & Jenni 2000b, Ottosson et al. 2001), there are only a few examples of within-species variation that could signal the existence of flexibility. For example, European populations of Sedge Warblers outside NW Europe do not appear to display the same rapid fuelling rates and consequent long haul strategy, as the birds studied by Bibby & Green (1981) in Britain and France (Bensch & Nielsen 1999). Dierschke & Delingat (2001) also reported divergent fuelling behaviour in two populations of Wheatear Oenanthe oenanthe using the same stopover site. However, whilst these examples show that one species is capable of more than one strategy, these differences were at the population level and there is no evidence that an individual from one population can perform both strategies.

In section 2.5, I demonstrated four very different fuelling behaviours within a population of Reed Warblers. This demonstrated that individuals are capable of performing a variety of fuelling behaviours and could therefore use behavioural plasticity to cope with rapid changes in the environment. Food supplementation experiments carried out on three migratory passerines have also demonstrated a degree of flexibility between individuals: Bluethroats Luscinia svecica, N = 8 (Lindström & Alerstam 1992), Whitethroats Sylvia communis, N = 12 (Fransson 1998a) and European Robins Erithacus rubecula, N = 10 (Danhardt & Lindström 2001). However, given that experimental birds were provided with an unlimited food supply and were compared to birds feeding under natural conditions, the degree of flexibility was not marked. Whilst
there was a fairly high degree of variation in FDR, there was little variation in departure mass.

In this study, I provided a different genus of migratory passerines (*Acrocephalus* warblers) with supplementary food and compared them to naturally fuelling birds, to further investigate the extent of flexibility.

**Summary and General Aims**

The contrast between the typical migration strategies of Reed and Sedge Warblers in NW Europe, demonstrates marked variation between congeners, but we know little about the degree of behavioural flexibility within species or populations. In the present study, I carried out food supplementation experiments to investigate the fuelling strategies adopted by free-living Reed and Sedge Warblers when food is potentially unlimited, and therefore fuelling decisions are constrained only by digestive and physiological constraints on food assimilation. This allowed me to examine further the causes, consequences and adaptive significance of the variation in strategy and to discover how increased food availability affects the fuelling behaviour of each species. In order to further investigate how fuelling migrants respond to food supplementation, I provided Reed Warblers in a different geographical region (northeast Spain) and a further species, the Great Reed Warbler *Acrocephalus arundinaceus*, with supplementary food.

The effect that food supplementation might have on each of these species is unclear. Under natural conditions Sedge Warblers typically have higher FDRs than Reed Warblers (Bibby & Green 1981), therefore, if prey abundance is the main constraint on Reed Warbler FDRs, food supplementation may remove this difference. Similarly, one might expect differences in fuel load between the two species (see page 95) to disappear. Very little is known about the fuelling behaviour of the Great Reed Warbler and it is difficult to predict how food supplementation might affect its migratory strategy or how it may behave relative the Reed and Sedge Warbler.

The food supplemented Reed and Sedge Warblers described in this chapter also provide the data for chapters 4 and 5. In these chapters, Reed (chapter 4) and Sedge Warblers (chapter 5) are treated separately in order to discover the underlying evolutionary pressures that have shaped the migratory strategies of these two species. This is achieved by comparing the data on fuelling birds to the predictions of theoretical
models of optimal migratory strategies. Further, additional data (not included in chapter 3) on fuelling Reed Warblers that attended feeders with restricted food availability are presented in chapter 4.

3.2 METHODS

Study Sites & Study Species

The experiments described in the following section took place at Icklesham, England (N50°54´, E0°41´) and Aiguamolls de L’Emporda natural park, NE Spain (N42°, W03°). See Chapter 2, section 2.2 for full descriptions of each site.

I studied three species of migratory warblers from the genus Acrocephalus: the Reed Warbler, Sedge Warbler and Great Reed Warbler. The Reed Warbler is described in detail in section 1.5. The Sedge Warbler’s morphology is similar to the Reed Warbler and its ecology (Cramp 1992) and migration (Bibby et al. 1976, Bibby & Green 1981) have been studied in some detail. The Great Reed Warbler is approximately twice the size of a Reed Warbler and has a more southerly breeding distribution. Aspects of the Great Reed Warbler’s ecology and migratory behaviour were described in Cramp (1992).

Timing of Fieldwork

Food supplementation experiments with Reed Warblers at Icklesham were carried out in the years 2001 and 2002. In 2001 the experiments were carried out between 1st August and 16th September whilst in 2002 experiments ran from 12th July to 30th September. Work on Sedge Warbles at Icklesham was carried out largely in 2003 between 6th August and 2nd September, however, data were also collected on one individual in August 2001 and on six individuals in August 2002. Data collection on Reed Warblers and Great Reed Warblers in NE Spain was carried out in 2001 from 24th April to 10th May and from 28th April to 24th May 2002. In 2001, data on one Reed Warbler were gathered and on two Reed Warblers and four Great Reed Warblers in 2002.
In the following analyses the results from food supplementation experiments were combined across years. This was justified in the case of Reed Warblers, as there was no significant difference in the main parameters between years (Daily FDR, t-test, \( t_{20} = -1.01, P = 0.324 \); Departure load, ANOVA, \( F_{1,24} = 0.49, P = 0.492 \), in analysis including departure date; Fuelling Duration, t-test, \( t_{20} = -1.11, P = 0.284 \)). In the case of Sedge Warblers, FDRs and fuelling durations did not vary between years (FDR, t-test, \( t_{10} = -0.97, P = 0.356 \); Fuelling Duration, t-test, \( t_{10} = -1.70, P = 0.120 \)) but departure loads did (t-test, \( t_{10} = -3.07, P = 0.012 \)). The difference in Sedge Warbler fuelling loads between years was taken into consideration when analysing the data and in the discussion.

**Experimental Design**

The experimental set up was the same at both sites and involved placing feeders that contained mealworms *Tenebrio molitor* in suitable habitat. The placing of feeders at Icklesham for Reed and Sedge Warblers is described in the methods sections of Chapters 4 and 5 respectively. At Aiguamolls, feeders were located in patches of *Phragmites* and within Tamarisk *Tamarix gallica* stands lining water filled ditches. The feeders consisted of a wooden box (25x40x15cm) attached to a stake that was typically 1.2–1.8m in length. A bowl was inserted into a purpose-made hole on the box top such that the bowl was immobile. One end of the box was open to allow an electronic balance to be inserted into the box (see Plate 1). For all the experiments described in this chapter, the feeders were kept topped up with at least 50 mealworms at all times. This type of feeder, which allows unlimited access to the food, shall be described as an *ad lib.* feeder from here on.

Birds attending the feeders were caught, when possible, using 6-10 metre long mist nets situated at least 10 metres away from the feeder. Mist nets were not placed any closer as to avoid birds forming an association between being caught and the feeder. When birds were caught they were fitted with an individual combination of colour rings (and a metal ring if they did not already have one). This allowed individual birds attending the feeders to be recognised. Before release, the age, fat score, wing length and body mass of birds were recorded (see section 2.2 for details). For birds not fitted with colour rings, it was still possible to identify the majority of individuals by a combination of factors. These included the weight of the bird; as the majority of birds...
were weighed in the morning and the evening, it was possible to differentiate between unmarked birds given that there was at least a 1g difference in weight. It is unlikely that a bird could increase by one gram more than another fuelling individual during the course of a day. Another useful feature was whether the birds had a metal ring attached or not. Individuals that could not be confidently identified were excluded from the analyses. Using the combination of unique features outlined above and the 1g rule, there is only one case in which two birds may have been confused (see Fig. 3.1). However as both these birds finished at approximately the same body mass, the resulting values for FDR and departure load will change little if these two birds were mixed up.

Body mass measurements of birds attending the feeders were taken using an electronic balance (Ohaus Scout II, Ohaus Corporation, Pine Brook, NJ 07058, USA) and a video camera (Sony CCD-TR748E Hi8, Sony Corporation). The balance was placed inside the box (described above) and a wooden perch was attached to the plate of the balance through a purpose made hole in the box top. A three-sided Perspex box was placed around the bowl of mealworms with the open side adjacent to the perch (Plate 1). The Perspex box prevented birds from accessing the mealworms unless they used the perch whilst still allowing them total visibility of the food supply. This set up had a number of advantages. First, the box surrounding the balance prevented the mass readout from being strongly affected by the wind, which can potentially cause large errors in mass measurements. A gust of wind can cause an unsheltered balance to register measurements of up to 0.5 g; as the body mass of Reed and Sedge Warblers attending the feeders typically increased by 1-2 g a day, this level of error would be unacceptable. Secondly, only one bird could sit on the perch at a time and thus one did not lose valuable measurements because of two birds feeding simultaneously. Remote weighing of birds in this way avoids the problems associated with catching birds, which can often result in mass loss.

The filming regimes for Reed and Sedge Warblers at Icklesham are described in Chapters 4 and 5. At Aiguamolls, each feeder was filmed every morning, between two and five hours after sunrise, and in the evening within two hours of sunset. Each filming session lasted between 45-90 min. In the evening this period was timed such that filming continued until approximately 20 min after sunset. However, at times more than two feeders were in use and as I only had two video cameras, one set of feeders would be filmed first before switching the cameras to the second set.
The experimental set up described above generally results in small sample sizes, however, even small samples can be very informative due to the quality of the resulting data. The main fallback of the set up is the difficulty of attracting birds to the feeders and the limited time during which birds are migrating (typically < 2 months). Past studies have highlighted this problem in a range of migratory species, as the following study durations and resulting sample sizes indicate: Robins, 2 months in one year, N = 10 (Danhardt & Lindström 2001); Whitethroats, 4.5 months over 3 years, N = variable, maximum 28 (Fransson 1998); Bluethroats, 2 months over 2 years, N = 8 (Lindström & Alerstam 1992).

**Calculating Fuel Deposition Rates and Departure Loads**

FDRs were calculated as the fraction of lean body mass deposited per day, as described in section 2.2. Lean body mass values were calculated for Reed Warblers as described in section 2.2. The lean body mass of Sedge Warblers was calculated by regressing the body mass of a dataset of 121 birds from Icklesham that had a fat score of zero on wing length. The same procedure was carried out for Great Reed Warblers using data on 34 birds caught at Aiguamolls in the years 1993-2002 in April and May. A detailed description of the selection process for the start mass and final mass, used in calculating FDRs is given in section 4.2. FDRs calculated using this method will be referred to as ‘daily FDRs’ in order to differentiate between ‘hourly FDRs’ detailed below.

Hourly FDRs were calculated by taking the earliest and latest body mass recordings for a bird on a given day and dividing by the number of hours between: giving a rate of gain in grams per hour. Recordings that were less than five hours apart were excluded, as they may not be representative of an entire day. As recording times were fairly constant, the majority of body masses were recorded between 8.5 and 10.5 h apart (mean time ± S.D = 9.34 ± 0.79) for Reed Warblers and between 10 and 11 h apart (mean time ± S.D = 10.43 ± 0.84) for Sedge Warblers.

**Fuelling Durations**

Fuelling durations were estimated from the number of days a bird was present at a feeder and gaining mass. The end of this period was always marked by the departure of individuals from the feeder. The start of the fuelling period was considered as the day
after which birds gained mass on three consecutive days: in some cases birds did not initially gain mass consistently at the feeders. In some instances, birds were present at the feeders for less than three days. In these cases the fuelling period was considered as the time spent at the feeder, unless these individuals were already carrying a large fuel load (>30% of lean body mass). Whilst these criteria will probably result in underestimates of fuelling duration for some individuals, they do not affect the most interesting variable which is the time spent actively fuelling at the feeders.

**Comparisons with Historical Datasets**

The collection of data described as ‘historical datasets’ in this chapter, was outlined in section 2.2. The data were not modified in any way for presentation in this chapter. Additional data not described in Chapter 2 were obtained on Great Reed Warblers at Aiguamolls from the Catalan Ornithological Institute.

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### 3.3 RESULTS

#### Body Mass Trajectories of Reed Warblers Attending the Feeders

The changes in body mass of Reed Warblers attending the *ad libitum* feeders at Icklesham are shown in Fig. 3.1. There are two striking features of these mass trajectories. Firstly, Reed Warblers did not necessarily begin fuelling as soon as they began attending the feeders, i.e. they did not simply maximise their energy reserves at all times. However, once they did begin to deposit fuel, FDRs were very high over a number of days, consistently exceeding 1g/day in many individuals. Secondly, these protracted periods of rapid mass gain resulted in very high fuel loads at departure, at a site where departure loads are normally low (see section 2.3.1).

#### Fuelling and Intake Rates of Reed Warblers

The ‘daily’ fuelling rates of Reed Warblers attending the feeders (food supplemented) and of birds under natural conditions (unmanipulated birds) at Icklesham are shown in Fig. 3.2. The rates of the food supplemented birds were clearly higher than those of unmanipulated individuals, and the mean rate of gain for food supplemented
FIGURE 3.1: Body mass trajectories of juvenile Reed Warblers attending *ad lib.* feeders at Icklesham during autumn migration in 2001 and 2002. Each point represents the mass of a bird on its last visit of the day to the feeders. To demonstrate that individual birds could not be confused, trajectories have been colour coded according to the following criteria. Black Line = 2001, Red Line = 2002, Green Circles = colour ringed bird, Blue Circle = bird with metal ring on right leg, Black Circle = unmarked bird unmarked, Blue Square = metal ring combined with individual plumage feature, e.g. fault bars, heavy moult, Large Blue Circle = indicates that a bird is at a different feeder to those with which it may be confused. It is important to note that any birds marked by green circles could not be confused with any other individuals as they were carrying a unique combination of colour rings. Only two birds of the 31 (6%) pictured here could have been confused (see two ringed birds fuelling in mid-late September in 2002).

TABLE 3.1: Descriptive statistics for the daily fuel deposition rate (fraction of LBM deposited in 24hrs), average hourly rate of mass gain (grams/hour) and hourly intake rate of mealworms (mealworms/hour) of juvenile Reed Warblers attending *ad lib.* feeders at Icklesham. The total number of birds attending the feeders was 27, however, some individuals were excluded due to insufficient data.

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>SE Mean</th>
<th>Lower Quartile</th>
<th>Upper Quartile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily FDR</td>
<td>22</td>
<td>0.094</td>
<td>0.021</td>
<td>0.004</td>
<td>0.079</td>
<td>0.109</td>
</tr>
<tr>
<td>Hourly FDR</td>
<td>22</td>
<td>0.144</td>
<td>0.034</td>
<td>0.007</td>
<td>0.119</td>
<td>0.160</td>
</tr>
<tr>
<td>Intake Rate</td>
<td>21</td>
<td>6.3</td>
<td>1.2</td>
<td>0.27</td>
<td>5.4</td>
<td>7.4</td>
</tr>
</tbody>
</table>
FIGURE 3.2: Daily fuel deposition rates (fraction of LBM accumulated in 24hrs) of unmanipulated Reed Warblers versus Reed Warblers attending the feeders at Icklesham. Unmanipulated birds (grey): All juvenile birds from 1997-2002 that were retrapped more than one day apart and had a positive FDR (N = 365, see section 2.2 for selection criteria). Food Supplemented birds (Black, N = 25): Juvenile birds that were provided with ad. lib. food. Due to the sample size differences, the number of food supplemented birds has been multiplied by a factor of 10 for ease of comparison.

TABLE 3.2: Descriptive statistics for departure body mass (g) and departure load (fuel store mass as a fraction of LBM) of juvenile Reed Warblers attending ad lib. feeders at Icklesham.

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>SE Mean</th>
<th>Lower Quartile</th>
<th>Upper Quartile</th>
</tr>
</thead>
<tbody>
<tr>
<td>Departure Mass</td>
<td>27</td>
<td>16.8</td>
<td>1.34</td>
<td>0.26</td>
<td>16.1</td>
<td>17.3</td>
</tr>
<tr>
<td>Departure Load</td>
<td>27</td>
<td>0.76</td>
<td>0.14</td>
<td>0.03</td>
<td>0.68</td>
<td>0.81</td>
</tr>
</tbody>
</table>

TABLE 3.3: Descriptive statistics for the fuelling duration of juvenile Reed Warblers attending ad lib. feeders at Icklesham. Five individuals were excluded as there were not sufficient data to estimate the duration.

<table>
<thead>
<tr>
<th>N</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>SE Mean</th>
<th>Lower Quartile</th>
<th>Upper Quartile</th>
</tr>
</thead>
<tbody>
<tr>
<td>22</td>
<td>5.86</td>
<td>1.36</td>
<td>0.29</td>
<td>5.0</td>
<td>7.0</td>
</tr>
</tbody>
</table>
birds (0.094, see Table 3.1) was over five times higher than unmanipulated birds (0.018, see also Table 2.3.5, section 2.3.1). In Table 3.1, descriptive statistics are given for both daily and hourly FDRs, and the rate at which Reed Warblers consume mealworms. The rate of consumption suggests a Reed Warbler could consume 84 mealworms during a day of typical length in August (approx 14 hours between sunrise and sunset). Assuming an average mass of 0.1 per mealworm, that is the equivalent of 8.4g of food per day.

**Body Masses and Final Departure Masses of Reed Warblers**

Reed Warblers attending the feeders attained very high body masses, which correspond to the deposition of large fuel loads (Table 3.2). The body masses attained by birds at the feeders were notably higher than those of unmanipulated birds at Icklesham. In Fig. 3.3, the frequency distribution of body masses recorded for food-supplemented birds is given. This distribution includes all morning mass recordings for all birds attending the feeders and gives an idea of the distribution that would be obtained if individuals at the feeders had been caught at random during normal ringing activities. The two body mass distributions show marked differences (Fig 3.3), suggesting that unmanipulated birds could not be performing the same fuelling strategy as birds at the feeders.

**Fuelling Durations of Reed Warblers**

The fuelling durations of Reed Warblers at the feeders (Table 3.3) were protracted relative to the durations calculated in section 2.3.1 (Table 2.3.8) and by other authors (e.g. Shaub & Jenni 2001). However, Shaub & Jenni (2001) calculated stopover durations, not fuelling durations, which are likely to be longer. The mean fuelling duration estimated in section 2.3.1 for unmanipulated birds at Icklesham, was likely to be an overestimate, as already discussed (section 2.3.1 & 2.5).
FIGURE 3.3: Body mass frequencies of unmanipulated Reed Warblers and food supplemented Reed Warblers at Icklesham.

A – Unmanipulated birds: includes all juvenile birds from 1998 –2002 that were caught between the 1st August and the 30th September between the hours of 4am and 12am (N = 11,139, Mean time ± St. Dev. of mass recording = 7.20am ± 1.59hrs).

B – Food supplemented birds: includes all mass recordings for juvenile birds that used the feeders. All mass recordings used were taken between the hours of 4am and 12 am (N = 137, Mean time ± St. Dev. of mass recording = 8.25am ± 1.21hrs).
Body Mass Trajectories of Sedge Warblers Attending the Feeders

Like the trajectories of Reed Warblers, those of Sedge Warblers were also striking with respect to the high rate of intake and, to a lesser degree, the body masses achieved (excluding the three birds that exceeded 20g in mass)(Fig. 3.4). Sedge Warblers fuelling under natural conditions at Icklesham rarely achieved high body masses, unlike the food-supplemented birds (Fig. 3.5).

Fuelling and Intake Rates of Sedge Warblers

The FDRs of Sedge Warblers attending the feeders were the highest of all species that attended the feeders (Table 3.4). Indeed, the mean daily FDR for Sedge Warblers (0.135) was significantly higher than that of Reed Warblers (0.094) (t-test, t_{14} = 3.19, P = 0.006). The high daily rates of FDR were reflected in both a high hourly FDR and a high intake rate of mealworms (Table 3.4). Intake rates were significantly higher than those of Reed Warblers (t-test, t_{16} = 3.52, P = 0.003) and may explain why Sedge Warblers achieved higher FDRs. Mean hourly FDRs were not significantly different between the two species (t-test, t_{32} = 0.39, P = 0.697). However, hourly FDR increased with decreasing day length in Reed Warblers (section 4.2) and by controlling for date, I found that Sedge Warblers had significantly higher hourly FDRs (ANOVA, F_{2,31} = 9.37, P = 0.005).

Body Masses and Final Departure Masses of Sedge Warblers

Despite having higher FDRs, many of the Sedge Warblers did not reach body masses as high as those observed in Reed Warblers (Table 3.5). However, the departure loads of Sedge Warblers attending the feeders were not significantly lower than Reed Warblers utilising the same food source but tended to be so (t-test, t_{15} = -0.41, P = 0.690). Indeed, excluding the three Sedge Warblers that fuelled for longer and attained notably higher fuel loads than the other individuals (see Fig. 3.4) from the analysis, renders the difference significant (t-test, t_{14} = -2.84, P = 0.013). It is also worth noting that these three individuals had departure body masses higher than any of the food supplemented Reed Warblers. Food supplemented Sedge Warblers appeared to attain
FIGURE 3.4: Body mass trajectories of 11 juvenile Sedge Warblers (black) and one adult (white) attending *ad lib.* feeders at Icklesham in 2001-2003.

![Body mass trajectories](image)

### TABLE 3.4: Descriptive statistics for the daily FDR (fraction of LBM deposited in 24hrs), average hourly FDR (grams/hour) and hourly intake rate of mealworms (mealworms/hour) of Sedge Warblers attending *ad lib* feeders at Icklesham.

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>SE Mean</th>
<th>Lower Quartile</th>
<th>Upper Quartile</th>
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<tbody>
<tr>
<td>Daily FDR</td>
<td>13</td>
<td>0.135</td>
<td>0.043</td>
<td>0.012</td>
<td>0.118</td>
<td>0.161</td>
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<tr>
<td>Hourly FDR</td>
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<td>0.148</td>
<td>0.022</td>
<td>0.006</td>
<td>0.127</td>
<td>0.164</td>
</tr>
<tr>
<td>Intake Rate</td>
<td>15</td>
<td>9.4</td>
<td>3.26</td>
<td>0.84</td>
<td>6.4</td>
<td>12.5</td>
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</tbody>
</table>

### TABLE 3.5: Descriptive statistics for departure body mass (g) and departure load (fuel store mass as a fraction of LBM ) of 13 juvenile Sedge Warblers and one adult attending *ad lib.* feeders at Icklesham.

<table>
<thead>
<tr>
<th>Variable</th>
<th>N</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>SE Mean</th>
<th>Lower Quartile</th>
<th>Upper Quartile</th>
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</thead>
<tbody>
<tr>
<td>Departure Mass</td>
<td>14</td>
<td>16.5</td>
<td>3.19</td>
<td>0.85</td>
<td>14.6</td>
<td>18.3</td>
</tr>
<tr>
<td>Departure Load</td>
<td>14</td>
<td>0.70</td>
<td>0.34</td>
<td>0.09</td>
<td>0.49</td>
<td>0.92</td>
</tr>
</tbody>
</table>
FIGURE 3.5: Body mass frequencies of unmanipulated Sedge Warblers and food supplemented Sedge Warblers at Icklesham.
A – Unmanipulated birds: includes all juvenile birds from 2001 –2002 that were caught between the 1st August and the 30th September between the hours of 4am and 12am (N = 2301, Mean time ± St. Dev. of mass recording = 7.30am ± 1.52hrs).
B – Experimental birds: includes all mass recordings of 12 juvenile and one adult bird that used the feeders. All mass recordings used were taken between the hours of 4am and 12 am (N = 38, Mean time ± St. Dev. of mass recording = 8.20am ± 0.59hrs).
higher body masses than Sedge Warblers fuelling under natural conditions at Icklesham (Fig. 3.5).

**Fuelling Durations of Sedge Warblers**

Sedge Warblers attending the feeders only fuelled for short periods (Table 3.6). The mean duration of 3.4 days is almost half as long as the mean time spent fuelling by Reed Warblers. Note though, that three of the Sedge Warblers had markedly longer durations than the majority of birds (up to 7 days; see Fig. 3.4) and thus the median of three days might be a better description.

**Reed Warblers and Great Reed Warblers in north-east Spain**

Only three Reed Warblers attended the feeders at Aiguamolls de L’Emporda. In contrast to the fuelling durations of birds at Icklesham, two of these birds stayed at the feeders for one day whilst the third stayed two days. These very short fuelling durations were in agreement with ringing data on unmanipulated birds (section 2.4.2) Unfortunately, fuelling rate data is only available for two of the Reed Warblers that attended the feeders, and only hourly FDRs could be calculated. However, these rates were higher than the maximum recorded for birds at Icklesham (rates at Aiguamolls: 0.25 & 0.22 grams/hour, maximum rate at Icklesham 0.21 grams/hour). The short fuelling durations resulted in departure masses (15.45 & 16.0 grams) that were at the lower end of those recorded at Icklesham.

Four Great Reed Warblers attended the feeders at Aiguamolls and had similarly short fuelling durations (Table 3.7), with all four birds only fuelling at the feeders for two days. Daily FDRs could be calculated for three of the birds (Table 3.7) and these were higher than those recorded for Reed Warblers at Icklesham and were more similar to the values recorded for Sedge Warblers. The departure loads of Great Reed Warblers were low relative to Reed Warblers at Icklesham but were similar to those of Sedge Warblers at Icklesham.
TABLE 3.6: Descriptive statistics for the fuelling duration of 14 juvenile Sedge Warblers and one adult attending *ad lib.* feeders at Icklesham.

<table>
<thead>
<tr>
<th>N</th>
<th>Mean</th>
<th>St. Dev.</th>
<th>SE Mean</th>
<th>Lower Quartile</th>
<th>Upper Quartile</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>3.4</td>
<td>2.17</td>
<td>0.56</td>
<td>2</td>
<td>4</td>
</tr>
</tbody>
</table>

TABLE 3.7: Daily FDR, departure load and fuelling duration of Great Reed Warblers attending *ad lib.* feeders at Aiguamolls de L’Emporda. Daily FDR could not be calculated for Bird 4 due to insufficient data.

<table>
<thead>
<tr>
<th>Bird</th>
<th>Daily FDR</th>
<th>Departure Load</th>
<th>Fuelling Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.111</td>
<td>0.53</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>0.124</td>
<td>0.43</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>0.141</td>
<td>0.49</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>0.35</td>
<td></td>
<td>2</td>
</tr>
</tbody>
</table>
3.4 DISCUSSION

Sedge Warblers and Reed Warblers

Migratory strategies show considerable variation between species (e.g. Alerstam 1990, Shaub & Jenni 2000b), but the selection pressures driving these differences are not always clear. Bibby & Green (1981) argued that contrasting prey choice was responsible for the different intake rates and therefore the differences in fuel deposition rate and resulting departure loads that they observed between Reed and Sedge Warblers. Higher intake rates have also been cited as the cause of the higher migration speeds observed in Sedge Warblers relative to Reed Warblers (Bensch & Nielsen 1999). Whilst prey choice may be one of the main reasons for higher fuelling rates in Sedge Warblers, my results suggest that prey choice may not be the only adaptation for increasing fuelling rates.

In my study, both Reed and Sedge Warblers were provided with an unlimited supply of food. With the differences in prey choice and food availability removed, one might no longer expect to see any differences in FDR. However, Sedge Warblers still had significantly higher FDRs than Reed Warblers, suggesting that behavioural or physiological adaptations beyond prey choice in Sedge Warblers, or constraints on Reed Warblers, accentuate the differences in FDR. The higher FDRs in food supplemented Sedge Warblers were probably largely due to a higher intake rate relative to Reed Warblers: this could be achieved by simply reducing predator awareness, thereby increasing feeding time. However, increasing intake rate may not achieve the desired effect unless it is coupled with physiological adaptations that enhance digestive efficiency (Klaassen 1996, McWilliams & Karasov 2001). Indeed, increasing intake without any change in the absorptive properties of the gut can lead to increased flow in the gut, which in turn may result in reduced digestive efficiency (McWilliams & Karasov 2001). Therefore, the benefits of increasing intake rates may be largely negated. Plasticity of the digestive organs has been demonstrated in a number of migrant birds (Piersma & Lindstrom 1997, Biebach 1998, Karasov & Pinshow 1998, Piersma 1998), suggesting that hypertrophy of the digestive organs, giving rise to increased digestive efficiency, could allow Sedge Warblers to support high intake rates. Increasing the surface area and volume of the gut appears to be the most effective
mechanism for supporting higher intake rates whilst maintaining digestive efficiency (McWilliams et al. 1999, McWilliams & Karasov 2001).

