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Research Papers

Site Safety and Food Affect Movements of Semipalmated Sandpipers (*Calidris pusilla*) Migrating Through the Upper Bay of Fundy

Effets de la sécurité du site et de la disponibilité de nourriture sur les déplacements des Bécasseaux semipalmés durant leur halte migratoire dans la partie amont de la baie de Fundy

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ABSTRACT. The upper Bay of Fundy is a critical stopover site for Semipalmated Sandpipers (*Calidris pusilla*) during their fall migration. However, little is known about factors that influence selection of feeding and roosting sites by these birds, or the extent to which birds move between different sites during their time in the region. Using radio-telemetry, we studied movement patterns, examined habitat use, and tested hypotheses associated with factors influencing foraging and roost-site selection. Movements of radio-tagged sandpipers were tracked in the upper Bay of Fundy in August 2004 and 2005. In 2004, sandpipers from the Minas Basin, Nova Scotia and Chignecto Bay, New Brunswick and Nova Scotia, were tracked, and in 2005, sandpipers were tracked only in Chignecto Bay. Sandpipers were highly mobile in both the Minas Basin 2004 and Chignecto Bay 2005, making daily movements of up to 20 km between foraging and roosting sites, although very little movement was detected in Chignecto Bay in 2004. Migrating sandpipers appeared to select foraging sites based on relative safety, as measured by distance to cover, provided that these sites offered an adequate food supply. Similarly, roosting sandpipers preferred sites that were far from nearby trees that might offer cover to predators. This preference for safe sites became more apparent later in their stay in the Bay of Fundy, when birds were heavier and, therefore, possibly more vulnerable to predation. Semipalmated Sandpipers appear to be flexible during their time in the upper Bay of Fundy, displaying year-to-year and site-to-site variability in movement and mudflat usage. Therefore, multiple, synchronized population counts should be conducted at known roost sites in order to more accurately estimate Semipalmated Sandpiper abundance in this region. Furthermore, in a highly dynamic system where food can be variable, landscape features such as distance to cover may be important factors to consider when selecting candidate sites for shorebird conservation measures.

RÉSUMÉ. La partie amont de la baie de Fundy est un arrêt migratoire critique pour le Bécasseau semipalmé (*Calidris pusilla*) à l’automne. Toutefois, les facteurs qui influencent la sélection des sites d’alimentation et de repos sont peu connus, tout comme les distances de déplacement entre différents sites durant leur séjour dans la région. À l’aide de la télémétrie, nous avons étudié les patrons de déplacement, examiné l’utilisation de l’habitat et testé les hypothèses associées aux facteurs influençant la sélection des sites d’alimentation et de repos. Les mouvements de bécasseaux munis d’émetteurs-radios ont été suivis dans la partie amont de la baie de Fundy en août 2004 et 2005. En 2004, des bécasseaux provenant du bassin de Minas, en Nouvelle-Écosse, et de la baie de Chignecto, au Nouveau-Brunswick et en Nouvelle-Écosse, ont été suivis. En 2005, les bécasseaux ont été suivis seulement dans la baie de Chignecto. Les bécasseaux étaient très mobiles à la fois dans le bassin de Minas en 2004 et dans la baie de Chignecto en 2005, parcourant jusqu’à 20 km par jour entre les sites d’alimentation et de repos. Cependant, peu de déplacements ont été observés dans la baie de Chignecto en 2004. Les bécasseaux migrateurs semblaient choisir des sites

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d'alimentation selon leur degré de sécurité, tel que mesuré par la distance au couvert, à condition que ces sites procurent une quantité de nourriture adéquate. De façon similaire, les bécasseaux au repos préféraient les sites éloignés d'arbres pouvant offrir un couvert aux prédateurs. Cette préférence des individus pour les sites sécuritaires était plus apparente plus tard durant leur passage dans la Baie de Fundy, lorsque les oiseaux sont plus lourds, donc possiblement plus vulnérables à la prédation. Les bécasseaux semblent être flexibles durant leur passage dans la partie amont de la baie de Fundy, démontrant une variabilité inter-annuelle ainsi qu'entre les sites dans leur utilisation des vasières. Il est donc nécessaire d'effectuer des décomptes multiples et synchronisés des populations aux sites de repos connus afin d'estimer correctement l'abondance des bécasseaux semipalmés dans la région. De plus, dans un système hautement dynamique où la quantité de nourriture est variable, les éléments du paysage tels que la distance au couvert peuvent être des facteurs importants à considérer lors de la sélection de sites potentiels pour la conservation des limicoles.

