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Experience and survival in migratory European Robins *Erithacus rubecula* and Song Thrushes *Turdus philomelos* negotiating the Baltic Sea

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ABSTRACT

Capsule: There were survival costs for adult European Robins *Erithacus rubecula* grounded at coastal sites following departure, but not for young Robins or Song Thrushes *Turdus philomelos*.

Aims: To compare survival costs of crossing the Baltic Sea in autumn in adults and young of two passerines: the smaller European Robin and the slightly larger Song Thrush.

Methods: We calculated the mortality of experienced adults and those embarking on their first migration, modelling survival in a capture-mark-recapture framework using ringing records from three bird observatories on the periphery of the Baltic Sea. We tested the subsequent age- and species-dependent 12-month interval survival of autumn migrants caught before, during and after the barrier.

Results: Survival did not differ in relation to the capture site, however, results revealed species-specific post-capture survival. Adult European Robins encountering an ecological barrier on autumn migration had lower survival probability than that of immature birds, and less than a third of adults at following intervals. Yet, in Song Thrushes, adult survival estimates were similar over all time intervals, and estimates for both age classes were comparable to those derived from breeding sites.

Conclusion: Experienced individuals of the smaller species are likely to become grounded at the periphery of the ecological barrier as a result of physiologically limiting conditions. Species- and age-dependent survival also highlights potential inherent biases of sampling birds at coastal bird observatories.

Overall, components of the migratory programme such as direction and seasonality are intrinsically controlled (Berthold 1996). However, many aspects of migratory behaviour are flexible, including routings and timings which are both components of stopovers (Alerstam *et al.* 2003, Wiltschko & Wiltschko 2012, Willemoes *et al.* 2015). Hence, stopover behaviours, fuelling and negotiating topographical features are all a function of genetic programming and a response to environmental and endogenous constraints (Alerstam & Christie 1993) and of behavioural manifestations, which can be expected to be more pronounced in first-year passerines migrating nocturnally and alone (Erni *et al.* 2003).

The migration routes of long- and medium-distance migratory songbirds invariably involve crossing topographical features where landing opportunities are unpredictable or impossible, where there are limited fuelling resources (e.g. in deserts and during water crossings) or high terrain which must be traversed.

These may be geographically imposing (Sahara desert or Arctic Ocean) or relatively small; but any feature, which can elicit a change in behaviour, is generally known as an ecological barrier. In most cases, these are not physically restrictive to flight, but it is likely that the risk of experiencing survival limiting events, such as starvation, disorientation and extreme weather, increases when crossing deserts or water bodies (Alerstam & Lindström 1990, Gill & Hays 2015).

Intrinsic factors such as age and morphology are expected to influence how individual birds fare in different phases throughout their annual cycle (Sherry & Holmes 1995) and how they respond to periods of extended endurance flight during migration. The age, and hence experience, of an individual has been well established to influence survival (Pollock 1981). Within the Scandinavian flyway, the vast majority of a migratory population does not stop at the periphery of the Baltic Sea, and it is assumed that those that fly overhead have sufficient fuel to continue their journeys

(Bruderer & Jenni 1990, Hüppop *et al.* 2016). This is apparently disproportionate between age classes (Ralph 1978), but in those individuals that do stopover at sites associated with an ecological barrier, any effect of a barrier is likely to be detected. At stopovers, young birds are potentially affected by socially dominant adults, are less efficient foragers and their survival is also likely to be influenced by naïve route selection in solitary migrant species. Size and therefore potential fuel loading and flight speed determine strategies for negotiating ecological barriers and subsequent survival (Newton & Dale 1996), while age has been demonstrated to influence migratory strategies in finches and warblers in response to barriers (Dunn & Nol 1980, Lindström & Alerstam 1986).

Migration is the least understood life history event in songbirds (Lebreton *et al.* 1992) largely due to the practical difficulties of monitoring birds on their migration (Klaassen *et al.* 2014) or of re-sighting individuals on both breeding and wintering grounds (Sherry & Holmes 1995). Under normal circumstances migration is not a dangerous journey but a predictable and well-regulated life-history stage (Wingfield 2003). However, the largest mortality is generally estimated to occur during the migratory periods (Johnson 1973, Sillett & Holmes 2002, Blackburn & Cresswell 2016, Paxton *et al.* 2017, Rockwell *et al.* 2017). The survival estimates for the wintering period or annual survival calculated on the wintering grounds for numerous migratory species is reported to be high (Sillett & Holmes 2002, Newton 2006, Blackburn & Cresswell 2016, Paxton *et al.* 2017) suggesting that variation in mortality between age groups can be attributed to the

period before arrival at the wintering grounds. In particular, lower survival of first-year birds has been connected with post-fledging mortality (Gruebler *et al.* 2014) and the autumn migration (Klaassen *et al.* 2014). Negotiating unfamiliar regions and the dangers associated with areas where it is impossible to alight, renders inexperienced birds more vulnerable to external hazards and inherent limitations of flight (Alerstam & Lindström 1990).

