Die Vogelwarte 40, 2000: 271–278

Habitat utilization by Northern Wheatears *(Oenanthe oenanthe)* stopping over on an offshore island during migration

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Abstract: Delingat J., & V. Dierschke (2000): Habitat utilization by Northern Wheatears (*Oenanthe oenanthe*) stopping over on an offshore island during migration. Vogelwarte 40: 271–278.

During migratory stopovers on the small offshore island Helgoland (North Sea), Northern Wheatears equally used grassland and beach habitats in spring. An increasing proportion of wheatears present in beach habitats during autumn migration can be attributed to declining food supplies in grassland habitats and abundant food supply in wrack beds on beaches, but habitat quality regarding protection from aerial predators was difficult to figure out. Individually colour-ringed birds revealed different patterns in utilization of the two habitat types. Grassland birds were transient and explorative with most individuals departing on the day of arrival and high mobility on the island. In contrast, higher proportions of beach birds stayed for at least one night and remained close to their place of ringing, often showing territorial behaviour (which was absent in grassland birds). The results underline the role of habitat quality in stopover behaviour, proposing that birds might quickly judge their expected refuelling capabilities in relation to the resulting migration speed (according to the hypothesis of time-minimization in optimal migration).

Key words: Northern Wheatear *(Oenanthe oenanthe)*, stopover behaviour, habitat quality.

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1. Introduction

During their movements between breeding site and winter quarter, migratory birds have to take care not only about suitable conditions for the migratory flight itself, but also to adjust stopover decisions regarding their migratory strategy. In order to manage migration in an optimal way, recent theories predict that birds should minimize either time spent on migration or total energy expenditure, with predation risk as a third criterion to be considered (Alerstam & Lindström 1990). Important test parameters identified in theoretical approaches are the rate of fuel deposition, which determines stopover length and body mass at departure, as well as protection against predators (Alerstam & Lindström 1990, Lindström 1995). These factors are strongly influenced by the kind of habitat which is chosen by a bird for stopover. Vegetation structure of the habitat determines locomotory abilities according to bird morphology (Bairlein 1981, 1992) and may provide shelter from predators (Lindström 1990, Cimprich & Moore 1999), whereas the food supply should allow the required rate of fuel deposition (Rappole & Warner 1976, Moore & Simons 1992).

During a migratory stopover, a bird does not necessarily find the kind of habitat to which it fits best by morphology or feeding habits, especially in landscapes which differ much from breeding or wintering area. After interrupting a migratory flight and landing in a given habitat, birds have to trade-off between staying in the habitat or investing time to search for a better habitat in the surrounding (Hutto 1985a, Moore & Simons 1992, Jenni-Eiermann & Jenni 1999). If a bird does not find adequate conditions for refuelling and/or surviving in a habitat, it would be expected to leave soon in order to find a better habitat following the next step of migration. This decision is important especially before crossing an ecological barrier, as no intermediate behaviour is possible with respect to the range of searching area: a bird has to stay or to depart ultimatively. In such a situation on a small offshore island, we studied the effect of habitat quality on the stopover behaviour in a migratory landbird, the Northern Wheatear (*Oenanthe oenanthe*). Two different habitats are available for wheatears on the island, grassland and beach. They differ by several features and, therefore, the birds were supposed to experience different suitability as a stopover habitat. Therefore, habitats should vary with respect to preference by wheatears and their stopover characteristics such as length of stay, dispersive behaviour, territoriality and food intake rates.

2. Study area

The island of Helgoland is situated in the North Sea (54 ° 11 ' N, 07 ° 55 ' E), 53 km off the German mainland coasts of Schleswig-Holstein and Niedersachsen and 43 km off the Wadden Sea island Wangerooge. The study concentrated on the main island (120 ha) which consists of a red sandstone rock and reclamated land. About 45 ha can be judged as grassland habitats which in part are grazed by cattle and sheep or are interspersed with open (sometimes rocky) patches. In addition to the close-by sand island ('Duene Island', 70 ha) not included in the study, three stretches of beach are found on the main island (500 m, 200 m and 100 m long; altogether 6.5 ha). Beach habitats are characterized by layers of brown algae washed ashore from the rocky inter- and subtidal surrounding the island. A small but consistent patch of algae thrown over a pier by the waves was also considered as a beach habitat.

