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

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# 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 that overlap with falcons, 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

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

These responses can create impacts on prey populations, competitors, and other trophic levels, together termed 'risk effects'. Over the past two decades it has become increasingly apparent that risk effects can propagate through entire ecosystems (e.g. Schmitz, Krivan & Ovadia, 2004). The risk effects on prey populations stemming from the large and expanding influence of humans on the planets oceans, particularly the great reductions in the abundance of top predators are well documented (Madin *et al.*, 2016; Myers & Worm, 2003). Heithaus *et al.* (2008) documented many novel repercussions of changing marine predator abundances (see also Estes *et al.*, 2011; Babcock *et al.*, 2010). Much of what is known about these effects relates to lethal effects (i.e. mortality inflicted directly by predators).

In contrast, the risk effects (e.g. influences of predator presence on prey behaviour and morphology; see Madin *et al.*, 2016, Box 1) are not as well studied, despite many advances in the past decade from the experimental literature (reviewed by Long & Hay, 2012).

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

Prey species have responded to this increased predator abundance in a variety of ways. The recovery of bald eagles (*Haliaeetus leucocephalus*) caused seabirds to shift to safer breeding locations within colonies, and to shift distributions between breeding colonies based on exposure to predators (Hipfner *et al.*, 2012). The increased presence of white-tailed sea eagles (*Haliaeetus alba*) in the Baltic Sea caused barnacle geese (*Branta leucopsis*) to alter migration timing and to shorten the duration of parental care (Jonker *et al.*, 2010). Falcon recovery drove Pacific dunlins (*C. alpina pacifica*) to lose their mid-winter fat store (in order to maintain escape performance), and to take up over-ocean flocking in place of roosting at high tide (Ydenberg *et al.*, 2010), and to shift the non-breeding distribution toward greater aggregation at safer sites (Ydenberg *et al.*, 2017). Wing lengths of semipalmated sandpipers (*C. pusilla*) and other calidridines shortened 1980 - 2015 as peregrine numbers increased, potentially due to selection for better predator

escape performance (Lank *et al.*, 2017; Anderson *et al.*, 2019). The risk effects, both direct and indirect, of these responses are unstudied as yet, but might be substantial.

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

Migrating birds encounter a variety of potential stopover sites with differing characteristics, and navigating appropriately among these sites is crucial for the successful completion of migration. Migration theory (Alerstam & Lindström, 1990) describe the usage of stopover sites to include site choice, the amount of fuel loaded and rate at which it is loaded (i.e. feeding intensity). Stopover usage at a site can vary based on characteristics of that site, such as the density of food available and the level of danger, based on to the attributes of other sites along the flyway, or even based on the condition of the migrants themselves (Weber, Ens & Houston, 1998). Most of the time during a migration is spent at stopover sites (Hedenström & Alerstam, 1997), foraging to acquire the large amounts of fuel necessary to sustain the prolonged flights (Houston, 1998; Cimprich, Woodrey

& Moore, 2005). This intensive foraging limits birds' ability to remain vigilant for predators, while the heavy fuel loads that they amass further contributes to making migrants vulnerable to predator attack. Habitat characteristics of stopover sites, such as the amount of cover available to predators to conceal their approach, or the distance between this cover and the feeding sites used by shorebirds, make the intrinsic danger of some sites greater than others (Lank & Ydenberg, 2003). When selecting sites, shorebirds must balance the risk of predation with the benefits of good foraging conditions, and previous studies have demonstrated that migrating sandpipers avoid sites that do not provide some element of food and safety (Sprague, Hamilton & Diamond, 2008; Pomeroy *et al.*, 2008). An increase in predator abundances is expected to shift the balances of these risks and rewards, and could lead to measurable changes in behaviour including a shift away from dangerous stopover sites and towards safer ones (Hope, 2018).

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

in aggregation at the safest sites.

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

# Methods

## Study region

The semipalmated sandpiper is a shorebird species with a hemispheric-spanning migration (Brown *et al.*, 2017). The breeding range stretches across arctic North America, and the non-breeding range across the northern coast of South America south to Peru and northern Brazil (Hicklin & Gratto-Trevor, 2010). Migrants moving from the breeding grounds either pass through the interior, migrate to the eastern coast of North America, or fly directly to Caribbean coasts. Of those that migrate to the east coast, the Maritime region of Canada holds the most numerically important staging areas (Hicklin, 1987), with numerous potential stopover sites, especially around the Bay of Fundy (Garrett, 1972; Hicklin & Smith, 1984;

Sprague, Hamilton & Diamond, 2008; Quinn & Hamilton, 2012). Migrants arrive from the central and eastern portions of the breeding range, load large amounts of fuel and depart out into the Atlantic Ocean (Lank, 1983). A large portion of the birds using the region migrate directly to South America in a single flight of over 4000 km (Lank, 1979).