Mortality on migration may increase on account of barrier crossings. In young raptors, the Sahara crossing accounted for approximately half the annual mortality and was significantly different between age classes (Strandberg *et al.* 2010). To estimate a potential survival cost associated with negotiating the Baltic Sea ecological barrier, we modelled the mortality of migrant European Robins *Erithacus rubecula* (hereafter Robin) and Song Thrushes *Turdus philomelos* caught and ringed at stations before, during, and after the Baltic: (a) Falsterbo, Sweden, a site just before the sea, (b) Christiansø, Denmark, an island in the sea and (c) Bukowo-Kopań, Poland, a site just after the sea with continental Europe beyond. We predicted higher mortality in first-time migrants and in the smaller species, the Robin. Furthermore, we *a priori* assumed that the survival cost of crossing would be reflected in lower survival of birds caught before, compared to after, the crossing; but that the greatest mortality cost would be associated with birds landing during the crossing (i.e. on an island) potentially unable to complete the water crossing in one flight. In addition, we explored the age composition of birds caught at each station and tested the relationship between navigating the barrier and the proportions of ages encountered.

Methods

Study sites and species

Data were obtained from standardized mist-netting across the Scandinavian to Northern Europe autumn migratory flyway (Figure 1) at three different sites on the Baltic Sea: Falsterbo, Sweden (pre-ecological barrier); Christiansø, Denmark (island in the Baltic Sea) and Bukowo-Kopań, Poland (post-ecological barrier). At Falsterbo Bird Observatory (55.384°N, 12.816°E) on the southern tip of Sweden, birds funnel down the Scandinavian Peninsula and then cross the Baltic primarily on a south-southeast (SSE) bearing towards Germany (Sjöberg *et al.* 2015), although an alternate and shorter water crossing to Denmark is available. Christiansø (55.320°N, 15.189°E) is only 800

Figure 1. Geographical locations of the three ringing stations situated on the Baltic Sea, from left to right, Falsterbo (Fbo) pre-barrier, Christainsø (Chø) island, and Bukowo-Kopań (Bu-Ko) post-barrier; and a schematic of treatment: land crossing (green) and potential or obligate water crossing (blue).

by 200 m in size and attracts large numbers of migrant passerines. The island is a minimum of 57 km from mainland Sweden and 120 km from the Polish coast, close to the ringing station of Bukowo-Kopań (55.354°N, 16.275°E). Thus birds are expected to respond to the ecological barrier by overflying it or circumnavigating it, before or after being captured and ringed. All sites ring many thousands of birds each autumn, have consistent long-term ringing effort and computerized records from 1980 until 2014.

Ringing data and dead recoveries were obtained for the most numerous ringed migrants that enabled survival modelling: Song Thrush and Robin. Both occur commonly throughout the Western Palearctic, and the Scandinavian breeding population winters in southwestern Europe (Cramp 1988). Food is mainly invertebrates. The Song Thrush is larger than the Robin (Song Thrush: average mass 78 g, wingspan 34 cm and length 23 cm; Robin: average mass 19 g, wingspan 21 cm and length 14 cm; Cramp 1988).

Survival modelling

Encounter histories were generated in the first instance to model survival for adult (older than one year) and first-year birds embarking on their initial migration. The data were not of sufficient size to enable modelling as a function of year of capture, so ringing and recovery data were combined to form encounter histories with the time interval of one year from the ordinal day of initial capture (i.e. an interval of autumn to autumn). Totals for each condition and species are shown in Table 1 with ringing effort and recoveries. On-site recoveries and recoveries where birds were targeted by ringing activities were discounted to reduce re-encounter bias, and a small number of birds were excluded from the data due to uncertainties in their recovery details. Probabilities of finding and reporting recoveries throughout Europe vary but all three sites are within a geographically analogous range targeting birds from the same population on an equivalent migratory path (online Figure S1).

Survival (S) and recovery (r) probabilities were estimated for one-year intervals from the Seber model (Seber 1970) using the MARK software (White & Burnham 1999). Species were treated as independent sets and recovery probabilities were modelled as a function of site for all cases. Candidate models for time and site variables were constructed; notation follows Lebreton et al. (1992). Annual survival (S) and recovery (r) probabilities were modelled as a function of site for both species. Annual S was modelled as a function of two distinguishable 'Age' classes: immature and adults (see glossary). Immature birds were defined as hatch-year birds on their first migration at the time of capture in autumn; aging criteria follow Svensson (1992). Age classes were also modelled as function of 'Time' as a 12-month period, resulting in a maximum of three 'TimeAge' variables (online Figure S2): Imm Ry1 and Adult Ry1 (S in the first year from capture for each age class) and Adult Ry2+ (Adult birds S in subsequent years). The same models were used for both species.

