

Behavioural and Physiological Reactions to Environmental Variation in Bird Migration: a Review

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1 Introduction

Many features of the migration of passerine birds are endogenously programmed and have a strong genetic basis. At least in inexperienced migrants, the general seasonal course of migration is endogenously controlled, such as the onset, the temporal pattern, the direction of migration and the seasonal pattern of energy stores. This leads to the conclusion that an endogenous spatiotemporal migration programme guides inexperienced migrants from their place of birth to their first winter quarters (summarized in Berthold 1996).

However, an endogenous spatiotemporal programme is probably not sufficient to lead birds to their first winter quarters (Gwinner 1996; Thorup and Rabøl 2001). Photoperiod acts as the most important synchronizer of circannual rhythms and accelerates or inhibits individual migration processes (Berthold 1996; Gwinner 1996). There is a large body of observations on environmental factors influencing bird migration. However, as concluded by Berthold (1996), many of these observations remain inconclusive with respect to whether and how exactly environmental factors influence migration and modify the endogenously programmed course of migration. Furthermore, many physiological constraints and adaptations have been shown to influence migration (Jenni and Jenni-Eiermann 1998; S. Jenni-Eiermann and L. Jenni, this Vol.).

Since the paper by Alerstam and Lindström (1990), bird migration has been examined under the aspects of optimality. The models, based on the theory of flight mechanics, more and more include behavioural reactions to environmental factors, such as wind, food availability, disposition of stop-over habitats (e.g. Weber and Houston 1997a; Weber et al. 1998b; Weber 1999). The models generally do not consider the endogenous framework within which the bird is able to migrate and react. Furthermore, the choice given to the model birds is only behavioural, rather than physiological. However, Bautista et al. (1998) have shown in the context of optimal foraging models that behaviour and physiology need to be integrated to fully account for the observed behaviour of the bird.

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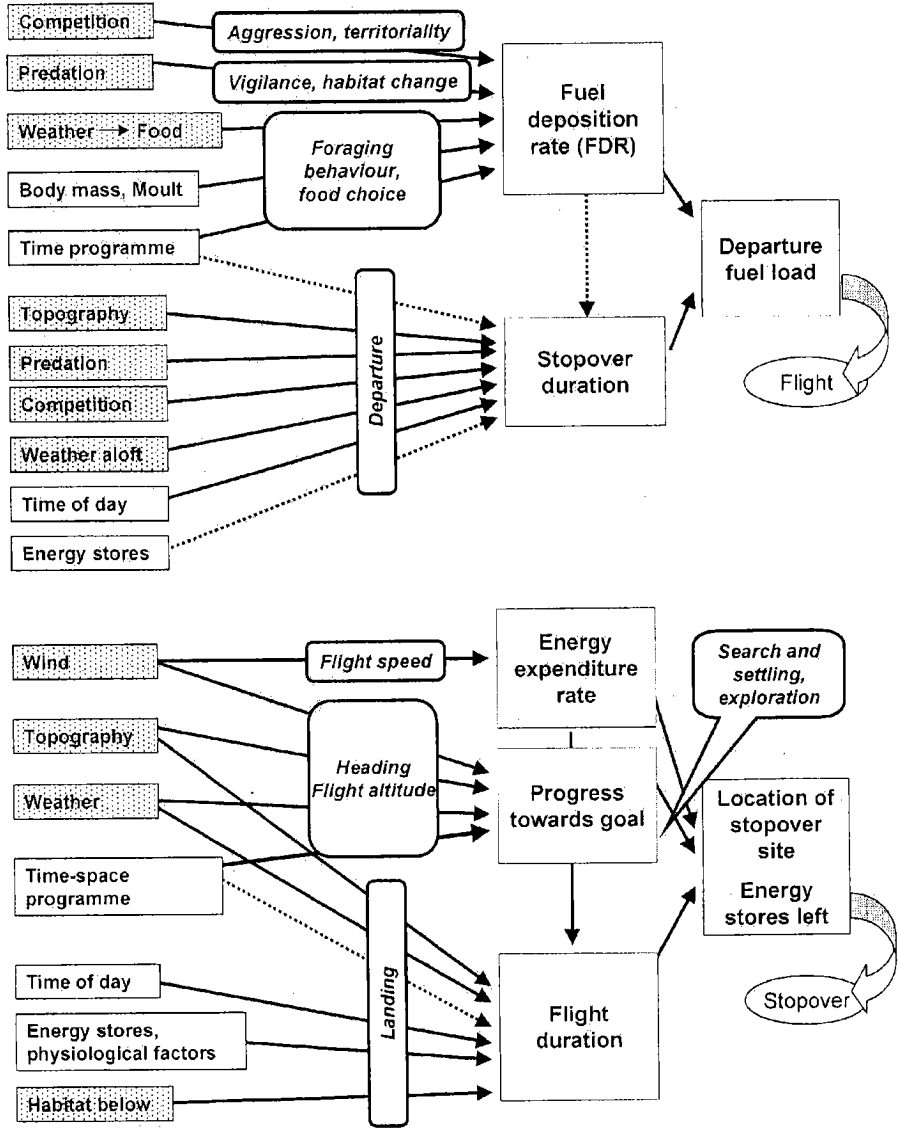