3. Methods

In 1998, during the migratory periods of Northern Wheatears (25 March to 8 June and 1 August to 12 November), the number of birds present was counted daily along a standardized route covering most of the island. Bird numbers were assigned to one of the two habitat types (grassland, beach), resulting in percentages of the stock using each habitat. In addition, the density of Northern Wheatears was calculated for each type of habitat.

Baited by mealworms, 439 and 472 Northern Wheatears were trapped with spring traps and ringed with individual combinations of three or four colour-rings in 1998 and 1999, respectively. During the daily routine, all wheatears present were checked for colour-ringed individuals. For those birds recognized, the exact location was noted and later related to the place of capture.

In order to quantify the potential food supply of wheatears, ground-dwelling invertebrates were trapped from March to November 1998 using pitfall traps controlled at regular intervals (the first day of each five-day-period, BERTHOLD 1973). The traps were filled with 3% formalin. Invertebrates were stored in 70% ethanol and later classified to family. At four sites in grassland habitats and at two sites in beach habitats, flying and grass-living invertebrates were netted by 20 standardized sweeps at each site daily around noon from 26 March to 30 September 1998. As the abundance of kelp fly larvae is very difficult to measure due to patchiness (density within a few meters varied from 24,500 to 136,400 m^{-2} in twelve samples taken on 3 August 1999, V.D. pers. obs.), a rough estimation was used in 1998 daily (6 April to 13 June and 9 August to 21 October) by estimating the number of larvae visible in a 10x10 cm patch immediately after uncovering the uppermost layer of wrack (3–4 times each at two different beaches). The estimate included four classes of abundance: 0 (no larvae), 1 (1–20 larvae), 2 (21–60 larvae) and 3 (> 60 larvae).

In both habitat types, foraging behaviour of Northern Wheatears was observed during spring and autumn migration in the second year of the study (1999). Focal birds were followed for 2 min, during which the number of pecks as well as the number of aggressive encounters (chases and fights) were recorded.

Acknowledgements: We are much indebted to the staff and volunteers of Institut für Vogelforschung who helped in many ways throughout the study, especially T. BLEIFUß, S. ENGEL, A. FISCHER and J. O. KRIEGS. Financial support was given by the Freunde und Förderer der Inselstation der Vogelwarte Helgoland e. V. O. HÜPPOP and F. BAIRLEIN kindly commented on the manuscript.

4. Results

In 1998, numbers of Northern Wheatears stopping over on Helgoland strongly fluctuated in both migratory seasons with maximum counts of 161 (1 May) and 429 birds (13 September), respectively. Due to the unregular occurrence of algae washed ashore and developmental cycles of the only numerous invertebrate taxon (kelp flies Coelopidae, at most *Coelopa frigida*), the food supply on beaches did not show a clear seasonal pattern (Fig. 1 C). In grassland habitats, invertebrates trapped in pitfall traps as well as caught by net sweeps increased during spring migration of wheatears, but decreased during autumn migration (Fig. 1 D). The most abundant taxa recorded in grassland habitats were Arachnida, Isopoda, Coleoptera (pitfall traps), Diptera and Rhynchota (net sweeps).

During spring migration, Northern Wheatears were present nearly equally in grassland and beach habitats (Fig. 1 B). There was neither a correlation between the percentage found in grassland habitats and ground-dwelling invertebrates (pitfall traps; R = - 0.154, P = 0.598, n = 14) and grass living invertebrates (net sweeps; R = - 0.402, P = 0.137, n = 15), respectively, nor a correlation between percentages seen in beach habitats and abundance of kelp flies (net sweeps; R = 0.169, P = 0.546, n = 15) and kelp fly larvae (density estimation; R_S = 0.291, P = 0.359, n = 12).

At the beginning of autum migration (August), most Northern Wheatears were found in grassland habitats, but during September and October the proportion of birds present in beach habitats increased gradually (Fig. 1 B). The change in habitat choice can at least in part be attributed to declining food supplies in grassland habitats, as the percentage of wheatears present in grassland is significantly correlated with invertebrates in net sweeps (R = 0.701, P = 0.016, n = 11) and close to significantly correlated to invertebrates in pitfall traps (R_S = 0.476, P = 0.062, n = 16). On the other hand, the percentage of wheatears observed in beach habitats increased with larger estimated abundances of kelp fly larvae (R_S = 0.537, P = 0.039, n = 15), while there was no such trend in relation to numbers of kelp fly imagines (net sweeps; R = 0.402, P = 0.196, n = 11). Taken as an additional measure of habitat quality, observed pecking rates tended to be higher on grassland than on the beach in spring, but were signifcantly higher on the beach in autumn (Table 1).

