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Source: *Ardea*, 99(2) : 157-165

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/078.099.0205>

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# Stopover behaviour and dominance: a case study of the Northern Wheatear *Oenanthe oenanthe*

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Arizaga J., Schmaljohann H. & Bairlein F. 2011. Stopover behaviour and dominance: a case study of the Northern Wheatear *Oenanthe oenanthe*. *Ardea* 99: 157–165.

In migrants that occupy and defend territories during migration, social status can determine access to preferred resources and alter stopover behaviour. The potential variation in stopover behaviour between dominant and subordinate individuals of the Northern Wheatear *Oenanthe oenanthe*, a territorial migrant bird species, was examined at an offshore stopover area on the island of Helgoland during the spring of 2009. Overall, territories were occupied and defended by dominant birds (identified as those that won  $\geq 50\%$  of the conspecific aggressive encounters). Dominant birds also initiated most conspecific aggression. Unable to settle and defend a territory, subordinates tended to be vagrant and stopped over for shorter periods of time. This is likely due to the fact that subordinates were continuously displaced by dominants, and therefore had less access to food. Subordinates also tended to forage at lower rates. Northern Wheatears were primarily found in zones with a higher number of shelters, supporting the idea that avoidance of predation plays a role in site selection.

Key words: asymmetric contests, body size, Helgoland, migration, social status, territoriality

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Migratory birds may divide their journey into periods of flight, when energy stores are consumed, and stopovers, when fuel reserves are replenished. Because low rates of fuel accumulation result in lower speeds of migration, which can have a negative impact on survival and/or fitness (Newton 2008), prompt refuelling is crucial at stopovers (Alerstam & Lindström 1990). In species that occupy and defend territories during migration (Lindström *et al.* 1990, Dänhardt & Lindström 2001, Dierschke & Delingat 2001), social status and hierarchy position can strongly determine access to food and/or shelter (Moore *et al.* 2003). This determines their stopover decision in terms of fuelling strategy or departure (Carpenter *et al.* 1993a, Dierschke *et al.* 2005).

An inherent question associated with any study analysing the influence of social status on behaviour is how dominance is measured. Age and/or sex often determine dominance, with adults and/or males often being dominant over juveniles or females, respectively

(Moore *et al.* 2003, Dierschke *et al.* 2005). In other cases, social status is determined by body size, with larger birds likely to be more dominant (Lindström *et al.* 1990). Although there is no clear evidence showing that fuel load determines social status in migrants, lean birds foraged at a higher rate than heavier birds after crossing the Gulf of Mexico during the spring (Loria & Moore 1990, Wang & Moore 1997). Such higher motivation to refuel before resuming migration may encourage leaner migrants to become dominant (i.e. to be able to expel other birds from a territory and therefore to have priority access to resources).

In this study, we tested hypotheses about differences in the stopover behaviour of dominant and subordinate individuals of a territorial migrant bird species, the Northern Wheatear *Oenanthe oenanthe*. This is a long-distance migratory passerine that breeds across most of the Holarctic and overwinters in Sahelian Africa (Cramp 1988). Two subspecies occur in W Europe: *O. o. oenanthe*, which breeds all across

Europe and Asia and reaches Alaska and NW Canada, and *O. o. leucorhoa*, which breeds in NE Canada, Iceland and Greenland (Conder 1989). Wheatears are insect-eating passerines that feed on small invertebrates found on the ground and in low vegetation and occasionally in the air (Cramp 1988).

**Territoriality and habitat use.** The “good feeding site” hypothesis states that a territory is placed in an optimal feeding area, where territorial birds increase survival likelihood by having consistent access to sufficient food (Davies & Houston 1981, Snow & Snow 1984). The relationship between territorial behaviour and social status has rarely been analysed in stopover migrants (but see Lindström *et al.* 1990, Carpenter *et al.* 1993a, Dierschke *et al.* 2005). Dominants are more likely to settle and establish a territory than subordinates (Carpenter *et al.* 1993a, Carpenter *et al.* 1993b), with such territories usually occurring in areas with abundant resources, such as food or shelter (Marra *et al.* 1993, Cuadrado 1995, 1997). Consequently, subordinates can adopt three alternative strategies: (1) depart from the stopover site, (2) establish a territory in a suboptimal habitat away from dominants (Marra *et al.* 1993, Stutchbury 1994), or (3) become vagrant (Sherry & Holmes 1996, Catry *et al.* 2004). The latter possibility would allow subordinates to briefly enter the territory of dominant birds to feed. In the Northern Wheatear, we hypothesize that dominants defend territories (Conder 1989, Dierschke *et al.* 2005), and subordinates are vagrant.

