Migrant semipalmated sandpipers (Calidris pusilla) have over four decades steadily shifted towards safer stopover locations

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2 ABSTRACT

Peregrine falcons (*Falco peregrinus*) have undergone a steady hemisphere-wide recovery since the ban on DDT in 1972, resulting in an ongoing increase in the level of danger posed for migrant birds, such as Arctic-breeding sandpipers. We anticipate that in response migrant semipalmated sandpipers (*Calidris pusilla*) have adjusted migratory behaviour, including a shift in stopover site usage towards locations offering greater safety from falcon predation.

We assessed semipalmated sandpiper stopover usage within the Atlantic Canada Shorebird Survey dataset. Based on 3,030 surveys (totalling ˜32M birds) made during southward migration, 1974 - 2017, at 198 stopover locations, we assessed the spatial distribution of site usage in each year (with a 'priority matching distribution' index, PMD) index in relation to the size (intertidal area) and danger (proportion of the intertidal area within 150m of the shoreline) of each location. The PMD index value is > 1 when usage is concentrated at dangerous locations, 1.0 when usage matches location size, and < 1 when usage is concentrated at safer locations.

A large majority of migrants are found at the safest sties in all years, however our analysis of the PMD demonstrated that the fraction increased over time. In 1974, 80% of birds were found at the safest 20% of the sites, while in 2017, this had increased to 97%. A sensitivity analysis shows that the shift was made specifically towards safer (and not just larger) sites. The shift as measured by a PMD index decline cannot be accounted for by possible biases inherent in the data set. We conclude that the data support the prediction that increasing predator danger has induced a shift by southbound migrant semipalmated sandpipers to safer sites.

Keywords: semipalmated sandpipers; peregrine falcons; predator response; stopover site selection; Atlantic Canada

1 INTRODUCTION

Prey animals often react to cues of predator presence with changes in morphology (Domenici et al., 2008) or behaviour. For example, songbirds reduce the amount and volume of singing after hearing a

25 predator (e.g. Ellison and Ydenberg, 2018). This occurs because singing makes a male conspicuous and so
26 more vulnerable to attack. Lowering the intensity of singing lowers conspicuousness and reduces the risk.
27 However, this comes at a cost because singing also has benefits (mate attraction, territorial defence) that are
28 presumably also reduced. Many such behavioural responses have been documented (Cooper et al., 2015).

29 These responses can create impacts on prey populations, competitors, and other trophic levels, together
30 termed 'risk effects'. Over the past two decades it has become increasingly apparent that risk effects can
31 propagate through entire ecosystems (e.g. Schmitz et al., 2004). The 'risk effects' on prey populations
32 stemming from the large and expanding influence of humans on the planet's oceans, particularly the
33 great reductions in the abundance of top predators are well documented (Madin et al., 2016; Myers and
34 Worm, 2003). Heithaus et al. (2008) documented many novel repercussions of changing marine predator
35 abundances (see also Estes et al., 2011; Babcock et al., 2010). Much of what is known about these effects
36 relates to lethal effects (i.e. mortality inflicted directly by predators). In contrast, the risk effects (e.g.
37 influences of predator presence on prey behaviour and morphology; see Madin et al., 2016, Box 1) are not
38 as well studied, despite many advances in the past decade from the experimental literature (reviewed by
39 Long and Hay, 2012).

40 In marine systems concern centres around consequences of reductions in the numbers and biomass of
41 top predators. In contrast, in some terrestrial systems top predators are increasing greatly in abundance
42 (Ydenberg et al., 2017). In particular, North American raptor populations are increasing strongly, attributed
43 to the 1973 ban on DDT usage, and to intense conservation efforts undertaken by wildlife agencies and
44 other groups. For example, captive-reared falcons were released to breed at various locations throughout
45 the continent (Amirault et al., 2004; Gahbauer et al., 2015; Watts et al., 2015).

46 Prey species have responded to this increased predator abundance in a variety of ways. The recovery of
47 bald eagles (*Haliaeetus leucocephalus*) caused seabirds to shift to safer breeding locations within colonies,
48 and to shift distributions between breeding colonies based on exposure to predators (Hipfner et al., 2012).
49 The increased presence of white-tailed sea eagles (*Haliaeetus alba*) in the Baltic Sea caused barnacle geese
50 (*Branta leucopsis*) to alter migration timing and to shorten the duration of parental care (Jonker et al.,
51 2010). Falcon recovery drove Pacific dunlins (*C. alpina pacifica*) to lose their mid-winter fat store (in
52 order to maintain escape performance), and to take up over-ocean flocking in place of roosting at high
53 tide (Ydenberg et al., 2010), and to shift the non-breeding distribution toward greater aggregation at safer
54 sites (Ydenberg et al., 2017). Wing lengths of semipalmated sandpipers (*C. pusilla*) and other calidridines
55 shortened 1980 - 2015 as peregrine numbers increased, potentially due to selection for better predator
56 escape performance (Lank et al., 2017; Anderson et al., 2019). The risk effects, both direct and indirect, of
57 these responses are unstudied as yet, but might be substantial.

58 The ongoing recovery of peregrines (*Falco peregrinus*) and merlins (*Falco columbarius*; Cade et al., 1988;
59 Cava et al., 2014; Ydenberg et al., 2017) constitutes an important environmental change for shorebirds.
60 Here we document a large-scale behavioural response of migratory shorebirds to this continental-scale
61 increase in predation danger. Many conditions have changed over recent decades for migratory birds,
62 including degraded or new habitats (Iwamura et al., 2013; Studds et al., 2017; Taft and Haig, 2006; Alves
63 et al., 2012), and climate change (Both and te Marvelde, 2007; Gordo, 2007; Cox, 2010; Sutherland et al.,
64 2015; Mann et al., 2017). These changing conditions can dramatically alter the costs and benefits of using a
65 stopover site during migration. However, we expect the effects of predator increase to be especially strong.