Table 1: Pecking rates of Northern Wheateras (pecks per 2-min-period; mean and s.d.) on grassland and beach during spring and autumn migration.

Tab. 1: Pickraten von Steinschmätzern (Anzahl Picks pro 2-Min.-Zeitraum; Mittelwert und Standardabweichung) im Grünland und am Strand während des Heim- und Wegzuges.

	pecks per 2-min-period			
	grassland	beach	T	P
spring	6.4 ± 4.3 (n=19)	4.4 ± 4.2 (n=273)	2.018	0.057 n.s.
autumn	6.5 ± 4.5 (n=68)	9.8 ± 5.7 (n=233)	4.421	< 0.001 ***

The density (birds per ha) was generally much higher in beach habitats during the migratory periods of Northern Wheatears, irrespective of percentages observed in absolute numbers (Fig. 1 B). Although birds were generally foraging in both habitat types, utilization of these habitats differed regarding stopover strategies. Nearly all individuals colour-ringed in grassland habitats disappeared during the day of ringing or in the subsequent night, whereas birds marked on beaches stayed at least until the next day (and up to 17 days) by 25 % in spring and 39 % in autumn, respectively (Table 2).

When resighted on the island, the majority of individuals was close to their place of ringing (Table 3). Only two birds moved to the adjacent Duene Island, which is situated in a minimum distance of 600 m to the main island. However, while present on Helgoland, birds marked in grassland habitats dispersed over significantly larger distances compared to birds marked on beaches in both spring and autumn (Table 3), but between seasons, no significant difference was observed in both habitat types (Table 3). In beach birds, 78 % (spring, n = 46) and 90 % (autumn, n = 107), respectively, remained in the same type of habitat, but in grassland birds, 57 % (spring, n = 7) and 50 % (autum, n = 26) switched at least during part of their stay to beach habitats.

The low mobility in beach habitats is underlined by the observed territoriality in some of the wheatear individuals while no such behaviour occurred in grassland habitats. Territories on beaches contained specific patches of wrack (up to 250 m^2) which were defended against conspecifics and other passerine birds. The different behaviour compared to grassland habitats is expressed by the higher rate of aggressive encounters observed on beaches (Table 4).

Table 2: Percentages of colour-marked Northern Wheatears not departing on the day of ringing (i.e. staying at least one night).

Tab. 2: Anteile farbberingter Steinschmätzer, die die Insel nicht am Tag der Beringung verlassen (d.h. mindestens einmal übernachtet) haben.

	% birds not departing (n) grassland	beach	χ^2	P
spring	6.2 (113)	24.5 (188)	604.978	< 0.001
autumn	8.6 (303)	38.5 (275)	73.453	< 0.001

Table 3: Maximum distance between place of ringing and sightings of colour-marked Northern Wheatears. The distance classes are frequented differently when comparing habitat types in spring (χ^2 =15.7, P < 0.001) and autumn (χ^2 = 12.2, P = 0.002), but no significant difference occurs between spring and autumn in either grassland (χ^2 = 2.02, P = 0.364) or beach habitats (χ^2 = 2.49, P = 0.288).

Tab. 3: Maximale Distanz zwischen Beringungsort und späteren Sichtungen bei farbberingten Steinschmätzern. Die Verteilung auf die Entfernungsklassen unterscheidet sich zwischen den Habitattypen sowohl im Frühjahr (χ^2 = 15,7, P < 0,001) als auch im Herbst (χ^2 = 12,2, P = 0,002) signifikant, nicht jedoch zwischen Heim- und Wegzug im Grünland (χ^2 = 2,02, P = 0,364) und am Strand (χ^2 = 2,49, P = 0,288).

	n	< 100 m	100–500 m	> 500 m
grassland	7	14 %	43 %	43 %
spring beach	46	80 %	15 %	4 %
grassland	26	42 %	19 %	35 %
autumn beach	107	72 %	17 %	11 %

Fig. 1: Occurrence and habitat choice of Northern Wheatears and abundance parameters of their prey on Helgoland in 1998 (March to November). A: Daily totals of wheatears on the main island (n = 6694). B: Density of wheatears in beach and grassland habitats per 5-day-period (columns) and the percentage of birds present in beach habitats (continuous line). C: Kelp fly abundance on beaches per 5-day-period (columns: estimation of larvae abundance per 10 x10 cm patch, see text; continuous line: average number of imagines netted per 20 net sweeps). D: Invertebrate abundance in grassland habitats per 5-day-period (columns: totals of invertebrates in four pitfall traps; continuous line: average number of invertebrates netted per 20 sweeps).