Fig. 1. Schematic representation of factors which have been shown to influence migration in field or laboratory studies. Various environmental (shaded boxes), intrinsic and endogenous factors influence via behavioural reactions (rounded boxes, text in italics) the main parameters of migration: during stopover (upper part) the two main parameters, fuel deposition rate (energy component) and stopover duration (time component), which determine departure fuel load, the starting point of flight; during flight (lower part) the three main parameters, energy expenditure rate (energy component), progress towards goal (spatial component) and flight duration (time component), which determine the location of the stopover site and remaining energy stores, the starting points of stopover. Dotted arrows indicate effects which are weak or hold under certain circumstances only (see text). The box time programme also includes the effects of photoperiod (progress of season)

Hence, three main questions appear regarding our understanding of the course of bird migration: what are the environmental factors influencing bird migration?; to which factors do the birds react behaviourally and physiologically, and how?; how do the behavioural and physiological reactions to environmental factors interact with the endogenous spatiotemporal migration programme? The aim of this chapter is to review the current literature about the proximate environmental influences on bird migration and the behavioural and physiological reactions of birds to the environmental situation during migration. This, we hope, is a step towards understanding the proximate rules of reaction to the environmental situation which complement, and help to implement, the endogenous spatiotemporal programme.

This discussion is based on small night-migrating passerine birds, because their endogenous control of migration has been investigated thoroughly and because our experience is with these birds. Most birds do not migrate in one flight bout, but divide their migration into phases of flights and stopovers. Thus, there are two alternating stages (stopover and flight) on which environmental factors can act. The distance may be covered in several small or a few long flight bouts. At good stopover sites, energy stores are deposited to be used partly or completely during the next flight bout.

The main variables which determine the progress and time schedule of migration are: fuel deposition rate and stopover duration which determine departure fuel load; energy expenditure during flight, direction of flight and duration of a flight bout which give the flight vector; and the time and energy needed to settle in a new stopover site (Fig. 1). The bird has to take two main decisions: when to depart from a stopover site, and when and where to land.

2 Stopover, Fuel Deposition and Departure Decision

2.1 Fuel Deposition Rates (FDR) and Behavioural Reactions

The seasonal onset of fattening and the main seasonal course of energy stores is endogenously controlled (reviewed in Gwinner 1990). Migrants endogenously start hyperphagia and deposit fat at the beginning of the migratory period and decrease fat deposits at the end (Berthold 1996).

FDR may be thought to depend mainly on food availability (Fig. 1). Evidence is provided by several studies demonstrating that differences in FDR between sites, and within sites between years, are correlated with food abundance (e.g. Bibby and Green 1981; Graber and Graber 1983). Supplemental feeding in the field increases FDR compared with conspecifics not receiving additional food (Fransson 1998; Dänhardt and Lindström 2001).

As known from the breeding season, food availability for most insectivores is influenced by weather. However, there are surprisingly few studies investigating effects of weather on FDR during stopover. FDR was dependent on weather in two insectivorous species, but not in the frugivorous garden war-

bler, *Sylvia borin* (Schaub and Jenni 2001b). We found decreasing FDR (measured by plasma metabolite levels, see Jenni-Eiermann and Jenni 1994) with increasing wind speed and just after rain in small passerines in autumn (own unpubl. data).

FDR depends not only on food availability, but on other environmental and intrinsic factors (Fig. 1). Among the environmental factors, birds have been shown to adjust their FDR in response to predation risk and competition.

