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1 *Running title: Migratory sandpiper behaviour at stopover sites*

2

3 **More Than Just Refuelling: Lengthy Stopover and Selection of**
4 **Departure Weather by Sandpipers Prior to Transoceanic and**
5 **Transcontinental Flights**
6

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21 Author contributions: SR helped to conceive the idea, did the analyses and drafted the
22 manuscript DBL conceived and designed the study, carried out the field work and critically
23 revised the manuscript. RP and EC helped to conceive the idea and revised the manuscript.

24 All authors gave final approval for publication.

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

49

50 **Keywords:** stopover decisions, migration, capture-recapture, Bayesian analysis, barrier effect

51

52 Migratory birds make their biannual movements between breeding and non-breeding areas in a
53 series of flights. Selection will favour flight strategies that include ‘hops skips or jumps’, and
54 variable stopover durations between flights (Schaub *et al.* 2008, Warnock 2010, Anderson *et*
55 *al.* 2019) that optimize fitness (Alerstam & Lindström 1990). Thus, birds’ internal conditions
56 and external situations when initiating flights should provide information about the nature of
57 selection during the subsequent migratory flight. As an extreme example, Bar-tailed Godwits
58 (*Limosa lapponica baueri*) departing on spectacular 6–9 day non-stop trans-Pacific Ocean
59 flights from Alaska to New Zealand carry fuel stores approximately equal to their airframe body
60 mass and do so when stronger tailwinds are available (Gill *et al.* 2009). Ecologically,
61 sufficiently food-rich and safe staging sites must be available to permit selection favouring the
62 evolution of such flights (Lank *et al.* 2003, Ydenberg *et al.* 2007). But generally, theory shows
63 that the costs of transporting excess fuel trades off against flight distance (Alerstam &
64 Lindström 1990). Thus, most migration routes consist of multiple stopover sites where migrants
65 prepare for successive stages of their journeys. Different migration strategies occur among
66 species, among populations traversing different routes, between age classes and sexes, at
67 different sites in a sequential journey, and even among individuals within these groups
68 (McKinnon *et al.* 2014, Deppe *et al.* 2015, Hua *et al.* 2017, Vansteelant *et al.* 2017).

69 The decision whether to depart from a stopover site at a particular time is understood to
70 be an evolved strategic decision rule conditioned proximately on internal state variables,
71 principally potential food acquisition rate and current fuel stores, and environmental factors,
72 especially weather conditions. Fuel stores can limit maximum flight ranges, and departure
73 decisions are therefore often related to them (e.g. Schaub *et al.* 2008, Arizaga *et al.* 2011,
74 Schmaljohann & Eikenaar 2017). Assessing an individual’s fuel and refuelling status usually
75 requires its physical capture and recapture, but changes in state following a captured bird’s
76 release are in most cases unmeasured (but see e.g. Schmaljohann *et al.* 2013). Fuelling rates

77 will vary largely as function of food abundance, predation danger, and seasonal time constraints
78 of the individual (e.g., Ydenberg & Hope 2019). A potentially useful alternative behavioural
79 metric that might index a bird's fuel status is the time the individual has spent at a stopover site,
80 hereafter "Time Since Arrival" (TSA) (Pledger *et al.* 2008, Roques *et al.* 2020). For migrants
81 following a classic model of stopover behaviour of 'arrive-fatten-depart', TSA could provide a
82 useful index of an individual's cumulative fuel acquisition and storage, and therefore be
83 predictive of its likelihood of departing from a site.

84 With respect to weather, wind strength and direction are strong general predictors of
85 migratory flight initiation (Richardson 1978, 1990, Ma *et al.* 2011, Gill *et al.* 2014). Stronger
86 tailwinds enable birds to fly further and/or arrive at subsequent sites with larger energy stores,
87 while stronger headwinds have the opposite effect and thus are expected to delay departures
88 from stopover sites (Butler *et al.* 1997, Åkesson & Hedenström 2000, Weber & Hedenström
89 2000, Grönroos *et al.* 2012). In addition, departure decisions have evolved with respect to
90 probable consequences further along the migration route and their potential carryover effects
91 on fitness consequences later in the birds' annual cycle (Alerstam & Lindström 1990,
92 Bednekoff & Houston 1994, Weber *et al.* 1998, Lank *et al.* 2003). For many northward
93 migrants, intraspecific competition for nesting sites and/or mates means that fitness declines
94 with arrival dates; southward migrants are generally thought to be under less time pressure (e.g.
95 Yohannes *et al.* 2009), but may still face deadlines in subsequent parts of their annual cycle,
96 including the timing of post-migratory flight feather moult, when birds are more vulnerable to
97 depredation (Lank *et al.* 2003, Ydenberg & Hope 2019). These broader strategic considerations
98 may be invoked to account for otherwise enigmatic observations of shorter or longer times spent
99 at migration stopovers.

100 In this study, we compared and contrasted the stopover departure decisions of southward
101 migrating Semipalmated Sandpipers (*Calidris pusilla*) prior to initiating flights to non-breeding

102 sites in South America via either a transoceanic flight from a coastal stopover site or an overland
103 flight from an inland site (Fig. 1, Lank 1979, 1983, Gratto-Trevor *et al.* 2012, Brown *et al.*
104 2017). Since using a successful transoceanic route requires a lengthy flight, we expected *a*
105 *priori* that migrants facing a transoceanic flight should (1) have stopover durations long enough
106 to obtain large fuel stores and (2) be highly selective about leaving in wind conditions that
107 would aid flight in the migratory direction. But what would inland birds do? Since birds leaving
108 the inland site have shorter flight range stopover options, they might leave after shorter stopover
109 durations with lower fuel stores and be somewhat less selective about the weather. Alerstam
110 (2001) proposed that “barrier effects” such as oceans should increase overall energetic cost and
111 danger relative to routes with stopover availabilities. In this case, all else being equal, inland
112 birds should adopt a lower energy and safer strategy, departing after shorter stopovers and
113 possibly being less selective about departure weather.

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

126 Adults and juvenile sandpipers were captured, marked, and resighted at a coastal and an
127 inland migratory stopover location. The age classes differ in that adults migrate about a month
128 ahead of juveniles and will undergo a post migratory wing moult, while juveniles will not.
129 Previous analyses of these data using simpler recapture models showed that birds remained at
130 both stopover sites for lengthy periods of time, declining at the end of the season (Lank 1983,
131 Hope 2011). Here, we estimated individual's Time Since Arrival using a capture-recapture
132 analytical approach that incorporates probabilities of entry prior to first capture and marking
133 (Pledger *et al.* 2008, Lyons *et al.* 2016, Roques *et al.* 2020). TSA was used as a potential index
134 of cumulative fuel storage, under the classic assumption that stopover activity consists of
135 arrival, fuel storage at a given rate, and departure (Schmaljohann & Eikenaar 2017, Roques *et*
136 *al.* 2020. Daily probabilities of leaving were then modelled with respect to TSA and daily
137 weather conditions. We interpret the stopover and departure patterns found in the context of the
138 flight options available and apparently utilized at each site, and in the context of the migrants'
139 annual cycle.

140

141 **METHODS**

142 **Study system**

143 The study system consisted of one coastal and one inland migratory stopover area for
144 Semipalmated Sandpipers at comparable latitudes during southward migration (Fig. 1, Lank
145 1983). The coastal site was Kent Island, New Brunswick, Canada (44°35'N, 60°27'W), in the
146 mouth of the strongly tidal Bay of Fundy. The inland site was the area around Sibley Lake,
147 North Dakota, United States of America (46°57'N, 99°43'W), which includes a mosaic of
148 shallow seasonal saline lakes. Both sites are intermediate stopovers situated between Arctic
149 breeding areas and South American wintering areas. Based on morphometrics, banding returns,
150 and subsequent tracking studies, birds at Kent Island likely originated at breeding grounds in

151 the central and eastern Canadian Arctic, may have previously staged along the shoreline of
152 James Bay, and were preparing for a transoceanic flight to northeastern South America (Lank
153 1979, 1983, Richardson 1979, Harrington & Morrison 1979, Morrison 1984, Gratto-Trevor *et*
154 *al.* 2012, Brown *et al.* 2017). Those at Sibley Lake were likely arriving from breeding grounds
155 in Alaska or the western Canadian Arctic, and departed heading towards the Caribbean and
156 northcentral or northwestern South America (Richardson & Gunn 1971, Lank 1979, 1983,
157 Gratto-Trevor *et al.* 2012). Adults pass through both areas in July and early August, and moult
158 flight feathers shortly after arrival on non-breeding grounds, while juveniles arrive through
159 August and into early September (Lank 1983, Lank *et al.* 2003). At both sites, birds acquire
160 substantial fuel for their next flight. A lean Semipalmated Sandpiper weighs ca. 20–22 g, but
161 many individuals at both sites nearly double this mass prior to departing on the next leg of their
162 journey (Lank 1983, Dunn *et al.* 1988).