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

## Shorebird Surveys

The Atlantic Canada Shorebird Survey (ACSS, named the Maritimes Shorebird Survey prior to 2005) is organized by the Canadian Wildlife Service and has been conducted annually since 1974 to identify important stopover sites for migrating shorebirds and to help assess population trends of these shorebird species. Surveyors attempt to census sites every second weekend during the southward migration period. Count methodology is described in more detail by Morrison et al. (1994; Gratto-Trevor, Smith, Morrison, Aubry & Cotter 2012; see also the ACSS survey protocol and guidelines - Environment and Climate Change Canada 2014).

Although protocols aim to make procedures consistent within sites across years, there is substantial variability in methodology and effort among sites.

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

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

## Site Characteristics

We assigned measures of size and danger to each location. We used the area of intertidal habitat in a 2500m radius around each location's geographic point as the measure of location size (Figure 3); sandpipers can traverse this distance in a few minutes (Reurink *et al.*, 2016). As defined by Lank & Ydenberg (2003) 'danger' represents the inherent riskiness of a location (see also Hugie & Dill, 1994). Danger is indexed as the proportion of the intertidal area lying within 150m of the shoreline, where foraging is most risky (Pomeroy, 2006; Dekker & Ydenberg, 2004; Pomeroy *et al.*, 2008). The sensitivity analyses reported in the Appendix vary both the 150m danger distance, and the 2500m radius.

We calculated the danger index from the CanVec map layers data set produced by Natural Resources Canada (acquired from:`www.GeoGratis.gc.ca`), which shows intertidal habitat and shoreline to a scale of 1:50,000. We extracted a polygon of intertidal as the waterbody features labelled as temporary under the Hydro feature category within the CanVec dataset. We also extracted the highwater line layer and created a buffer of 150m around that line, which was then clipped to the intertidal layer. For each Universal Transverse Mercator (UTM) region, we transformed each polygon layer from original geographic projection (North American Datum (NAD) 1983 CSRS; Spheroid: GRS 1980; WKID: 4617) to the UTM region projection (UTM 19-22N WGS84) and clipped it to that grid. Around each site location we created a buffer 2500m in radius and defined the area of intertidal habitat as the area of the intertidal polygons that fell within that buffer (Figure 3).

## Priority Matching Distribution index

We describe the distribution of sandpipers across locations in each year using a 'Priority Matching Distribution' (PMD) index. The PMD index assesses how closely the measured distribution of sandpipers matches various distribution possibilities, ranging from sandpipers aggregating at dangerous locations, to spreading evenly over locations, to aggregating at safer locations (Ydenberg *et al.*, 2017).

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

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

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

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

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

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

Calculation of the PMD index involves comparing the area under the curve

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

$$\mathrm{AUC_A} = \sum_{i=2}^{k} \frac{(y_i - y_{i-1})(cA_i + cA_{i+1})}{2} \tag{3}$$

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

$$\mathrm{AUC_U} = \sum_{i=2}^{k} \frac{(y_i - y_{i-1})(cU_i + cU_{i+1})}{2} \tag{4}$$

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

The Priority Matching Distribution index is calculated as

$$PMD = \frac{\mathrm{AUC_U}}{\mathrm{AUC_A}} \tag{5}$$

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

## Analysis

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

Our analysis focused on two questions: 1) how do semipalmated sandpipers distribute across potential stopover locations?, and 2) has the distribution of semipalmated sandpipers changed systematically since surveys began in 1974? We calculated the PMD index for each survey year. We examined annual change using a linear model, centred and rescaled by year to provide a meaningful intercept and provide a more accurate effect size (Gelman & Hill, 2006). We used Akaike Information Criterion (AIC) to compare support for a linear trend by competing a null model, a linear interannual trend model, a model with a quadratic term, and a model with the log of the interannual trend. We assessed the fit to the linear trend by bootstrapping the original count data to compute 95% confidence intervals of the intercept and interannual trend estimates.

