

More than just refuelling: lengthy stopover and selection of departure weather by sandpipers prior to transoceanic and transcontinental flights

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The evolutionary and behavioural ecology of migratory birds has received much theoretical and empirical attention. We contribute to this field by contrasting the weather at departure and stopover durations of a long-distance migratory sandpiper prior to initiating lengthy transoceanic vs. transcontinental flights of potentially variable duration. Transoceanic flights provide few if any stopover options. We predicted that transoceanic migrants should therefore be more selective of energetically favourable weather at departure and have longer stopover durations prior to departing, using time as a surrogate for cumulative fuel acquisition, compared with transcontinental migrants. We used recent advances in capture–recapture modelling to quantify how weather conditions, length of stay, including estimated residence time prior to capture, and age class correlated with daily departure probabilities of Semipalmated Sandpipers *Calidris pusilla* at a coastal and an inland stopover site at comparable latitude. As expected, departure probabilities from both sites were higher with increasing strength of tailwinds, and the strength of this effect was larger for birds facing transoceanic vs. transcontinental flights. Cloud cover and temperature conditions at departure converged between sites at intermediate values from different background distributions. Stopover durations at both sites were substantially longer than needed if the birds were pursuing a simple tactic of arrive–fatten–leave at the stopover site. We infer that both sites provided high levels of both food and safety relative to other stages in the birds’ annual cycle, favouring lengthy stopovers and subsequent use of lengthy flights from both sites. Our study shows that recent advances of capture–recapture models can provide additional resolution to studies of the migration strategies of birds and refine our perspective on global patterns of migration routes and stopover decisions.

Keywords: barrier effect migration, Bayesian analysis, capture–recapture, stopover decisions.

Migratory birds make their biannual movements between breeding and non-breeding areas in a series of flights. Selection will favour flight strategies that include ‘hops, skips or jumps’ and variable stopover durations between flights (Schaub *et al.*

2008, Warnock 2010, Anderson *et al.* 2019) that optimize fitness (Alerstam & Lindström 1990). Thus, birds’ internal conditions and external situations when initiating flights should provide information about the nature of selection during the subsequent migratory flight. As an extreme example, Bar-tailed Godwits *Limosa lapponica baueri* departing on spectacular 6- to 9-day non-stop trans-Pacific Ocean flights from Alaska to New

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Zealand carry fuel stores approximately equal to their airframe body mass and do so when stronger tailwinds are available (Gill *et al.* 2009). Ecologically, sufficiently food-rich and safe staging sites must be available to permit selection favouring the evolution of such flights (Lank *et al.* 2003, Ydenberg *et al.* 2007). However, generally, theory shows that the costs of transporting excess fuel trades off against flight distance (Alerstam & Lindström 1990). Thus, most migration routes consist of multiple stopover sites where migrants prepare for successive stages of their journeys. Different migration strategies occur among species, among populations traversing different routes, between age classes and sexes, at different sites in a sequential journey, and even among individuals within these groups (McKinnon *et al.* 2014, Deppe *et al.* 2015, Hua *et al.* 2017, Vansteelant *et al.* 2017).

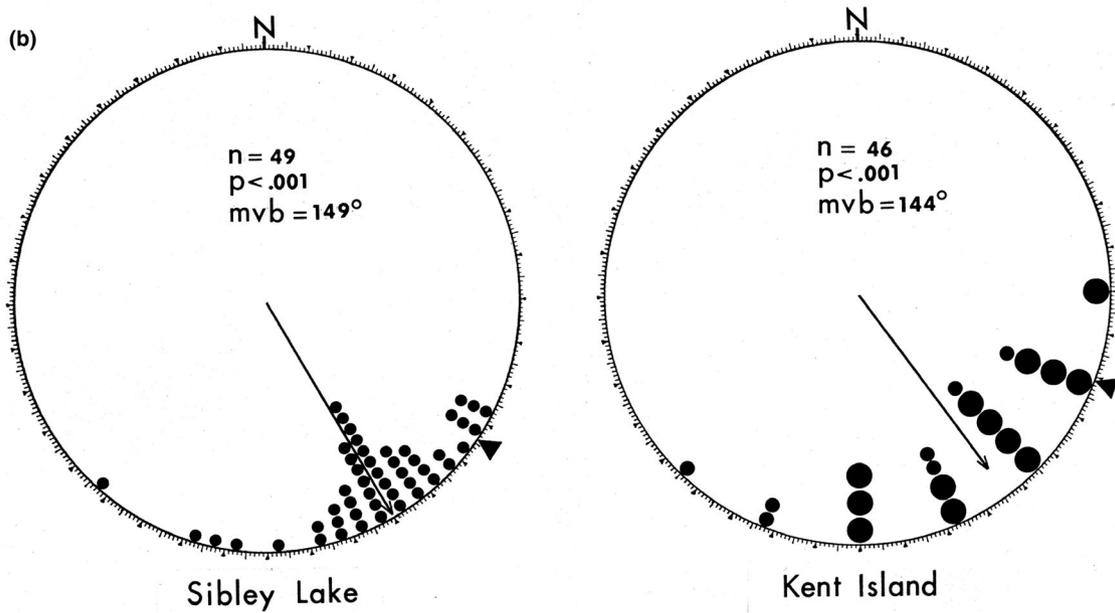
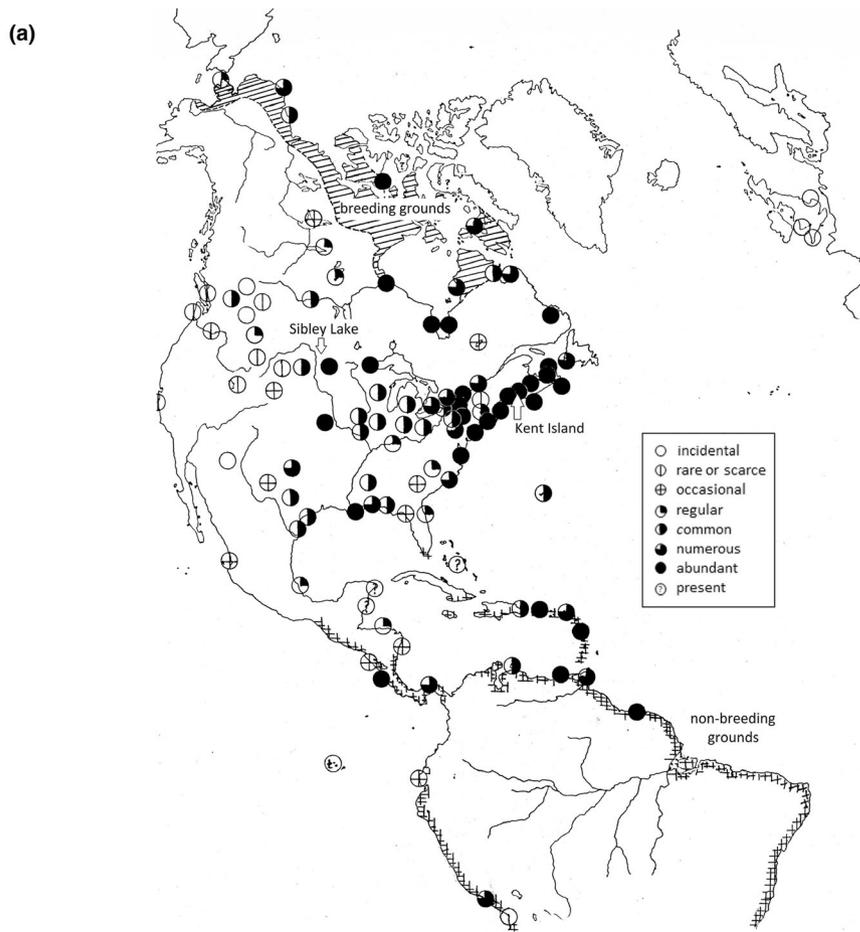
The decision whether to depart from a stopover site at a particular time is understood to be an evolved strategic decision rule conditioned proximately on internal state variables, principally potential food acquisition rate and current fuel stores, and environmental factors, especially weather conditions. Fuel stores can limit maximum flight ranges, and departure decisions are therefore often related to them (Schaub *et al.* 2008, Arizaga *et al.* 2011, Schmaljohann & Eikeenaar 2017). Assessing an individual's fuel and refuelling status usually requires its physical capture and recapture, but changes in state following a captured bird's release are in most cases unmeasured (but see e.g. Schmaljohann *et al.* 2013). Fuelling rates will vary largely as a function of food abundance, predation danger and seasonal time constraints of the individual (Ydenberg & Hope 2019). A potentially useful alternative behavioural metric that might index a bird's fuel status is the time the individual has spent at a stopover site, hereafter 'time since arrival' (TSA; Pledger *et al.* 2008, Roques *et al.* 2020). For migrants following a classic model of stopover behaviour of