Bootstrap goodness-of-fit tests of the general model to the data indicated some over-dispersion. Residuals were visually inspected and did not indicate a structural issue. Models were adjusted for median-$\hat{c}$: Robin 1.809, Song Thrush 3.142 (White & Burnham 1999). Models were selected based on quasi Akaike's information criteria corrected for small sample size (QAICc) and (adjusted for median-$\hat{c}$; Akaike 1973) and QΔAICc was used to assess evidence for statistical differences in site, age and time, and to identify best estimates for annual survival for Robins and Song Thrushes.

Body condition and age composition

Fat scores (based on Pettersson & Hasselquist (1985), but adapted for Falsterbo Bird Observatory with classes 0–9) were measured for a representative subsample of birds ringed at Falsterbo since 1985. Data were obtained for a 20-year period for adult and immature birds of both species, and differences between age-classes were tested (Mann–Whitney U).

Table 1. Autumn ringing totals, annual mean and range, and subsequent recoveries for the period 1980–2014 at each Bird Observatory.

	Robin						Song Thrush					
	Falsterbo		Christainsø		Bukowo-Kopań		Falsterbo		Christainsø		Bukowo-Kopań	
	Ad	Imm	Ad	Imm	Ad	Imm	Ad	Imm	Ad	Imm	Ad	Imm
ringed	10694	74310	9038	87689	6663	57073	1404	7676	2004	23374	910	7022
$\bar{x}$	306	2123	258.2	2505.4	190.4	1630.7	40	219	62.2	708.3	26	200.6
range	78–822	745–3348	0–1459	1–6799	24–516	103–3863	12–87	56–525	1–286	82–1724	0–100	0–550
recov T	12	108	14	130	6	76	11	88	18	229	5	60
recov yr1	11	88	12	102	5	60	4	56	10	152	3	41
recov yr2+	1	20	2	28	1	16	7	32	8	77	2	19

Observations that the majority of birds landing at the periphery of ecological barriers were birds on their first migration, were tested. The proportion of age classes of both species caught and ringed each year was compared between the three sites using sign tests. Mean age ratios were consistent between the two species, with a significantly greater ratio of young birds to adults at the island site (16.1:1 for Robin, 28.6:1 for Song Thrush) compared to the post-barrier site (10.6:1 for Robin and 10.5:1 for Song Thrush; $z = 2.26$, $P = 0.0024$ and $z = 2.56$, $P = 0.011$, respectively) and pre-barrier site (7.8:1 and 5.8:1; $z = 3.31$ and $z = 4.24$, respectively, $P < 0.001$ for both species). The differences observed between the pre- and post-barrier sites were also significant ($z = 3.21$, $P = 0.0013$ and $z = 2.96$, $P = 0.0031$, respectively).

Glossary

S – Survival probability; r – Recovery probability; Imm Ry1 – immature birds, time interval 12 months post-ringing; Ad Ry1 – adult birds, time interval 12 months post-ringing; Ad Ry2+ – adult birds, subsequent autumn to autumn 12-month intervals.

Results

Our models supported pronounced differences in survival probabilities between Robin and Song Thrush age classes, although site differences were not reflected in the best supported models in either species (Table 2, online Table S1). For Robins, site differences accounted for some QAICc weight (0.11) with survival overall increasing in birds captured at sites progressing southwards. Furthermore, for Robins we found strong support (QAICc weight = 0.67, ΔQAICc

= 3.60) for a difference between the two age classes (immature and adult) and the time interval since ringing (year 1 and year 2+). At all sites, adult Robins had a survival probability in the first 12 months after ringing of less than a third of adults at subsequent intervals, and lower than that of immature birds. Survival was lower in young Robins than the annual survival of adults in the years following initial capture (immature: 0.20 ± 0.02; adult year 2+: 0.41 ± 0.05); however, the lowest survival estimate was of adult birds in the first year after capture (adult year 1: 0.12 ± 0.06; Figure 2). This result was consistent across the three sites with the lowest survival estimate from the pre-ecological barrier site and the greatest at the post-ecological barrier site, but the large standard error of the results gave little support within the model for site differences. In adult Song Thrushes, there was no support for a difference in annual survival over the two 'Time' intervals investigated; and the expected lower survival of first-year birds compared to adults was maintained (immature: 0.34 ± 0.02; adult: 0.48 ± 0.03; Figure 2).

