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Nocturnal exploratory flights, departure time and, direction in a migratory songbird

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Abstract

Stopover studies have concentrated so far mostly on mechanisms regulating the temporal organisation on the day-to-day level. Taking advantage of the small and isolated island of Helgoland in the North Sea, we investigated the stopover and departure behaviour of a nocturnal migrant by using radio telemetry. Special attention was paid particularly to nocturnal behaviour, their departure times within the night, and departure directions. Here we show that Northern Wheatears, *Oenanthe oenanthe*, performed regularly nocturnal exploratory flights on nights before and on departure night, which might be a common behaviour of nocturnal migrants to evaluate meteorological conditions aloft prior to departure. We proposed that migrants being prepared for an endurance flight would depart early in the night within a short time window, whereas individuals departing with low fuel load would be less prone to take off early. Our data, however, could not support this hypothesis. In respect of the migratory direction there was a significant correlation between departure direction and departure fuel load. Northern Wheatears with high departure fuel loads headed more towards north than lean migrants, which departed mostly towards the nearest coastline, i.e. east to south. Thus, birds with high fuel loads showed their seasonally appropriate migratory direction irrespectively of the ecological barrier ahead, whereas lean birds avoided this direction. To our knowledge, this is the first study that investigates the relationship of fuel load and departure direction in a free-flying songbird.

Keywords: Northern Wheatear · exploratory flight · departure time · departure direction · radio telemetry

Introduction

While migrating between breeding and wintering areas, birds spend far more of their time and energy at stopover sites than they do flying along their routes (Hedenström & Ålerstam 1997; Wikelski et al. 2003). Stopover ecology has taken over a major role in building up an understanding of how bird migration is organized. The optimal migration strategies from Ålerstam & Lindström (1990) predict how birds should organize their stopover in respect of time, energy, and predation (Houston 1998), which was confirmed by several studies (Hedenström 2007). It is now well understood, why migrants decide setting off from a stopover site during the season (Jenni & Schaub 2003; Schaub et al. 2004; Tsvey et al. 2007; Schaub et al. 2008; Goymann et al. 2010) and what influences migrants' general flight directions (Liechti & Bruderer 1998; Liechti 2006). Only little is, however, known about the nocturnal behaviour on the ground prior departure and why birds depart at a certain night-time and in a certain direction from a stopover site.

To investigate these issues, we conducted a radio telemetry study on an island in the German North Sea. Helgoland offers favourable conditions to investigate nocturnal behaviour of migrants, because (1) owing to its small size (1 km²) presence/absence can be precisely determined, (2) birds having left the island can be treated as having continued their migration, because next stopover sites are at least 50 km away, and (3) birds performing local nocturnal flights will not be misidentified as departing birds, because detection range of radio transmitters is larger than the study area itself. As the study species, we chose the Northern Wheatear, *Oenanthe oenanthe*, a trans-Saharan migrant, which assembles frequently in two subspecies on Helgoland during migration (Dierschke & Delingat 2003). These birds of the nominate subspecies, *O. o. oenanthe* (*oenanthe* wheatears hereafter), breed in Scandinavia, whereas the subspecies *O. o. leucorhoa* (*leucorhoa* wheatears hereafter) breeds on Iceland, Greenland, and Eastern Canada. Individuals stopping over are, hence, from the same species but face different migratory goals during spring migration.

Migrants having decided not to set off at a certain night might seek for a sheltered site and rest to recover from sleep deprivation of the previous migratory flight (Schwilch et al. 2002). Thus, these birds are supposed to rest during the night, whereas birds preparing for departure might show a higher nocturnal activity prior their departure, which might include screening the horizon for compass

calibration (Cochran et al. 2004; Mouritsen et al. 2004), exploring weather conditions, and possibly performing short nocturnal flights to test meteorological conditions aloft (Liechti 2006). We hypothesize that nocturnally migrating songbirds show a higher night-time activity on departure night than on nights before.

Prior to departure, migrants need to calibrate their compasses for orientation. The appropriate cues are best available during the twilight period, hence nocturnally migrating songbirds are supposed to depart after this period (Moore 1987; Muheim et al. 2006a). This coincides well with the majority of departure events (Bruderer & Liechti 1995; Liechti et al. 1997; Bruderer & Liechti 1999; Gauthreaux & Belser 1999; Bolshakov et al. 2003; Bulyuk & Tsevy 2006; Schmaljohann et al. 2007). However, such radar and mist-net data do not provide spatial and temporal information about departure events of a priori specifically selected individuals. Radio telemetry studies do so (Cooke et al. 2004) and revealed that individual departure events may occur much later in the night than the exodus of migrants after sunset might suggest (Cochran et al. 1967; Åkesson et al. 1996a; Moore & Aborn 1996; Åkesson et al. 2001; Bolshakov & Chernetsov 2004; Bolshakov et al. 2007), see also Bulyuk & Tsvey (2006).

Factors influencing the day-to-day departure decision are also supposed to control for migrants' departure time within the night. These decisions are, generally, ruled by an interplay of environmental and endogenous factors (Jenni & Schaub 2003) with meteorological conditions having a paramount effect on flight (Liechti 2006) and orientation performance (Åkesson et al. 2001), while other environmental factors such as predation danger (Fransson & Weber 1997; Schmaljohann & Dierschke 2005) and competition (Rappole & Warner 1976; Dierschke et al. 2005) seem to play a less important role. Fuel deposition rate and stopover duration determine departure fuel load, which in turn defines the potential flight range. Combining the potential flight range with the direction provides the potential flight vector. Migrants with high fuel loads can reach their next migratory goal by a direct flight and can keep their seasonal appropriate migratory direction, whereas leaner birds may need to fly towards the nearest available stopover site. The latter may, hence, be forced to select a flight direction differing from the seasonal appropriate one, if stopover sites are not in the same direction as their overall migratory goal. The length of the potential flight vector might initiate the departure

96 decision within the night: Intended long flights need to be initiated soon after sunset, whereas migrants
97 with short flight vectors do not need to depart early to accomplish their flight during the dark. We
98 hypothesize that migrant's nocturnal departure time is driven by its potential flight vector.

99 Migrant's potential flight vector plays also an important role for the departure direction, when
100 birds face a particularly inhospitable range of their journey. Long potential flight vectors allow
101 crossing any obstacle by a non-stop flight and keeping the seasonal appropriate migratory direction,
102 whereas short flight vectors drive birds to a detour avoiding the barrier (Alerstam 2001; Sandberg
103 2003). Unfavourable weather conditions (Richardson 1982) and the inability to orientate sufficiently
104 well (Komenda-Zehnder et al. 2002; Zehnder et al. 2002) might deviate birds' flight direction from the
105 expected one as well. Departure direction can, therefore, only be explained in the light of bird's
106 potential flight vector (Alerstam 1978; Lindström & Alerstam 1986; Sandberg 1994; Åkesson et al.
107 1996b; Moore & Aborn 1996; Sandberg & Moore 1996; Sandberg 2003 ; Deutschlander & Muheim
108 2009). We hypothesize that migrants with long potential flight vectors will adjust their departure
109 direction more towards their migratory goal than migrants with short potential flight vectors. In
110 respect of the subspecies, we hypothesize that *oenanthe* wheatears with long potential flight vectors
111 depart towards north to northeast and *leucorhoa* birds towards northwest (Dierschke & Delingat
112 2003), whereas lean birds of either subspecies might depart in any direction directly towards the
113 mainland.

116 **Methods**

117 *Study site*

118 The study was conducted on the German island of Helgoland in the North Sea (54°11'N,
119 07°55'E); the distance to the nearest coast is about 50 km. Helgoland consists of two islands: the main
120 island (1 km², Helgoland hereafter), on which the field study was carried out, and the small Düne
121 island (0.7 km², Düne hereafter), which lies 800 m to the east of Helgoland. The term "island" refers
122 to both.