'arrive–fatten–depart', TSA could provide a useful index of an individual's cumulative fuel acquisition and storage, and therefore be predictive of its likelihood of departing from a site.

With respect to weather, wind strength and direction are strong general predictors of migratory flight initiation (Richardson 1978, 1990, Ma *et al.* 2011, Gill *et al.* 2014). Stronger tailwinds enable birds to fly further and/or arrive at subsequent sites with larger energy stores, whereas stronger headwinds have the opposite effect and thus are expected to delay departures from stopover sites (Butler *et al.* 1997, Åkesson & Hedenström 2000, Weber & Hedenström 2000, Grönroos *et al.* 2012). In addition, departure decisions have evolved with respect to probable consequences further along the migration route and their potential carryover effects on fitness consequences later in the birds' annual cycle (Alerstam & Lindström 1990, Bednekoff & Houston 1994, Weber *et al.* 1998, Lank *et al.* 2003). For many northward migrants, intraspecific competition for nesting sites and/or mates means that fitness declines with arrival dates; southward migrants are generally thought to be under less time pressure (Yohannes *et al.* 2009) but may still face deadlines in subsequent parts of their annual cycle, including the timing of post-migratory flight feather moult, when birds are more vulnerable to depredation (Lank *et al.* 2003, Ydenberg & Hope 2019). These broader strategic considerations may be invoked to account for otherwise enigmatic observations of shorter or longer times spent at migration stopovers.

In this study, we compared and contrasted the stopover departure decisions of southward migrating Semipalmated Sandpipers *Calidris pusilla* prior to initiating flights to non-breeding sites in South America via either a transoceanic flight from a coastal stopover site or an overland flight from an inland site (Fig. 1; Lank 1979, 1983, Gratto-Trevor *et al.* 2012, Brown *et al.* 2017). As a successful

Figure 1. (a) Breeding (diagonal hatching) and non-breeding grounds (cross-hatching) of Semipalmated Sandpipers, study site locations, and relative abundances of migrant Semipalmated Sandpipers reported during southward migration. Abundance classes at migration sites were compiled from regional accounts in literature prior to 1980. (b) The directional distribution of presumed migratory departures of Semipalmated Sandpipers from Sibley Lake and Kent Island. Flocks leaving each study site were followed optically until they disappeared from view (details in Lank 1983, 1989). Vanishing bearings were assigned to one of 16 compass points at Kent Island or to the nearest compass degree at Sibley Lake. Mean vector bearings (mvp) and statistical significance (*P*) were calculated using Baschelet (1981). The black triangle on the outside of each circle shows the mean direction towards which surface winds were blowing at the time of the departures. Both figures were adapted from Lank (1983), which provides references to the migration site accounts used in (a).



transoceanic route requires a lengthy flight, we expected *a priori* that migrants facing a transoceanic flight should (1) have stopover durations long enough to obtain large fuel stores and (2) be highly selective about leaving in wind conditions that would aid flight in the migratory direction. But what would inland birds do? As birds leaving the inland site have shorter flight range stopover options, they might leave after shorter stopover durations with lower fuel stores and be somewhat less selective about the weather. Alerstam (2001) proposed that 'barrier effects' such as oceans should increase overall energetic cost and danger relative to routes with stopover availabilities. In this case, all else being equal, inland birds should adopt a lower energy and safer strategy, departing after shorter stopovers and possibly being less selective about departure weather.

Alternatively, despite the potential availability of additional stopover sites *en route*, making a lengthy flight might be the selected strategy from the perspective of the full annual cycle, contingent on the relative refuelling rates and safety of alternative sites. In the context of classical optimal migration theory (Alerstam & Lindström 1990), we ask whether birds following the transcontinental route behave more as energy or time minimizers, compared with coastal birds. Energy minimizers avoid the energetic cost of carrying excess fuel by departing with lighter fuel loads after shorter stopover durations. Time minimizers achieve faster overall migration speeds by carrying heavier fuel loads, despite higher energy requirements overall. Our interpretation of the patterns seen also considers trade-offs with predation danger at stopover sites, a third dimension that interacts with and can alter predictions from simpler time vs. energy trade-offs (e.g. Ydenberg & Hope 2019 and references therein).

Adult and juvenile Sandpipers were captured, marked and resighted at a coastal and an inland migratory stopover location. The age classes differ in that adults migrate about a month ahead of juveniles and will undergo a post-migratory wing moult, whereas juveniles will not. Previous analyses of these data using simpler recapture models showed that birds remained at both stopover sites for lengthy periods of time, decreasing at the end of the season (Lank 1983, Hope *et al.*, 2011). Here, we estimated an individual's TSA using a capture–recapture analytical approach that incorporates probabilities of entry prior to first capture

and marking (Pledger *et al.* 2008, Lyons *et al.* 2016, Roques *et al.* 2020). TSA was used as a potential index of cumulative fuel storage, under the classic assumption that stopover activity consists of arrival, fuel storage at a given rate, and departure (Schmaljohann & Eikenaar 2017, Roques *et al.* 2020). Daily probabilities of leaving were then modelled with respect to TSA and daily weather conditions. We interpret the stopover and departure patterns found in the context of the flight options available and apparently utilized at each site, and in the context of the migrants' annual cycle.

METHODS

Study system

The study system consisted of one coastal and one inland migratory stopover area for Semipalmated Sandpipers at comparable latitudes during southward migration (Fig. 1; Lank 1983). The coastal site was Kent Island, New Brunswick, Canada (44°35'N, 60°27'W), in the mouth of the strongly tidal Bay of Fundy. The inland site was the area around Sibley Lake, North Dakota, USA (46°57'N, 99°43'W), which includes a mosaic of shallow seasonal saline lakes. Both sites are intermediate stopovers situated between Arctic breeding areas and South American wintering areas. Based on morphometrics, banding returns and subsequent tracking studies, birds at Kent Island probably originated at breeding grounds in the central and eastern Canadian Arctic, may have previously staged along the shoreline of James Bay, and were preparing for a transoceanic flight to northeastern South America (Harrington & Morrison 1979, Lank 1979, 1983, Richardson 1979, Morrison 1984, Gratto-Trevor *et al.* 2012, Brown *et al.* 2017). Those at Sibley Lake were probably arriving from breeding grounds in Alaska or the western Canadian Arctic, and departed heading towards the Caribbean and northcentral or northwestern South America (Richardson & Gunn 1971, Lank 1979, 1983, Gratto-Trevor *et al.* 2012). Adults pass through both areas in July and early August, and moult flight feathers shortly after arrival on non-breeding grounds, whereas juveniles arrive throughout August and into early September (Lank 1983, Lank *et al.* 2003). At both sites, birds acquire substantial fuel for their next flight. A lean Semipalmated Sandpiper weighs

c. 20–22 g, but many individuals at both sites nearly double this mass prior to departing on the next leg of their journey (Lank 1983, Dunn *et al.* 1988).