Plasticity in behaviour and physiology as a means of increasing FDRs may not be restricted to Sedge Warblers. Indeed, food supplemented Reed Warblers in NE Spain appeared to have higher FDRs than birds at Icklesham with access to an equivalent food supply. Whilst more evidence is needed to prove this difference between food supplemented birds, unmanipulated Reed Warblers in NE Spain had the highest FDRs relative to birds at three other sites examined in Chapter 2. Organ hypertrophy coupled with behavioural changes may be an important mechanism for increasing FDRs in time-selected migrants and therefore warrants further investigation.

Flexibility and Constraint in Reed Warbler Fuelling Strategies

Food supplementation had a profound effect on the fuelling strategies of Reed Warblers at Icklesham, resulting in both higher FDRs and departure loads. This demonstrates that food availability is an important constraint on fuelling behaviour in Reed Warblers and that environmental changes leading to changes in prey abundance could have a dramatic effect on the success of their migratory journey. This is the first time such a high degree of flexibility has been demonstrated in a migratory bird and suggests that migrants may be able to adjust to rapid changes in fuelling site quality and availability through behavioural flexibility. Further, it has recently been argued that such plastic responses to changed environmental conditions could subsequently become genetically based through directional natural selection (see Price et al. 2003).

Whilst food supplemented Reed Warblers showed a dramatic shift in fuelling behaviour, it is unclear as to whether naturally fuelling birds have this degree of flexibility or that these changes lead to a change in strategy. Most individuals fuelling under natural conditions at Icklesham achieved low FDRs and fuel loads (section 2.3.1), however, some individuals fuelled in a manner similar to food-supplemented birds (Fig. 3.6, see also Ormerod 1990). Whilst these individuals had not achieved an equivalent fuel load to food supplemented birds on their last capture, if they had continued to fuel at the same rate for two or more days they would have (Fig. 3.6). It is unclear what these individuals were feeding on but I speculate that they may have exploited a temporarily superabundant food source. Reed Warblers approaching the Sahara in SW
Portugal also routinely achieve very high fuel loads, so this behaviour is by no means unusual for this species (see section 2.3.2).

None of the birds that attended the feeders were caught or found dead on their journey south (although three birds returned in following years, proving that they survived) and thus it was not possible to determine the strategy they adopted. However, we do know (from ringing records) about the subsequent migratory flights of a small number of Reed Warblers that reached high fuel loads in NW Europe under natural conditions. For example, a Reed Warbler captured at a mass of 16.2g at Falsterbo, Sweden (N56°4´ E12°8´) was retrapped at Quinta da Rocha, Portugal (N37°8´, W8°43.5´) at 10.0g only 16 days later. This movement of approximately 2,620 km (= 163 km/day) was considerably faster than would be expected for a bird that had to make one or more refuelling stops en route, suggesting a single flight stage south across Europe. Observations such as this indicate that Reed Warblers that reach high fuel loads in NW Europe can (and do) make longer than normal flights on departure.

Whist Reed Warblers appear to have real flexibility in their fuelling strategy it is unclear whether other species of migratory bird share this flexibility. Food supplementation experiments on three other species pointed to other species being flexible but the degree of flexibility was not as marked as in Reed Warblers (section 3.1). For example, the FDRs of food supplemented Whitethroats were approximately twice those observed under natural conditions (supplemented and un-supplemented means ± SE: 1.01 ± 0.07 g/day, 0.43 ± 0.07 g/day) but they did not show a marked increase in departure load (un-supplemented birds ≈ 35% of LBM, supplemented birds mean = 55.2%; Fransson 1998a). Indeed, the maximum departure load for juvenile Whitethroats provided with unlimited food was 82% of LBM whilst Reed Warblers had a mean load of 76% and the maximum load was greater than 100% under the same conditions. A similar relationship between the departure loads of experimental versus non-experimental birds was found for Robins (un-supplemented birds mean = 34% of LBM, supplemented birds mean = 53%; Danhardt & Lindström 2001). Further, the true departure loads of non-experimental birds were likely to have been underestimated in these two studies, as the authors had no means of determining when these birds left the study site, indeed, the mean for Robins was based on just 14 birds (Danhardt & Lindström 2001).

My results showed that food supplemented Sedge Warblers also had flexibility in their fuelling behaviour, having both higher FDRs and departure loads than naturally
fuelling birds. However, the extent of flexibility in supplemented Sedge Warblers appeared to be constrained by behavioural programs for short fuelling durations, which resulted in lower fuel loads relative to Reed Warblers. Indeed, a small proportion of naturally fuelling Sedge Warblers at sites in the UK have been shown to accumulate larger fuel loads than these food supplemented birds (Bibby et al. 1976, Bibby & Green 1981). Predetermined fuelling durations also appeared to constrain the fuel loads of Reed Warblers and Great Reed Warblers in NE Spain. Whilst I provided both species with unlimited food, they accumulated smaller fuel loads than Reed Warblers fuelling at Icklesham. For both species fuelling durations were just two days in length, which was also the strategy adopted by un-supplemented birds (section 2.4.2). These results suggest that fuel loads may be constrained by endogenously controlled fuelling durations (see Chapter 5 for further discussion).

It was not just fuelling behaviour that was highly flexible in food-supplemented Reed Warblers. The extremely high FDRs that these birds achieved relative to un-supplemented individuals suggests that Reed Warblers typically had considerable spare capacity with respect to their digestive efficiency, although I have also presented evidence that points to Reed Warblers at Icklesham being digestively constrained relative to Sedge Warblers. The degree of spare capacity and therefore flexibility in digestive efficiency a migrant maintains is likely to be a trade-off between the probability and subsequent benefits of needing the extra capacity (e.g. the probability of encountering highly abundant food sources) and the costs of carrying extra gut mass on flight performance (McWilliams & Karasov 2001). In this case, I hypothesise that the benefits of additional capacity are greater for Sedge Warblers that actively seek out superabundant food sources than they are for Reed Warblers.

**Behavioural Flexibility and Environmental Change**

Environmental change, whether it be gradual or as rapid as the degradation or destruction of fuelling sites by man, could potentially pose a threat to migratory birds that require a large network of fuelling habitats. Previous studies have demonstrated that migratory strategies can evolve to keep up with fairly rapid environmental change (Berthold 1988, Berthold & Terrill 1988, Berthold et al. 1992), however, some changes are immediate (man induced) or too rapid to be closely tracked by evolutionary changes. My results show that there can be considerable quantitative behavioural flexibility in...
migration strategies when and where ecological conditions allow, which may allow migrants to adapt to change.

Wetland habitats are under considerable pressure from man and thus Reed and Sedge Warblers may be particularly prone to man-induced changes at stopover habitats. Throughout Europe, wetlands have been drained for agriculture, tourism and industry. The pressure on wetlands is particularly acute in southern Europe where the need for water for irrigation and tourism means there is little water left to maintain healthy wetland habitats. The Algarve coast of southern Portugal, that I identified as a key fuelling area for migrating Reed Warblers in section 2.5, is a popular tourist destination and further development could have dramatic consequences for Reed Warblers fuelling in this region. Theoretical work has predicted that habitat loss at such sites could have a major impact on migration strategies and the success or failure of migration (Weber, Houston & Ens 1999).

My results show that the fuelling strategies of Reed and Sedge Warblers are sensitive to food availability and highlight the importance of conserving stopover sites with adequate food supplies for migrating birds. Further, a network of high quality sites must be conserved such that birds can accumulate sufficient reserves to fly between increasingly widely separated sites.

Summary

This study underscores the importance of stopover sites in determining migratory strategies. It is clear that both the quality (in terms of prey abundance) and availability of stopover sites could impact on the success or failure of migration, especially with regards to species that are reliant on localised habitats as fuelling sites. I have highlighted that whilst fuelling behaviour can be a flexible response to food availability, it will be constrained to a varying degree between species by the time spent fuelling, which appears to be fairly inflexible. Finally, variation in migratory strategies may not only be caused by environmental and behavioural variability; physiological adaptations, such as plasticity of the digestive organs, may also play an important role.
CHAPTER 4

THE FUELLING BEHAVIOUR OF REED WARBLERS ON AUTUMN MIGRATION: TESTING OPTIMAL MIGRATION MODELS

4.1 INTRODUCTION

For a typical trans-Saharan migrant much of a migratory journey will be spent on the ground fuelling, not in the air. Indeed, Hedenström & Alerstam (1997) estimate that 80-90% of the time and approximately 67% of the energy expended during migration is spent during fuelling phases. A number of authors, starting with Alerstam & Lindström (1990), have therefore argued that fuelling phases are a crucial determinant of the time course, organisation and energetic cost of a migratory journey (section 1.3).

Exactly how a migrant should regulate its energy reserves, foraging behaviour and length of stay whilst fuelling has been the subject of a large body of theoretical work. Alerstam & Lindström (1990) were the first to suggest that migrants have been selected to optimise their behaviour according to an overall migration strategy. Two key strategies have received the most attention from theoreticians: a time-minimising strategy and an overall energy-minimising strategy. Alternative strategies may be to reduce the energy cost of transport or to minimise predation risk during migration (Alerstam & Lindström 1990, Hedenström & Alerstam 1997, Weber, Ens & Houston 1998). Recently, weather conditions have been included in models to determine how they may influence departure decisions and therefore the duration of fuelling (see Chapter 6).

Minimising Time, Energy or the Cost of Transport

Time-minimisation was proposed as a possible strategy on the assumption that by minimising time spent on migration, migrants may maximise their fitness by arriving before competitors at wintering/breeding sites, leaving breeding/wintering areas before resources are depleted, or by minimising the time spent at stopover sites where a lack of
local knowledge may threaten survival (Alerstam & Lindström 1990, Weber & Houston 1997a, Danhardt & Lindström 2001). In the case of the overall energy-minimising strategy, it is hypothesised that energy expended in one life stage affects the amount energy that can be expended on another. For example, it has been demonstrated that reproductive effort in one year is directly linked to effort in the following year (Gustafsson et al. 1994). By minimising the energy spent on migration, more energy can be invested in reproduction or survival, thus directly increasing fitness. Minimising energy expenditure may also be optimal when resources are low and a high-energy budget cannot be supported. Selection for minimising the cost of transport is only expected to act on short to medium distance migrants for which keeping flight costs to a minimum, rather than minimising the total energy expended on flights and fuelling periods, may have the greatest fitness consequences (Hedenström & Alerstam 1997).

Various models of optimal strategies have generated unique predictions regarding the relationship between the fuel deposition rate (FDR) and departure load (the amount of fuel available for flight at departure), which may be used to differentiate between strategies (Lindström & Alerstam 1990, Weber & Houston 1997a & 1997b, Hedenström & Alerstam 1997, Houston 1998, Weber, Ens & Houston 1998, Clark & Mangel 2000). All these models rely on three key assumptions:

1 – There is a decelerating relationship between the fuel load and the potential flight range, such that at higher fuel loads the increase in distance gained from additional fuel is minimal. This relationship directly influences that between the stopover duration and flight range, as fuel load increases with stopover duration (see Fig 4.1.1, page 120). This assumption is derived from flight mechanical theory (e.g. Pennycuick 1975, 1989) and gives rise to the negatively accelerated function defining the relationship between the departure load and FDR (see curve A or B in Fig. 4.1.2, page 120).

2 – There is a cost associated with stopping over, often described as a search and settling cost, that may manifest itself as both a time cost in days and an energy cost. On arrival at a stopover site, birds are said to need to locate suitable resources and in some cases set up and defend territories. Other authors have suggested that the digestive machinery must be switched from metabolising fat to storing fat, a change that introduces a time cost (Gannes 2002). The mean
value of this cost from a range of studies has been put at 2.5 days (Alerstam & Lindström 1990). However, some studies have concluded that there is no stopover cost, including one on Reed Warblers (Schwilch & Jenni 2001).

3 – The fuel deposition rate is constant from one day to the next. Whilst this assumption makes computation of the models easier, recent evidence suggests that FDRs are not constant (Fransson 1998b, Danhardt & Lindström 2001).

Hedenström & Alerstam (1997), who modelled three different migratory strategies, predicted that departure load should be an increasing function of FDR if migrants are minimising either time or energy, although the relationship should be steeper for time-minimisation (Fig. 4.1.2). It is important to note that this increase in departure load is not brought about by an increase in duration but rather durations are expected to decrease with increasing FDR. This is due to the nature of the relationship illustrated in Fig. 4.1.1, whereby an increase in FDR will result in a steeper relationship but a decrease in the optimal duration. This prediction is contrary to a number of examples from foraging theory in which foraging time increases with patch quality (equivalent to increasing FDR), thereby maximising resource intake (McNair 1982, Lima 1984), however, migrants are expected to be simultaneously maximising their intake whilst also minimising either their overall expenditure of time or energy, and are therefore not expected to spend longer in high quality patches.

For birds selected to minimise the cost of transport, departure load should be independent of FDR (Fig. 4.1.2) and again stopover duration is expected to decrease with increasing patch quality. It is important to note that migrants could have mixed strategies and thus observed values may, for example, fall between the predictions for energy- and time-minimisation.

A further time-minimising model developed by Weber & Houston (1997a) included a finite distance for the journey length, unlike the model of Hedenström & Alerstam (1997) that assumed an infinite distance. Rather than predicting a continuous relationship between FDR and departure load, this model predicted a stepwise relationship in which the predicted departure mass does not change over small ranges of FDR. This pattern emerges because the optimal strategy is to complete a journey in steps of equal length. However, this is only applicable on a landscape where fuelling
FIGURE 4.1.1: The decelerating relationship between flight range and stopover duration when FDR remains constant across the stopover, as determined by flight mechanical theory (e.g. Pennycuick 1975). The optimal stopover duration \( t^* \) for a bird minimising time can be obtained graphically by drawing a tangent (straight line) to the curved line, which identifies the point at which flight range is maximised, for the minimum time spent fuelling \( t^* \). The starting point of this line is determined by the stopover cost \( t_0 \), thus the smaller the cost, the shorter the optimal duration will be. Further, at higher FDRs, the relationship between duration and flight range will be steeper and the optimal duration will also decrease. As fuel load is a function of the fuel deposition rate and the fuelling duration, the curved line also describes the relationship between the fuel load and flight range.

FIGURE 4.1.2: Predicted relationships between fuel deposition rate (FDR) and departure load according to strategy: A – time minimisation; B – overall energy minimisation; C – cost of transport minimisation (Adapted from Hedenström & Alerstam 1997).
opportunities are continuous, as this is rarely the case it is unclear as to whether fuelling behaviour will have been optimised in this way.

For migrants minimising either time or energy, the relationship between their FDR and departure load is expected vary depending on how they interpret variation in FDRs between sites. Two hypotheses have been put forward regarding how this variation is interpreted (Houston 1998):

(a) *local variation* i.e. birds have a fixed expectation of FDRs along the length of the migratory route, therefore the FDR experienced at one site does not change the expected FDR at future sites.

(b) *global variation* i.e. locally experienced variation in FDR represents variation along the entire migratory route.

Selection might have favoured birds with a fixed expectation (local variation), as they will make the most of fuelling opportunities when they encounter FDRs higher than their expectation whilst birds using a global rule will not. However, if FDR varies considerably between sites and years, it may not be possible for selection to shape a fixed expectation and thus the global rule may perform better. Houston (1998) predicted that migrants using a local rule will have a much steeper relationship between their FDR and departure load than birds using a global rule, thus it should be possible to discern which rule is generally used.

Finally, it has been suggested that birds may have a fixed expectation of fuelling conditions improving or deteriorating along the route (Lindström & Alerstam 1992, Weber & Hedenström 1997a, Houston 1998). If such expectations have evolved, fuel loads are predicted to decrease if fuelling conditions are expected to improve, or increase if conditions are expected to deteriorate.

**Tests of the Models**

There have been few formal tests of optimal migration models and they have only been carried out on four species (Table 4.1.1). As migratory strategies may vary between species that migrate different distances, and winter and breed in different areas, the conclusions from these tests may not be generalised to other species until further tests have been carried out. Further, all four studies had small sample sizes (see Table 4.1.1) and therefore the power of these studies to detect real patterns must be queried.
TABLE 4.1.1: Description of studies that have tested the predictions from models of optimal migration, giving the following details: species; class of migrant in terms of distance to migratory goal; sample size; state of study birds i.e. whether they were fuelling naturally or were provided with additional food; the model the results most closely fitted; the manner in which variation in FDR was interpreted. Questions marks denote conclusions that were not entirely supported by the results.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Rufous Hummingbird <em>Selasphorus rufus</em></td>
<td>Bluethroat <em>Luscinia svecica</em></td>
<td>Whitethroats <em>Sylvia communis</em></td>
<td>European Robins <em>Erithacus rubecula</em></td>
</tr>
<tr>
<td>Type of Migrant</td>
<td>Medium-long distance</td>
<td>Medium-long distance</td>
<td>Long distance</td>
<td>Short-medium distance</td>
</tr>
<tr>
<td>State of Study Birds</td>
<td>Natural</td>
<td>Food supplemented</td>
<td>Food supplemented</td>
<td>Food supplemented</td>
</tr>
<tr>
<td>Sample Size</td>
<td>8</td>
<td>8</td>
<td>12</td>
<td>10</td>
</tr>
<tr>
<td>Currency Minimised</td>
<td>Time</td>
<td>Time/ Energy</td>
<td>Time? (only true when naturally fuelling birds were included in analyses)</td>
<td>Cost of Transport?</td>
</tr>
<tr>
<td>Interpretation of Variation in FDR</td>
<td>Global/Local</td>
<td>Global</td>
<td>Global</td>
<td>Not tested</td>
</tr>
</tbody>
</table>
Three of the studies, which were all on medium to long distance migrants, found a positive relationship between FDR and departure load and it was argued that the birds had been selected to minimise time but overall energy-minimisation was not formally ruled out. Indeed, Hedenström & Alerstam (1997) argued that the study on Bluethroats did not explicitly rule out either time- or energy-minimisation, and that more experiments were urgently needed.

Further, food supplemented Whitethroats did not have a significant relationship between their FDR and departure load when analysed alone and it was only when experimental birds were compared to estimates for naturally fuelling birds that a significant relationship was found (Fransson 1998a). The reliability of the estimates for naturally fuelling birds must be called into question in this case.

The fourth study (European Robins) found no significant correlation between FDR and departure load and the authors suggested that Robins might have been minimising the cost of transport (Danhardt & Lindström 2001). However, the authors admit that the lack of power was acute and that none of the strategies could be ruled out. It is unclear from these four studies which currencies migrants have been selected to minimise, if they have at all, I therefore intend to test the models with another species of long distance migrant and with a larger and hopefully more informative sample size.

Data from three of the studies were analysed by Weber, Fransson & Houston (1999) to determine how migrants interpret local variation in FDR with respect to FDRs at future sites (see Table 2.1.1). They concluded that migrants base their expectations of FDR at different sites entirely using the global rule. This has important implications for the outcomes of optimal migration models. A bird encountering a high FDR during its first fuelling phase will accumulate a larger fuel load if it is using the local rule, given that its expectation of FDR is lower than that experienced, relative to a bird using the global rule. Thus a bird using the global rule may take longer to complete its migration as it fails to recognise and capitalise on abundant food sources.

**Minimising Predation Risk**

Weber, Ens & Houston (1998) introduced three forms of perceived predation risk into models of optimal migration. These were mass-dependent (MD) predation risk, foraging-intensity dependent (FID) predation risk and a combination of the two. The models predicted that birds experiencing MD predation risk will forage at maximum
intensities whilst birds only experiencing FID predation risk will forage at rates below
the maximum. In both cases, FDRs are expected to be constant throughout the fuelling
period. If birds are experiencing both forms of predation risk then foraging intensities
should be below their maximum and are expected to decrease as the final departure load
is approached. There have been no formal tests of these predictions.

**Behavioural Programs for Optimisation**

All the optimal migration models assume that a migrant can accurately calculate
its FDR. No mechanism for achieving this has been proposed, let alone tested, and the
accuracy of any method of estimation that a bird may possess must therefore be
questioned. A recent computer simulation of migratory journeys under several different
criteria highlights the fact that complex behavioural rules for optimising departure times
and fuel loads, as described above, may be unnecessarily complicated (Erni et al. 2002).
Erni et al. compared the outcome of 6 different models on the total time spent
completing a migration of 4000 km on a simulated landscape. Four of these models
were of the time-minimising strategy in four different conditions: infinite or finite
distance coupled with local or global variation. The other two models were extremely
simple with just one rule. The first rule said that a bird should stay at a stopover site
until a given fuel load had been attained whilst the second said that a bird should remain
at a stopover site for a set number of days (CSD). The second of these two new models
(CSD) resulted in remarkably similar values for the total time spent on migration
relative to the best performing time-minimising model (infinite distance coupled with
global rule). In fact, durations using the CSD rule were only 2.5 days longer under a
wide range of conditions (total duration of journey ≈ 55 days). On the basis of this
outcome, Erni et al. (2002) argued that a fairly simple behavioural rule could govern the
time spent fuelling and have little effect on the overall speed of migration whilst other
factors may be much more important.

**Summary & General Aims**

Optimal migration models have generated a number of unique predictions that
can be tested in order to understand that selection pressures that have shaped migratory
behaviour. Few studies have tested these models and no general consensus has been
reached regarding the selection pressures acting on migratory behaviour. Studies have
indicated that time-minimisation may be important, however, the lack of direct agreement with the predictions, coupled with small sample sizes, suggests that further studies are crucial.

In order to address this uncertainty, I provided free-living Reed Warblers on autumn migration with a supplementary food source and obtained measurements of FDRs and departure loads from attendant birds. Using these data, I aimed to test the unique predictions regarding the relationship between FDR and departure load (Fig. 4.1.2) and therefore identify the selection pressures acting on Reed Warblers. A positive relationship would indicate that either energy or time are being minimised whilst a constant departure load, regardless of FDR, would indicate that the cost of transport is being minimised. By investigating variation in the daily FDR of individual birds, I intend to discover whether other selection pressures such as predation risk have shaped fuelling behaviour.

Whilst migrants are expected to be minimising one of the proposed currencies, the behavioural mechanisms by which this is achieved are completely unknown. If migrants are ‘true’ time or energy minimisers then their fuelling duration should decrease as their FDR increases, however, birds may simply have a fixed fuelling duration (Erni et al. 2002). By examining the relationship between the fuelling duration and FDR of Reed Warblers, I aimed to discover the behavioural rules governing fuelling behaviour.

Time-minimising behaviour may be identified by other means apart from the relationship between FDR and departure load. Time-minimising birds are always expected to fuel at maximum rates and thus if FDRs vary with date as Fransson (1998a) found then this could indicate that time is not the only currency under selection. I intend to look for similar patterns in Reed Warblers that could indicate that a currency such as predation risk is also being minimised.

4.2 METHODS

Study Site

The feeding experiments described in this chapter were carried out at Icklesham (N50°54′; E0°41′); for a detailed description of the site see section 2.2.
Experimental Birds

Experiments were carried out in two successive autumns: 1st August to 16th September 2001 and 12th July to 30th September 2002. At the beginning of each field season, a number of feeders were set up in the reedbed. For a description of the feeder design see section 3.2. The feeders were placed at sites that were chosen subjectively according to their usage by Reed Warblers. These sites were typically within bushes (Salix species) that varied in height from 2-3m. The bushes were always located in extensive areas of Phragmites reeds. In 2001, feeders were placed at four different sites, however, for much of the season only two of these feeders, which attracted the majority of birds, were operated. In 2002, four feeders were operated at a total of nine different sites. A number of these sites were vacated due to Reed Warblers being driven away by large numbers of Blue Tits Parus caeruleus, which had been attracted to the feeders. The number of feeders at which data were collected on any one day depended on whether Reed Warblers were present or not. The maximum number of Reed Warblers attending any one feeder was seven in 2002.

In 2001, all feeders were ‘ad lib’ as described in section 3.2. However, during 2002 two different types of feeder were used, the first being an ad lib feeder as in 2001. The second, called a ‘half rate feeder’, only allowed access to the mealworms for approximately half an hour in every hour and was expected to reduce the FDR of attendant birds, relative to those at ad lib feeders. This was achieved by integrating a clock mechanism into the feeder. Instead of a minute hand, a straw was attached vertically to the mechanism and a circular piece of transparency was then glued horizontally to the straw. Within the transparency, a wedge was cut that would circle the bowl every hour. Underneath the transparency and attached to the bowl was a wire mesh, approximately 4 cm from the base of the bowl, that also had a wedge cut in it. The size of the wedge in the wire mesh and the transparency was such that when one passed over the other, the mealworms were accessible for approximately half an hour. Whilst the mealworms were inaccessible, birds were still able to see the mealworms through the transparency. Although more birds were attracted to the ad lib feeders, six birds attended the half rate feeders, two them adults. In some cases, both types of feeder were covered overnight due to the attentions of small rodents.

Birds attending the feeders were individually identified using the methods described in section 3.2. As stated in that section, birds that could not be individually
identified were excluded from the analyses. Body mass recordings of these birds were taken using the methods described in section 3.2, using the combination of an electronic balance and a video camera (Plate 2). Filming in 2001 was carried out most mornings between 0700 and 1000h and in the evening between 1600 and 1900h, giving rise to 104 filming sessions. Each filming session was typically between 45 min and 90 min in length. In 2002, two cameras were used and each feeder was filmed for at least 45 min each evening and morning, giving rise to 321 filming sessions. If just two feeders were operating they would be filmed simultaneously until just after sunset. The end of filming after sunset depended on the time of year and the timing of the last feed on the previous evening. If three or four feeders were in operation, one/two feeders would be filmed before switching the cameras to the second set of feeders approximately 45 min before sunset. In this set up, the half rate feeders would always be filmed first as the food would be largely inaccessible between the end of filming and sunset, thus only a small mass increase would be likely. The video tapes were analysed on a colour television and the identity, time of visit (to the nearest minute), body mass (to the nearest 0.01g if possible, otherwise to 0.1g) and the number of mealworms eaten on each visit were recorded.

Calculating Fuel Deposition Rates and Departure Loads

Fuel Deposition Rates (FDRs) were calculated by dividing the change in body mass whilst attending the feeder by the number of days over which it took place and then dividing by the lean body mass (LBM, for calculation see Chapter 2). The first and last evenings that define the fuelling period were chosen using the criteria described in section 3.2.

The calculation of departure load and its relationship to FDR is critically dependent on the assumption that the final sighting of a bird is a reliable indicator of when a bird departed on migration. All the birds included in these analyses were present at a feeder for at least three days before the assumed departure and made regular visits to the feeder. No individuals were caught or sighted after they ceased to use the feeder, despite there being over 800m of mist net within the reed bed. Further, the mean number of visits to a feeder during two hours of filming on a bird’s final day was 10.6 (N = 22, StDev = 3.68, Min = 5, Max = 18). Given this rate of visitation, the probability of recording no visits during two hours of filming on the following day is significant at
0.002 (if one assumes a normal distribution with mean = 10.6 and StDev = 3.68). Therefore, it is highly unlikely that any individuals remained within the study area after they were no longer recorded at the feeder.

The exact evening body mass that was used varied between years due to different filming regimes. In 2002, the body mass of the majority of birds was recorded just before or after sunset and this was considered to be the mass at their last feed. In these cases, the mass recordings for any one bird in the half hour before its last feed were summed and the mean value taken. This measure was used rather than the mass at the last feed because part of the body mass at the last feed is due to the presence of food (mealworms) in the gut. By taking the average over a half hour, I hoped to produce an estimate that was closer to the mass of a bird once the food had been digested and the unwanted material expelled. Further, this procedure reduced the inflated mass of any birds that had a large last feed (three mealworms weigh 0.3g) which could potentially cause appreciable differences in departure load between birds. Birds attending the half rate feeders were not filmed up until sunset and thus their final mass could not be estimated in this way. As these birds only had limited access to the feeder post filming and were therefore unlikely to show a large increase in mass, the last recorded mass was used.