Chronological trends in site survey dates or danger indices could bias our results. We examined the sensitivity of the results to the temporal distribution of these factors to explore this possibility. To explore the assumptions behind the PMD we modified the estimation of the index by changing the radius around each point used to calculate $A_i$ from 2.5km to 1km and 5km, and modifying the distance from shore that was classified as dangerous from 150m to 50m, 300m, and 450m. We also expanded the dates of surveys to include the 60th, 90th, 95th, 98th quantiles of dates, and with all surveys between July and October. To separate out the potential that any shift was driven by site size and not site safety, we modified the calculation of the PMD index by arranging sites from smallest to largest instead of most dangerous to safest. We also recalculated the PMD in each year excluding Mary's Point and Johnsons Mills. To control for the site bias towards a greater number of dangerous sites in later years we binned sites into 0.1 bins of safety $y_i$. We sampled one site from each bin in each year, creating equal numbers of sites in all years. We resampled 1000 times and calculated the slope and intercept of the calculated PMD for each draw. Finally, we simulated the impact of sea level rise by reducing the total area of habitat available by the rate described in Murray *et al.* (2019), recalculating the danger index and redistributing total number of birds counted in that year across the site using a $Beta(1, 14)$ distribution. For each simulation we calculated the PMD for each year and recalculated the intercept and rate of change in the linear interannual trend model. The results of these simulations and modifications of the PMD are described in Figure A.2

# Results

## Location Characteristics

The 198 locations are arrayed over 4.6 degrees of latitude and 7.2 degrees of longitude, and are located mostly around of Bay of Fundy (mean: 46°N, -64°W; Figure 1). They range in size from 0.002 $km^2$ to 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 small and relatively dangerous (Figure 5). On average, 27 locations were censused per year (range 12 - 44), averaging 3.2 surveys each per year (range 1.9-4.3). More surveys were conducted at large, safe locations (Figure 2 and Figure 6). The total annual count (summed over all locations) of semipalmated sandpipers varies between 35,636 birds (1,987) and 421,982 birds (1,992) with a mean of 100,486, and no trend across years ($\beta$=0.0021 [-0.018, 0.021], using a log link).

## Sandpiper distribution

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

Linear and log-linear models both estimate a decline in the PMD index over years (Table 3), and have approximately equal support from the data ($w_i = 0.37$ and $w_i = 0.45$ respectively). The quadratic model is less well supported ($w_i =$

0.16), and the null model not at all ($w_i = 0.019$). There is little deviation from linearity in the estimated trends for the log-linear model, and we therefore consider only the linear model. It shows that the PMD index falls at a standardized rate of -0.11 (95% CIs [-0.18, -0.034]) per SD of years (13 y), equivalent to -0.004 per year, for a 0.18-point decline in the PMD index between 1974 and 2017. This decline could be created either by (i) birds crowding into fewer sites (90% of birds at the 27% (1974) safest sites, shifting to the 13% (2017) safest sites); (ii) more birds crowding into the 20% safest sites (from 80% of birds in 1974 to 97% in 2017); (iii) a population decline some combination of the two. Despite the extensive variability in methodology and the irregular coverage, the regression provides a reasonable fit ($r^2 = 0.21$) to the data.

The sensitivity analyses demonstrate that the variation in the number or danger levels of the sites surveyed each year do not bias the PMD index estimates, and are therefore unlikely to explain the interannual trend. Likewise, the modifications to the assumptions governing either the selection of data or underlying the PMD calculation do not alter the results (Figure A.2). Simulating a response to sea-level rise (i.e. sites becoming smaller), or limiting the counts to the peak of migration (20-60th quantile of counts) erases the interannual trend in the PMD. Importantly, when locations are ranked 'small to large' rather than 'safe to 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 A.2). 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.

# 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 (Marys Point and Johnsons 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 A.2).

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

For most of the twentieth century, these regions were essentially predator-free during the sandpiper passage, so stopover site choices and behaviour by migrant sandpipers could be based primarily on food availability and ignore the danger

posed by falcons. In fact, during the late 1970s, some individual semipalmated sandpipers at Kent Island in the Bay of Fundy were so encumbered by the fat they had accumulated that they could be captured by gulls (Lank, 1983). But as reported for western sandpipers in the Strait of Georgia (Ydenberg *et al.*, 2004), semipalmated sandpiper fuel loads in the Bay of Fundy have decreased at small dangerous locations such as Kent Island, but not at large locations such as Johnson's Mills (Hope, 2010). This shift is attributed to the reduced predator escape performance induced by large fuel loads (Burns & Ydenberg, 2002), consistent with the hypothesis that stopover site choices depend on the trade off between fuel loading and predation danger (Pomeroy *et al.*, 2008; Taylor *et al.*, 2007). The locations at which sandpipers aggregate are relatively safe, even when their large size is considered. As the number of falcons increases, the extra benefit that habitat safety provides, no matter how small, should become increasingly important. The marginal benefit to spending time in dangerous habitat has likely been reduced as predator numbers have increased.