Key Words: *Bay of Fundy; habitat selection; intertidal mudflats; migration staging area; radiotracking; Semipalmated Sandpipers*

INTRODUCTION

Each fall, shorebirds undertake a long-distance migration, often traveling thousands of kilometers from northern breeding grounds to Central and South America where they overwinter (Hicklin 1987). Because long-distance migrants cannot complete such journeys without periodically replenishing their fat reserves, stopover sites become critical to the success of migration and the birds' survival (Myers 1983, Myers et al. 1987, Skagen and Knopf 1994). Only a few studies have examined movements of and habitat use by shorebirds during migration stopovers. van Gils and Piersma (1999) found that Red Knots (*Calidris canutus*) staging in the Wadden Sea moved an average distance of 10.6 km, with individuals moving distances of over 30 km during a single tidal cycle. Farmer and Parent (1997) found that Pectoral Sandpipers (*Calidris melanotos*) made only localized movements during spring migration stopovers in the Great Plains, with 90% of radio-tagged birds moving less than 10 km from their original release site. Similarly, Butler et al. (2002) radio-tracked Western Sandpipers (*Calidris mauri*) during their fall migration stopover in the Fraser River Delta, British Columbia. They found that individual birds tended to remain on one site and moved only 4 to 6 km, following the tide up and down the beach.

Semipalmated Sandpipers (*Calidris pusilla*) migrate from breeding grounds in the North American Arctic tundra to the northeastern coast of South America, where they overwinter (Morrison 1984, Morrison and Ross 1989, Gratto-Trevor 1992, Gratto-Trevor and Dickson 1994, Harrington and Morrison 1997). During fall migration, central and eastern breeding populations stop in the upper Bay of Fundy, where they feed, roughly doubling their mass during their approximate 2-week stay (Hicklin and Smith 1984), in preparation for a 3000–4000 km transatlantic flight to the wintering grounds. In recognition of the importance of this site, the upper Bay of Fundy has been designated as a site of critical importance by the Western Hemisphere Shorebird Reserve Network (Hicklin 1988a, b).

Although the upper Bay of Fundy is crucial to migrating sandpipers, little is known about how sandpipers select foraging and roosting sites or to what extent birds move between these sites during their time in the Bay of Fundy. In the only previous movement study conducted in the region, Hicklin (1987) found that 86% of color-marked shorebirds used only one mudflat for foraging and roosting at Grande Anse, Chignecto Bay. However, other sites around the Bay were not checked daily and resighting color-marked birds can be challenging (P. W. Hicklin, pers. comm.). A more quantitative approach, such as radiotelemetry, provides more detailed information on movement (Haig et al. 1998) and is required to address this question.

The objectives of our study were to track movements of individual sandpipers in the Bay of Fundy and test hypotheses about sandpiper foraging and roost site choice. Shorebirds are generally thought to distribute themselves by balancing their energetic needs with the risk of predation (Ydenberg at al. 2002, Pomeroy 2006). We hypothesized that movement by sandpipers among and within sites may be influenced by two main factors: (1) the abundance and size distribution of their main prey, the amphipod *Corophium volutator* and (2) relative safety of a site, as measured by both physical characteristics of the site and predation threats by raptors.