For birds attending the feeders in 2001, the situation was more complicated. Mass recordings were taken between 1600 and 1900h and thus the pre-dusk mass had to be extrapolated from the data. Extrapolations were only made if a bird’s mass had been recorded both in the morning and evening on the day in question. If these conditions were met, then a regression equation was generated for the mass gain on that day. Rather than using a linear regression, a 1/X transformation, characterised by a de-accelerating mass gain curve, was employed. This transformation was selected because five out of seven birds, for which mass recordings had been taken during at least three separate time periods on the same day, fitted this model best. The time to which body mass was extrapolated, was calculated by determining the timing of last feeds by birds in 2002. The time of all last feeds was regressed against date and the subsequent regression equation was used to predict the time of the last feed for a given date. Finally, body mass was extrapolated to 15 minutes before the last feed in order to mimic the half hour correction used in 2002.

Once appropriate masses were calculated, the mass change was divided by the number of days between and then by the lean body mass to give an estimate of the FDR.
These will be referred to as daily FDRs, in order to differentiate between hourly FDRs described in section 3.2. Departure loads were calculated by subtracting the LBM from the body mass on the last evening (as calculated above) and then dividing by the LBM (Lindström & Alerstam 1992, Fransson 1998a etc).

**Optimal Migration Models**

The predictions of two models were calculated using the information provided in Hedenström & Alerstam (1997). The first of these was a time-minimising model, for which the assumptions of a constant FDR along the length of the migratory journey, an infinite migratory distance, and variation in FDR being interpreted as ‘global’ variation, were made. The model also assumes that there is a cost to initiating a stopover that comes in the form of a time cost and an energy cost. Equation 3 in Hedenström & Alerstam (1997) is the basis of the time-minimising model and was used to generate an optimal value for $t$, the number of days spent at a stopover site, which is written as $t^*$. I varied the following key variables to see how they affect $t^*$:

- $t_0 =$ the time cost of stopping over expressed in whole days.
- $f_0 =$ the energy cost of stopping over, expressed as a percentage of LBM.
- $k =$ FDR, expressed as the proportion of LBM accumulated per day.

Taking the values for $t^*$, the model was used to generate a series of predictions relating the fuel deposition rate ($k$) to the optimal departure load ($f^*$). The departure load was calculated using the following equation: $f = kt$. As the model predicts values of $t^*$ that are not integers, the predictions of the model can be altered slightly by rounding the values of $t^*$ up to full days. This results in higher values for the departure load in all cases.

In the second model, the total energy cost of migration was minimised. The assumptions made above apply to this model and similarly the values of $t_0$, $f_0$ and $k$ could be varied to give different predictions. Additional variables included:

- $q =$ proportion of the energy spent on search/settling costs derived from fuel stores or from foraging. If all the energy is derived from the fuel stores, $q = 0$. Conversely, if all the energy is from foraging then $q = 1$. For the predictions given here $q = 1$. This value of $q$ results in maximal values for the departure load
and allows one to exclude total energy-minimisation as a strategy if observed values are yet higher.

$a =$ energy density of the fuel. Although the fuel is likely to consist in part of protein, the value for fat, $3.9 \times 10^4 \text{ kJ}^{-1}$, was used. If protein is included, the energy content of the fuel decreases and the predicted departure load increases. The magnitude of this increase is small e.g. for an FDR of 0.02 then the predicted departure load if the fuel store only consists of fat = 0.40, whilst it only increases to 0.41 if the fuel store consists entirely protein.

$t_x =$ the existence metabolism or field metabolic rate during stopover. The value of $6.25 \cdot m^{0.724}$ given by Hedenstrom & Alerstam (1997) was used, where $m$ is the body mass.

Both the models described above give predictions for the departure load of a bird experiencing a given FDR. This departure load is expressed as a fraction of the body mass at which a bird started fuelling, which in the case of the models is assumed to be the LBM of the bird in question. Reed Warblers attending the feeders at Icklesham began fuelling at higher body masses than the key estimates for LBM presented in Chapter 2, table 2.2.2. Therefore to insure that the departure loads of experimental birds were suitable for comparison with the model predictions, the estimates of LBM at Icklesham alone were used. These values were higher than the values used in previous analyses and are therefore more likely to reflect the start mass of birds attending the feeders. These modified departure loads appear in Fig. 4.3.5 to 4.3.8. The consequence of not knowing exact start masses is discussed in section 4.4.

For all other models discussed in this chapter, qualitative predictions, not quantitative, were used.

**Estimating Fuelling Duration**

The methods for calculating fuelling durations were described in section 3.2.
4.3 RESULTS & DISCUSSION

Departure Loads and Fuel Deposition Rates

The form of the relationship between the departure load and the fuel deposition rate is one of the key predictions arising from the models of optimal migration. Before examining this relationship, I have examined the relationship between the departure load and other factors, in order that they were corrected for if necessary.

The departure loads of juvenile Reed Warblers at *ad lib* feeders varied with the square of date (squaring improved linearity) such that loads were significantly higher later in the autumn (Regression, \( F_{1,24} = 10.83, P = 0.003, \text{adjusted } R^2 = 28.2\% \)). To illustrate this relationship clearly (Fig. 4.3.1), I regressed departure masses on date\(^2\) (Departure Mass = 15.8 + 0.001*Date\(^2\), \( F_{1,24} = 10.67, P = 0.003, \text{adjusted } R^2 = 27.9\% \)). Juveniles attending half rate feeders and adults were excluded from these two analyses because sample sizes were too small to allow for a suitable correction.

The increase in departure load with date could be a product of either increasing FDRs or longer fuelling durations. Hourly FDR showed a significant linear increase with date (Regression, \( F_{1,96} = 36.6, P <0.001, \text{adjusted } R^2 = 27.6\% \); Fig. 4.3.2). However, day length decreases whilst night length increases as the autumn progresses and to maintain the same daily FDR, hourly FDRs must increase to compensate for the reduced feeding time (daylight hours) and the increased fasting time (hours of darkness). Compensation may also be achieved by feeding later in the evening and earlier in the morning as the autumn progresses: I found that the last feeds of Reed Warblers were closer to sunset at the end of the migration period relative to the beginning (Fig. 4.3.3). Increasing hourly FDRs may therefore only compensate for reduced feeding time. Indeed, whilst hourly FDR increases with date, daily FDR did not increase significantly with date (Regression, \( F_{1,19} = 3.01, P = 0.099, \text{adjusted } R^2 = 9.1\% \)). However, if one bird, still in heavy post-juvenile moult whilst attending the feeder in late September, was removed from the dataset, the relationship became significant (Regression, \( F_{1,18} = 5.40, P = 0.032, \text{adjusted } R^2 = 18.8\% \)). Removing this bird can be justified on the grounds that FDRs are suppressed by moult (section 2.3.1) and all other study birds had either completed their moult or were close to completion.
FIGURE 4.3.1: Relationship between departure mass and date for juvenile Reed Warblers attending *ad lib* feeders at Icklesham. Black symbols = raw data. Regression line: Departure Mass = 15.8 + 0.001* date², where date = days from 15th August – 30th September.

![Graph showing relationship between departure mass and date](image)

FIGURE 4.3.2: Regression plot of hourly FDR against date. FDR is measured in grams per hour. Black symbols = raw data. Regression equation: Hourly FDR = 0.069 + 0.0019*Date.

![Graph showing hourly FDR against date](image)
FIGURE 4.3.3: Timing of last feeds by Reed Warblers relative to sunset. Raw data are indicated by symbols. Regression line: Time of Last Feed = 20.1 – 0.023*Date (P < 0.001).

FIGURE 4.3.4: Regression plot of departure load against FDR for juvenile Reed Warblers attending both types of feeder at Icklesham. Raw data is represented by the black (juveniles) and white symbols (adults). Regression equation (juveniles only): Departure load = 0.326 + 4.54*Fuel Deposition Rate.
Variation between feeders might have caused some of the variation in departure load. Birds attending half rate feeders had significantly lower departure loads than birds at *ad lib* feeders (t-test, variances not pooled, t₄ = -3.15, P = 0.034). However, as the experiment was designed to cause this effect, there was no need to control for it. Differences between feeders providing the same level of food do need to be controlled for but I found no significant difference in the departure loads of birds attending four different *ad lib* feeders in a model including date (ANOVA, F₃,₂₁ = 1.26, P = 0.314).

Differences between individual half rate feeders could not be examined due to the small number of birds attending them.

Adult Reed Warblers accumulated smaller loads than juvenile Reed Warblers (t-test, variance not pooled, t-value t₁₁ = -3.71, P = 0.003), but the sample size for adults was small (N=3) and more data are needed to confirm this result. After correcting for date, there was no between-year difference in the departure loads of juveniles attending *ad lib* feeders (t-test, variances pooled, t₂₃ = 0.16, P = 0.877).

To analyse the relationship between departure load and FDR, adults were excluded, as the sample was too small to allow for a suitable correction, and no correction was made for feeder number, year or date (due to the correlation between FDR and date). Departure load increased significantly with FDR (Fig. 4.3.4) when juvenile birds attending both *ad lib* and half rate feeders were examined (Regression, F₁,₂₄ = 19.74, P<0.001, adjusted R² = 41.9%, Departure load = 0.326 + 4.54*FDR). This positive relationship is consistent with selection for both time- and energy-minimisation, but rules out the cost of transport as a currency under selection. To differentiate between the time and energy strategies, it is necessary to examine the exact predictions of the models.

**Model Predictions**

Migrants may have been selected to respond to variation in FDR using either a local or a global rule (section 4.1). The model predictions presented in Fig. 4.3.5 assumed a global rule and it is evident that this approach provides a reasonable fit to the data on Reed Warblers. The local rule results in an appreciably steeper relationship between departure load and FDR (see Houston 1998, Page 397, Fig. 2 for a graphical representation) and could not be acting alone in the case of Reed Warblers.
The fit of either the energy or time-minimising models to the data on Reed Warblers depends on the stopover cost \((t_o)\) entered into the model (see Fig. 4.3.5). To discover which value of \(t_o\) generates the closest fit to the observed data, I calculated the sum of squares for three values of \(t_o\) for each model \((t_o = 1, 2 \text{ or } 3); \text{ these are considered realistic values, given the current data on stopover costs; see page 119): the model with the smallest sum of squares is considered the best fit according to Akaike Information Criteria. A value of \(t_o\) of two days provided the closest fit for the time minimising model (sums of squares, 1 day = 0.95, 2 days = 0.43, 3 days = 0.75), whilst a stopover cost of 3 days gave the closest fit for the energy minimising model (sums of squares, 1 day = 1.39, 2 days = 0.63, 3 days = 0.48). The best fitting model is therefore a time-minimising model with a stopover cost of two days (Fig. 4.3.5), although the energy minimising model with a stopover cost of three days also provided a similar fit. Whilst a stopover cost of three days is possible, current evidence suggests that this value is too high, especially when one considers that Schwilch & Jenni (2001) found no evidence for a stopover cost in Reed Warblers. Further, the value of one of the variables \((q = 1); \text{ see methods) entered into the energy-minimising model was chosen to give maximal values for departure load. If one chooses a more realistic value \((q = 0.75), then the sum of squares for an energy-minimising model with a stopover cost of three day is 0.52.

Based on the evidence for stopover costs we have to date, it would appear that a time-minimising model with a stopover cost of two days provides the closest fit to the data on Reed Warblers. However, examination of Fig. 4.3.5 reveals that the departure loads of Reed Warblers show many deviations from the model predictions, therefore some of the model assumptions may not appropriate for Reed Warblers. Note, in particular, that lower FDRs resulted in departure loads that were smaller than the predictions of both the energy- and time-minimising models.

The time-minimising model used here generated values for \(t^*\), the optimum number of days to spend on stopover. However these values were not integers and as a bird will not leave half way through a day, the predictions will alter if the value of \(t^*\) is rounded up to a whole day. By rounding the value of \(t^*\) up, the predicted departure load increases in all cases and may explain departure loads greater than the predictions in Fig. 4.3.5. The optimal stopover duration \((t^*)\) was also predicted to be high at low FDRs but to rapidly decrease as FDRs increased, before levelling off (Fig. 4.3.6). This relationship would suggest that a bird with a low FDR (<0.02) might avoid the
FIGURE 4.3.5: The relationship between FDR ($k$) and Departure Load ($f^*$) for time minimisation (black lines) and energy minimisation (blue line). To calculate the predictions, variation in FDR was interpreted as ‘global’ variation. The value for $f_0 = 0.03$ and the value of $t_0$ was varied between 0.5 days and 4 days, as indicated by the values on the right of the plot area. For energy, $f_0 = 0.03$, $t_0 = 2$, $q = 1$, $m = 0.0105$ and $a = 39000$. The symbols represent the data from food-supplemented Reed Warblers at Icklesham (diamonds = juveniles, squares = adults, black symbols = birds at *ad lib* feeders, white = birds at half rate feeders).
associated time cost (>17 days) by moving sites in search of a higher FDR. The predicted optimal durations did not appear to fit the data on food-supplemented Reed Warblers in all cases, especially at lower values of k (Fig. 4.3.6).

Whilst a time-minimising model provides an approximate fit to the observed relationship between FDR and departure load, it is evident that a linear model may be more appropriate than the non-linear relationship predicted for a time-minimising bird. Therefore, it seems likely that some of the assumptions of the time-minimising model, i.e. that stopover durations decrease with increasing FDR (see below), may not hold true for Reed Warblers.

**Fuelling Duration**

The number of days spent fuelling should decrease with increasing FDR, if time is minimised according to the models used here (Fig. 4.3.6). The fuelling duration of food-supplemented Reed Warblers varied little and the mean duration rounded to a whole day was 6 days (see Table 4.1). The mean duration did not decrease significantly as FDR increased (Pearson $r^2 = -0.079$, $P = 0.698$). The date at the start of fuelling was the only factor to have a significant effect on the duration of fuelling, such that duration increased as the autumn progressed (ANOVA, $F_{1,23} = 7.59$, $P = 0.011$). This increase in duration with date could be partly responsible for the increase in departure load with date (see Fig. 4.3.1). Age and body mass at the start of fuelling did not contribute significantly to variation in fuelling duration (ANOVA, $P>0.35$ for both variables).

The lack of variation in the mean fuelling duration suggests that fuelling durations could be largely fixed (section 4.1). This is supported by the similarity in departure load between hypothetical birds with a fixed duration of six days and the experimental birds described here (see Fig. 4.3.7). Therefore, it would appear that whilst Reed Warblers approximate to time-minimising behaviour, they are not adopting the ‘true’ time-minimising behaviour predicted by optimality models.

**Variation in FDR between Days**

One of the underlying assumptions of optimal migration models is that the FDR of fuelling birds does not vary between days. However, FDR may decrease as departure approaches if metabolic demands increase in line with body mass. FDR is also predicted
FIGURE 4.3.6: The relationship between Optimal Stopover Duration ($t^*$), expressed in days, and the Fuel Deposition Rate ($k$). Here $t_0 = 2$ days and $f_0 = 0.03$ (values for best fit line judged by eye in Fig. 4.3.5). Fuelling durations for juvenile Reed Warblers that attended the feeders at Icklesham are given by the diamonds (black = birds at *ad lib* feeders, white = birds at half rate feeders).

TABLE 4.1: Descriptive statistics for the fuelling durations (days) of all Reed Warblers that attended the feeders at Icklesham for which duration could be calculated (29 of 32).

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>ST. DEV.</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
</tr>
</thead>
<tbody>
<tr>
<td>29</td>
<td>5.6</td>
<td>1.3</td>
<td>0.24</td>
<td>5.0</td>
<td>6.0</td>
</tr>
</tbody>
</table>
FIGURE 4.3.7: Comparison of the relationship between FDR and departure load for a constant fuelling duration model (solid black line – duration 6 days) and a time-minimising model (solid white line, durations were rounded to nearest day). The relationship for juvenile Reed Warblers at Icklesham is shown by the diamond symbols (black = birds at ad lib feeders, white = birds at half rate feeders).
to decrease, if fuelling behaviour has evolved to reduce both MD and FID predation risk (section 4.1).

If neither increasing metabolic demands or the combination of MD and FID predation influence FDRs, then one would expect to see no relationship between FDR and time relative to departure (equivalent to increasing body mass). An analysis of hourly FDR against day relative to departure of 17 juvenile Reed Warblers attending *ad lib* feeders, for which hourly FDR could be calculated on at least three days, found no evidence for rejecting the null hypothesis (ANOVA, $F_{1,49} = 0.05$, $P = 0.830$; Fig. 4.3.8). This was supported by a nested analysis in which bird was nested within day relative to departure (ANOVA, $F_{17,39} = 1.31$, $P = 0.240$).

Whilst the lack of relationship between hourly FDR and time spent fuelling, suggests that the combination of MD and FID predation risk are not acting on fuelling birds, it does not rule out the possibility that increased metabolic demands are compensated for by day, through increased intake, but not at night. By analysing the total mass gain between evenings for the same set of birds as above, I found that mass gain decreased as departure approached and therefore as body mass increased (ANOVA, $F_{1,60} = 5.57$, $P = 0.022$; Fig 4.3.8). This was still true if bird was nested within day relative to departure (ANOVA, $F_{17,47} = 2.15$, $P = 0.020$).

Whilst the lack of relationship between hourly FDR and time spent fuelling, suggests that the combination of MD and FID predation risk are not acting on fuelling birds, it does not rule out the possibility that increased metabolic demands are compensated for by day, through increased intake, but not at night. By analysing the total mass gain between evenings for the same set of birds as above, I found that mass gain decreased as departure approached and therefore as body mass increased (ANOVA, $F_{1,60} = 5.57$, $P = 0.022$; Fig. 4.3.8). This was still true if bird was nested within day relative to departure (ANOVA, $F_{17,47} = 2.15$, $P = 0.020$).

Whilst it was not possible to examine overnight loss, it was possible to test whether the actual rate of intake of mealworms increased by day to compensate for increased metabolic costs. The hourly rate of intake increased significantly as the day of departure approached (ANOVA, $F_{1,60} = 5.37$, $P = 0.024$) and was still significant if bird was nested within day relative to departure (ANOVA, $F_{15,46} = 2.88$, $P = 0.003$; Fig 4.3.8).

Whilst the patterns described above were significant at the population level and when nesting was employed (Fig. 4.3.8), there was considerably variation within individual birds. When these patterns were analysed day by day using paired t-tests, no significant differences were found except for decreases in three measures of fuelling between the penultimate day and the day of departure (hourly FDR, $t_{5} = -2.89$, $P = 0.028$, daily mass gain, $t_{14} = -2.83$, $P = 0.013$, intake rate, $t_{13} = -2.67$, $P = 0.018$). The varying values for the degrees of freedom are because each data variable could not be calculated for all birds on all days.
FIGURE 4.3.8: Variation in three variables with day relative to departure: hourly FDR, daily mass gain and intake rate (of mealworms). Boxes define the median and the inter-quartile ranges, and whiskers show the range for 17 juvenile Reed Warblers attending *ad lib* feeders at Icklesham. The black dots represent the population mean. The departure day = 0.
4.4 GENERAL DISCUSSION

Food-supplemented Reed Warblers at Icklesham were not trying to attain a specific departure load but instead their departure load was a positive function of their fuel deposition rate. The departure loads of Reed Warblers and their speed of migration will therefore be influenced by the FDRs they encounter, suggesting that fuelling site quality could have important fitness consequences. As FDRs directly influence fuelling behaviour, food availability is likely to have a significant impact on the time-course and organisation of migratory journeys made by Reed Warblers (Lindström & Alerstam 1990).

Optimality in Migratory Strategies

Optimality models of migratory behaviour predict that departure loads should be a positive function of FDRs if migrants have been selected to minimise either time or energy during migration (Hedenström & Alerstam 1997). I found that the relationship between departure load and FDR for Reed Warblers most closely approximated to the predictions of a time-minimising model. This result is the clearest demonstration to date that the fuelling behaviour of a migratory bird has been at least been partly shaped by selection for time-minimisation. Previous studies have suggested that this was most likely the case for three other species (Table 2.1.1), but further investigation, for the Whitethroat and Bluethroat in particular, is needed to confirm this (Lindström & Alerstam 1992, Fransson 1998a, Houston 1998). These apparently time-selected species were all medium-long distance migrants, like the Reed Warbler. Further, the Whitethroat bred in Europe and had to cross the Sahara to reach wintering grounds in Africa. That the Reed Warbler and this species have been selected to minimise time, suggests that there are important fitness rewards for early arrival on the wintering grounds in Africa, or, alternatively, that remaining in Europe too long is detrimental to fitness or even threatens survival. Therefore Reed Warblers may be particularly sensitive to environmental changes that result in a slower speed of migration.

The FDRs and ‘apparent’ departure loads of non-experimental birds at Icklesham provide further support for the conclusion that Reed Warbler migratory behaviour has been influenced by selection for time-minimisation (section 2.3.1). These
FDRs and ‘apparent’ departure loads (departure load cannot be determined exactly from ringing data) were lower than those of experimental birds, further demonstrating sensitivity to FDR. Fransson (1998a) obtained a similar result for Whitethroats. A clearer indication of time-minimising behaviour was the increase in FDR and departure load with date in experimental birds (Fig. 4.3.1 & 4.3.2). Both these increases will act to increase the potential speed of migration, and presumably reflect the expectation that the strength of selection for time-minimisation will increase as the time available for completing migration decreases (Fransson 1998a). The increase in daily FDR towards the end of the season was also reflected by a linear increase in hourly FDR as the autumn progressed (Fig. 4.3.2). I believe this increase in hourly FDR is, in part, a mechanism for compensating for the reduction in feeding time as day length decreases.

Whilst increases in FDR and departure load with date support the case for time-minimisation, they also suggest, as other authors have not previously noted (Fransson 1998a, Schaub & Jenni 2000a), that FDRs must have been constrained earlier in the season. The nature of this constraint is open to speculation but it suggests that Reed Warbler fuelling behaviour has not been shaped by selection for time-minimisation alone. A second currency under selection could be predation risk, although a bird trying to minimise MD predation risk should always fuel at maximum rates, thereby reducing the time spent at higher body masses (Weber, Ens & Houston 1998). However, a bird selected to minimise just its FID predation risk is expected to forage/fuel at rates below maximum, thereby increasing awareness (Weber, Ens & Houston 1998). Therefore, Reed Warblers may have been selected to minimise both time and FID predation risk: although the selection pressure for time-minimisation may increase to the degree that it overrides other considerations by the end of the migratory season. Further support for Reed Warblers being selected to minimise both currencies comes from the increasing foraging risks birds take by feeding closer and closer to sunset, and even after sunset, as day length decreases (Fig. 4.3.3). Low light levels and high predator activity may make sunset a dangerous time to forage (Lima 1988, Krams 2000), therefore birds that fuelled earlier in the season presumably reduced their predation risk by not foraging close to sunset. Evidence for the minimisation of FID predation risk or simultaneous selection for two currencies, has not been shown in a migratory bird before.

Another explanation for non-maximal FDRs is the possibility that maximum levels of energy turnover are detrimental to fitness, through side affects such as lowered immunity or heightened cellular damage (Klaassen 1996, Hedenström & Alerstam
1997). Whilst this possibility cannot be ruled out, there is good evidence that predation risk can influence foraging decisions (Cresswell 1994, Fransson & Weber 1997, Brown 1999, Krams 2000, Lilliendahl 2000). Regardless of the exact constraint, it is apparent that foraging at high intensities, or having a high-energy turnover, has negative fitness consequences that must be balanced against the benefits of increasing foraging rates in order to minimise time.

**Discrepancies between the Raw Data and the Model Predictions**

The time-minimising model used to generate the predictions presented in this chapter assumed that migrants optimise their fuelling behaviour according to two expectations: A) the existence of a stopover cost, B) that currently experienced variation in FDR reflects variation in FDR at future stopover sites (global rule, see section 4.1). Stopover durations and therefore departure loads are expected to increase as a bird’s perception of the magnitude of stopover costs increases (Hedenström & Alerstam 1997). The departure loads of food supplemented Reed Warblers suggested that their fuelling behaviour had evolved to account for a stopover cost of approximately two days (Fig 4.3.5). Previous studies on caged migrants pointed to a cost of similar magnitude (Klaassen & Biebach 1994, Hume & Biebach 1996) and a review of a number of field studies found an average cost of 2.5 days (Alerstam & Lindström 1990). However, the departure masses of food supplemented Reed Warblers, with FDRs in the range found in naturally fuelling birds at Icklesham (0.01-0.03, section 2.3.1), were lower than the predictions of a model including a cost of two days. The ‘apparent’ departure loads of naturally fuelling birds were also low and both these observations suggest that stopover costs could be in the order of one day or less (Fig. 4.3.5). Indeed, Schwilch & Jenni (2001) found no evidence for a stopover cost in Reed Warblers. Further work is still needed to discover the true extent of stopover costs in migrating birds.

The true value of the stopover cost will determine the slope of the relationship between departure load and FDR. The slope is also expected to be dependent on how a bird interprets variation in FDR with respect to the FDR it expects to experience at future sites (Houston 1998, Weber, Fransson & Houston 1999). If Reed Warblers have evolved to account for a stopover cost of two days, then my data on food-supplemented birds suggest that birds were using a global rule, i.e., local variation reflects variation at
future sites. However, if stopover costs were low or non-existent, as indicated by naturally attained fuel loads, then the slope of the relationship for experimental Reed Warblers is steeper than expected and indicates that birds may have a fixed expectation of future FDRs. An alternative explanation is that Reed Warblers use a combination of both rules, such that they have a fixed expectation of FDRs but also integrate current experience as an indication as to whether their fixed expectation may be too high or too low. Houston (1998) argued that this could be the case for Bluethroats. Indeed, the slope of the relationship for Reed Warblers was steeper than for any of the three species reviewed by Weber, Fransson & Houston (1999) and this difference in fuelling behaviour suggests Reed Warblers may be using a rule other than the global rule on its own. This has important implications for Reed Warbler fuelling behaviour because it means they will capitalise on unusually high food availability. This could explain why food supplemented Reed Warblers appeared to attain higher departure loads than other species provided with supplementary food (Lindström & Alerstam 1992, Fransson 1998a, Danhardt & Lindström 2001).

Unlike the model prediction of a smooth relationship between departure load and FDR, the data from food supplemented Reed Warblers showed considerable variation in departure load, even when FDRs were similar. This variation may have a number of causes. Firstly, the models assume that birds are carrying no fuel when they start fuelling and therefore have similar body masses (Lindström & Alerstam 1990). Experimental birds had a range of body masses when they started fuelling and this may have caused the observed difference in departure mass of birds with similar FDRs (Fig. 4.3.5). Secondly, departures by birds from the study site may have been delayed by adverse weather conditions (see Chapter 6). Delayed birds, assuming they continued to fuel whilst waiting for suitable departure conditions, will have inflated departure loads (Weber, Houston & Ens 1999).

**Individual Variation in FDR**

The predictions of the time-minimising model used in this study (Hedenström & Alerstam 1997) were also based on the assumption that the FDR remained constant during the fuelling period. The majority of Reed Warblers broke this assumption and therefore I do not expect an exact fit between the data and model predictions. Further, it has been argued that if either metabolic rate increases in line with the fuel stores or if
birds have been selected to minimise both MD and FID predation risk, then FDR should decrease over the fuelling period in a predictable way (Klaassen & Lindström 1996, Weber, Ens & Houston 1998). Reed Warblers attending the feeders showed a significant decrease in FDR on the day of departure but support for a gradual decrease over the fuelling period was only weak. Indeed, it seems that the actual rate of mass gain varied little between days but instead, the mass lost during overnight fasting increased as body mass increased. Therefore, it may be the case that increased metabolic demands were compensated for during daylight hours, by increasing the foraging/intake rate, but not at night when feeding was impossible. This theory does not receive significant statistical support from the data presented here but neither is it ruled out. However, the increase in intake rate is of interest, because again it points to intake rates having been constrained by FID predation risk.

Previous studies have noted similar reductions in FDR on the day of departure but have not looked for the trends suggested here (e.g. Fransson 1998b, Danhardt & Lindström 2001). More detailed data is needed to discover whether these trends really exist and whether they are common to species other than the Reed Warbler. Further, if these trends are real, then they will affect the optimal strategy of a time-minimising bird. A decreasing FDR is expected to result in shorter optimal fuelling durations; therefore departure loads will be lower relative to a situation in which FDR remains constant.