124 *Study species*

125 During spring season 2008 138 Northern Wheatears were trapped with spring traps baited with
126 mealworms, *Tenebrio molitor*, throughout the daylight period from 6th April to 23rd May 2008.
127 Within 5 min until release, Northern Wheatears were aged and sexed by plumage colouration
128 according to Svensson (1992), measured (maximum wing length to the nearest 0.5 mm after Svensson
129 (1992)) and weighed to the nearest 0.2 g with a Pesola balance. Fat score was estimated on a nine-
130 class (Kaiser 1993) and size of the breast muscle on a four-class scale (Bairlein 1994). Each bird was
131 marked with an individual combination of one aluminium and four split colour-rings. Wing length was
132 used to identify the subspecies: males and females with wing lengths exceeding 102 mm and 97 mm,
133 respectively, were treated as belonging to the Iceland/Greenland subspecies *O. o. leucorhoa*, whereas
134 wing lengths below 99 mm (males) and 96 mm (females) indicated nominate birds (Svensson 1992).
135 Birds with wing length from the range of overlap were not assigned to a subspecies.

136
137 *Departure fuel load*

138 We compared fuel loads rather than body masses owing to the large size differences [range of
139 wing length in this study: 92.5 – 110.5 mm]. Lean body mass resulted from a linear regression of body
140 mass from 220 Northern Wheatears with fat score < 2 (only traces of fat visible) and muscle score < 2
141 (low in breast muscle) caught on Helgoland in the years 1998-2002 and 2008:

142
143
$$\text{lean body mass}_i = 0.29 \times \text{wing length}_i - 6.85 \quad (1)$$

144
145 ($F_{1,218} = 95.07$, $\text{adj-}R^2 = 0.30$, $n = 220$, $P > 0.0001$). Departure fuel load was calculated for each
146 individual as:

147
148
$$\text{departure fuel load}_i = (\text{departure body mass}_i - \text{lean body mass}_i) / \text{lean body mass}_i \quad (2)$$

149
150 We obtained birds' departure body mass by either remote weighing or modelling. For remote
151 weighing bowls supplied with mealworms ad libitum were placed on electric balances so that body

mass development of individually ringed Northern Wheatears could be surveyed; for further information about this technique see Schmaljohann and Dierschke (2005). Birds' body mass from the evening of departure (later than 7 pm) was defined as departure body mass. This procedure was successful for four birds. Departure body masses of the others were modelled. Based on field data from our northern wheatear research group on Helgoland, we estimated the 24 h' (day + night) body mass increase to be 0.9 g (Delingat et al. 2006, 2009).

Flight range calculation

The potential flight range of a bird depends on its departure fuel load, which corresponds to the available energy reserves. According to Delingat et al. (2008), flight range Y [km] can be estimated as:

$$Y_i = 100 U \ln(1 + \text{departure fuel load}_i), \quad (3)$$

with U as the average airspeed of a northern wheatear, which is 46 km/h (13 m/s) after Bruderer & Boldt (2001).

Direct flights to the breeding grounds lead *leucorhoa* wheatears towards northwest for 1700 km to Iceland or 2400 km to Greenland. No resting and refuelling sites are available en route for at least 700 km (Scotland). We divided *leucorhoa* wheatears into two groups: 1) with an estimated flight range exceeding 800 km (corresponding to departure fuel loads ≥ 0.19) and 2) with shorter flight ranges. *Leucorhoa* wheatears of the latter group had insufficient fuel to cross the North Sea without any wind assistance. The breeding areas of *oenanthe* wheatears are to the north and east and hence, the next potential stopover sites are reachable with rather low fuel loads (Dierschke & Delingat 2003; Delingat et al. 2008).

Radio transmitters

Radio transmitters were constructed by the Swiss Ornithological Institute in cooperation with the University of Applied Sciences in Burgdorf, Switzerland (Naef-Daenzer 1993; Naef-Daenzer et al.

2005). They were attached to 26 Northern Wheatears using a Rappole-type harness made from 0.5 mm elastic cord (Rappole & Tipton 1990); length of leg-loops were adjusted individually to birds according to Naef-Daenzer (2007). The elastic cord degraded when exposed to air, and radio transmitters fell eventually off. Although radio-tagging birds is an interference, no adverse effects were found, when transmitters had been fitted properly (Naef-Daenzer et al. 2001), and increase in flight costs seemed to be low (Irvine et al. 2007). Radio transmitters, including battery and harness, weighed 0.8 g. Because lowest body mass of the Northern Wheatears was 21 g (mean \pm SD: 23.7 ± 3 g) in the present study, mass of radio transmitters represents at maximum 4% (mean: 3.4%) of birds body mass. Thus, the relative load was lower than 5%, which is suggested to be the upper permissible load limit (Cochran 1980; Caccamise & Hedin 1985).

Detection properties

Batteries' lifetime was about 30 days. Detection range was tested by placing a radio transmitter on a ferry leaving the island and locating its position every few seconds by means of a GPS device. We tracked the radio transmitter with Yagi 3EL2 antennas (Vårgårda, Sweden) in combination with hand-held receivers, YAESU FT-290RII, from Helgoland. The detection range of the radio transmitters depends on the orientation of transmitter's antenna, when pointing towards Helgoland detection range was 8 km, when turned by 45° 10 km and when being perpendicular towards Helgoland 15 km, respectively. We tracked departing birds for (mean \pm SD) 15.3 ± 8.5 min ($n = 26$). Because Northern Wheatear's airspeed is about 13 m/s (Bruderer & Boldt 2001), detection range was approximately 12 km, which coincided well with the predicted detection range from the ferry experiment.

Telemetry routine

The 26 radio-tagged Northern Wheatears were tracked during all nights until their departure. For convenient use each antenna was attached to a 2 m high wooden pole, where a compass was aligned with the antenna axis. Location of the bird was from where the strongest signal came. To test our accuracy of detection, we determined blindfolded the location of a fixed radio-transmitter in a

distance of about 750 m (mean \pm SD, deviation: $3 \pm 5^\circ$, $n = 49$). We estimated our recordings of departing Northern Wheatears to be correct to the nearest 3° ($n = 4$), 5° ($n = 19$), and 10° ($n = 3$) owing to our field experience. We searched the whole island shortly after each individual departure event and during the following day, but departed birds never recurred.

Nocturnal behaviour

We present here a first attempt to quantify bird's nocturnal behaviour on the ground. We assigned for each individual the different fluctuations in the received signal strength to different activity classes. This assignment was based on visual observations during daylight and the twilight period, when we could link fluctuations in the signal strength to defined activity classes.

Unknown: Bird was located, but small fluctuations in the signal strength could not be recorded due to general tracking problems, strong wind or more than one bird to be tracked.

Motionless: The signal strength was constant, hence, birds did not move.

Little activity: Fluctuations in signal strength were present but weak. We defined this category as small changes in bird's location, i.e. turning around or moving slightly for less than a metre.

High activity: Fluctuations in signal strength were strong, but birds did not fly. We defined such changes as high activity including movements for several meters. We observed that Northern Wheatears were searching for food during day time and the twilight periods producing as strong fluctuations in the signal strength as we recorded during night-times. This suggests that Northern Wheatears had fed during the night, which is supported by feeding until the onset of darkness (Palmgren 1949; Ramenofsky et al. 2003) or even later (Morton 1967).

Exploratory flights: Northern Wheatears performed nocturnal flights for several minutes and landed afterwards at the same or a different site.

To compare the nocturnal behaviour, we present here data of the first four activity classes as relative proportions of the whole observation period per bird and corresponding night. Thus, the different activity values sum up to 100% for the different groups (see Figs 1 and 2), but might be based on differently long observation periods per bird and night depending on departure time and end of observation. For some birds and nights no such data could be recorded.

Weather data

We had two sources of meteorological data. From the Helgoland station of the German Weather Service we obtained cloud cover [$\times/8$], cloud height [max 2500 m], wind speed [m/s] and direction [10°], amount [mm], and duration [min] of precipitation at 2 m above sea level on an hourly basis. From the National Oceanic and Atmospheric Administration (NOAA, Boulder, Colorado, USA) we downloaded NCEP Reanalysis wind speed and direction data (<http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.html>). We used data from four different pressure levels (1000, 925, 850, and 700 mbar) representing four altitude intervals (ground level – 445, 445 – 1145, 1145 – 2375, and 2375 – 4000 m, respectively). Because departure time was in all cases closest to the 0 a.m. data of NOAA, we considered only these data for our analyses. NOAA wind data correlated significantly with wind speed ($r = 0.41$, $n = 61$, $P = 0.0001$), and wind direction ($r_{C-C} = 0.523$, $n = 61$, $P = 0.0002$ (Jammalamadaka & SenGupta 2001)) data from German Weather Service, so that we had confidence in considering NOAA data from higher altitudes for our analyses.