Kent Island was monitored from 11 July to 23 September 1977 and Sibley Lake from 13 July to 27 September 1978. At each site, Semipalmated Sandpipers were captured almost daily using mist-nets and/or walk-in traps at Sibley Lake, individually marked with conspicuous individually coded wing-tags (Lank 1979) and released. Marked birds were subsequently recaptured or resighted during daily surveys of the local areas. Kent Island resightings were made exclusively on the intertidal mudflats surrounding the island; Sibley Lake resightings occurred along the shore of saline Sibley Lake and adjacent wetlands. Further details on capture, marking and resighting effort are given in Lank (1979, 1983).

Birds initially landing at a site may not remain present to rest and refuel (i.e. actual 'stopover'; Warnock, 2010). Inclusion of 'transients' will usually bias low estimates of 'migratory' emigration rates (Bächler & Schaub 2007, Schaub *et al.* 2008). At Kent Island, 26% of birds marked were never re-encountered, nor were 36% of those marked at Sibley Lake (Lank 1983). Initial analyses of this dataset in a methodological paper showed that daily survivorship estimates distinguishing first vs. later captures of individuals provided better model fits than ignoring a possible capture/transient effect (Brownie & Robson 1983). Local population size may also have affected transience probability (Lank 1983). As our interest was on the effects of meteorology and length of stay on departure decisions, we analysed only capture histories of individuals that were subsequently re-encountered. The numbers of capture histories included were: 928 at Kent Island, with 759 adults and 169 juveniles, resighted 4.5 times on average; and 1073 at Sibley Lake, with 520 adults and 553 juveniles, resighted 5.3 times on average.

Weather variables

To describe how meteorological conditions relate to the departure decisions of Sandpipers, we chose four weather covariates, measured daily at sunset, when most migratory departures occurred (Richardson & Gunn 1971, Richardson 1978, Lank 1989). Based on earlier analyses of this dataset and other information on the timing of migratory

departures (Lank 1983, 1989), our metric for wind was the 24-h trend in the strength of the tailwind–headwind component of wind direction (hereafter, 'wind'), which was the wind metric most predictive of departure decision. Radar studies and direct observations show that at that season, shorebird migration in both regions occurs in along a northwest to southeast axis (Fig. 1; Richardson & Gunn 1971, Lank 1979, 1983, Richardson 1979), which we therefore defined as the expected migratory direction. The wind effect value at sunset was calculated as follows:

$$\text{Wind} = V \times \cos(\alpha - 45)$$

where V is wind speed (in m/s) and α the direction from where the wind comes, in degrees ($^{\circ}$). Subtracting 45° from the wind direction creates a vector with positive values for tailwinds blowing from the northwest towards the southeast, the migratory direction. The 24-h trend in wind was calculated as the vector value each day minus that of the previous day. Thus, positive values indicated that tailwinds were getting stronger, and negative values that they were becoming weaker. Additional meteorological variables modelled were: temperature ($^{\circ}\text{C}$), percentage cloud cover and relative humidity, measured at sunset.

Collinearity between weather covariates can lead to erroneous conclusions about the effect of particular focal weather covariates. We tested for collinearity between the weather covariates and found that some significantly correlated, but not with high correlation coefficients (Lank 1983). Nonetheless, to characterize the weather patterns with respect to synoptically covarying meteorological conditions, we ran a principal component analysis (PCA) on the four meteorological variables pooled across both sites, which clearly distinguished two axes explaining 80% of the variation (Fig. 2, see Table S3 of Appendix S1 for details). We modelled departure probability with respect to both individual variables and the first two PCs.

Statistical analyses of mark–recapture data

We used a Bayesian state-space formulation of an open population capture–recapture model that incorporates entry probabilities to a sampling area (Pledger *et al.* 2008, Lyons *et al.* 2016). This