**Behavioural Control**

Whilst there is support for Reed Warblers being time-selected during autumn migration, the mechanism by which time-minimisation is achieved is unclear. I will discuss three mechanisms:

1) Migrants have behavioural programs that measure FDRs and then monitor fuel stores until the optimal departure load is reached (Houston 1998).

2) Behavioural programs measure FDR, calculate the optimal fuelling duration and promote fuelling until this period is over.

3) Migrants fuel for a fixed duration that has been shaped by selection to be optimal with respect to the range of FDRs typically encountered (Erni *et al.* 2002).
Mechanism one and two require complex behavioural programs and therefore may be least likely to arise through natural selection. Of these two, mechanism 2 seems more likely, as estimating the time spent fuelling should be easier than estimating current fuel load. Indeed, caged migrants demonstrate fairly precise rhythms of migratory restlessness that could reflect these fuelling periods (Gwinner 1986, 1996). However, the fuelling durations arising from both these mechanisms should vary with FDR. Reed Warbler fuelling durations were relatively constant, regardless of FDR, and only seemed to vary with date. This supports the third mechanism in which birds always fuel for a period of set length. Whilst mechanism 3 does not give rise to ‘true’ time-minimisation (Erni et al. 2002), its simplicity favours its evolution by natural selection and fits with a number of observations:

A) Gwinner (1986, 1996) observed fairly precise periods of migratory restlessness in caged migrants, which suggest a hard-wired stopover/fuelling length.

B) Constant fuelling durations provide a flexible system when other factors such as barriers must be incorporated into fuelling strategies. For example, migrants preparing to the cross the Sahara must accumulate large fuel loads to achieve a safe crossing and typically need to fuel for longer than would be optimal under time-minimisation. Whilst adjusting the relationship between the FDR and optimum stopover length would be relatively complex, to alter the length of a fixed fuelling duration is potentially relatively simple. Indeed, Fransson et al. (2001) showed that magnetic cues could trigger changes in fuelling duration (section 1.3).

C) Helbig (1996) argued that cues leading to shifts in migratory direction are already in place and therefore could also bring about changes in fuelling behaviour.

A number of observations have been put forward to refute the constant fuelling duration hypothesis. Firstly, birds fuelling under natural conditions have a degree of variability in their fuelling/stopover durations. So-called fixed fuelling durations, however, do not always have to be exact, as delays due to poor flying conditions (see Chapter 6) and variability as a consequence of more than one allele for duration length, are part of my view of this hypothesis. Further, the fuelling durations of naturally fuelling birds have never been measured exactly; rather stopover durations have been calculated using complex probability models. This method of calculation will lead to
inherent variability in stopover durations that may not reflect the real world. The ringing data used for these calculations will also include birds that had yet to commence fuelling and even birds that were close to finishing fuelling on first capture, further increasing variability in estimates. Finally, despite the unreliability of these estimates of stopover duration, Schaub & Jenni (2001) remarked that their estimates of stopover durations across a wide range of sites within Europe showed surprisingly little variation.

A second argument against the fixed duration hypothesis is that it does not take into account the need to cross barriers. This is a rather short sighted objection as I do not expect the same fixed duration to apply along the entire length of the migratory journey, indeed I would expect selection to have shaped fixed durations according to the journey ahead, such that the duration is optimised with respect to the geographic position of a fuelling site.

If fuelling durations are fixed within geographic regions, then there is the problem that the optimal duration should vary with date as the time available for fuelling decreases with day length. However, in the case of Reed Warblers it seems that by increasing foraging rates and by foraging closer to sunset, they are able compensate for decreases in day length. How this compensation is controlled behaviourally is unclear but perhaps motivation for foraging is linked to a time program, which monitors the time available for migration and adjusts foraging motivation appropriately.

**Summary**

The fuelling behaviour of Reed Warblers on autumn migration shows the hallmarks of an overall migratory strategy in which time is the key currency under selection. However, whilst time is shaping the overall strategy, fuelling decisions are still partly influenced by other variables which act to keep FDRs below their maximum for much of the migratory period: contrary to the expected behaviour of a ‘true’ time-minimising migrant. Reed Warblers must therefore be minimising a second currency such as FID predation risk. Minimisation of FID predation risk or simultaneous selection for the minimisation of two contrasting currencies has not been shown previously.

The approximation of fuelling behaviour to ‘true’ time-minimising behaviour has now been demonstrated in four different species of long distance migrant, including the Reed Warbler, and may prove to be widespread or even general among long
distance migrants. However, long distance migrants are subject to a wide range of ecological and physiological variables that in some instances may negate the importance of time; only further study will identify these. It is also important to note that the small sample sizes in previous studies only allowed for tentative conclusions to be drawn, and further work may refute previous conclusions.

Whilst time may be a currency common to many long distance migrants, the behavioural means by which time-minimisation is achieved is a question that must now be addressed. This is the first empirical study to suggest that a constant fuelling duration may be the mechanism at work and future studies must identify methods that accurately obtain not only a range of FDRs but also fuelling/stopover durations in order to test this further. I have shown that fuelling durations vary on a geographical scale (section 2.5) and it is therefore important to identify the cues that give rise to different durations. It would also be of great interest to identify the constraints that suppressed Reed Warbler FDRs for much of the migratory season. These results also suggest that optimality models must be reworked to include alternative ways by which migrants may approximate to time-minimisation, without the need for complex behavioural rules.
CHAPTER 5

THE FUELLING BEHAVIOUR OF SEDGE WARBLERS ON AUTUMN MIGRATION

5.1 INTRODUCTION

Migration is an energetically demanding process and therefore migratory strategies are likely to be influenced by the distribution of food supplies both in space and in time (Alerstam 1990). Morphology directly influences feeding ecology, including both habitat and prey choice, and hence morphological differences may give rise to a diversity of migratory strategies. The differences in the autumn migration strategy of Reed and Sedge Warblers in north-west Europe are well documented (section 3.1), and yet the two species show considerable morphological similarities except for subtle differences in leg and bill morphology (Bibby & Green 1981). These subtle differences appear to allow Sedge Warblers to efficiently utilise superabundant supplies of reed aphids as a food source and consequently perform a remarkable long stage migration from fuelling sites in southern England and northern France to sub-Saharan Africa without the need to refuel.

Sedge Warbler Fuelling Behaviour

Whilst Sedge Warblers have been shown to undergo enormous weight gains (80-120% of their lean body mass) in some reedbeds in northwest Europe, at many others no such gains are observed. Bibby et al. (1976) noted that the actual proportion of birds making such weight gains at a site in southern England was relatively small, and that the majority of birds only remained at the site for short periods (3 days or less) and gained little weight. Indeed in a year when aphid abundance was low, approximately 85% of birds remained at the site for two days or less. At my study site in southern England, I artificially increased food abundance and therefore expected to observe both these fuelling behaviours.
Similar behaviour may be true of Scandinavian Sedge Warblers. Bensch & Nielsen (1999) reported rapid movements between sites by Sedge Warblers migrating southwards from Scandinavia and noted that these movements were considerably faster than those of Reed Warblers. These rapid movements suggest that these birds had short fuelling durations, like some birds in southern England, and were unlikely to be gaining large fuel stores. These birds were probably heading to sites further south in order to fuel extensively. One such site may be Illmitz in central Europe, where fuelling durations were found to be highly variable between years (Schaub & Jenni 2001): presumably reflecting differing proportions of extensively fuelling birds depending on food availability.

Given the low proportions of birds making large weight gains at sites in southern England and even in northern France, which is perceived as one the key fuelling areas (Bibby & Green 1981), it is unclear what the cue for extensive fuelling is. The obvious suggestion would be that food abundance determines where Sedge Warblers fuel extensively. However, evidence from southern England indicates that high food abundance does not necessarily result in a high proportion of fuelling birds (Bibby et al. 1976) and thus a geographical cue may also be involved.

These periods of extensive fuelling, whether they be in southern England or northern France, must result in extremely high fuel loads if birds are to fly to the Sahel without refuelling. To achieve a single flight stage from a site such as Icklesham to the Sahel region of West Africa (approx. 3,800-4,200km), a bird must theoretically reach a body mass of 20g or more (equivalent to a fuel load > 100% of LBM), given that the additional body mass consisted of 75% fat and 25% protein (Klaassen 1996) and the bird flew in still air conditions (see section 7.2 for method of calculation).

Sedge Warblers and Models of Optimal Migration

Given our current knowledge of Sedge Warbler migration, how would we expect Sedge Warblers to behave with respect to theoretical ideas about optimal migration strategies? Bensch & Nielsen (1999) suggested that the rapid movements they observed were consistent with time-minimising behaviour but were unable to conclude how Sedge Warblers achieved a higher speed of migration relative to Reed Warblers. They hypothesised that Sedge Warblers could shorten stopover durations by either being more efficient at finding good feeding sites or by have a higher FDR but found no
evidence for either hypothesis. However, I have demonstrated that Sedge Warblers had higher FDRs than Reed Warblers when utilising the same unlimited food source (section 3.3). These higher rates may have led in part to the shorter fuelling durations that I also found (section 3.3).

The selective pressure driving these short fuelling durations was likely to have been time-minimisation due to the temporal availability of aphids within the key areas where Sedge Warblers undergo extensive fuelling. Bibby & Green (1981) reported that the peak abundance of aphids in mid-August coincided with the peak passage of Sedge Warblers and from late August onwards there was a rapid decline in aphid abundance. This contracted period of prey abundance suggests that Sedge Warblers migrating to key fuelling areas should have been strongly selected to minimise time and would therefore be expected to show a positive relationship between their departure load and FDR (section 4.1, Fig 4.1.2). However, under both the time-minimising and energy-minimising hypotheses, the expectation of good conditions further south is predicted to lead to lower fuel loads than if fuelling conditions were constant (Alerstam & Lindström 1990, Weber & Houston 1997a). Thus a shallower relationship between departure load and FDR is predicted, relative to a scenario where fuelling conditions are expected to be homogenous between sites.

Whilst time is expected to be the key currency driving Sedge Warbler fuelling behaviour, other factors such as FID predation risk and rising metabolic costs may be influential (see section 4.1).

**General Aims**

In this study I provided free-living Sedge Warblers with an unlimited supply of food at a site in southern England where extensive fuelling was rare but had been noted in some years (S.J. Rumsey, *pers. comm.*). Therefore, if an abundant food supply was the cue for switching from a strategy of short stops and rapid onward movements to a large fuel gain, I expected all Sedge Warblers attending the feeders to fuel extensively. However, if the cue was temporal or geographical, mediated through magnetic cues for example (Fransson *et al.* 2001), then I expected that birds would make short stops and respond to their FDR in the manner predicted for time-minimising migrants. Alternatively if the cue for extensive fuelling was a combination of the above, then I expected to see both strategies arising amongst experimental birds: both strategies were
recorded in mist netted birds in southern England (Bibby 1976), suggesting that the exact cue for initiating extensive fuelling may vary between populations. Using data on fuelling Sedge Warblers attending an artificial food source, I aimed to test these different predictions and the predictions of optimal migration models.

5.2 METHODS

Study Site

The feeding experiments described in this chapter were carried out at Icklesham in southern England (N50°54´, E0°41´); for a detailed description of the site see section 2.2.

Experimental Birds

Experiments were carried out in three successive autumns in the years 2001 to 2003. In 2001 and 2002, whilst the main purpose of the experiments was to gather data on Reed Warblers, data were collected on Sedge Warblers attending the feeders. As a result, data were gathered on one Sedge Warbler in 2001 and on six individuals in 2002. Of the six individuals in 2002, two of the birds were only recorded at the feeder on one evening. Both these individuals were feeding rapidly from the feeders and were therefore assumed to have departed the same evening, rather than having ignored the feeders the following day. Consequently, only one of the variables of interest could be calculated for these birds and they therefore appear in few of the analyses presented in section 5.3. In 2003, I concentrated on collecting data on Sedge Warblers and a total of eight birds attended the feeders. One of these individuals was prevented from using the feeder on its last evening by intense competition from Reed Warblers and consequently does not appear in all the analyses, as its departure load could not be calculated.

The feeder design used in all three years is described in section 3.2 (see also Plate 3). In total six different feeder positions were utilised by Sedge Warblers across the three years. The main similarity between the positions of these feeders was their proximity to the edge of the reedbed, areas of open grass and medium to tall stands of plants such as Willowherbs, Chamerion & Epilobium spp. The edge of the reedbed was
typically 5-10 m away from feeders. Five of the feeders were placed in or next to water: two in reeds (*Phragmites*) along the borders of a long drainage ditch (attended by 6 birds) and three around the edges of pools fringed by reeds (attended by 6 birds). The sixth feeder was placed in a strip of reeds, between a track and a dried area of open water (attended by 3 birds).

All the feeders attended by Sedge Warblers were kept topped up with at least 50 mealworms (*Tenebrio molitor*) from dawn till dusk and were therefore all ad lib feeders. In 2003 in particular, the feeders were emptied after sunset each evening and refilled each morning before sunrise in order to prevent small rodents discovering the feeders. In 2001 and 2002 Sedge Warblers discovered the feeders by chance, although the presence of other birds at the feeders probably aided this process. In 2003, in order to increase attendance by Sedge Warblers, I played a tape of Sedge Warbler two to three metres from the feeders, which was audible at a maximum distance of approximately 30 m. Typically the tape was played for one to three hours every other morning at each feeder. However, the use of the tape depended on whether a feeder had a Sedge Warbler present already and whether or not the more commonly used feeders had a Sedge Warbler present.

Individual birds were identified using a combination of factors. These included the presence/absence of a metal ring and body mass. For justification of the use of these see section 3.2. I avoided catching and marking Sedge Warblers with individual colour rings in 2003, as experience with Reed Warblers had taught me that the process of catching and marking often caused birds not to return to a feeder.

The methods for the recording of visits and the taking of mass measurements for birds visiting the feeders were described in detail in section 3.2. The timing of recordings for 2001 and 2002 was described in section 4.2. In 2003, four different feeders were deployed and as I only had two video cameras, the filming of visits had to be staggered. Each feeder was filmed twice daily, once between 0700-1000h and once between 1800-2030h, giving a total of 161 filming sessions. Each filming session lasted between 45-90 minutes. In the evening, the second set of feeders was filmed until after sunset (birds rarely fed after sunset, see also Fig. 4.3.3) and feeders with Sedge Warblers present were prioritised for the later filming session. At no stage in 2003 were more than two feeders being used by Sedge Warblers, therefore all final mass recordings represent the mass of a bird at their last feed of the day (from the feeder). The videotapes were analysed on a colour television and the identity, time of visit (to
the nearest minute), body mass (to the nearest 0.01g if possible) and the number of mealworms eaten on each visit were recorded.

**Calculating Fuel Deposition Rates and Departure Loads**

The methods for calculating the daily fuel deposition rate and departure load of fuelling birds were laid out in section 4.2. The key measurements for both these variables are the body mass on the first evening of fuelling and the body mass on the final evening. For Sedge Warblers attending the feeders in 2001 and 2002, the same method of calculation described for Reed Warblers in section 4.2 was used. In 2003, all Sedge Warblers had mass recordings up until sunset on both their first and last evenings at the feeders. This mirrors the situation for Reed Warblers in 2002 and so the evening mass was calculated taking the average of all mass recordings in the half hour before the final feed. For justification of this method see section 4.2. The calculation of lean body mass estimates for Sedge Warblers is described in section 3.2. As the wing length of Sedge Warblers attending the feeders was unknown, the LBM estimate for the mean wing length of birds caught at Icklesham was used (mean wing length = 65mm, LBM = 9.55g).

The hourly FDRs of birds were calculated by taking the first mass recording in the morning and the first mass recording in the evening and dividing by the number of hours between: giving a rate in grams per hour. All recordings were greater than 7.5 hours apart (mean time ± S.D = 10.43 ± 0.84).

The accurate estimation of departure loads depends on how certain one can be that a bird left on the evening after which it no longer attended the feeder. Sedge Warblers made an average of 9.6 visits (StDev = 3.6, Min = 4, Max = 16) over two hours of filming on their last day. Given this rate of visitation, the probability of a bird making no visits to a feeder the following day is significant at p = 0.003, if one models the visitation rate as a normal distribution. Therefore, it is very unlikely that a bird remained at the site after it ceased to use the feeder.

**Optimal Migration Models**

Details of the energy-minimising and time-minimising models presented in this chapter are described in section 4.2. Predictions were generated using the same methods described in that section. Two additional time-minimising models are illustrated in
section 5.3 of this chapter. The predictions from these models were not generated but modified from figures 2a and 3 of Weber & Houston (1997). The key differences between these models and the time-minimising model described in section 4.2, is that the migratory distance is considered finite and that FDRs are not expected to be constant along the migratory route.

All the models described so far assume that migrants start fuelling with a body mass equivalent to their LBM. Sedge Warblers did not start fuelling at their LBM and in order to make comparisons to the models possible, a value of 11g was chosen for LBM in the calculation of departure loads presented in Fig. 5.3. This is the approximate start mass of five of the Sedge Warblers that attended the feeders but probably underestimates the start mass of some of the birds. In a different approach, I raised the model predictions in Fig. 5.4 by 1.5g in order to account for the fuel load that experimental birds already had, without altering the ‘true’ departure load of these birds. Thus departure loads differ between Fig. 5.3 and 5.4, with those presented in Fig. 5.4 being the most realistic values. The models only provide a guide to the strategy adopted by migrants and thus small discrepancies caused by different starting points will not affect the conclusions drawn. All other figures use data based on the value of LBM described in section 3.2.

**Estimating Fuelling Durations**

All Sedge Warblers attending the feeders increased in mass on all the days that they were present at the feeders. Therefore the start of the fuelling period was considered as the first day on which they appeared at the feeder, whilst the end of the fuelling period was the last day on which they were present. The fuelling duration was therefore calculated as the number of days a bird was present at a feeder. Of the 15 birds for which fuelling durations were calculated, 13 birds were estimated to have begun fuelling at the feeder with a low level of reserves (body masses of between 10-12g), which may have been accumulated at another site prior to arriving at Icklesham. I am therefore confident that the fuelling duration of these birds is fairly accurate. The other two individuals began fuelling with a medium level of reserves (body mass of 14-15.5g) and may have already been fuelling for three to six days under natural conditions. Alternatively they may have gained the fuel at another site. I have taken the possible inaccuracy in the fuelling durations of these birds into account when interpreting the data.
5.3 RESULTS & DISCUSSION

Departure Load as a function of Fuel Deposition Rate

The relationship between departure load and fuel deposition rate is the key prediction of the optimality models and may inform us about which currency governs a migrant’s fuelling behaviour. Both FDR and departure load may be influenced by other factors that must be taken into account when interpreting the relationship between the departure load and FDR.

Year was found to have no affect on FDR (Mann-Whitney, N = 13, w = 19, P = 0.27), however, the small sample size may have reduced the probability of detecting an effect. Departure load did differ between years (Mann-Whitney, N = 13, w = 25, P = 0.018), however, when three birds that had extremely high values for departure load were removed, significance was lost (Mann-Whitney, N = 10, w = 25, P = 0.11, see also Fig. 5.1). Time of year may affect both the final departure load and the FDR of migrants, especially if they are time-minimising. The departure load of Sedge Warblers showed no relationship with date after controlling for year (ANOVA, F_{2,10} = 0.91, P = 0.363), but increased with date in 2003 (Regression, F_{1,5} = 15.61, P = 0.011, adjusted R² = 70.9%). The relationship found in 2003 may have occurred by chance as the sample size was very small, but may also reflect a propensity to attain higher fuel loads as the time available to complete the migratory journey decreases. Daily FDR showed no apparent relationship with date after controlling for year (ANOVA, F_{2,9} = 0.63, P = 0.449). Sample sizes were small in the above three analyses and therefore the power to detect any effect was low, therefore I cannot rule out relationships between either pair of variables.

Decreasing day length with date may lead to increases in hourly rates of gain by way of compensation for reduced feeding time (section 4.3). No such relationship was found for Sedge Warblers (Regression, F_{1,35} = 0.62, P = 0.438, adjusted R² = 0.0%).

As neither FDR nor departure load showed a significant relationship with date, I did not consider date when interpreting the relationship between the departure load and FDR. Birds were combined across years, as there was no significant difference in FDR and the differences in departure load (see above) were dealt with by separating the data into two distinct groups (see below). Fig. 5.1 shows the relationship between FDR and departure load for 12 Sedge Warblers for which both the FDR and departure load could
FIGURE 5.1: Relationship between the fuel deposition rate and departure load of 11 juvenile Sedge Warblers (squares) and one adult (triangle) attending *ad lib.* feeders at Icklesham. Year of attendance is differentiated by colour: grey = 2001, black = 2002, white = 2003. The dotted line separates the two subsets of birds that showed strategic differences with respect to the time spent fuelling (a difference that leads to the observed differences in departure load). Note that the departure load at which this line is placed, is estimated to be sufficient for reaching the Sahel without refuelling (section 5.1). The solid regression line is from the analysis of the nine birds in subset A: Departure load = 0.326 + 2.4*Fuel Deposition Rate.
FIGURE 5.2: Fuelling curves of 11 juvenile and one adult Sedge Warbler that attended *ad lib.* feeders in the autumns of 2001-2003. Markers represent the final body mass recording made each evening, except for those birds for which the morning mass on their first day is marked. Note the two individuals that start at body masses above 15g and presumably had been fuelling on a natural food source before discovering a feeder. The horizontal line at 20g indicates the mass above which Sedge Warblers can theoretically make a flight to the Sahel from southern England without refuelling (section 5.1): it also serves to differentiate between individuals in subsets A and B.
be calculated. A regression analysis of the data in its raw form suggested that there was not a significant relationship between FDR and departure load (Regression, $F_{1,10} = 3.08$, $P = 0.110$, adjusted $R^2 = 15.9\%$). However, the data suggest that there were two different groups of birds as I predicted in section 5.1: one that had departure loads below 90% (9 birds) and the other with loads in excess of 110% (3 birds) (Fig. 5.1). The difference between these two groups is further highlighted in Fig. 5.2, where the extended fuelling durations of the birds in the second group are also evident (mean = 7 days vs mean = 2.5 days). The differences between these groups were not caused by a significant difference in start mass (Mann Whitney test, $w = 56$, $P = 0.71$) or the start date of fuelling (Mann Whitney test, $w = 53$, $P = 0.35$). This suggests that birds adopted two different strategies and should therefore be analysed separately. From here on I shall refer to two subsets of birds: subset A with fuelling durations of 4 days or less and subset B with fuelling durations of 5 days or more.

The sample sizes were only sufficient for an analysis of subset A. For that subset, departure load increased significantly with FDR (Departure load = 0.326 + 2.4*FDR, $F_{1,7} = 7.12$, $P = 0.032$, adjusted $R^2 = 43.3\%$). This positive relationship (see Fig. 5.1) between FDR and departure load for birds in subset A is consistent with the time- and energy-minimising hypotheses but not the cost of transport hypothesis.

**Model Predictions**

Subset A of Sedge Warblers had a relationship between their FDR and departure load that is consistent with either time-minimising or energy-minimising behaviour. Both these currencies may be minimised using either a local or a global rule for the interpretation of variation in FDR (see section 4.1). The fit between the Sedge Warbler data and the model predictions in Fig. 5.3, which were generated using a global rule, suggested that Sedge Warblers used a global rule. Birds adopting a local rule would show a considerably steeper relationship between the two variables (section 5.3). Indeed, even the three birds in subset B did not accumulate large enough fuel loads to conform to the predictions of a model incorporating the local rule.

Fig. 5.3 shows the relationship between the raw data and the model predictions for both time- and energy-minimising scenarios. Unlike in the case of Reed Warblers (section 4.3), it is not possible to determine exactly which of the two currencies were influencing the fuelling decisions of Sedge Warblers in subset A. Which ever currency
FIGURE 5.3: Model predictions for a time-minimising model (black lines) and an energy-minimising model (blue lines). The black and blue numbers adjacent to the right hand axis represent the stopover cost in days used to generate the black and blue lines respectively. For the time minimising predictions, the energy cost of stopping over was held constant at 3% of LBM, except for the model where the cost in days was 0.1 and the energy cost was set to zero (this model approximates to a cost of zero days which cannot be modelled as the value of the cost must be divisible in the calculations). For the energy minimising models, the predictions arising from a time cost of 2 days were generated using an energy cost of 3% of LBM and ‘maximising’ values for the other variables in the model, \( a \) and \( q \) (see section 4.2). The second energy minimising prediction gives a more realistic scenario in which the energy cost is still 3% but the value for \( a \) is 0.5 and the value for \( q \) is \( 3.063 \times 10^4 \) kJ kg\(^{-1}\) (assumes that the fuel store is 75% fat and 25% protein, as suggested by Klaassen & Biebach (1994) and Hedenström & Alerstam (1997)). The raw data is divided into subsets A (black squares) and B (white squares). N.B. Departure masses are lower than their ‘true’ values in order to be consistent with the methods used to calculate the model predictions (see section 5.2).
FIGURE 5.4: Qualitative predictions of two alternative time minimising models adapted from Weber & Houston (1997). Model 1 (solid line): departure fuel load as a function of FDR when FDR is increasing along the route. Model 2 (dotted line): departure fuel load as a function of FDR when FDR is decreasing along the route. In both cases the distance to the migratory goal is finite, rather than infinite as in Fig. 5.3, which leads to the stepped function. The experimental Sedge Warblers in Subset A are marked in black and are expected to fit model 1 whilst those in subset B are marked in white and are expected to fit model 2.

TABLE 5.1: Fuelling durations in days of Sedge Warblers at Icklesham. The table is divided into the two subsets of birds: A) those that fuelled for four days or less, B) those that fuelled for five days or more.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>MEAN</th>
<th>ST. DEV.</th>
<th>SE MEAN</th>
<th>LOWER QUARTILE</th>
<th>UPPER QUARTILE</th>
</tr>
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<tbody>
<tr>
<td>A</td>
<td>12</td>
<td>2.5</td>
<td>1</td>
<td>0.29</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Duration 1-4 days</td>
<td></td>
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<tr>
<td>B</td>
<td>3</td>
<td>7</td>
<td>1.73</td>
<td>1</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Duration 5-8 days</td>
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</table>
the birds were minimising, it is apparent that the stopover cost incurred by these birds was low, accounting for one day or less of the stopover duration.

The birds in subset B were clearly not minimising energy and did not appear to fit the time-minimising predictions presented here: a stopover cost of three or more days is unlikely, especially when one considers that birds in subset A fitted a model with a cost of one day or less. However, such high departure loads are likely to be a function of time-minimisation in one form another, with the discrepancy being caused by birds adopting a local rule (see above) or having a low expectation of future fuelling conditions.

In Fig. 5.4, I have presented two alternative models adapted from Weber & Houston (1997) that may be appropriate for interpreting the fuelling behaviour observed in Sedge Warblers. The first model assumes that birds have a fixed expectation of higher FDRs at future stopover sites, or at least that high FDRs will be encountered at some future stopover sites. This model, appears to fit some of the properties displayed by the Sedge Warblers in subset A and also ties in with present knowledge of where Sedge Warblers experience high FDRs and undergo extensive fuelling (section 5.1 & 5.4). The second model describes a situation in which birds have a fixed expectation of FDRs decreasing along the route. The predictions show similarities to the behaviour of birds in subset B. This apparent duality in strategy is discussed in detail in section 5.4.

The ‘step’ relationship resulting from Weber & Houston’s (1997) models is predicted if migratory strategies have been optimised with respect to a set distance to the migratory goal (finite distance models). This aspect of the models was not supported by the Sedge Warbler data (Fig. 5.4). However, if the finite distance assumption is removed, smooth curves with slopes of different magnitude are expected, which would best explain the Sedge Warbler data.

**Fuelling Duration**

Birds minimising either time or energy are predicted to show a distinctive relationship between their FDR and the number of days spent fuelling (Fig. 5.5). With regards to the Sedge Warblers in subset A, fuelling durations approximated to optimal durations at high FDRs but birds with low FDRs did not fit the predictions of the models. Further, there is no evidence for the predicted decrease in duration as FDR increases, for subset A (Regression, $F_{1,8} = 1.39$, $P = 0.273$, adjusted $R^2 = 4.1\%$). This
FIGURE 5.5: Relationship between FDR and optimal stopover duration ($t^*$, expressed in days), as predicted by a time-minimising model when $t_0 = 1$ day and $f_0 = 0.03$ (black line). The fuelling durations for Sedge Warblers are presented for comparison: birds in subset A are marked by black squares and by white squares for birds in subset B. N.B. the bird marked in white with a duration of five days arrived at the feeder with a body mass of >15g, suggesting that the bird had already been fuelling for a number of days.

