Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain

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Migratory birds replenishing their fuel stores have to decide when to leave their stopover site for the next flight bout. We studied whether the decision to leave a stopover site depends on wind and rain conditions. From capture–recapture data of 1153 European robins collected during three autumns at a stopover site in Switzerland, we estimated the daily emigration probability with a newly developed multistate capture–recapture model that accounts for the occurrence of transients. We tested whether the variation in the daily emigration probabilities can be explained by wind speed, wind direction (both on the ground and 300 m above ground) or rain. Variation in emigration probability was largely explained by variation in wind at 300 m and rain. The emigration probability was highest (0.5) during nights with no or weak (<1.5 m/s) winds at 300 m and no rain, intermediate (0.15–0.2) on nights without rain and with medium wind (>1.5 m/s), and on nights with weak winds (<1.5 m/s) and rain; and almost zero during nights with rain and strong winds at 300 m. Wind direction at 300 m and wind conditions (speed and direction) on the ground had no influence on departure decision. We suggest that birds may consider cues other than wind speed at ground level to predict wind speed at higher altitudes, and that they consider wind direction only when aloft by selecting an optimal flight altitude. Wind speed aloft and rain appeared to be significant factors that synchronize bird migration spatially and temporally.

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During their first year, the timing, direction and distance of autumn migration of passerine birds is, to a large extent, endogenously governed (Berthold 1996). The expression of their spatiotemporal programme is, however, modified by environmental factors (Jenni & Schaub 2003). This is particularly important when migratory birds divide their migration from the breeding to the wintering grounds and back into several periods of flights and stopovers to replenish their energy stores (e.g. Moore & Yong 1991; Schaub & Jenni 2000, 2001; Dierschke & Delingat 2001). Based on the endogenous time programme and on environmental information, migrants have to decide at each stopover site when to stop accumulating energy and start on the next flight bout. This departure decision controls the time the bird spends at the current stopover site, the potential flight range (maximum amount of usable energy) and, in part, the realized flight path (weather conditions during flight). The overall speed of migration and the flight path are therefore largely dependent on the departure decisions at the intermittent stopover sites. Achieving an optimal flight

path is fundamental for migrants, because it ensures that they arrive at further stopover sites, at the wintering or the breeding grounds in an optimal time window, so that survival and reproductive output are maximized (Farmer & Wiens 1999).

Wind and rain are thought to be the most important environmental factors determining departure from a stopover site. Because wind speed is often as high as or higher than flight speed, it is an important component of the ground speed and direction of flying birds. Birds may consider the current wind conditions for their departure decision, or start in any wind condition and select the air layer with the most profitable wind (Alerstam 1978; Cochran & Kjos 1985; Bruderer et al. 1995), as wind speed and direction can vary dramatically with altitude (Liechti & Bruderer 1998). If wind conditions are considered, it would be best to have information about wind at the usual flight altitude.

Avoiding flying in rain is important for several reasons: during rain, visibility, and thus ability to orient visually, is severely compromised, and increased drag, the negative effects of turbulent air (from rain drops) on the air flow around the wings, and the eventually wet plumage all increase flight costs.

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The density of migrating birds aloft commonly depends on weather factors, most importantly wind speed and direction and rain (Nisbet & Drury 1968; Richardson 1978, 1990; Erni et al. 2002). However, the density of migrating birds is an estimate of the number of birds that have taken off, and is not well suited to judge the proportion of migrants that have decided to depart from a stopover site. The density of migrants measured aloft depends on the number of birds resting the day before in the take-off area (potential recruitment), and on the accuracy of the measurement, which itself depends on the method used (Rabøl 1978; Richardson 1978; Bruderer 1997). The effects of weather on the departure behaviour of migrants may therefore be evaluated by estimating the proportion of birds taking off out of the birds present at a stopover site every day (Rabøl 1978; Richardson 1990). While estimating the number of birds aloft includes mainly birds setting off on a migratory flight of some reasonable distance, estimating the proportion of departing birds includes those landing soon after take-off because of, for example, bad weather.

Most studies have investigated the role of weather conditions on departure decisions by directly counting the number of departing birds (Chan 1995; Bolshakov & Rezvyi 1998; Bolshakov & Bulyuk 1999), which increases on nights without rain, and with high visibility, low wind speed and low cloud cover. However, observed variation depends not only on the weather conditions at time of departure, but also on the number of birds that are present at the stopover site. Again, it would be preferable to consider the proportion of departing birds rather than their number.