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

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

Food and danger both influence location usage in semipalmated and western sandpipers (Pomeroy *et al.*, 2008; Sprague, Hamilton & Diamond, 2008), and changes in either could contribute to the shift in distribution measured here. If locations were to experience a uniform increase in food abundance, or if they become more uniform in their food abundance, sandpipers could find the marginal benefit of visiting a dangerous, but food abundant location to be reduced and shift towards safer locations. *Corophium volutator*, a major prey item for semipalmated sandpipers in the Bay of Fundy, appears to vary in abundance between locations and within each year, but variation between years does not appear to be substantial (Barbeau *et al.*, 2009), though other studies have shown variation between years when looking at a wider array of potential food sources (Quinn & Hamilton, 2012). It appears that semipalmated sandpipers have a lot of flexibility in their food sources (Quinn, Hamilton & Hebert, 2017), meaning that a change in one prey type abundance at a location could be compensated by other potential

food sources. We found no evidence for a longer-term trend in food overall abundance or a hypothesised change within the literature that would lead to a shift in sandpiper distributions.

The size of the sandpiper population moving through the region could influence the distribution of birds across locations. Analyses of migratory census counts suggest there has been a sharp decrease in the population size since the 1970s, though the decline may have begun to reverse in recent years (Bart *et al.*, 2007; Andres *et al.*, 2012; Gratto-Trevor *et al.*, 2012). There is also evidence from both the breeding and non-breeding grounds suggestive of a decline in the sandpipers population (Smith *et al.*, 2012; Morrison *et al.*, 2012). Owing to biases and variation in survey effort and methodology, and due to the large area that encompasses these portions of the semipalmated sandpipers life cycle, it has been difficult to determine with certainty the population consequences of these survey declines, but a true population decline could shape the distribution across locations under specific conditions. For example, a reduction in the number of birds moving through a region could allow a greater proportion of birds to occupy the most preferred sites. If these preferred sites happened to be also the safest, the observed distribution shift should appear similar to one caused by increasing predator abundance. Simulation modelling of other migratory systems has suggested that population declines do not necessarily lead to redistributions across migratory site types (Taylor *et al.*, 2007), if migratory stopover densities of birds are below the sites carrying capacities. The Government of Canadas index of semipalmated sandpiper population (Government of Canada, 2014) shows a correlated decline with our shift in the PMD index, but these are generated from the same data set, which complicates any interpretation. Repeating the analysis using data from other parts of the fly-

way without resident falcons might elucidate the underlying cause of the measured redistribution in bird usage.

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

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# Tables

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 |

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 |

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

# Figures

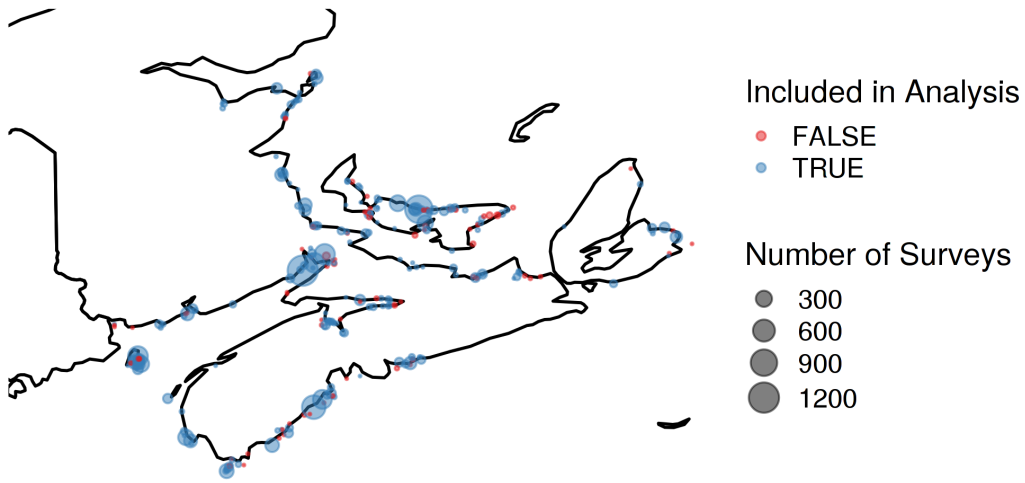


Figure 1: Map of survey locations (n = 198) from the Maritimes portion of the Atlantic Canada Shorebird Survey. The size of each point is related to the number of surveys conducted at that site. Sites that were excluded from the final analysis are shown in red (n = 77).