**Foraging.** Subordinate birds are often forced to either utilize suboptimal habitat (Figuerola *et al.* 2001) or to have intermittent access to food in higher quality habitat (i.e. entering a territory to feed; Carpenter *et al.* 1993b, Dierschke *et al.* 2005), resulting in lower foraging rates compared to dominants holding territories. Alternatively, subordinates could reach a mean foraging rate similar to that of dominants under super-abundant food availability (Ellegren 1991, Carpenter *et al.* 1993b, Dierschke *et al.* 2005). This happens when subordinates are able to increase their foraging rates (Carpenter *et al.* 1993b, Dierschke *et al.* 2005). Such a strategy, however, could be valid only for a fraction of subordinates and under particular conditions (Dierschke *et al.* 2003). We hypothesized that subordinate Northern Wheatears have lower foraging rates than dominants, indicating less access to food.

**Aggression.** Subordinates may be involved in more aggressive encounters with dominant birds (Dierschke *et al.* 2005) since subordinate birds forage in widely spread areas along which they cross the territories of dominants. Alternatively, subordinates may not be

considered as a threat by dominant birds and could be less frequently attacked (Davies & Houston 1981, Carpenter *et al.* 1993b). Subordinates could also show high rates of aggressive encounters if they fight among each other.

**Stopover duration.** Subordinate birds could adopt two strategies in relation to their stopover duration: (1) depart from the stopover site to look for better conditions in other areas, resulting in shorter stopover periods than dominants (Weber *et al.* 1999, Dierschke *et al.* 2005), or (2) remain at the site and adopt alternative strategies, such as vagrancy and/or the occupancy of less suitable habitats within the stopover locality, resulting in similar or longer stopovers than dominants. In the case of high food abundance, subordinates should gain weight and depart with fuel loads similar to dominants (Dierschke *et al.* 2005). This suggests that subordinates are able to compensate for their worse situation in comparison with dominants (Dierschke *et al.* 2005). Such compensation, however, could only be possible when food is very abundant (Carpenter *et al.* 1993b, Dierschke *et al.* 2005). We hypothesize that, except in case of superabundance of food, subordinates stop over for shorter periods of time than dominants.

## METHODS

### Sampling area and protocol

Helgoland is a 1.5 km<sup>2</sup> island in the North Sea approximately 50 km from the coast of north Germany. Helgoland contains open grasslands and beach as chief habitats. It is used as a stopover site by *O. o. oenanthe* and *O. o. leucorhoa* during both the autumn and spring migration (Dierschke & Delingat 2001, 2003). During spring, *O. o. leucorhoa* faces a longer flight from Helgoland over the sea than *O. o. oenanthe* to reach its breeding grounds (*O. o. leucorhoa* to Iceland/ Greenland/E Canada; *O. o. oenanthe* to Scandinavia).

Data were collected during the spring migration period from 15 April to 21 May 2009. Wheatears in Helgoland tend to concentrate along the beach, where food availability is normally higher (Delingat & Dierschke 2000), and birds are more territorial than in other areas (Dierschke & Delingat 2001). Accordingly, the study was carried out on the northeastern beach (550 × 30 m). The most northeastern part of the beach was bordered by a seawall flanked by blocks of stone with many cavities; such cavities were consistently used by Wheatears as shelter (J. Arizaga, pers. obs.). The opposite (northwest) extreme of the beach was bordered by a cliff that is more than 40 m high, at the

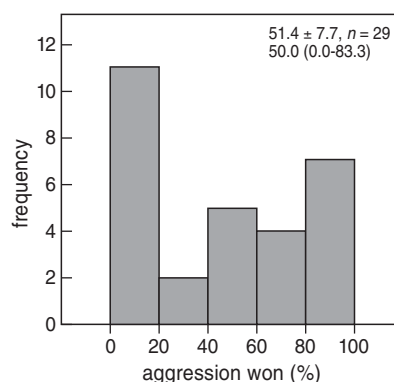
base of which there were many large rocks, also providing shelter for Wheatears. The rest of the beach was open sand, devoid of rocks and other types of shelter. Behind the beach there was a narrow dune-line followed by a shrubby area.

Wheatears were captured with spring traps baited with mealworms. Upon capture they were ringed both with metal and coloured rings (code: metal-colour on the left leg/colour-colour-colour on the right leg). Birds were sighted with a telescope (magnification 60×). Trapping mainly occurred from 12:00 to 16:00. The island's size allowed almost all of the migrant birds landing on Helgoland to be detected upon arrival; studies of colour-ringed birds showed a re-sighting likelihood of up to 83% (Schmaljohann & Dierschke 2005). This allows for reliable measures of stopover duration based on mark-resight data, because the ringing day and the day of the last sighting can be considered to be roughly the day of arrival and departure in Helgoland, respectively (Dierschke & Delingat 2001). Ringed birds were aged (2y, birds in their second year of life; >2y, older birds), and sexed. Wing length ( $\pm 0.5$  mm; method III by Svensson 1992), tarsus length ( $\pm 0.1$  mm), body mass ( $\pm 0.5$  g) were also recorded for each bird.