Abb. 1: Vorkommen und Habitatwahl von Steinschmätzern und Abundanz-Parameter ihrer Beute von März bis November 1998 auf Helgoland. A: Tagessummen auf der Hauptinsel gezählter Steinschmätzer (n = 6694). B: Dichte von Steinschmätzern am Strand und im Grünland pro Pentade (Säulen) und der Anteil der am Strand gezählten Vögel (durchgezogene Linie). C: Abundanz der Tangfliegen pro Pentade (Säulen: Schätzung der Larvenabundanz auf 10 x 10 cm Flächen, s. Text; durchgezogene Linie: mittlere Anzahl von Imagines bei 20 Käscherschlägen). D: Abundanz von Wirbellosen im Grünland pro Pentade (Säulen: Summen von Wirbellosen in vier Barberfallen; durchgezogene Linie: mittlere Anzahl von Wirbellosen bei 20 Käscherschlägen).

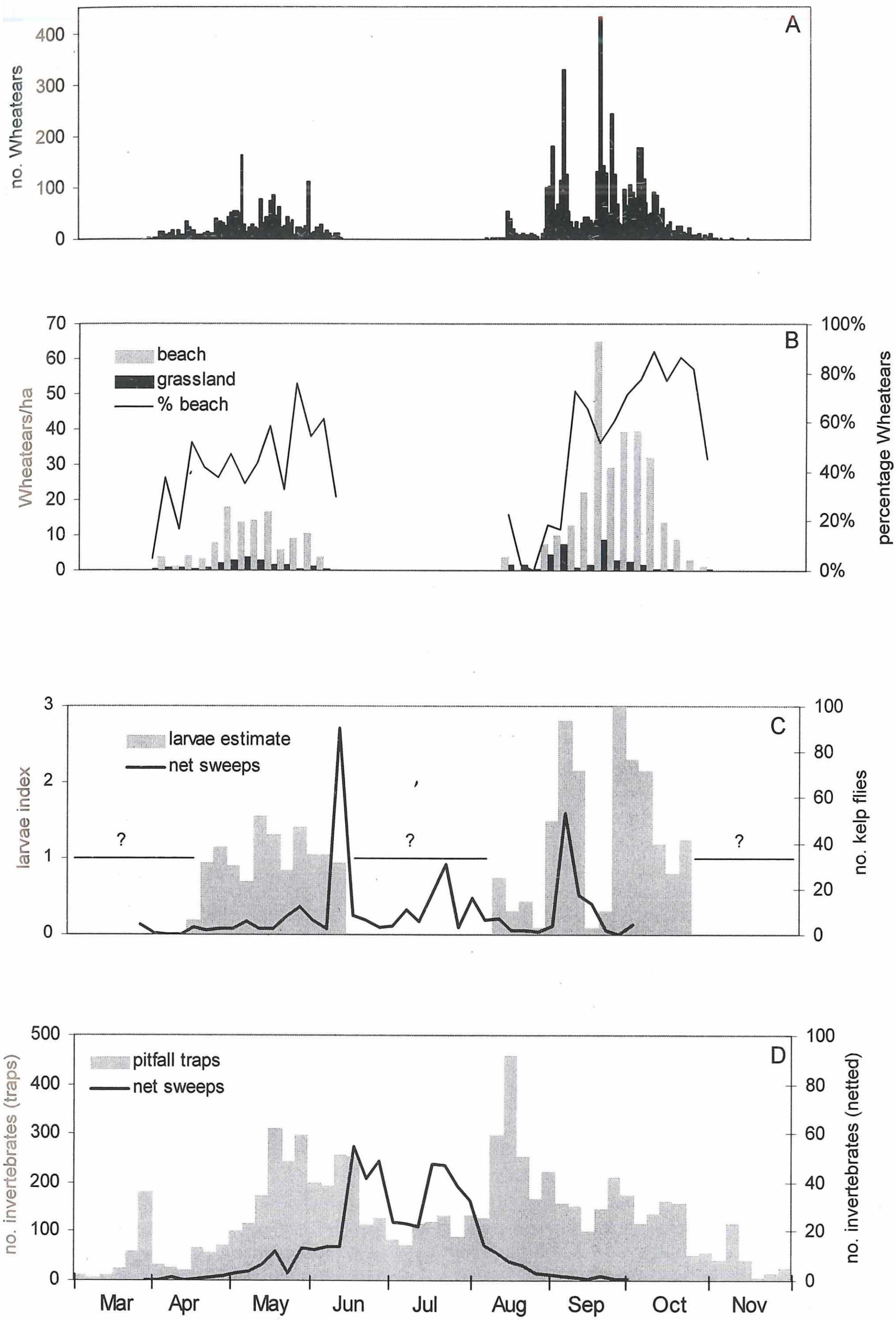
A
no. Wheatears
400
300
200
100
0
B
beach
grassland
% beach
Wheatears/ha
70
60
50
40
30
20
10
0
100%
80%
60%
40%
20%
0%
percentage Wheatears
C
larvae estimate
net sweeps
larvae index
3
2
1
0
?
?
?
100
80
60
40
20
0
no. kelp flies
D
pitfall traps
net sweeps
no. invertebrates (traps)
500
400
300
200
100
0
100
80
60
40
20
0
no. invertebrates (netted)
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Table 4: Aggressive encounters between focal Northern Wheatears and other birds in the two habitat types during n 2-min-periods of observation. The difference is significant according to MANN-WHITNEY U-test ($Z = 3.630$, $P < 0.001$). [a] *Motacilla alba*; [b] Including Yellow Wagtail *Motacilla flava* (twice), Redstart *Ph. phoenicurus* and Starling *Sturnus vulgaris.*