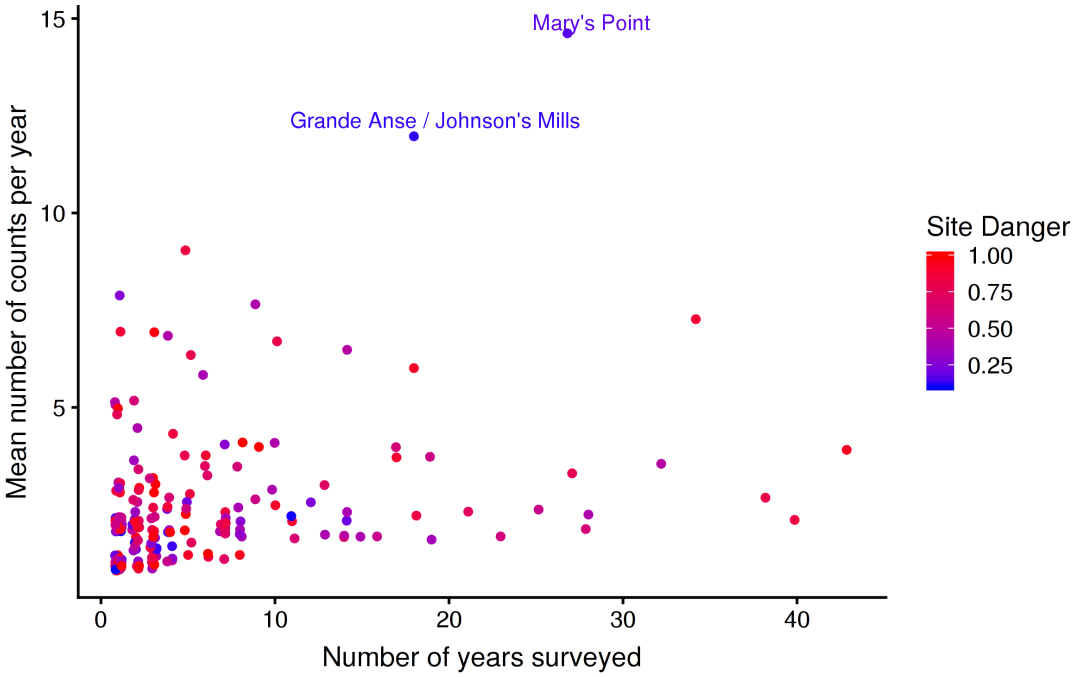


Figure 2: Number of years surveyed and the number of surveys per year for each location. The colour of the point is related to the proportion of the site within 150m of cover.

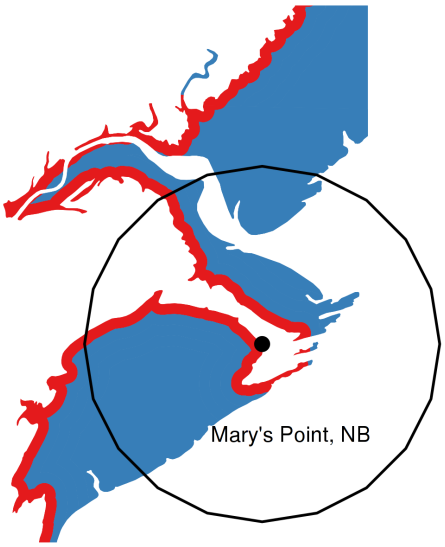


Figure 3: Example showing the safe (blue) and dangerous (red) portions of a habitat. Mary's Point, NB is shown with its geographic location highlighted by the point. The 2,500 m radius habitat circle is shown around this point. Intertidal mudflat habitat is shown in blue or red.

