动物学报 52(Supplement): 594–598, 2006
Acta Zoologica Sinica

S34-3 Factors determining stopover decisions in migrating passerines on an offshore island

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Abstract Factors influencing decisions in small migrating passerines to stopover on small islands or press on were investigated in a five-year study on Helgoland Island in the North Sea, using the northern wheatear as the focal species. Assessment of foraging opportunities focused on rate of prey intake and the related effort of finding food. Northern wheatears prolonged their stopovers and defended territories whenever rich food patches occurred. The density of passerines also affected departures due to crowding and interference. Raptors, as a measure of predation, played little part in departure decisions, but cloud cover and head winds seemed to hold up departures, particularly in Greenlandic wheatears in spring before their sea crossing to breeding grounds. Body condition was not a factor in forcing birds to land on Helgoland, judged by its uniformity in early departing and resting birds. Because the number of migrants passing over Helgoland annually is unknown, it is difficult to assess its importance as a stopover. Stopovers seem to occur randomly, but in favorable conditions, migrants will take the opportunity to refuel.

Key words Stopover ecology, Departure decision, Foraging opportunity, Climatic factors, Crowding, Northern wheatear

1 Introduction

The migration of birds between breeding and wintering areas is generally controlled endogenously (Berthold, 1996). Many environmental factors, however, modify the behavior of birds during migration, particularly weather (Richardson, 1990) and the quality of stopover sites for refueling in transit (Rabøl and Hansen, 1978; Bibby and Green, 1981). Because most time and energy is spent at stopover sites during migration (Hedenström and Alerstam, 1997), such sites play a major role in successful migration. For birds, the choice of whether to use a stopover site or not involves balancing refueling conditions, flight conditions and body condition (Jenni and Schaub, 2003). After landing in any environment, a bird has to check quickly whether the site is suitable for a stopover and to decide between staying or moving on. Such decisions are best observed on small, isolated stopover sites where it is easy to separate those that stay and those that move on. That is why I chose the small offshore island of Helgoland in the North Sea to determine factors influencing stopover decisions in migrating passerines. The results are summarized here.

2 Methods

The island of Helgoland (1.5 km^2) is situated 50 km off the German North Sea coast (54°11' N, 07°55' E). For more than 90 years, migrating birds have been trapped regularly there during stopovers by a daily trapping routine of seven rounds using three large funnel traps (for details, see Moritz, 1982). In a field study from 1998 to 2002, northern wheatears (*Oenanthe oenanthe*) were trapped with spring traps outside the funnel-tarp site and marked with individual combinations of color-rings (Delingat and Dierschke, 2000). All birds trapped or retrapped during spring and autumn migration were measured and weighed (Dierschke and Bindrich, 2001); visual fat stores were scored according to a nine-class scale (Kaiser, 1993). Birds were treated as staying on the island if recaptured or resighted on days following the day of ringing, but were considered to have departed if not recaptured or resighted after the day of arrival. Strong fluctuations in the daily number of birds present (Delingat and Dierschke, 2000) suggest that most birds were trapped on their day of arrival. The very low rate of recaptures elsewhere on the island (< 1% away from the funnel traps, Dierschke and Bindrich, 2001), and the high search effort for color-ringed wheatears, make these estimates of length of stay highly reliable.

3 Results

3.1 Body condition

On both spring and autumn migration, passerines generally cross the southeastern North Sea with low or intermediate fat stores; high fuel loads are rarely observed in trapped birds (Dierschke and Bindrich, 2001). In the funnel traps, recapture rates are much higher for lean birds (fat scores 0–1) than for birds with larger amounts of visible fat stores (Fig. 1). Therefore, the degree of fuel store depletion is a considerable factor in the decision to skip or stopover.

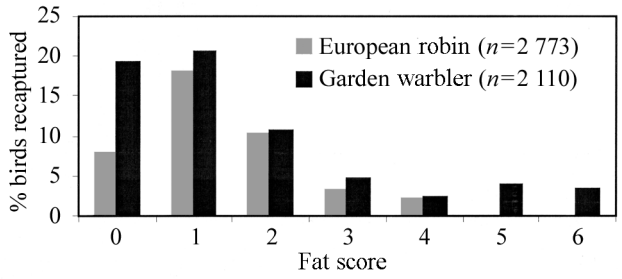

Fig. 1 Proportion of birds recaptured in relation to visible fat stores at initial capture during autumn migration (1996–2001)

Note that fat scores 5 and 6 were not found in European robins.

3.2 Season

Northern wheatears of the nominate subspecies which breeds in Scandinavia showed a much higher tendency to stay on Helgoland during the first part of spring migration (20%–80% of individuals staying in early and mid April) compared to the period from late April to late May (0%–10% of individuals staying) (Dierschke and Delingat, 2001). Comparison with other migratory passerines is needed to determine whether this is a general pattern for passerine spring migration.