Tab. 4: Aggressive Interaktionen zwischen Steinschmätzern und anderen Vögeln während zweiminütiger Beobachtungszeiträume in den beiden Habitattypen. Der Unterschied ist nach MANN-WHITNEY U-Test signifikant ($Z = 3{,}630$, $P < 0{,}001$). [a] *Motacilla alba*; [b] inklusive Schafstelze *Motacilla flava* (zweimal), Gartenrotschwanz *Ph. phoenicurus* und Star *Sturnus vulgaris.*

	n	Wheatear	White Wagtail [a]	others [b]	total	encounter rate (min^{-1})
beach	480	132	27	4	163	0.17
grassland	86	3	0	0	3	0.02

5. Discussion

Stopover behaviour of Northern Wheatears clearly differs between the two habitat types studied on Helgoland. Compared to birds in beach habitats, grassland birds depart much sooner and in case their stay on the island exceeds the day of arrival, they disperse over larger distances and more often switch to the other kind of habitat. In general, the birds ringed in grassland habitats seem to be transient while beach birds show the tendency to settle for some days in a restricted patch of beach, often including territorial behaviour.

As earlier studies have found correlations between habitat choice and food supply (BIBBY & GREEN 1983, HUTTO 1985b, MARTIN & KARR 1986), it seems reasonable to relate the differences in habitat utilization observed at Helgoland to habitat quality regarding food supply. Wrack beds holding large amounts of kelp flies and their larvae are well known as feeding habitats for a broad spectrum of migrant birds (GOETHE 1936, LIFJELD 1984) and allow very high rates of energy intake and thus fattening in waders (DIERSCHKE 1998). In Northern Wheatears on Helgoland, this is reflected by a high pecking rate in autumn and by a high rate of body mass increase: recaptured or automatically weighed individuals gained mass by 1.7 g d^{-1} in spring ($n = 6$) and 1.8 g d^{-1} in autumn ($n = 17$; J. D. and V. D. unpubl.) which for a passerine of an estimated lean mass of c. 20–25 g is close to a maximum rate of mass increase (LINDSTRÖM 1991). In contrast, the food supply in grassland habitats is more diverse, but strongly decreasing in the course of autumn migration season (Fig. 1 D). Wheatears do not decide to settle there and in case of staying on the island often switch to the apparently more profitable beach habitats.