66 Migrating birds encounter a variety of potential stopover sites with differing characteristics, and navigating
67 appropriately among these sites is crucial for the successful completion of migration. Migration theory

68 (Alerstam and Lindström, 1990) describe the usage of stopover sites to include site choice, the amount of
69 fuel loaded and rate at which it is loaded (i.e. feeding intensity). Stopover usage at a site can vary based on
70 characteristics of that site, such as the density of food available and the level of danger, based on to the
71 attributes of other sites along the flyway, or even based on the condition of the migrants themselves (Weber
72 et al., 1998). Most of the time during a migration is spent at stopover sites (Hedenström and Alerstam,
73 1997), foraging to acquire the large amounts of fuel necessary to sustain the prolonged flights (Houston,
74 1998; Cimprich et al., 2005). This intensive foraging limits birds' ability to remain vigilant for predators,
75 while the heavy fuel loads that they amass further contributes to making migrants vulnerable to predator
76 attack. Habitat characteristics of stopover sites, such as the amount of cover available to predators to
77 conceal their approach, or the distance between this cover and the feeding sites used by shorebirds, make
78 the intrinsic danger of some sites greater than others (Lank and Ydenberg, 2003). When selecting sites,
79 shorebirds must balance the risk of predation with the benefits of good foraging conditions, and previous
80 studies have demonstrated that migrating sandpipers avoid sites that do not provide some element of food
81 and safety (Sprague et al., 2008; Pomeroy et al., 2008). An increase in predator abundances is expected to
82 shift the balances of these risks and rewards, and could lead to measurable changes in behaviour including
83 a shift away from dangerous stopover sites and towards safer ones (Hope, 2018).

84 Semipalmated sandpipers display many of the attributes of mortality-minimizing migrants (Hope et al.,
85 2011; Duijns et al., 2019), and hence we expect that safety is important to their stopover decisions. As
86 demonstrated by Ydenberg et al. (2004; Pomeroy et al., 2006), safer sites are those at which sandpipers
87 can feed distant from the shoreline, where cover provides falcons the opportunity for stealth hunts (Dekker
88 and Ydenberg, 2004), which are far more successful than open hunting in which peregrines have to pursue
89 prey for lengthy periods to make captures. Consequently, we predict that as predator populations increased,
90 sandpipers increasingly prioritized safety on migration and as such should have shifted their usage towards
91 the safest sites over the survey period. As semipalmated sandpipers are a gregarious species and large
92 flocks can further reduce individual vulnerability to predation we expect this shift towards safety will also
93 have led to an increase in aggregation at the safest sites.

94 We used a survey dataset of counts of sandpipers from stopover sites to determine if semipalmated
95 sandpipers changed their site preferences between 1974 and 2017. Based on the local reintroduction of
96 breeding falcons (Amirault et al., 2004) and the continental recovery of peregrine populations, we expected
97 to see a shift in bird usage towards safer sites as migrating birds increasingly prioritized the reductions
98 in predation danger afforded to birds utilizing safer sites. To quantify how sandpipers prioritized safety,
99 aggregation, and habitat availability, we developed an index of the annual distribution of birds and utilized
100 both statistical methods and simulations to diagnose whether semipalmated sandpipers adjusted stopover
101 site selection as predator abundance increased.

2 METHODS

2.1 Study region

103 The semipalmated sandpiper is a shorebird species with a hemispheric-spanning migration (Brown et al.,
104 2017). The breeding range stretches across arctic North America, and the non-breeding range across the
105 northern coast of South America south to Peru and northern Brazil (Hicklin and Gratto-Trevor, 2010).
106 Migrants moving from the breeding grounds either pass through the interior, migrate to the eastern coast of
107 North America, or fly directly to Caribbean coasts. Of those that migrate to the east coast, the Maritime
108 region of Canada holds the most numerically important staging areas (Hicklin, 1987), with numerous

109 potential stopover sites, especially around the Bay of Fundy (Garrett, 1972; Hicklin and Smith, 1984;
110 Sprague et al., 2008; Quinn and Hamilton, 2012). Migrants arrive from the central and eastern portions of
111 the breeding range, load large amounts of fuel and depart out into the Atlantic Ocean (Lank, 1983). A large
112 portion of the birds using the region migrate directly to South America in a single flight of over 4000 km
113 (Lank, 1979).

114 Migrant shorebirds passing through the Maritime region of Canada encounter both peregrines migrating
115 from their own northern breeding areas, as well as peregrines breeding locally, descended from those
116 introduced 1982 -1991 (peregrines were extirpated here by 1956; Amirault et al., 2004). At least 30 pairs
117 are currently known to breed round the Bay of Fundy (Dekker et al., 2011). Migratory peregrines begin to
118 arrive in the region in September, and overlap with the final weeks of semipalmated sandpiper migration
119 (Hope et al., 2011, Ydenberg & Lank unpublished data). Both migratory and breeding peregrines have
120 increased steadily since the mid- 1970s.

2.2 Shorebird Surveys

122 The Atlantic Canada Shorebird Survey (ACSS, named the Maritimes Shorebird Survey prior to 2005)
123 is organized by the Canadian Wildlife Service and has been conducted annually since 1974 to identify
124 important stopover sites for migrating shorebirds and to help assess population trends of these shorebird
125 species. Surveyors attempt to census sites every second weekend during the southward migration period.
126 Count methodology is described in more detail by Morrison et al. (1994; Gratto-Trevor, Smith, Morrison,
127 Aubry, and Cotter 2012; see also the ACSS survey protocol and guidelines - Environment and Climate
128 Change Canada 2014). Although protocols aim to make procedures consistent within sites across years,
129 there is substantial variability in methodology and effort among sites.

130 The data for the analysis reported here were accessed through Bird Studies Canada's Nature Counts
131 database (Environment and Climate Change Canada, 2008). We focused on semipalmated sandpiper
132 counts made 1974-2017 throughout Nova Scotia, New Brunswick, and Prince Edward Island (Figure 1).
133 Sites in Newfoundland (due to their position ancillary to the main semipalmated sandpiper migration
134 route) and those at which semipalmated sandpipers have never been recorded were excluded. We included
135 counts during the main migratory period, defined as falling within the 10th (July 28) and 90th (August
136 21) quantiles of all semipalmated sandpipers counted between July and October. After this filtering, our
137 analysis incorporated 3,030 of the 20,064 surveys, and 471 of the 769 survey sites in the full dataset.