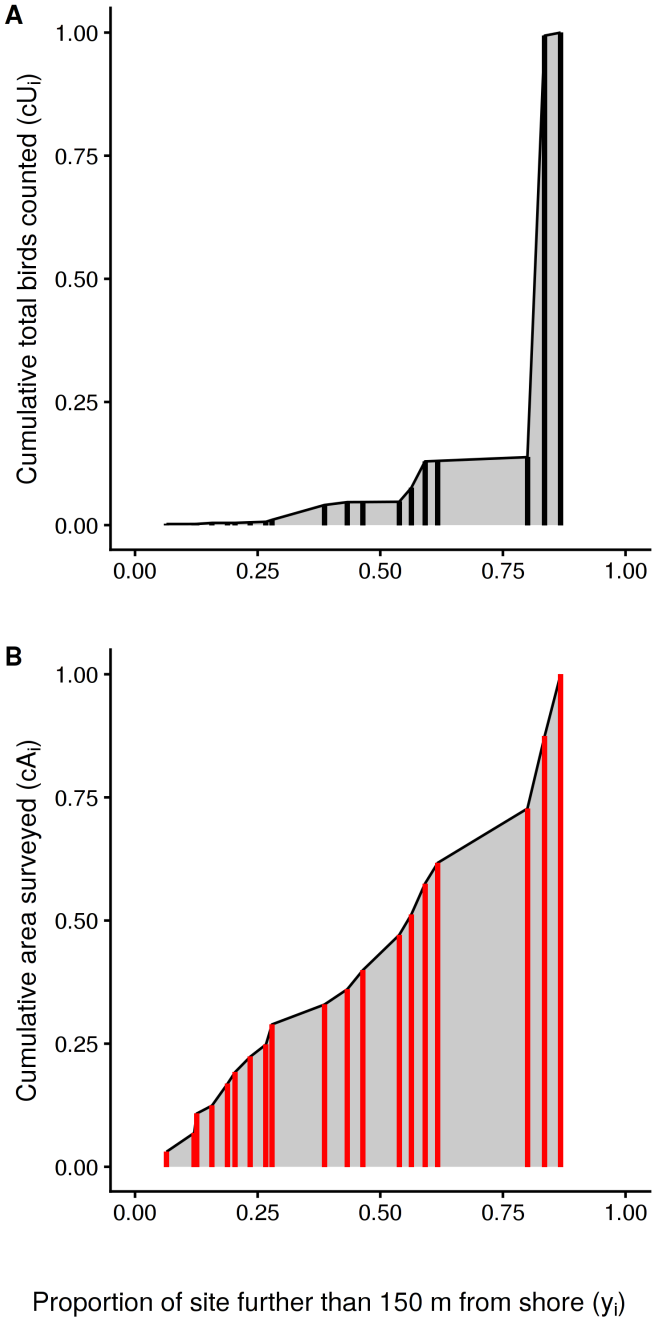


Figure 4: Example of the construction of the Priority Matching Distribution index for a given year (1985 in example). The sites (red and black bars, though sites of equivalent safety will be stacked) surveyed in a year are arranged along the x-axis from dangerous to safe with the cumulative proportional 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.