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

171 Birds initially landing at a site may not remain present to rest and refuel (i.e. actual
172 ‘stopover’; Warnock, 2010). Inclusion of ‘transients’ will usually bias low estimates of
173 ‘migratory’ emigration rates (Bächler & Schaub 2007, Schaub *et al.* 2008). At Kent Island, 26%
174 of birds marked were never reencountered, nor were 36% of those marked at Sibley Lake (Lank
175 1983). A initial analyses of this dataset in a methodological paper, showed that daily

176 survivorship estimates distinguishing first versus later captures of individuals provided better
177 model fits than ignoring a possible capture/transient effect (Brownie & Robson 1983). Local
178 population size may also have affected transience probability (Lank 1983). Since our interest
179 was on the effects of meteorology and length of stay on departure decisions, we analysed only
180 capture histories of individuals that were subsequently reencountered. The numbers of capture
181 histories included were: 928 at Kent Island, with 759 adults and 169 juveniles, resighted 4.5
182 times, on average; and 1073 at Sibley Lake, with 520 adults and 553 juveniles, resighted 5.3
183 times on average.

184

185 **Weather variables**

186 To describe how meteorological conditions relate to the departure decisions of sandpipers, we
187 chose four weather covariates, measured daily at sunset, when most migratory departures
188 occurred (Richardson & Gunn 1971, Richardson 1977, Lank 1989). Based on earlier analyses
189 of this data set and other information on the timing of migratory departures (Lank 1983, 1989),
190 our metric for wind was the 24-hour-trend in the strength of the tailwind-headwind component
191 of wind direction (hereafter ‘wind’), which was the wind metric most predictive of departure
192 decision. Radar studies and direct observations show that at that season shorebird migration in
193 both regions occurs in along a northwest towards southeast axis (Fig. 1, Richardson & Gunn
194 1971, Lank 1979, Richardson 1979, Lank 1983), which we therefore defined as the expected
195 migratory direction. The wind effect value at sunset was calculated as follows:

$$196 \quad \text{Wind} = V * \cos(\alpha - 45)$$

197 where V is wind speed (in *m/s*) and α the direction where the wind comes from, in $^{\circ}$.
198 Subtracting 45° from the wind direction creates a vector with positive values for tailwinds
199 blowing from the northwest towards the southeast, the migratory direction. The 24-hour-trend
200 in wind was calculated as the vector’s value each day minus that of the previous day. Thus

201 positive values indicated that tailwinds were getting stronger, and negative values that they
202 were becoming weaker. Additional meteorological variables modeled were: temperature (°C),
203 percent cloud cover and relative humidity, measured at sunset.

204 Collinearity between weather covariates can lead to erroneous conclusions about the
205 effect of particular focal weather covariates. We tested for collinearity between the weather
206 covariates and found some significantly correlated, but not with high correlation coefficients
207 (Lank 1983). Nonetheless, to characterize the weather patterns with respect to synoptically
208 covarying meteorological conditions, we ran a Principal Component Analysis on the 4
209 meteorological variables pooled across both sites, which clearly distinguished two axes
210 explaining 80% of the variation (Fig. 2, see Table S3 for details). We modelled departure
211 probability with respect to both individual variables and the first two PCs.

212

213 **Statistical analyses of mark-recapture data**

214 We used a Bayesian, state-space formulation of an open population capture-recapture model
215 that incorporates entry probabilities to a sampling area (Pledger *et al.* 2009, Lyons *et al.*
216 2016). This formulation allows modelling both birds' arrival at and departure from the
217 stopover site. The parameters of the model are:

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

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

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

223 $psight_t$ Probability of visual recapture (encounter) at the sampling occasion t given the
224 individual has been captured and marked (wing-tagged) but has not yet departed

225 This formulation contains one submodel for the state process (states are “not yet arrived”,
 226 “present in the stopover site”, “departed”), and one submodel for the observations encoded in
 227 the individual capture histories. The observation process is conditional on the current state. For
 228 each individual capture history h_i , there is a true state history accounted for by the vector z_i .
 229 This vector of binary state variables describes if an individual i is present, $z_{i,t} = 1$, or not, $z_{i,t} =$
 230 0 , in the stopover area on day t . In our study, individuals can be physically captured or simply
 231 visually resighted, thus we separated the physical capture probability from the resighting
 232 probability, noted respectively as p and $psight$. Birds can also be captured and resighted during
 233 the same sampling occasion. To deal with this, we used a multi-state formulation of the
 234 observation process. Consequently, in an individual capture history, we distinguished four
 235 potential events (Pradel 2005) denoted as 0: not seen, 1: physically captured, 2: resighted, 3:
 236 physically captured and resighted during the same occasion. This resulted in the following
 237 observation matrix $\theta_{i,t}$ that applies to an individual present:

$$238 \quad \begin{bmatrix} 1 - p_t - psight_t + (p_t * psight_t) \\ p_t * (1 - psight_t) \\ psight_t * (1 - p_t) \\ p_t * psight_t \end{bmatrix}$$

239

240 For an individual i that has not yet entered the stopover area or has left it ($z_{i,t} = 0$), $h_{i,t} =$
 241 0 with probability equal to 1. This formulation allows us to estimate the time since arrival (TSA)
 242 for each individual. This covariate is a non-observable variable that can be computed with the
 243 sum of the true states $z_{i,t}$ up to time t , and represents the time of presence of the individual i at
 244 time t in the stopover area:

$$245 \quad TSA_{i,t} = \sum_{s=1}^{t-1} z_{i,s} \quad (1)$$

246

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

$$249 \quad SOD = \frac{\sum_i \sum_t z_{i,t}}{n} \quad (2)$$

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

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

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

$$260 \quad \text{Logit}(\phi_t) = a + \beta_{age} * TSA_t + \beta * Cov_t \quad (3)$$

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

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

$$265 \quad \text{Logit}(\phi_t) = a + \beta_{age} * TSA_t + \beta_1 * PC1_t + \beta_2 * PC2_t \quad (4)$$

266 Then, to test effects of each weather covariate, we ran one model for each weather covariate for
267 each site according to formula (3) to avoid collinearity problem (Harrison *et al.* 2018). This
268 resulted into 8 different slope values for each weather covariate for each site (Table 2).

269 Analyses were performed with JAGS (Hornik *et al.* 2003) using R version 3.6.1 (R
270 Development Core Team 3.0.1. 2013). Models were run with 120,000 iterations with non-
271 informative priors, and we checked chain mixing and the convergence (Kéry & Schaub 2011).
272 The JAGS code is available in Appendix S2.

273

274 **RESULTS**

275 **Stopover duration, time since arrival, and recapture probability**

276 The mean stopover duration estimates were 9–10 days longer at Kent Island than at Sibley
277 Lake, being 42.0 versus 33.7 days, respectively, but the CIs are wide for both estimates (Table
278 1 and Fig. 3). At Kent Island, the stopover durations of adults appear shorter than that of
279 juveniles, being 40.0 versus 51.2 respectively, again with large CIs, but quite similar at Sibley
280 Lake, averaging 32.8 versus 34.5 days (Table 1 and Fig. 3).

281 The probability of departure increased for all classes of individuals as their residency times
282 increased. The coefficients of the TSA effects were significant and estimated with a high
283 precision at both sites (see the 95% CI Table 2). The strongest TSA estimated effect was for
284 adults at Kent Island, with a 0.13 estimated slope on the logit scale. Kent Island juveniles had
285 estimates, of 0.09, close to values at Sibley Lake of 0.08 for adults and 0.09 for juveniles,
286 with overlapping 95% CIs (Table 2). Controlling for weather covariates, departure
287 probabilities remained below ca. 0.1 for over 30 days since initial arrival (Figures 4C and
288 4D).