Seasonal variation in the capture dates of adults at all sites indicated that those birds that died within 12 months of ringing, and hence contributing to the year 1 survival statistic, were later-arriving birds in the case of the Robin, but there was no difference for the Song Thrush (Figure 3). Low sample size precluded incorporation of ordinal day of capture into the model.

Recovery probabilities were similar between sites but parameters were maintained due to the anticipated variability, mortality of individuals at sea or recovery bias between the geographically different positions of ringing stations. Recovery probability differed between species; ranges were 0.0013-0.0015 and 0.0082-0.011 for Robin and Song Thrush, respectively.

Table 2. Annual survival model (log link function) for European Robin and Song Thrush, second-order Akaike's information criterion values (QAICc), differences in QAICc, weights, model likelihood and number of estimable parameters. For survival (S) and recovery (r) probabilities, parameterization variables are given in parenthesis: Age represents the two age classes; TimeAge represents the combined effect of age class and time interval since ringing – Imm Ry1, Ad Ry1 and Ad Ry2+ (see glossary); site denotes the three ringing stations.

|	Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Num. Par.
Robin	{S(TimeAge)r(Site)}	3179.602	0	0.66624	1	6
	{S(Age)r(Site)}	3183.206	3.604	0.10991	0.165	5
	{S(TimeAge[Imm Ry1]*Site,TimeAge[Ad Ry1,Ad Ry2 +])r(Site)}	3183.401	3.7995	0.09967	0.1496	8
	{S(TimeAge[Ad Ry1]*Site,TimeAge[Imm Ry1,Ad Ry2 +])r(Site)}	3183.415	3.8128	0.09901	0.1486	8
	{S(TimeAge[Imm Ry1,Ad Ry1]*Site,TimeAge[Ad Ry2 +])r(Site)}	3187.214	7.6123	0.01481	0.0222	10
	{S(Age*Site)r(Site)}	3189.882	10.2804	0.0039	0.0059	9
	{S(Site)r(Site)}	3189.954	10.3519	0.00376	0.0056	6
	{S(TimeAge*Site)r(Site)}	3190.628	11.0261	0.00269	0.004	12
Song Thrush	{S(Age)r(Site)}	1771.913	0	0.68688	1	5
	{S(TimeAge)r(Site)}	1773.891	1.9775	0.25555	0.372	6
	{S(Site)r(Site)}	1777.794	5.881	0.03629	0.0528	6
	{S(Age*Site)r(Site)}	1779.644	7.7311	0.01439	0.0209	9
	{S(TimeAge[Imm Ry1,Ad Ry1]*Site,TimeAge[Ad Ry2 +])r(Site)}	1781.375	9.4615	0.00606	0.0088	10
	{S(TimeAge*Site)r(Site)}	1785.347	13.4334	0.00083	0.0012	12
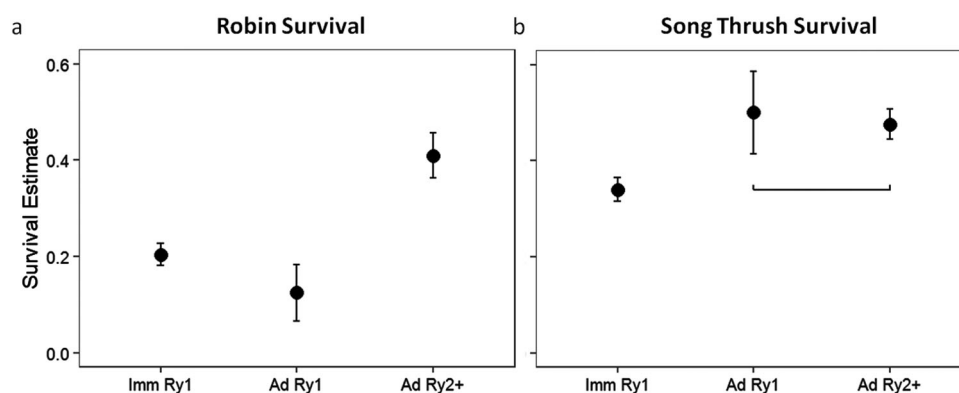
Figure 2. Survival estimates (mean with se represented by whiskers) for the three TimeAge classes: immature and adult 12-month interval following ringing (Ry1) subsequent 12-month intervals (Ry2+) for (a) European Robin and (b) Song Thrush. The bar represents there was no model support to separate these two parameters.
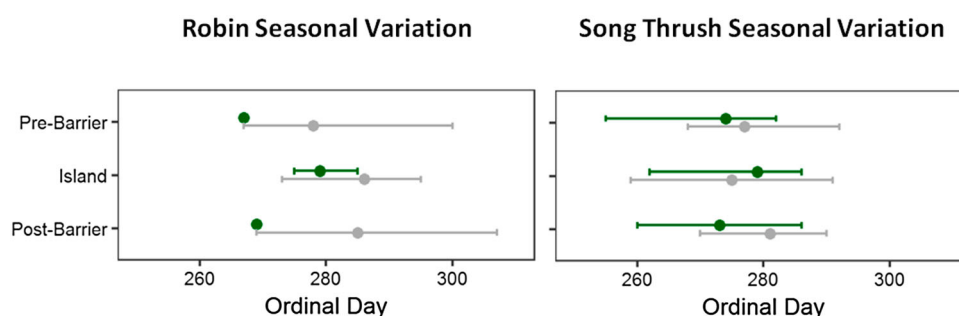