Under risk of predation, migrants may react in different ways, depending on whether the risk of predation is independent of, or increasing with, increasing time spent foraging (Fransson and Weber 1997; Weber et al. 1998b). With predation risk independent of foraging time, birds should increase foraging intensity in order to shorten stopover duration, as shown in an experiment (Fransson and Weber 1997). If predation risk increases with foraging time, birds should decrease foraging time, as found in a field study (Cimprich and Moore 1999). Another reaction is to select a habitat with less predation despite a lower food intake rate, thus minimizing the predation risk per energy intake (Lindström 1990). As suggested from optimal migration models (Weber et al. 1998b), predation is potentially an important factor shaping fuel deposition.

FDR may be affected by inter- and intraspecific competition (e.g. Moore and Yong 1991) and dominance may be correlated with size (Lindström et al. 1990). Subordinate birds (e.g. females) may compensate for their subordination by feeding longer and may have a similar FDR as dominants (Carpenter et al. 1993). Certain species establish temporal feeding territories necessary for efficient fuel deposition (e.g. Rappole and Warner 1976; Bibby and Green 1980; Dierschke and Delingat 2001). Species feeding on superabundant food resources are not aggressive to conspecifics (e.g. Bibby and Green 1981; Fransson 1998). It is unclear whether the establishment of territories varies in response to competition or food distribution.

Among the intrinsic factors, moult and current body mass affect FDR (Fig. 1). Moulting birds do not deposit fuel or have a lower FDR than birds at the end or after moult (Lindström et al. 1990; Fransson 1998; Schaub and Jenni 2000b).

FDR was found to be positively or negatively or not related with current body mass. FDR was higher in fat birds than in lean birds in a study investigating four species of passerines migrating over Europe during autumn, i.e. before crossing an ecological barrier (Schaub and Jenni 2001b). High energy reserves during stopover impair predator escape (e.g. Lind et al. 1999; Kullberg et al. 2000) and increase costs of maintenance, flight and foraging (Klaassen and Lindström 1996). Hence birds may shorten the period of high body mass at a stopover site by feeding at maximum intensity, as suggested by the model of Weber et al. (1998b), if predation risk is not dependent on foraging intensity. In contrast, in birds having crossed an ecological barrier, lean birds were found to have a higher FDR at arrival than fat birds (Loria and Moore 1990; Kuenzi et al. 1991). After crossing an ecological barrier, lean

birds may have a stronger urge to restore energy stores than fat birds. White-throats, *Sylvia communis*, had a lower FDR on the last day before departure (Fransson 1998), but other species showed a constant FDR during stopover (Lindström et al. 1990; Lindström and Alerstam 1992; Merom et al. 2000; Dänhardt and Lindström 2001). This demonstrates that birds are able to compensate for the increasing costs of a high body mass when their body mass increases.

An important factor influencing FDR is the progress of season (e.g. decreasing photoperiod in autumn, summarized under time programme in Fig. 1). The progress of season accelerates autumnal migratory fuel deposition in caged birds and in the field (e.g. Lindström et al. 1994; Fransson 1998; Bairlein 2000; Schaub and Jenni 2000b; Dänhardt and Lindström 2001). This accords with the finding that late-migrating individuals have higher fuel stores and higher FDR and seem to travel at a higher speed (e.g. Ellegren 1993; Fransson 1995; Schaub and Jenni 2000a,b).

The increased FDR later in the season of insectivorous passerines in autumn is surprising, because daylength (foraging time) and insect densities generally decrease with progressing season (Bibby and Green 1981; Turrian and Jenni 1991). The variable FDR suggests that migrants show a large behavioural flexibility in foraging depending on the urge to refuel. Indeed, light birds were shown to exhibit a more risk-prone foraging behaviour after a long non-stop flight than fat birds and a higher refuelling rate (Loria and Moore 1990).

2.2 Fuel Deposition and Physiology

There are a number of physiological and metabolic adaptations to endurance flight (summarized in Jenni and Jenni-Eiermann 1998; Butler and Bishop 2000). However, little is known about whether these physiological adaptations vary as a response to endogenous or environmental factors or whether they form a constant (species- or population-specific) set of adaptations. For instance, it could be imagined that a reduction in overnight basal metabolic rate (cf. e.g. Piersma et al. 1996; Bautista et al. 1998) or an increase in the efficiency of food utilization (cf. Bairlein 1985b) may facilitate fattening under stringent environmental conditions. Reduction of digestive organs prior to the onset of a flight bout has been considered as a means to increase flight range in waders crossing large oceans (e.g. Piersma and Gill 1998; Battley et al. 2000), but no such study was conducted in passerines. A low proportion of protein to fat deposited and concomitant adaptations to maximum fat catabolism may increase flight range (Jenni and Jenni-Eiermann 1998, 1999).