We used NOAA data to estimate the possible available tailwind component at the four different pressure levels per day around midnight. We defined the overall migratory goal for *oenanthe* wheatears as 80° (mean departure direction in this study, see Fig. 1) and for *leucorhoa* wheatears as 315° (direction towards Iceland and Greenland, see Fig. 2). Individual tailwind component was calculated as:

$$\text{tailwind component}_i = \cos(\text{wind direction}_i - \text{migratory goal}_i) \times \text{wind speed}_i. \quad (4)$$

Predation danger

We defined predation danger here according to Lank & Ydenberg (2003), as the probability of becoming a prey if no antipredator behaviour was shown. Predation danger was assessed by daily counts as the abundance of raptors posing a potential threat to Northern Wheatears: Eurasian sparrowhawk, *Accipiter nisus*, common kestrel, *Falco tinnunculus*, merlin, *F. columbarius*, Eurasian hobby, *F. subbuteo*, and peregrine falcon *F. peregrinus*.

Northern wheatear abundance

Daily counts of Northern Wheatears on Helgoland provided information about species' abundance indicating intraspecific competition.

Position of Sun

We used a freely available internet calculator for astronomical data (http://www.sunearthtools.com/dp/tools/pos_sun.php) to determine sun's elevation at the time of the exploratory flights and departures. Sun's elevation defines the different twilight periods: The Civil Twilight starts at sunset, when sun's elevation is at 0° and ends when the top edge of the sun is 6° below the horizon. The Nautical and Astronomical Twilight periods end at sun's elevation of -12° and -18° , respectively (Fig. 3; Rozenberg 1966).

Statistics

Statistics were calculated using the statistical software package R (R Development Core Team 2009) including packages "circular", "boot", and "bootstrap". Uniformity of directions was tested with the Rayleigh's Test of Uniformity (Batschelet 1981; Jammalamadaka & SenGupta 2001). Circular-circular and circular-linear correlations were calculated following Jammalamadaka & SenGupta (2001). The p-value for a circular-linear correlation was approximated by bootstrapping. Out of each circular and linear variable a certain number of values (here 26 equalling sample size of the radio-tagged Northern Wheatears) were sampled randomly with replacement and their circular-linear correlation coefficient estimated. This was bootstrapped 2000 times in all cases. The number of such bootstraps with a correlation coefficient larger than the one of the original data set divided by the total number of bootstraps gives a robust estimate of the corresponding p-value (Crawley 2005).

We analysed different variables possibly influencing sun's elevation at departure by Spearman's rank correlations. Although sun's position below the horizon is more crucial for departure decisions having a more important effect on orientation cues than simply the time elapsed after sunset, we conducted the same analyses also with departure time after sunset as the response variable to

compare our results with other studies. Duration from sunset to certain twilight periods changes in course of the season, i.e., at a certain time after sunset sun's position varies with time of season (see Fig. 3).

Results

Here we present data from 26 radio-tagged Northern Wheatears, including 17 *oenanthe* (all 2nd year males) and 9 *leucorhoa* (five 2nd year, two adult males, and two 2nd year females) birds. Stopover duration after radio-tagging varied between 1 and 6 days (mean \pm SD: 1.9 ± 1.3 days, $n = 26$); 15 birds stayed on Helgoland only for one day. Stopover duration did not differ between subspecies (Wilcoxon signed-ranks test: $T = 76$, $n_{oenanthe} = 17$, $n_{leucorhoa} = 9$, $P = 1$).

Nocturnal behaviour

Of the 26 radio-tagged birds, we could identify the nocturnal behaviour of 23 birds during departure night, of ten during the night before, of five during two nights before departure and of four on earlier nights, respectively. Nocturnal activity did not differ between the two nights before departure and departure night (see Fig. 4) and was generally rather low. Some birds showed only sometimes high activity on the ground. Although *leucorhoa* wheatears had a higher temporal proportion of little activity than *oenanthe* wheatears during departure night (Fig. 5), this difference was not statistically significant (ANOVA: $F_{83,1} = 0.0122$, $P = 0.912$) and *oenanthe* wheatears' behaviour was often categorized as unknown, which might disguise little activity.

Exploratory flights

During departure night ten out of 23 Northern Wheatears performed single exploratory flights, of which two birds showed twice such flight behaviour. The exploratory flights lasted between 1 and 9 min (mean \pm SD: 2.5 ± 2.5 min, $n = 12$) and occurred from 48 to 314 min after sunset. Sun's elevation during the exploratory flights varied between 0.23° and -18.90° . In four cases birds landed in the same area, from where they had initiated their exploratory flights. They landed eight times at different sites

on the island. Although we could estimate neither flight altitude nor range during the exploratory flights, three birds covered at least 1 km during such flights, because they landed on the Düne before resuming migration. Actual departure after the first exploratory flight occurred when the sun was $8.7 \pm 4.6^\circ$ (mean \pm SD, range = $0.6 - 14.3^\circ$, $n = 10$) further below the horizon or after 67 ± 36 min (mean \pm SD, $n = 10$, range = $15 - 120$ min; compare Fig. 6). The three Northern Wheatears that had rested on the Düne before departure set off from there after 60, 79, and 110 min, respectively. The time of the first exploratory flight until departure did not correlate significantly with sun's elevation at departure (Spearman rank correlation: $r_s = 0.36$, $n = 10$, $P = 0.313$; Fig. 6).

Northern Wheatears performed exploratory flights also on nights before departure: Sun's elevation was $-14.3 \pm -6.1^\circ$ (mean \pm SD, range = $-0.88 - -22.4^\circ$, $n = 11$) and time after sunset was 173 ± 71 min (mean \pm SD, range = $55 - 168$ min, $n = 11$). During one night before departure four out of ten birds performed exploratory flights: One did three (-14.4° , -17.2° , -18.1° and 159, 213, 258 min after sunset), two birds two flights (-0.9° , -15.5° and 55, 187 min; -20.1° , -22.4° and 213, 268 min after sunset, respectively) and one bird only one flight (-10.7° and 122 min after sunset). Only one out of five (-17.3° and 225 min after sunset) and one out of three (-7.2° , -13.3° and 73, 133 min after sunset) birds showed exploratory flights during two and three nights before departure, respectively. The ratios of birds performing and not performing exploratory flights per night did not differ significantly between the nights before departure and departure night (all 2-sample tests for equality of proportions: $P > 0.05$). Although birds staying on the island could have performed their exploratory flights at lower sun's elevation than birds departing, sun's elevation of the first exploratory flights did not differ between these two (Wilcoxon signed-ranks test: $T = 42$, $n_{\text{departure night}} = 10$, $n_{\text{nights before departure}} = 6$, $P = 0.22$). Northern Wheatears performing exploratory flights on the night before departure did not seem to have been prevented from setting off by unfavourable meteorological conditions, because they did not differ between their departure and previous night (tested for cloud cover, wind speed, wind direction, and rain duration, all Wilcoxon signed-ranks tests: $P > 0.15$).

Sun's elevation at departure and departure time

i. departure in relation to sun's elevation and time after sunset

All Northern Wheatears departed well after the end of civil twilight, when the sun was at least 6° below the horizon; mean sun's elevation \pm SD at departure was $-14.8 \pm 3.4^\circ$ ($n = 26$; median = -14.1°). Significantly more Northern Wheatears departed after the Nautical Twilight Period (sun's elevation -12°) compared to the Nautical Twilight Period and before ($\chi^2 = 13$, $Df = 1$, $n_{after\ NTP} = 20$, $n_{NTP\ and\ before} = 6$, $P = 0.0003$; Fig. 3). There was no significant difference between the two subspecies in sun's elevation (mean \pm SD) at departure (*oenanthe* $-14 \pm 3.0^\circ$, median = -13° ; *leucorhoa* $-16 \pm 4.0^\circ$, median = -16° , Wilcoxon signed-ranks test: $T = 102$, $n_{oenanthe} = 17$, $n_{leucorhoa} = 9$, $P = 0.1815$) and departure time after sunset (mean \pm SD, *oenanthe* 172 ± 56 min, median = 163 min; *leucorhoa* 203 ± 81 min, median = 208 min, Wilcoxon signed-ranks test: $T = 57$, $n_{oenanthe} = 17$, $n_{leucorhoa} = 9$, $P = 0.3057$). Mean \pm SD departure time after sunset was 183 ± 66 min ($n = 26$, median = 176 min).