Figure 3. Capture dates of adult birds, median (dot), minimum and maximum, where grey dots show those recovered in 12 months from capure (Ry1) and green dots represent those recovered in subsequent 12-month intervals (Ry2+) for (a) European Robin and (b) Song Thrush.

In both species, mean fat scores at Falsterbo ranged from 0 to 7 for both age classes. For both species, significant differences in the fat score by age were found, $P < 0.0001$, $U = 7.2\ e^7$ and $P < 0.0001$, $U = 2.1\ e^6$ for Robins and Song Thrushes, respectively, although median values only differed in Robins, adults = 3 and immatures = 2. Mean values were higher in adults than immature birds: Robin 3.1 and 2.4, for adults and immatures, respectively, and Song Thrush 3.2 and 2.6, respectively (Table 2).

Discussion

We found no support for a difference in survival between sites across the autumn migration of the Baltic Sea which would have reflected a cost of the crossing itself. However, 12-month adult survival immediately following stopovers at the periphery of the ecological barrier was disproportionately low for the smaller species, the Robin. In contrast, such an effect was not found in young Robins or Song Thrushes. Potentially, adult Robins stop out of necessity whereas young birds stop out of naïvety. Whereas in the larger species, the Song Thrush, which is better equipped to deal with the Baltic crossing, stopover behaviour and subsequent survival was not influenced by this premise.

Though the numbers of ringed birds were large, our recovery rates were low and the sample sizes of some of our recovery groups consequently small, necessitating caution when interpreting results. Our findings rest on a number of important assumptions regarding the ringing and recovery data. Most importantly, recovery probabilities across age classes were assumed to be equal. Our data did not allow for separating these but the assumption seemed reasonable for dead recoveries and, for example, Thomson *et al.* (1997) detected no such differences for Song Thrushes. A number of other biases in ringing data might challenge our conclusions. Potentially, age-specific differences in reactions to bad conditions could influence whether individuals reach the coastline. However, our annual survival rates for immature and adults were, in general, similar to published estimates, making strong biases in our data less likely.

Annual survival estimates for Song Thrushes (0.34 for immature birds and 0.48 for adults) are similar to those reported in the Baltic region (Courish Spit 0.37–0.42 and 0.56-0.63, respectively and Sweden approximately 0.4 and 0.5, respectively (Lack 1948, Payevsky & Vysotsky 2003, Fransson & Hall-Karlsson 2008)) but lower than those estimated for Britain and Ireland 0.37–0.66 (Thomson et al. 1997, Siriwardena et al. 1998, Robinson et al. 2004), potentially reflecting less migratory behaviour in the subspecies hebridensis and clarkei than the nominate considered in our study. Hunting pressure on European migrants may also contribute to the lower survival of these populations compared to the British Isles (Payevsky & Vysotsky 2003).

Published survival estimates for adult Robins (0.38 and 0.42 in the British Isles (Lack 1948, Siriwardena et al. 1998) and approximately 0.35 in Sweden (Fransson & Hall-Karlsson 2008)) were similar to our estimate (0.41) for birds recovered in subsequent years after ringing (Ad Ry2+). First-year birds from Sweden had a similar survival of 0.213 compared to our estimate of 0.20. Estimates for all age-classes of migrating Robins in Britain and Ireland, the majority of which can be supposed to be immature, were 0.23 and 0.25 (Lack 1948, Korner-Nievergelt et al. 2014), respectively, while first-year Robins ringed in Britain had a survival of 0.34–0.40 (Lack 1948, Siriwardena et al. 1998). Indeed, survival of the largely resident Robins from the British Isles (Snow 1966, Ambrosini et al. 2016) did not differ between age classes (Siriwardena et al. 1998).

As several studies have reported similar first-year and adult survival after the post-fledging period (Sillett & Holmes 2002 and papers therein), we infer that the higher mortality of birds undertaking their first migration, and of adult Robins, is likely to be due to the autumn migration as the birds were all sampled en route during this interval. Timing of migration in adult Robins may affect their subsequent survival, where late arrival at ringing sites resulted in a lower survival, due to a potential variation in environment, delayed poorer-condition individuals or reflect population specific effects (Lerche-Jørgensen et al. 2018). Timing differences were not observed in Song Thrushes, where there was no difference in interval survival.