289 The physical recapture probability p was similar between the two sites (Kent Island:
290 0.03, Sibley Lake: 0.04), but the resighting probability $psight$ was lower at Kent Island than at
291 Sibley Lake (0.14 and 0.22, respectively, Table 1).

292

293 **Weather Covariate Effects**

294 The first two principle component dimensions accounted for 52% and 29%, respectively, of the
295 total variances of the four meteorological variables (Table S3). PC1 captured covariation in
296 temperature, humidity and cloud cover (Fig. 2A, Table S3), patterns of which clearly differed
297 between sites (Fig. 2B, Table S1). Mean values of PC1 were -0.8 ± 1.3 at Kent Island and 0.8
298 ± 1.1 at Sibley Lake (Table S3). Kent Island had the cooler, more humid and cloudier conditions
299 expected from a marine site, contrasting with warmer and drier inland conditions at Sibley Lake
300 (Fig. 2B). PC2 largely captured the independent variation in 24-hour wind trend (Fig. 2A),
301 which ranged similarly between favourable and unfavourable conditions at both sites (Fig. 2B).
302 Mean values of PC2 were -0.2 ± 1.2 and 0.2 ± 0.9 at Kent Island, and Sibley Lake, respectively.

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

314 opposite trends produce some convergence of temperature and cloud cover conditions at
315 intermediate values from both sites.

316 PC1, primarily capturing variation in temperature, humidity and cloud cover (Fig. 1A),
317 had a significant negative effect on departure probability at Kent Island, but not at Sibley Lake
318 (Table 2, Fig. 4A). Negative values on PC1 represent strengthening tailwinds, since the
319 correlation between PC1 and wind is 0.20 (Table S3). The effect of PC1 appears larger at Kent
320 Island than at Sibley Lake; the CIs overlap, but that at Kent Island does not overlap zero. PC2,
321 associated strongly with the independent variation in 24 hour wind (Fig. 2, Fig 4B, Table S3),
322 had no significant effect at either site, thus most of the variation responsible for the univariate
323 relationship with wind must have been represented through covariation in PC1. The
324 environmental conditions correlating with departure are the ones that maximize the component
325 $\beta_1*PC1 + \beta_2*PC2$, corresponding to the direction (β_1, β_2) on plane 1,2 of the PCA. The
326 intensity of their effects are reflected by the length of the site-specific vectors shown in Fig. 2A
327 for each site.

328

329 **DISCUSSION**

330 We estimated the stopover durations, effects of Time Since Arrival and meteorological
331 conditions on the daily departure probabilities of Semipalmated Sandpipers from stopover sites
332 during southeastward migratory journeys. Birds at Kent Island, New Brunswick were preparing
333 for a lengthy transoceanic flight, while those at Sibley Lake, North Dakota, were preparing for
334 overland flights of unknown lengths. We proposed that contrasting the stopover durations and
335 departure behaviour of migrants from the sites would provide information about the migratory
336 strategies of comparable sandpiper populations when the migratory routes did or did not provide
337 access to intermediate downstream stopover sites. At both sites, birds departed with favourable
338 winds, and had lengthy stopover durations for most of the season, suggesting preparation for

339 lengthy migratory flights even when intermediate sites were available. However, birds at both
340 sites stayed substantially longer than necessary to simply refuel and continue migratory
341 journeys, suggesting that in the context of the birds' annual cycles, being at each of these
342 locations at those seasons had high fitness value. There were, however, quantitative differences
343 between migrants' behaviour at the two sites. Birds at Kent Island had somewhat greater
344 selectivity with respect to wind conditions at departure, and adults at that site had longer stays
345 than juveniles or birds at Sibley Island. Below, we interpret the patterns found as adjustment of
346 migratory strategy related to the differences in the downstream stopover options of each
347 migratory route, within the context of the birds' annual cycles.

348

349 **Weather effects**

350 At both sites, birds had higher probabilities of initiating migratory flight after tailwinds had
351 been strengthening for the past 24 hours. Departure with stronger tailwinds is expected on first
352 principles and from previous studies (Table 1, Richardson & Gunn 1971, Richardson 1978,
353 1979, 1990, Alerstam 1990, Weber *et al.* 1998, Åkesson & Hedenström 2000, Loonstra *et al.*
354 2019). Surface winds assisting southeastwardly flight were blowing when migratory departures
355 were directly observed (Fig 1B). From a synoptic weather point of view, as expected,
356 sandpipers from both sites thus do depart on days with tailwinds, reducing cost of flight per
357 kilometre travelled (Tsvey *et al.* 2007, Arizaga *et al.* 2011, Ma *et al.* 2011, Grönroos *et al.* 2012,
358 Dossman *et al.* 2016).

359 We predicted that birds facing transoceanic flight would show greater selectivity in
360 departure conditions than those facing transcontinental flight, and indeed, the effect size of
361 change in headwind component was stronger at Kent Island than at Sibley Lake. Kent Island
362 birds also showed stronger relationships with the integrated measures of meteorological
363 covariation than the birds at Sibley Lake. Although the background weather regimes differed

364 with respect to temperature, cloud cover and humidity, they were similarly variable in terms of
365 the general distributions of favourable winds (Fig. 2). In the current study, favourable weather
366 for migration occurred at fairly regular 4–5 day intervals at both sites throughout the migration
367 season, with regular passage of cyclonic and anticyclonic weather systems, and the patterns in
368 the specific years studied were typical of longer term weather regimes (Lank 1983). Thus,
369 systematic differences in meteorological migration opportunities do not account for differences
370 in selectivity between sites. Greater selectivity for wind assistance can trade-off against speed
371 of migration; McCabe *et al.* (2018), argued that in general, time minimizers might be less
372 selective because of fitness decreases associated with waiting for favourable weather
373 conditions. In our cases, however the lengthy stopover durations shown by both of our
374 migratory populations indicate that neither were time minimizers during much of the season
375 (see below), and both populations selected tailwinds for departure.

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

383 The direction of temperature and cloud cover effects were opposite at the two sites.
384 Sandpipers were more likely to leave Kent Island with higher than average temperatures and
385 less cloud cover for that site, while those at Sibley Lake left with lower than average
386 temperatures and greater cloud cover for the site. Since Kent was generally cooler and cloudier
387 than Sibley Lake (Fig. 2), this pattern produces a convergence of departure conditions between
388 sites under intermediate conditions of both variables. Greater cloud cover decreases the

389 visibility of the sky, and since migratory birds use the stars for the orientation (Wiltschko &
390 Wiltschko 1988), including Semipalmated Sandpipers (Lank 1973), dense cloud cover could
391 present initial navigational difficulties. Low cloud cover in particular may have a strong
392 negative impact on the probability of departing from a stopover area, while high altitude clouds
393 will have little effect (Martin 1990, Koistinen 2000).

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

401

402 **Modelling Considerations**

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

409 Lank (1983, unpublished analyses) tested for relationships between daily emigration
410 rates and prevailing daily weather conditions, using emigration rates estimated using a simpler
411 capture-recapture model (Brownie & Robson 1983). The emigration rate-meteorology
412 relationships in that study were weaker than those shown here (Table 2), suggesting that the
413 approach taken in the current study provided more useful estimates. Lank (1983) speculated

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

430

431 **Lengthy Stopover Durations**

432 As argued in the introduction, preparing for a non-stop transoceanic flight rather than an
433 overland flight should favour the acquisition of larger fuel stores, since the latter provides
434 opportunities for shorter flights from the stopover sites. Consistent with our prediction,
435 estimated stopover durations were ca. 10–15 days longer prior to transoceanic relative to
436 transcontinental flights for adults and juveniles, respectively (Table 1, Fig.3). Further, the
437 samples of birds captured and tagged at Kent Island averaged 3.4 g. heavier than those caught
438 at Sibley Lake (33.0 versus 29.6 g, Lank (1983)).

439 We motivated this study in part by suggesting that stopover duration might be a useful
440 index of cumulative refuelling that could be estimated without recapturing marked individuals,
441 assuming a classical model of stopover behaviour as ‘arrive-fatten-depart’. As expected under
442 this model, the effects of estimated Time Since Arrival were positive and predictive of departure
443 probabilities. Rapid refuelling often has been found at stopover sites, and the TSA approach
444 used here should work best in analyses of such situations, namely for time-minimizing migrants
445 whose stopover behaviour fits (Alerstam & Lindström 1990).