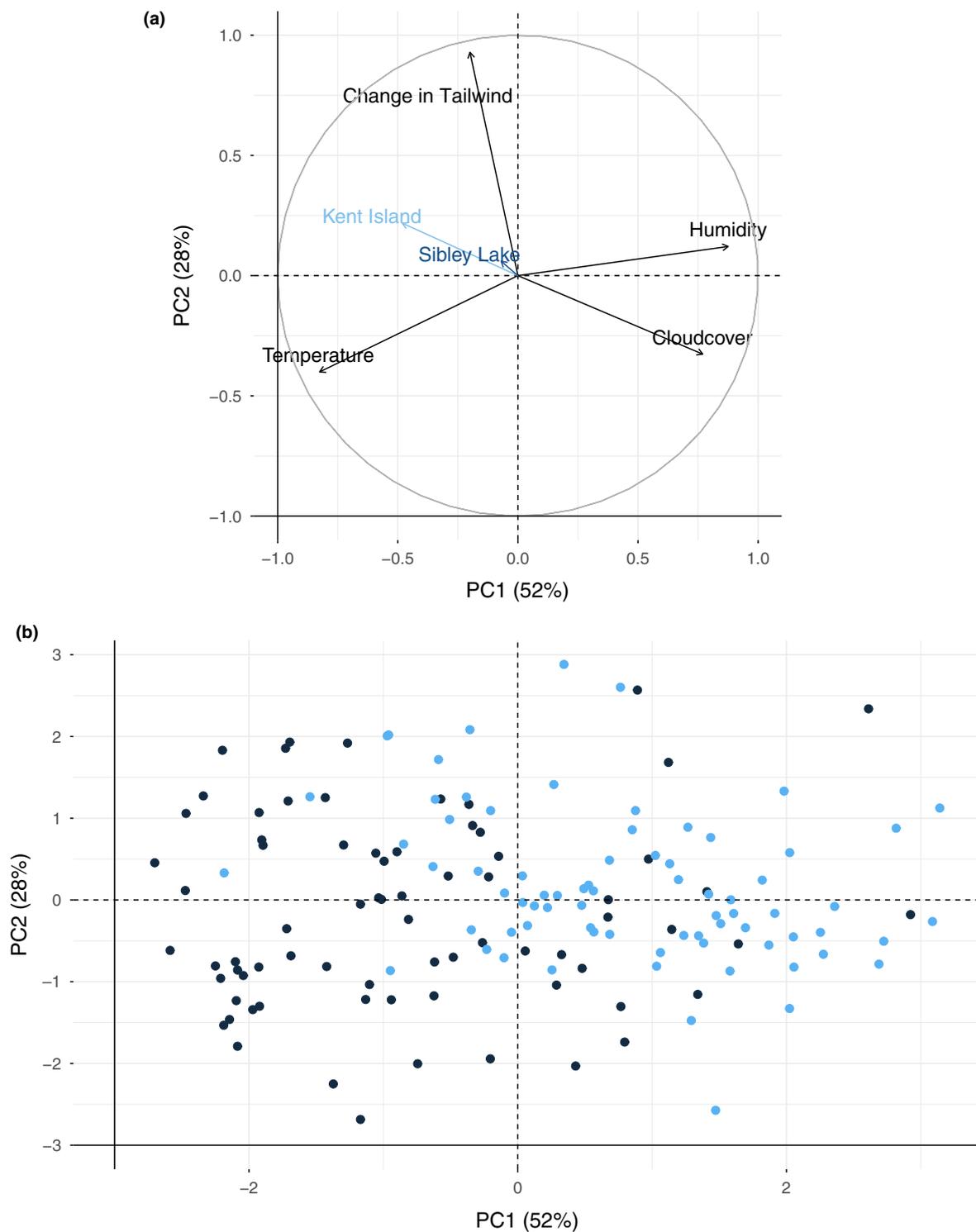


Figure 2. Principal component analysis of the four weather variables. (a) Length and direction of vectors shows the relative weightings of the four weather variables along the two first axes of the PC (black arrows). PC1 largely captures covariation in temperature, humidity and cloud cover, and PC2 primarily captures the independent variation in wind direction. Vectors representing the conditions favouring departure of Semipalmated Sandpipers are plotted for Kent Island and Sibley Lake with light and dark blue arrows, respectively (Table 2). (b) Scatterplot of daily local weather observations with respect to PC1 and PC2 scores (light blue: Kent Island, dark blue: Sibley Lake).

formulation allows modelling of both birds' arrival at and departure from the stopover site. The parameters of the model are:

ϕ_t Probability of departure from sampling area between the sampling occasions t and $t + 1$

η_t Probability of arriving at the stopover area at sampling occasion t given that the individual was not there before

p_t Probability of physical capture at the sampling occasion t given the individual has arrived but not yet departed

$psight_t$ Probability of visual recapture (encounter) at the sampling occasion t given the individual has been captured and marked (wing-tagged) but has not yet departed

This formulation contains one submodel for the state process (states are 'not yet arrived', 'present in the stopover site', 'departed') and one submodel for the observations encoded in the individual capture histories. The observation process is conditional on the current state. For each individual capture history h_i , there is a true state history accounted for by the vector z_i . This vector of binary state variables describes whether an individual i is present, $z_{i,t} = 1$, or not, $z_{i,t} = 0$, in the stopover area on day t . In our study, individuals can be physically captured or simply visually resighted, and thus we separated the physical capture probability from the resighting probability, noted respectively as p and $psight$. Birds can also be captured and resighted during the same sampling occasion. To deal with this, we used a multi-state formulation of the observation process. Consequently, in an individual capture history, we distinguished four potential events (Pradel 2005): 0: not seen, 1: physically captured, 2: resighted, 3: physically captured and resighted during the same occasion. This resulted in the following observation matrix $\theta_{i,t}$ that applies to an individual present:

$$\begin{bmatrix} 1 - p_t - psight_t + (p_t \times psight_t) \\ p_t \times (1 - psight_t) \\ psight_t \times (1 - p_t) \\ p_t \times psight_t \end{bmatrix}$$

For an individual i that has not yet entered the stopover area or has left it ($z_{i,t} = 0$), $h_{i,t} = 0$ with a probability equal to 1. This formulation allows us

to estimate the TSA for each individual. This covariate is a non-observable variable that can be computed with the sum of the true states $z_{i,t}$ up to time t , and represents the time individual i was present at time t in the stopover area:

$$TSA_{i,t} = \sum_{s=1}^{t-1} z_{i,s} \quad (1)$$

The state vector z_i also allows us to use a new formulation of the stopover duration described by Lyons *et al.* (2016). We computed the mean stopover duration (in days) as follows:

$$SOD = \frac{\sum_i \sum_t z_{i,t}}{n} \quad (2)$$

where n is the number of individuals and $z_{i,t}$ the true state variable (which defines whether an individual i was present or not at the stopover area on day t). Juvenile individuals arrive later in the season at the stopover area. Thus, the entry probability (η_t) was modelled as age- and time-dependent.

The probability of departure from the site between 2 days was written as a function of all previously defined weather covariates and TSA, with a slope to be estimated for each covariate. When the slope for an effect had a 95% confidence interval that did not include 0, the effect was considered statistically significant (Kéry & Schaub 2011).

Using the logit link, the probability of departure from the stopover area between t and $t + 1$ was formulated as:

$$\text{Logit}(\phi_t) = a + \beta_{\text{age}} \times TSA_t + \beta \times Cov_t \quad (3)$$

where a is the intercept, β_{age} is the age-specific TSA effect to estimate, Cov_t is the weather covariate and β is the associated slope to estimate.

To incorporate potential effects of meteorological variables, we first ran one model for each site with the two PC axes as covariates as follows:

$$\text{Logit}(\phi_t) = a + \beta_{\text{age}} \times TSA_t + \beta_1 \times PC1_t + \beta_2 \times PC2_t \quad (4)$$

Then, to test effects of each weather covariate, we ran one model for each weather covariate for each site according to Equation 3 to avoid a collinearity problem (Harrison *et al.* 2018). This

Table 1. Mean and credible intervals (CI) of the resighting probability ($psight$), capture probability (p) and stopover duration by age of southward migrating Semipalmated Sandpipers estimated from the models following Equation 4.

	Kent Island		Sibley Lake	
	Mean	CI	Mean	CI
Resighting probability ($psight$)	0.14	0.02, 0.30	0.22	0.11, 0.39
Capture probability (p)	0.03	0.01, 0.08	0.04	0.01, 0.10
Mean stopover duration (days)	42.07	21.65, 60.21	33.67	12.21, 55.52
Adult stopover duration (days)	40.04	19.30, 53.60	32.76	11.03, 59.32
Juvenile stopover duration (days)	51.19	37.46, 63.54	34.52	12.13, 50.44

Estimates from Kent Island were derived from 4178 encounters in capture histories from 759 adults and 169 juveniles; those from Sibley Lake were derived from 5613 encounters in capture histories from 520 adults and 553 juveniles.