138 Each survey site is associated with a name describing the geographic locality, and a latitude and longitude
139 in decimal degrees. To reduce possible pseudoreplication due to spatial autocorrelation, we pooled sites
140 that were within 375m of each other, reducing the 448 'sites' into 198 'locations'. To reduce any bias
141 possibly arising with variation in the number of counts per location (which tend to vary positively with the
142 number of sandpipers; Figure 2), we used the mean of all the site-surveys in a year at a location, whatever
143 the methodology, to represent that location.

2.3 Site Characteristics

145 We assigned measures of size and danger to each location. We used the area of intertidal habitat in a
146 2500m radius around each location's geographic point as the measure of location size (Figure 3); sandpipers
147 can traverse this distance in a few minutes (Reurink et al., 2016). As defined by Lank and Ydenberg (2003)
148 'danger' represents the inherent riskiness of a location (see also Hugie and Dill, 1994). Danger is indexed
149 as the proportion of the intertidal area lying within 150m of the shoreline, where foraging is most risky
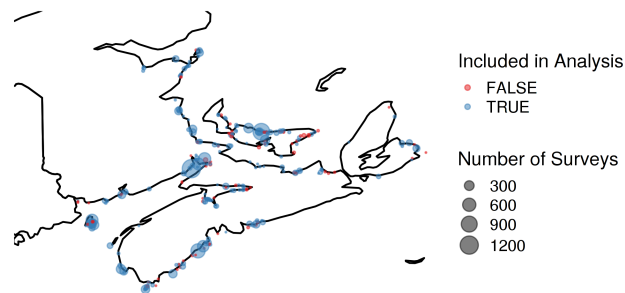
Figure 1. Map of survey locations (n = 198) from the Maritimes portion of the Atlantic Canada Shorebird Survey. The size of each point is related to the number of surveys conducted at that site. Sites that were excluded from the final analysis are shown in red (n = 77).
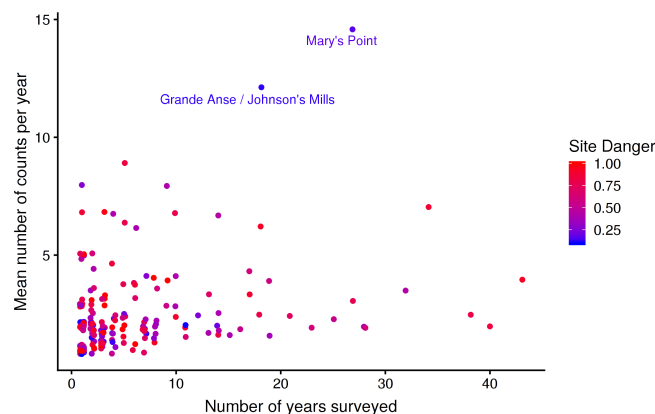

Figure 2. Number of years surveyed and the number of surveys per year for each location. The colour of the point is related to the proportion of the site within 150m of cover.

150 (Pomeroy, 2006; Dekker and Ydenberg, 2004; Pomeroy et al., 2008). The sensitivity analyses reported in
151 Figure S2 vary both the 150m danger distance, and the 2500m radius.

152   We calculated the danger index from the CanVec map layers data set produced by Natural Resources
153 Canada (acquired from:`www.GeoGratis.gc.ca`), which shows intertidal habitat and shoreline to a
154 scale of 1:50,000. We extracted a polygon of intertidal as the waterbody features labelled as 'temporary'
155 under the "Hydro" feature category within the CanVec dataset. We also extracted the highwater line layer
156 and created a buffer of 150m around that line, which was then clipped to the intertidal layer. For each
157 Universal Transverse Mercator (UTM) region, we transformed each polygon layer from original geographic
158 projection (North American Datum (NAD) 1983 CSRS; Spheroid: GRS 1980; WKID: 4617) to the UTM
159 region projection (UTM 19-22N WGS84) and clipped it to that grid. Around each site location we created
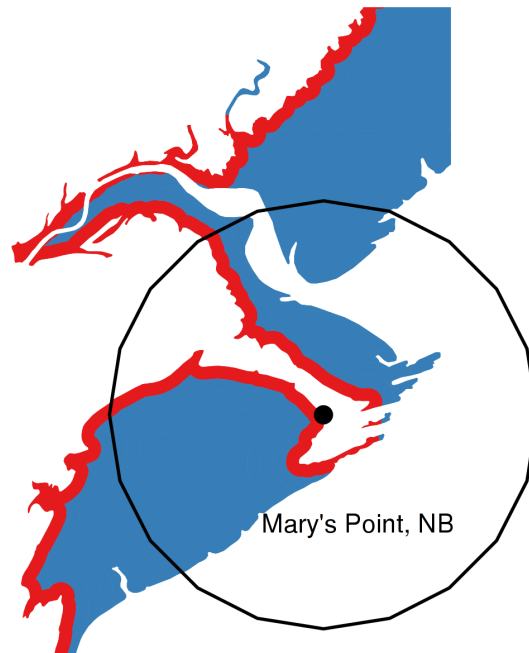
Figure 3. Example showing the safe (blue) and dangerous (red) portions of a habitat. Mary's Point, NB is shown with its geographic location highlighted by the point. The 2,500 m radius habitat circle is shown around this point. Intertidal mudflat habitat is shown in blue or red.

160 a buffer 2500m in radius and defined the area of intertidal habitat as the area of the intertidal polygons that
161 fell within that buffer (Figure 3).

2.4 Priority Matching Distribution index

163   We describe the distribution of sandpipers across locations in each year using a 'Priority Matching
164 Distribution' (PMD) index. The PMD index assesses how closely the measured distribution of sandpipers

165 matches various distribution possibilities, ranging from sandpipers aggregating at dangerous locations, to
166 spreading evenly over locations, to aggregating at safer locations (Ydenberg et al., 2017).

167 The PMD index is calculated as follows. The (mean, across all surveys) number of sandpipers censused
168 ('usage') at location i in a given year is denoted U_i. The total area of intertidal habitat at that location is
169 denoted A_i. The safety index for the site, y_i is the proportion of the site's total intertidal area that lies more
170 than 150m from the shoreline (Figure 3B).