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

458 At Kent Island, Lank (1983) estimated that adults arrived with an average of 5–6 g of
459 fuel. Some, identified by colour-dyed breasts, had previously staged further north along the east
460 coast of James Bay. Juveniles arrived at Kent Island lighter than adults. At Sibley Lake, many
461 birds of both ages arrived with little or no fuel stores, potentially having flown directly from
462 western Nearctic breeding grounds. Lank estimated fattening rates of up to 2.5 g/day at Kent
463 Island and 1.5 g/day at Sibley Lake. The rate for Kent Island is high relative to those estimated

464 for shorebirds at other sites (Alerstam & Lindström 1990, Anderson *et al.* 2019). But even at a
465 lower rate, birds arriving completely lean at both sites could have added the 20–24 g of fuel
466 needed to support maximal transoceanic or trans-continental flights in ca. 15 days, far fewer
467 than their estimated mean stopover durations of 40.0 and 51.2 d for adults and juveniles at Kent
468 Island, respectively, and 33.7 and 32.8 d at Sibley Lake (Table 1). If birds fit the classic model,
469 we would expect clear inverse relationships between mass at capture and subsequent length of
470 stay, as has indeed been found in many other situations (e.g. Schaub *et al.* 2008). No such
471 relationship occurred at either Kent Island or Sibley Lake (Lank 1983), or at Dunn *et al.*'s
472 (1988) coastal site. Since favourable departure weather occurs at regular 4–5 day intervals
473 (Lank 1983, see above), waiting for favourable departure conditions (e.g. McCabe *et al.* 2018)
474 would not add more than a few days to stopover durations. None of the sandpipers captured at
475 these sites in our study was moulting, which can explain lengthy stays at stopover sites (Jehl
476 1990). We conclude that for most of the season the sandpipers at both sites were not in a hurry
477 to undertake their next, lengthy, migratory flight. At James Bay, a major stopover site for central
478 and eastern migrants further north, the relationship between length of stay and fuel loads at
479 capture for Semipalmated Sandpipers and other shorebirds was actually positive early in the
480 season, but did become negative towards the end (Anderson *et al.* 2019). This finding also
481 points towards a relatively leisurely southward migration schedule.

482

483 **Life History Perspectives**

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

489 Adults had shorter stopover durations than juveniles (Fig. 3). If we assume that at both
490 age classes were preparing for similar migratory flights, the shorter duration for adults could
491 indicate that their refuelling rate was higher, and/or reflect their arrival at Kent Island with
492 higher fat stores, which did occur. Lank (1983) concluded that adults and juveniles present
493 concurrently at Kent Island had similar daily mass increases. In addition, at Kent Island, adults
494 may have been more likely than juveniles to be preparing for a direct transoceanic flight. In
495 both Lank's (1983) and Dunn *et al.* (1988)'s studies, fewer juveniles than would be expected
496 demographically utilized the coastal stopover sites. There is evidence that juvenile
497 Semipalmated Sandpipers generally make shorter transoceanic flights by leaving from sites
498 further south, possibly after first moving southwesterly down the Atlantic coast (Harrington &
499 Morrison 1979, Anderson *et al.* 2019: their supplementary Fig. 3). Thus, adults had shorter
500 lengths of stay despite being more likely to be preparing for a longer journey. In conclusion, as
501 argued above, since none of these birds were fattening as rapidly as possible, stopover duration
502 and fuel levels were to a considerable extent decoupled for these birds. Thus, we will look for
503 alternative explanations for lengthy stopovers.

504 Lank *et al.* (2003) argued that the evolution of migratory routes involving lengthy
505 migratory flights depends not only on the existence of staging sites with sufficient food to fuel
506 flights, but also, critically, low predation danger at such sites, since birds become quite
507 vulnerable when carrying stores needed to fuel such flights. Schedules of migrating falcons
508 may thus influence both the timing and routes of migration, including Semipalmated Sandpipers
509 in particular (Lank *et al.* 2003, Ydenberg *et al.* 2007). Models of migration's role within annual
510 cycles stress the importance of date in the season, usually with fitness penalties for late arrivals
511 (e.g. Weber *et al.* 1998). For southward migrating Semipalmated Sandpipers, Lank *et al.* (2003)
512 argued that adults face stronger seasonal deadlines than juveniles to arrive at their non-breeding
513 grounds by a given date, in order to mitigate the increased vulnerability they experience during

514 post-migratory wing moult to later-migrating avian predators. Since juveniles do not replace
515 their feathers immediately on arrival, adults should put a higher priority on earlier arrivals on
516 moulting sites further south, and thus have shorter stopover durations particularly later in the
517 season. Hope et al. (2011) showed that conditional residency times calculated from this dataset
518 were truncated at the end of the season, coinciding with the approach of migrant Peregrine
519 Falcons (*Falco peregrinus*) towards the stopover sites.

520 When the observations reported here were made in the late 1970s, falcon populations
521 were in fact relatively low, due to residual effects from the extensive use of DDT, and during
522 the migratory seasons both sites were quite safe with respect to avian predators (Ydenberg *et*
523 *al.* 2017). No attacks from falcons were observed at Kent Island. At Sibley Lake, only a few
524 observations of Prairie Falcons (*Falco mexicanus*) and resident Short-eared Owls (*Asio*
525 *flammeus*) attacking sandpipers were made (Lank 1979). Although proximate disturbance and
526 danger was lacking, from an evolutionary sense, the predictable seasonal pattern of increasing
527 danger may indeed have influenced birds' departure decisions towards the end of the season
528 (Lank *et al.* 2003, Hope *et al.* 2011, Ydenberg & Hope 2019), but for much of the time there
529 was little direct threat.

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

534

535 **Conclusions**

536 Migratory populations of the same species of sandpipers traversing different migration routes
537 had different relationships between departure probabilities with respect to time present at the
538 site and meteorological variables. The open population capture-recapture model we used

539 incorporates entry probabilities to a sampling area and provided novel estimates of stopover
540 durations and departure probabilities. As expected, strong tailwinds favoured migratory
541 departures, somewhat more strongly along a route where birds were initiating a non-stop
542 transoceanic flight compared with a transcontinental flight that allowed for stopovers at shorter
543 distances. However, stopover durations were lengthy at both sites studied, suggesting that birds
544 were not simply arriving, refuelling, and leaving as quickly as possible. Time since arrival was
545 nonetheless predictive of departure, despite likely violations in this case of seasonal
546 homogeneity in departure probability, an underlying assumption of the modelling approach.
547 We recommend the further application of this approach, particularly for time minimizing
548 migrants, combined with counts if available (Lyons *et al.* 2016, Lok *et al.* 2019) towards the
549 analysis of migratory stopover and departure probabilities.

550

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556

557 **DATA AVAILABILITY STATEMENT**

558 All data used here are available on the personal correspondence author github account.

559

560 **REFERENCES**

561 **Åkesson, S. & Hedenström, A.** 2000. Wind selectivity of migratory flight departures in
562 birds. *Behav. Ecol. Sociobiol.* **47**: 140–144.

563 **Åkesson, S., Walinder, G., Karlsson, L., & Ehnbohm, S.** 2001. Reed warbler orientation:

564 initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk.
565 *Anim. Behav.* **61**: 181-189.

566 **Alerstam, T.** 1990. *Bird migration*. Cambridge: Cambridge University Press.

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

570 **Alerstam, T.** 2001. Detours in bird migration. *J. Theor. Biol.* 209(3), 319-331.

571 **Anderson, A.M., Duijns, S., Smith, P.A., Friis, C. & Nol, E.** 2019. Migration distance and
572 body condition influence shorebird migration strategies and stopover decisions during
573 southbound migration. *Front. Ecol. Evol.* **7**: 251.

574 **Arizaga, J., Belda, E.J. & Barba, E.** 2011. Effect of fuel load, date, rain and wind on
575 departure decisions of a migratory passerine. *J. Ornithol.* **152**: 991–999.

576 **Bächler, E. & Schaub, M.** 2007. The effects of permanent local emigration and encounter
577 technique on stopover duration estimates as revealed by telemetry and mark-recapture.
578 *Condor* **109**: 142–154.