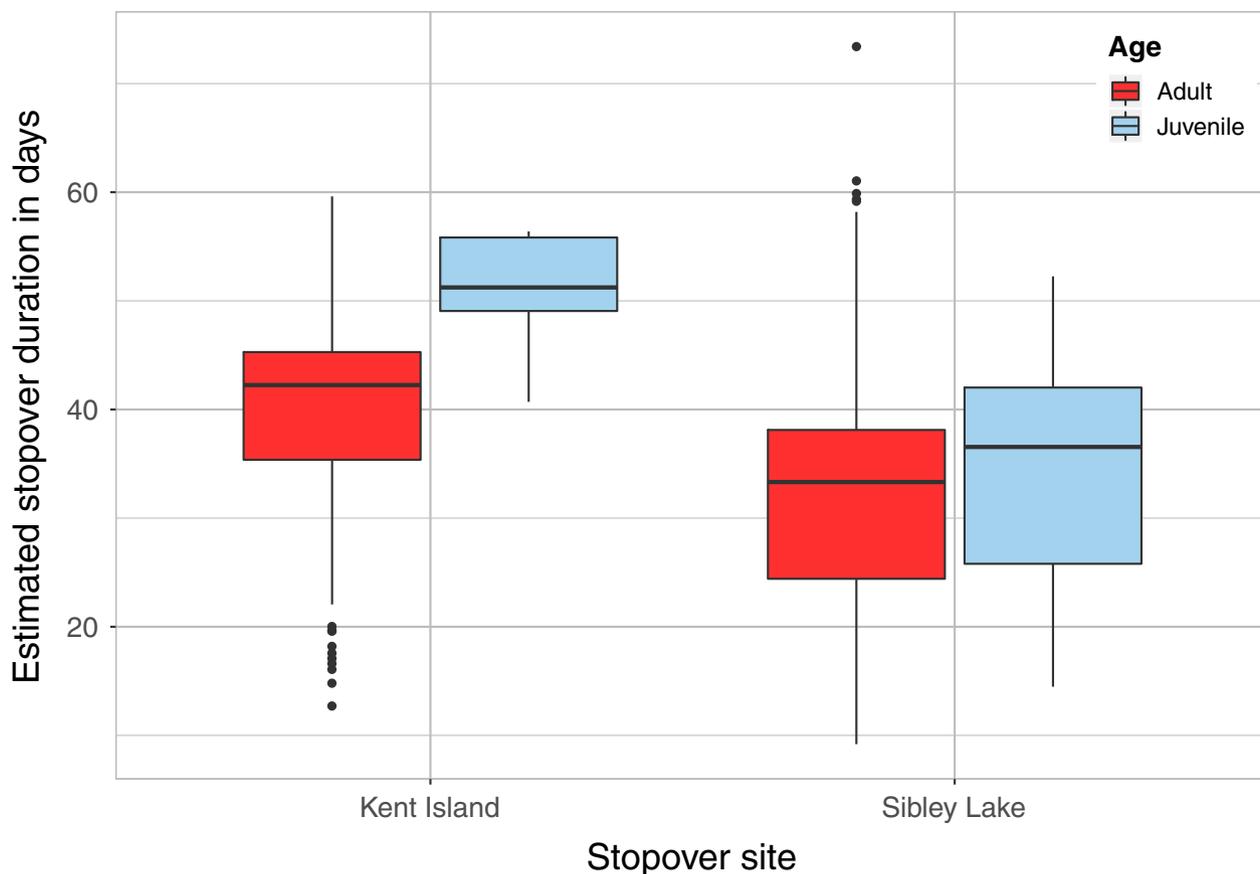
resulted in eight different slope values for each weather covariate for each site (Table 2).

Analyses were performed with JAGS (Hornik *et al.* 2003) using R version 3.6.1 (R Development Core Team 2013). Models were run with 120 000 iterations with non-informative priors, and we checked chain mixing and the convergence (Kéry & Schaub 2011). The JAGS code is available in Appendix S2.

RESULTS

Stopover duration, time since arrival and recapture probability

Mean stopover duration estimates were 9–10 days longer at Kent Island than at Sibley Lake, 42.0 vs. 33.7 days, respectively, but the credible intervals are wide for both estimates (Table 1, Fig. 3). At

**Figure 3.** Estimated stopover duration by age classes at Kent Island and Sibley Lake. Adults: red, juveniles: blue. Box plots show median (thick line) and first- and third-quartile boundaries. Lines extend to 1.5 times the box boundaries. Black dots show outliers.

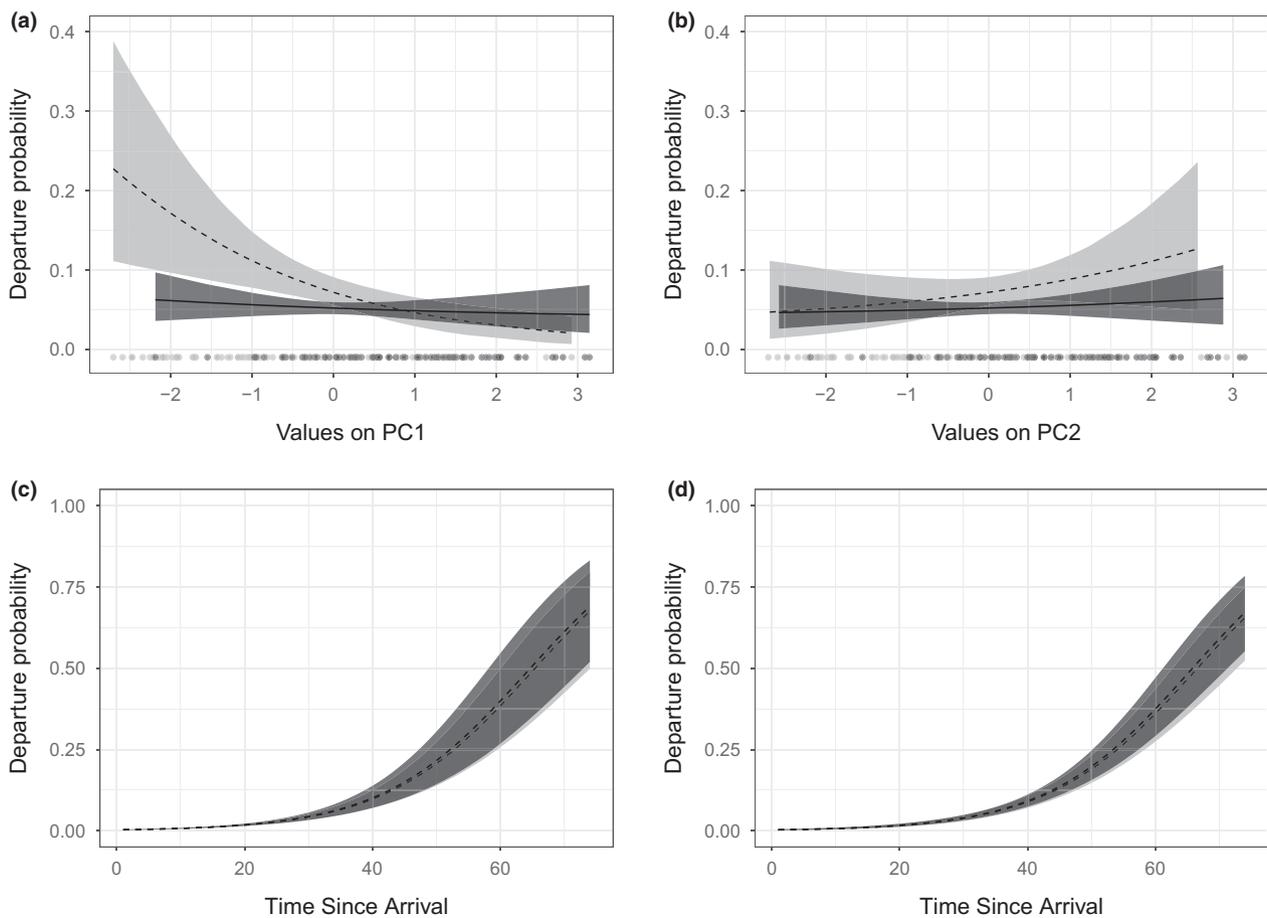


Figure 4. Predicted effects of (a) the first and (b) the second PC axes on the departure probability of Semipalmated Sandpipers at both sites, given birds are at their mean stopover duration (Kent Island: light grey, Sibley Lake: dark grey). (a,b) The light and dark grey points show the values encountered respectively at Kent Island and Sibley Lake. (c,d) The TSA on departure probability given weather values are at their mean values at both sites (c: Kent Island, d: Sibley Lake) for both ages (dark grey: adults; light grey: juveniles). For all figures the dashed lines represent the mean values and the grey areas represent the 95% credible intervals.

Kent Island, the stopover durations of adults appear shorter than those of juveniles, 40.0 vs. 51.2 days, respectively, again with large credible intervals, but quite similar to those at Sibley Lake, which averaged 32.8 vs. 34.5 days (Table 1, Fig. 3).