Another approach is to observe the departure of marked birds. Passerines usually select the best weather conditions (tail wind assistance, no rain, low cloud cover) for their departure (Åkesson & Hedenström 2000; Åkesson et al. 2001, 2002; Dänhardt & Lindström 2001). Sample size is often quite low with such an approach, which may be why Fransson (1998) did not find a relation between departure and wind conditions. A further problem is that it is not always certain whether the departure night is the night after the last observation. The probability of encountering a bird that is still at the site is usually less than one (Schaub et al. 2001), unless the bird is equipped with a transmitter (Åkesson & Hedenström 2000; Åkesson et al. 2001, 2002).

Few studies have tried to relate the proportion of departing birds to weather conditions. Rabøl & Hansen (1978) calculated the emigration ratio (estimated by capture–recapture methods as the quotient of the number of birds that have left the site on night i and the number of birds present on the preceding day) of European robins to be higher when the sky was clear than when it was cloudy, but no relation was found between the emigration ratio and wind speed or wind direction. Pyle et al. (1993), however, found that low wind speed, clear sky, rising barometric pressure and high visibility resulted in an increased proportion of departing landbirds. Wind direction was not important for the departure decision.

In summary, despite the different methods used, there is clear evidence that departure of passerines from stopover sites depends on wind speed. However, the role of the wind direction is not clear. Furthermore, it is not clear whether and how the potential influence of wind and rain interact. Emigration may be reduced by the same constant amount when it is raining for all wind conditions or the influence of the rain may vary with wind conditions. Furthermore, it is unknown whether wind conditions on the ground or aloft are considered for departure.

In this study we assessed whether wind conditions (speed and/or direction) aloft or on the ground and rain were important for the decision to leave the stopover site. To overcome the methodological problems mentioned above, we analysed with product multinomial models capture–recapture data of European robins obtained at a stopover site in Switzerland (Lebreton et al. 1992; Lebreton & Pradel 2002). With these models, the daily emigration probability is estimated independently of the resighting probability. This approach has several advantages: (1) we can estimate the probability that an individual leaves the stopover area on a given night, which is the target parameter for studying the departure decision; (2) we can relax the assumption that the night after the last observation was the departure night; and (3) we can test rigorously whether the emigration probability is a function of weather characteristics.

Robins are short-distance, nocturnal migrants. Individuals that migrate through Switzerland mainly originate from areas north-northeast of Switzerland up to Fennoscandia (Jenni 1987) and spend the winter in the Mediterranean area, as shown by ring recoveries. During stopovers, the majority of robins defend small territories for a few days (Johnstone 1998; Titov 1999; Lajda 2001). Individuals that cannot occupy a territory after arrival leave the stopover site very quickly (Johnstone 1998; Titov 1999; Lajda 2001). They may fly the next night, probably without replenishing their energy stores (Szulc-Olech 1965), or they may just move outside the study area in search of a free territory. We therefore tested whether the departure decision of robins that stop over for some days (thus probably occupy territories) depends on wind and rain.

METHODS

Study Site and Data Collection

The capture–recapture data of robins were collected during three autumn migration seasons (1987–1989) at Portalban (46°55′N, 6°57′E; 430 m above sea level), situated at the southeastern shore of Lake Neuchâtel, Switzerland. We captured birds daily with a total length of 429 m of mist nets placed in different habitats such as reeds, bushes within woods and wood edges (for a detailed description of the study site, see Jenni & Widmer 1996). Robins were caught and ringed in all habitats, but were most frequent in the bushes within woods (Jenni & Widmer 1996). We included data from the beginning of the main migration season of the robin (3 October) until the end of the catching season (28 October), and considered only nonmoulting robins, because moulting

robins are not likely to be on migration (personal observation). In total, we captured 1153 nonmoulting robins during this period. Of these, 95 were recaptured once and 41 more than once. No robin was captured in 2 different years.

We used two sources of wind data. First, we collected ground wind data at Portalban each evening between 1800 and 2100 hours. Wind speed was estimated using the Beaufort scale and its direction classified into eight categories. Second, we used wind data measured at the meteorological station Payerne (46°49′N, 6°56′E; 450 m above sea level), 10 km south of Portalban. Wind speed and direction were measured with radio sondes each night at midnight. We used data of 925 hPa which corresponds to an altitude of about 300 m above ground. These wind measurements were more precise than those estimated at Portalban. Wind speed from both sources was grouped into three classes (zero: 0−1.5 m/s; moderate: >1.5−4.6 m/s; high: >4.6 m/s) and the wind directions into head wind (between 145° and 325°; 180° around mean autumn migration direction of 235°, Bruderer & Jenni 1990) and tail wind (other directions). Thus, every evening was characterized by one of five wind conditions (zero wind had no direction). Table 1 summarizes the number of nights within each class. The amount of rainfall during the night (from 1900 to 0700 hours) was used to classify each night as 'no rain' (<2 mm) and rain (≥2 mm). Rainfall data were sampled at Payerne by the meteorological station.