ii. influence of environmental factors on sun's elevation at departure

Sun's elevation at departure of Northern Wheatears did neither correlate with wind direction ($r_{C-L} = 0.15$, $n = 26$, $F_{2,23} \approx 0.57$, $P > 0.05$) nor wind speed at ground level ($r_S = 0.05$, $n = 26$, $P = 0.793$). There was also no significant correlation between sun's elevation and either tailwind component at the four pressure levels (all r_S : $P > 0.15$). Cloud cover varied in general very little, but was slightly less at departure (mean \pm SD, 0.7 ± 1.0) than around sunset (mean \pm SD, 2.1 ± 2.0 ; Wilcoxon signed-ranked test: $T = 177$, $n = 26$, $P = 0.002$). The statistical difference in cloud cover at departure and around sunset has only little biological significance, because cloud cover at sunset was in comparison to overcast situations very low. Cloud height did not have an influence on sun's elevation at departure ($r_S = 0.40$, $n = 26$, $P = 0.40$). Precipitation was very low; it rained on three days during the whole study period and only two birds departed during nights when light drizzle occurred. We, consequently, omitted precipitation from our analysis. Time of season did not influence departure time after sunset ($r_S = -0.1876$, $n = 26$, $P = 0.3587$); here we could not test sun's elevation at departure because of its apparent correlation with season. As in the abiotic factors, predation pressure ($r_S = -0.15$, $n = 26$, $P = 0.478$) and competition did not have an effect on the sun's elevation at departure (r_S

= -0.15, $n = 26$, $P = 0.472$)). Instead of sun's elevation at departure we calculated these correlations also with departure time after sunset, but none was significant.

iii. influence of endogenous factors on sun's elevation at departure

There was no correlation of sun's elevation at departure with stopover duration ($r_s = -0.037$, $n = 26$, $P = 0.856$), departure fuel load ($r_s = -0.093$, $n = 26$, $P = 0.652$), and deviation of the departure direction from the final migratory goal ($r_{C-L} = 0.033$, $n = 26$, $F_{2,23} \approx 0.79$, $P \approx 0.693$). We tested the effect of the flight vector on sun's elevation by combining departure fuel load, flight direction and their interactions in a linear model. To accommodate the departure direction in the linear model, we included the corresponding sine and cosine values instead of the angular values. This model did not explain a significant proportion of the variability in the departure time of Northern Wheatears ($F_{5,20} = 2.47$, $adj-R^2 = 0.227$, $n = 26$, $P = 0.068$). We calculated these correlations and model also with departure time after sunset, but none proved to be significant either.

Departure direction

Oenanthe wheatears departed in directions between northwest and southeast (Fig. 1). Distribution of departure direction was unimodal (Rayleigh's test: $z = 0.69$, $n = 17$, $P < 0.001$) with a mean direction of 80° ($r = 0.69$, $n = 17$). In contrast, *leucorhoa* wheatears did not show a preferred departure direction (Rayleigh's test: $z = 0.08$, $n = 9$, $P = 0.94$; Fig. 2). There was no effect of season on the departure direction for both subspecies separately and combined (for all three correlations $r_{C-L} < 0.10$, $F < 1.5$, $P > 0.50$).

i. influence of weather on departure direction

Wind direction did not correlate with departure direction of Northern Wheatears; this was neither the case for German Weather Service, NOAA data, nor in respect of the subspecies (r_{C-C} : all $P > 0.05$). Departure direction did not correlate with available tailwind component at the four different pressure levels (for all four correlations $r_{C-L} < 0.25$, $n = 26$, $F_{2,23} < 1.4$, $P > 0.05$), though all correlation

coefficients were positive. The lacking effect of tailwind component on departure direction might be explained by low values of tailwind: at 1000 mb pressure level tailwind component was (mean \pm SD) 1.23 ± 4.48 m/s [1st quantile: -2.8 m/s, 3rd quantile: 4.7 m/s], at 925 mb 0.45 ± 4.35 m/s [-2.1 m/s, 2.9 m/s], at 850 mb 0.11 ± 3.64 m/s [-2.0 m/s, 2.3 m/s], and at 700 mb 0.05 ± 4.31 m/s [-3.0 m/s, 3.5 m/s] ($n = 26$), respectively.

ii. effect of departure fuel load on departure direction

Departure fuel load did not differ significantly between *oenanthe* (mean \pm SD: 0.14 ± 0.08 , $n = 17$) and *leucorhoa* wheatears (mean \pm SD: 0.22 ± 0.23 , $n = 9$; Wilcoxon signed-ranks test: $T = 71$, $P = 0.787$). Departure direction of all Northern Wheatears correlated significantly with departure fuel load ($r_{C-L} = 0.59$, $n = 26$, $F_{2,23} \approx 8.4$, bootstrap: $n = 2000$, $P \approx 0.021$; Fig. 7). This means the higher the departure fuel load, the stronger was the northwards component in the departure direction. Such circular-linear correlations were not significant on the subspecies-level (for both correlations: $r_{C-L} < 0.37$, $F < 3.48$, $P > 0.23$). *Leucorhoa* wheatears having departed towards northwest carried high fat loads enabling flight bouts of more than 700 km (800, 1312, and 2521 km). Birds departing in any other direction had in general lower fuel loads and hence, lower flight ranges. Only one of those had a potential flight range of about 1380 km but flew southwards (162°); mean flight range \pm SD of the remaining five birds was 331 ± 251 km ($n = 5$; Fig. 2).

Discussion

Departure behaviour

Migrants did not show a higher activity on the ground during departure night than on previous nights (Fig. 4). Birds are either generally resistant to sleep deprivation during migration (Rattenborg et al. 2004), or might recover from the overall lack of sleep by some diurnal naps (Fuchs et al. 2006). Some Northern Wheatears showed a high activity on the ground even after sunset suggesting feeding

behaviour, as shown and implied by other studies (Palmgren 1949; Morton 1967; Ramenofsky et al. 2003).

About one half of the birds performed exploratory flights on departure nights and before. It seems unlikely that these flights could have been initiated by disturbance, because flights lasted up to several minutes and some birds returned to the initial site, which seems unlikely in case of disturbance. One might assume that early exploratory flights should indicate early departures from the stopover site and hence indicate a temporal relation between both of them. However, the time of the first exploratory flight until departure did not correlate with sun's elevation at departure (Fig. 6). The reason for this remains unclear. Although some of the exploratory flights shown on Helgoland might be aborted migratory flights of birds being reluctant to continue flying when facing the large sea crossing, we suppose that the exploratory flights are a general behaviour of nocturnal migrants. They might serve (1) to test orientation abilities (Mukhin et al. 2005), (2) to familiarize themselves with the environment for upcoming departure, here e.g. detecting the distance to the nearest coast, (3) to examine the meteorological conditions aloft for potential departure, or (4) might be caused by strong migratory restlessness ("Zugunruhe"; Gwinner 1990). Similar but longer lasting exploratory flights were detected in young Reed Warblers, *Acrocephalus scirpaceus*. These were interpreted as pre-migratory flights to develop stellar compass and for gathering information of geographical cues (Mukhin et al. 2005). We suggest that exploratory flights are a common behaviour of nocturnally migrating songbirds to evaluate meteorological conditions aloft, as suggested by Liechti (2006). Schaub et al. (2004) even pointed out that a crucial point for understanding departure decisions of migrants is to discover, how migrants predict wind conditions aloft.

Departure time

Northern Wheatears did not depart within a fixed time window after sunset but significantly more departed after the Nautical Twilight Period than before (Fig. 3), which are both in line with other radio telemetry studies (Cochran et al. 1967; Åkesson et al. 1996a; Moore & Aborn 1996; Åkesson et al. 2001; Bolshakov & Chernetsov 2004; Cochran et al. 2004; Bolshakov et al. 2007) or mist-netting studies (Bolshakov et al. 2003; Bulyuk & Tsvey 2006). The skylight polarization pattern, used to

calibrate the compass systems (Cochran et al. 2004; Muheim et al. 2006b, 2007), is available before and during but not after the Nautical Twilight Period. Birds departing after this period might have explored the polarization pattern until its disappearance. Even under overcast situations the skylight polarization pattern is available (Hegedüs et al. 2007), so that the availability of stars or in turn the cloud cover is not likely to influence the schedule of nocturnal departure, as in our and other study species: Summer Tanagers, *Piranga rubra*, Reed Warblers, and European Robins, *Erithacus rubecula* (Moore & Aborn 1996; Åkesson et al. 2001; Bulyuk & Tsvey 2006; Bolshakov et al. 2007). However, *Hylochicla* thrushes from North America departed later at night with an increasing cloud cover (Cochran et al. 1967).