579 **Baschelet, E.** 1981. *Circular Statistics in Biology*. London: Academic Press.

580 **Bednekoff, P.A. & Houston, A.I.** 1994. Dynamic models of mass-dependent predation, risk-
581 sensitive foraging, and premigratory fattening in birds. *Ecology* **75**: 1131–1140.

582 **Brown, S., Gratto-Trevor, C., Porter, R., Weiser, E.L., Mizrahi, D., Bentzen, R.,**
583 **Boldenow, M., Clay, R., Freeman, S., Giroux, M.-A., Kwon, E., Lank, D.B.,**
584 **Lecomte, N., Liebezeit, J., Loverti, V., Rausch, J., Sandercock, B.K., Schulte, S.,**
585 **Smith, P., Taylor, A., Winn, B., Yezerinac, S. & Lanctot, R.B.** 2017. Migratory
586 connectivity of Semipalmated Sandpipers and implications for conservation. *Condor*
587 **119**: 207–224.

588 **Brownie, C. & Robson, D.S.** 1983. Estimation of time-specific survival rates from tag-

589 resighting samples: A generalization of the Jolly-Seber Model. *Biometrics* **39**: 437.

590 **Butler, R.W., Williams, T.D., Warnock, N. & Bishop, M.A.** 1997. Wind assistance: A
591 requirement for migration of shorebirds? *Auk* **114**: 456–466.

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

598 **Dossman, B.C., Mitchell, G.W., Norris, D.R., Taylor, P.D., Guglielmo, C.G., Matthews,**
599 **S.N. & Rodewald, P.G.** 2016. The effects of wind and fuel stores on stopover departure
600 behavior across a migratory barrier. *Behav. Ecol.* **27**: 567–574.

601 **Dunn, P.O., May, T.A., McCollough, M.A. & Howe, M.A.** 1988. Length of stay and fat
602 content of migrant Semipalmated Sandpipers in eastern Maine. *Condor* **90**: 824–835.

603 **Gill, R.E., Douglas, D.C., Handel, C.M., Tibbitts, T.L., Hufford, G. & Piersma, T.** 2014.
604 Hemispheric-scale wind selection facilitates bar-tailed godwit circum-migration of the
605 Pacific. *Anim. Behav.* **90**: 117–130.

606 **Gill, R.E., Tibbitts, T.L., Douglas, D.C., Handel, C.M., Mulcahy, D.M., Gottschalck,**
607 **J.C., Warnock, N., McCaffery, B.J., Battley, P.F. & Piersma, T.** 2009. Extreme
608 endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather
609 than barrier? *Proc. R. Soc. Lond. B.* **276**: 447–457.

610 **Gratto-Trevor, C., Morrison, R.I.G., Mizrahi, D., Lank, D.B., Hicklin, P. & Spaans,**
611 **A.L.** 2012. Migratory connectivity of Semipalmated Sandpipers: Winter distribution and
612 migration routes of breeding populations. *Waterbirds* **35**: 83–95.

613 **Grönroos, J., Green, M. & Alerstam, T.** 2012. To fly or not to fly depending on winds:

614 shorebird migration in different seasonal wind regimes. *Anim. Behav.* **83**: 1449–1457.

615 **Harrington, B.A. & Morrison, R.I.G.** 1979. Semiplumated Sandpiper migration in North
616 America. *Stud. Avian Biol.* **2**: 83–100.

617 **Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin,**
618 **C.E.D., Robinson, B.S., Hodgson, D.J. & Inger, R.** 2018. A brief introduction to
619 mixed effects modelling and multi-model inference in ecology. *PeerJ* **2018**.

620 **Hope, D.D., Lank, D.B., Smith, B.D. & Ydenberg, R.C.** 2011. Migration of two calidrid
621 sandpiper species on the predator landscape: How stopover time and hence migration
622 speed vary with geographical proximity to danger. *J. Avian Biol.* **42**: 522–529.

623 **Hornik, K., Leisch, F., Zeileis, A. & Plummer, M.** 2003. JAGS: A program for analysis of
624 Bayesian graphical models using Gibbs sampling. Available at:
625 <http://www.ci.tuwien.ac.at/Conferences/DSC-2003/>.

626 **Houston, A.I.** 1998. Models of optimal avian migration: state, time and predation. *J. Avian*
627 *Biol.* **29**: 395–404..

628 **Hua, N., Åkesson, S., Zhou, Q., Ma, Z.** 2017. Springtime migratory restlessness and
629 departure orientation of Great Knots (*Calidris tenuirostris*) in the south compared to the
630 north Yellow Sea. *Avian Res.* **8**, 20 (2017). <https://doi.org/10.1186/s40657-017-0078-1>

631 **Jehl, J.R.** 1990. Aspects of the molt migration. In: Gwinner, E. (ed) *Bird Migration*: 102–
632 113. Berlin: Springer Verlag.

633 **Kéry, M. & Schaub, M.** 2011. Bayesian population analysis using WinBUGS: A hierarchical
634 perspective. 1–554.

635 **Koistinen, J.** 2000. Bird migration patterns on weather radars. *Phys. Chem. Earth, Part B*
636 *Hydrol. Ocean. Atmos.* **25**: 1185–1193.

637 **Lank, D.** 1989. Why fly by night? Inferences from tidally-induced migratory departures of
638 sandpipers. *J. Field Ornithol.* **60**: 154–161.

- 639 **Lank, D.B.** 1973. *Celestial Orientation by Migrating Sandpipers*. B.Sc. thesis, Marlboro
640 College, Marlboro, Vermont, USA. (71 pp).
- 641 **Lank, D.B.** 1979. Dispersal and predation rates of wing-tagged Semipalmated Sandpipers
642 *Calidris pusilla* and an evaluation of the technique. *Wader Study Group Bull.* **27**: 41–46.
- 643 **Lank, D.B.** 1983. *Migratory behavior of Semipalmated Sandpipers at Inland and Coastal*
644 *Staging Areas*. PhD. Thesis, Cornell University, Ithaca, USA. (285 pp).
- 645 **Lank, D.B., Butler, R.W., Ireland, J. & Ydenberg, R.C.** 2003. Effects of predation danger
646 on migration strategies of sandpipers. *Oikos* **103**: 303–319.
- 647 **Lok, T., Hassell, C.J., Piersma, T., Pradel, R. & Gimenez, O.** 2019. Accounting for
648 heterogeneity when estimating stopover duration, timing and population size of red knots
649 along the Luannan Coast of Bohai Bay, China. *Ecol. Evol.* **9**: 6176–6188.
- 650 **Loonstra, A.H.J., Verhoeven, M.A., Senner, N.R., Both, C. & Piersma, T.** 2019. Adverse
651 wind conditions during northward Sahara crossings increase the in-flight mortality of
652 Black-tailed Godwits. *Ecol. Lett.* **22**: 2060–2066.
- 653 **Lyons, J.E., Kendall, W.L., Royle, J.A., Converse, S.J., Andres, B.A. & Buchanan, J.B.**
654 2016. Population size and stopover duration estimation using mark-resight data and
655 Bayesian analysis of a superpopulation model. *Biometrics* **72**: 262–271.
- 656 **Ma, Z., Hua, N., Zhang, X., Guo, H., Zhao, B., Ma, Q., Xue, W. & Tang, C.** 2011. Wind
657 conditions affect stopover decisions and fuel stores of shorebirds migrating through the
658 south Yellow Sea. *Ibis* **153**: 755–767.
- 659 **Martin, G.R.** 1990. The Visual Problems of Nocturnal Migration. In: Gwinner, E. (ed) *Bird*
660 *Migration*: 185–197. Berlin Springer Verlag.
- 661 **McCabe, J.D., Olsen, B.J., Osti, B. & Koons, P.O.** 2018. The influence of wind selectivity
662 on migratory behavioral strategies. *Behav. Ecol.* **29**: 160–168.
- 663 **McKinnon, E.A., Fraser, K.C., Stanley, C.Q. & Stutchbury, B.J.M.** 2014. Tracking from

664 the tropics reveals behaviour of juvenile songbirds on their first spring migration. *PLoS*
665 *One* **9**: e105605.