There is evidence that food composition influences the composition of fuel types stored (the ratio of protein to fat) which, in turn, determines the fuel types catabolized during flight and, hence, flight range (S. Jenni-Eiermann and L. Jenni, this Vol.). A complete or partial change from insectivory to frugivory (e.g. Bairlein and Gwinner 1994) or to insects rich in lipids or car-

bohydrates may facilitate fattening during stopover, which accords with field studies (S. Jenni-Eiermann and L. Jenni, this Vol.). If particular food types are necessary for rapid fuel deposition, selection of favourable stopover sites may be of much higher relevance than previously thought.

2.3 Stopover Duration, Departure Fuel Load and Departure Decision

Experiments with caged birds have shown that food availability and current fuel stores combined determine whether birds exhibit migratory restlessness or not (Biebach 1985; Gwinner et al. 1985; Yong and Moore 1993). Birds with high fuel stores, and birds with low fuel stores but without food, show migratory restlessness, while birds with low fuel stores and food do not. From these experiments, we would expect that birds should depart as soon as possible when there is no food and that birds with food available depart when a certain threshold of fuel is attained.

The first prediction is supported by field studies. Birds with a negative or a very low FDR are very likely to move on (e.g. Rappole and Warner 1976; Biebach et al. 1986; Kuenzi et al. 1991). The second prediction (departure at threshold fuel stores) is difficult to test with field data, because departure fuel loads are very difficult to determine and because a threshold of fuel stores most likely varies along the migration route and possibly between individuals.

A number of studies suggest that lean birds at capture stay longer than fat birds (e.g. Cherry 1982; Bairlein 1985a; Biebach et al. 1986; Moore and Kerlinger 1987; Loria and Moore 1990; Dierschke and Delingat 2001). However, stopover duration has not been measured reliably in some of these studies (see Schaub et al. 2001) or sample size was small. In the same or other studies, body mass at capture was unrelated to stopover duration (DeWolfe et al. 1973; Safriel and Lavee 1988; Kuenzi et al. 1991; Ellegren 1991; Morris et al. 1996; Dierschke and Delingat 2001). Along the migration route of three species of passerine birds, FDR varied substantially between sites (Schaub and Jenni 2000b, 2001b), but stopover duration was remarkably constant (Schaub and Jenni 2001a), indicating that birds did not vary their stopover duration in relation to FDR.

Many species deposit large fuel stores only just before crossing the Mediterranean Sea or the Sahara Desert (e.g. Schaub and Jenni 2000a). Although the endogenous course of fuel stores shows highest fat stores at a time when conspecifics normally cross these barriers (Berthold 1996), it seems unlikely that the endogenous programme is so precise as to increase fuel stores just before crossing barriers. It is more likely that birds react to some environmental cue (such as the magnetic field; Fransson et al. 2001) that announces an oncoming barrier and increase fat stores. Reversed migration before sea crossings has been interpreted as such a behaviour (Sandberg et al. 1988; Åkesson et al. 1996b; R. Sandberg, this Vol.).

In summary, it is evident that stopover duration is very short if FDR is low or negative. However, it remains unclear how stopover duration is regulated

when FDR is positive. It appears that stopover duration is frequently unrelated to both FDR and current energy stores, e.g. when migrating over areas with many stopover sites (dotted lines in Fig. 1). On the other hand, there is evidence that lean birds stay longer than fat birds before crossing an ecological barrier or when lean birds land in a desert oasis.

An endogenous rhythm of flight and refuelling may provide the framework of stopover duration. Rhythmic body mass changes of about 2 weeks may hint at such a regulation (Bairlein 1986). Also Safriel and Lavee (1988) suggest that departure from a stopover site is under a strong influence of the endogenous time programme, because a negative correlation between stopover duration and initial mass (hence reaching a certain departure fuel load) is absent even before crossing the Sahara.

Departure of night-migrating passerines is usually restricted to nighttime and departure of day migrants usually to the early morning hours. Although most night migrants appear to depart within 0.5–1.5 h after sunset (e.g. Bruderer 1997), there may be more variability than usually thought (e.g. Hebrard 1971; Cochran and Kjos 1985; Moore and Aborn 1996; Åkesson et al. 1996a, 2001; Bolshakov and Bulyuk 2001).