The probability of departure increased for all classes of individuals as their residency times increased. The coefficients of the TSA effects were significant and estimated with a high precision at both sites (see the 95% credible interval (CI), Table 2). The strongest TSA estimated effect was for adults at Kent Island, with a 0.13 estimated slope on the logit scale. Kent Island juveniles had estimates of 0.09, close to values at Sibley Lake of 0.08 for adults and 0.09 for juveniles, with overlapping 95% CIs (Table 2). Controlling for

weather covariates, departure probabilities remained below *c.* 0.1 for over 30 days since initial arrival (Fig. 4c,d).

The physical recapture probability p was similar between the two sites (Kent Island: 0.03, Sibley Lake: 0.04), but the resighting probability $psight$ was lower at Kent Island than at Sibley Lake (0.14 and 0.22, respectively, Table 1).

Weather covariate effects

The first two principal component dimensions accounted for 52 and 29%, respectively, of the total variances of the four meteorological variables (Table S3 of Appendix S1). PC1 captured covariation in temperature, humidity and cloud cover (Fig. 2a, Table S3 of Appendix S1), patterns of

Table 2. Mean, standard deviation (sd) and credible intervals (CI) of the estimated effects of covariates on departure probability.

	Kent Island			Sibley Lake		
	Mean	sd	CI	Mean	sd	CI
Intercept	-8.85	0.55	-9.17, -7.94	-9.44	0.68	-10.87, -8.20
(β_{1adult}) TSA	0.13	0.01	0.11, 0.14	0.08	0.01	0.07, 0.10
($\beta_{1juvenile}$) TSA	0.09	0.01	0.06, 0.10	0.09	0.01	0.07, 0.10
PCA Axis 1	-0.48	0.15	-0.80, -0.20	-0.08	0.12	-0.30, 0.15
PCA Axis 2	0.22	0.19	-0.16, 0.58	0.06	0.11	-0.18, 0.26
(β_2) Wind	0.77	0.13	0.52, 1.01	0.39	0.08	0.23, 0.54
(β_3) Temperature	0.84	0.16	0.52, 1.15	-0.19	0.05	-0.30, -0.09
(β_4) Humidity	-0.58	0.18	-0.95, -0.23	-1.06	0.17	-1.43, -0.73
(β_5) Cloud cover	-0.33	0.16	-0.66, -0.02	0.42	0.11	0.20, 0.65

The first part of the table shows the results from Equation 4 with TSA (β_{1age}) and PCA axes covariates. The second part of the table shows the results from Equation 3, which included TSA (β_{1age}) and coefficients for weather covariates effects (β_2 , β_3 , β_4 , β_5). Estimated values of intercept and TSA effects for each univariate models are not shown in this table as they are mostly similar to those of Equation 4.

which clearly differed between sites (Fig. 2b, Table S1 of Appendix S1). Mean values of PC1 were -0.8 ± 1.3 at Kent Island and 0.8 ± 1.1 at Sibley Lake (Table S3 of Appendix S1). Kent Island had the cooler, more humid and cloudier conditions expected from a marine site, contrasting with the warmer and drier inland conditions at Sibley Lake (Fig. 2b). PC2 largely captured the independent variation in 24-h wind trend (Fig. 2a), which ranged similarly between favourable and unfavourable conditions at both sites (Fig. 2b). Mean values of PC2 were -0.2 ± 1.2 and 0.2 ± 0.9 at Kent Island and Sibley Lake, respectively.

In univariate models of each weather covariate at each site, the coefficient for 24-h trend in headwind effect was positive at both sites (Table 2). Strengthening winds from the northwest, defined as tailwinds, increased the probability of leaving the stopover area between t and $t + 1$. The magnitude of the effect was 0.77 at Kent Island, larger than 0.39 at Sibley Lake, with marginally overlapping 95% CIs. Each of the other weather covariates tested also had significant univariate relationships with the probability of departing from the stopover site. At both sites, lower humidity was associated with higher departure probabilities. However, the relationships with temperature and cloud cover differed in direction between sites. At Kent Island, where the weather was generally cooler and cloudier (Fig. 2b), birds were more likely to leave under warmer and clearer skies. In contrast, at Sibley Lake, where warmer and clearer

conditions prevailed, birds were more likely to leave in colder and cloudier local weather. These opposite trends produce some convergence of temperature and cloud cover conditions at intermediate values from both sites.

PC1, primarily capturing variation in temperature, humidity and cloud cover (Fig. 1a), had a significant negative effect on departure probability at Kent Island but not at Sibley Lake (Table 2, Fig. 4a). Negative values on PC1 represent strengthening tailwinds, as the correlation between PC1 and wind is 0.20 (Table S3 of Appendix S1). The effect of PC1 appears larger at Kent Island than at Sibley Lake; the credible intervals overlap, but the CI does not overlap zero at Kent Island. PC2, associated strongly with the independent variation in 24-h wind (Figs 2 and 4b, Table S3 of Appendix S1), had no significant effect at either site, and thus most of the variation responsible for the univariate relationship with wind must have been represented by covariation in PC1. The environmental conditions correlating with departure are those that maximize the component $\beta_1*PC1 + \beta_2*PC2$, corresponding to the direction (β_1 , β_2) on plane 1,2 of the PCA. The intensity of their effects are reflected by the length of the site-specific vectors shown in Fig. 2(a) for each site.

DISCUSSION

We estimated the stopover durations, effects of TSA and meteorological conditions on the daily

departure probabilities of Semipalmated Sandpipers from stopover sites during southeastward migratory journeys. Birds at Kent Island, New Brunswick, were preparing for a lengthy transoceanic flight, whereas those at Sibley Lake, North Dakota, were preparing for overland flights of unknown lengths. We proposed that contrasting the stopover durations and departure behaviour of migrants from the sites would provide information about the migratory strategies of comparable Sandpiper populations when the migratory routes did or did not provide access to intermediate downstream stopover sites. At both sites, birds departed with favourable winds and had lengthy stopover durations for most of the season, suggesting preparation for lengthy migratory flights even when intermediate sites were available. However, birds at both sites stayed substantially longer than necessary simply to refuel and continue migratory journeys, suggesting that in the context of the birds' annual cycles, being at each of these locations at those seasons had high fitness value. There were, however, quantitative differences between migrants' behaviour at the two sites. Birds at Kent Island had somewhat greater selectivity with respect to wind conditions at departure, and adults at that site had longer stays than juveniles or birds at Sibley Island. Below, we interpret the patterns found as adjustment of migratory strategy related to the differences in the downstream stopover options of each migratory route, within the context of the birds' annual cycles.

Weather effects

At both sites, birds had higher probabilities of initiating migratory flight after tailwinds had been strengthening for the past 24 h. Departure with stronger tailwinds is expected on first principles and from previous studies (Table 1; Richardson & Gunn 1971, Richardson 1978, 1979, 1990, Alerstam 1990, Weber *et al.* 1998, Åkesson & Hedenström 2000, Loonstra *et al.* 2019). Surface winds assisting southeastwardly flight were blowing when migratory departures were directly observed (Fig. 1b). From a synoptic weather point of view, as expected, Sandpipers from both sites thus do depart on days with tailwinds, reducing the cost of flight per kilometre travelled (Tsvey *et al.* 2007, Arizaga *et al.* 2011, Ma *et al.* 2011, Grönroos *et al.* 2012, Dossman *et al.* 2016).