Ringed birds ( $n = 41$ ) were surveyed for 2 min time periods between 08:00 and 12:00, and 16:00 and 20:00 (mean survey period/bird: 36 min; range 1.5 to 144.5; 1.5 was due to a bird that departed from the area before the 2 min-survey was complete). During the survey period the number of hops, pecks, flights and aggressive encounters per each 2-min period were recorded (Dierschke & Delingat 2001). We measured home ranges as the linear distance between the two most distant locations at which a bird was observed.

Previous studies have classified dominant birds as those winning most of the aggressive encounters in which they are involved (Lindström *et al.* 1990, Dierschke *et al.* 2005). In our study, the proportion of aggressive encounters that were won by each bird showed a U-shape distribution curve; a high fraction of birds never or seldom won a contest and another high fraction were clearly winners (Fig. 1). Therefore, we classified dominant birds as those that won  $\geq 50\%$  of the encounters in which they were involved ( $n = 16$ ); the remaining Wheatears were classified as subordinates ( $n = 9$ ).

To analyse the spatial distribution of Wheatears, the beach was divided into two main sections: (1) the two edges, which contain abundant shelter (large rocks with many cavities), and (2) the middle area, constituted by open sand, which does not contain any shelter.



**Figure 1.** Frequency distribution of the percentage of aggressive encounters won by Northern Wheatears stopping-over on Helgoland. Mean  $\pm$  SE, sample size and median (together with percentiles 25 and 75) values are shown.

Wheatears at the beach fed mostly on kelp larvae (see for further details Delingat & Dierschke 2000).

### Statistical analyses

We compared the (1) behaviour (foraging rate, foraging effort, aggressiveness, stopover duration, home ranges), (2) individual features (sex, subspecies, body size and fuel load), and (3) spatial distribution between subordinate and dominant Wheatears during their entire stopover in Helgoland. Only those birds involved in at least one aggressive conspecific encounter throughout their stopover in Helgoland were included in this analysis ( $n = 25$  out of 42; Table 1).

Although all the quantitative data (foraging rate, foraging effort, aggressiveness, stopover duration, home ranges, body size and fuel load; see Tables 2 and 3 for more details) were normally distributed (Kolmogorov test,  $P > 0.05$ ), the variance was very high for the behaviour-associated variables (mean coefficients of variation for dominants: 64.2%; subordinates: 77.7%) compared to body size and fuel load (mean coefficients of variation for dominants: 30.8%; subordinates: 23.6%). Therefore, behavioural data were log-transformed to reduce variance (mean coefficients of variation for dominants: 36.2%; subordinates: 53.5%). We used both wing length (Gosler *et al.* 1998) and tarsus length (Senar & Pascual 1997) as proxies of body size. Fuel load (FL) was calculated as  $FL = (BM - LBM) / LBM$ ; where BM was the actual body mass and LBM was lean body mass. LBM was calculated for each individual  $i$  as  $LBM_i = 22.7 + 0.28(97.0 - WL_i)$ , where  $WL_i$  is wing length (in mm) (Dierschke *et al.* 2005). Capture time (hour) was not correlated with fuel load ( $r = -0.167$ ,  $P = 0.424$ ,  $n = 25$ ), probably

because all birds were captured within a short time period (cf. Delingat *et al.* 2009). Therefore, body mass was not corrected for capture time. Both behaviour and body size and fuel load-associated data of dominant and subordinate birds were compared with t-tests (significance level:  $P < 0.05$ ). Since P-values depend on sample size, and the sample size here was relatively low (Table 1), we complementary calculated the effect size (Arizaga & Barba 2009) as  $d = (\text{mean}_a - \text{mean}_b) / \text{SD}_{\text{pooled}}$ , and the  $\text{SD}_{\text{pooled}} = [((n_a - 1)\text{SD}_a^2 + (n_b - 1)\text{SD}_b^2) / (n_a + n_b)]^{0.5}$ , where a and b are the two groups compared and  $n$  is the sample size. An effect size  $> 0.5$  (difference between means accounts for  $> 50\%$  of the pooled SD) was considered to indicate a significant difference between samples (Cohen 1969).

We used contingency tables to see whether the proportion of dominant/subordinates differed in relation to sex, subspecies, or location on the study beach (significance level:  $P < 0.05$ ). A Pearson's correlation test was used to test if foraging rate was correlated to population size (number of Wheatears counted on the beach per day).

SPSS 15.0 software was used for statistical procedures. Google Earth was used for territory mapping (see above for definition of a territory). All means are given  $\pm 95\%$  confidence interval (CI), and median values are given with the 25th and 75th percentiles.

RESULTS

Of 42 colour-ringed birds surveyed during the spring migration period, 27 (65.9%) were observed to be involved in one or more aggressive interactions (131 encounters registered in 933.8 min). Most contests (90.1%) were conspecific (i.e. Wheatear–Wheatear interactions), and the rest involved other small passer-

ines (pipits *Anthus* spp., wagtails *Motacilla* spp. and one Common Starling *Sturnus vulgaris*). We did not detect any conspecific interaction in two out of 27 Wheatears, so the actual sample size of Wheatears where we could determine social status was 25. 38.9% of conspecific aggressions were found between birds of the same sex, without significant differences between sexes ( $\chi_1^2 = 1.33$ ,  $P = 0.249$ ). This result was biased from a 1:1 proportion ( $\chi_1^2 = 5.33$ ,  $P = 0.021$ ), and significantly more aggression was between individuals of the opposite sex. Most conspecific aggressive encounters were won by the initiator (83.1%;  $\chi_1^2 = 51.56$ ,  $P < 0.001$ ), indicating that a bird initiating an aggression was more likely to win it and therefore to become dominant.