Where species can be tracked remotely (Strandberg et al. 2010) it is possible to attribute mortality events to distinct periods in the bird's life cycle. In young diurnal migrating raptors, the Sahara crossing accounted for about half the annual mortality and was significantly different between age classes. For colour-ring or museum collection studies in normally nocturnally migrating passerines, where the annual cycle is partitioned, the greatest mortality is during the migratory periods (Johnson 1973, Sillett & Holmes 2002, Blackburn & Cresswell 2016, Paxton et al. 2017, Rockwell et al. 2017). Our data did not support site differences, presumably because of the low statistical power and other factors having a greater relative influence. Nevertheless, in Robins, site accounted for around 10% of the variation, and survival tended to increase for Robins captured progressively southwards across the Baltic, consistent with a survival cost of the sea crossing. An opposite tendency in Song Thrushes may indicate a smaller effect on the larger species, although there was less than 5% support for a site effect in this species. This, however, cannot explain the large mortality found in Robins stopping at the edge of the Baltic that have previously undertaken the journey.

Fat stores, the principle fuel for migratory flight (Jenni & Jenni-Eiermann 1998), have been shown to affect departure orientation in numerous passerines including Robins (Sandberg 1994, Tsvey et al. 2007, Schaub et al. 2008), and it is expected that fuel carried must be sufficient for periods of non-stop flight. We found no difference in fat scores at the point of capture between age-classes in the two species. The available data do not suggest that these adult Robins carried a lower fuel load than Song Thrushes and cannot explain the difference in patterns of survival. In both species, fat scores were significantly different, but less than one condition-score greater in adults than young. While there was no evidence that adult Robins had poorer body condition than young Robins, it is possible that in contrast to grounded juveniles, adult Robins are physiologically compromised regardless of fuel load compared to those that do not stopover at the periphery of the Baltic Sea.

Flexibility in migratory strategies (e.g. route selection with respect to geographical features) may explain the survival effects described here. The larger Song Thrush may be better equipped to negotiate the Baltic Sea so that a direct crossing or stopping at the coast may be inconsequential. Radiotelemetry studies from Falsterbo indicate a higher propensity for Song Thrushes to make the direct sea crossing than for Robins (Sjöberg 2015). In the smaller Robin, selecting the optimal route may have a greater impact on subsequent survival in experienced individuals, something which naïve, first-year birds cannot incorporate into their migratory strategy (Ralph 1978). Similarly, Red-eyed Vireos Vireo olivaceus confronted with the Gulf of Mexico were more likely to depart inland compared to the larger thrush species: Swainson's Thrush Catharus ustulatus and Wood Thrush Hylocichla mustelina (Deppe et al.

2015). The ecological barrier had a greater impact on the smaller species which could not be explained by fat load, biogeography or flight performance. This migratory behaviour is analogous to our two study species and may explain their subsequent survival.

The age composition (87.2% young birds, aggregate) verified that proportions of birds encountered at coastal sites are weighted toward immature individuals in North America (Ralph 1978, Woodrey & Moore 1997) and for Robins in Europe (85% at Ottenby, Pettersson 1983; 88% at Falsterbo, Ehnbom *et al.* 1993). This pattern was particularly prominent on the island (mean 93.7%, Robins) and far exceeds that expected from productivity of small songbirds in this region (Robinson 2016) and specifically 70–75% for Robins (Lack & Gillmor 1965). Under-representation of adults suggests differences in migratory routing, stopover preferences or endurance (i.e. range between stopovers). Lindstrom *et al.* (1996) proposed that birds on their first migration are ignorant of the fuel required to negotiate environmental barriers, which contributes to a higher proportion of young at coastal sites and poorer survival. Different migratory strategies reflected in the proportions of age classes may also be attributed to the increased flight capacity of adults, necessitating fewer stopovers. It has been proposed that episodes of unexpected poor weather may briefly ground a proportionate sample of migrants transiting an area (Lindström *et al.* 1996). These factors may lead to a higher proportion of birds lost within the barrier itself, but this was not reflected in the recovery statistic.

While the age composition of birds at coastal ringing sites was not proportionate to the total migratory population, the contrast in survival between juveniles and adults suggests that adult individuals caught at the periphery of an ecological barrier may not be representative of the physiological condition of the migratory adult population.

In conclusion, our findings indicate that in experienced migrants, stopping over in relation to an ecological barrier is not adaptive but likely results from individuals experiencing difficulties. The findings have implications for the interpretation of studies of migrants conducted at major ringing stations, and suggests that there may be additional inherent bias in the sample population.