We predicted that birds facing transoceanic flight would show greater selectivity in departure conditions than those facing transcontinental flight and, indeed, the effect size of change in headwind component was stronger at Kent Island than at Sibley Lake. Kent Island birds also showed stronger relationships with the integrated measures of meteorological covariation compared with the birds at Sibley Lake. Although the background weather regimens differed with respect to temperature, cloud cover and humidity, they were similarly variable in terms of the general distributions of favourable winds (Fig. 2). In the present study, favourable weather for migration occurred at fairly regular 4- to 5-day intervals at both sites throughout the migration season, with regular passage of cyclonic and anticyclonic weather systems, and the patterns in the specific years studied were typical of longer term weather regimens (Lank 1983). Thus, systematic differences in meteorological migration opportunities do not account for differences in selectivity between sites. Greater selectivity for wind assistance can trade-off against speed of migration; McCabe *et al.* (2018) argued that, in general, time minimizers might be less selective because of fitness decreases associated with waiting for favourable weather conditions. In our cases, however, the lengthy stopover durations shown by both of our migratory populations indicate that neither were time minimizers during much of the season (see below) and both populations selected tailwinds for departure.

Despite lower values of humidity in general at Sibley Lake (Fig. 2), the relationship between relative humidity and departure probability was negative at both sites. This is sensible in a synoptic sense, as northwesterly winds at both sites would probably bring in drier air. This effect may reflect a direct effect of rain, but also the fact that more humid air increases the cost of flight and decreases visibility (Åkesson *et al.* 2001). Similar effects have been found in other situations (Åkesson *et al.* 2001, Deppe *et al.* 2015, Roques *et al.* 2020), such as passerines selecting nights with lower humidity to cross the Gulf of Mexico (Deppe *et al.* 2015).

The direction of temperature and cloud cover effects were opposite at the two sites. Sandpipers were more likely to leave Kent Island with higher than average temperatures and less cloud cover for that site, whereas those at Sibley Lake left with lower than average temperatures and greater cloud

cover for the site. As Kent Island was generally cooler and cloudier than Sibley Lake (Fig. 2), this pattern produces a convergence of departure conditions between sites under intermediate conditions of both variables. Greater cloud cover decreases the visibility of the sky, and as migratory birds use the stars for orientation (Wiltschko & Wiltschko 1988), including Semipalmated Sandpipers (Lank 1973), dense cloud cover could present initial navigational difficulties. Low cloud cover in particular may have a strong negative impact on the probability of departing from a stopover area, whereas high-altitude clouds will have little effect (Martin 1990, Koistinen 2000).

PC1, which was strongly and approximately evenly weighted by humidity, cloud cover and temperature, captured most of the covariation in departure probability from both stopover sites. Despite being heavily weighted by tailwind trend, PC2 was not strongly related to departure probability, although it may have been more so at Kent Island than at Sibley Lake. This means that most of the univariate relationship between departure probability and wind trend had been captured by PC1 through covariation between wind and the other variables (Table S2 of Appendix S1).

Modelling considerations

The stopover durations estimated in this study incorporate estimates of entry probabilities to a sampling area prior to first capture. They are thus longer than the minimum lengths of stay (marking to last sighting) presented by Lank (1983), the conditional residence times estimated from Lank's data by Hope *et al.* (2011), and the minimum lengths of stay found in a separate study on the coast of Maine (Dunn *et al.* 1988). Including time prior to capture should make the values estimated in the current study more realistic.

Lank (1983, unpublished analyses) tested for relationships between daily emigration rates and prevailing daily weather conditions using emigration rates estimated with a simpler capture–recapture model (Brownie & Robson 1983). The emigration rate–meteorology relationships in that study were weaker than those shown here (Table 2), suggesting that the approach taken in the present study provided more useful estimates. Lank (1983) speculated that permanent local dispersal may have partially obscured relationships between the emigration rates and actual migratory

departure probability, which also applies to our analysis (Bächler & Schaub 2007, Schmaljohann & Eikenaar 2017). Our study provided some perspective on the local dispersal issue by distinguishing between physical and visual recapture events in the modelling process. The sites had similar physical recapture rates but the visual re-encounter rate was lower at Kent Island than at Sibley Lake (Table 2). Regular surveys at Kent Island were restricted to birds visible from the island itself; small numbers of *ad hoc* sightings of wing-tagged birds by local bird watchers at nearby sites were not included in the capture history. In contrast, regular surveys were made at additional waterbodies near Sibley Lake when these sites were used by birds as a function of changing rainfall conditions. The higher visual re-encounter rate at Sibley Lake probably reflects the observers' greater ability to track local movements of birds at that stopover site. Separate parameterization of physical and visual re-encounters thus added precision and highlighted sampling patterns between sites and data sources. We conclude from this that the potential effects of local dispersal would have weakened relationships with meteorological variables more at Kent Island than at Sibley Lake. If so, our conclusion of greater selectivity in departure weather at Kent Island is conservative.

Lengthy stopover durations

As argued in the Introduction, preparing for a non-stop transoceanic flight rather than an overland flight should favour the acquisition of larger fuel stores, as the latter provides opportunities for shorter flights from the stopover sites. Consistent with our prediction, estimated stopover durations were *c.* 10–15 days longer prior to transoceanic relative to transcontinental flights for adults and juveniles, respectively (Table 1, Fig. 3). Furthermore, the samples of birds captured and tagged at Kent Island were on average 3.4 g heavier than those caught at Sibley Lake (33.0 vs. 29.6 g, Lank 1983).

A motivation for this study was in part that stopover duration might be a useful index of cumulative refuelling that could be estimated without recapturing marked individuals, assuming a classical model of stopover behaviour as 'arrive–fatten–depart'. As expected under this model, the effects of estimated TSA were positive and predictive of departure probabilities. Rapid refuelling has

often been found at stopover sites and the TSA approach used here should work best in analyses of such situations, namely for time-minimizing migrants whose stopover behaviour fits (Alerstam & Lindström 1990).

Despite the utility of TSA as a predictor of departures in our study, the stopover durations of most Sandpipers at both sites are substantially longer than those expected if the stopover behaviour of these migrants is a good fit with the classical model. The model coefficients for TSA were small and quite similar at both sites (Table 2). Also, the departure probability curves as a function of TSA were low and nearly flat for the first 30 days (Fig. 4c,d). Lank (1983) provided information on the arrival mass, fattening rate and departure masses at each site, inferred by comparing the masses of the daily samples of Sandpipers caught throughout the season, and on successive days when weather was or was not favourable for southeastward migration. Lank estimated that departure masses from Sibley Lake were only about 2 g less than those from Kent Island (e.g. 16 vs. 18 g on birds with lean masses of 20–22 g). Thus, despite the availability of stopover opportunities *en route*, the transcontinental migrants were also preparing for lengthy flights.