171 For each location, we calculated the proportional area for that location in relation to the total area surveyed
172 for all locations sampled in a given year (p_i), and proportion of the total bird usage (q_i) in a given year at
173 each location i.

174 Within each year, sites are ordered from most dangerous to safest (i.e. lowest to highest safety index) so
175 that the cumulative proportion of total area surveyed up to location i is

$$cA_i = \sum_{n=1}^{i} p_n \tag{1}$$

176 where the cumulative proportional area of all k sites surveyed in a year $cA_k = 1$. Analogously, the
177 cumulative proportion of usage up to location i is calculated as

$$cU_i = \sum_{n=1}^{i} q_n \tag{2}$$

178 Calculation of the PMD index involves comparing the area under the curve ('AUC') of measured sandpiper
179 usage (Equation 2), with that expected if sandpipers are distributed in relation to the intertidal area of each
180 location (Equation 1; Figure 4). AUC is calculated using a trapezoidal function. The trapezoid function for
181 area of habitat surveyed is defined as

$$\text{AUC}_\text{A} = \sum_{i=2}^{k} \frac{(y_i - y_{i-1})(cA_i + cA_{i+1})}{2} \tag{3}$$

182 where i is a given location and $i-1$ is the next most dangerous location. For bird usage the area under the
183 distribution is calculated as

$$\text{AUC}_\text{U} = \sum_{i=2}^{k} \frac{(y_i - y_{i-1})(cU_i + cU_{i+1})}{2} \tag{4}$$

184 We used the trapezoid function because its estimate lies between that generated by the 'upper-step' and
185 'lower-step' functions. Sensitivity analyses using these step functions in place of the trapezoidal function
186 produce only minor differences in the results.

187 The Priority Matching Distribution index is calculated as

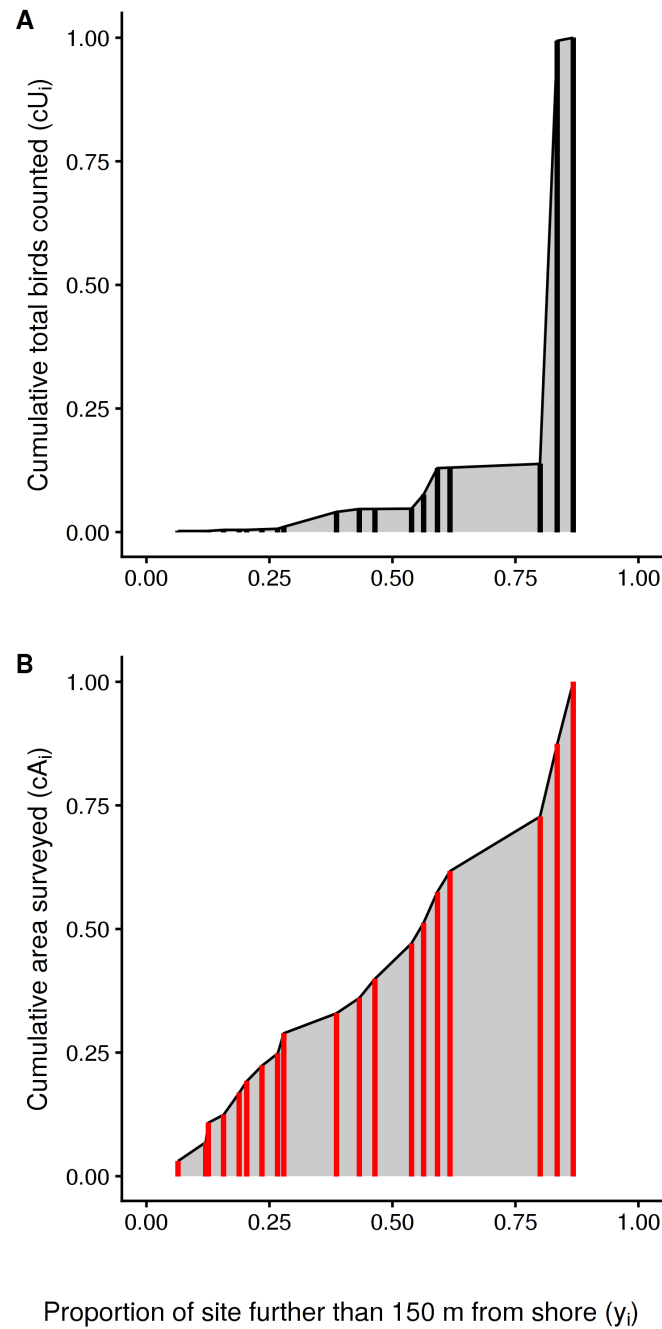$$PMD = \frac{\text{AUC}_\text{U}}{\text{AUC}_\text{A}} \tag{5}$$

Figure 4. Example of the construction of the Priority Matching Distribution index for a given year (1985 in example). The sites (red and black bars, though sites of equivalent safety will be stacked) surveyed in a year are arranged along the x-axis from dangerous to safe with the cumulative proportional usage (A; numerator of the PMD index) and intertidal area (B; denominator of the PMD index) shown by the height of the vertical bar. The grey area in each plot shows the area under the distribution (AUD) used to calculate the PMD index.

188   Values of the PMD index vary systematically with the distribution of sandpipers across locations, as
189   summarized in Table 1 and shown in Figure S1.

Table 1. Simulated values of the PMD index as the usage distribution of semipalmated sandpipers over 100 simulated census locations. A bootstrap was used to estimate 95% CI intervals.