Furthermore, there are three environmental factors to which birds may adjust their stopover duration: predation risk, competition and weather aloft (Fig. 1). Predation risk may influence stopover duration, as suggested by an experiment (Fransson and Weber 1997), but there is no convincing field evidence (Dierschke and Delingat 2001). Probably, birds are more likely to continue migration when arriving at a crowded stopover site (Dierschke and Delingat 2001), especially in species establishing temporary territories (e.g. Rappole and Warner 1976).

Stopover duration is influenced by weather conditions aloft, particularly wind conditions. Birds increase potential flight range by selecting nights with favourable winds (Liechti and Bruderer 1998; Weber et al. 1998a). In radar studies, the number of birds aloft is considerably higher in favourable than in bad weather conditions, with rain, wind speed and wind direction as the main factors (Richardson 1990; Erni et al. 2002). Takeoff of grounded migrants was found to be more likely in nights with good visibility, no overcast, no rain and light or following winds (Cochran and Kjos 1985; Safriel and Lavee 1988; Bolshakov and Bulyuk 1999; Åkesson and Hedenström 2000; Åkesson et al. 2001; Dierschke and Delingat 2001; Dänhardt and Lindström 2001).

2.4 Conclusions

It appears that stopover duration is only loosely dependent on FDR and current fuel stores, except when FDR is negative and possibly when birds are facing an ecological barrier (Fig. 1). There may be two reasons for that. First, there seems to be a strong endogenous component determining FDR and possibly stopover duration which may overrule any relationship between

stopover duration and FDR. Second, stopover duration may be predominantly determined by weather aloft in areas of variable wind conditions (Liechti and Bruderer 1998).

It is likely that the dependence of stopover duration, FDR and departure fuel load on endogenous versus environmental factors varies according to the specific phase of migration. When birds migrate over areas with frequent stopover sites, endogenous factors may predominate, while birds before an oncoming barrier may put more emphasis on environmental factors (reaction to the barrier) and current body stores. Similarly, birds migrating early may be able to behaviourally adjust more easily to environmental factors, while birds migrating late (time-pressed) are governed predominantly by their time programme. Hence, behavioural reactions to environmental factors and the importance of the time programme are likely to depend on the environmental context (e.g. topography) and specific phase of migration (early or late migrants, beginning or end of migration).

FDR is often well below the maximum rate as derived from values observed in rapidly fattening free-living populations (Schaub and Jenni 2000b) and shows a large variation, especially between stopover sites (Schaub and Jenni 2001b). FDR seems to be quite flexible and is probably determined by complex tradeoffs between food availability, competition, predation risk, body mass and the time programme.

In the case of adequate food resources, it is largely unknown whether FDR is mainly determined by the endogenous time programme (photoperiod) or predominantly by environmental factors interacting with each other in a set of trade-offs, or by a combination thereof: (1) the endogenous time programme may lead birds to refuel and to migrate slowly at the beginning of the migration season; (2) adverse factors such as competition or predation might be more severe for early-migrating birds; (3) early-migrating birds are more risk-sensitive and adopt a lower FDR under predation risk or competition than late-migrating conspecifics which maximize FDR by taking a higher risk. In any of these cases, this would imply that early-migrating birds are not strict time-minimizers.

3 Flight, Landing Decision and Stopover Site Selection

3.1 Flight and Behavioural Reactions

Overall flight distance to the wintering quarters, the general direction of migration and the time of day of migratory flight seem to be endogenously controlled, at least in inexperienced migrants (Berthold 1996). During migratory flight, birds react to the environmental factors topography and weather, particularly wind and rain (Fig. 1).

Night migration of small passerines is clearly influenced by topography at several spatial scales. On a continental scale, migration of passerines converges as a guided broad-front migration towards landbridges, i.e. in Europe towards the Iberian peninsula and towards the Near East (Bruderer and Liechti 1999). This might have a genetic component as there are endogenous migration directions which change during migration in accordance with the land masses (Gwinner and Wiltschko 1978; Beck and Wiltschko 1988; Helbig et al. 1989). However, the genetic programme is unlikely to bring some species to their winter quarters and birds probably use information of landscape topography (Thorup and Rabøl 2001).