Statistical Analysis

Cormack−Jolly−Seber models allow us to estimate separately local survival probability (ϕ_i: probability that a marked individual survived and remained at the study site during the time intervals i and $i+1$) and recapture probability (p_i: probability that a marked individual that is alive and at the study site at i is captured at i) by using capture−recapture data. Under the assumption that survival probability from one day to the next is 1 (the annual survival rate of robins is about 0.4, Siriwardena et al. 1998; thus the daily survival rate is 0.997), the estimated local survival rate is the probability of remaining at the study site during the next day. Its complement to one is an estimate of the daily probability of leaving the study site (see Schaub et al. 2001 for a detailed description of the method).

Robins at stopover places consist of two groups: individuals that hold a territory for some time and individuals that visit the study area in search of a territory (Szulc-Olech 1965; Johnstone 1998; Titov 1999; Lajda 2001). Individuals of the latter group leave the site quickly after landing and appear as transients (i.e. the emigration probability just after initial capture is 1). To obtain unbiased estimates of the emigration probability of the nontransients, we opted for a capture−recapture model that accounts for transients. This could have been done using an age-dependent structure for the local survival rate (Pradel et al. 1997), but the proportion of transients among newly caught individuals (hereafter proportion of transients) and the emigration probability of the non-transients cannot always be modelled independently from each other with this approach. To overcome this problem, we formulated a multistate capture−recapture model (Nichols et al. 1992; Lebreton & Pradel 2002) to model and estimate the proportion of transients and the emigration probability of the nontransients. Compared with one-state models, multistate models are parameterized with additional parameters to estimate movement between states. In the three-state model we defined here, all robins are in the state 'initial' when they are captured for the first time. All these robins are forced to move to another state until the next capture occasion: the transients move to the state 'transients' and the non-transients to the state 'nontransients'. The movement probabilities are now the probabilities that a bird is either a transient (τ) or a nontransient ($1-\tau$). Transients leave the study site thereafter with probability 1 and cannot be recaptured. Nontransients leave the stopover site with probability $\varepsilon = 1 - \phi$, and are recaptured with probability p. The transition matrix and the vectors of state-specific emigration and recapture probabilities are

$$\begin{bmatrix} 0 & 1-\tau & \tau \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}_t \begin{bmatrix} 0 \\ \varepsilon \\ 1 \end{bmatrix}_t \begin{bmatrix} 0 \\ p \\ 0 \end{bmatrix}_t \qquad (1)$$

where the subscript t denotes time dependence, and the states are initial, nontransient and transient from top to bottom. If the emigration probability of the state initial were ε instead of 0, this model would be identical to the one-state transient model of Pradel et al. (1997).

The input data for this model are in the form of a matrix with the individual capture histories. The elements of an individual capture history are 1 on the day the robin was caught for the first time (state initial), 2 on days when it was recaptured (representing state nontransient) and 0 on days when it was not captured. The third state transient does not occur in the data, because transients cannot be recaptured. We pooled the data from the 3 years longitudinally, so that the complete capture−recapture matrix consisted of nine submatrices. The three submatrices in the diagonal are the year-specific capture−recapture data as described above. The six off-diagonal submatrices contain only zeros. The first capture occasion of the complete matrix was 3 October 1987, the last one 28 October 1989. To ensure that no bird 'remains' at the

Table 1. Wind speeds recorded during the study at ground level in Portalban and at about 300 m above ground in Payerne

	Ground level	At 300 m
No wind	0.63 ± 0.51 (36)	1.06 ± 0.35 (19)
Moderate, head	3.42 ± 1.22 (22)	3.09 ± 0.91 (17)
Moderate, tail	3.26 ± 1.03 (9)	2.99 ± 0.66 (14)
High, head	6.70 (8)	8.25 ± 2.74 (20)
High, tail	— (0)	6.38 ± 0.57 (5)

No wind: 0−1.5 m/s; moderate: >1.5−4.6 m/s; high: >4.6 m/s; head: direction 145°−325°; tail: direction 325°−145°. Means are given ± SD, with sample sizes in parentheses.

stopover site from one year to the other, we fixed the emigration probabilities from 28 October 1987 to 3 October 1988 and from 28 October 1988 to 3 October 1989 to one. We also fixed the recapture probability of the nontransient robins on 3 October 1988 and 1989 to zero, because no robin could be recaptured then. The complete capture history was then a matrix of size 1153 (individuals) times 77 (capture occasions).

The most complex model that we fitted and used to test the goodness-of-fit (GOF) considered time-specific (i.e. different each day) emigration, transients and recapture probabilities (ε_t, τ_t, p_t). The GOF test was done with U-CARE (Choquet et al. 2001; see also Pradel et al. 1997) and was not significant (chi-square test: $\chi^2_{67} = 79.1$, NS); thus the model adequately fitted the data. Models with fewer parameters were nested within the most complex model. We used MARK (White & Burnham 1999) for modelling and for the estimation of the parameters.