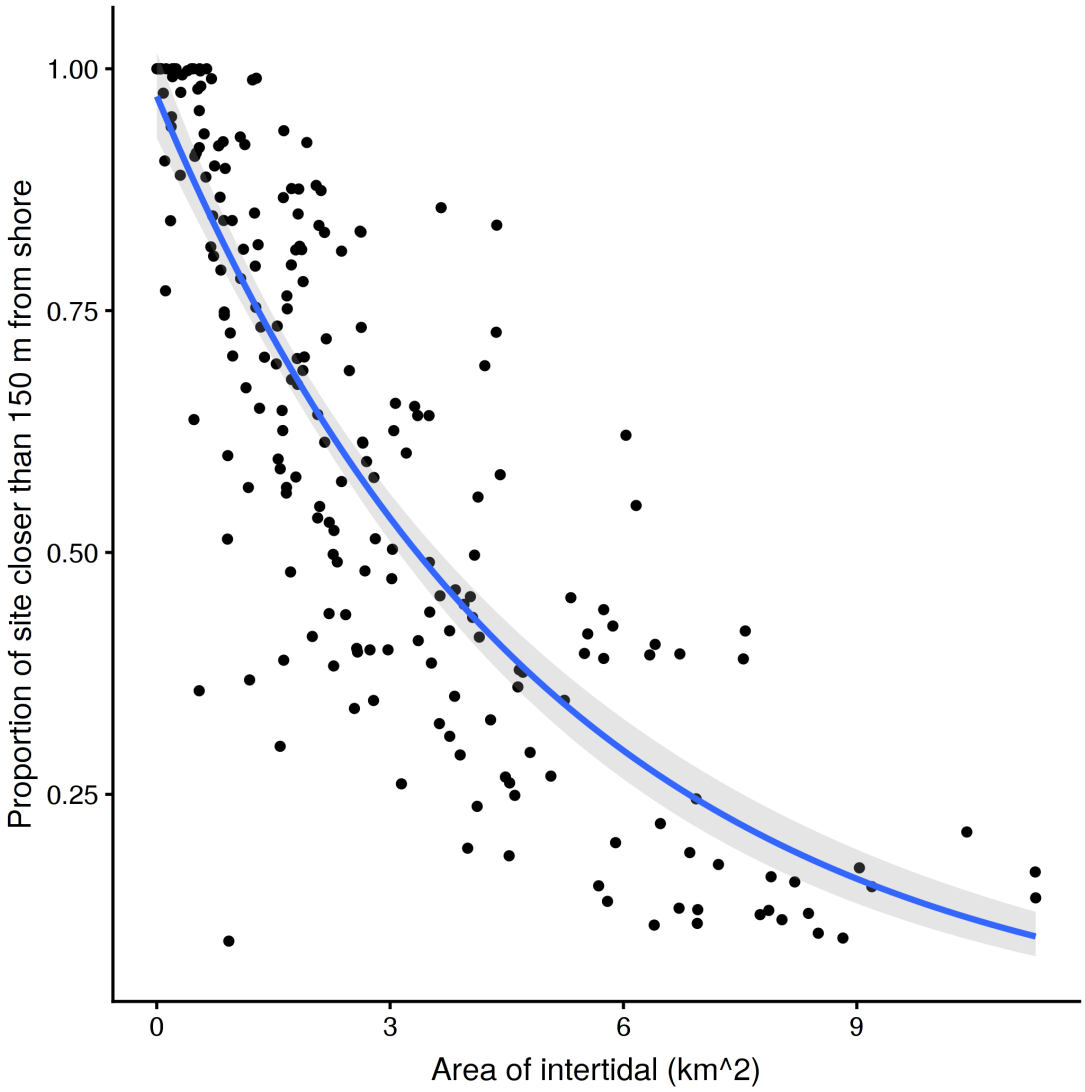


Figure 5: Location danger as a function of size. The fitted line shows the log-linear trend of danger with intertidal area. Larger sites are generally less dangerous, but the danger index varies widely between sites of a given size.

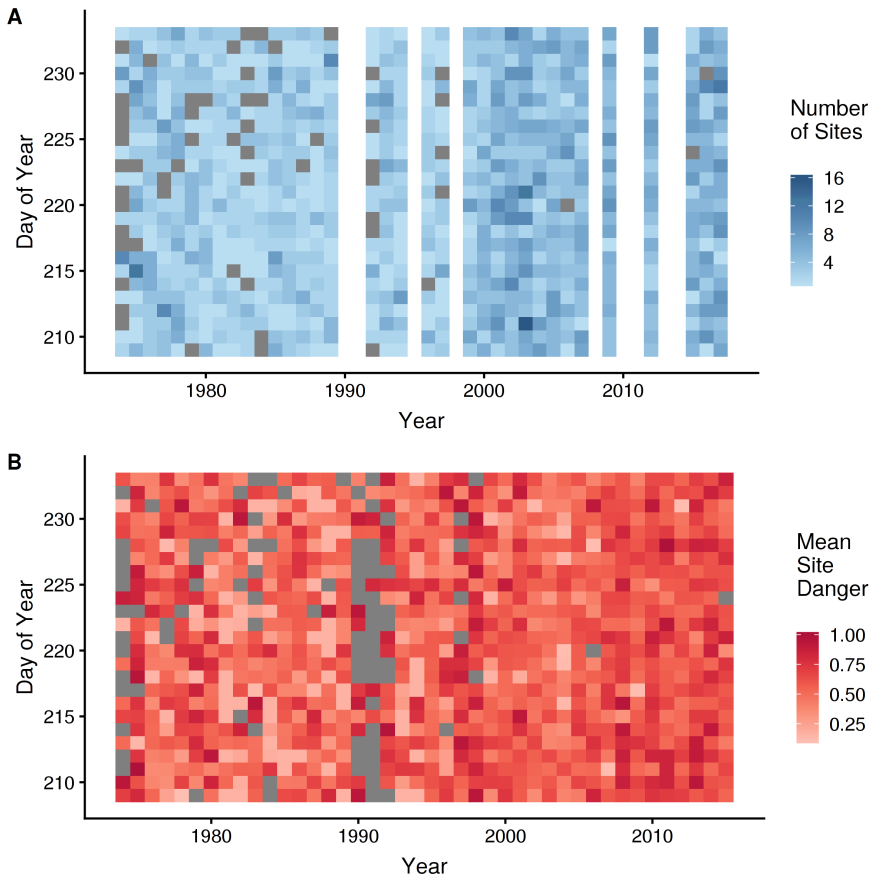


Figure 6: Biases and variation in site survey effort across years and dates. (A) Number of sites surveyed in a given day across years where darker blue shows more sites surveyed on a given day of year in a year. (B) Mean danger of sites surveyed in a given day across years where red indicates more dangerous sites surveyed for a given day and green shows safer sites surveyed on that day. Grey represents zero surveys in both figures.