In contrast to the high variation in departure times after sunset found in individually radio-tagged songbirds (Moore & Aborn 1996; Åkesson et al. 2001; Bolshakov et al. 2007; this study) and the two **hours** lasting exodus of nocturnal migrants detected by radar (Liechti et al. 1997, Bruderer & Liechti 1999), Cochran (1987) found a very restricted time period (range 9-13 min after evening civil twilight) for one migratory Swainson's Thrush, *Catharus ustulata*, being radio tracked for seven successive nights. In accordance with this result is a consistency in the initiation of flight activity of captive Redstarts, *Phoenicurus phoenicurus*, in consecutive nights demonstrating that the internal clock might govern the timing of migratory behaviour (Coppack et al. 2008), though contrary results were shown by Palmgren (1949). These studies indicate that individual migrants might have a preferred departure time within the night. Because we could track our study birds only once, we could not assess whether individuals departed at the same time in consecutive nights. An autonomous circadian clock might purport the preferred time window for departure, environmental and migrant's body condition will, however, most likely modulate the exact time of the departure within the genetically predetermined time window (Åkesson et al. 2001; Bulyuk & Tsvey 2006). The relation between the environment and the endogenous rhythms might be highly complex, which might disguise clear effects of single meteorological conditions on departure time within the night (Bulyuk & Tseyv 2006).

Departure direction

In contrast to other studies (Åkesson & Hedenström 2000, Åkesson et al. 2002, Schaub et al. 2004, Liechti 2006), wind direction did not have an influence on the departure direction of Northern Wheatears. Because experienced tailwind (mean: 1 m/s; 1st quantile: -3.0 m/s, 3rd quantile: 4.7 m/s) and general wind speed (seasonal mean \pm SD: 6.6 ± 2.6 m/s, $n = 34$) were much lower than bird's potential airspeed of 13 m/s (Bruderer and Boldt 2001), and because only strong winds (headwinds > 5 m/s) were assumed to influence departure direction (Åkesson et al. 2002) and departure decision (Erni et al. 2002; Schaub et al. 2004), both were not influenced as strongly by wind in this study than as in others.

The mean departure direction of *oenanthe* wheatears (80° , $r = 0.69$, $n = 17$; Fig. 1) in this study differed significantly from the more northwards orientated direction determined by Dierschke & Delingat (2003) during a release experiment on Helgoland (10° , $r = 0.63$, $n = 17$; Watson's Two-Sample Test of Homogeneity: *test statistic* = 0.256, $P < 0.05$). Birds from Dierschke & Delingat (2003) were kept in captivity with food ad libitum for several days and were released after sunset with a light stick attached to their tail feathers allowing tracking them for about 1 km by means of binoculars. Owing to the more northbound departure direction, we would expect higher departure fuel loads and with that longer flight ranges in their *oenanthe* wheatears than in our birds. However, the contrary was the case (mean departure fuel load \pm SD: Dierschke & Delingat (2003), 0.07 ± 0.09 , $n = 17$; this study, 0.14 ± 0.08 ; Wilcoxon signed-ranks test: $W = 81$, $n_{oenanthe} = 17$, $P = 0.0287$). Besides body condition, birds' origin might explain deviant departure directions in the two studies. Only few wheatears of British origin were probably in our study, because mean wind direction was 67° (Rayleigh's test: $z = 0.42$, $n = 863$, $P < 0.0001$, 24 measurements per day on ground) and westerly wind prevailed only on two days. In Dierschke & Delingat's (2003) study, wind came from westerly directions during one third of the study period, so that a higher proportion of British wheatears might have been drifted towards Helgoland than in our study. Thus, more birds could have departed towards northwest in their than in our study to compensate for the drift.

Departure direction of *oenanthe* and *leucorhoa* wheatears correlated significantly with their departure fuel load. Migrants with a high departure fuel load headed further northwards than lean

birds, which generally headed towards the nearest coastline. Similar results were found in orientation experiments of thrushes and larks also during spring migration (Sandberg & Moore 1996; Sandberg 2003; Deutschlander & Muheim 2009). There, only birds with high fuel loads showed their seasonally appropriate migratory direction in orientation cages in front of an ecological barrier, whereas lean birds avoided this direction. A similar, though owing to the small sample size not statistically verifiable phenomenon was shown by our *leucorhoa* wheatears. The three *leucorhoa* wheatears that departed towards northwest carried sufficient fuel loads for a successful flight of at least 700 km to cross the North Sea without any wind assistance (mean \pm SD: 1544 \pm 883 km, $n = 3$). Also the two *oenanthe* wheatears departing towards northwest or north had such high fuel loads (Fig. 7). Other *leucorhoa* wheatears had generally lower fuel loads and departed in any other direction. This tendency is supported by the release experiment from Dierschke & Delingat (2003). Their *leucorhoa* wheatears had relatively high mean departure fuel loads corresponding to mean \pm SD potential flight ranges of 967 \pm 641 km ($n = 8$). If considering only those birds with a flight range exceeding 700 km, distribution of departure direction was unimodal towards northwest (298°; Rayleigh test: $z = 0.70$, $n = 6$, $P = 0.0474$). Thus, there are hints that *leucorhoa* wheatears only cross the North Sea towards northwest, if they possess high departure fuel loads, whereas lean migrants are more reluctant to proceed their migration across ecological barriers (Alerstam 1978, 2001; Sandberg & Moore 1996; Sandberg 2003; Deutschlander & Muheim 2009). Deviations from the seasonal appropriated migratory direction were known from field observations (Koch 1934; von Haartman 1945; von Haartman et al. 1946; Rabøl 1969; Alerstam 1978; Richardson 1982), ring recovery analyses (Åkesson et al. 1996b), orientation cage experiments (Sandberg & Moore 1996; Sandberg et al. 2002; Sandberg 2003; Deutschlander & Muheim 2009), radar (Richardson 1982; Liechti & Bruderer 1995; Komenda-Zehnder et al. 2002), and infra-red studies (Zehnder et al. 2002). Migrants might have left the stopover sites because of strong competition (Rappole & Warner 1976; Moore & Yong 1991), high predation danger (Lindström 1990; Moore 1994; Fransson & Weber 1997), and/or low quality stopover sites (Ktitorov et al. 2008). Orientation away from any inhospitable habitat seems to be an adaptive behaviour for lean birds (Alerstam 1978; Lindström & Alerstam 1986; Sandberg & Moore 1996; Sandberg et al. 2002; Sandberg 2003; Deutschlander & Muheim 2009) and might reduce the apparent

high mortality rate on migration (Sillett & Holmes 2002). Although unfavourable weather (Richardson 1990) and errors in orientation (Komenda-Zehnder et al. 2002; Zehnder et al. 2002) will lead to reverse migration as well, most reverse migration is an individual-based and intended reaction up on the actual stopover situation.

Coming from their Sahelian wintering areas *leucorhoa* wheatears have to eventually switch their migratory direction from north to northwest or even west to reach their breeding areas on Iceland, Greenland or Eastern Canada during spring migration. Such a switch in the migratory direction is likely to be genetically determined (Gwinner & Wiltschko, 1978; Helbig et al. 1989), but in *leucorhoa* wheatears such a change in the migratory direction is only of use, if birds have stored sufficient fuel load and selected favourable meteorological conditions to successfully cross the Atlantic. Migrants are, therefore, supposed to refuel intensively before crossing this marine obstacle as many songbird migrants do before crossing the Sahara (Odum 1963). We hypothesize that the trigger to actually perform the genetically determined migratory shift towards northwest might be the interplay of migrant's high fuel load and favourable meteorological conditions for the Atlantic crossing.

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Figure 1. Nocturnal activity on the ground two and one days before departure and departure night. Given are means and standard error of percentage, for further information see Methods. “dep day” stands for “departure day” (solid triangle), “dep day – 1” for “one day before departure day” (solid circle) and “dep day – 2” for “two days before departure day” (solid square), respectively. Values per specific day sum up to 1.