Name	DESCRIPTION of DISTRIBUTION	lci	PMD index value	uci
Danger Aggregation	90% of usage at the most dangerous 20% of sites	1.68	2.06	2.57
Site Matching	Usage equal on all locations	1.20	1.41	1.69
Intermediate Aggregation	Aggregation on mid-safety locations	0.93	1.29	1.78
Area Matching	Usage proportional to intertidal area	1.00	1.00	1.00
Safe Area Matching	Usage proportional to safe intertidal area	0.56	0.67	0.78
Safety Aggregation	90% of usage at the safest 20% of sites	0.19	0.29	1.24

2.5 Analysis

190
191   Locations vary in the number of surveys, both within and between years (Figure 2), with some missed
192   entirely in some years. To examine the potential influence of individual locations we calculated the PMD
193   index with and without each location ('leverage', see Table 2). Based on this, we excluded from the analysis
194   10 of 44 years that did not include surveys at least one of the two most surveyed locations, namely Mary's
195   Point, NB (45.72°N, 64.65°W) and Johnsons Mills, NS (45.81°N, 64.5°W). We calculated and analyzed
196   trends in the PMD with both locations excluded to ensure the results were not driven entirely by these
197   locations (see Figure S2). We also excluded 1995, which had an extremely high count at a site surveyed in
198   no other year that had a strong influence on the annual PMD. Our final data set included 3,030 surveys
199   at 198 stopover locations, made 1974-2017 (excluding 1990, 1991, 1995, 1998, 2008, 2010, 2011, 2013,
200   2014).

Table 2. Sites with the most influence on the Priority Matching Distribution index across all years within the survey dataset. Leverage is defined as the total difference in the PMD index with and without each location across all survey years.

Site Name	Danger	Area (km^2)	Number of Years	Leverage
Mary's Point	0.16	7.90	27	426.03
Grande Anse / Johnson's Mills	0.12	6.95	18	232.54
Saints Rest Marsh and Beach	0.61	2.16	17	9.16
Economy	0.20	5.90	14	4.80
Daniels Flats	0.10	8.82	11	3.03
Selma	0.13	8.38	3	2.93
Little Dyke	0.13	6.71	4	2.68
Cape Sable (Hawk Flats)	0.41	3.36	28	2.61
Egmont Bay (lower Bedeque area)	0.19	4.00	1	2.54
Daniel Head	0.91	0.51	10	2.41
Bedeque Bay	0.27	5.07	7	2.37
Cooks Beach	0.62	6.03	28	1.58
Lusbys Marsh/John Lusby Saltmarsh	0.11	6.40	2	1.36

201   Our analysis focused on two questions: 1) how do semipalmated sandpipers distribute across potential
202   stopover locations?, and 2) has the distribution of semipalmated sandpipers changed systematically since
203   surveys began in 1974? We calculated the PMD index for each survey year. We examined annual change
204   using a linear model, centred and rescaled by year to provide a meaningful intercept and provide a more
205   accurate effect size (Gelman and Hill, 2006). We used Akaike Information Criterion (AIC) to compare
206   support for a linear trend by competing a null model, a linear interannual trend model, a model with a
207   quadratic term, and a model with the log of the interannual trend. We assessed the fit to the linear trend by

208 bootstrapping the original count data to compute 95% confidence intervals of the intercept and interannual
209 trend estimates.

210   Chronological trends in site survey dates or danger indices could bias our results. We examined the
211 sensitivity of the results to the temporal distribution of these factors to explore this possibility. To explore
212 the assumptions behind the PMD we modified the estimation of the index by changing the radius around
213 each point used to calculate A_i from 2.5km to 1km and 5km, and modifying the distance from shore that
214 was classified as dangerous from 150m to 50m, 300m, and 450m. We also expanded the dates of surveys
215 to include the 60th, 90th, 95th, 98th quantiles of dates, and with all surveys between July and October.
216 To separate out the potential that any shift was driven by site size and not site safety, we modified the
217 calculation of the PMD index by arranging sites from smallest to largest instead of most dangerous to
218 safest. We also recalculated the PMD in each year excluding Mary's Point and Johnsons Mills. To control
219 for the site bias towards a greater number of dangerous sites in later years we binned sites into 0.1 bins of
220 safety y_i. We sampled one site from each bin in each year, creating equal numbers of sites in all years. We
221 resampled 1000 times and calculated the slope and intercept of the calculated PMD for each draw. Finally,
222 we simulated the impact of sea level rise by reducing the total area of habitat available by the rate described
223 in Murray et al. (2019), recalculating the danger index and redistributing total number of birds counted
224 in that year across the site using a $Beta(1, 14)$ distribution. For each simulation we calculated the PMD
225 for each year and recalculated the intercept and rate of change in the linear interannual trend model. The
226 results of these simulations and modifications of the PMD are described in Figure S2

3   RESULTS

3.1   Location Characteristics

228   The 198 locations are arrayed over 4.6 degrees of latitude and 7.2 degrees of longitude, and are located
229 mostly around of Bay of Fundy (mean: 46°N, -64°W; Figure 1). They range in size from 0.002 km^2 to
230 11 km^2, with a mean of 3 km^2. Danger indices ranged from 0.098 to 1.0 with a mean of 0.57. Most are
231 small and relatively dangerous (Figure 5). On average, 27 locations were censused per year (range 12 - 44),
232 averaging 3.2 surveys each per year (range 1.9-4.3). More surveys were conducted at large, safe locations
233 (Figure 2 and Figure 6). The total annual count (summed over all locations) of semipalmated sandpipers
234 varies between 35,636 birds (1987) and 421,982 birds (1992) with a mean of 100,486, and no trend across
235 years (β=0.0021 [-0.018, 0.021], using a log link).

3.2   Sandpiper distribution

237   Annual PMD index values range from 0.61 to 0.11 with an overall mean of 0.3 (95% CI [0.28, 0.36]).
238 None of the confidence intervals of the annual PMD index values overlap one and most estimates of the
239 PMD index are well below 0.50 indicating that semipalmated sandpipers aggregate at safer locations
240 (Figure 7). The overall annual mean value of 0.3 corresponds with that expected when 90% of usage occurs
241 at the safest 20% of locations (see Table 1).