666 **Morrison, R.I.G.** 1984. Migration systems of some New World shorebirds. In Burger, J. &
667 Olla, B.L. (eds.) *Shorebirds: Migration and Foraging Behavior*: 125–202. New York:
668 Plenum Press.

669 **Pledger, S., Efford, M., Pollock, K., Collazo, J. & Lyons, J.** 2008. Stopover duration
670 analysis with departure probability dependent on unknown time since arrival. In
671 Thomson D.L., Cooch E.G., Conroy M.J. (eds) *Modeling Demographic Processes In*
672 *Marked Populations. Environmental and Ecological Statistics, vol 3*: 349-363. Boston,
673 MA: Springer.

674 **Pomeroy, A.C., Acevedo Seaman, D.A., Butler, R.W., Elner, R.W., Williams, T.D. &**
675 **Ydenberg, R.C.** 2008. Feeding-danger trade-offs underlie stopover site selection by
676 migrants. *Avian Conserv. Ecol.* **3**: 7.

677 **Pradel, R.** 2005. Multievent: An extension of multistate capture-recapture models to
678 uncertain states. *Biometrics* **61**: 442–447.

679 **R Development Core Team 3.0.1.** 2013. A language and environment for statistical
680 computing. *R Found. Stat. Comput.* **2**: <https://www.R-project.org>.

681 **Richardson, W.J.** 1978. Timing and amount of bird migration in relation to weather: A
682 review. *Oikos* **30**: 224–272.

683 **Richardson, W.J.** 1979. Southeastward shorebird migration over Nova Scotia and New
684 Brunswick in autumn: a radar study. *Can. J. Zool.* **57**: 107–124.

685 **Richardson, W.J.** 1990. Timing of bird migration in relation to weather: Updated review. In
686 Gwinner, E. (ed) *Bird Migration*: 78–101. Berlin: Springer Verlag.

687 **Richardson, W.J. & Gunn, W.W.H.** 1971. Radar observations of bird movements in east-
688 central Alberta. *Stud. Bird Hazards to Aircraft* 35–68.

689 **Roques, S., Henry, P.-Y., Guyot, G., Bargain, B., Cam, E. & Pradel, R.** 2020. When to
690 depart from a stopover site? Time-since-arrival matters more than weather conditions.
691 *bioRxiv* 2020.02.05.933788.

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

694 **Schmaljohann, H., Korner-Nievergelt, F., Naef-Daenzer, B., Nagel, R., Maggini, I.,**
695 **Bulte, M., & Bairlein, F.** 2013. Stopover optimization in a long-distance migrant: the
696 role of fuel load and nocturnal take-off time in Alaskan northern wheatears (*Oenanthe*
697 *oenanthe*). *Front. Zool.* **10**: 26. <https://doi.org/10.1186/1742-9994-10-26>

698 **Schmaljohann, H. & Eikenaar, C.** 2017. How do energy stores and changes in these affect
699 departure decisions by migratory birds? A critical view on stopover ecology studies and
700 some future perspectives. *J. Comp. Physiol. A.* **203**: 411–429.

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

704 **Vansteelant, W.M.G., Kekkonen, J. & Byholm, P.** 2017. Wind conditions and geography
705 shape the first outbound migration of juvenile honey buzzards and their distribution
706 across sub-Saharan Africa. *Proc. R. Soc. Lond. B.* **284**: 20170387.

707 **Warnock, N.** 2010. Stopping vs. staging: The difference between a hop and a jump. *J. Avian*
708 *Biol.* **41**: 621–626.

709 **Weber, T.P., Ens, B.J. & Houston, A.I.** 1998. Optimal avian migration: A dynamic model
710 of fuel stores and site use. *Evol. Ecol.* **12**: 377–401.

711 **Weber, T.P., Fransson, T. & Houston, A.I.** 1999. Should I stay or should I go? Testing
712 optimality models of stopover decisions in migrating birds. *Behav. Ecol. Sociobiol.* **46**:
713 280–286.

- 714 **Weber, T.P. & Hedenström, A.** 2000. Optimal stopover decisions under wind influence: The
715 effects of correlated winds. *J. Theor. Biol.* **205**: 95–104.
- 716 **Wiltshko, W. & Wiltshko, R.** 1988. Magnetic versus celestial orientation in migrating
717 birds.
- 718 **Ydenberg, R.C., Butler, R.W. & Lank, D.B.** 2007. Effects of predator landscapes on the
719 evolutionary ecology of routing, timing and molt by long-distance migrants. *J. Avian*
720 *Biol.* **38**: 523–529.
- 721 **Ydenberg, R.C, Barrett, J., Lank, D.B., Xu, C. & Faber M.** 2017. The redistribution of
722 non-breeding dunlins in response to the post-DDT recovery of falcons. *Oecologia* **183**:
723 1101–1110. DOI 10.1007/s00442-017-3835-2
- 724 **Ydenberg, R.C. & Hope, D.D.** 2019. Danger management and the seasonal adjustment of
725 migratory speed by sandpipers. *J. Avian Biol.* **50**: jav.02202.
- 726 **Yohannes, E., Biebach, H., Nikolaus, G. & Pearson, D.J.** 2009. Migration speeds among
727 eleven species of long-distance migrating passerines across Europe, the desert and
728 eastern Africa. *J. Avian Biol.* **40**: 126-134. doi:[10.1111/j.1600-048X.2008.04403.x](https://doi.org/10.1111/j.1600-048X.2008.04403.x)

730 **Tables**

731 **Table 1.** Mean and credible intervals (CI) of the resighting probability (*psight*), the capture
732 probability (*p*) and stopover duration by age of southward migrating Semipalmated Sandpipers
733 estimated from the models following equation 4. Estimates from Kent Island derived from 4178
734 encounters in capture histories from 759 adults and 169 juveniles; those from Sibley Lake
735 derived from 5613 encounters in capture histories from 520 adults and 553 juveniles.

736

Kent Island	Sibley Lake
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	Mean	CI	Mean	CI
Resighting probability (<i>psight</i>)	0.14	0.02, 0.30	0.22	0.11, 0.39
Capture probability (<i>p</i>)	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

737

738 **Table 2.** Mean, standard deviation (Sd) and credible intervals (CI) of the estimated effects of
739 covariates on departure probability. The first part of the table shows the results from the
740 equation 4 with TSA (β_{1age}) and PCA axes covariates. The second part of the table shows the
741 results from the equation 3, which included TSA (β_{1age}) and coefficients for weather covariates
742 effects ($\beta_2, \beta_3, \beta_4, \beta_5$). Estimated values of intercept and TSA effects for each univariate
743 models are not shown in this table as they are mostly similar to the ones of equation 4.

	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) Cloudcover	-0.33	0.16	-0.66, -0.02	0.42	0.11	0.20, 0.65