We did not detect significant behavioural differences between subordinate and dominant birds during their first day of stopover, but differences were detected over the entire stopover period (Table 2). Dominant birds were found to occupy smaller home ranges than subordinates (Table 2). Moreover, effect size values (but not  $P$  values from  $t$ -tests) also indicated that subordinates tended to have lower foraging rates, move (fly) less and remain at the site for shorter periods than dominants (Table 2). Thus, 70% of subordinates had a one-day stopover, whereas only 40% of dominants left the area after one-day stopover. Dominants were attacked less often than subordinates (9.1% vs. 100%;  $\chi_1^2 = 16.78$ ,  $P < 0.001$ ). Wheatears that initiated more than 50% of the contests had nearly significantly larger fuel loads ( $21.7 \pm 5.4\%$ ,  $n = 12$ ) than those that seldom initiated a contest ( $10.5 \pm 9.9\%$ ,  $n = 13$ ,  $t = 1.892$ ,  $P = 0.068$ ),

Neither the sex ratio nor the subspecies differed between dominants and subordinates (male–female ratios: 10:6 vs. 7:2,  $\chi_1^2 = 0.62$ ,  $P = 0.661$ ; *O. o. leucorhoa* – *O. o. oenanthe* ratios: 3:1 vs. 11:5,  $\chi_1^2 = 0.06$ ,

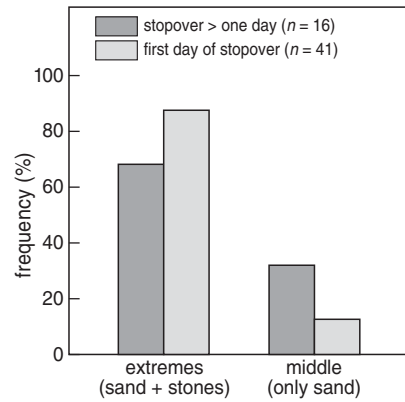
**Table 1.** Number of colour-ringed migratory Northern Wheatears ( $n = 42$ ) surveyed when stopping-over on Helgoland, during the spring migration period of 2009. Social status was determined for birds involved in one or more conspecific aggressive encounters. Wheatears winning  $\geq 50\%$  of contests were classified as dominant. Individuals classified by length of stay (1 day or longer).

Subspecies	Sex	No aggressions		Aggressions			
		1 day	>1 day	Subordinate		Dominant	
				1 day	>1 day	1 day	>1 day
Unknown	Male	6	0	5	0	0	0
	Female	0	0	0	0	0	0
<i>O. o. oenanthe</i>	Male	2	0	0	1	2	2
	Female	0	1	0	0	0	1
<i>O. o. leucorhoa</i>	Male	3	2	0	1	2	4
	Female	2	1	1	1	2	3



$P = 0.999$ ). Dominants tended to be larger and had more fuel over lean body mass, although the difference was only significant (based on effect size, but not  $P$ -value) for tarsus length (Table 2). Fuel load was not correlated with stopover duration ( $r = -0.315$ ,  $P = 0.125$ ,  $n = 25$ ).

Birds were not randomly distributed along the beach. Most were established far from the middle part of the beach for both the first day ( $\chi^2_1 = 5.49$ ,  $P = 0.019$ ) and subsequent days ( $\chi^2_1 = 9.00$ ,  $P = 0.003$ ) (Fig. 2). Such a preference for the sheltered areas did not differ between the first day and subsequent days ( $\chi^2_1 = 2.19$ ,  $P = 0.139$ ). The behaviour (foraging rate, movement rate, home ranges) of the Wheatears did not differ between the beach edges and the middle part (data provided for the first day on the beach; Table 3). As foraging rate of Wheatears did not differ between the beach edges and the middle part, we assume that



**Figure 2.** Percentage of Northern Wheatear territories occurring on beach edges ('extremes') and open beach area ('middle') during spring 2009 stopovers on Helgoland.

**Table 2.** Stopover behaviours and biometrics of dominant and subordinate Northern Wheatears during spring stopover on Helgoland. Significant values from the  $t$ -test and effect size values  $>0.5$  are in bold. Values reported as mean  $\pm$  95% CI. Data on behaviour and stopover duration were log-transformed for the analyses. Original data in parentheses, except for body size and fuel load, for which the original data are shown.

