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Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea

Sissel Sjöberg [a,*], Thomas Alerstam [a], Susanne Åkesson [a], Axel Schulz [b], Alexander Weidauer [b], Timothy Coppack [b], Rachel Muheim [a]

[a] Department of Biology, Lund University, Lund, Sweden
[b] Institute of Applied Ecology (IfAÖ), Rostock, Germany

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Departure decisions of how and when to leave a stopover site may be of critical importance for the migration performance of birds. We used an automated radiotelemetry system at Falsterbo peninsula, Sweden, to study stopover behaviour and route choice in free-flying passerines departing on flights across the Baltic Sea during autumn migration. In addition, we had an offshore receiver station (FINO 2) located about 50 km southeast from Falsterbo. Of 91 birds equipped with radiotransmitters, 19 passed FINO 2. The probability that a departing migrant passed near FINO 2 was primarily affected by winds and timing of departure. Probably, the migrants were subjected to drift by westerly winds, leading to southeasterly flight paths and an enhanced probability of passing FINO 2. Most birds passing the offshore station departed early in the night, which indicates that southward departures across the Baltic Sea usually take place during this time window. Wind condition was the dominant factor explaining the variation in flight duration between Falsterbo and FINO 2. After considering wind influence, we found additional effects of fat score and cloud cover. Birds with a higher fat score performed the flight faster than leaner individuals, as did birds that departed under clear skies compared to birds departing during overcast skies. These effects may reflect a difference in migratory motivation and airspeed between lean and fat birds together with difficulties in controlling orientation in overcast situations on oversea flights when celestial cues are unavailable. Thus, winds, clouds and fuel reserves were the primary factors determining departure and flight decisions in passerine migrants at Falsterbo in autumn.

Migrating songbirds accomplish their journeys by intermittent flights with stopovers for resting and refuelling (e.g. Schaub & Jenni, 2001). Most time and energy are spent at stopover sites (Hedenström & Alerstam, 1997; Wikelski et al., 2003). Decisions about when and how to leave a stopover site may affect the overall success of migration (Alerstam & Hedenström, 1998; Alerstam & Lindström, 1990; Newton, 2006), especially at coastal stopover sites where competition and risk of predation are expected to be high (Newton, 2008; Woodworth, Francis, & Taylor, 2014). It is highly relevant to analyse departure decisions of individual songbird migrants facing ecological barriers, such as deserts, large ice caps or extended bodies of water. In particular, it is important to understand how migrants establish their orientation and flight schedule under variable wind and weather conditions in environments that lack perceivable landmarks and predictable stopover possibilities. During stopover ahead of a barrier the risk associated with a direct flight needs to be balanced against the cost in terms of the time and energy that a detour around the barrier would incur. Passerine migrants have been shown to be highly variable in their strategies when facing a barrier. Straight barrier crossings and longer detours are regularly observed in migratory birds (e.g. Åkesson, Klaassen, Holmgren, Fox, & Hedenström, 2012; Alerstam, 2001; Stutchbury et al., 2009). Furthermore, reverse migratory directions away from the barrier (Åkesson, Karlsson, Walinder, & Alerstam, 1996; Alerstam, 1978; Woodworth et al., 2014) and postponement of the departure for more favourable weather conditions (Åkesson & Hedenström, 2000) have been observed, indicating that the decisions made at stopovers before flights over unfavourable habitats play an essential part in their migratory schedules.

Here, we investigated departure decisions and flight behaviours in free-flying migratory passerines crossing the Baltic Sea during autumn migration. We used an automatic radiotelemetry system

* Correspondence: S. Sjöberg, Department of Biology, Lund University, Biology Building, Sölvegatan 35, 223 62 Lund, Sweden.
E-mail address: Sissel.Sjoberg@biol.lu.se (S. Sjöberg).

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covering the coastal region at Falsterbo, Sweden, and an additional receiver station on the remote offshore platform FINO 2 about 50 km off the Swedish coast towards the southeast (Fig. 1). The crossing of the Baltic Sea from Falsterbo is associated with a flight of 23–100 km over open sea. This may not be comparable with a crossing of a larger ecological barrier, such as the Saharan desert, but may nevertheless be sufficiently large to make birds hesitate before the sea crossing. Furthermore, it has been described earlier that birds more often perform reverse migration in this area than at an inland site (Åkesson, 1999). A route southwest from Falsterbo is associated with a sea crossing of 23–50 km. On the other hand, one towards the southeast from Falsterbo, involving a passage of the offshore receiver station at FINO 2, requires a sea crossing of at least 80 km (Fig. 1c).

The Falsterbo peninsula, located at the southwestern tip of Scandinavia, is one of the focal sites for migratory birds during autumn migration, and large numbers of migrants concentrate in this area. We know much about the pattern of migration, species composition, phenology and the condition of birds migrating through Falsterbo from ringing and bird migration counts at Falsterbo Bird Observatory (Karlsson, 2009; Zehnder, Akesson, Liechti, & Bruderer, 2001). However, far less is known about the birds' flight and stopover decisions at the individual level when they are confronted with the sea after long migratory flights over land (cf. Åkesson, Alerstam, et al., 1996; Åkesson, Karlsson, et al., 1996). Radiotelemetry is ideally suited for following avian migrants during stopover in this area, since the peninsula has a flat topography, is fairly small and is to a large extent surrounded by water.