3.3 Foraging conditions

A fundamental component of foraging conditions is the availability of food. Its presence or absence should thus have an impact on stopover decisions. During post-breeding migration, many European passerines are frugivorous, and berries of Black Elder *Sambucus nigra* have been found to be a very profitable food source for them (Simons and Bairlein, 1990). On Helgoland, large quantities of elder berries become available from early September onwards, but are nearly completely depleted by birds by mid October. In two highly frugivorous species, the garden warbler (*Sylvia borin*) and the blackcap (*Sylvia atricapilla*), recapture rates in funnel traps are much higher during periods of high availability of berries (Table 1). The importance of food supply in the stopover decision is further illustrated by those northern wheatears that visited grassland habitats poor in invertebrate food, to linger there for a much shorter time than conspecifics in food-rich wrack beds on the beach (Delingat and Dierschke, 2000). In a field experiment, a much higher proportion of northern wheatears stayed on in the poor grassland when they were offered mealworms ad libitum (Table 2).

The effects of foraging conditions are not only explained by food availability, but also by competition for food among the birds stopping over. It was expected that at least interference competition would act when high bird densities occurred. For funnel trapping, no absolute values of bird density are available; instead, the number of birds trapped per day was used as an estimate. For a number of species, the proportion of birds recaptured on days after ringing decreased with increasing bird density, most clearly so in pied flycatchers (*Ficedula hypoleuca*) which are territorial during migration (Table 3). This is consistent with observations during big fallouts, when most of the thousands of grounded birds leave by morning (Dierschke and Bindrich, 2001). In such circumstances, it appears that the food supply for frugivorous birds is not sufficient to allow refueling for all birds present at one time; the number of birds exceeds the carrying capacity of the island. In the color-ringing study with northern wheatears, high bird density and concomitant interference competition was also identified as a factor leading to early departures (Dierschke and Delingat, 2001).

3.4 Predation risk

Predation risk was quantified as the number of sparrowhawks (*Accipiter nisus*) and various falcons (*Falco* spp.) flying over the study site per hour. In both spring and autumn migration, the rates of raptor flights did not differ for northern wheatears on or leaving on the day of arrival

Table 1 Effect of high and low availability of elder berries

	No/few elder berries available		Copious elder berries available			
	n	Recapture rate	*n*	Recapture rate	χ^2	*P*
Garden warbler, *Sylvia borin*	732	6.3%	878	14.9%	31.6	<0.001
Blackcap, *Sylvia atricapilla*	483	0.8%	2226	9.0%	38.3	<0.001

Proportion of birds recaptured after 1 day during periods of high availability (1 September to 10 October) and low availability (1–31 August, garden warbler; 11 October to 30 November, blackcap).

Table 2 Proportion of color-ringed northern wheatears resighted in grassland habitat with and without additional food

	No additional food		Mealworms ad libitum			
	n	Resighting rate	*n*	Resighting rate	χ^2	*P*
Spring migration	174	11.5%	226	33.2%	25.5	<0.001
Autumn migration	170	5.9%	178	32.0%	38.2	<0.001

Table 3 Proportion of birds recaptured during autumn migration (1990–2000) in relation to bird density

	Garden warbler, *Sylvia borin*		Pied flycatcher, *Ficedula hypoleuca*	
Bird density (number of birds trapped)	*n*	Recapture rate	*n*	Recapture rate
1–10	1 247	11.4%	771	10.0%
11–20	658	8.8%	173	4.0%
21–30	365	9.6%	70	2.9%
31–50	189	4.2%	129	0.0%
>50	242	2.1%		

Proportion expressed as the number of conspecifics trapped on the day of ringing

(Dierschke and Delingat, 2001). Because freezing in response to raptors lasted up to 30 minutes, however, there may be an indirect effect through reduced foraging time and thus lower fuel deposition rate.

3.5 Weather

Apart from stopover site characteristics, the decision to take off on migratory flight is influenced by weather: strong headwinds or drift will increase fuel consumption and overcast conditions can compromise orientation. During spring migration, wheatears tended to stay when cloud cover was high (Dierschke and Delingat, 2001). Whereas nominate birds breeding in Scandinavia with a short flight to the next stopover left regardless of weather conditions, those of the subspecies *O. o. leucorhoa*, which breed in Iceland and Greenland and face a long nonstop flight, stayed on much longer when wind and overcast combined in adverse conditions (Dierschke and Delingat, 2001). Nevertheless, much more information is needed to understand the effect of weather on patterns of landing and departure.

3.6 Migration route

Migration route may be involved too in the decision-making of migrating birds. In order to combine the effects of the factors analyzed above, logistic regressions were calculated using the observed departure decision of color-ringed northern wheatears as the dependent variable (0 = staying, 1 = departing). The regressions were calculated separately for groups of birds facing a long-flight (*O. o. leucorhoa* in spring) and those facing a short flight (*O. o. oenanthe* in spring, all birds in autumn). For both groups, data are available for unmanipulated situations as well as for experiments with food offered ad libitum. The factors involved affected the two groups significantly. Whereas birds facing long flights focused on site use with respect to factors reflecting foraging conditions and weather, those facing short flights were more diverse in their decision making. In contrast to the first group, moreover, the second factored in body condition and, in spring, the time of the season, early or late (Table 4). The significance of predation risk for Greenlandic/Icelandic spring migrants was probably related to weather conditions, which favored migration (and thus departures) in both wheatears and raptors (Dierschke and Delingat, 2001).