Variable	Subordinates (n = 9)	Dominants (n = 16)	t-value	P-value	Effect size
<b>Behaviour (first day on the beach)</b>					
Peck/min	0.44 $\pm$ 0.22 (2.5 $\pm$ 0.8)	0.54 $\pm$ 0.14 (3.4 $\pm$ 0.8)	0.847	0.406	0.368
Hops/min	0.81 $\pm$ 0.37 (10.4 $\pm$ 3.4)	0.87 $\pm$ 0.18 (8.7 $\pm$ 1.5)	0.342	0.735	0.149
Flight/min	0.23 $\pm$ 0.11 (0.8 $\pm$ 0.2)	0.29 $\pm$ 0.10 (1.2 $\pm$ 0.3)	0.757	0.457	0.329
Aggression/min	0.15 $\pm$ 0.12 (0.6 $\pm$ 0.3)	0.23 $\pm$ 0.10 (1.0 $\pm$ 0.3)	0.962	0.346	0.418
Home range (m)	1.83 $\pm$ 0.48 (121 $\pm$ 33)	1.51 $\pm$ 0.39 (79 $\pm$ 25)	0.996	0.329	0.433
<b>Behaviour (entire stopover)</b>					
Peck/min	0.55 $\pm$ 0.18 (3.1 $\pm$ 0.6)	0.69 $\pm$ 0.09 (4.4 $\pm$ 0.7)	1.618	0.119	<b>0.703</b>
Hops/min	0.93 $\pm$ 0.31 (11.7 $\pm$ 3.1)	1.02 $\pm$ 0.11 (10.6 $\pm$ 1.2)	0.511	0.621	0.269
Flight/min	0.20 $\pm$ 0.10 (0.7 $\pm$ 0.2)	0.29 $\pm$ 0.07 (1.0 $\pm$ 0.2)	1.455	0.159	<b>0.632</b>
Aggression/min	0.07 $\pm$ 0.04 (0.2 $\pm$ 0.1)	0.08 $\pm$ 0.03 (0.2 $\pm$ 0.1)	0.449	0.658	0.195
Home range (m)	2.07 $\pm$ 0.19 (141 $\pm$ 30)	1.75 $\pm$ 0.13 (64 $\pm$ 9)	2.888	<b>0.008</b>	<b>1.255</b>
Stopover duration (days)	0.39 $\pm$ 0.09 (1.6 $\pm$ 0.3)	0.48 $\pm$ 0.09 (2.3 $\pm$ 0.4)	1.330	0.197	<b>0.578</b>
<b>Body size and fuel load</b>					
Wing length (mm)	100.7 $\pm$ 2.9	101.6 $\pm$ 2.1	0.468	0.644	0.203
Tarsus length (mm)	27.4 $\pm$ 0.7	28.0 $\pm$ 0.5	1.363	0.186	<b>0.592</b>
Fuel load (% over lean mass)	12.2 $\pm$ 5.9	18.6 $\pm$ 8.9	0.992	0.331	0.431

the main difference between these zones was due to different amount of shelter. The proportion of birds that were found in the beach edges did not differ in relation to social status ( $\chi^2_1 = 0.672$ ,  $P = 0.630$ ), with most birds being detected in the beach edges. Only four out of the 16 colour-ringed Wheatears with stopovers longer than one day changed territory location, and in all cases the birds moved from the middle part of the beach to the extremes regardless of their social status ( $\chi^2_1 = 1.73$ ,  $P = 0.497$ ).

Foraging rate was not correlated with population size ( $r = -0.159$ ,  $P = 0.316$ ,  $n = 42$ ; data provided for the first day on the beach). This same result was obtained for Wheatears with different social rank (dominants:  $r = 0.112$ ,  $P = 0.680$ ; subordinates:  $r = -0.379$ ,  $P = 0.314$ ).

DISCUSSION

Nearly 70% of Northern Wheatears stopping-over on Helgoland during the spring migration period were observed in one or more aggressive encounters, suggesting resource competition. In agreement with previous studies, we found that birds initiating an aggressive encounter were more likely to win (Bibby & Green 1980; Dierschke *et al.* 2005).

Behavioural differences between subordinate and dominant birds were found only when data for the entire stopover were pooled; no such differences were detected when data from the first day of the stopover were analysed. This may be because during the first day on the beach, newly arrived birds could experience settling/search costs that included coping with the existing social environment and/or the determination

of their own social status. However, we cannot reject a possible sampling bias; many Wheatears were captured around noon, and therefore the survey period was shorter for the first day (mean 9.7 min/bird/day) than for subsequent days (mean 23.0 min/bird/day). Such a short survey period would have been insufficient to properly document stopover behaviour. It is also possible that dominance may not be a characteristic of a bird at arrival, but a status that is reached after winning one or several contests, so differences in behaviour are difficult to detect for the first day.