744

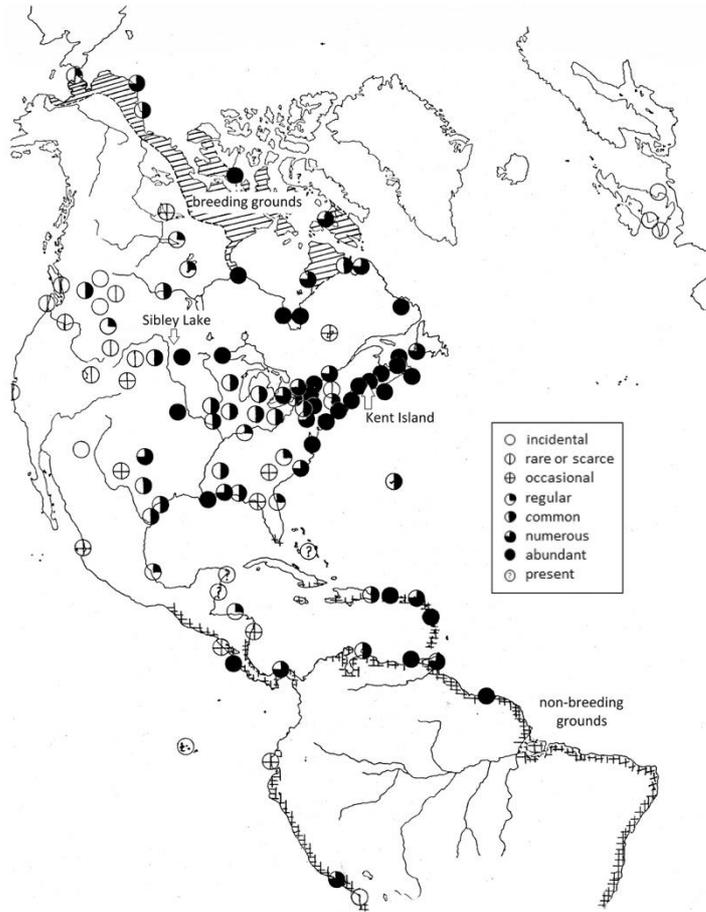
745

746 **Figure legends**

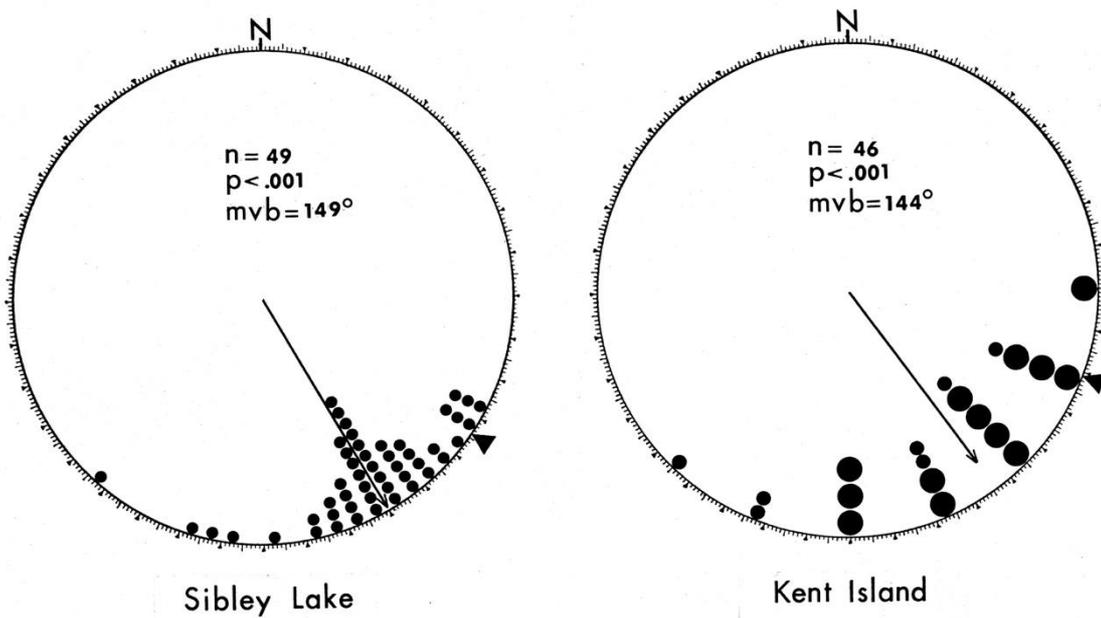
747 Figure 1: A. Breeding (diagonal hatching) and nonbreeding grounds (crosshatching) of
748 Semipalmated Sandpipers, study site locations, and relative abundances of migrant
749 Semipalmated Sandpipers reported during southward migration. Abundance classes at
750 migration sites were compiled from regional accounts in literature prior to 1980. B. The
751 directional distribution of presumed migratory departures of Semipalmated Sandpipers from
752 Sibley Lake and Kent Island. Flocks leaving each study site were followed optically until they
753 disappeared from view (details in Lank 1983, 1989). Vanishing bearings were assigned to one
754 of 16 compass points at Kent Island, or to the nearest compass degree at Sibley Lake. Mean
755 vector bearings (mvb) and statistical significance (p) were calculated using Baschelet (1981).
756 The black triangle on the outside of each circle shows the mean direction towards which surface
757 winds were blowing at the time of the departures. Both figures adapted from Lank (1983),
758 which provides references to the migration site accounts used in A.

759

A

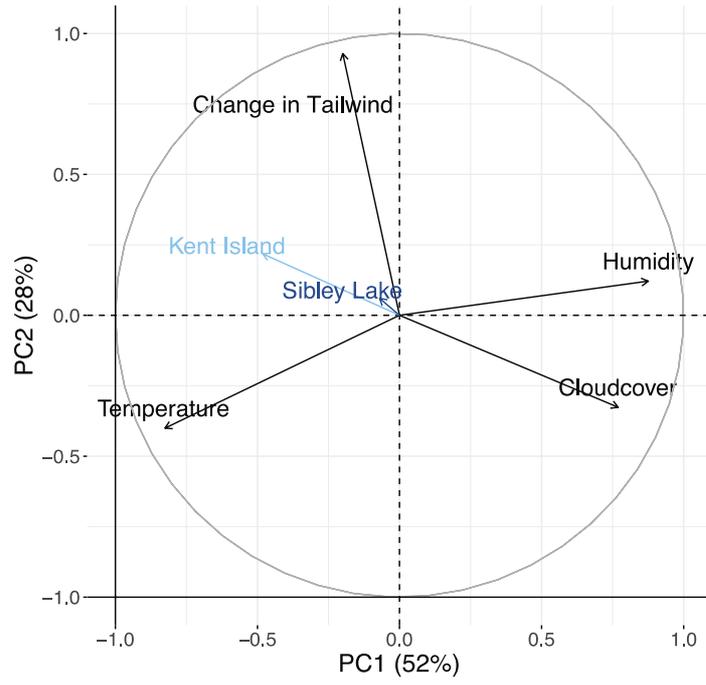


B

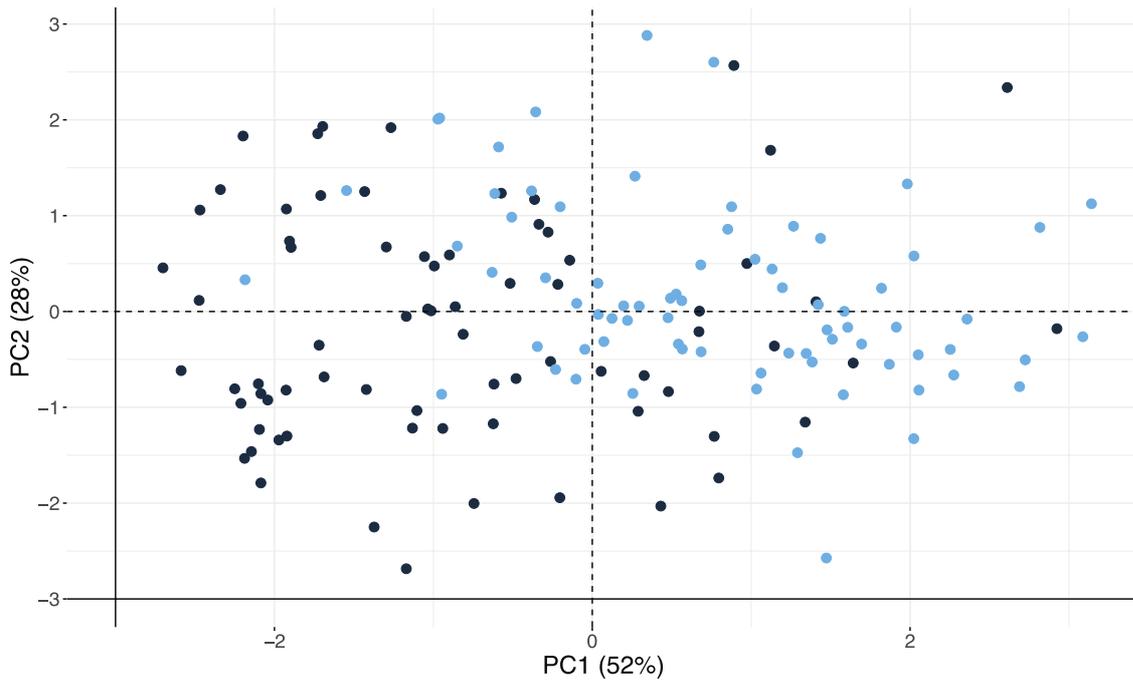


761 Figure 2. Principal component analysis of the four weather variables. A) Length and direction
762 of vectors shows the relative weightings of the 4 weather variables along the two first axes of
763 the PC (black arrows). PC1 largely captures covariation in temperature, humidity and cloud
764 cover, while PC2 primarily captures the independent variation in wind direction. Vectors
765 representing the conditions favouring departure of Semipalmated Sandpipers are plotted for
766 Kent Island and Sibley Lake with light and dark blue arrows, respectively (Table 2). B)
767 Scatterplot of daily local weather observations with respect to PC1 and PC2 scores (light blue:
768 Kent Island, dark blue: Sibley Lake).