FIGURE 5.6: Comparison of the constant fuelling duration model (solid and dotted lines) and a time minimising model (solid line with white points). The lines for the constant fuelling duration models represent the predictions arising from durations of 2, 3 and 4 days from bottom to top of the graph. Only Sedge Warblers in subset A are figured (black squares).
supports the hypothesis put forward in section 4.4 that fuelling behaviour may be controlled by a fixed fuelling/stopover duration (see also Table 5.1). For a comparison of the predictions from a constant fuelling duration model and a time-minimising model, see Fig. 5.6.

Table 5.1 includes a further three individuals in subset A which are not included in Fig. 5.5, as one of the variables could not be calculated. The additional three individuals support the conclusion that a shorter fuelling duration was the commonest strategy amongst Sedge Warblers at Icklesham. The three Sedge Warblers in subset B (Fig. 5.5, white points) have lengthier durations than predicted by the models, suggesting that their fuelling behaviour was being influenced by an additional factor.

**Variation in Fuelling Rate between Days**

A constant FDR between days is one of the underlying assumptions of the optimal modelling approach. A declining FDR across the fuelling period has been predicted under two main scenarios: (1) if metabolic demands increase as body mass increases; (2) if FID and MD predation risk are acting together (section 4.1).

At a population level, Sedge Warblers showed a gradual decrease in hourly FDR and daily mass gain (evening to evening, thereby including overnight mass loss) as departure approached (Fig. 5.7; result of ANOVA: hourly FDR, $F_{1,27} = 6.54$, $P = 0.016$; daily mass gain, $F_{1,23} = 10.97$, $P = 0.003$). No trend was found in the intake rate of mealworms as departure approached (ANOVA, $F_{1,30} = 1.41$, $P = 0.245$).

When individual birds were nested within ‘day relative to departure’, hourly FDR still decreased as departure approached (ANOVA, $F_{9,11} = 4.40$, $P = 0.012$) but the change in daily mass gain became marginally non-significant (ANOVA, $F_{8,9} = 2.62$, $P = 0.087$).
FIGURE 5.7: Variation in three variables with day relative to departure: hourly FDR, daily mass gain and intake rate (of mealworms). Boxes define the median and inter-quartile ranges, black dots the population mean and whiskers show the total range for nine Sedge Warblers attending *ad lib.* feeders. The departure day = 0. Note: sample size varies between days.
5.4 GENERAL DISCUSSION

The brief period in which aphids are superabundant in northern European reedbeds (Bibby & Green 1981) suggests that time could be the most important currency under selection for Sedge Warblers on autumn migration. Further, Sedge Warblers breeding in northwest Europe winter largely in the Sahel region of West Africa (Morel & Morel 1992, Wernham et al. 2002) and seasonality in food abundance there may produce an additional time pressure. The erratic Sahelian rainy season lasts from June to October, producing a single annual flush of invertebrates that rapidly dwindle in numbers after the rains. Sedge Warblers undergo a complete moult on arriving in the Sahel and therefore require a good food supply to fuel this energetically demanding process (Jenni & Winkler 1994). Late arrival in this region may therefore compromise the ability of birds to successfully complete their moult before the onset of the dry season (Bensch et al. 1991). The combined action of these two pressures suggests that Sedge Warblers should be particularly time stressed and therefore one might expect the signature of time-minimisation in their fuelling behaviour.

Optimisation of Sedge Warbler Fuelling Behaviour

One of the key predictions of time-minimising models is a positive relationship between departure load and FDR of birds on stopover (Alerstam & Lindström 1990, Hedenström & Alerstam 1997). Food supplemented Sedge Warblers in subset A demonstrate such a relationship, but the shallowness of the observed relationship could also be a consequence of selection for energy-minimisation. The high departure loads of Sedge Warblers in subset B, however, could only be a consequence of time-minimising behaviour. Further, if birds expect to encounter higher FDRs at future stopover sites then they are predicted to have a shallower relationship between their FDR and departure load under a time-minimising model (section 5.1). Only a low percentage of Sedge Warblers passing through southern England fuel extensively, whilst at sites in northern and western France a higher percentage of birds do so, indicating improved fuelling conditions in this region (Bibby & Green 1981). If this picture is accurate, the shallow relationship between FDR and departure load for birds in subset A supports theoretical predictions that hard wired expectations of future FDRs can influence time-minimising behaviour. Conversely, the high departure loads of birds in subset B support
theoretical predictions concerning the optimal behaviour of birds that have a low expectation of future FDRs. Whilst this may seem strange, as many migrants find suitable fuelling opportunities in southern Europe, reedbeds in southern Europe senesce earlier than those in northern Europe and thus aphid supplies would be low by the time Sedge Warblers reached these areas.

A direct comparison of the relationship between FDR and departure load of Sedge and Reed Warblers can be seen in Fig. 5.8. This highlights the shallowness of the relationship observed in Sedge Warblers and demonstrates how fuelling strategies can differ if hard-wired expectations of future conditions vary between species (Reed Warblers are hypothesised to have a constant expectation of future conditions).

**Behavioural Control of Time-Minimising Behaviour**

Our current knowledge of Sedge Warbler migration and the evidence from this study point strongly to selection for time-minimisation being one of the key determinants of Sedge Warbler fuelling behaviour and therefore their overall migratory strategy. However, the fuelling behaviour of Sedge Warblers in subset A does not appear to mirror the behaviour of ‘true’ time-minimising birds. Migrants achieving true time-minimisation are predicted to increase their fuelling/stopover duration as their FDR decreases. Sedge Warblers, as was also the case for Reed Warblers (section 4.3), did not appear to respond to their FDR in such a precise way: in both cases this was most striking for birds with low FDRs. Indeed, as I argued for Reed Warblers (section 4.4), it would appear that Sedge Warblers have a constant fuelling duration which means that they do not achieve ‘true’ time-minimising behaviour but approximate to it fairly accurately (Erni et al. 2002). The constant fuelling duration model appeared to fit the data better than a ‘true’ time-minimising model, especially if there is small degree of variation in duration between birds (Fig 5.6).

Variation in the length of a ‘fixed’ duration may be present for a number of reasons. Firstly, unfavourable weather conditions on the final evening of the period may result in delayed departure and consequently longer durations (section 6.1). Secondly, the energetic status of a bird at the start of a fuelling period could influence its duration, especially if a bird already has a large fuel reserve from a previous fuelling stage. Finally, there might be heritable variation in this trait. This is likely if food availability shows considerable fluctuations between years (see Bibby et al. 1976), such that in
FIGURE 5.8: Comparison of the relationship between the fuel deposition rate and departure load of food supplemented juvenile Sedge and Reed Warblers at Icklesham. Reed Warblers (white squares), regression line: departure load = 0.326 + 4.54*FDR. Sedge Warblers (black squares), regression line: departure load = 0.326 + 2.40*FDR. The slopes of the regression lines are significantly different (one-sample t-test, $t_8 = -7.16$, $P < 0.05$) but the intercepts are not (one-sample t-test, $t_8 = 0.01$, $P > 0.05$). The birds included in this comparison were fuelling in order to reach sites where they would begin fuelling to make long haul flights to south of the Sahara. Extensive fuelling by two juvenile Sedge Warblers in subset B suggests they had already reached such a site and were therefore at a different stage in their migration. Consequently they have not been included in this comparison.
some years longer or shorter durations are favoured, relative to the population mean. For example, when aphid supplies are high in much of northern Europe, birds with a shorter fuelling duration will have a faster overall migration and therefore may have a competitive advantage over birds with longer fuelling durations, as they will reach the wintering grounds earlier. Conversely, in a poor aphid year, birds with shorter durations will have to make more stops and if a stopover cost exists, will have a lower overall speed of migration.

**Daily Variation in FDR**

Like Reed Warblers (section 4.1), Sedge Warblers had lower FDRs as the day of departure approached. A constant FDR between days is one of the assumptions of the optimal migration models (Alerstam & Hedenström 1997), therefore this assumption must be relaxed in future models. More importantly though, this pattern can tell us about variables that influence FDRs. Food supplemented Sedge Warblers demonstrated a gradual decrease in both their hourly FDR and daily FDR, yet their intake rate of mealworms remained constant. Whilst minimising both mass dependent and foraging-intensity dependent predation risk might explain this, it seems more likely that rising metabolic costs associated with an increasing fuel store, caused a gradual decrease in FDR. In contrast, the hourly FDR of Reed Warblers only declined significantly on the day of departure; presumably because additional metabolic costs were compensated for by increasing intake rate (Fig. 4.3.8).

That Sedge Warblers were apparently unable to compensate for a rise in metabolic expenditure and that their intake rate remained constant, suggests that Sedge Warblers were already fuelling at maximum rates. Maximum rates are predicted if birds are time-minimising (Lindström & Alerstam 1990), especially if the associated cost in terms of increased predation risk is ignored. Minimising time rather than predation risk may increase mortality rates in Sedge Warblers relative to Reed Warblers during migration, contributing to the shorter life spans observed in Sedge Warblers (Peach et al. 1990).

**Dual Strategies**

It has long been documented that Sedge Warblers adopt two different fuelling strategies at sites in southern England, with the majority of birds only making small fuel
gains and stopping for short times whilst a small proportion of birds make long stops and large fuel gains (Bibby et al. 1976). In my study, this duality in strategy was also apparent and, despite having access to an unlimited food supply, only 20% of birds fuelled extensively. Thus the cue for extensive fuelling does not appear to be food availability alone, as was previously thought (Bibby et al. 1976, Bibby & Green 1981). Instead, I hypothesise that a combination of high food availability and a geographic cue are probably responsible for triggering this behaviour. The low frequency of this behaviour in southern England suggests that there may have been selection for a polymorphism. The highly variable occurrence of abundant aphid crops between years and sites could have resulted in selection for a number of alleles that promote extensive fuelling in different regions. Frequency dependent selection could also be acting, if increasing competition prevents birds from accumulating sufficient fuel to reach the Sahel, as an allele for fuelling in southern England becomes commoner.

A second alternative is that the cue to initiate extensive fuelling is embedded within a time programme such that a typical bird will be in northern France when the cue comes, whilst later migrating birds are more likely to fuel at increasingly northerly sites. Such a rule could be actively selected for as reedbeds senesce earlier in southerly latitudes, directly affecting aphid abundance (Bibby & Green 1981). Therefore a late migrating bird should encounter higher aphid abundance if it were to remain in southern England rather than continuing southwards. However, I found no statistical support for late migrating birds being more likely to fuel extensively.

**Summary**

The migratory strategy of Sedge Warblers appears to be driven by a time pressure arising from the temporal changes in food availability in northern Europe (aphids in reedbeds) and their Sahelian wintering grounds (rainy season invertebrates). Ultimately, Sedge Warblers adopt a high-risk strategy that is dependent on a highly variable food source, both in time and space, and expose themselves to a high level of predation risk by fuelling at maximum intensities and compromising their escape ability by grossly increasing their body mass. The success of Sedge Warbler migration is likely to be highly sensitive to climate change, just as their over-winter survival is sensitive to erratic rainfall in the Sahel (Peach et al. 1991). Hotter summers in northern Europe are known to reduce aphid crops (Bibby & Green 1981), and were these to become more
frequent, Sedge Warblers may be forced to fuel up further and further north and make increasingly longer flight stages without refuelling, or adopt a new strategy.

The positive relationship found between FDR and departure load, generated through an apparently fixed stopover duration, and the maximal FDRs observed in Sedge Warblers, can only suggest that hard-wired behaviours can give rise to time-minimising behaviour in a migratory passerine. Furthermore, this fuelling behaviour can be selected and refined such that it is optimal with regards to future fuelling conditions, allowing migrants, unbeknownst to them, to see into the future and successfully complete their migration.
CHAPTER 6

THE DECISION TO DEPART – IS WEATHER IMPORTANT?

6.1 INTRODUCTION

Fuelling phases have been recognised as a crucial influence on the time course and organisation of a migratory journey (Alerstam & Lindström 1990), but they are not necessarily the overriding influence nor are they the most hazardous phase. During every migration season, there is clear evidence that birds make mistakes during flight phases. These mistakes can have severe consequences for both survival and future reproductive success. From Europe to the Americas to South-East Asia, the occurrence of ‘falls’ is recognised (Elkins 1988). A typical fall occurs when large numbers of birds have encountered adverse weather conditions whilst making a sea crossing, causing them to land exhausted on the first piece of land they reach. It is clear from reports of numerous dead birds being washed up on beaches in adverse conditions, that not all birds make landfall (Elkins 1988). It is also evident that adverse conditions can cause birds to be blown a long way off course: every autumn, large Atlantic depressions off North America blast birds, ‘intending’ to winter in South America, across the ocean to make landfall on the Atlantic coasts of Europe (Elkins 1988, Alerstam 1990). Even if these birds survive there is little chance of them re-crossing the Atlantic or of encountering a mate in Europe (some wildfowl and waders excluded).

The Importance of Wind

Such threats to survival and reproductive success are expected to have selected for birds to avoid adverse conditions when initiating a flight but less dramatic factors may also have shaped departure decisions. During stopover phases, migrants are expected to remain at fuelling sites until they have optimised their fuel load, with respect to a currency such as time, and then initiate a migratory flight (Alerstam & Lindström 1990, Hedenström & Alerstam 1997). However, the decision to depart may
not only depend on the level of fuel stored and the probability of encountering adverse conditions but also on whether the flight conditions allow the fuel load to be used to its maximum potential. Indeed, we have long known that the intensity of migration varies with subtle differences in wind direction and strength, and with levels of cloud cover and precipitation (Able 1973, Richardson 1978, Alerstam 1979, 1990, Elkins 1988). Of the various weather variables, wind is likely to be a key factor. If the wind is blowing against a migrant, it will have to increase its energy expenditure in order to maintain forward flight and the additional loss of energy will reduce the potential flight range for a given fuel load (Liechti & Bruderer 1998).

Theoretical work has shown that not paying attention to wind direction and strength could have a dramatic impact on flight range and therefore wind should be a key factor in shaping optimal departure decisions (Liechti & Bruderer 1998). Indeed, it has been argued that optimising a departure decision with respect to wind can, in some cases, be more important than optimising fuelling behaviour whilst on stopover. Using real wind data from various part of Europe, it has been shown that leaving at random could in some cases cost a migrant up to 60% of its potential flight range (Liechti & Bruderer 1998).

It is intuitive that the extent to which wind-driven departure decisions will determine fuel loads depends on the frequency of favourable winds. If wind conditions are often unfavourable for example, then a bird may depart during a window of favourable conditions regardless of whether it has optimised its fuel load with respect to time (section 4.1). Conversely, if favourable conditions are the norm, then other factors may be more important in deciding the departure day and departure load. Thus the variability of wind conditions is likely to determine a migrant’s sensitivity to wind. Further, as fuel load increases so does the potential difference in flight range, thus sensitivity to wind conditions is expected to increase with fuel load (Liechti & Bruderer 1998).

Modelling of Optimal Departure Decisions

Weber, Alerstam & Hedenström (1998) developed these ideas further and suggested that a ‘departure window’ may exist. During the departure window, birds are expected to depart as soon as favourable conditions arise whilst continuing to fuel in the meantime. If the end of the departure window is reached without such conditions
arising, a bird is predicted to depart regardless of conditions. Modelling departure
decisions within the framework of time-minimisation, has shown that the departure
window should commence on different days depending on the probability of favourable
winds (Weber, Alerstam & Hedenström 1998). The higher the probability, the closer the
first departure will be to the day predicted by wind-free time-minimising models, whilst
lower values may result in departures 1 or 2 days before (Fig. 6.1).

Regardless of the probability of favourable conditions, this model leads to
deviations from the relationship between the FDR and the departure load predicted by
wind-free models of stopover behaviour (Alerstam & Lindström 1990, Hedenström &
Alerstam 1997, see section 4.1). When favourable winds are rare, the majority of birds
are predicted to depart with fuel loads just below the optimum predicted by wind-free
models, whilst a smaller percentage may leave with greatly elevated loads. As
favourable conditions become more common, the mean departure load approaches the
wind-free optimum and the number of birds departing with elevated loads decreases. In
cases, except when the probability of a tailwind occurring is very low, all birds are
expected to leave with a tailwind. An important prediction from this model is that
variability in departure load will increase with increasing FDR. Further, Weber,
Alerstam & Hedenström (1988) suggest that if departure windows are short, then birds
with the highest fuel loads are likely to leave in less favourable conditions at the end of
the window, relative to birds with lower loads that encountered favourable conditions
during the window.

A later model extended that of Weber, Alerstam & Hedenström, by modelling
the effects of correlated winds, i.e., situations in which wind direction changes little
between successive days due to a prevailing weather system (Weber & Hedenström
stochastic factor. The implications of Weber & Hedenström’s model on fuel loads were
qualitatively and quantitatively similar to Weber, Alerstam & Hedenström’s (1998)
model, although deviations from the wind-free optimum were reduced. Decreasing
correlation between winds has the same affect as an increasing probability of favourable
winds. Whether birds can actually use current weather conditions to form an expectation
of future wind conditions is unclear, although birds departing from North America fly
through decaying fronts and reach the predictable and favourable trade winds on the
other side (Williams & Williams 1990, Nisbet et al. 1995). Whether or not departure
FIGURE 6.1: Probability of a bird leaving a stopover site with respect to the occurrence of favourable winds. All departures occur in favourable winds but the probability of favourable winds is either high \( (p = 0.6) \) or low \( (p = 0.25) \). The situation is modelled when FDR = 0.04, the wind assistance factor = 1.2, and the stopover cost = 2 days. (Figure adapted from Weber, Alerstam & Hedenström 1998). The probability of departure should be equivalent to the proportion of birds that leave on a given day.
decisions have evolved to account for correlated winds, the predictions from these wind driven models of stopover behaviour are still unique and testable.

**Empirical Studies of Departure Decisions**

A number of tests of the relationship between weather conditions and departure decisions have been carried out. Fransson (1998b) looked at the departure decisions of Whitethroats attending an *ad lib* food source. A sample of 28 Whitethroats showed no correlation between departure and the wind conditions at ground level and only showed a slight but non-significant tendency to depart with reduced cloud cover. Danhardt & Lindström (2001) examined the departure decisions of European Robins from southern Sweden and also found no correlation with wind conditions. Most Robins, however, departed on a day with more favourable conditions than on the previous day or the day after departure. The authors argued that as the winds were rarely ‘favourable’ over southern Sweden, the birds were in fact choosing the best conditions available, by limiting the headwind component. The Robins also departed on days when air pressure was increasing which the authors present as evidence for birds using increasing pressure as an indication of improving weather.

Butler *et al.* (1997) looked at the departure decisions of Western Sandpipers *Calidris mauri* and in contrast to the studies on passerines described above, they found a significant correlation between departure decisions and wind conditions. In fact Butler *et al.* argued that wind was the main determinant of stopover length in Western Sandpipers and that FDRs were relatively unimportant. A further study by Åkesson & Hedenstrom (2000) used radiotransmitters in order to track individual birds of four species (*Luscinia luscinia, Erithacus rubecula, Turdus merula* and *T. philomelos*) and thus pinpoint the exact timing of departure. The authors found a strong association between departures and the occurrence of tail winds, despite headwinds predominating during the departure period.

When relating weather conditions to departure decisions, the timing of the decision to depart is crucial. Recent data suggest that there are preparations beyond fuelling that are undertaken before a flight phase commences. The Bar Tailed Godwit (*Limosa lapponica*, a migratory non-passerine) was found to dramatically reduce its digestive apparatus prior to departure (Piersma & Lindström 1997). However, similar pre-flight reductions have yet to be demonstrated in migratory passerines, although
some migrants using artificial food sources reduce their FDR on the day of departure, which may be associated with preparations for flight (Klaassen & Biebach 1994, Fransson & Weber 1997, Fransson 1998b, my study). If passerines make such preparations, it suggests that the decision to depart could be made a day earlier, rather than just after sunset when most flights initiated (Åkesson et al. 2001).

Summary

Despite the theoretical importance of wind conditions on stopover length and departure decisions, and the consequent effect on fuel loads, there is still a limited body of empirical work testing these predictions. Indeed, none of the previous studies have linked delayed departures to inflated departure loads as predicted by the models (Weber, Alerstam & Hedenström 1998, Weber & Hedenström 2000). In this chapter, the departure decisions and fuel loads of 34 Reed Warblers and three Sedge Warblers attending an artificial food source were related to the weather conditions around the time of departure.

A radio tracking study on actively migrating Reed Warblers has already been carried out in southern Sweden (Åkesson et al. 2001 & 2002). The departure decisions of these Reed Warblers were found to be related to cloud cover and thus the availability of celestial cues, and were significantly correlated with rising air pressure. Further, there was significantly less precipitation on departure nights. However, there was no significant association between departure decisions and wind assistance, with only 11 of 21 Reed Warblers, which departed in the preferred migratory direction, selecting tailwinds (Åkesson et al. 2002).

Given the preference for low levels of cloud cover and rising air pressure found by Åkesson et al. (2002), I expected to see similar preferences in the Reed Warblers in my study. Further, variation in the departure loads/fuelling durations outlined in section 4.4 may have been explained by delays due to unfavourable departure conditions. Therefore, I investigated interactions between fuelling durations and the weather conditions at, and prior to, departure. It was unclear as to whether my experimental Reed Warblers would be sensitive to wind conditions but as all the Reed Warblers that attended the experimental set up reached high fuel loads (section 3.3), I expected, as Liechti & Bruderer (1998) predicted, that the experimental birds should be particularly sensitive to wind conditions.
6.2 METHODS

Study Site

The experiments described in this chapter were carried out at Icklesham (N50°54’, E0°41’); for a full site description see section 2.2.

Experimental Birds

During the years 2001 and 2002, feeders containing mealworms were set up in the reedbed at Icklesham (see sections 3.2 & 4.2). Reed Warblers attending the feeders were weighed on an electronic balance every evening of their stay and regularly in the morning. Individual Reed Warblers could be identified using a range of characters (see section 3.2 for more details).

The timing of departure for individual Reed Warblers was taken as the evening after which they no longer appeared at the feeder. To minimise the chance that birds had simply left the feeder but not the study site, only birds that had regularly visited a feeder for at least three consecutive days including the day of departure were included. Body mass on the night of departure was calculated by two different methods depending on the year in which the bird attended the feeder (see section 4.2). The hour of departure was taken to be two hours after local sunset, based on the study by Åkesson et al. (2001) in which the mean time of departure for 28 Reed Warblers was 128 minutes after local sunset.

Data on 34 Reed Warblers were used in the following analyses; all were juveniles that attended ad lib feeders except for one adult at an ad lib feeder and two adults and four juveniles that attended half rate feeders (section 4.2). Three Sedge Warblers that attended ad lib feeders in 2002 were also examined.

Weather Data

Weather data for August and September of the years 2001 and 2002 were obtained from the Metrological Office. The data were collected at the Herstmonceux
station (N50°89´, E00°32´, altitude 52m), which was approximately 25 km from the study site. The data included hourly recordings of wind strength and direction, cloud cover, precipitation, air pressure at sea level and air temperature. Weather conditions recorded closest to the time of sunset plus two hours were used as the representative conditions for the time of departure (based on Åkesson et al. 2001).

The migratory direction of birds departing from Icklesham was taken as 225º (southwest), which is approximately the mean direction of Reed Warblers ringed in Britain and later retrapped in southern Europe (Wernham et al. 2002). Therefore a ‘perfect’ tailwind would come from 45º, the opposite compass direction to 225º. To calculate the head or tail wind component, the methods laid out in Fransson (1998b) were used. Firstly v was calculated which was the deviation from 45º for winds between 337.5º and 112.5º, and the deviation from 225º for winds between 157.5º and 292.5º. The component was then calculated as follows: cos (v) x observed wind speed (m/s). Observations between 112.5º - 157.5º and 292.5º - 337.5º resulted in zero values as they correspond to cross winds. Components resulting from winds between 157.5º and 292.5º were assigned negative values as they correspond to headwinds.

To analyse the preference of Reed Warblers for rising or decreasing air pressure, the air pressure difference between the expected time of departure and 12 hours before was calculated. If air pressure changed by more than one millibar, it was scored as -1 for decreasing and +1 for increasing. If the change in air pressure was less than 1 millibar, a score of 0 was given.

**Statistical Methods**

Chi-squared statistics have been used throughout this chapter. The calculation of expected values is described in the relevant body of text and to calculate \( \chi^2 \) the standard equation was used: \( \frac{(\text{observed} - \text{expected})^2}{\text{expected}} \). Deconstructed Chi-squared tests were also used, following the methods laid out in Siegal & Castellan (1989).
6.3 RESULTS & DISCUSSION

Departures Decisions and Wind Conditions

Of the 34 Reed Warblers that attended the feeders, 24 departed with tailwinds, six in crosswinds, and four against headwinds (light in 3 cases < 2 m/s). Of the six birds that departed with crosswinds, conditions on the evening of departure were more favourable than on evenings a day either side in all six cases (see departures where wind component = 0 in Fig. 6.3). In five of these cases there were headwinds on the days either side and in the sixth case, there was a headwind the day before and a stronger crosswind on the day after departure. The frequency of birds departing in the three main wind conditions (head, cross and tail winds) was significantly different from the distribution of conditions if birds had left at random on any of the days during their stay (Chi-Squared test, $\chi^2 = 11.05$, $P = 0.004$, see Table 6.1). Inspection of the data reveals that this largely reflected an avoidance of headwinds (largest contribution to chi-squared, see Table 6.1). Deconstruction of the chi-squared analysis revealed that tailwinds were also linked with departures more often than would be expected ($\chi^2 = 5.84$, $P = 0.016$, see Table 6.2).

The majority of Reed Warblers departed with a positive wind component (Fig. 6.2). The mean wind component on departure days ($n = 23$) was $0.73 \pm 1.76$ m/s (tailwind). On non-departure days when fuelling birds were present ($n = 54$), the mean was $-0.44 \pm 2.85$ m/s (headwind). The difference in wind component between departure days and non-departure days was very nearly significant (data Box-Cox transformed, $t$-test, $t_{55} = 2.0$, $P = 0.051$). The non-significant difference between departure days and non-departure days is likely to be due to the regular occurrence of favourable wind components when birds were present at the feeders.

With the regular occurrence of favourable wind components, the association between departures and positive wind components could have happened by chance. To test this, wind component was divided into 12 categories and the frequency of occurrence of each wind component was calculated for when birds were present at the feeders (Table 6.3). The two years were treated separately at this stage. The expected number of birds in each category, if birds left at random, was then calculated by
TABLE 6.1: Frequency of the three main wind conditions whilst Reed Warblers were attending the feeders in 2001 and 2002. The expected frequency of birds leaving in each wind condition by year is given by multiplying the frequency of wind conditions by the number of birds present (2001 = 15, 2002 = 19). For the chi-squared statistic, the expected frequencies in each year were combined and compared to the observed frequencies for both years.

<table>
<thead>
<tr>
<th>Wind Condition</th>
<th>Frequency 2001</th>
<th>Frequency 2002</th>
<th>Expected 2001</th>
<th>Expected 2002</th>
<th>Joint Expected</th>
<th>Observed</th>
<th>(O-E)^2/E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Headwind</td>
<td>0.474</td>
<td>0.281</td>
<td>7.11</td>
<td>5.34</td>
<td>12.45</td>
<td>4</td>
<td>5.74</td>
</tr>
<tr>
<td>Crosswind</td>
<td>0.211</td>
<td>0.175</td>
<td>3.17</td>
<td>3.33</td>
<td>6.49</td>
<td>6</td>
<td>0.04</td>
</tr>
<tr>
<td>Tailwind</td>
<td>0.316</td>
<td>0.544</td>
<td>4.74</td>
<td>10.3</td>
<td>15.08</td>
<td>24</td>
<td>5.28</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$\chi^2$ (DF=2)</td>
<td>11.05</td>
<td></td>
</tr>
</tbody>
</table>

TABLE 6.2: Deconstructed analysis of the chi-squared test presented in Table 6.1.