We focused our study on two main questions: which factors (1) lead to longer than necessary sea crossings across the Baltic Sea and (2) affect the flight duration for a specific flight distance?

(1) Environmental conditions, e.g. winds and weather, are hypothesized to affect the flight route of migrating birds. The prevailing wind situation has been shown to play a prominent role in determining the patterns and speed of bird migration (Alerstam, 1979; Liechti & Bruderer, 1998; Richardson, 1990). Reed warblers, *Acrocephalus scirpaceus*, have been observed to be more scattered in their departure directions in overcast weather (Åkesson, Walinder, Karlsson, & Ehnbom, 2001). Individual characteristics and differences in behaviour (departure timing and directions) are also hypothesized to be important for route choice. Adult individuals and individuals with larger fuel reserves have been shown to be less likely to perform a detour around an area of unfavourable habitat (e.g. Sandberg, Pettersson, & Persson, 1991; Schmaljohann & Naef-Daenzer, 2011; Smolinsky et al., 2013). There are also indications that true migratory departures in the preferred migratory directions mainly occur shortly after evening civil twilight (Åkesson, Alerstam, et al., 1996; Åkesson, Karlsson, et al., 1996; Åkesson, Walinder, Karlsson, & Ehnbom, 2002; Mills, Thurber, & Mackenzie, 2011), which made us hypothesize that departure time could also be related to route choice.

From these hypotheses and earlier tests and studies related to them we predicted that: (1) southeasterly departures leading the birds on the longer flight across the Baltic would primarily occur in crosswinds from the west, promoting a certain degree of wind drift from the main migratory course to the southeast; (2) overcast skies and low visibility would increase the likelihood of a longer sea crossing; (3) adult individuals and individuals with larger fuel stores would be more likely to perform this longer sea crossing; (4) early night-time departures would have a higher probability of being true migratory departures and have a longer sea crossing; (5) birds orienting and departing from Falsterbo in southeasterly directions would more often take the longer sea crossing and fly via FINO 2, assuming that they keep a straight flight path after take-off.

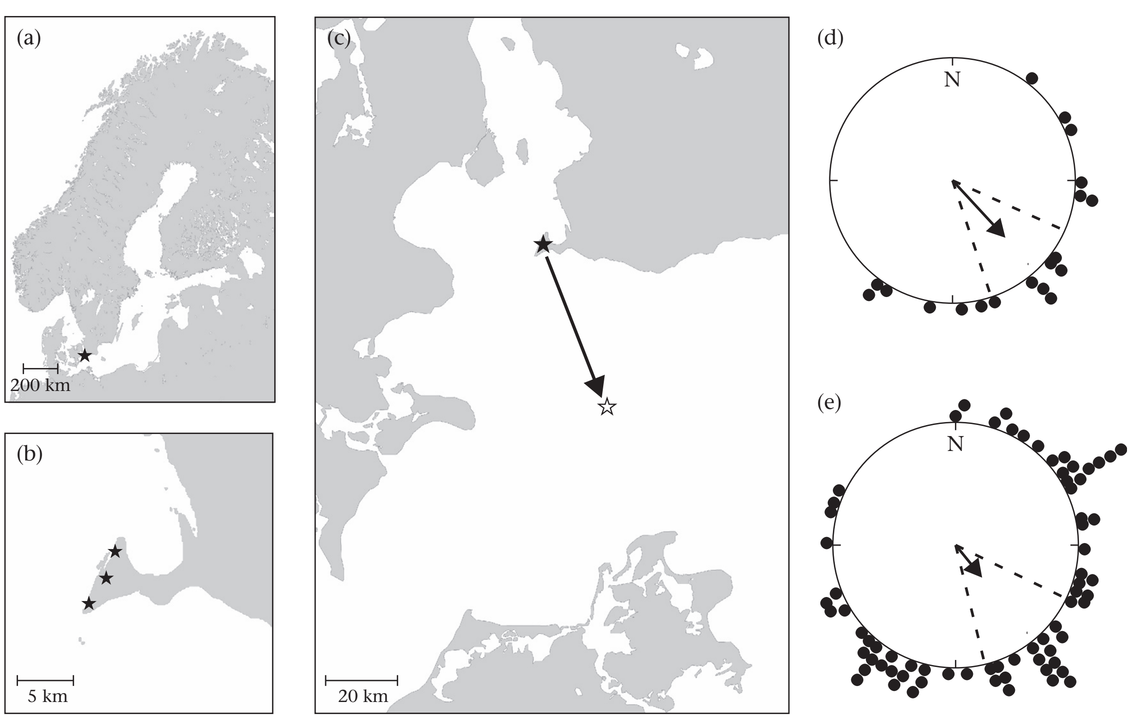

Figure 1. Maps showing the location of (a) Falsterbo in Scandinavia (black star), (b) telemetry stations at Falsterbo peninsula and (c) FINO 2 (white star). The arrow in (c) shows the direct flight route from Falsterbo to FINO 2. (d) Mean departure directions of birds that passed and (e) did not pass FINO 2. In circular plots the arrow indicates the mean direction and the length of each arrow is a measure of concentration (*r*) of the departures drawn relative to the radius of the circle. Broken lines give ±95% confidence intervals. Maps from Maptool (Seaturtle.org, 2002).