The main difference between social classes was that dominant individuals occupied smaller home ranges than subordinates. Rather than having larger home ranges, this suggests that subordinates did not defend a territory (Chernetsov & Titov 2001); hence subordinates tended to forage over a larger area (a vagrancy strategy of subordinates vs. a territorial behaviour of dominants). Vagrancy, however, was likely to be a suboptimal alternative for Wheatears unable to defend a territory (Rappole & Warner 1976; Sherry & Holmes 1996). Although we need more studies to determine whether vagrancy is in fact a suboptimal strategy, some of our results support this hypothesis: subordinates tended to have lower foraging rates and stop over for shorter periods. Both behaviours are consistent with the idea that subordinate birds found it difficult to forage at a sufficient rate, and were forced to leave the beach. Dierschke *et al.* (2005) showed that stopover duration did not differ between territorial and non-territorial (vagrant) Northern Wheatears stopping-over more than one day on Helgoland, and that most territories were held by dominants. This result does not contradict our findings if only a fraction of the vagrants are able to remain on the beach for more than one day

**Table 3.** Microhabitat-associated stopover features of Northern Wheatears. The edges ('extremes') of the beach had a high number of shelters (rocks) that were absent from the middle part of the beach where there was only sand. Data provided for the first day on the beach. All variables are log-transformed. Original data in parentheses.

Variable	Extremes ( <i>n</i> = 28)	Middle ( <i>n</i> = 13)	<i>t</i> -value	<i>P</i> -value	Effect size
Peck/min	0.54 ± 0.11 (3.3 ± 0.6)	0.58 ± 0.15 (3.4 ± 0.6)	0.391	0.698	0.135
Hops/min	0.92 ± 0.14 (9.9 ± 1.3)	1.03 ± 0.24 (13.3 ± 2.2)	0.791	0.433	0.272
Flight/min	0.27 ± 0.05 (1.0 ± 0.1)	0.24 ± 0.13 (1.0 ± 0.4)	0.479	0.635	0.165
Aggression/min	0.14 ± 0.07 (0.6 ± 0.2)	0.09 ± 0.09 (0.4 ± 0.2)	0.749	0.458	0.258
Home range (m)	1.54 ± 0.28 (69 ± 10)	1.61 ± 0.45 (108 ± 37)	0.275	0.785	0.095

(the others are presumably displaced by territory owners).

To some extent, a higher foraging rate of dominants is consistent with the good feeding site hypothesis, according to which dominant birds defend sites where there is more food (Cuadrado 1997). A higher foraging rate would allow dominant birds to reach a higher fuel deposition rate than subordinates (Dierschke *et al.* 2005). However, we cannot completely rule out the prediction that subordinates could also reach similar rates of fuel accumulation than dominants by increasing their foraging rates (Davies & Houston 1981, Carpenter *et al.* 1993b). In previous studies, non-territorial birds were found to take more food per unit time than territorial Wheatears when attracted to an artificial feeder (Dierschke *et al.* 2005). We did not detect such a compensatory strategy. A possible reason explaining this result is that this strategy is possible only when food is superabundant (Dierschke *et al.* 2003, Dierschke *et al.* 2005). On Helgoland, this is associated with episodes of high accumulation of kelp algae along the beach, which give rise to noticeable demographic explosions of kelp flies (Delingat & Dierschke 2000). During the spring of 2009, however, the amount of kelp at the study beach was relatively low (J. Arizaga & H. Schmaljohann, pers. obs.).

Dominants tended to remain on the island for a longer period, indicating that they had better access to food than subordinates. This is in agreement with previous studies (Dierschke *et al.* 2005), and supports the hypothesis that when unable to defend a territory, subordinates departed from the area, and likely the island, as most birds leaving the beach were never seen again (J. Arizaga, pers. obs.). Such a difference, however, was not so obvious if we consider in the analysis not only birds that stopped-over for more than one day, but also those that stayed one day. Most subordinates stayed on Helgoland for one day and they had a mean fuel load of 12.2% over lean body mass upon capture. Most *O. o. leucorhoa* (which was the most abundant subspecies, 70%) subordinates stopping-over on the island for only one day did not have sufficient fuel load to cover the large sea crossing until reaching their breeding areas in Iceland/Greenland (Dierschke & Delingat 2003). In this case, they could continue their migration towards southern Scandinavia or even perform a reverse migration towards the south where the possibility to refuel should have been higher (Schmaljohann *et al.* 2011).

The habitat was not homogeneous along the beach, with a higher availability of shelter at beach edges. Noticeably, most Wheatears were concentrated in the

beach edges and even subordinates were not more abundant in the middle zone, indicating that when unable to settle and/or forage in a sufficiently good habitat they left the stopover site. Moreover, all migrants stopping-over for two or more days that changed the location of their home range ( $n = 4$ ) moved from the middle part toward the beach edge. Thus, our results are also in agreement with the anti-predation hypothesis (Cuadrado 1997); Northern Wheatear may minimize predation risk during stopover by avoiding those sites where exposure to predators is very high. Previous studies on the Northern Wheatear demonstrated that the presence of raptors did not affect departure decisions directly (Dierschke & Delingat 2001), but was negatively correlated with fuel deposition rate (Schmaljohann & Dierschke 2005). In our study, under the presence of predators (e.g. a raptor), Wheatears adopted a “freezing” behaviour (Schmaljohann & Dierschke 2005) or flew to nearby shelters (J. Arizaga, pers. obs.). Wheatears did not feed during this time, and therefore their refuelling rates presumably decreased.