We ranked all models considered (see below) by means of the small-sample-size-adjusted Akaike's Information Criterion (AICc), an information-theoretical measure that provides a good balance between over- and underfitting (Burnham & Anderson 1998). We calculated the Akaike weight for each model, which can be interpreted as the probability that the current model is the best one given the data and the set of candidate models (Burnham & Anderson 1998). Finally, based on the Akaike weights we calculated model-averaged parameter estimates and drew inferences from them. Model averaging has the advantage that model selection uncertainty is taken into account for the estimation of the parameters and for inferences and that the standard errors of the parameter estimates are conditional on the set of candidate models rather than on a single model, and thus are more realistic (Burnham & Anderson 1998).

Hypotheses

We defined a priori several biologically meaningful models. For each parameter type (ε, τ, p), different hypotheses were formulated. We examined all hypotheses of the parameter types which resulted in 44 different models.

The emigration probabilities of the nontransients might have been time dependent (ε_t), if the departure of the robins had been determined by external factors. Possible external factors that might have synchronized the emigration probability of robins are either wind or rain, or both. First, robins may consider only wind conditions such as wind speed and direction ($\varepsilon_{speed*direction}$). We predicted birds would favour strong tail winds, whereas strong head winds would hamper emigration. Alternatively, robins may consider only wind speed (ε_{speed}), or only wind direction ($\varepsilon_{direction}$). We would expect emigration to be higher on nights with low wind speed in the former model, and on nights with a tail wind in the latter model. Second, robins may consider only rain (ε_{rain}) and we would expect emigration probability to be lower during rainy nights. Third, robins may consider both main factors for the departure decision. They may consider wind speed or direction and rain in such a way

that emigration is reduced by a constant amount during rainy nights for all possible wind situations. This is expressed in additive models ($\varepsilon_{speed+rain}$ or $\varepsilon_{direction+rain}$). It may also be that emigration is high only at a specific combination of wind and rain situations. This is expressed in models with interactions ($\varepsilon_{speed*rain}$, $\varepsilon_{direction*rain}$ and $\varepsilon_{speed*direction*rain}$). The emigration probability may also appear to be the same on each night (ε), if robins do not consider wind condition or rain or another external cue that synchronizes emigration, but rather base their departure decision on intrinsic characteristics such as the amount of accumulated fuel or the fuel deposition rate. The proportion of transients and the recapture probability were not of particular biological interest for this study. For both parameter types we considered a time-dependent model (τ_t, p_t) to take account of possible temporal variation, and a constant model (τ, p) to try to increase parsimony.

To study whether robins consider local ground wind or wind condition aloft for the departure decision, the hypotheses outlined above were tested using wind data at ground level and at 300 m.

RESULTS

Weather Conditions

The wind conditions were very variable over the study period (Fig. 1, Table 1). The most frequent wind directions were southwest (on the ground and aloft) and northeast (aloft). As the main migration direction of robins in autumn is southwest, they encounter either a head or a tail wind component. Wind speed was higher and more variable aloft than on the ground (Fig. 1) and the two speeds were positively correlated (Spearman rank correlation: $r_S = 0.46$, $N = 77$, $P < 0.001$). The amount of rainfall during a rainy night varied between 2.2 and 36.2 mm ($\overline{X} \pm SD = 8.9 \pm 8.7$ mm, $N = 16$) and on nonrainy nights between 0 and 1.5 mm (0.1 ± 0.3 mm, $N = 59$).

Modelling of Departure Probability

In our first analysis, we considered the local ground wind and rain. Model selection revealed that four models had substantial support (Table 2). The common feature of the best models was that the proportion of transients (model averaged mean 0.73, 95% unconditional confidence interval 0.66–0.79) and the daily recapture probability (model averaged mean 0.17, 95% unconditional confidence interval 0.13–0.20) were constant during the study period and that the emigration probability was a function of the rain. Model averaged estimates indicate that the daily emigration probability was at least double during nights without rain than during nights with rain. In the second to the fourth best models wind speed and direction were included in addition to rain, but emigration probability did not differ between nights with different wind conditions (Fig. 2a).