At a regional and local scale, birds clearly react to the topography, such as the Alps (reviewed in Bruderer and Jenni 1990). Crossing the Alps (and probably other ecological barriers) depends on flight capabilities, habitat requirements for stopover, approach direction, flight altitude, energy stores and prevailing weather and wind (Jenni and Naef-Daenzer 1986; Bruderer and Jenni 1990). Hence, there is a differential reaction to the Alps according to extrinsic and intrinsic factors of the approaching birds. Similarly, birds react differentially to a coastline depending on time of day and weather, particularly wind (Bruderer and Liechti 1998a,b; Fortin et al. 1999).

Migration progress aloft is crucially dependent on prevailing winds, and birds adjust their flight path (heading and flight altitude) in response to the wind. Birds choose a flight altitude with favourable winds (Cochran and Kjos 1985; Bruderer et al. 1995; Liechti et al. 2000). Passerines compensate wind drift fully when wind speed is weak, but only partially when wind speed is stronger (Liechti 1993). Flight speed is adapted to the tailwind component in order to maximize progress towards the goal (Liechti 1993, 1995; Liechti et al. 1994).

3.2 Flight Duration and Landing Decision

The time of day of migratory flight is endogenously determined (Fig. 1). Since night migrants land at sunrise at the latest (except when over inhospitable areas), this provides a maximum duration of a flight bout when migrating over areas where birds can stop over. However, radar studies have shown that many night migrants flying over inland areas land after only a few hours of flight during the night (e.g. Bruderer et al. 2000). Therefore, similar to departure time, the time of landing, and hence flight duration, is quite variable. Energy stores provide another maximum for flight duration (e.g. Weber and Houston 1997b).

Possibly, seasonal time pressure (photoperiod) has the effect of increasing the duration of a flight bout and delay landing, as suggested by Safriel and Lavee (1988). Because overall migration speed is increasing with season (e.g. Fransson 1995), we may expect this to happen, but to our knowledge, there is no convincing evidence that flight duration is increasing rather than stopover duration decreasing.

Flight duration (or landing decision) is determined by a number of environmental factors. When landing and selecting a stopover site, the bird makes a decision based on the conditions aloft and the conditions on the ground. The factors topography, weather and habitat below were shown to influence the decision when and where to land (Fig. 1).

Migrants are more prone to land when encountering an ecological barrier late during the night than earlier (Bruderer and Liechti 1998b). Birds generally land when they risk flying into bad weather (e.g. Cochran and Kjos 1985; Moore and Kerlinger 1987). Night migrants flying over continental Europe are found in their species-specific habitats, if available at a regional scale, from the early morning (e.g. Bairlein 1983; Jenni and Widmer 1996; Jenni-Eiermann and Jenni 1999). Therefore, they must be able to recognize their habitat at night while flying overhead. Visual and acoustic cues have been shown to be used (Herremans 1990; Jenni 1996; Jenni-Eiermann and Jenni 1999; Schaub et al. 1999).

Energy rate and progress towards the goal can influence flight duration. For instance, birds prolong their nocturnal flight into the morning if they happen to be in a low-altitude jet stream (Liechti and Schaller 1999).

Apart from the limitations imposed by overall energy stores, there are a number of other physiological factors possibly influencing flight duration. As discussed in the context of desert crossings, water may limit flight duration (Carmi et al. 1992; Klaassen 1995, 1996; Klaassen et al. 1999), but field evidence for water limitation in small birds is still absent (Liechti et al. 2000; Landys et al. 2000; own unpubl. data). Because birds during endurance flight need to catabolize a certain amount of protein, protein utilization results in a functional or structural loss and may limit flight duration (Klaassen and Biebach 1994; Hume and Biebach 1996; Biebach 1998; Jenni and Jenni-Eiermann 1998). Adverse effects of a moderate protein catabolism during flight may be more than compensated for by the savings in costs of transport and maintenance (Piersma 1998; Piersma and Lindström 1997). However, if protein catabolism attains high levels (i.e. entering phase III of fasting with a highly elevated protein breakdown; Jenni et al. 2000), there is certainly a net adverse effect on flight performance and subsequent recovery which should be avoided. Also, glycogen stores should not be exhausted during flight to allow burst flights for predator escape and for catching mobile prey when landed (Jenni-Eiermann and Jenni 2001). A factor not considered so far is sleep deprivation during nocturnal flight as a potential factor influencing flight duration (Schwilch et al. 2002).