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References

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Proceedings of the 2nd International Symposium on Information. Czaki, Akademiai Kiado, Budapest.

Alerstam, T. & Christie, D.A. 1993. *Bird Migration*. Cambridge University Press, Cambridge.

Alerstam, T., Hedenström, A. & Åkesson, S. 2003. Long-distance migration: evolution and determinants. *Oikos* **103**: 247–260.

Alerstam, T. & Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In Gwinner, E. (ed) *Bird Migration*: 331–351. Springer, Berlin.

Ambrosini, R., Cuervo, J.J., Feu, C., Fiedler, W., Musitelli, F., Rubolini, D., Sicurella, B., Spina, F., Saino, N. & Møller, A.P. 2016. Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin *Erithacus rubecula*: a continent-wide analysis. *J. Anim. Ecol.* **85**: 749–760.

Berthold, P. 1996. *Control of Bird Migration*. Chapman & Hall, London.

Blackburn, E. & Cresswell, W. 2016. High within-winter and annual survival rates in a declining Afro-Palaearctic migratory bird suggest that wintering conditions do not limit populations. *Ibis* **158**: 92–105.

Bruderer, B. & Jenni, L. 1990. Migration across the Alps. In Gwinner, E. (ed) *Bird Migration: physiology and ecophysiology*, 60–77. Springer, Berlin.

Cramp, S. 1988. *Handbook of the Birds of Europe, the Middle East and North Africa: birds of the Western Palearctic: Vol 5*. Oxford University Press, Oxford.

Deppe, J.L., Ward, M.P., Bolus, R.T., Diehl, R.H., Celis-Murillo, A., Zenzal, T.J., Jr., Moore, F.R., Benson, T.J., Smolinsky, J.A., Schofield, L.N., Enstrom, D.A., Paxton, E.H., Bohrer, G., Beveroth, T.A., Raim, A., Obringer, R.L., Delaney, D. & Cochran, W.W. 2015. Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. *Proc. Natl. Acad. Sci. USA* **112**: E6331–E6338.

Dunn, E.H. & Nol, E. 1980. Age-related migratory behavior of warblers. *J. Field Ornithol.* **51**: 254–269.

Ehnbom, S., Karlsson, L., Ylvén, R. & Åkesson, S. 1993. A comparison of autumn migration strategies in robins *Erithacus rubecula* at a coastal and an inland site in southern Sweden. *Ringing Migr.* **14**: 84–93.

Erni, B., Liechti, F. & Bruderer, B. 2003. How does a first year passerine migrant find its way? Simulating migration mechanisms and behavioural adaptations. *Oikos* **103**: 333–340.

Fransson, T. & Hall-Karlsson, S. 2008. *Svensk ringmarkningsatlas*. Naturhistoriska riksmuseet & Sveriges Ornitologiska Forening, Stockholm.

Gill, J.A. & Hays, G. 2015. Encountering extreme weather during migration: individual strategies and their consequences. *J. Animal Ecol.* **84**: 1141–1143.

Gruebler, M.U., Korner-Nievergelt, F. & Naef-Daenzer, B. 2014. Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. *Ecol. Evol.* **4**: 756–765.

Hüppop, O., Hüppop, K., Dierschke, J. & Hill, R. 2016. Bird collisions at an offshore platform in the North Sea. *Bird Study* **63**: 73–82.

Jenni, L. & Jenni-Eiermann, S. 1998. Fuel supply and metabolic constraints in migrating birds. *J. Avian Biol.* **29**: 521–528.

Johnson, N.K. 1973. Spring migration of the Western Flycatcher, with notes on seasonal changes in sex and age ratios. *Bird-Banding* **44**: 205–220.

Klaassen, R.H., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.M., Bairlein, F. & Alerstam, T. 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *J. Animal Ecol.* **83**: 176–184.

Korner-Nievergelt, F., Liechti, F. & Thorup, K. 2014. A bird distribution model for ring recovery data: where do the European robins go? *Ecol. Evol.* **4**: 720–731.

Lack, D. 1948. Notes on the ecology of the robin. *Ibis* **90**: 252–279.

Lack, D. & Gillmor, R. 1965. *The Life of the Robin*. Witherby, London.

Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**: 67–118.

Lerche-Jørgensen, M., Korner-Nievergelt, F., Tøttrup, A.P., Willemoes, M. & Thorup, K. 2018. Early returning long-distance migrant males do pay a survival cost. *Ecol. Evol.* **8**: 11434–11449.

Lindström, Å. & Alerstam, T. 1986. The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden. *Behav. Ecol. Sociobiol.* **19**: 417–424.