In the second analysis, wind conditions at 300 m above ground and rain were considered (Table 3). Model

Ground level
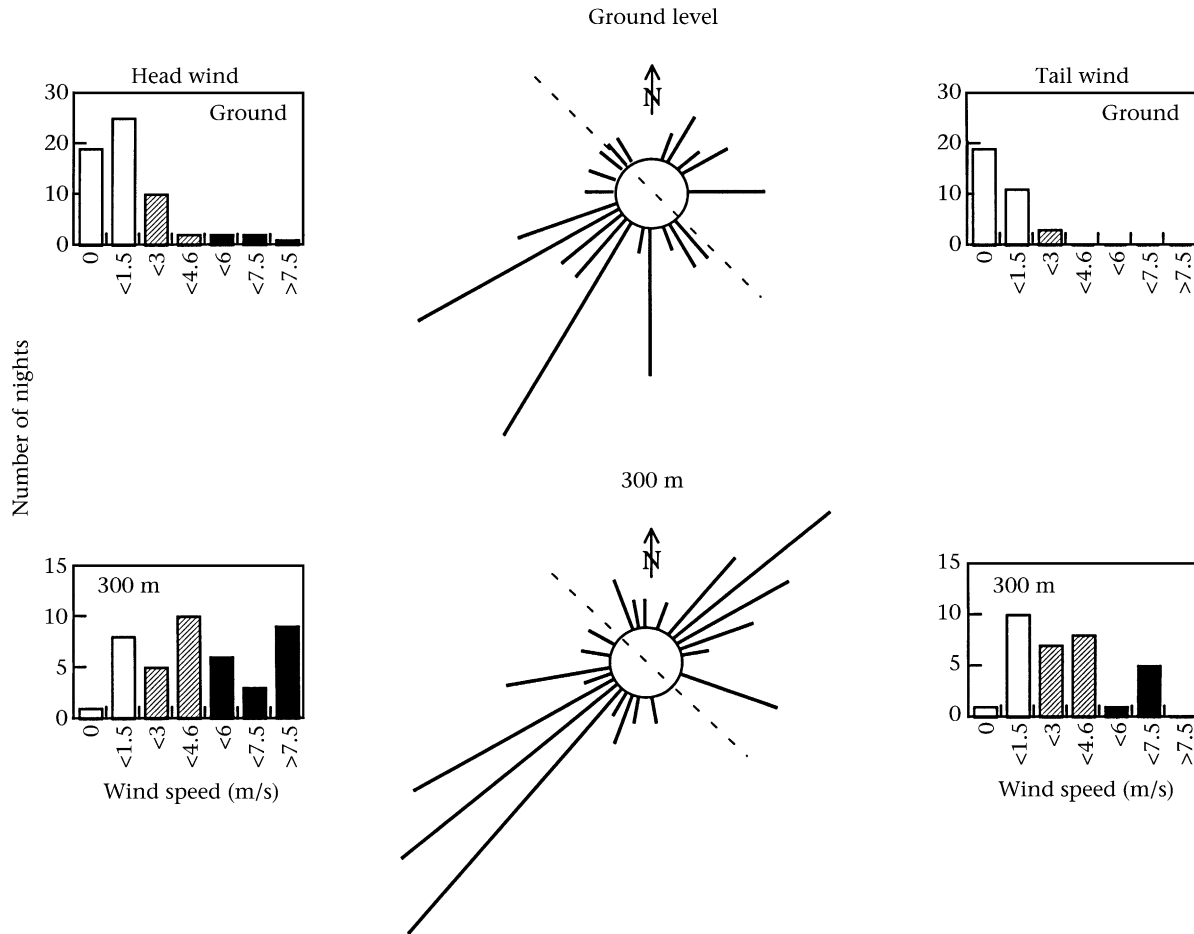
Figure 1. Frequency distribution of wind directions from 3 to 28 October 1987–1989 measured at 1900 hours at Portalban and at midnight at about 300 m aloft. For the two main wind directions 'tail' and 'head' the frequency of wind speeds at each site is shown in the bar charts. The number of nights with wind speed 0 is shown in both charts of the corresponding site, as it could not be allocated to a direction. The shading of the columns indicates the different wind speed classes used for the analysis: □: no wind; ▨: moderate wind speed; ■: high wind speed.

selection was unambiguous, as only two models had substantial support. The common feature of both models was that the proportion of transients (model averaged mean 0.73, 95% unconditional confidence interval 0.66–0.79) and the daily recapture probability (model averaged mean 0.16, 95% unconditional confidence interval 0.13–0.20) were constant during the study period; the emigration probability was a function of the wind aloft and of the rain. Models in which emigration was a function of only wind aloft or rain were clearly worse (Table 3). Model-averaged emigration probabilities were highest during nights when there was no wind aloft and no rain (Fig. 2b); about 50% of the nontransient robins left the stopover site during such nights. Daily emigration probability was intermediate (15–20%) during nights with rain, but no wind aloft and during nights without rain, but wind aloft (regardless of its direction and speed). Almost no robin left the stopover site during nights with rain and with wind aloft.

The lower AICc value of the best models that considered wind aloft and rain (Table 3) compared with the best models that considered local ground wind and rain (Table 2) indicates that the former explained more of the

temporal variation of the daily emigration probabilities than the latter.