4 Discussion

The results of field studies and field experiments on the offshore island Helgoland demonstrate that a number of factors play a role in the stopover decisions of migrating passerines. So far, only single factors have been shown to be important in experiments: food supply for refueling (Gwinner et al., 1985), overcast as a factor influencing orientation (Åkesson and Bäckman, 1999), tail wind for helping migratory flight (Åkesson and Hedenström, 2000), and fuel loads as crucial energy stores for the crossing of ecological barriers (Biebach, 1985; Sandberg et al., 1991). Predation risk has also been shown to influence departures (Fransson and Weber, 1997), but seemed to be negligible for northern wheatears on Helgoland, both in field studies (Dierschke and Delingat 2001, this study) and in an indoor experiment (V.D. and A. Walter, unpubl.). Beyond these factors, a seasonal component, reflected in early spring migrants staying on, and, more importantly, foraging and thus refueling conditions, was also found to be incorporated into decision-making.

Given appropriate body condition, opportunity for refueling as a combination of food supply and competition seems to be the most important factor in the stopover decision for migrating passerines. This fits well with a strategy of time-minimization which incorporates departure from a stopover site if the fuel deposition rate is equivalent to an instantaneous speed of migration below the expected average (Alerstam and Lindström, 1990). Accordingly, factors decreasing the fuel deposition rate directly (low food supply, high density of competitors) were found to promote early departures in this study. However, the indirect impacts of weather (Schaub and Jenni, 2001), and predation risk which hindered foraging, were not investigated or did not prove to be significant, respectively. The minor influence of predation risk on departure decision and the emphasis on refueling is in accord with other studies (Metcalfe and Furness, 1984; Moore, 1994). Despite the underlying significance of refueling factors, flight and orientation conditions affected by local weather can dictate decisions, even preventing departures. This was especially the case for wheatears facing a long flight from Helgoland.

The importance of refueling conditions writ small in Helgoland may be writ big on large continental landscapes. Fragmentation of habitats suitable for stopovers will lead to a higher concentration of birds at local sites and thus to increased competition for and exploitation of resources (Moore and Yong, 1991; Ottich and Dierschke, in prep.). High concentrations of passerines on Helgoland created an imbalance between food supply and energy demand, with carrying capacity overloaded more than four-fold (Ottich and Dierschke, in prep.). Because habitat availabil-

Table 4 Results of logistic regressions using departure or stay in color-ringed northern wheatears as the dependent variable and physiological and environmental factors as independent variables

Flight faced	Long-distance flight		Short-distance flight			
Season	Spring	Spring	Spring	Spring	Autumn	Autumn
Subspecies	*leucorhoa*	*leucorhoa*	*oenanthe*	*oenanthe*	both	both
	field obs.	experiment	field obs.	experiment	field obs.	experiment
Season						
five-day period	no	no	yes	no	no	no
Body condition						
fat score	no	no	yes	yes	no	
body mass/fuel load	no	no	no	no	no	yes
Foraging conditions						
rate of successful pecks					yes	
fuel deposition rate						no
total number wheatears	yes	no	no	no	no	no
aggression rate					no	
Predation risk						
rate of raptor flights		no	no		no	no
total number raptors	yes		no			
Weather						
cloud cover	no	no	no	no	no	yes
wind velocity	no	yes	no	no	no	no
tail wind component	yes	no	no	no	yes	no

"Yes" or "no" indicate variables that are significant or not. Results are split into birds facing long-distance flights in spring (*O. o. leucorhoa*) and those facing short-distance flights in spring and autumn (*O. o. oenanthe* in spring, both subspecies in autumn) from Helgoland. "Field obs." refers to unmanipulated conditions, and "experiment" to birds offered food ad libitum.

ity on a landscape-scale is a central issue in conservation (Simons et al., 2000), understanding of processes at stopover sites becomes important, despite high flexibility in habitat use by passerine migrants (Bairlein, 1981).

Acknowledgements I am much indebted to Franz Bairlein for encouraging and enabling my studies on Helgoland. Results were achieved through cooperation from staff and candidates at the Institut für Vogelforschung Helgoland, notably O. Hüppop, T. Bleifub, F. Bindrich, J. Delingat, B. Mendel, I. Ottich, H. Schmaljohann and A. Walter), and many volunteers. The manuscript was kindly reviewed by F. Bairlein and L. Jenni. My studies were supported financially by the "Freunde und Förderer der Inselstation der Vogelwarte Helgoland e.V.".

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