Figure 2. Nocturnal activity on the ground on the day of departure of *oenanthe* (solid circles) and *leucorhoa* (open triangles) wheatears. Given are means and standard error of percentage, for further information see Methods. Values per subspecies sum up to 1.

Figure 3. Departure directions of 17 Northern Wheatears of the *oenanthe* subspecies. Their mean departure direction was 80° ($r = 0.69$, $n = 17$; Rayleigh’s test: $z = 0.69$, $n = 17$, $P < 0.001$) and is indicated by the arrow.

Figure 4. Departure directions of nine Northern Wheatears of the *leucorhoa* subspecies, which did not show a preferred departure direction (Rayleigh’s test: $z = 0.08$, $n = 9$, $P = 0.94$). Birds with a departure fuel load of > 0.19 (solid circles) had sufficient fuel load to perform a 800 km long non-stop flight and could reach Scotland without any additional refuelling.

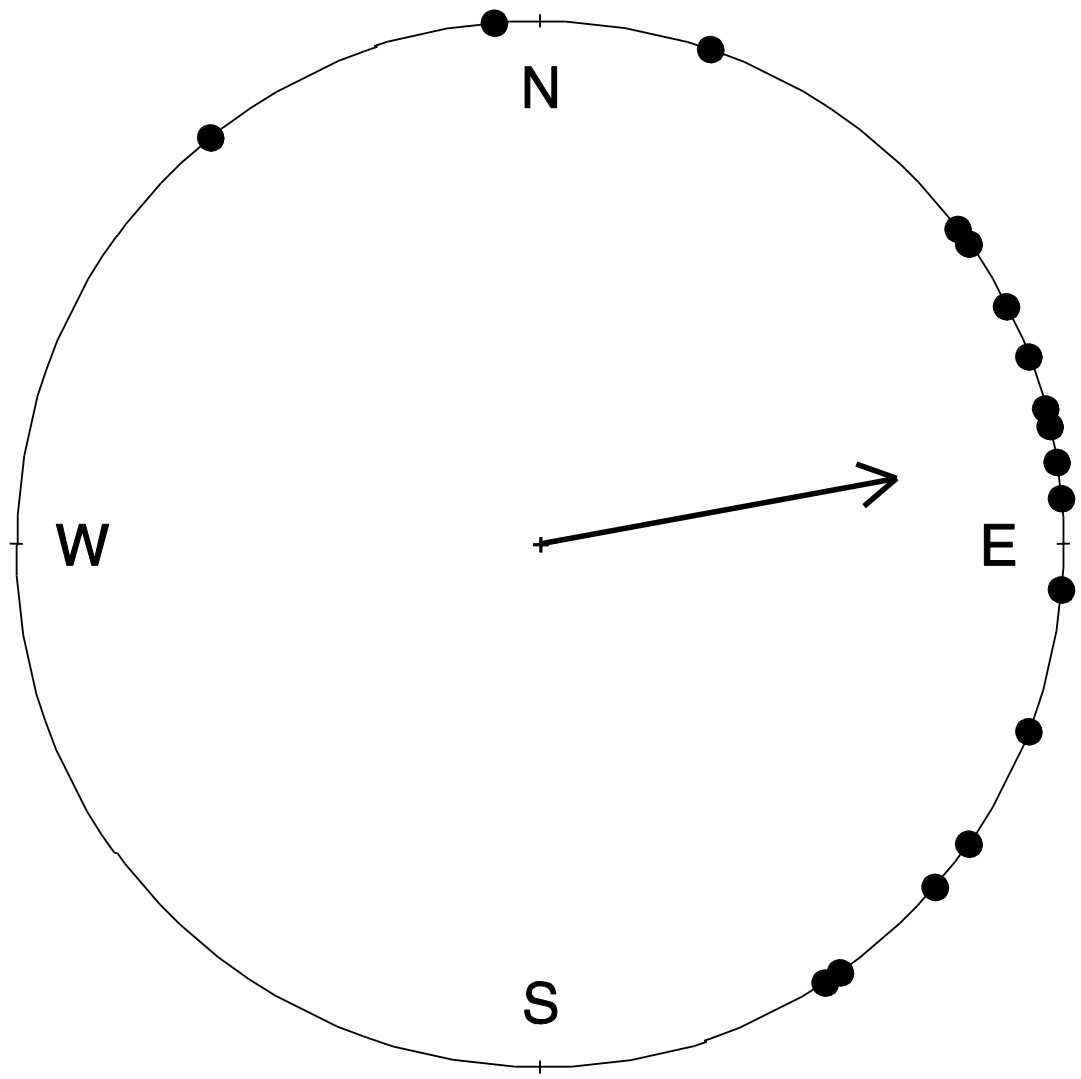
Figure 5. Time of departure of radio-tagged Northern Wheatears in relation to elevation of the sun on Helgoland in spring. Solid circles refer to *oenanthe* and open triangles to *leucorhoa* wheatears, respectively. At Civil Twilight (CT) sun is defined to be 6° , at Nautical Twilight Period (NT) 12° , and at Astronomical Twilight (AT) 18° below the horizon, respectively. Duration from sunset to certain twilight periods changes in course of the season, i.e., at a certain time after sunset sun’s position varies with time of season.

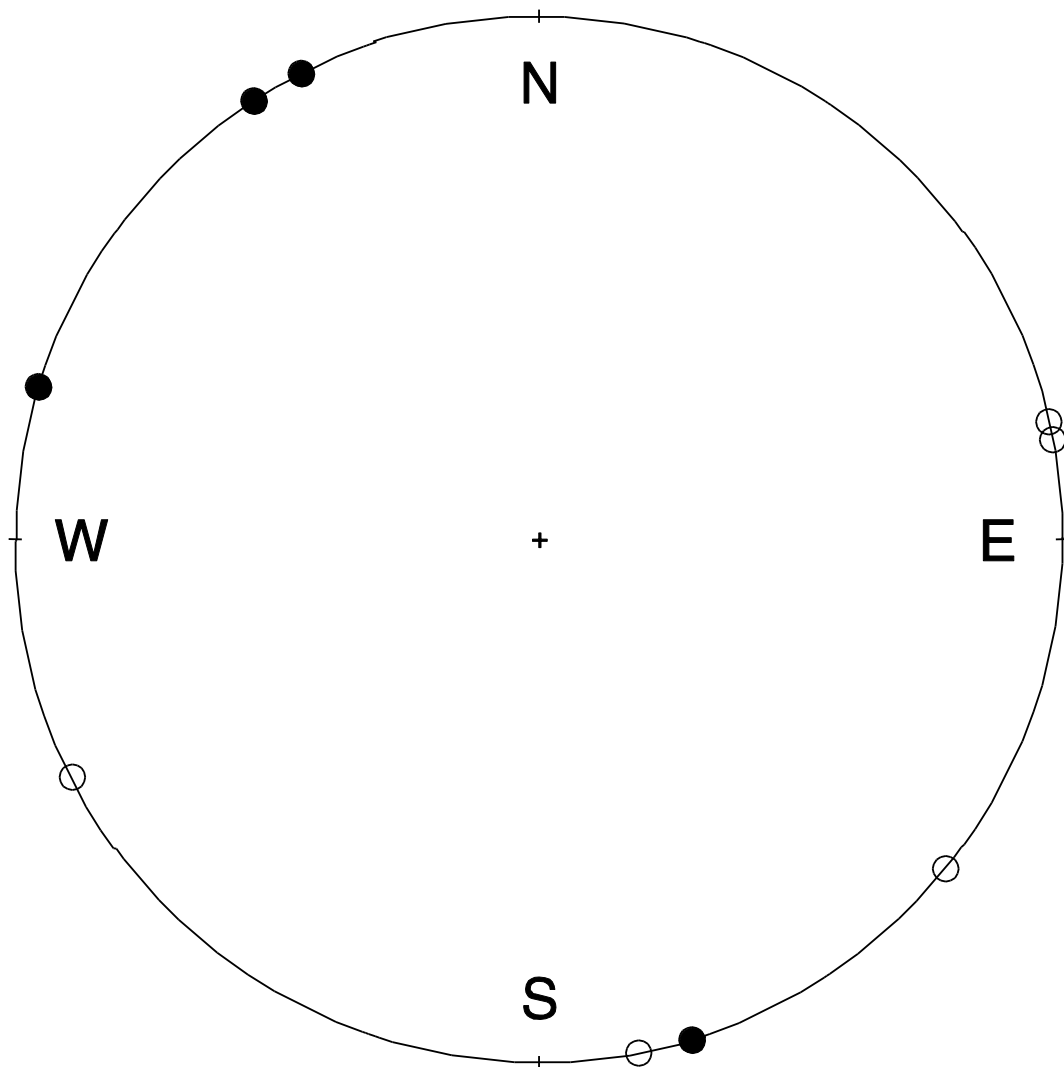
Figure 6. Sun’s elevation against time of first exploratory flight until departure. There is no apparent relationship between both variables (Spearman rank correlation: $r_s = 0.36$, $n = 10$, $P = 0.313$).