<table>
<thead>
<tr>
<th>Wind Condition</th>
<th>Headwind</th>
<th>No Headwind</th>
<th>Tailwind</th>
<th>Crosswind</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed</td>
<td>4</td>
<td>30</td>
<td>Observed</td>
<td>24</td>
</tr>
<tr>
<td>Expected</td>
<td>12.45</td>
<td>21.55</td>
<td>Expected</td>
<td>15.08</td>
</tr>
<tr>
<td>$\chi^2_1$</td>
<td>6.08</td>
<td></td>
<td></td>
<td>5.84</td>
</tr>
<tr>
<td>$P$</td>
<td>0.014</td>
<td></td>
<td></td>
<td>0.016</td>
</tr>
</tbody>
</table>
TABLE 6.3: Frequency of wind components across 12 categories when Reed Warblers were present at the feeders in the years 2001 and 2002. The expected number of birds departing in each category was calculated by multiplying the frequency by the number of birds departing in each year (2001 = 15, 2002 = 19). To generate the final expected number of birds in each category, categories were amalgamated so that there were at least five birds in each category. The amalgamation of categories made the data more suitable for analysis using a chi-squared test. Exp. = expected, Obs. = observed.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt; -7</td>
<td>0.053</td>
<td>0</td>
<td>0.789</td>
<td>0</td>
<td>0.789</td>
<td>6.464</td>
<td>1</td>
</tr>
<tr>
<td>-6</td>
<td>0.053</td>
<td>0</td>
<td>0.789</td>
<td>0</td>
<td>0.789</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-5</td>
<td>0.079</td>
<td>1.184</td>
<td>0</td>
<td>1.184</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-4</td>
<td>0.079</td>
<td>0.018</td>
<td>1.184</td>
<td>0.333</td>
<td>1.518</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-3</td>
<td>0.079</td>
<td>0.053</td>
<td>1.184</td>
<td>1</td>
<td>2.184</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-2</td>
<td>0.053</td>
<td>0.035</td>
<td>0.789</td>
<td>0.667</td>
<td>1.456</td>
<td>5.974</td>
<td>1</td>
</tr>
<tr>
<td>-1</td>
<td>0.079</td>
<td>0.175</td>
<td>1.184</td>
<td>3.333</td>
<td>4.518</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0.211</td>
<td>0.175</td>
<td>3.158</td>
<td>3.333</td>
<td>6.491</td>
<td>6.491</td>
<td>10</td>
</tr>
<tr>
<td>1</td>
<td>0.079</td>
<td>0.333</td>
<td>1.184</td>
<td>6.333</td>
<td>7.518</td>
<td>7.518</td>
<td>10</td>
</tr>
<tr>
<td>2</td>
<td>0.053</td>
<td>0.105</td>
<td>0.789</td>
<td>2</td>
<td>2.789</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>0.158</td>
<td>0.105</td>
<td>2.368</td>
<td>2</td>
<td>4.368</td>
<td>7.552</td>
<td>12</td>
</tr>
<tr>
<td>4</td>
<td>0.026</td>
<td>0</td>
<td>0.395</td>
<td>0</td>
<td>0.395</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

FIGURE 6.2: Distribution of wind components on nights of departure by Reed Warblers attending feeders at Icklesham in the autumns 2001 and 2002 (black bars). The distribution of wind components on nights when Reed Warblers were present at the feeders is also presented (black line). Wind component was calculated as: cos (wind direction) x observed wind speed (m/s). Values of wind component >0 = tailwind, <0 = headwind, 0 = crosswind. Increasing values of wind component indicate increasingly favourable conditions for migration.
multiplying the number of birds departing in each year by the frequencies for each category. Comparing the expected distribution of wind components to the observed distribution involved combining the two years and reducing the number of categories to 5 (Table 6.3). A chi-squared test found that the two distributions were significantly different, rejecting the null hypothesis that the observed distribution could have happened by chance (Chi-Squared test, $\chi^2 = 14.10$, $P = 0.007$).

Departing birds are expected to choose the best conditions within a given window when fuel reserves are ‘optimal’ with respect to a currency such as the minimisation of time. Reed Warblers departed with a more favourable wind component relative to the day before departure (paired t-test, $N = 34$, $t = 2.97$, $P = 0.006$). The same significant difference was true of the departure day relative to the wind conditions two days before departure (paired t-test, $N = 33$, $t = 2.39$, $P = 0.023$). Finally conditions on the day of departure were not quite significantly different from the conditions on the day after departure (paired t-test, $N=34$, $t = 1.96$, $P = 0.058$). These results suggest that birds typically chose the best conditions for departure within a four day window, although conditions the day after departure were often as favourable as on the actual departure day (see Fig. 6.3 for raw data). Fig. 6.4 illustrates the greater range of wind components occurring on the days before departure relative to the day of departure.

The extent to which birds picked the most favourable day varied between years. By analysing the years separately, I found that the difference in conditions between the departure day and the previous day was still significant for 2001 (paired t-test, $N = 15$, $t = 2.83$, $P = 0.013$) but was not so in 2002 (paired t-test, $N = 19$, $t = 1.44$, $P = 0.166$). Whilst part of the effect may be due to reduced sample sizes and the consequent loss of power, the frequency of unfavourable conditions in 2001 may also have had an effect. Unfavourable conditions occurred on 48% of days in 2001 but only on 28% of days in 2002. Thus whilst birds in 2001 regularly chose between unfavourable and favourable days, birds in 2002 often just had a choice of favourable days and may therefore have been less likely to show decisive choices between days.

Birds with larger fuel loads are expected to be more sensitive to wind conditions than birds with smaller loads. In this study, there was no relationship between the strength of the wind component and the fuel load a bird was carrying on the night of departure (Regression, $F_{1,32} = 0.0$, $P = 0.984$, adjusted $R^2 = 0.0\%$). Neither was there a significant difference in fuel load between birds that departed in more favourable
FIGURE 6.3: Pattern of wind components between nights at Icklesham in the years 2001 and 2002. White diamonds (◊) indicate nights with departures by Reed Warblers, accompanying numbers indicate when more than one bird departed on a given night. In 2002, the departures of three Sedge Warblers are highlighted by white squares (□).
FIGURE 6.4: Distribution of wind components two days before departure (-2), one day before departure (-1), on the day of departure and on the day after departure (+1) for 34 Reed Warblers at Icklesham. The boxplots define the inter-quartile range and the median, the whiskers define the total range and the black circles correspond to the population mean.
conditions, relative to the previous day, than those that did not (t-test, \( t_{19} = -0.05, P = 0.962 \)). The majority of birds departing from the feeders attained high fuel loads, thus one would expect all the birds to be equally sensitive, which might explain the lack of a sensitivity gradient.

**Optimal Modelling of Departure Decisions**

The key predictions of the models introduced by Weber, Alerstam & Hedenström (1998) and Weber & Hedenström (2000) are dependent on the probability of favourable wind conditions. The probability of favourable wind conditions (tailwinds only in these models) varied between the two years at Icklesham: \( P = 0.32 \) in 2001 and 0.62 in 2002. Weber, Alerstam & Hedenström’s (1998) model predicts that when the probability is low, some birds may leave before the ‘optimum day’ and many will leave several days after (up to 6 days). At a medium/high probability (e.g. 0.6), the majority of birds are predicted to leave on the ‘optimal’ day and 95% of birds are expected to have departed 3 days later.

If winds are correlated between evenings rather than occurring at random then subtle differences in the pattern of departure may occur (Weber & Hedenstrom 2000). To test whether winds were correlated, I classed winds as either favourable (tailwinds only) or unfavourable (head or crosswinds). I then used a runs test to see whether the pattern of conditions between successive nights were likely to have occurred at random i.e. conditions between nights were independent (Siegal & Castellan 1989). In both 2001 and 2002, there were more runs than would be expected by chance (Runs test, \( P = 0.035 \) and 0.017 respectively), which suggests that wind conditions between nights were non-independent and therefore it was likely that the wind conditions on the next day were similar to those experienced on the current day. Examination of the data showed that in 2001 the probability of unfavourable conditions occurring on successive days was more likely than for favourable conditions (probability = 0.80 and 0.57 respectively). In 2002, the probability of favourable conditions occurring in succession was more likely than the probability for unfavourable conditions (p = 0.73 and 0.57 respectively).

In 2001, given the probability of unfavourable conditions and the likelihood that unfavourable conditions occur on successive nights, the models of Weber, Alerstam & Hedenström (1998) and Weber & Hedenström (2000) predict that some birds would
FIGURE 6.5: Frequency of fuelling durations (days) of 25 Reed Warblers attending *ad lib.* feeders at Icklesham in the years 2001 (black) and 2002 (white). Only birds with an FDR between 0.07-0.14 were included in the sample because the time-minimising models described in Chapter 4 predicts that birds with FDRs in this range should have fuelling durations of similar length (only varying by two days). Birds with lower FDRs are expected to show much greater variation in duration. Bars represent the cumulative frequency across the two years.
depart before the ‘optimum’ day and that a decreasing number of birds would depart over the following 1-15 days. Conversely in 2002, when the probability of favourable conditions was high, they predict that the majority of birds would depart on the ‘optimum’ day and a decreasing number of birds should depart 1 to 4 days later. Fig. 6.5 shows the number of days spent fuelling by 25 birds across both years. If one assumes that day five is the ‘optimum’ departure day, then there is some agreement with the models but also some disagreement (See section 6.4 for further discussion).

Air Pressure

Air pressure was generally high on departure days but there was no apparent difference between days with departures and days when birds were present but did not depart (means ± s.d: Departure days (n = 23), 1018.3 ± 6.1, Non Departure days (n=53), 1018.1 ± 5.7). High-pressure systems were common in the autumn of 2002 and these may have obscured any potential difference in pressure between departure and non-departure days. Rising pressure is a potential cue for favourable conditions and in this study 21 out of 34 Reed Warblers departed on days on which pressure was increasing. A further four birds departed in stable air pressure whilst only 9 birds departed when air pressure was decreasing (Fig. 6.6). To test whether birds were choosing rising air pressure or whether it was occurring by chance, I calculated the frequency of days on which air pressure was either increasing, decreasing or stable, for days on which Reed Warblers were present at the feeders (Table 6.4). In 2001, the observed distribution of departures with respect to air pressure was significantly different from that expected by chance (Chi-Squared Test, \( \chi^2 = 7.36, P = 0.025 \)). This affect seemed largely due to birds avoiding dropping air pressure (largest contribution to chi-squared, Table 6.4) rather than choosing rising air pressure. In 2002, when high pressure prevailed for much of the period in which Reed Warblers were using the feeders, there was a significant difference between the observed and expected distributions (Chi-Squared Test, \( \chi^2 = 6.19, P = 0.045 \)), however, this appears to be largely due to birds not departing in stable air (largest contribution to chi-squared, Table 6.4). The lack of support for birds choosing rising air pressure in 2002, may be because air pressure was high even when pressure was dropping (Fig. 6.6).

High pressure systems over Britain are often accompanied by winds from the north-east and east which are favourable for Reed Warbler migration and thus birds may
TABLE 6.4: Frequency of decreasing pressure (-1), stable pressure (0) and increasing pressure (+1) in the years 2001 and 2002 when Reed Warblers were present at the feeders. Expected frequencies were calculated by multiplying the frequency of each condition by the number of birds departing in the given year (2001 = 15, 2002 = 19). The calculations required for the chi-squared statistic are given in the columns labelled \((\text{obs} – \text{exp})^2/\text{exp}\).

<table>
<thead>
<tr>
<th>Air Pressure</th>
<th>Frequency</th>
<th>Expected Frequency</th>
<th>Observed Frequency</th>
<th>((\text{obs} – \text{exp})^2/\text{exp})</th>
</tr>
</thead>
<tbody>
<tr>
<td>2001</td>
<td>-1</td>
<td>0.395</td>
<td>5.921</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0.132</td>
<td>1.974</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>+1</td>
<td>0.474</td>
<td>7.105</td>
<td>10</td>
</tr>
<tr>
<td>2002</td>
<td>-1</td>
<td>0.375</td>
<td>7.125</td>
<td>8</td>
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<td></td>
<td>0</td>
<td>0.232</td>
<td>4.411</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>+1</td>
<td>0.393</td>
<td>7.464</td>
<td>11</td>
</tr>
</tbody>
</table>

FIGURE 6.6: Air pressure at departure for 34 Reed Warblers departing in either decreasing, stable or rising air pressure from Icklesham (symbols). N.B birds departing when air pressure was decreasing do so when air pressure is relatively high, except for one individual. The frequency distribution of air pressures on nights when Reed Warblers were present at the feeders is given on the left of the figure (black line).
not be responding to rising pressure but to the presence of favourable winds instead. Indeed, wind component showed a significant linear increase with air pressure (Wind Component = -191 + 0.189 Pressure, $F_{1,93} = 20.5$, $P<0.001$, adjusted $R^2 = 17.2\%$), such that the most favourable wind components during the autumns of 2001 and 2002 occurred during periods of high pressure.

**Cloud Cover and Rain**

The distribution of departures relative to cloud cover can be seen in Fig. 6.7. Over 50% of Reed Warblers departed when there was no cloud cover at all and only two birds departed when cloud cover was total. Birds are expected to choose nights with reduced cloud cover and to test this I calculated the frequency of nine classes of cloud cover on nights when Reed Warblers were present at the feeders. Expected frequencies were then calculated and the number of classes was reduced to four so that a chi-squared test could be performed. The observed distribution of cloud cover on nights when Reed Warblers departed was not significantly different from the distribution one would expect by chance (Chi-Squared Test, $\chi^2_4 = 7.89$, $P = 0.096$) but the p-value suggests a tendency to leave on nights when cloud cover is low (see Fig. 6.7 also)

However, whilst most birds may be choosing reduced cloud levels for the concordant availability of celestial cues for navigation (Åkesson & Backman 1999, Åkesson *et al.* 2001), reduced cloud cover was significantly related to positive wind components and therefore tailwinds in this study (Regression, $F_{1,92} = 8.91$, $P = 0.004$, adjusted $R^2 = 7.8\%$). Further, cloud cover decreased significantly as pressure increased (Regression, $F_{1,92} = 7.02$, $P = 0.009$, adjusted $R^2 = 6.1\%$), as would be expected. Thus the association between departures and both low cloud cover and high pressure, could be a by-product of choosing tailwinds or vice-versa.

Cloud cover on days of departure was not significantly less than on the day prior to departure (paired t-test, $N = 34$, $t = -1.60$, $P = 0.118$), although the trend was in that direction. Given the that there was no cloud cover on 55% of days on which Reed Warblers were present in 2002, it is not surprising that cloud cover levels changed little between the penultimate evening and the departure evening.

Rain did not occur at the approximate time of departure on any of the nights when Reed Warblers departed from the site. Further, no rain fell in the 6 hours prior to
FIGURE 6.7: Frequency of departures by 34 Reed Warblers according to the level of cloud cover. Cloud cover was measured on a 9 point scale such that 0 represented no cloud cover and 8 total cloud cover.

![Frequency of departures by 34 Reed Warblers according to the level of cloud cover.](image)

TABLE 6.5: Descriptive statistics for the percentage increase in flight range that Reed Warblers achieved by departing on the evening that they did, rather than the previous evening. The two years are separated, with 2001 presented first followed by 2002. Birds were assumed to have a flight speed of 10m/s in still air (Åkesson et al. 2002).

<table>
<thead>
<tr>
<th>N</th>
<th>MEAN</th>
<th>STDEV</th>
<th>SE MEAN</th>
<th>Q1</th>
<th>Q2</th>
<th>MAX</th>
<th>MIN</th>
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<tbody>
<tr>
<td>15</td>
<td>43.1%</td>
<td>50.4</td>
<td>13</td>
<td>19.1%</td>
<td>82.9%</td>
<td>116%</td>
<td>-35.8%</td>
</tr>
<tr>
<td>19</td>
<td>5.3%</td>
<td>13.2</td>
<td>3.0</td>
<td>-3.7%</td>
<td>17.1%</td>
<td>27.2%</td>
<td>-19.5%</td>
</tr>
</tbody>
</table>
the estimated departure time for all 34 experimental birds. For 5 of the 34 departures, rain had fallen on the previous night and may therefore have delayed departure.

**Sedge Warblers**

All three Sedge Warblers attending feeders in 2002 departed with a tailwind (Fig. 6.3). Conditions on the evening of departure were more favourable than the previous two evenings in all three cases, with regards to the wind component. All three birds departed when the cloud cover was total and only one bird departed in rising air pressure. No precipitation occurred within 6 hours of departure in all cases.

Weather data for the autumn of 2003 was not obtained in time for inclusion in this thesis and thus the departure decisions of Sedge Warblers in 2003 could not be related to weather conditions (Chapter 5).

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### 6.4 GENERAL DISCUSSION

The intensity of migration has long been known to vary with weather conditions such as wind direction, in particular, levels of cloud cover and precipitation (Able 1973, Richardson 1978, Alerstam 1979, 1990, Elkins 1988). In a recent study, the intensity of nocturnal migration over central Europe was measured using radar over the course of an entire autumn (Erni *et al.* 2002). It was found that wind direction (classed as favourable or unfavourable), rain and previous precipitation explained up to 70% of variance in intensities. It was concluded that unsuitable weather conditions may often delay the departure of migrants from stopover sites and could be responsible for the low correspondence of empirical data with the predictions of wind-free optimal migration models.

**The Influence of Wind on Departure Decisions by Reed Warblers**

Whilst the evidence for the influence of various weather variables on the intensity of migration is convincing, data relating known departures of individual birds from stopover sites to favourable conditions is not so supportive (see section 6.1). Indeed, whilst the majority of individual birds in these studies showed a preference for
low levels of cloud cover and precipitation, few appeared to chose ‘favourable’ (tailwinds) wind conditions (Fransson 1998b, Danhardt & Lindström 2001, Åkesson et al. 2001). In my study, the decision to depart appeared to be influenced by the presence/absence of tailwinds, with Reed Warblers favouring tailwinds (as did three Sedge Warblers). However, a number of individuals departed in crosswinds and thus the behaviour observed may reflect an avoidance of headwinds rather than a preference for tailwinds. This result is striking given that Åkesson et al. (2001) found no preference for avoiding headwinds or choosing tailwinds in a study of Reed Warblers in southern Sweden, despite a similar sample size (Sweden, N = 28, my study, N = 34).

Liechti & Bruderer (1998) argued that choosing the most favourable conditions within a theoretical ‘departure window’ could make a considerable difference to the potential flight range of a migrant. I found evidence that Reed Warblers were selecting the most favourable conditions for migration within a window of about 3 days. In many cases, this meant that birds avoided departing against a headwind and departed with tailwinds instead, thereby increasing their potential flight range (Table 6.5). The difference in potential range was most striking in 2001, when favourable conditions were rare (Table 6.5). Even the small number of Reed Warblers departing in crosswinds increased their flight range in 5 out of 6 cases by not departing against a headwind the previous evening. The departure decisions of Reed Warblers support the assertion that migrants are sensitive to wind conditions and therefore stopover lengths and consequent fuel loads may not be determined by fuelling behaviour alone.

Wind Driven Models of Departure Decisions

The theoretical models developed by Weber, Alerstam & Hedenström (1998) and Weber & Hedenström (2000) assume that birds should always depart with a tailwind unless the probability of a tailwind occurring is particularly low (<0.2). Under this assumption, it is predicted that as the probability of tailwinds occurring decreases, the degree of variability in stopover durations and fuel loads will increase (Fig. 6.1). During 2001, the probability of tailwinds at my study site was low but variation in fuelling duration did not reflect this (Fig. 6.5). The propensity of birds to leave in crosswinds, 5 out of 15 birds did so in 2001, rather than waiting for a tailwind may explain this lack of variation. Indeed, two Reed Warblers left against a headwind in 2001. The possibility of birds considering crosswinds ‘favourable’ was not considered
by previous authors, and including this as a criterion, when the probability of a tailwind drops below a certain threshold, could be an important modification for future models. Had these 5 individuals waited for a tailwind, 4 would have waited a further four days and the fifth would have waited 2 days (see Fig. 6.3). Consequently, fuelling durations would have been much closer to the model predictions if birds had only departed in tailwinds.

Weber, Alerstam & Hedenström (1998) also predict that when the probability of tailwinds is low, some birds may depart one day before the ‘optimum’ day, given favourable conditions. If one assumes that the wind-free optimum duration is 5 days (modal value for the whole data set, see Fig. 6.5) then any longer durations should be due to birds waiting for favourable conditions (Weber, Alerstam & Hedenström 1998). In 2001, 8 birds deviated from this hypothetical five-day optimum. In 5 of these cases there was clear evidence of birds avoiding headwinds and waiting for tail/cross winds but not in the other 3. Indeed, two of the birds departed after 4 days, supporting the model prediction of early departure when the probability of tailwinds is low. However, neither of these two birds had experienced a run of unfavourable winds and it is unclear at what stage their expectation of wind direction might have been formed, or indeed if it had been formed at all.

In 2002, the probability of tailwinds was high and the distribution of fuelling lengths seemed to support the theoretical models, with the majority of birds leaving on day 5 or the following day (71%). However, in all eight cases of deviation from the assumed five day ‘optimum’, there was no support for delayed departure by unfavourable conditions. Indeed, in many cases stronger tailwinds occurred on days without departure. The lack of support for delayed departure in 2002 may be because the assumed optimum fuelling duration is incorrect. Indeed, duration could vary between birds for a number of reasons, including time of year, level of reserves at the start of fuelling, origin or even errors in the estimation of durations. Therefore, using a more conservative assumption that the optimum duration may be five or six days, I found that only 4 cases of increased duration in 2002 could not be explained.

Interestingly, the Reed Warbler that stayed for 9 days in 2002, showed a dramatic decrease in FDR on day 5 (see Fig. 3.1), which is usually associated with departure (section 4.4). Why this bird appeared to reverse its decision to depart is unclear, as all the weather variables were favourable.
Departure Decisions in Relation to Cloud Cover, Pressure and Rain

Reed Warblers departing from Icklesham showed a tendency to depart when cloud cover was minimal and air pressure was either rising or stable, and in no cases did birds leave when there had been precipitation in the 6 hours prior to departure. Precipitation can severely hamper the flight of small passerines and cloud cover can obscure important navigational cues, thus the advantages of departing without either are clear (Erni et al. 2002). Rising pressure is indicative of the recent passage of a cyclone from west to east in Europe and is typically accompanied by decreasing cloud cover and, in many cases, tailwinds during autumn migration (Åkesson et al. 2001). Therefore, Reed Warblers may be using rising pressure as a cue for improving flight conditions. However, rising pressure, low cloud cover and a lack of precipitation were all correlated with favourable wind components in the datasets examined here and some of the apparent preferences observed may be by-products of selection for just one variable. If wind direction and strength are considered the most important variables determining departure decisions, then one can argue that the other variables may not in fact be favoured: except the avoidance of precipitation. However, in other studies when no clear preferences for tailwinds were found, birds still selected nights with reduced cloud cover and in many cases rising pressure (Fransson 1998b, Åkesson et al. 2001, Danhardt & Lindström 2001), thus a preference for such conditions appears to have been selected for.

Comparisons to Previous Studies

So why do Reed Warblers in southern England show a significant preference for departing with tailwinds, when migrants in other studies, including Reed Warblers in Scandinavia, do not appear to? The three main studies discussed here (Fransson 1998b, Åkesson et al. 2001, Danhardt & Lindström 2001) were all carried out in southern Sweden where in some autumns, headwinds from the south/southwest predominated. This appeared to explain the high proportion of departures against headwinds found by Danhardt & Lindström, although Fransson (1998b) states that the frequencies of head and tail winds were roughly equal during his study period. Could it be that migrants have a fixed expectation of the probability of favourable conditions within a given
region and thus will await favourable conditions when the expectation is high but will leave against weak headwinds if the expectation is low?

A second possibility is that the high fuel loads attained by Reed Warblers at Icklesham may have made them more sensitive to conditions. Fuel loads were higher in experimental Reed Warblers than in either Robins (Danhardt & Lindström 2001) or Whitethroats (Fransson 1998a) despite equivalent food sources (see section 3.4) and it is predicted that sensitivity should increase as fuel loads do (Liechti & Bruderer 1998). However, I found no support for this trend in Reed Warblers alone but this may be because fuel loads were consistently high (section 3.3).

Summary

I have shown that the departure decisions of Reed Warblers were influenced by wind conditions, contrary to previous studies, and to an unknown degree by the extent of cloud cover, recent precipitation and changes in air pressure. Reed Warblers typically chose the best conditions within a ‘departure window’ and thus may be capable of forming an expectation of future weather conditions: a valuable ability in any migratory species. Whilst the majority of birds departed with a tailwind, crosswinds were also selected and it may be that Reed Warblers simply class winds into favourable and unfavourable such that they actively avoid headwinds but do not wait for the ‘perfect’ tailwind. This conclusion was also reached by a recent study in which the same preferences were noted in a wide range of nocturnal migrants recorded by radar (Erni et al. 2002)

Comparisons with wind based models of departure decisions suggest that waiting for favourable conditions can delay Reed Warbler departures, causing birds to stay longer than the wind-free ‘optimal’ stopover duration. Thus the sensitivity of Reed Warblers, and presumably other migrants, to wind direction is likely to cause deviations from the predictions of wind-free optimality models (Lindström & Alerstam 1990, Hedenström & Alerstam 1997). However, these deviations may not be as large as expected (Liechti & Bruderer 1998) or predicted (Weber, Alerstam & Hedenström 1998, Weber & Hedenstrom 2000). My study suggests that Reed Warblers will typically leave within four days, at most, after the wind-free optimal departure day, rather than the much lengthier delays predicted. Therefore, future models may need to incorporate
the disposition of migrants to depart in crosswinds thus shortening expected delays considerably.

Unlike the assertions of a number of authors (Liechti & Bruderer 1998, Weber, Alerstam & Hedenström 1998, Weber & Hedenström 2000), the evidence I have presented for Reed Warblers suggests that wind does not have a large influence on stopover durations. Therefore, the level of fuel accumulated and its impact on the course of a migratory journey may be largely influenced by time-selected optimal stopover durations (section 4.4 & 5.4), rather than the probability of favourable winds occurring. This may be especially true of naturally fuelling Reed Warblers at Icklesham, whose low FDRs would not result in a large increase in fuel load during short delays (section 2.3.1).
FINAL DISCUSSION

In the following two sections I have used my results from both the analysis of historical data sets and experiments, firstly to discuss how the results may be generalised to migratory behaviour across a range of species, and secondly to look in depth at the migratory behaviour of one species. In section 7.1, I therefore discuss the key variables that influence fuelling behaviour and consequently the migratory strategies of passerines. Whilst the conclusions drawn may apply to non-passerines as well, many of the generalisations are expected to be most applicable to long distance migratory passerines. I also discuss the relative importance of behaviour during fuelling phases versus flight phases in determining migratory strategies. Finally I suggest work that could be carried out in this field in future.

In section 7.2, I discuss in detail the migratory strategy of the Reed Warbler and the implications this knowledge has for the conservation of fuelling habitats. This section is expected to provide a model for how a variety of data, including the analysis of ringing data, recovery information, experimental work and theoretical estimates of flight ranges can be combined to give a greater understanding of migratory strategies in terms of habitat use, and to help identify key fuelling regions. A final summary is presented in section 7.3.

7.1 THE FUELLING BEHAVIOUR OF LONG DISTANCE MIGRATORY BIRDS AND ITS IMPORTANCE IN DETERMINING MIGRATORY STRATEGIES

The behaviour of migratory birds during fuelling phases is expected to have a strong influence on the time course of migration and the overall strategy a migrant adopts (Alerstam & Lindström 1990). Fuelling behaviour and its outcome may be defined by three key variables: the fuel deposition rate (FDR), the number of days spent
fuelling and the fuel load a bird has on departure. The departure load is the most important determinant of a bird’s onward progress, both in terms of distance covered in one flight stage and the number of flight stages required to reach the migratory goal (see section 7.2). However, the final departure load is entirely determined by the rate and length of fuelling, therefore the value of these two variables will directly influence the overall strategy.