DISCUSSION

Methodological Aspects

We consider the application of capture–recapture models as a complementary method to study departure behaviour. As outlined in the Introduction, it has several advantages over other methods. However, for a rigorous interpretation of the results, the significance of the estimated emigration probability must be kept in mind. It is the probability that the birds have left the area that is covered by the nets. Therefore it cannot be inferred that all emigrating birds perform a true migratory flight. For example, some birds may have left the study area during the day while feeding. However, as nontransient robins defend small territories during stopover (Johnstone 1998; Titov 1999; Lajda 2001), this is not a cause for concern here, but may be problematic in species with a different spatial behaviour at stopover sites (Chernetsov 2002). Furthermore, departing birds that encounter unsuitable

Table 2. Model selection of the emigration and transience behaviour of robins at Portalban with respect to local ground wind and rain

Model	Deviance	No. of parameters	AICc	ΔAICc	AICc weight
ε_{rain}, τ, p	762.7	4	1742.5	0.00	0.30
$\varepsilon_{rain+speed}$, τ, p	758.9	6	1742.7	0.21	0.27
$\varepsilon_{rain+direction}$, τ, p	759.2	6	1743.0	0.50	0.23
$\varepsilon_{rain*speed}$, τ, p	756.3	8	1744.2	1.71	0.13
$\varepsilon_{rain*direction}$, τ, p	759.6	8	1747.4	4.97	0.02
$\varepsilon_{rain*direction*speed}$, τ, p	755.9	10	1747.8	5.35	0.02
ε_{speed}, τ, p	766.5	5	1748.3	5.82	0.02
$\varepsilon_{direction}$, τ, p	766.7	5	1748.5	6.01	0.01
ε, τ, p	772.9	3	1750.7	8.17	0.00
$\varepsilon_{speed*direction}$, τ, p	766.0	7	1751.8	9.35	0.00
ε_t, τ_t, p_t	515.7	216	2002.9	260.37	0.00

Of the 44 fitted models, only the best model, the nine best alternative models and the global model are shown. We indicate the deviance, given by MARK, the number of estimated parameters in the model, the small-sample-size-adjusted Akaike's Information Criterion (AICc), the difference in AICc between the best and the actual model (ΔAICc) and the AICc weights. ε denotes the emigration probability, τ the proportion of transients and p the recapture probability.

flight conditions after take-off may land after a short time. As such birds have left the study area, they are treated as emigrants in capture–recapture models. Hence, the definition of the departure decision that applies here is a wide one; it does not involve additional assumptions about the distance of movement or the flight duration after departure.

We developed a multistate capture–recapture model to estimate and account for the presence of transients. Hitherto, one-state capture–recapture models with an age structure have been used for that purpose (Pradel et al. 1997). The multistate approach has the advantage that it is more flexible. The proportion of transients and the survival or emigration rates of the nontransients can be modelled independently of each other, whereas in the one-state context they cannot.

Influence of Weather on Departure

Our analyses showed that the daily emigration probabilities of robins from the stopover site were strongly influenced by the prevailing rain and wind conditions aloft during the night, but not by the local ground wind conditions. As expected, robins were much more likely to depart from the stopover site during nights when wind speed aloft was low than during nights when it was moderate or high. During rainy nights this pattern was more or less maintained, but the emigration probability was much reduced. These findings agree well with the main conclusions of other studies (e.g. Richardson 1978, 1990; Bolshakov & Rezvyi 1998; Bolshakov & Bulyuk 1999; Erni et al. 2002) and with theoretical models (Liechti & Bruderer 1998; Weber et al. 1998).

For migrating robins it seems to pay to wait for an evening when there is no wind aloft and then take off. The benefit of flying in low wind speeds is to minimize the losses of potential flight range in the head winds that prevail at the study site (Fig. 1) and in western Europe (Liechti & Bruderer 1998).

Departure was almost independent of wind conditions on the ground, but dependent on wind conditions aloft. As small passerines such as robins fly up to 1000 m above ground (Bruderer 1971), wind conditions aloft are more important to maximize flight range than ground winds; hence robins behaved optimally in this respect. The crucial point is how robins are able to predict wind conditions aloft. Wind speeds aloft and on the ground were positively correlated, so robins could predict wind speed aloft from ground wind speed. However, departure was almost independent of wind conditions on the ground and it seems that wind speed aloft is predicted by other means. A possible cue is the general weather situation. Of the 16 nights with a high proportion of departing robins, 11 were described by stable high-pressure conditions. During 2 nights, westerly fronts passed slowly and during 3 nights a centre of a low-pressure area with no wind was prevailing. Robins may be able to predict wind speed aloft by changes in air pressure, as evidenced in pigeons, *Columba livia* (Kreithen & Keeton 1974). It is a common observation that the number of passerine migrants aloft is high during high-pressure conditions (Hilgerloh 1981). Erni et al. (2002) found a good correlation between the component of the wind in migratory direction and 24-h change in air pressure. Since other cues such as cloud movements or infrasound might also be used by the birds, which is the most important factor is still unclear.