Another factor ruling the habitat choice might be safety from aerial predators (LINDSTRÖM 1990, CIMPRICH & MOORE 1999). Migrant raptors occur at Helgoland during all of the migratory season of Northern Wheatears (V. D. in prep.). The shape of the beach habitats presents good opportunities to quickly hide between boulders and other structures when a predator is approaching. On the other hand, the more open grassland habitats generally give a better overall view which should allow easier detection of surprise attacking raptors. Therefore, it is difficult to evaluate the role of safety in this case. However, the only small movements made and even the territories held on the beach demonstrate an advantage to remain at a certain place, probably including the knowledge of efficient escape tactics.

Thus, Northern Wheatears behave as expected since many of them settle in the high quality habitat to which they should become familiar during their stopover – irrespective of the much higher bird density in the beach habitats. In contrast, birds in grassland habitats seemed to be explorative and either ended up in beach habitats – paralleling rapid dispersal away from unfavourable habitats observed elsewhere (BRUDERER & JENNI 1988, MOORE et al. 1990, JENNI 1996) – or even left the island immediately. According to our observations and especially on peak migration days, there is a high turnover of individuals during the day with birds arriving all day and low percentages of colour-ringed individuals still present in the evening. Therefore, although at least 43 km offshore and generally being nocturnal migrants, many wheatears continue migration during daylight and refuse resting and feeding. These observations are in line with those sometimes made on the nearby and much larger Wadden Sea islands Wangerooge and Langeoog, where Northern Wheatears were streaming along dunes and beaches during daytime (HANTGE & SCHMIDT-KOENIG 1958). Perhaps, the wheatears are able to judge feeding conditions and thus the potential of refuelling in a stopover habitat quickly. According to optimality models, time-minimizing migrant birds would have to leave the site when the expected refuelling rate would drop the instantaneous speed of migration to an average speed of migration (ALERSTAM & LINDSTRÖM 1990, LINDSTRÖM & ALERSTAM 1992, WEBER et al. 1999), which might happen much earlier when stopping over in Helgoland grassland habitats compared to beach habitats.

Without doubt, the stopover behaviour even on the very small island of Helgoland, which is much restricted in space and habitat diversity, shows large variation with lengths of stay ranging from several minutes to two weeks. Further studies will have to show whether this variation is influenced by other factors than habitat quality such as predation risk, weather and body condition.

6. Zusammenfassung

Habitatnutzung durch rastende Steinschmätzer (*Oenanthe oenanthe*) während des Zuges auf einer Meeresinsel

Bei Rastaufenthalten auf der Hochseeinsel Helgoland (Deutsche Bucht, Nordsee) nutzen Steinschmätzer (*Oenanthe oenanthe*) auf dem Heimzug (März bis Mai) gleichermaßen Grünlandbereiche und am Strand angespülte Tanghaufen als Rasthabitat. Im Laufe des Wegzuges ist von August bis Oktober ein wachsender Anteil der Steinschmätzer am Strand zu finden, was vor allem am schwindenden Nahrungsangebot in den Grünlandbereichen und dem gleichzeitigen massenhaften Angebot von Tangfliegen (Coelopidae) und deren Larven am Strand liegt. Schwer zu beurteilen ist dagegen die Habitatqualität im Hinblick auf Schutz vor fliegenden Prädatoren (Greifvögel). Anhand von individuell farbberingten Vögeln konnten unterschiedliche Muster der Habitatnutzung in den beiden Lebensräumen gezeigt werden. Im Grünland beringte Steinschmätzer streiften meist weiträumig umher und verließen meist noch am Tag der Ankunft die Insel. Von den am Strand beringten Vögeln verweilte dagegen ein deutlich größerer Anteil über mindestens eine Nacht hinweg, wobei diese Vögel in der Regel nahe dem Beringungsort blieben und häufig Territorien etablierten (im Grünland nie vorkommend). Die Ergebnisse unterstreichen die Rolle der Habitatqualität beim Rastverhalten, denn Steinschmätzer scheinen schon kurz nach der Ankunft in einem potentiellen Rastgebiet die Möglichkeiten zur Erneuerung der Energiereserven im Verhältnis zur resultierenden Zuggeschwindigkeit beurteilen zu können (im Hinblick auf die Minimierung der Zuggeschwindigkeit als Optimalitätskriterium beim Vogelzug).

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