At Kent Island, Lank (1983) estimated that adults arrived with an average of 5–6 g of fuel. Some, identified by colour-dyed breasts, had previously staged further north along the east coast of James Bay. Juveniles arrived at Kent Island lighter than adults. At Sibley Lake, many birds of both ages arrived with little or no fuel stores, potentially having flown directly from western Nearctic breeding grounds. Lank estimated fattening rates of up to 2.5 g/day at Kent Island and 1.5 g/day at Sibley Lake. The rate for Kent Island is high relative to those estimated for shorebirds at other sites (Alerstam & Lindström 1990, Anderson *et al.* 2019). However, even at a lower rate, birds arriving completely lean at both sites could have added the 20–24 g of fuel needed to support maximal transoceanic or transcontinental flights in *c.* 15 days, far less than their estimated mean stopover durations of respectively 40.0 and 51.2 days for adults and juveniles at Kent Island and 33.7 and 32.8 days at Sibley Lake (Table 1). If birds fit the classic model, we would expect clear inverse relationships between mass at capture and subsequent length of stay, as has indeed been found in many other situations (Schaub *et al.* 2008). No such relationship

occurred at either Kent Island or Sibley Lake (Lank 1983) or at Dunn *et al.*'s (1988) coastal site. As favourable departure weather occurs at regular 4- to 5-day intervals (Lank 1983, see above), waiting for favourable departure conditions (McCabe *et al.* 2018) would not add more than a few days to stopover durations. None of the Sandpipers captured at these sites in our study was moulting, which can explain lengthy stays at stopover sites (Jehl 1990). We conclude that for most of the season the Sandpipers at both sites were not in a hurry to undertake their next lengthy migratory flight. At James Bay, a major stopover site for central and eastern migrants further north, the relationship between length of stay and fuel loads at capture for Semipalmated Sandpipers and other shorebirds was actually positive early in the season, but it did become negative towards the end (Anderson *et al.* 2019). This finding also points towards a relatively leisurely southward migration schedule.

Life history perspectives

Why were stopover durations so long at both sites, despite the apparent availability of food resources and favourable weather for departures at regular intervals? Answering this question requires taking a life history perspective, including migrants' age and prospects at subsequent stages of their annual cycles (Bednekoff & Houston 1994, Weber *et al.* 1998, 1999, Houston 1998).

Adults had shorter stopover durations than juveniles (Fig. 3). If we assume that both ages classes were preparing for similar migratory flights, the shorter duration for adults could indicate that their refuelling rate was higher and/or this could reflect their arrival at Kent Island with higher fat stores, which did occur. Lank (1983) concluded that adults and juveniles present concurrently at Kent Island had similar daily mass increases. In addition, at Kent Island, adults may have been more likely than juveniles to be preparing for a direct transoceanic flight. In both Lank's (1983) and Dunn *et al.*'s (1988) studies, fewer juveniles than would be expected demographically utilized the coastal stopover sites. There is evidence that juvenile Semipalmated Sandpipers generally make shorter transoceanic flights by leaving from sites further south, possibly after first moving southwesterly down the Atlantic coast (Harrington & Morrison 1979, Anderson *et al.* 2019: their

supplementary fig. 3). Thus, adults had shorter lengths of stay despite being more likely to be preparing for a longer journey. In conclusion, as argued above, as none of these birds were fattening as rapidly as possible, stopover duration and fuel levels were to a considerable extent decoupled for these birds. Thus, we will look for alternative explanations for lengthy stopovers.

Lank *et al.* (2003) argued that the evolution of migratory routes involving lengthy migratory flights depends not only on the existence of staging sites with sufficient food to fuel flights but also, critically, on low predation danger at such sites, as birds become quite vulnerable when carrying stores needed to fuel such flights. Schedules of migrating falcons may thus influence both the timing and the routes of migration, including those of Semipalmated Sandpipers in particular (Lank *et al.* 2003, Ydenberg *et al.* 2007). Models of migration's role within annual cycles stress the importance of date in the season, usually with fitness penalties for late arrivals (Weber *et al.* 1998). For southward migrating Semipalmated Sandpipers, Lank *et al.* (2003) argued that adults face stronger seasonal deadlines than juveniles to arrive at their non-breeding grounds by a given date, in order to mitigate the increased vulnerability they experience during post-migratory wing moult to later-migrating avian predators. As juveniles do not replace their feathers immediately on arrival, adults should put a higher priority on earlier arrivals on moulting sites further south, and thus have shorter stopover durations particularly later in the season. Hope *et al.* (2011) showed that conditional residency times calculated from this dataset were truncated at the end of the season, coinciding with the approach of migrant Peregrine Falcons *Falco peregrinus* towards the stopover sites.

When the observations reported here were made in the late 1970s, falcon populations were in fact relatively low, due to residual effects from the extensive use of DDT, and during the migratory seasons, both sites were quite safe with respect to avian predators (Ydenberg *et al.* 2017). No attacks from falcons were observed at Kent Island. At Sibley Lake, only a few observations of Prairie Falcons *Falco mexicanus* and resident Short-eared Owls *Asio flammeus* attacking Sandpipers were made (Lank 1979). Although proximate disturbance and danger was lacking, from an evolutionary sense, the predictable seasonal pattern of increasing danger may indeed have influenced birds' departure decisions

towards the end of the season (Lank *et al.* 2003, Hope *et al.* 2011, Ydenberg & Hope 2019), but for much of the time there was little direct threat.

We infer that during most of the season, both these sites provided quite favourable habitat for Semipalmated Sandpipers, making these ideal places to stage on migration (Pomeroy *et al.* 2008) or indeed to allocate time to, broadly considered in the context of the full annual cycle.

CONCLUSIONS

Migratory populations of the same species of sandpipers traversing different migration routes had different relationships between departure probabilities with respect to time present at the site and meteorological variables. The open population capture–recapture model we used incorporates entry probabilities to a sampling area and provided novel estimates of stopover durations and departure probabilities. As expected, strong tailwinds favoured migratory departures, somewhat more strongly along a route where birds were initiating a non-stop transoceanic flight compared with a transcontinental flight that allowed for stopovers at shorter distances. However, stopover durations were lengthy at both sites studied, suggesting that birds were not simply arriving, refuelling and leaving as quickly as possible. TSA was nonetheless predictive of departure, despite likely violations in this case of seasonal homogeneity in departure probability, an underlying assumption of the modelling approach. We recommend the further application of this approach, particularly for time-minimizing migrants, combined with counts if available (Lyons *et al.* 2016, Lok *et al.* 2019), towards the analysis of migratory stopover and departure probabilities.

Data collection by D.B.L. was supported by NSF grants BNS-7518905 and 7813016 to Stephen T. Emlen and William T. Keeton. D.B.L. thanks Stephen Emlen for his input and patience with respect to publication of this work. E.C. was supported by the French Laboratory of Excellence project 'TULIP' (ANR-10-LABX-41; ANR-11-IDEX-0002-02). We thank three anonymous reviewers, the Associate Editor and Editor for their helpful comments.

AUTHOR CONTRIBUTIONS

Sébastien Roques: Conceptualization (equal); Data curation (equal); Formal analysis (lead);

Methodology (equal); Resources (supporting); Software (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (equal). **David Lank:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Methodology (supporting); Resources (lead); Visualization (equal); Writing-original draft (equal); Writing-review & editing (lead). **Emmanuelle Cam:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Writing-original draft (supporting). **Roger Pradel:** Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Methodology (equal); Visualization (supporting); Writing-original draft (equal); Writing-review & editing (equal).

AUTHOR CONTRIBUTIONS

S.R. helped to conceive the idea, did the analyses and drafted the manuscript. D.B.L. conceived and designed the study, carried out the fieldwork and critically revised the manuscript. R.P. and E.C. helped to conceive the idea and revised the manuscript. All authors gave final approval for publication.

Data availability statement

All data used here are available on the corresponding author github account at: <https://github.com/sebroques/Ibis2020stopover>.

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Received 11 February 2020;
 revision accepted 21 September 2020.
 Associate Editor: Auriel Fournier.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Details about environmental covariates and principal component analysis.

Table S1. Mean and standard deviation of the weather variables at both sites.

Table S2. Pearson correlation coefficients of weather variables at Kent Island (upper part of the table) and Sibley Lake (lower part of the table).

Table S3. Correlations between weather covariates and dimensions. Eigenvalues and % of variance of dimensions are also displayed.

Appendix S2. JAGS code of the statistical model used in our study.