242   Linear and log-linear models both estimate a decline in the PMD index over years (Table 3), and have
243 approximately equal support from the data ($w_i = 0.37$ and $w_i = 0.45$ respectively). The quadratic model is
244 less well supported ($w_i = 0.16$), and the null model not at all ($w_i = 0.019$). There is little deviation from
245 linearity in the estimated trends for the log-linear model, and we therefore consider only the linear model.
246 It shows that the PMD index falls at a standardized rate of -0.11 (95% CIs [-0.18, -0.034]) per SD of years
247 (13 y), equivalent to -0.004 per year, for a 0.18-point decline in the PMD index between 1974 and 2017.
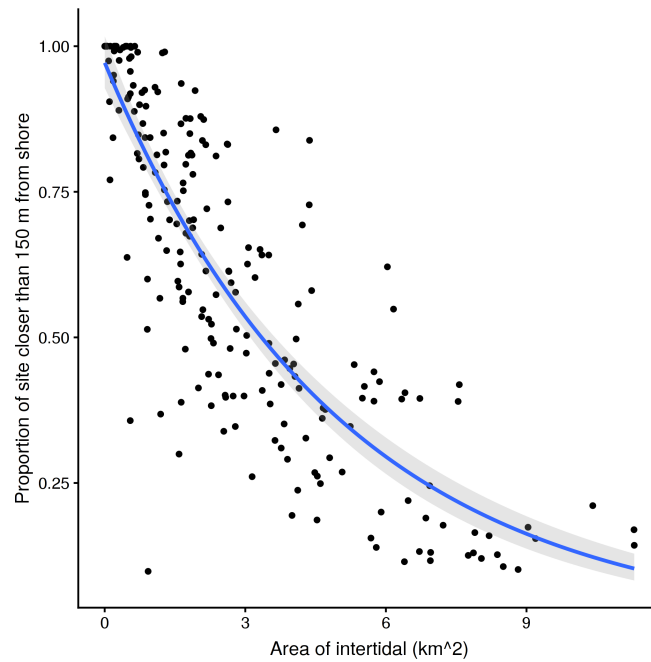
Figure 5. Location danger as a function of size. The fitted line shows the log-linear trend of danger with intertidal area. Larger sites are generally less dangerous, but the danger index varies widely between sites of a given size.

Table 3. Support for models of interannual trends in the Priority Matching Distribution. Models other than the null model use a centred and standardized variable for Year. The log-linear model is a linear generalized linear model with a log link function for the gaussian distribution. All other models are linear models with the identity link function. We used AICc values to correct for biases in the Akaike's information criterion in models with low sample sizes, log(L) is the log-likelihood value, $\triangle_i$ is the difference in AICc value from that of the top model (i.e., lowest AICc), K is the number of parameters in each model and w_i is the Akaike weight. r^2 are listed to show improvement of model fit between null and fitted model

Interannual Trend	log(L)	$\triangle_i$	K	w_i	r^2
Log Linear	30.28	0.00	3.00	0.45	
Linear	30.08	0.40	3.00	0.37	0.21
Quadratic	30.52	2.09	4.00	0.16	0.23
None	25.94	6.29	2.00	0.02	0.00

AICc = -53.79; n = 35

248 This decline could be created either by (i) birds crowding into fewer sites (90% of birds at the 27% (1974)
249 safest sites, shifting to the 13% (2017) safest sites); (ii) more birds crowding into the 20% safest sites
250 (from 80% of birds in 1974 to 97% in 2017); (iii) or some combination of the two. Despite the extensive
251 variability in methodology and the irregular coverage, the regression provides a reasonable fit ($r^2 = 0.21$)
252 to the data.

253 The sensitivity analyses demonstrate that the variation in the number or danger levels of the sites surveyed
254 each year do not bias the PMD index estimates, and are therefore unlikely to explain the interannual trend.
255 Likewise, the modifications to the assumptions governing either the selection of data or underlying the
256 PMD calculation do not alter the results (Figure S2). Simulating a response to sea-level rise (i.e. sites
257 becoming smaller), or limiting the counts to the peak of migration (20-60th quantile of counts) erases the
258 interannual trend in the PMD. Importantly, when locations are ranked 'small to large' rather than 'safe to
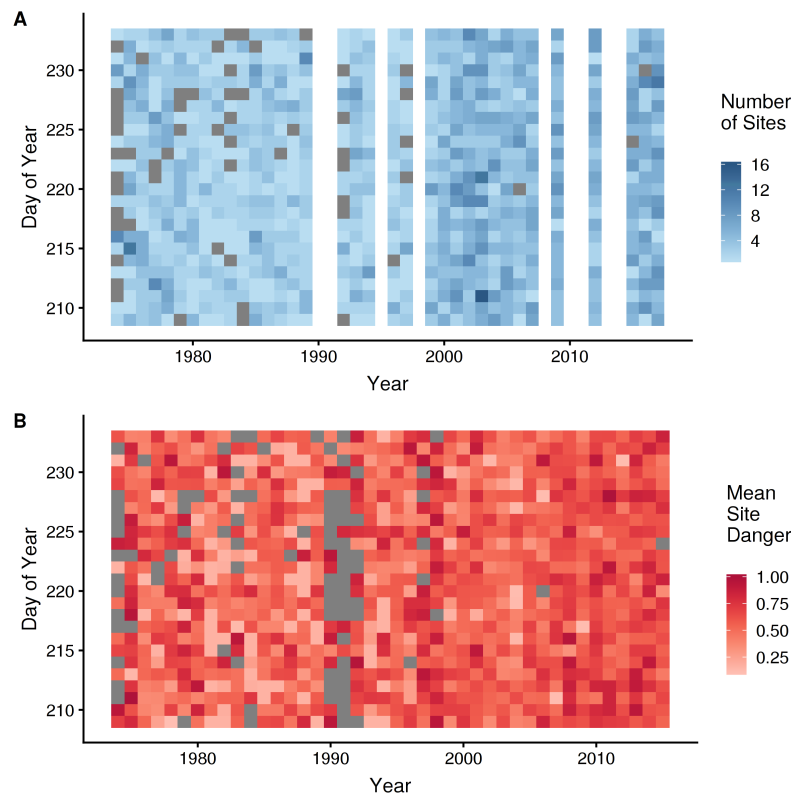
Figure 6. Biases and variation in site survey effort across years and dates. (A) Number of sites surveyed in a given day across years where darker blue shows more sites surveyed on a given day of year in a year. (B) Mean danger of sites surveyed in a given day across years where red indicates more dangerous sites surveyed for a given day and green shows safer sites surveyed on that day. Grey represents zero surveys in both figures.

dangerous' (the "Area Sorted PMD" analysis), the temporal trend is eliminated altogether, showing that the PMD index shift is not the result of a move to larger sites, but indeed a shift towards safer sites (interannual trend: 0.0049 95% CI[-0.11, 0.12];Figure S2). Binning the sites did not change the mean interannual trend of the PMD index (-0.07), but it did decrease the precision (95% CI[-0.16, 0.034]. This is not surprising as, we drew only one site per bin per year and therefore there should be a greater variation between draws depending on the sites drawn.