A



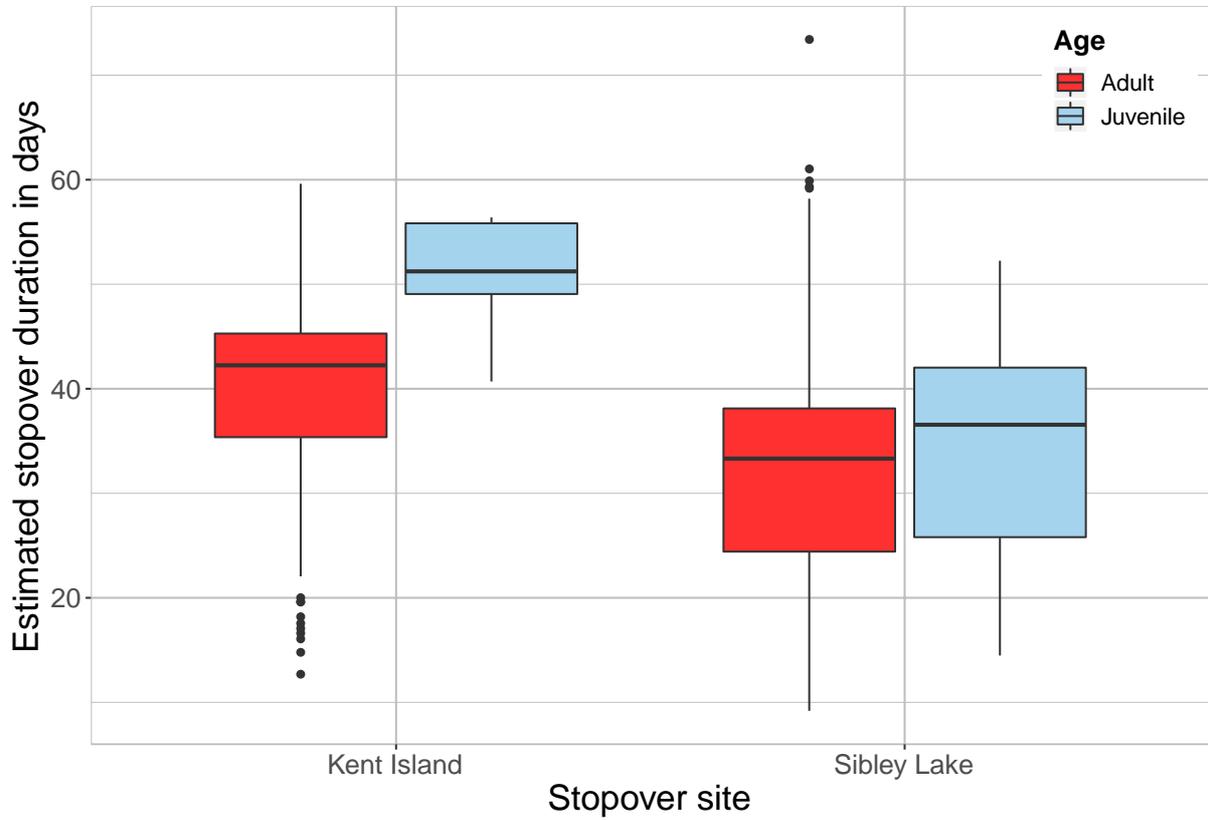
B



769

770

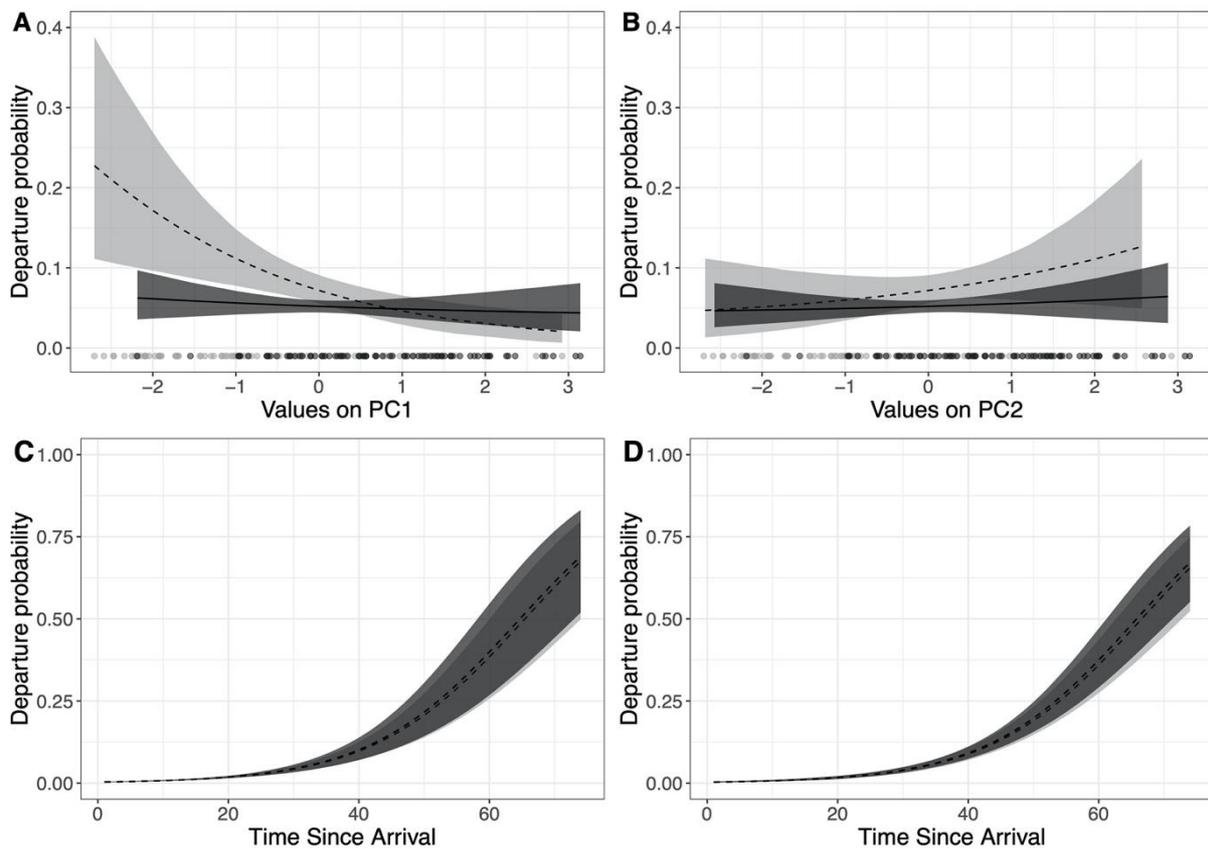
771 Figure 3. Estimated stopover duration by age classes at Kent Island and Sibley Lake. Adults:
772 red, Juveniles: blue. Box plots show: median (thick line), first and third quartiles boundaries,
773 lines extend to 1.5 times the box boundaries, and black dots show outliers.



774

775 Figure 4. Predicted effects of: A,B) the first and the second PC axes (respectively A and B) on
776 the departure probability of Semipalmated Sandpipers at both sites given birds are at their mean
777 stopover duration (Kent Island : light grey, Sibley Lake : dark grey). In figures A and B, the
778 light and dark grey points show the values encountered respectively at Kent Island and Sibley
779 Lake. C,D) the TSA on departure probability given weather values are at their mean values at
780 both sites (C: Kent Island, D: Sibley Lake) for both ages (Dark grey: Adults, Light grey:
781 Juveniles). For all figures the dashed lines represent the mean values, and grey areas represent
782 the 95% credible intervals.

783



784

785 **SUPPORTING INFORMATION**

786

787 Additional supporting information may be found online in the Supporting Information section

788 at the end of the article.

789 **Appendix S1.** Details about environmental covariates and Principal Component Analysis

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

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

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

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