Lindström, Å., Hedenstroem, A. & Pettersson, J. 1996. The autumn migration of Willow Warblers *Phylloscopus trochilus* in Sweden: results from a nation-wide co-operative project. *Ornis Svec.* **6**: 145–172.

Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *J. Ornithol.* **147**: 146–166.

Newton, I. & Dale, L. 1996. Relationship between migration and latitude among west European birds. *J. Animal Ecol.* **65**: 137–146.

Paxton, E.H., Durst, S.L., Sogge, M.K., Koronkiewicz, T.J. & Paxton, K.L. 2017. Survivorship across the annual cycle of a migratory passerine, the willow flycatcher. *J. Avian Biol.* **48**: 6.

Payevsky, V.A. & Vysotsky, V.G. 2003. Migratory Song Thrushes *Turdus philomelos* hunted in Europe: survival rates and other demographic parameters. *Avian Science* **3**: 13–20.

Pettersson, J. 1983. Rödhakens *Erithacus rubecula* höstflyttning vid Ottenby. *Vår Fågelvärld* **42**: 333–342.

Pettersson, J. & Hasselquist, D. 1985. Fat deposition and migration capacity of robins *Erithacus rebecula* and goldcrests *Regulus regulus* at Ottenby, Sweden. *Ringing Migr.* **6**: 66–76.

Pollock, K.H. 1981. Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics* **37**: 521–529.

Ralph, C.J. 1978. Disorientation and possible fate of young passerine coastal migrants. *Bird-Banding* **49**: 237–247.

Robinson, R.A., Green, R.E., Baillie, S.R., Peach, W.J. & Thomson, D.L. 2004. Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. *J. Animal Ecol.* **73**: 670–682.

Robinson, R.A., Leech, D.I., Massimino, D., Woodward, I., Hammond, M.J., Harris, S.J., Noble, D.G., Walker, R.H., Eglington, S.M., Marchant, J.H., Sullivan, M.J.P., & Baillie, S.R. 2016. *BirdTrends 2016: trends in numbers, breeding success and survival for UK breeding birds*. BTO, Thetford.

Rockwell, S.M., Wunderle, J.M., Jr., Sillett, T.S., Bocetti, C.I., Ewert, D.N., Currie, D., White, J.D. & Marra, P.P. 2017. Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation. *Oecologia* **183**: 715–726.

Sandberg, R. 1994. Interaction of body condition and magnetic orientation in autumn migrating robins, *Erithacus rubecula*. *Anim. Behav.* **47**: 679–686.

Schaub, M., Jenni, L. & Bairlein, F. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behav. Ecol.* **19**: 657–666.

Seber, G. 1970. Estimating time-specific survival and reporting rates for adult birds from band returns. *Biometrika* **57**: 313–318.

Sherry, T.W. & Holmes, R.T. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence. In T. Martin & D. Finch (eds) *Ecology and Management of Neotropical Migratory Birds*, 85–120. Oxford University Press, New York.

Sillett, T.S. & Holmes, R.T. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Animal Ecol.* **71**: 296–308.

Siriwardena, G., Baillie, S. & Wilson, J. 1998. Variation in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study* **45**: 276–292.

Sjöberg, S. 2015. Stopover behaviour in migratory songbird. PhD, Lund University.

Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, T. & Muheim, R. 2015. Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. *Anim. Behav.* **104**: 59–68.

Snow, D. 1966. Movements of British Robins as shown by ringing. *Brit. Birds* **59:** 67–74.

Strandberg, R., Klaassen, R.H., Hake, M. & Alerstam, T. 2010. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biol. Lett.* **6:** 297–300.

Svensson, L. 1992. *Identification Guide to European Passerines*. L. Svensson, Stockholm.

Thomson, D.L., Baillie, S.R. & Peach, W.J. 1997. The demography and age-specific annual survival of song thrushes during periods of population stability and decline. *J. Animal Ecol.* **66:** 414–424.

Tsvey, A., Bulyuk, V.N. & Kosarev, V. 2007. Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site. *Behav. Ecol. Sociobiol.* **61:** 1665–1674.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46:** S120–S139.

Willemoes, M., Blas, J., Wikelski, M. & Thorup, K. 2015. Flexible navigation response in common cuckoos *Cuculus canorus* displaced experimentally during migration. *Sci. Rep* **5:** 16402.

Wiltschko, W. & Wiltschko, R. 2012. Global navigation in migratory birds: tracks, strategies, and interactions between mechanisms. *Curr. Opin. Neurobiol.* **22:** 328–335.

Wingfield, J.C. 2003. Avian migration: regulation of facultative-type movements. In Berthold, P., Gwinner, E. & Sonnenschein, E. (eds) *Avian Migration*: 113–125. Springer, Berlin.

Woodrey, M.S. & Moore, F.R. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* **114:** 695–707.