In the following two sub-sections (7.1.1 & 7.1.2), I discuss variables that can influence the rate of fuelling and then the duration of fuelling, thereby influencing the final departure load and the overall migratory strategy. However it is important to note that choices made during flights could also influence migratory strategies and in sub-section 7.1.3 I discuss the relative importance of behaviour during fuelling phases versus flight phases in defining the strategies of migratory birds. In sub-section 7.1.4 I discuss future work that could be carried out in this field. In section 7.3, I summarise the key points and findings discussed below and from the thesis as a whole. These key findings are now summarised in concise form.

- The fuelling behaviour of Reed Warblers showed marked variation between four sites separated by both their geographical position and by the season in which birds were studied. These differences were noted in FDRs and fuelling durations, and appeared to be partly predetermined but also due to interactions with the environment (Chapter 2).
- The lean body mass of Reed Warblers varied with time of year (Chapter 2).
- Food-supplemented Reed Warblers differed significantly in the FDRs and departure loads they achieved relative to naturally fuelling birds. The outcome of fuelling behaviour is therefore flexible, not fixed (Chapter 3).
- Food supplemented Sedge Warblers and Great Reed Warblers did not differ in fuelling behaviour to the same extent as Reed Warblers when compared to naturally fuelling birds. Fuelling duration appeared to be the main constraint on these two species (Chapter 3).
- Reed Warbler FDRs increased with date, indicating that the selection pressure for time-minimisation increased as the time available for completing migration decreased. Selection for a reduced foraging-intensity dependent predation risk probably constrained FDRs when time was not the overriding selective force (Chapter 4).
• Reed Warbler fuelling behaviour was consistent with the predictions of time-minimising models of migration (Chapter 4).
• Evidence from spring migrating Reed Warblers and experimental birds suggested that stopover costs were minimal or non-existent (Chapter 2 & 4).
• Reed Warblers partly compensated for increasing metabolic costs as fuel load increased by increasing their foraging/intake rate (Chapter 4).
• Sedge Warbler fuelling behaviour was consistent with the predictions of a time-minimising model in which migrants have a fixed expectation of higher FDRs at future stopover sites and only pay a small stopover cost (Chapter 5).
• Food supplemented Sedge Warblers showed remarkable duality in fuelling behaviour at the same site. Therefore the cue for extensive fuelling in Sedge Warblers was not food availability alone (Chapter 5).
• Sedge Warblers appeared to be fuelling at their maximum capacity, although FDRs decreased as fuel load increased, probably as a result of rising metabolic costs (Chapter 5).
• Fuelling durations in Reed and Sedge Warblers appeared to be fixed, rather than a functional response to their FDR (Chapter 4 & 5).
• Reed Warbler departure decisions were influenced by a preference for avoiding headwinds and precipitation, and to some extent by cloud cover and air pressure (Chapter 6).
• Delays due to unfavourable winds resulted in delayed departure in some Reed Warblers. These delays were shorter than models have predicted (Chapter 6).

7.1.1 INFLUENCES ON FUEL DEPOSITION RATES

Morphology and Feeding Ecology

The morphology of a migrant directly impacts on its feeding ecology, influencing both prey choice and habitat preferences. Therefore the feeding opportunities encountered during migration may be directly related to morphology. Some species show remarkable switches in feeding ecology when fuelling e.g. the
dramatic switch made by a number of species of *Sylvia* warblers from insectivory to frugivory, allowing them to attain high FDRs by utilising highly clumped and fat rich food sources (Alerstam 1990). In contrast, insectivores such as the Pied Flycatcher are constrained by their feeding ecology, as flying insects are rarely highly abundant and therefore FDRs are typically low in these species, leading to shorter flight stages and slower migrations (Schaub & Jenni 2000b).

Reed and Sedge Warblers remain insectivores during migration and yet despite strong ecological and morphological similarities, the two species have distinctly different fuelling strategies (Bibby & Green 1981). Subtle differences in morphology may allow Reed Warblers to behave as generalists, fuelling in a variety of habitats throughout Europe, whilst Sedge Warblers are largely restricted to reedbeds, in which they have become dependent on a highly clumped food source only found in northern Europe. An alternative explanation may be that the divergent strategies observed in these ecologically similar species have evolved in order to avoid competition. Either way, it is clear that morphology will impact on feeding ecology and therefore the level of food availability a migrant encounters, which in turn will directly influence FDRs.

**Food Availability**

Fuelling rates are expected to increase with increasing food availability, making food availability an important determinant of the FDRs of migratory birds. In section 3.3, the FDRs of three species of long distance migrants, the Reed Warbler, Sedge Warbler and Great Reed Warbler, were all shown to be a positive function of food availability. Three further species - Whitethroat (Fransson 1998a), Bluethroat (Lindström & Alerstam 1992) and Robin (Danhardt & Lindström 2001) – have also been found to increase their FDR when food supplemented. However, note that food availability is not determined by the environment alone but also by constraints on feeding opportunities imposed by a migrant’s morphology and feeding ecology.

I found that Reed Warblers with access to unlimited food did not show an all or nothing response, i.e. they did not fuel at maximum rates at all times. FDRs may therefore be suppressed below their maximum by other variables (see below). Given a fixed level of food, maximum FDRs will also be determined by digestive capacity and a bird’s basal metabolic rate, which may vary with fuel load and the simultaneous
occurrence of energetically demanding processes such as moult or the feeding of young (sections 2.1.1 & 2.3.1).

**Digestive Capacity/Efficiency**

The digestive capacity, and therefore digestive efficiency, of a migratory bird may not be constant. In section 2.5, I showed for the first time that the lean body mass of Reed Warblers varied on both geographical and temporal scales. Variability in lean body mass cannot be attributed to one cause but variation in the length and therefore mass of the digestive organs is a strong candidate, given the evidence, both theoretical and empirical, for organ hypertrophy in migrating birds (McWilliams & Karasov 2001, Weber & Hedenström 2001; Jehl 1997, Piersma & Lindström 1997, Biebach 1998, Piersma 1998). Whilst hypertrophy of the digestive organs may initially impose both a time and energy cost and also a subsequent maintenance cost, these costs may be overridden by the benefits of an increased speed of migration through higher FDRs for a time-selected migrant.

I found further evidence for variation in digestive capacity in the difference in FDR between birds provided with an unlimited supply of food (section 3.3). Reed Warblers in northeast Spain had significantly higher FDRs than birds in southern England: a difference that also exists between birds fuelling under natural conditions (section 2.4.2). Whilst these differences could be a result of trading-off an increased foraging-intensity dependent (FID) predation risk against a higher intake rate, differential digestive efficiency is an equally plausible explanation. The marked difference in FDR and intake rate between Reed and Sedge Warblers could also be explained by a greater digestive capacity in Sedge Warblers. That Sedge Warblers were more time stressed than Reed Warblers would suggest that they were more likely to trade off costs associated with organ hypertrophy for a higher FDR than Reed Warblers. However, it can also be argued that Sedge Warblers may be more prepared to trade off a higher FID predation risk for an increased speed of migration. The relative contribution of increased digestive capacity versus an increased FID predation risk in determining intake rates and therefore FDRs is an important topic for future work (see section 7.2.4).
Metabolic Costs Associated with Increasing Fuel Loads

Fuelling rates may decrease as body mass increases for two reasons. First, if there is an increase in the basal metabolic rate associated with maintaining and transporting larger fuel loads (Klaassen & Lindström 1996). Second, if mass-dependent (MD) and FID predation risk are both minimised during fuelling (section 4.1, Houston 1998). Both of these processes may in fact act together to decrease FDRs. I found that the FDR of individual food supplemented Reed Warblers gradually decreased over the period in which they were fuelling (section 4.3), but the decrease was not as dramatic as the case for food supplemented Sedge Warblers (section 5.3). The key difference was that Reed Warblers compensated for increased energetic demands during daylight hours by increasing their intake rate, whilst Sedge Warblers did not increase their intake rate, showing no compensation. This points to a number of possibilities. In the case of Reed Warblers, the reduced FDR would appear to be largely a consequence of increased metabolic costs, as the increased intake rate is not consistent with the expected behaviour of a bird selected to minimise its FID predation risk. The constant intake rate in Sedge Warblers could be explained by either assuming that intake rates were already maximised or that birds were not prepared to increase their predation risk. Therefore the decrease in FDR may be either due to increasing metabolic costs alone or due to the combined action of increasing metabolic costs and maintaining a low predation risk.

This is the first time such patterns in FDRs have been discovered and further work is required to test their generality. However, Fransson (1998b) noted that Whitethroats had a reduced FDR on the day of departure, a pattern I identified in both my datasets (sections 4.3 & 5.3). The important discovery here is that metabolic costs increase with increasing fuel loads, leading to lower FDRs. Consequently, final fuel loads may be reduced or migrants may have been selected to increase their fuelling duration to compensate, thereby increasing the time spent migrating. As the metabolic costs associated with small fuel loads are likely to be small, increasing metabolic costs may have only shaped fuelling behaviour at times when large fuel loads are accumulated, e.g. when crossing large barriers.
Selection for Minimising Time and/or Predation Risk

Migrants that have been selected to minimise the time they spend migrating are expected to fuel at maximum rates (Lindström & Alerstam 1990) and this would appear to be the case for Sedge Warblers (see above and section 5.4). However, migrants selected to reduce or minimise their FID predation risk are expected to fuel at below maximum rates (see above also). Reed Warblers provided with unlimited food did not fuel at maximum rates at all times. Indeed, the hourly rate of gain and therefore intake rate of Reed Warblers increased as the time available for migration decreased (Fig. 4.3.2): a response that also appeared to compensate for the gradual reduction in the time available for feeding as day length decreased. Thus as Reed Warblers became more time stressed they gradually increased their intake rate and therefore their FID predation risk. It is important to note that this was not an all or nothing response but occurred on a continuous scale such that FDRs were modified to account for reduced feeding time on a regular basis. This response was also noted in the FDRs of birds fuelling under natural conditions (section 2.3.1). This active modification, which has never previously been shown, could also be seen in the manner in which food supplemented birds had their last feed closer to sunset, as the time available for migration decreased (Fig. 4.3.3).

Selection for time-minimisation may therefore result in a graded behaviour, according to the amount of time available to complete a migration. The behaviour of Reed Warblers also indicates that FID predation is a more potent force in shaping their fuelling behaviour than MD predation (since a bird minimising MD predation risk is predicted to fuel at maximum rates thereby minimising the time spent at high body masses). However, caged Blackcaps whose perceived predation risk was artificially increased, responded in a manner consistent with the expected behaviour of a bird minimising MD predation risk (Fransson & Weber 1997).

Therefore, whilst time may be the main selective force acting on FDRs, migrants may have been selected to minimise their FID predation risk at times during their migration when time is not an overriding selective force. For species in which time is not the only selective force, this will result in longer but ‘safer’ migrations. For long distance migrants, time should typically be the most important currency to be minimised, except for early migrating individuals of some species. Short distance migrants, however, may not be so time stressed and the importance of safety may have selected for lower FDRs. Indeed, the mean FDR for a food supplemented short-distance
migrant, the Robin (mean ± s.d. = 0.054 ± 0.023; Danhardt & Lindström 2001), was close to half the mean rate I found for Reed and Sedge Warblers (mean ± s.d: Reed 0.094 ± 0.021; Sedge 0.135 ± 0.043).

Weather

Without the security of an unlimited and sheltered food source, weather conditions may directly impact on daily FDRs. Weather variables such as wind, temperature and rain can potentially reduce insect abundance and activity, giving rise to reduced FDRs in insectivorous migrants. Conversely, birds feeding largely on fruits may be unaffected by such conditions. The impact of persistent rain on the FDRs of two Reed Warblers can be seen in Fig. 7.1. These birds were part of a preliminary study during August 2003 in which mealworms were provided for just three hours in the morning and two hours in the evening. During this study, two birds experienced persistent rain on two days during the hours when no food was provided. Examination of Fig. 7.1 makes it clear that if these birds had not received supplementary food, they would have lost mass over the two days. Further investigation of the effect of weather on FDRs would clearly be profitable (see section 7.2.4).

7.1.2 INFLUENCES ON FUELLING DURATIONS

Time-Selected Fixed Durations

Theoretical work has predicted that a migrant demonstrating ‘true’ time-minimising behaviour should regulate the length of its fuelling period according to its FDR (Hedenström & Alerstam 1997). In my study both Reed (section 4.3) and Sedge Warblers (section 5.3) failed to conform to this prediction and instead showed little variation in their fuelling duration across a wide range of FDRs (0.02-0.2). I also re-examined Fransson’s (1998a, Fig. 2) data on Whitethroats and found that ten out of twelve birds fuelled for exactly five days. Fransson did not draw attention to this important difference between his data and the predictions of a time-minimising model. Therefore, rather than fuelling durations being a predetermined function of the FDR, I hypothesise that they are of fixed length, presumably regulated through a bird’s
FIGURE 7.1: Mass gains by two Reed Warblers at a feeder where mealworms were provided between dawn and 0900h and between 1800h and sunset during August 2003. The gains pictured were from the last mass recording before mealworms were removed in the morning and the first recording after mealworms were replaced in the evening. On days four and five there was persistent rain throughout the day. Unfortunately on day four the heavy rain in the evening made it impossible to attach the perch to the balance so mass recordings could not be taken.
circadian clock (Gwinner 1996). Possible reasons for variation in fuelling duration were given in sections 4.4, 5.4, & 6.4. I have already argued that both Reed and Sedge Warbles have been selected to minimise time to varying degrees and I expect that fixed fuelling durations will have been selected to be of optimal length with respect to the range of FDRs typically experienced and the total time spent migrating. Indeed, it was found that by fine tuning the fuelling duration of birds crossing a computer simulated landscape on which FDRs varied within the range typically experienced by migratory passerines, migrants using a fixed rule only under-performed birds adopting ‘true’ minimising behaviour by two days on a journey approximately 50 days in length (Erni et al. 2002).

If fixed durations are one of the keys to fuelling behaviour, then durations must vary on a geographic scale, allowing ecological barriers to be crossed successfully. I would therefore expect a behavioural program in which fixed durations vary between sites according to the journey ahead. The cue for changes in duration may be built into the time programme apparently governing the behaviour of migrants (Gwinner 1996) or be a response to variables that vary on a geographic scale such as day length or the Earth’s magnetic field (Fransson et al. 2001). In some cases food availability may be an appropriate cue. However, Sedge Warblers might be expected to increase their fuelling durations when high food availability is encountered but I found that fuelling behaviour was not altered in all cases in response to food supplementation (section 5.3). Therefore a second cue acting alone or together with food availability must exist (section 5.4). Having fixed fuelling durations that vary between geographic regions is a simple but elegant solution for approximating to time-minimising behaviour along the length of a migratory journey. Therefore, time-selected durations are a crucial determinant of not only departure loads but of migratory strategies.

Fuelling duration will also influence the degree of variability within a migrant’s strategy. If the FDRs of individual migrants vary, then where species have short durations, one would expect to see relatively little variation in departure load and therefore the onward strategy. However, for birds with longer durations the variation between individuals will increase and I would expect to see a continuum of possible strategies arising. This may be the case for Reed Warblers at sites in southern England where they have durations twice the length of a typical Sedge Warbler (Chapter 3). Consequently, I would expect free-living Reed Warblers to show greater variance in body mass than Sedge Warblers, which is indeed the case (Fig. 7.2; Test for Equal
FIGURE 7.2: Body mass distributions of juvenile Reed and Sedge Warblers caught at Icklesham. All Reed Warblers had a moult score of 0 and had therefore completed their moult and begun fuelling/migrating. Only a relatively small number of pairs of Sedge Warblers bred at Icklesham and therefore the majority of individuals were already actively migrating.
Variances, F-Test Statistic = 0.708, P<0.001). The larger range in Sedge Warblers is due to a very small percentage of birds fuelling extensively, rather than making short fuelling stops (Fig. 7.2)

**Expectation of Future Conditions**

Fuelling durations could have simply been optimised to minimise the time spent on migration given a constant expectation of future fuelling conditions. However, if food availability and therefore FDRs are higher or lower at future sites then the optimum duration changes (Weber & Houston 1997a). Therefore fuelling durations and strategies might have evolved to take into account geographical variation in FDR. I have presented the first empirical evidence for a migrant’s (Sedge Warblers) fuelling duration and resulting fuel load having been optimised with respect to future expectations (Chapter 5). Indeed, the short fuelling durations of the majority of Sedge Warblers, relative to Reed Warblers, point to Sedge Warblers having an expectation of higher FDRs at future sites. This conclusion is consistent with current knowledge of the migratory strategy of Sedge Warblers (Bibby & Green 1981; section 5.4). Fuelling durations, departure loads and overall strategies might therefore have been shaped by predictable variation in the fuelling rates achievable at sites along the length of the migratory journey.

**Ecological Barriers**

Ecological barriers vary in length and the fuelling opportunities they provide, and therefore in the amount of fuel required for a successful crossing. For Wheatears *Oenanthe oenanthe leucorhoa* making the journey from southern Greenland to west Europe, a flight of 2,500 km over the Atlantic Ocean must be made, with no chance of making landfall or refuelling (Alerstam 1990). Conversely, the many passerines that cross the Sahara desert in autumn can at least rest and may be able to find food in widely scattered oases (Biebach et al. 2000). The fuel loads required to cross both these barriers are larger than those typically observed in birds crossing areas where refuelling opportunities are plentiful (Schaub & Jenni 2000b) and therefore fuelling behaviour must be modified in order to cross these barriers. I have already pointed out that FDRs can be increased but this may also need to be coupled with an increase in fuelling
duration. Reed Warblers in southern Portugal (section 2.3.2) were not found to have significantly longer fuelling durations than birds in southern England. However, the experimental work suggests that durations in southern England were overestimated and thus the mean duration of 10 days for birds in southern Portugal may represent a change in strategy from the mean duration of six days for experimental birds in England (section 4.3). A more striking case of an increase in fuelling duration was that of Reed Warblers fuelling in Senegal where extremely low food availability led to mean durations of 19 days: the true duration is expected to be longer as the probability of recapture in Senegal was very low (section 2.4.1).

I have shown that the need to cross a large ecological barrier has selected for longer fuelling durations in both Reed and Sedge Warblers. Where and when increases in duration occur, however, may be dependent on where suitable fuelling opportunities exist. This can be seen in the striking differences in strategy between Reed and Sedge Warblers.

**Delayed Departure – Paying Attention to the Weather**

I have argued that the fuelling durations of Reed and Sedge Warblers, and probably many long distance migrants, are fixed at distinct stages in the migratory journey but that the exact duration will vary between stages. However, I do not expect a bird to adhere to this duration if the conditions for flying on the night of departure are unfavourable for onward migration. Therefore, fuelling durations may be extended in response to conditions such as precipitation or strong headwinds. The extent of these delays and their impact on departure loads, and therefore the strategy adopted by a migrant, depends on a number of factors.

Firstly, the sensitivity of a migrant to flying conditions will determine how often it is delayed by unfavourable conditions. I found that Reed Warblers, whilst being highly sensitive to headwinds, were apparently undeterred from migrating in crosswinds (section 6.4). Thus for Reed Warblers, which do not wait for the ‘perfect’ tailwind, delays are likely to be relatively short. As Reed Warblers fuelling under natural conditions throughout much of Europe have relatively low FDRs (Schaub & Jenni 2000a), a delay of one or two days will not dramatically affect the fuel load a bird attains and therefore the overall strategy of such a migrant will not be strongly influenced by weather. However, there may be times when Reed Warblers and other
migrants are highly sensitive to weather conditions and in these cases delays may have a marked impact on the overall time taken to complete the migratory journey and the strategy adopted. For example, if Reed Warblers fuelling in southern Portugal are regularly delayed by three or more days before they attempt to cross the Sahara, then some birds may accumulate enough fuel to fly all the way to their wintering grounds. Non-delayed birds, however, may only have enough fuel to cross the Sahara and will have to refuel in order to reach their wintering grounds. Finally, if favourable conditions are particularly rare, then delays may also be commonplace.

7.1.3 THE RELATIVE IMPORTANCE OF BEHAVIOUR ON FUELLING PHASES VERSUS FLIGHT PHASES IN DETERMIING MIGRATORY STRATEGIES AND THE TIME COURSE OF A MIGRATORY JOURNEY

Much of the theoretical work on optimal fuelling behaviour is based on the premise that fuelling behaviour is a key determinant of the strategy a migrant adopts, and that fuelling stages account for a considerable proportion of the time and energy a bird spends migrating (Hedenström & Alerstam 1997). However, it has been argued that if migrants are highly sensitive to flying conditions, then suitable conditions are more likely to determine fuelling durations. Therefore the distance covered in each flight stage may be more sensitive to the extent of support from following winds than the actual fuel load a migrant achieves during fuelling (Liechti & Bruderer 1998). Further, Erni et al. (2002) point out that if a migrant can regulate its fuelling behaviour according to a fixed duration and still closely approximate to time minimisation then wind assistance and the accuracy with which flight direction is chosen may have a greater impact on the time spent migrating than fuelling behaviour.

Whilst unfavourable conditions for flight may delay migrants from leaving a fuelling site, I found that delays were relatively short for Reed Warblers and were therefore unlikely to have significant impact on fuel loads (section 7.1.2). This conclusion is further supported by the lack of evidence for other migrants choosing optimal departure conditions; rather birds appeared to depart in the least unfavourable conditions available (Fransson 1998b, Danhardt & Lindstrom 2001, Åkesson et al. 2002). If the availability of favourable flight conditions does not alter departure loads
significantly then the efficiency with which a fuel load is used may have a greater impact.

The efficiency with which fuel loads are used, in terms of the distance covered towards the migratory goal, is at present an unknown quantity. Although there are examples of individual birds that appear to have utilised their fuel load efficiently, both in terms of the distance covered and the time taken in doing so (see example of a Reed Warbler in section 3.4), there is also evidence that flights can be sub-optimal. Wind drift often causes the displacement of birds from their preferred migratory route (Elkins 1988) and such movements may result in longer migrations and a departure from the optimal strategy. A number of long distance migrants have also been shown to make regular movements away from their preferred migratory direction: these are particularly evident in the easterly and westerly movements of Sedge and Reed Warblers along the south coast of Britain in autumn (Wernham et al. 2002). Whilst these movements may be considered as sub-optimal, they may actually be a searching behaviour, adopted by birds that have yet to begin fuelling for the journey southwards, for locating good fuelling sites (Insley & Boswell 1978).

For birds that have accumulated medium to large fuel loads, the direction and strength of the wind during flight could have a dramatic impact on flight range (section 6.1). However, the evidence from Reed Warblers suggests that birds are not trying to pick a near ‘perfect’ tailwind. Therefore, whilst such winds may occur on nights of departure (greatly increasing the range of some birds), on average the support from wind may not dramatically increase range. Therefore, for Reed Warblers and probably other long distance migrants, the fuel load as opposed the choice of flying conditions may be a more important determinant of flight stage length. This may be particularly true when one considers that a flight stage could last up to 8 days and therefore favourable conditions may be balanced out by less favourable conditions on other nights. Indeed, delaying departure until near perfect conditions occur could actually result in longer migratory durations even if such conditions occur 50% of the time.

I have argued that Reed Warblers, and by implication some other long-distance migrants facing a similar journey, are not highly sensitive to flight conditions and therefore fuelling behaviour and resulting departures loads are the most important influences on the time course of a migratory journey and the strategy adopted. However, there are species of long distance migrant for which this does not hold true. Wheatears migrating across the Atlantic from Greenland to western Europe and Blackpoll
Warblers *Dendroica striata* migrating from northeast North America to the northern coast of South America could only complete these spectacular journeys with wind assistance (Alerstam 1990). Therefore the time spent at a fuelling site and the evolution of such strategies will be largely determined by the occurrence of winds that make these journeys possible. Thus the relative importance of fuelling phases and flight phases will depend on the strategy a migrant adopts but for most long distance migrants travelling from Europe to sub-Saharan Africa, I propose that fuelling behaviour plays the greatest role.

### 7.1.4 FUTURE WORK

**The Reed/Sedge Warbler System**

The system I developed for manipulating and measuring the FDRs of Reed and Sedge Warblers may be used to answer yet more questions about the fuelling behaviour of long distance migrants.

An investigation of the control of fuelling durations and the selective pressures shaping them is an important avenue for future work. This could be examined by investigating the behaviour of migrants using feeders at sites where fuelling durations are expected to vary. For example, Reed Warblers in Portugal in autumn or in Senegal in spring would be ideal study subjects (sections 2.3.2 & 2.4.1). Indeed, Dr Rob Thomas was carrying out work on Reed Warblers in Portugal in the autumn of 2003, having previously tested my system at a site in Wales.

Of the Reed and Sedge Warblers I gathered data on, few of the individuals had low FDRs, especially within the range typical of birds fuelling under natural conditions. By restricting access to food it is possible induce lower FDRs and generate data that could provide further support for my claim that fuelling durations are fixed. In the autumn of 2003, I manipulated food availability at one of the feeders by only providing mealworms for three hours each morning and two hours each evening. Whilst some individuals no longer attended the feeder after food availability was reduced, three individuals continued to use the feeder whilst also finding food in the surrounding area.
when the mealworms were absent. My experience with altering food availability suggests that food availability could be further reduced without birds ceasing to visit the feeder. It is important that feeders with higher food availability are not placed within at least 200 m of a feeder with low availability, as Reed Warblers were noted to have moved between feeders placed approximately 100 m apart.

Feeders with reduced food availability could also be used to test the effects of weather conditions on FDRs. At Icklesham, Reed Warblers continued to fuel under natural conditions when food was removed and adverse weather conditions were shown to dramatically reduce FDRs when food was absent (Fig. 7.1). Evidence for the effect of weather can also be looked for using a combination of historical ringing and weather data. Indeed, after the same period of rain covered in Fig. 7.1, I observed that Reed and Sedge Warblers caught in mist nets were in notably poorer condition relative to birds caught before the two days of rain. Further, direct comparisons could be made between frugivores and insectivores to see if conditions, such as persistent rain, differentially affect species that differ in prey choice.

In line with fuelling durations, sensitivity to flight conditions may vary at different points along the migratory journey. For example, Reed Warblers attempting to overfly the Mediterranean Sea and the Sahara desert from Portugal might be more likely to delay departure, whilst waiting for a tailwind, than birds crossing Europe. By combining data from a feeding experiment with weather data, increased sensitivity just before ecological barriers could be tested for.

Finally, the Reed/Sedge Warbler system could be used to test how a migrant’s perception of its predation risk alters its fuelling behaviour. Whilst increasing perceived predation risk is difficult to achieve in a quantitative way, a method such as playing alarm calls periodically within the vicinity of a feeder may provide an interesting insight, without the complications of trying to introduce a live or model predator into the system.

Other Species

Future work may also concentrate on other species of migrants to test whether my conclusions from Reed and Sedge Warbler fuelling behaviour apply to a wider range of species. Whilst running food supplementation experiments in Spain, I had a number of Great Reed Warblers attend the feeders and therefore this species would be
an ideal candidate for further investigation. Nightingales were also regularly seen at the feeders in Spain, but all of these birds were believed to be breeding at the site. However, migrating Nightingales would presumably also provide an ideal study subject. Reed Warblers of the eastern race *fuscus* would also be a very interesting candidate for future studies as they follow a different route to the race I studied.

**Organ Hypertrophy**

The existence of organ hypertrophy is still a contentious subject with regard to migratory passerines. The striking difference in FDRs between Reed and Sedge Warblers suggests that examining the digestive organs of ethically obtained corpses of these two species could provide some answers concerning this phenomenon.

**Optimal Modelling**

Future optimality models of migration should take into account some of the key findings of this study. These are that stopover costs appear to be minimal; fuelling durations are not a function of FDR but are fixed; fuelling behaviours can be selected to be optimal with regards to an expectation of future conditions; and that departure decisions will alter fuelling durations but not to the extent previously predicted, as sensitivity to flight conditions is lower than has been assumed.
Habitat degradation and destruction, climate change and agricultural intensification have all been cited as pressures responsible for causing declines in bird populations (Mead 2000). A number of migratory species within in Europe have declined in recent years (Marchant 1992, Wernham et al. 2002) and may be at particular risk from further environmental change. Migratory birds not only require intact breeding and wintering habitats (Sutherland & Dolman 1994, Sutherland 1996), they are also reliant on stopover habitats along the length of the migratory route (Farmer & Wiens 1998, Weber, Houston & Ens 1999). Changes to any of the habitats used by a migratory species could cause population declines, and simply conserving breeding habitats is not enough to ensure the survival of these species. To formulate a sound conservation plan for migratory species it is essential that we not only identify both breeding and wintering habitats but that we also evaluate specific migratory routes, identify key fuelling areas and have a sufficient understanding of migratory strategies to create a network of stopover habitats that allow the successful completion of migration (Bairlein 2000, Wernham et al. 2002).