Dominant birds were found to be larger than subordinates, regardless of subspecies or sex, suggesting that social status in the Northern Wheatear is partly associated with body size. Similarly, larger Bluethroats *Luscinia svecica* were observed to be dominant over smaller ones during migration (Lindström *et al.* 1990). The fact that Dierschke *et al.* (2005) found males to frequently be dominant over females could be due to the fact that Northern Wheatear males are larger than females (Svensson 1992). Fuel load also tended to be higher among dominant birds, but the difference was not significant. However, Wheatears that initiated more than 50% of the contests had nearly significantly larger fuel loads than those that seldom initiated a contest, contradicting to some extent the prediction that Wheatears with lower fuel reserves were more motivated to fight for the resources.

In conclusion, Northern Wheatears stopping-over on Helgoland compete for resources, including food (Delingat & Dierschke 2000) and probably shelter. Dominant birds were found to be territorial. Unable to settle and defend a territory, subordinates tend to be vagrants until they leave the beach, and usually the island, resulting in shorter stopover periods. This decision is likely caused by the fact that subordinates are continuously displaced from high quality areas by dominant birds, and they therefore have less access to food (which could give rise to a negative energy budget) and were probably exposed to a higher risk of predation.



## ACKNOWLEDGEMENTS

The field work was supported by the staff and volunteers of the Institute of Avian Research "Vogelwarte Helgoland". We are especially indebted to M. Burgh, B. Holtmann, O. Hüppop, and S. Stadtmann. The financial support was given by the Basque Government (post-doctoral fellowship to J. Arizaga). The methods used in this work comply with the laws of the Federal Republic of Germany and Schleswig-Holstein. Two anonymous reviewers and Kees van Oers provided valuable comments that helped us to improve and earlier version of this work.