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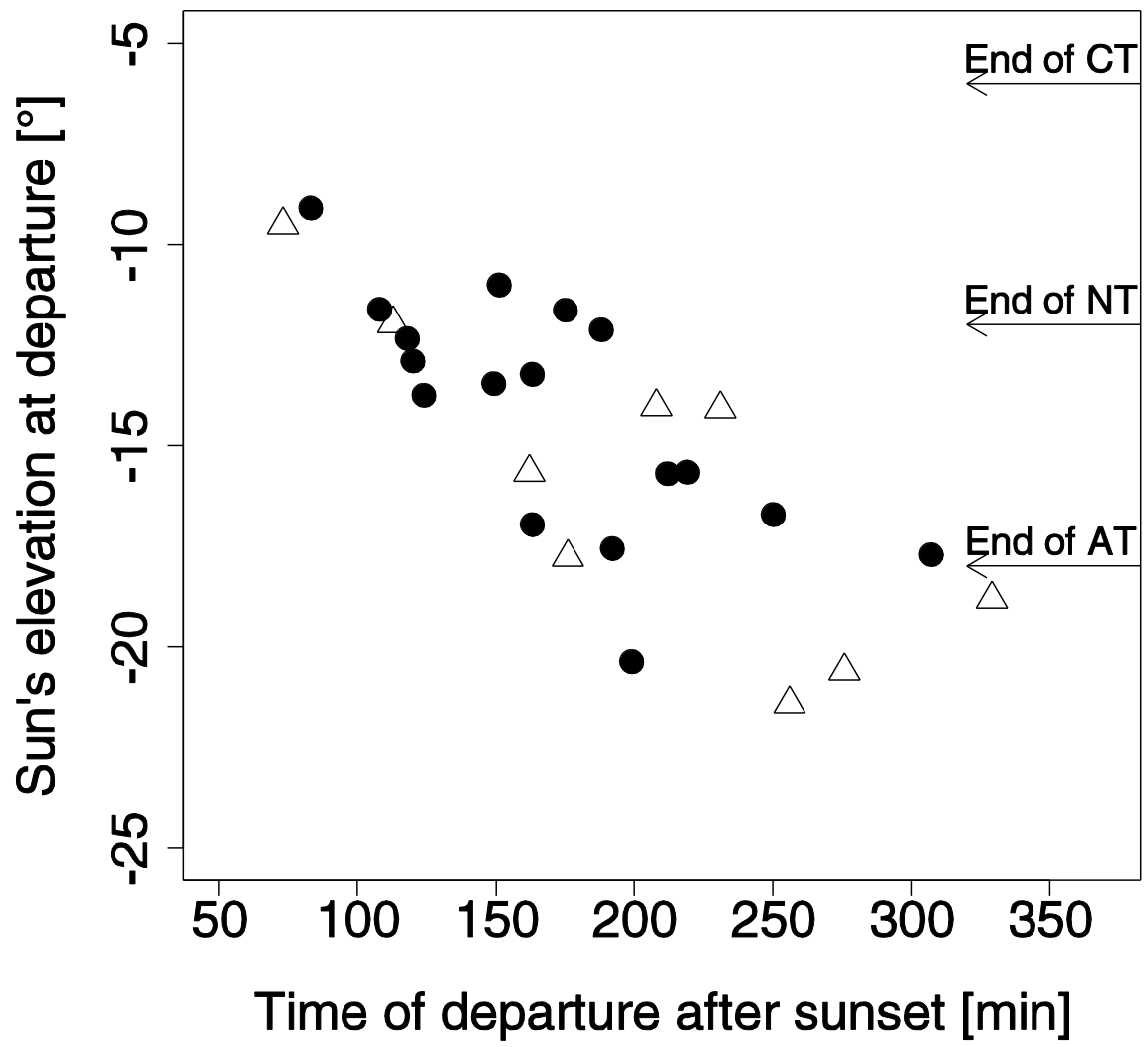
807 Figure 7. Departure direction against departure fuel load. For clarity reasons y-axis does not start with
808 0° but 180°, otherwise trend line would be truncated and its meaning not straightforward. Solid circles
809 refer to *oenanthe* and open triangles to *leucorhoa* wheatears, respectively. The trend line indicates the
810 direction of the circular-linear correlation (circular-linear correlation: $r = 0.59$, $n = 26$, $F_{2,23} \approx 8.4$,
811 bootstrap: $n = 2000$, $P \approx 0.021$; for statistical details see method section). The directions between north
812 and northwest are highlighted in light grey. All birds departing in any of these directions had a
813 departure fuel load of ≥ 0.19 enabling flights of 800 km without any wind assistance.