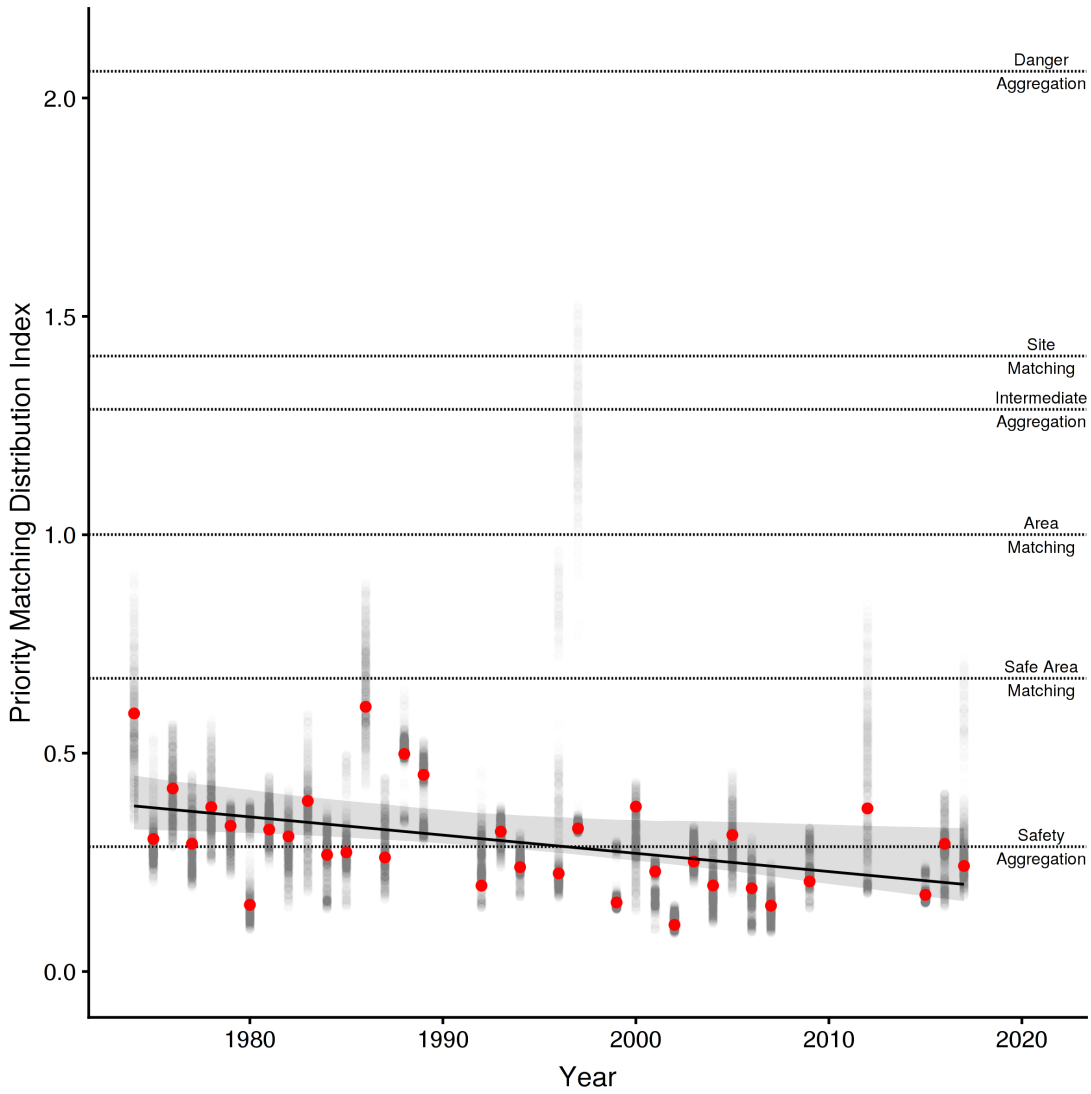


Figure 7: Interannual trend in the Priority Matching Distribution index (PMD) with the 95% bootstrapped confidence intervals. Points are the PMD for each year (red points) with the 95th inner quantiles of variation in the estimate shown in the grey points. The expected distributions for site-matching, area-matching, safe-area-matching, and safe and danger aggregation are shown as horizontally dashed lines.