## REFERENCES

- Alerstam T. & Lindström A. 1990. Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E. (ed.) Bird migration: the physiology and ecophysiology. Springer-Verlag, Berlin, pp. 331–351.
- Arizaga J. & Barba E. 2009. Importance of sampling frequency to detect differential timing of migration: a case study with Blackcaps *Sylvia atricapilla*. *Ardea* 97: 297–304.
- Bibby C.J. & Green R.E. 1980. Foraging behaviour of migrant pied flycatchers, *Ficedula hypoleuca*, on temporary territories. *J. Anim. Ecol.* 49: 507–521.
- Carpenter F.L., Hixon M.A., Russell R.W., Paton D.C. & Temeles E.J. 1993a. Interference asymmetries among age-sex classes of rufous hummingbirds during migratory stopovers. *Behav. Ecol. Sociobiol.* 33: 297–304.
- Carpenter F.L., Hixon M.A., Temeles E.J., Russell R.W. & Paton D.C. 1993b. Exploitative compensation by subordinate age-sex classes of migrant rufous hummingbirds. *Behav. Ecol. Sociobiol.* 33: 305–312.
- Catry P., Campos A., Almada V. & Cresswell W. 2004. Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. *J. Avian Biol.* 35: 204–209.
- Chernetsov N. & Titov N.V. 2001. Movement patterns of European reed warblers *Acrocephalus scirpaceus* and sedge warblers *A. schoenobaenus* before and during autumn migration. *Ardea* 89: 509–515.
- Cohen J. 1969. Statistical power analysis for the behavioral sciences. Academic press, New York.
- Conder P. 1989. The Wheatear. Christopher Helm, London.
- Cramp S. 1988. Handbook of the Birds of Europe, the Middle East and North Africa. Vol. 5. Oxford University Press, Oxford.
- Cuadrado M. 1995. Territory characteristics and the attacks against intruders in migrant robins *Erithacus rubecula*. *Ardeola* 42: 147–160.
- Cuadrado M. 1997. Why are migrant Robins (*Erithacus rubecula*) territorial in winter?: The importance of the anti-predatory behaviour. *Ethol. Ecol. Evol.* 9: 77–88.
- Dänhardt J. & Lindström A. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Anim. Behav.* 62: 235–243.
- Davies N.B. & Houston A.I. 1981. Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. *J. Anim. Ecol.* 50: 157–180.
- Delingat J. & Dierschke V. 2000. Habitat utilization by Northern Wheatears (*Oenanthe oenanthe*) stopping over on an offshore island during migration. *Vogelwarte* 40: 271–278.
- Delingat J., Dierschke V., Schmaljohann H. & Bairlein F. 2009. Diurnal patterns of body mass change during stopover in a migrating songbird, the northern wheatear *Oenanthe oenanthe*. *J. Avian Biol.* 40: 625–634.
- Dierschke V. & Delingat J. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. *Behav. Ecol. Sociobiol.* 50: 535–545.
- Dierschke V. & Delingat J. 2003. Stopover of Northern Wheatears *Oenanthe oenanthe* at Helgoland: where do the migratory routes of Scandinavian and Nearctic birds join and split? *Ornis Svecica* 13: 53–61.
- Dierschke V., Delingat J. & Schmaljohann H. 2003. Time allocation in migrating Northern Wheatears (*Oenanthe oenanthe*) during stopover: is refuelling limited by food availability or metabolically? *J. Ornithol.* 144: 33–44.
- Dierschke V., Mendel B. & Schmaljohann H. 2005. Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? *Behav. Ecol. Sociobiol.* 57: 470–480.
- Ellegren H. 1991. Stopover ecology of autumn migrating bluethroats *Luscinia svecica svecica* in relation to age and sex. *Ornis Scand.* 22: 340–348.
- Figuerola J., Jovani R. & Sol D. 2001. Age-related habitat segregation by Robins *Erithacus rubecula* during the winter. *Bird Study* 48: 252–255.
- Gosler A.G., Greenwood J.J.D., Baker J.K. & Davidson N.C. 1998. The field determination of body size and condition in passerines: a report to the British Ringing Committee. *Bird Study* 45: 92–103.
- Lindström A., Hasselquist D., Bensch S. & Grahm M. 1990. Asymmetric contests over resources for survival and migration a field experiment with bluethroats. *Anim. Behav.* 40: 453–461.
- Loria D.E. & Moore F.R. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. *Behav. Ecol.* 1: 24–35.
- Marra P.P., Sherry T.W. & Holmes R.T. 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica - a removal experiment with American redstarts (*Setophaga ruticilla*). *Auk* 110: 565–572.
- Moore F.R., Mabey S. & Woodrey M. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries. In: Berthold P., Gwinner E. & Sonnenschein E. (eds) Avian migration. Springer-Verlag, Berlin, pp. 281–291.
- Newton I. 2008. The migration ecology of birds. Academic Press, London.
- Rappole J.H. & Warner D.W. 1976. Relationships between behaviour, physiology and wheatear in avian transients at a migration stopover site. *Oecologia* 26: 193–212.
- Schmaljohann H. & Dierschke V. 2005. Optimal bird migration and predation risk: a field experiment with northern wheatears *Oenanthe oenanthe*. *J. Anim. Ecol.* 74: 131–138.
- Schmaljohann H., Becker P.H., Karaardic H., Liechti F., Naef-Daenzer B. & Grande C. 2011. Nocturnal exploratory flights, departure time, and direction in a migratory songbird. *J. Ornithol.* 152: 439–452.
- Senar J.C. & Pascual J. 1997. Keel and tarsus length may provide a good predictor of avian body size. *Ardea* 85: 269–274.
- Sherry T.W. & Holmes R.T. 1996. Winter habitat quality, population limitation, and conservation of neotropical nearctic migrant birds. *Ecology* 77: 36–48.

- Snow B.K. & Snow D.W. 1984. Long-term defence of fruit by Mistle Thrushes *Turdus viscivorus*. *Ibis* 126: 39–49.
- Stutchbury B.J. 1994. Competition for winter territories in a neotropical migrant: the role of age, sex and color. *Auk* 111: 63–69.
- Svensson L. 1992. Identification guide to European passerines. Fourth edition. Lars Svensson, Stockholm.
- Wang Y. & Moore F.R. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. *Auk* 114: 263–278.
- Weber T.P., Fransson T. & Houston A.I. 1999. Should I stay or should I go? Testing optimality models of stopover decisions in migrating birds. *Behav. Ecol. Sociobiol.* 46: 280–286.

## SAMENVATTING

Sommige vogelsoorten bezetten niet alleen territoria gedurende de broedtijd maar vertonen ook territoriumgedrag tijdens de trek. Territoriale dieren kunnen onderweg op pleisterplaatsen

gunstige plekken monopoliseren wat betreft voedsel en beschutting. De sociale status die individuen hebben op deze pleisterplaatsen, zou dus een grote invloed kunnen hebben op het gedrag dat zij vertonen tijdens de trek. In het onderhavige onderzoek vergeleken de auteurs het gedrag van dominante en subdominante Tapuiten *Oenanthe oenanthe* op een pleisterplaats op het eiland Helgoland gedurende de voorjaars trek van 2009. Zij vonden dat dieren die veel agressieve interacties initieerden met soortgenoten en die in meer dan 50% van de gevallen wonnen, overwegend de territoria bezetten en verdedigden. Dieren die niet in staat waren een territorium te bemachtigen, werden voortdurend door territoriale individuen van de goede foerageerplekken verjaagd. Dit resulteerde in een voor de subdominante vogels verlaagde voedselopnamesnelheid. Tevens neigden zij ernaar de periode dat zij op het eiland pleisterden, te verkorten en eerder door te trekken. (KvO)

*Corresponding editor: Kees van Oers*

*Received 27 December 2010; accepted 28 August 2011*