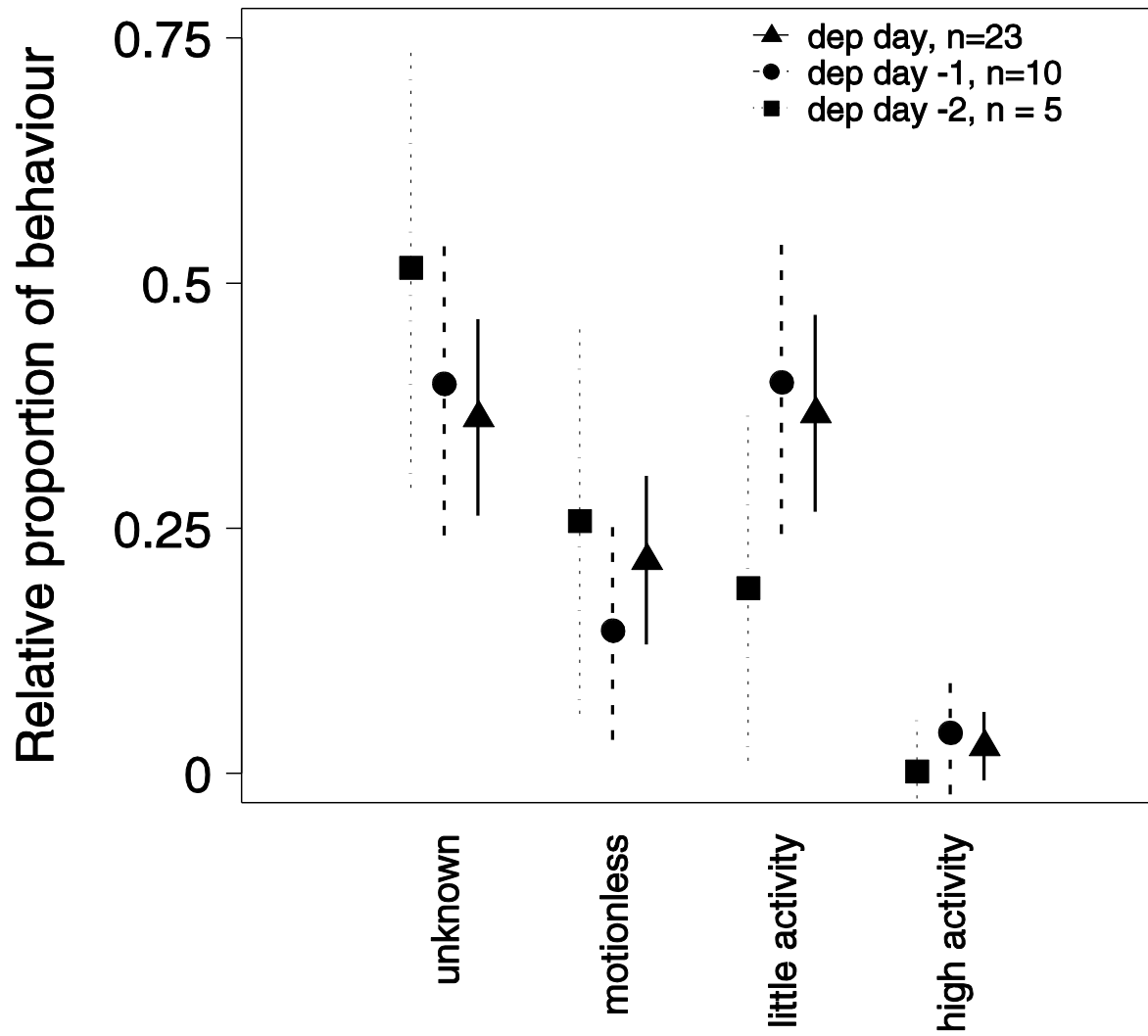
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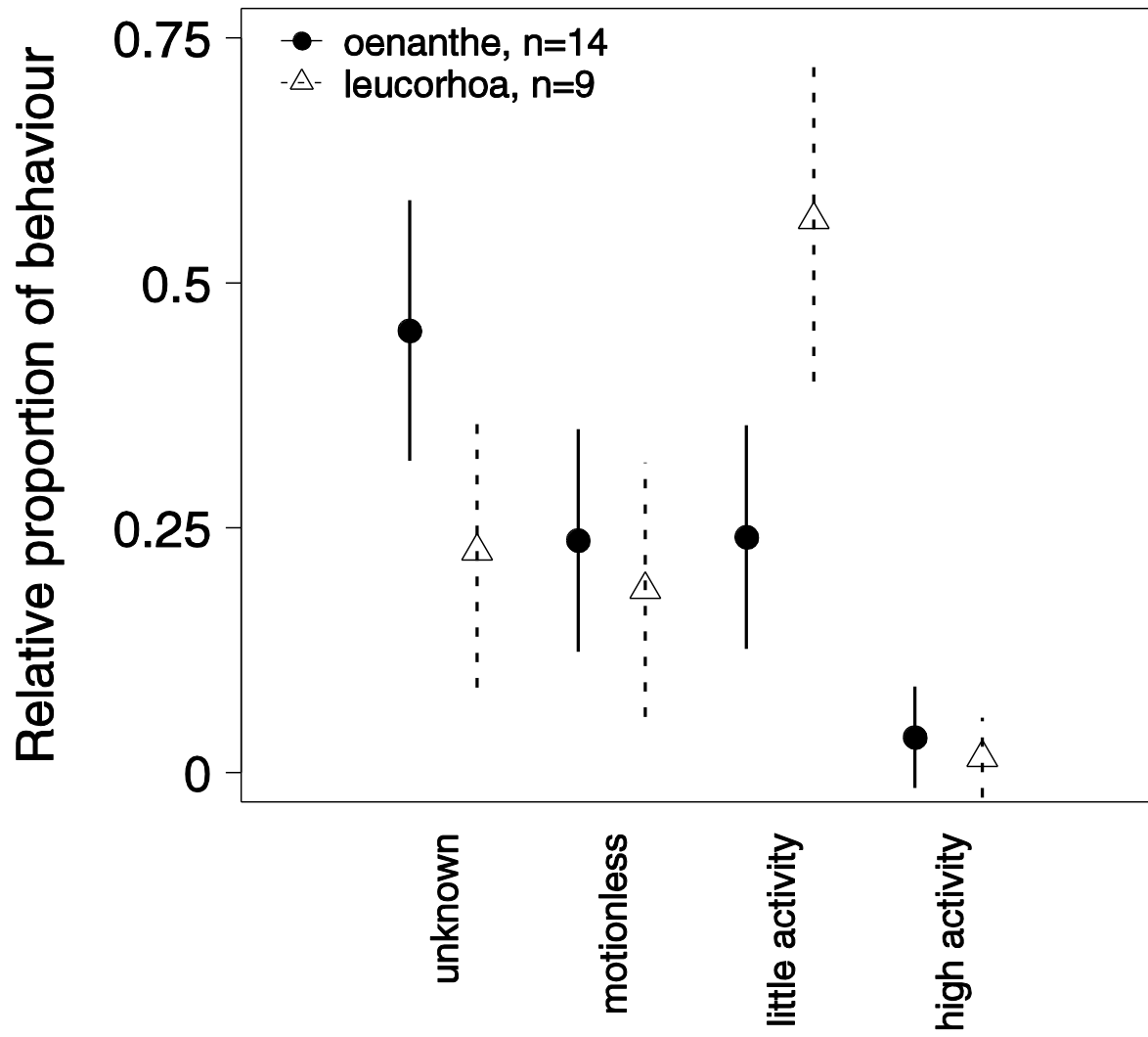


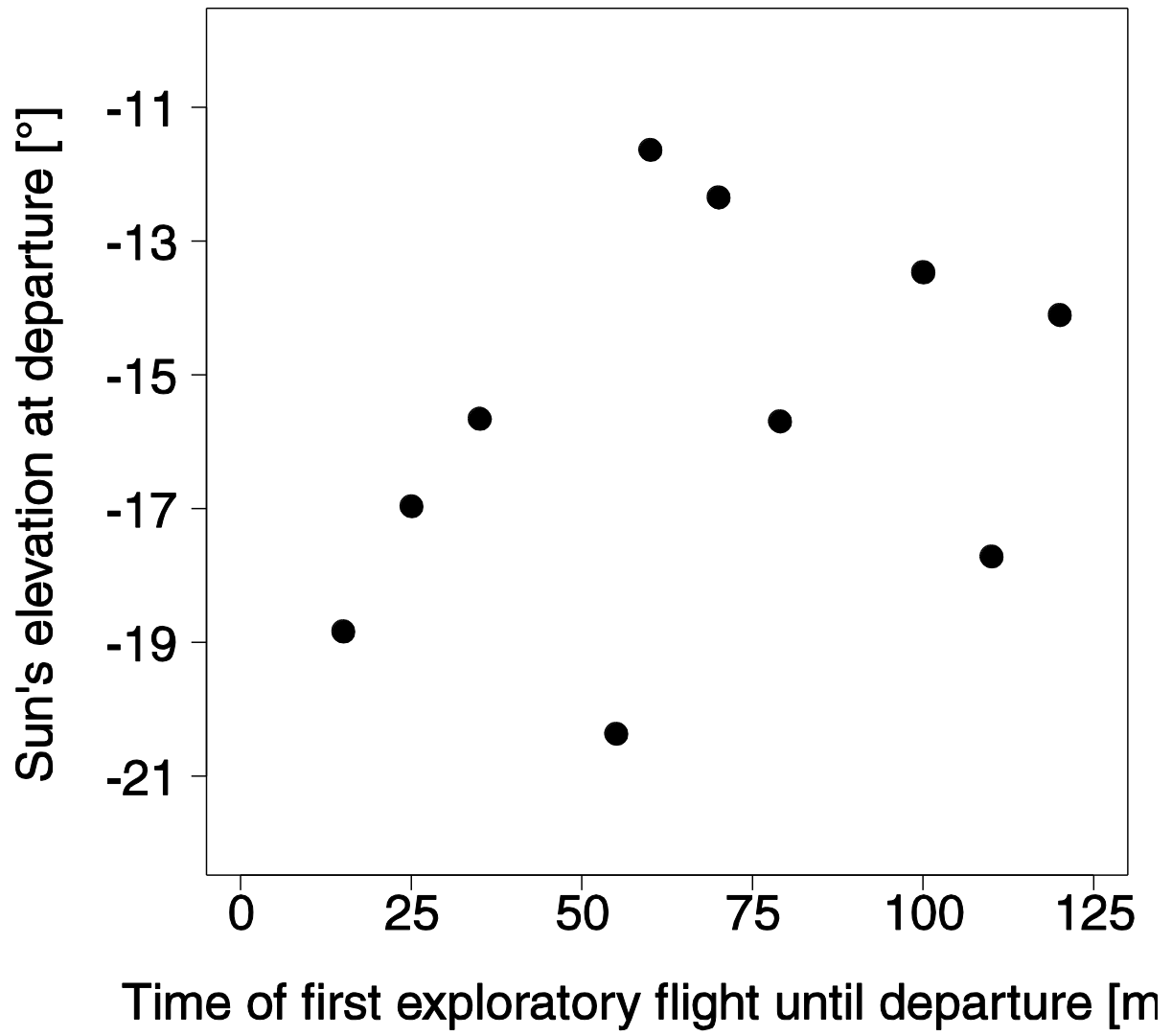


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