The landing decisions when migrating across the Sahara are thought to depend mainly on current fuel stores, the availability of oases and time of day, as shown in a decision-making flow chart (Biebach et al. 1986), but the endogenous time programme (Safriel and Lavee 1988) as well as wind and temperature conditions at different flight altitudes (Biebach 1990) have been considered as well. While the importance of wind direction was confirmed,

the effects of temperature and humidity (influencing water budget) remain unclear (Liechti et al. 2000).

The decision to land is apparently the outcome of a complex interaction of (1) the endogenous diurnal rhythm of migration, (2) current energy stores and physiological factors (water budget, sleep, glycogen, protein), (3) possibly time pressure (endogenous time programme), (4) current and expected conditions aloft (weather, topography) and (5) expected conditions on the ground (topography, habitat). Depending on the environmental circumstances and possibly the time programme, the relative importance of the factors varies.

3.3 Selection of Stopover Site After Landing

Birds land in a new environment and usually stay for only a short period. Exploration is costly and needs to be balanced against the probability of finding significantly better conditions (see Jenni-Eiermann and Jenni 1999). There is evidence of birds searching for a better habitat nearby (Bairlein 1983; own unpubl. obs.), for instance when they landed in foggy conditions (Jenni 1996). Exploration movements after landing were observed in summer tanagers, *Piranga rubra*, but only over small distances of about 500 m (Aborn and Moore 1997).

It has been suggested that many birds do not fatten up just after landing, but need time and energy before they can do so. However, it remains still unclear under which conditions such a search-and-settling period and an initially low refuelling rate occurs (see Schwilch and Jenni 2001).

3.4 Conclusions

While a number of environmental factors and behavioural reactions have been identified in birds during migratory flight (Fig. 1), it is still unclear how strongly the time programme influences the duration of a flight bout. However, this is a crucial parameter of overall migration speed.

The behaviour during flight has been mainly analyzed in the context of optimizing the migration route and progress towards the goal. For instance, this is certainly the case when birds look for the flight altitude with the most favourable wind. However, other behavioural reactions may mainly serve to optimize the probability of finding an appropriate stopover site or minimizing mortality, for instance reactions to topography. Therefore, we suggest that the search for an appropriate habitat while flying may be the reason for many observed behavioural reactions during flight. We suggest that the spatial distribution of appropriate stopover sites (i.e. the landscape aspect of stopover) is one of the important variables in migration research, which has received only little attention (e.g. Evans et al. 1991; Farmer and Wiens 1999; Simons et al. 2000).

4 Conclusions and Perspectives

This review of the current knowledge about factors influencing bird migration shows that there is still considerable uncertainty as to what degree the main parameters and decisions during flight and during stopover are determined by endogenous or environmental factors, respectively.

Furthermore, the interdependence of flight and stopover is not fully understood. Two examples: first, the decision where to land determines the whole suite of environmental factors influencing stopover. However, we have a very incomplete knowledge about how birds adjust their flight path to the landscape below, how they determine where to land and whether birds explore the surroundings. Second, weather as an environmental factor influences both flight and stopover (Fig. 1). In bad weather, the bird is in a difficult situation, especially in central Europe, where bad weather in autumn is normally associated with headwinds. Birds in such a situation may depart in headwind conditions in order to find a stopover site with good weather across the weather front. This would not be in accord with the existing optimal behaviour models (Liechti and Bruderer 1998; Weber et al. 1998a). Therefore, without appreciating the effects of weather on both refuelling rates and flight, we cannot fully understand the departure and landing rules.

It appears that there are predominant effects of the time programme on route and FDR, and possibly on stopover duration and flight duration. The endogenous time programme seems to break up possible optimal behavioural reactions to environmental factors, so that, for instance, FDR and stopover duration are only loosely interrelated. It seems that the time programme is providing important and simple rules for the behaviour during migration which might then be modified by environmental factors.

There is a strong effect of photoperiod or time pressure on many aspects of migration. As suggested above, early-migrating birds may migrate more slowly. Late-migrating birds migrate faster, but probably have to take more risks. Hence, the endogenous programme is likely to be more important in late than in early migrants. An important approach to understand the interaction of endogenous and environmental factors, therefore, would be the comparison of early- and late-migrating individuals, an approach so far underexploited.

Field studies will be important to advance our understanding of the relative importance of endogenous and environmental factors and about the behavioural and physiological reactions of birds. This should lead to an understanding of the proximal mechanisms working during migration and the probably simple rules the birds are using during migration, as advocated for by Wehner (1998).

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