Rain has not yet been considered in theoretical models of bird migration, because the costs of flying in rain are difficult to quantify. We think that this cost may have several components, such as increased mortality, increased energy expenditure because of increased drag, turbulence and wet plumage, and increased frequency of misorientation. As our results show, rain has a large influence on the probability of take-off and thus on the spatial and temporal pattern of migration. Therefore, the occurrence of rain should be included in refinements of theoretical bird migration models.
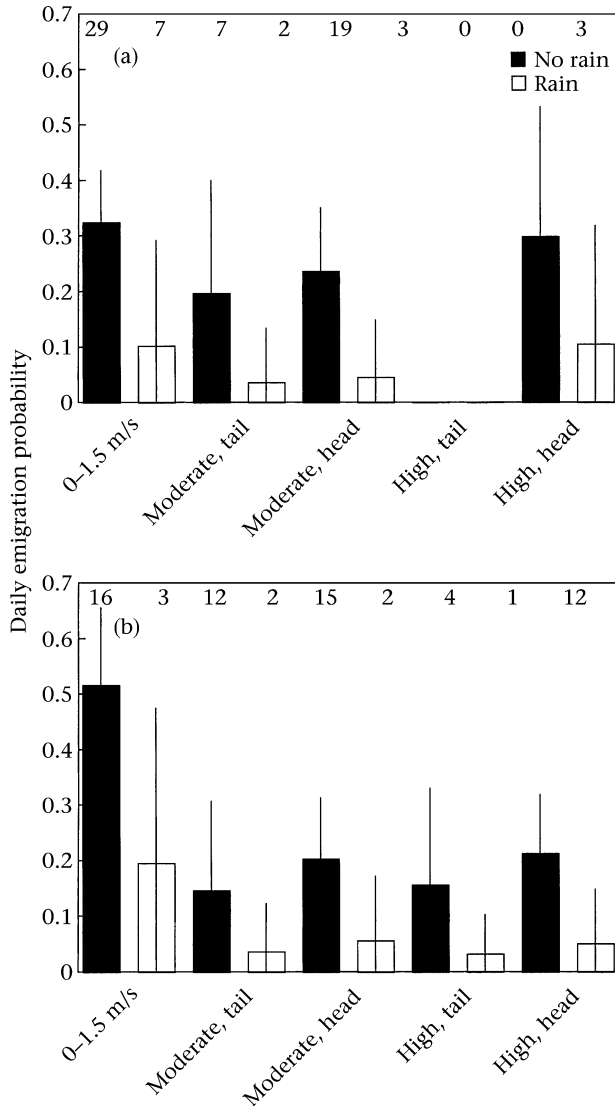
Figure 2. Model-averaged daily emigration probabilities of non-transient robins from the stopover site Portalban under different wind and rain conditions. (a) At ground level, (b) at 300 m above ground. Vertical lines indicate 95% confidence intervals. For the classification of the wind situations see Table 1. The classification of the nights according to rain was: 'no rain' (<2 mm during the night), 'rain' (≥2 mm during the night). The numbers above the columns indicate the sample size (number of nights).

Considering the results of the model selection (Table 3), we conclude that wind direction aloft was slightly more important than wind speed. However, in the model with wind direction there is in fact also a component of wind speed, because no wind direction was assigned to winds that were zero or weak (class zero). Therefore the model name 'direction' may be slightly misleading. The most pronounced feature of the wind direction model was that the emigration probability was highest during nights without wind and much lower during all the other nights without any marked effect of wind direction (Fig. 2b). This pattern remained the same when wind speeds between 1 and 1.5 m/s were allocated to the moderate instead of the 'no' wind speed category. Thus, we conclude that most

robins selected nights without wind for their departure and did not consider its direction.