Long distance migrants may be more at risk than short distance migrants as they can be affected by changes over a much larger geographic area. For example, the Chiffchaff Phylloscopus collybita and the Willow Warbler Phylloscopus trochilus share morphological and ecological similarities but winter in the Mediterranean and sub-Saharan Africa respectively. The former has shown a consistent increase over the last 40 years or so in Britain whilst the latter showed a dramatic decline about 10 years ago, particularly in southern Britain, although the population is now recovering (Mead 2000). Other long distance migrants have also been through dramatic population declines (especially in the 1970s) linked to the levels of rainfall in West Africa (Marchant et al. 1990): a factor that does not affect short distance migrants. Climate change appears to be having a more adverse affect on long distance migrants than short distance migrants. Jenni & Kéry (2003) argued that the earlier onset of the dry season in the Sahel region of Africa is causing some trans-Saharan migrants to fly south earlier, curtailing their breeding season and placing an increasing time pressure on their migration. Earlier departure dates are apparently not compensated for by earlier return
dates in spring that are less variable and thus constrain the start of reproduction (Both & Visser 2001).

The Reed Warbler is a typical trans-Saharan migrant and here I demonstrate that through a combination of analysing historical datasets, experimental work and theoretical work, it is possible to make informed conclusions about the migratory strategy and therefore the habitat requirements of this species during migration. I hope that this approach can be used to assess the requirements of other migratory species.

To estimate the distance migrants cover during flight phases, it is necessary to know the efficiency with which fuel stores are used and whether fuelling occurs during what would be considered a flight phase. The efficiency of fuel store use in terms of the directness of flights towards the migratory goal is an unknown quantity whilst estimates of the distances that can be covered on a given fuel store are becoming increasingly accurate (Pennycuick 1998). In the following calculations and discussions I have assumed that migrants use accumulated fuel stores with a high degree of efficiency. This approach can be justified on the grounds that in most of the calculations I present, I have assumed that a bird has no assistance from tailwinds. As some birds will receive wind assistance during flights whether by chance or through choice, the increased efficiency of fuel use during such flights will compensate for overestimates of the efficiency of fuel use in still air conditions.

Fuelling during ‘flight phases’ is also an unknown quantity and a number of scenarios may arise. For migrants that migrate only by night, daytime stops between flights may provide suitable refuelling opportunities. However, it is unknown whether birds only obtain enough energy to meet their daily energy requirements or if fuel is deposited during stops. Fuelling during daytime stops would be the optimal behaviour, but physiological changes associated with endurance flights may constrain the ability of birds to fuel during daytime stops (Klaassen & Biebach 1994). Clearly for some birds flying over water or even desert, stopping is not an option, or at least a stop will not provide any refuelling opportunities.

### 7.2.1 REED WABLER MIGRATION STRATEGIES

In the following section, I will discuss and frame hypotheses on the autumn migration strategy of Reed Warblers breeding in the UK. However, I will also make
inferences about populations elsewhere in Europe and the strategy used by spring migrating birds.

Ringing recoveries have highlighted the routes and destinations of Reed Warblers breeding in the British Isles and it is clear that many birds migrate to southern Portugal or to the far southwest of Spain where they are widely believed to accumulate fuel loads sufficient for crossing the Sahara desert. The distribution of recoveries along the way points to many birds utilising the western seaboard of France as an area for refuelling or resting between flights (Wernham et al. 2003). Although the distribution of ringing recoveries cannot be taken at face value, as there are many inherent biases in their distribution, I will use them as a guide in the following analyses.

Southern England to Southern Portugal

Experimental work on Reed Warblers at Icklesham suggested that a fixed fuelling duration rather than a variable response to the FDR largely determined fuelling behaviour. The mean duration of food-supplemented birds was six days (rounded to whole day) whilst un-supplemented birds had a mean duration of 10 days (likely to be an overestimate, see section 2.5). Schaub & Jenni (2001) found that stopover durations were remarkably constant between 12 widely spaced sites in Europe and gave a mean duration and standard deviation of $9.5 \pm 2.2$ days. A similar finding for Garden Warblers also points to stopover/fuelling durations being under fixed across a wide range of European sites. As the authors were calculating stopover durations and not fuelling durations, the actual time spent fuelling is likely to be shorter (see section 2.5 & 4.4). Therefore, I shall assume a fuelling duration of six days for the following calculations, as this is the most accurate estimate of fuelling duration I have.

The mean ‘positive’ FDR of naturally fuelling birds at Icklesham was 0.018 (fraction of LBM/day). Therefore if a bird fuelled at this rate for six days it would accumulate 1 g of fuel. Assuming that a bird starts fuelling at 10.5 g (mean body mass for Reed Warblers carrying no visible fat at Icklesham) then a bird would have a final body mass of 11.5 g and would be capable of a flight to the Atlantic seaboard of France, a distance of between 500-700 km (Fig. 7.3 & 7.4): where recoveries of British ringed birds are common. If the bird fuelled at the same rate at subsequent stopover sites, it would take two more fuelling stages before the bird reached key fuelling areas in
FIGURE 7.3: Flight ranges of Reed Warblers carrying different fuel loads departing from Icklesham in southern England. Flight ranges were calculated using the latest version of Pennycuick’s flight program (Flight 1.11, accessed 17/01/03, http://nhsbig.inhs.uiuc.edu/wes/pennycuick.html). Birds were set up with a wingspan of 0.195m, a wing area of 0.00723m² and a flight altitude of 500m. The default setting of 0.17 was used for the flight muscle fraction. The fat mass was calculated by subtracting the lean body mass of a bird of average wing length (wing = 65 mm, LBM = 10 g) from the ‘empty body mass’ and taking 75% or 85% of that figure. Thus 75% or 85% of any mass increase is expected to be fat whilst the rest is expected to be protein combined with water that may contribute to the flight muscles or to any other protein based structures in the body. Exact fat percentages of fuel stores are unknown but most studies suggest a figure between 65-85% (Klaassen 1996). The figures next to each curve give firstly the fat percentage of the fuel store and secondly the wind assistance received in m/s. For all other factors, the default settings were used. The labels (e.g. France) indicate the distance from Icklesham, England, to certain geographical regions.
Portugal. However, FDRs at Icklesham were likely to have been underestimated for the same reasons as fuelling durations were (see section 2.5).

Having discovered from experimental work that fuelling durations are only six days in length, it makes sense to look at the FDRs of birds that were retrapped over short periods and were therefore likely to be fuelling for the entire time between captures. This approach may be advisable in future studies if accurate measures of FDRs are to be obtained from ringing data. By taking birds that were present for between one to three days at Icklesham and making a conservative assumption that a fuelling bird can gain at least 0.1 g a day (a single prey item may weigh 0.1 g), the mean FDR for Reed Warblers became 0.033 (N = 115). This would result in a fuel load of 1.9 g and a final body mass of 12.4 g, if a bird commenced fuelling at 10.5 g and fuelled for six days. This is only slightly higher than the mean body mass of non-moulting juvenile Reed Warblers at Icklesham (12.2 g), a similarity that supports a fuelling duration of six days for non-experimental birds. A fuel load of this magnitude would enable a bird to fly at least 800 km and reach areas in southwest France close to the Spanish border and therefore only one stopover would be required in order to reach fuelling areas in Portugal (distance from Icklesham to Quinta da Roche \(\approx\) 1700 km; Fig. 7.4).

To reach southern Portugal in one stage without refuelling, a Reed Warbler would require a body mass of approximately 13.5 g or greater (Fig. 7.3). Of the 115 birds used to calculate the mean FDR of 0.033 above, 15% of them would have achieved a fuel load of 13.5 g or more if they had fuelled for six days. Thus a single stage strategy could be relatively common amongst Reed Warblers at Icklesham. This is further supported by the percentage of non-moulting juveniles that weighed more than 13.5 g. Excluding birds weighing less than 11.25 g on the assumption that they had not finished fuelling, 25% (117 birds out of 459) of non-moulting juveniles caught at Icklesham could complete the journey to southwest Portugal without refuelling.

The calculations presented in the last two paragraphs do not take into account two mechanisms by which migrant birds could increase their flight range with a given starting fuel load:

A – The intensity of migration has long been known to vary with weather conditions (Able 1973, Richardson 1978, Alerstam 1979, 1990, Elkins 1988). In Chapter 6 I demonstrated that the departure decisions of Reed Warblers were influenced by wind
conditions and that the majority of birds departed with a tailwind. The mean assistance for Reed Warblers choosing tailwinds was a 1.8 m/s increase in flight speed. If a bird flies at 10 m/s (Åkesson et al. 2002), the mean level of assistance would increase flight range by 18%. Therefore, with wind assistance a bird weighing approximately 12.5 g or more could complete the journey to southern Portugal without refuelling. Further a body mass of 11.25 g could enable a bird to complete the journey with just one refuelling stop (Fig. 7.3). Assuming that Reed Warbler flight ranges are regularly increased by tailwinds then approximately 50% of non-moultng juvenile Reed Warblers at Icklesham had sufficient fuel to fly to Portugal without the need to refuel.

B - Passerines on autumn migration migrate almost exclusively by night (Alerstam 1990) and rest in suitable habitat by day. Thus a migrant that has accumulated enough fuel to fly for two or more consecutive nights has the option of accumulating additional fuel during daytime stops. Whether birds routinely gain fuel, simply rest or only obtain enough energy to maintain their present fuel store during these stops is unknown. Migrants stopping in Saharan oases for a day rarely gained mass (Biebach et al. 1986, Safriel & Lavee 1988), whilst Reed Warblers in spring in NE Spain routinely increased their mass during daytime stops (section 2.4.2), as do a number of spring migrating North American species (Moore & Keling 1987, Yong & Moore 1997). For highly time-stressed spring migrants, fuel gains between nights with successive flights may represent their main fuelling strategy and these fuelling bouts are part of what we term stopovers. However, in the case of autumn migrants that show distinct stopovers several days in length, it is difficult to define whether fuel gains during daytime stops are stopovers or an as yet undefined phenomenon. Fuel gains by birds stopping for one day in autumn have yet to be proven and would seem to be an important avenue for future research.

Making the conservative assumption that a Reed Warbler flies for six hours each night with no wind assistance at a speed of 10 m/s (estimate used in Åkesson et al. 2002), it could fly approximately 216 km in a night. A Reed Warbler flying some 2,620km from Falsterbo, Sweden (N56°4´ E12°8´) took 16 days to reach Quinta da Rocha, Portugal (N37°8´, W8°43.5´), equivalent to a speed of 163 km/day (assuming that the bird flew every night and departed on the day of capture from Falsterbo and was caught on the day of arrival in Portugal). If this bird did not fly on every available evening, an estimate of 216 km a night seems reasonable. For a Reed Warbler covering
216 km per night it would take eight nights and seven daytime stops to fly from Icklesham to fuelling areas in southern Portugal (≈1650 km), if there were no interruptions. If one makes a further conservative assumption that a bird only accumulates an additional 0.2g of fuel on each daytime stop (birds in NE Spain regularly increased in mass by 1g over an entire day), across seven stops this results in an additional 1.4g of fuel. Thus under this scenario a bird leaving Icklesham with a fuel load of 12.1g could reach Portugal in one flight stage with the extra fuel. Therefore, if birds at Icklesham adopted this strategy, approximately 70% of non-moulting juvenile Reed Warblers could reach Portugal without having to initiate a refuelling stop longer than one day. Clearly such a strategy requires there to be suitable fuelling habitats to make daytime stops in.

If migrants regularly adopt a strategy of fuelling on daytime stops, then our present interpretation of strategies, based on the fuel loads of birds at departure from stopover sites, may greatly underestimate the distance a bird can cover on an initial fuel load. Our present understanding of specific migratory strategies could therefore change dramatically if fuelling occurs both during distinct stopover phases and between successive night flights.

**Moulting Reed Warblers**

In all the calculations and estimates made above, I have only considered non-moulting juveniles. However, a large percentage of the birds caught at Icklesham were moulting and many appeared to be migrating whilst still actively moulting (section 2.3.1, Schaub & Jenni 2000a). The ‘apparent’ fuel loads of moulting birds were lower than those of non-moulting birds (section 2.3.1) and therefore flight stages were probably short in these birds until they completed their moult. Even so these birds would be capable of flights of approximately 300-400 km from Icklesham, after which a body mass of 11.5 g or more would be sufficient to cover the remaining 1,200 km to southern Portugal. Therefore moulting birds may still be able to reach southern Portugal with just one refuelling stop.
FIGURE 7.4: Theoretical Reed Warbler migration strategies from southeast England. The green areas represent fuelling areas that are potentially crucial for Reed Warblers following a typical strategy. Red dots connecting arrows represent fuelling stops. The strategies are as follows:

1 – One stage flight to southern Portugal/southwest Spain without refuelling. Birds attaining 13.5g or above could use this strategy, as could birds with smaller fuel loads (body mass of >12.5g) if they had wind assistance or fuelled during daytime stops between flights. The lack of recoveries from the north coast of Spain (Wernham et al. 2002) suggest that few birds make direct flights across the Bay of Biscay and instead birds migrate firstly to southwest France and then cross the Iberian peninsula to southern Portugal.

2 – Two stage strategy, using the Atlantic coast of France as a fuelling stop. Birds with a body mass of 11.5g and above could use this two-stage strategy.

3 – Possible strategy adopted by moulting juveniles. A short stage to northern France may be made whilst the moult is completed, before flying to Portugal in two stages. Alternatively, a single stage to Portugal from northern France could be made with sufficient fuel.

The percentage of juveniles adopting each strategy, based on the body mass distribution of birds which had completed or nearly completed their moult at Icklesham, are presented in the figure. These are conservative estimates as they assume that birds receive no wind assistance and do not fuel during day time stops. Therefore the percentage of birds adopting strategies 1 and 2 may be considerably higher e.g. 45% could achieve strategy 1 if birds fuel on day time stops.
Portugal to sub-Saharan Africa

The distance from a site such as Quinta da Roche, SW Portugal to Djoudj in West Africa is approximately 2,420 km. Reed Warblers would therefore require a body mass of approximately 16 g or more to over fly the Sahara and complete the journey without refuelling. Reed Warblers at Quinta da Roche regularly had body masses of this magnitude or greater (section 2.3.2) and would therefore be capable of a non-stop flight from SW Portugal to suitable habitat in sub-Saharan Africa. Ringing recoveries of British birds showed that stops in Northern Morocco were made (Wernham et al. 2002) and therefore birds leaving Portugal with loads less than 16 g may be able to use sites in Morocco to accumulate the extra fuel needed cross the Sahara. Birds with body masses less than 16 g may be able to use wind assistance to make the Sahara crossing possible. Indeed, Moreau (1961) estimated that a tailwind of 16 km h⁻¹ blew over the Sahara for 60% of the time in autumn.

Djoudj, Senegal to North Africa/Southern Europe

Reed Warblers migrating north from Djoudj in spring attained smaller fuel loads than birds migrating south from Portugal in autumn. This suggests that birds were not making non-stop flights to southern Europe but instead were stopping at suitable habitat in N Africa to refuel. N Africa is at its most fertile at this time of year and thus this would be a plausible strategy (Alerstam 1990). A flight from Djoudj to N Africa would require a body mass of approximately 14-15g. Fuelling birds at Djoudj regularly achieve such fuel loads and would therefore be capable of a single stage flight north across the Sahara (section 2.4.1).

Spring Migration through Europe

Reed Warblers in NE Spain regularly increased in body mass by one gram over the course of a single day. These increases would provide sufficient fuel for a flight of 400 km. If the length of night flights is approximately 200 km, then these rapid fuelling bouts could provide enough fuel for two nights flying. The Reed Warblers caught in NE Spain were mainly destined for Central and Eastern Europe (unpublished recovery data) and therefore it is unclear whether Reed Warblers of British origin adopt the same
strategy. However, if British Reed Warblers do make these rapid fuelling gains, then they could complete the journey from southern Europe to the UK in 8-9 days without having to make a fuelling stop longer than one day.

7.2.2 IMPLICATIONS FOR FUELLING/STOPOVER HABITAT CONSERVATION

The breeding population of Reed Warblers in Britain has been stable if not increasing over the last 50 years. Indeed, Reed Warblers have colonised many new areas in both the north and west of Britain and have even expanded into Ireland (Mead 2000). However, Reed Warblers have declined in southern Europe (Cramp 1992, Snow & Perrins 1998) and the increase in Britain may be associated with global warming as the range where ecological conditions are suitable shifts gradually northwards (Travis 2003). The effects of continued global warming and habitat destruction will have an unknown affect on Reed Warblers and other migratory species, thus it is important to understand their migratory strategy and identify key fuelling areas for this species and others now.

I have shown that non-moulting juvenile and adult Reed Warblers on autumn migration in southern England typically accumulate sufficient fuel to make the flight to important fuelling areas in southern Portugal and SW Spain without the need to refuel or by making just one refuelling stop. This suggests that there are two key fuelling areas for birds migrating from Britain to Portugal. The first is in Britain itself, where the breeding habitats must double as crucial fuelling habitats. Whilst Reed Warblers will breed in relatively small areas of reeds e.g. patches lining ditches, more extensive areas may be important for fuelling birds in the autumn. The second area is likely to be the Atlantic coast of France from around Nantes (N47°20’, W2°25’) south to the border with Spain where the high mountains of the Pyrenees begin (N43°23’, W2°15’). This is a long stretch of coast with some large wetland areas that provide suitable fuelling habitat for Reed Warblers and numerous recoveries of British ringed birds have come from this region (Wernham et al. 2002). There have also been many recoveries of Sedge Warblers in the same region (Wernham et al. 2002), which suggests that it is also an important fuelling area for this species. Indeed Bibby and Green (1981) showed that Sedge Warblers attained high FDRs and departure loads in the north of this region and
therefore it is likely that this coast is a crucial staging area for Sedge Warblers before they embark on a flight to sub-Saharan Africa without refuelling (see section 5.1).

Juvenile Reed Warblers that are still moulting are reliant on other areas for fuelling as well. As they are likely to only make short flight stages from southern England until they have finished moulting, wetland areas in northern France may be of particular importance to these birds. Indeed, ringing recoveries show that juveniles regularly stop in northern France whilst adults rarely do (Bibby & Green 1981), a difference that could result from the constraints placed on fuelling by moult (section 2.3.1).

The conservation of suitable wetland habitats within the UK, northern France and along the Atlantic coast of France is vital for the continued success of Reed Warbler migration. If these habitats are degraded or destroyed then the FDRs that Reed Warblers are able to achieve are likely to decrease, resulting in longer migration times. For example, under present conditions the journey from southern England to Portugal given a fixed fuelling duration of six days and an FDR of 0.033 would involve 12 days of fuelling and approximately nine nights of flying. Allowing for interruptions and search and settling costs one might expect the entire journey to take between 21 and 30 days. If FDRs at all sites were to drop as low as 0.015, then birds would require three fuelling stops totalling 18 days and a further nine days would be required for flight. Again allowing for interruptions this would lead to a total duration of between 27 and 36 days. Given that Reed Warblers have been selected to minimise time during migration (Chapter 4), longer durations of this nature may have important fitness consequences.

Further, my finding that fuelling durations are fixed and not a flexible response to FDRs, suggests that fuelling behaviour will not respond flexibly to lowered food availability and therefore FDRs in real time. Instead, the optimum fuelling duration will have to evolve in response to new levels of food availability. This is likely to be a slow and gradual process and thus rapid changes in fuelling site quality could have a dramatic effect on migrating Reed Warblers.

The fuelling habitats in southern Portugal and SW Spain may play an even more crucial role in the strategy of autumn migrating Reed Warblers. These habitats provide sufficient fuelling resources for birds to make the long journey across the Sahara desert: if these habitats are destroyed or degraded, the ability of Reed Warblers to cross the Sahara may be severely impaired. This problem could be compounded by the gradual widening of the Sahara Desert, which was vegetated as recently as 5,500 years ago (e.g.
The recent reductions in rainfall in the Sahel region south of the Sahara may also add to this problem: it has already been shown to have a dramatic affect on Whitethroat (Winstanley et al. 1974) and Sedge Warbler populations (Peach et al. 1991). If global warming and the actions of humans cause further expansion of the desert, further reducing the quality of the Sahel region, then the preservation of fuelling sites either side of the Sahara may be one of the most important tools for aiding the survival of Reed Warblers and other trans-Saharan migrants. Some of these sites are already at risk: damming and flood prevention measures have already significantly reduced the area of wetland around the Senegal River delta, of which Djoudj is part (section 2.2).

Conserving sites that are known for high concentrations of fuelling migrants may also benefit species that show high site fidelity. Cantos & Telleria (1994) and Merom et al. (2000) demonstrated that long distance migrants show a relatively high degree of fidelity to stopover sites on the Iberian peninsula and in Israel respectively. Indeed Reed Warblers showed higher levels than the other species studied. This suggests that familiarity with high quality sites may be an important mechanism by which adults make rapid and successful migrations. Identifying and conserving sites to which birds show a high fidelity may be an important mechanism for maintaining a suitable network of stopover sites.

The effect of the destruction of individual fuelling sites is difficult to predict. If for example a high-quality fuelling site on the Atlantic seaboard of France was drained, the effect on migrating Reed Warblers may be minimal unless there were few similar sites nearby. Indeed, if Reed Warblers maintain a basic level of reserves, equivalent to 0.5 g of fuel for example, then this would allow them to make a flight of approximately 200 km in search of an alternative fuelling site. Thus if we could conserve extensive wetland habitats, spaced approximately 150 km apart along the coast, then the impact on migrating Reed Warblers would be minimal if sites between were destroyed due to the pressures of human activity. A similar approach may be appropriate for other migratory species.

7.2.3 SUMMARY

By investigating Reed Warbler fuelling behaviour I have been able to obtain insights into the migratory strategy of this species that complement the knowledge we
already have from ringing and recovery data. By having a fuller understanding of fuelling behaviour and therefore the fuel loads birds may attain, it has been possible to validate whether the pattern of recoveries to date gives an accurate picture of site use, given the feasibility of accumulating the fuel loads required to reach them. Knowing the fuelling duration of a typical Reed Warbler at Icklesham also enables one to see through the very confusing picture created by ringing data alone. A straightforward analysis of ringing data can lead to underestimates of FDRs because fuelling durations are typically overestimated leading to the inclusion of periods during which birds are not fuelling. Consequently, departure fuel loads are underestimated because birds with low fuel loads are thought to be a product of low FDRs rather than being recognised as individuals that have not started or not finished fuelling. It was this approach using just ringing and recovery data that led to the conclusion that juvenile Reed Warblers make two or more refuelling stops in order to reach southern Portugal from southern England (Bibby & Green 1981, Wernham et al. 2002). However, the approach I have taken points to juvenile Reed Warblers typically completing the journey without needing to refuel or just refuelling once in southwest France, unless they are moulting. This view is in agreement with the pattern of recoveries to date and suggests that recoveries away from coastal northern France, the Atlantic coast of France and southern Spain/Portugal are probably due to birds making daytime stops. This could explain why recoveries in the key regions that I have outlined are numerous, as birds are actually stopping for several days, whilst recoveries from other areas are scarce as birds are only stopping for a day at a time, and therefore the probability of capture is low.

Further detailed experimental studies of fuelling behaviour may shed light on the strategies of species for which ringing and recovery information is scarce, allowing a more accurate picture of site use to be generated.
7.3 FINAL SUMMARY

The fuel load attained at the end of a fuelling phase determines the distance a migrant can fly during subsequent flight phases, the choice of and distance between refuelling sites, and the amount of time and energy it takes to complete a migratory journey successfully. The fuel load itself is a function of two key variables: the rate of fuelling and the duration of fuelling (Fig. 7.5).

For long distance migrants such as Reed and Sedge Warblers, I found that the fuel deposition rate is not simply a response to food availability and quality, although food availability is probably the most influential factor. Migrants selected to minimise the total time spent on migration will typically maximise their FDR. However, where the advantages of minimising time are outweighed by other considerations, rates can be below the physiological maximum. For example, foraging rates and therefore FDRs may be suppressed in order to maintain vigilance and therefore avoid the heightened predation risk associated with high foraging intensities. Phenotypic flexibility of the digestive organs can lead to higher FDRs through an increase in digestive capacity/flexibility: this phenomenon has been demonstrated in a number of migratory species, although the contribution organ flexibility makes to the fuelling behaviour of long distance passerines is unknown. However, I found extremely high FDRs in Sedge Warblers relative to Reed Warblers and also showed that Reed Warblers had marked variation in their lean body mass during the annual cycle: these two findings might be explained by differences in the mass and capacity of the digestive organs.

The range of FDRs observed in the majority of migratory passerines fuelling under natural conditions is small (Schaub & Jenni 2000a) and therefore fuelling durations may contribute more to variation in fuel loads between species than FDRs. I found that the fuelling durations of Reed and Sedge Warblers were significantly different between species but strikingly constant within each species, and therefore appear pre-determined, rather than a functional response to a variable such as food availability. This novel conclusion is supported by work both on caged migrants that displayed distinct temporal patterns of restlessness (Gwinner 1996) and by crossing experiments in which the periods of restlessness of intermediate length found in hybrids, pointed to a genetic basis (Berthold 1999). Fuelling durations in the case of Reed and Sedge Warblers and presumably other long-distance migrant passerines, are likely to have been shaped by the range of FDRs typically encountered coupled with selection for minimising the total time spent on migration.
Whilst the length of predetermined fuelling durations will significantly impact on the final fuel load accumulated, durations, and therefore fuel loads, will vary to a limited degree due to unfavourable weather conditions (wind direction in particular) delaying departure. Further, fuelling durations will not be constant along the length of the migratory journey. Indeed temporal, magnetic or environmental cues are expected to bring about switches in duration according to the journey ahead. Thus longer durations occur when the expectation of future fuelling conditions is low, e.g. when a migrant is approaching a barrier, whilst shorter durations will occur when future conditions are expected to be better than those currently experienced. Expectations such as these must be hard wired and have evolved in response to patterns of resource availability over time; otherwise juvenile birds migrating for the first time would be unlikely to successfully cross large ecological barriers such as the Sahara desert. I found strong evidence that an expectation of future conditions had shaped the fuelling behaviour of Sedge Warblers in southern England. Finally, I would expect there to be a mechanism by which the fuelling period can be re-started if fuelling has been particularly unsuccessful and a threshold level of fuel has not been achieved.

I have contributed to our knowledge of migratory behaviour by demonstrating that two further species of long distance migrants have evolved to minimise time whilst migrating. Therefore, time-minimisation may be the most important selective force shaping the behaviour of long-distance migrants. However, I have also shown that the fuelling behaviour of both these species has not been shaped by time alone. I have presented evidence that suggests that two further variables, FID predation risk in Reed Warblers and a fixed expectation of future FDRs in Sedge Warblers, can influence fuelling strategies: neither has previously been linked to fuelling behaviour. I have also presented striking evidence that fuelling durations are fixed and do not vary with FDR as has been predicted by optimality models. This is an important step in our understanding of the control of fuelling behaviour. It suggests that fuelling durations are likely to be controlled by an endogenous time program linked to the circadian clock. Finally, I have made an important contribution to our understanding of departure decisions in migrating birds with respect to weather conditions.

In summary, fuelling rates, determined by prey choice and abundance, coupled with fixed fuelling durations selected by time and resource availability are the most important determinants of the strategies of long-distance migratory passerines (see Fig. 7.5 for pictorial summary of conclusions).
FIGURE 7.5: A summary model of the variables influencing fuelling behaviour for long distance migrants, based on the fuelling behaviour of Reed Warblers and Sedge Warblers. Positive and negative signs next to arrows indicate the influence a variable has. Arrow thickness indicates the hypothesised strength of each variable’s contribution. The chapter(s) in which I have increased our knowledge of the influence of a given variable is also indicated.
REFERENCE LIST