4 DISCUSSION

Our results show that semipalmated sandpipers aggregate at the safest migratory stopovers, and that this distribution has shifted since 1974 towards stronger aggregation at safer sites. Extensive sensitivity analyses establish that this shift is specifically toward sites of higher safety rather than larger size. Further, the shift cannot be accounted for by inclusion (or exclusion) of the two sites exerting most leverage (Mary's Point and Johnson's Mills; see Table 2), by possible confounds arising from habitat reduction, by the selection of survey dates included in the analysis, or by modifications in the definitions of site size and danger (Figure S2).

The shift in semipalmated sandpiper distribution matches our predicted response to the well-established increase in continental falcon populations. Of particular note is the introduction of captive-reared peregrines in the 1970s and '80s to major stopover areas such as the Bay of Fundy (Dekker et al., 2011) and Delaware
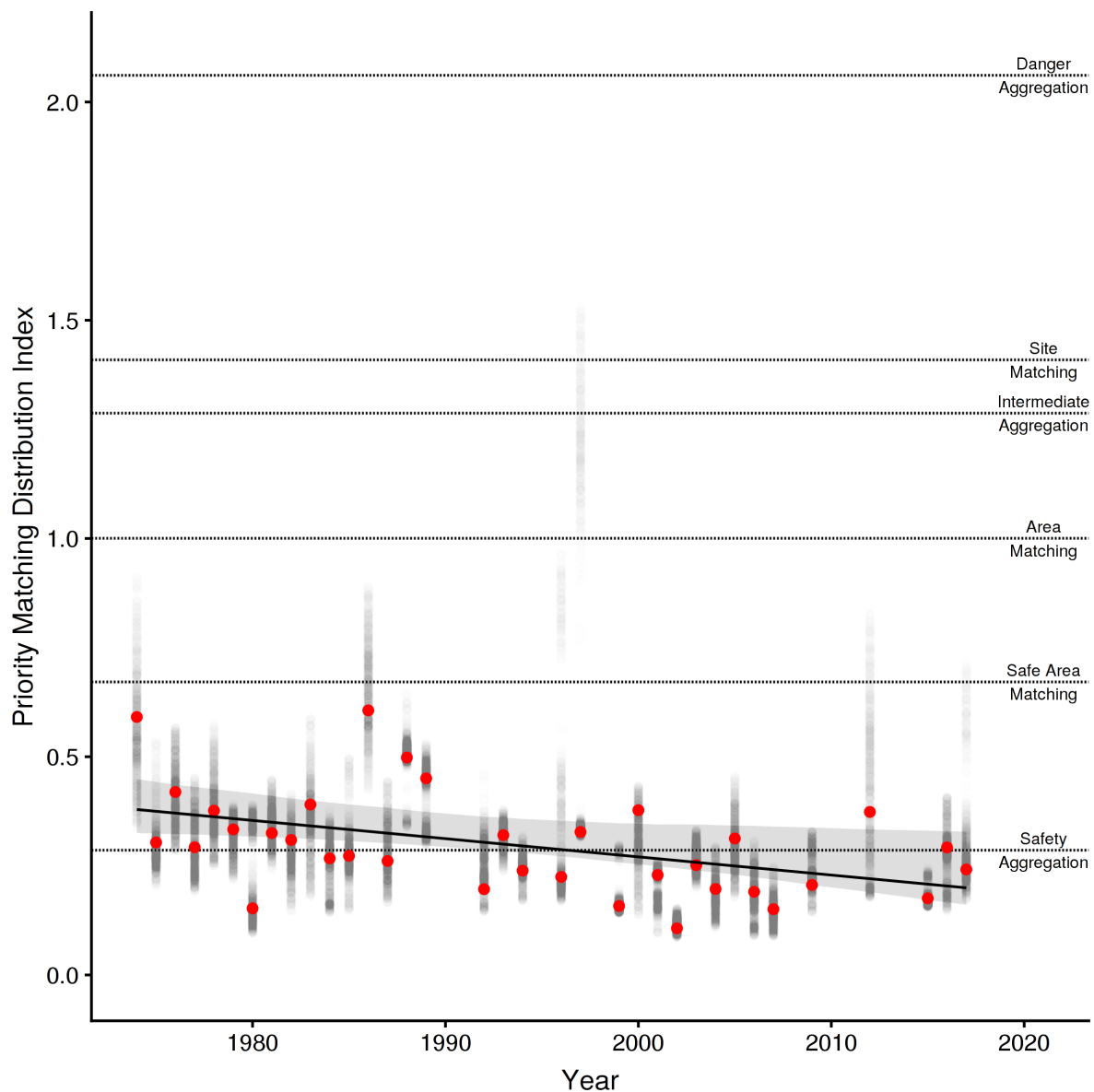
Figure 7. Interannual trend in the Priority Matching Distribution index (PMD) with the 95% bootstrapped confidence intervals. Points are the PMD for each year (red points) with the 95th inner quantiles of variation in the estimate shown in the grey points. The expected distributions for site-matching, area-matching, safe-area-matching, and safe and danger aggregation are shown as horizontally dashed lines.

275   and Chesapeake Bays and their environs (Watts et al., 2015), where scores of pairs now breed. With a
276   home range estimated to be between 123 and 1175 km^2 and a daily range of 23 km^2 around the breeding
277   locations (Enderson and Craig, 1997; Jenkins and Benn, 1998; Ganusevich et al., 2004), the effect of falcon
278   reintroduction is widespread throughout both regions.