This finding is somewhat surprising, because optimal migration theory predicts that birds should be sensitive to wind direction and speed (Liechti & Bruderer 1998; Weber et al. 1998). From radar studies, there is clear evidence that the number of migrants aloft is higher in tail than in head wind conditions (e.g. Richardson 1978, 1990; Erni et al. 2002). This indicates that birds actively select the most profitable air layer (Alerstam 1978; Cochran & Kjos 1985; Bruderer et al. 1995), or that birds break off or shorten their flights in head winds, or that birds predominantly depart in tail winds (but see Introduction). The results of studies focusing on direct observations of departing birds or on the estimation of the proportion of departing birds are controversial. While some studies did not find evidence of an influence of wind direction on departure behaviour (Rabøl & Hansen 1978; Pyle et al. 1993; Fransson 1998; this study), others did (Åkesson & Hedenström 2000; Dänhardt & Lindström 2001). Åkesson et al. (2002) found that wind direction was important only when wind speed was high (>4 m/s). At our study site most winds were weak. Therefore, it may not be surprising that robins did not consider wind direction at ground level for departure, because especially weak winds are strongly dependent on local topography and wind directions often change with altitude. In contrast, wind speed aloft is usually positively correlated with wind speed at ground level. Based on the available information on the ground (general weather situation, wind speed at ground level) it therefore appears possible that a robin can predict wind speed aloft but not its direction. Once the robin is aloft, it experiences wind direction and can choose the most profitable air layer (Alerstam 1978; Cochran & Kjos 1985; Bruderer et al. 1995), or may break off the flight when no profitable wind layer can be found. Whether robins consider wind direction when winds are stronger remains an open question.

Transients

It is well known that not all robins become territorial immediately after arrival (Titov 1999; Lajda 2001), but the proportion doing so has not yet been quantified. Here we estimated that almost three-quarters of all robins at the stopover site behaved as transients. They had definitively left the area that was covered by the mist nets. However, a transient, as defined here, need not have undertaken a long migratory flight during the nights before and after the capture day. Transients also include individuals that move through the area during the day, for example while feeding, but without becoming resident (Jenni 1996). The question whether and how many robins make migratory flights on two successive nights must be addressed by other methods (see e.g. Cochran & Kjos 1985); the occurrence of transients is a presumption but not a proof and the proportion of transients is an upper limit.

Perspectives

Wind and rain appear to be important factors determining the end of a stopover period. However, they are

Table 3. Model selection of the emigration and transience behaviour of robins at Portalban with respect to wind aloft (300 m above ground) and rain

Model	Deviance	No. of parameters	AICc	ΔAICc	AICc weight
$\varepsilon_{\text{rain+direction}}$, τ, p	751.6	6	1735.4	0.00	0.48
$\varepsilon_{\text{rain+speed}}$, τ, p	752.4	6	1736.3	0.84	0.32
$\varepsilon_{\text{rain*direction}}$, τ, p	751.1	8	1739.0	3.58	0.08
$\varepsilon_{\text{rain*speed}}$, τ, p	751.7	8	1739.6	4.16	0.06
$\varepsilon_{\text{direction}}$, τ, p	759.6	5	1741.4	6.01	0.02
$\varepsilon_{\text{rain}}$, τ, p	762.7	4	1742.5	7.07	0.01
$\varepsilon_{\text{speed}}$, τ, p	761.1	5	1742.9	7.47	0.01
$\varepsilon_{\text{speed*direction}}$, τ, p	758.5	7	1744.3	8.93	0.01
$\varepsilon_{\text{rain*direction*speed}}$, τ, p	750.1	12	1746.1	10.71	0.00
ε, τ, p	772.9	3	1750.7	15.24	0.00
ε_t, τ_t, p_t	515.7	216	2002.9	267.44	0.00

Of the 44 fitted models, only the best model, the nine best alternative models and the global model are shown. We indicate the deviance, given by MARK, the number of estimated parameters in the model, the small-sample-size-adjusted Akaike's Information Criterion (AICc), the difference in AICc between the best and the actual model (ΔAICc) and the AICc weights. ε denotes the emigration probability, τ the proportion of transients and p the recapture probability.

unlikely to be the only determinants for the departure decision. In addition, intrinsic factors such as the amount of fuel reserves, the fuel deposition rate, predation risk and expectations about the quality of further stopover sites are likely to be considered by migrants (reviewed by Jenni & Schaub 2003). Further studies should focus on a combined analysis that takes the most important factors into account (Schaub, in press). Such a study could determine the possible hierarchical structure of the decisions to take off (Able 1973).

Wind and rain as environmental factors synchronize the flights of most migrants. As a result, one can observe waves of arriving and of departing individuals. Although flying under favourable wind and rain conditions has the advantage that the flight range is maximized, the synchronization of individual behaviour may have drawbacks. Intraspecific competition at stopover places may become high, which in turn may reduce fuel deposition rate (Rappole & Warner 1976; Moore & Yong 1991). A high proportion of transients may be the result of this. Some robins find territories immediately after arrival whereas others have to search for a place to take on fuel. Individuals of the latter group may lose time because they cannot start feeding immediately on arrival. Apparently, the gain while flying under good weather conditions outweighs the drawbacks of delayed fuel deposition. We suggest that flying in good weather situations includes not only energetic advantages (cf. Liechti & Bruderer 1998; Weber et al. 1998), but also life history components such as reducing direct mortality during flight (Butler 2000).

Acknowledgments

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