279   For most of the twentieth century, these regions were essentially predator-free during the sandpiper
280   passage, so stopover site choices and behaviour by migrant sandpipers could be based primarily on
281   food availability and ignore the danger posed by falcons. In fact, during the late 1970s, some individual
282   semipalmated sandpipers at Kent Island in the Bay of Fundy were so encumbered by the fat they had
283   accumulated that they could be captured by gulls (Lank, 1983). But as reported for western sandpipers in

284 the Strait of Georgia (Ydenberg et al., 2004), semipalmated sandpiper fuel loads in the Bay of Fundy have
285 decreased at small dangerous locations such as Kent Island, but not at large locations such as Johnson's
286 Mills (Hope, 2010). This shift is attributed to the reduced predator escape performance induced by large
287 fuel loads (Burns and Ydenberg, 2002), consistent with the hypothesis that stopover site choices depend on
288 the trade off between fuel loading and predation danger (Pomeroy et al., 2008; Taylor et al., 2007). The
289 locations at which sandpipers aggregate are relatively safe, even when their large size is considered. As the
290 number of falcons increases, the extra benefit that habitat safety provides, no matter how small, should
291 become increasingly important. The marginal benefit to spending time in dangerous habitat has likely been
292 reduced as predator numbers have increased.

293   Aggregating in large groups also has the benefits of reducing the likelihood of being selected by a predator
294 (dilution) and increased detection of predator attacks (many eyes Roberts, 1996; Bednekoff and Lima,
295 1998; Fernández-Juricic et al., 2007; Pays et al., 2013). With predation dilution can also come increased
296 competition during foraging (Stillman et al., 1997; Vahl et al., 2005; Minderman et al., 2006). While the
297 Bay of Fundy provides rich and widespread food for refuelling sandpipers, competitive interactions that
298 reduce foraging efficiency still occur at small scales (Vahl, 2005; Beauchamp, 2009, 2014). For most
299 semipalmated sandpipers, the benefits of large aggregations appear to outweigh the costs to foraging
300 efficiency.

301   Migrant sandpipers have previously been shown to be sensitive to predation danger on migration. The
302 migratory behaviours that shift in response to predation include flock size, vigilance, over-ocean flocking
303 during high tides, length of stay at dangerous locations, location selection, habitat selection within a
304 location, and fuel load (Dekker, 1998; Ydenberg et al., 2004; Pomeroy, 2006; Pomeroy et al., 2008;
305 Sprague et al., 2008). On a longer time scale, wing lengths of semipalmated sandpipers and other small
306 shorebirds utilizing the Bay of Fundy have shortened, enhancing escape performance (Lank et al., 2017;
307 Anderson et al., 2019). Migrant sandpipers also change their behaviour within seasons based on their
308 geographic position relative to that of their temporal proximity to the arrival of migrant peregrines (Hope
309 et al., 2014, 2011).

310   Food and danger both influence location usage in semipalmated and western sandpipers (Pomeroy et al.,
311 2008; Sprague et al., 2008), and changes in either could contribute to the shift in distribution measured here.
312 If locations were to experience a uniform increase in food abundance, or if they become more uniform in
313 their food abundance, sandpipers could find the marginal benefit of visiting a dangerous, but food abundant
314 location to be reduced and shift towards safer locations. *Corophium volutator*, a major prey item for
315 semipalmated sandpipers in the Bay of Fundy, appears to vary in abundance between locations and within
316 each year, but variation between years does not appear to be substantial (Barbeau et al., 2009), though other
317 studies have shown variation between years when looking at a wider array of potential food sources (Quinn
318 and Hamilton, 2012). It appears that semipalmated sandpipers have a lot of flexibility in their food sources
319 (Quinn et al., 2017), meaning that a change in one prey type abundance at a location could be compensated
320 by other potential food sources. We found no evidence for a longer-term trend in food overall abundance or
321 a hypothesised change within the literature that would lead to a shift in sandpiper distributions.

322   Recent analyses of shorebird population censuses including breeding, migration as well as non-breeding
323 surveys all point to decreases since the 1970s in many species, including Semipalmated Sandpipers (Bart
324 et al., 2007; Andres et al., 2012; Gratto-Trevor et al., 2012; Smith et al., 2012; Morrison et al., 2012). A
325 population decline (or increase) would not change the value of the PMD index unless accompanied by a
326 change in the distribution of usage across sites, because the PMD index depends only on the distribution,
327 and is independent of the numbers of birds. Hence a population decline could not on its own explain the

328 PMD trend reported here. Simulation modelling of other migratory systems has suggested that a population
329 decline does not necessarily lead to redistribution (Taylor et al., 2007), if stopover densities of birds are
330 below the sites' carrying capacities. A population decline could alter the food/safety trade-off at different
331 sites by affecting dilution benefits or the intensity of food competition. But depending on the distribution
332 of the quality (size, danger and food density) of stopover sites, this could drive the PMD index either up or
333 down (see discussion on redistribution in Ydenberg et al., 2017).

334 In conclusion, semipalmated sandpipers aggregate in large numbers at a few large and safe sites and have
335 increasingly shifted towards aggregating at the safest sites between 1974 and 2018. The detection of the
336 shift highlights the potential for stopover distributions to shift, and distributions should not be assumed to
337 be static in population trend analyses. We attribute the observed trend as a response to increased predator
338 populations and the reintroduction of predators into the migratory route. An increasing list of studies
339 highlight the important role that predators play in shaping the lives of their prey, and we believe predation
340 danger is likely influencing stopover decisions in this Maritime flyway. While biases do have the potential
341 to affect our priority matching distribution index, our results are robust to most moderate biases, and this
342 index can be used (with relevant checks of its assumption) to explore migratory distributions in a number
343 of settings. The next step is to explore other landscapes and other species to see if a similar pattern holds.

CONFLICT OF INTEREST STATEMENT

344 The authors declare that the research was conducted in the absence of any commercial or financial
345 relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

346 DH, RY, and DL conceived of the study. PS and JP provided advice on the data use to fit with the study
347 goals. JP organized data collection and cleaning. DH, with RY and DL designed the PMD index. DH
348 performed the analysis, simulations. DH, RY, and DL wrote the paper with input from PS and JP.

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