C. volutator is estimated to make up approximately 80%–100% of Semipalmated Sandpiper diet while in the Bay of Fundy (Hicklin and Smith 1979, 1984, Gratto et al. 1984, Peer et al. 1986), with the larger adult amphipods preferred over the smaller juveniles (Boates and Smith 1979, Peer et al. 1986, Wilson 1990). One may predict that sandpipers would distribute themselves in an ideal free manner, in which highest densities of birds are found at sites with highest densities of *C. volutator*. Although there is some evidence of that (Hamilton et al. 2003), others have suggested that a threshold prey density, above which birds can feed profitably, leads to an asymptotic relationship between bird density and prey abundance (Hicklin and Smith 1984, Wilson 1990).

The main predators of shorebirds in the Bay of Fundy are Peregrine Falcons (*Falco peregrinus*) and Merlins (*F. columbarius*). These raptors have altered shorebird stopover behavior elsewhere. Western Sandpipers with lower body mass were found to select sites with a higher predation risk whereas shorebirds with higher body mass (and, therefore, lower maneuverability—see below) selected safer sites (Ydenberg et al. 2002). We predict that shorebirds would avoid sites with high predator activity, especially if these sites also have *C. volutator* density below a threshold of profitability, as discussed above. Where food is plentiful and predator activity is high, they should change their behavior to reduce risk of predation, for example by forming into large flocks.

Furthermore, mudflat area, and shape and composition of surrounding landscape are indicators of site safety. Sites where birds can forage away from cover, which is often the source of predator attacks (Whitfield 2003), may be safer. Therefore, we predict that sites bordered by forest and lacking open marshland may be visited less frequently by sandpipers. This prediction can be further refined based on when birds are tracked during their stay. Predation risk to the sandpipers may increase as they gain mass because increased fat reserves could impair a bird's ability to escape from a predator, both through reduced take-off ability and through impaired performance in flight (Whitfield 2003, Dietz et al. 2007). Therefore, newly arriving light birds may be less likely to avoid potentially dangerous sites if such areas offer quality foraging habitat because they are less vulnerable to predation (Ydenberg et al. 2002). To further test this final hypothesis, we quantified habitat use relative to number of days since individuals were tagged (a surrogate for mass given that we tagged light birds and they gain mass during their stay). We predicted that over time, as they gained mass, birds would become less likely to visit dangerous sites.

Understanding how birds move within the area will help to estimate more accurately the number of birds using the bay, and help monitor any population changes. If it is found that individual birds use multiple sites, then counts must be conducted simultaneously at various roost sites in order to ensure that individuals are not being counted twice at different sites. This is especially critical for species such as the Semipalmated Sandpiper, for which population declines have been documented in the Bay of Fundy (Morrison et al. 1994). Improved population estimates will also help predict future responses of shorebirds to human-induced changes in the ecosystem, such as the damming of tidal rivers and the subsequent removal of these barriers, which may alter sediment transport and mudflat composition. Migrating shorebirds tend to concentrate, with large proportions of the population occurring at a restricted number of sites, which makes them particularly vulnerable to loss or degradation of foraging and roosting habitat in such areas (Myers et al. 1987, Morrison et al. 1994). Finally, understanding which factors influence shorebird stopover site selection will help identify potential sites for implementation of conservation measures.

METHODS

Study Area

Our study was conducted in three areas of the upper Bay of Fundy: Nova Scotia's Minas Basin (45º 09' N, 64º 17' W), and both arms of Chignecto Bay–Shepody Bay (45º 49' N, 64º 31' W) in New

Brunswick and Cumberland Basin between Nova Scotia and New Brunswick (45º 48' N, 64º 23' W). Tides in the upper Bay of Fundy rise and fall 12–15 m twice daily and, at mean low water, about 35 000 ha of mud and sand flats are exposed (Hicklin 1987). We selected eight mudflats in the upper Bay of Fundy (Grande Anse, Daniel's Flats, Peck's Cove, Mary's Point, and Minudie in Chignecto Bay, and Avonport, Evangeline Beach, and Cheverie in the Minas Basin) to monitor during the study (Fig. 1). In Chignecto Bay, all sites except Daniel's Flats and Peck's Cove had exposed beaches at high tide where shorebirds could roost. In the Minas Basin, only Evangeline Beach provided roosting habitat.

Radio Tracking

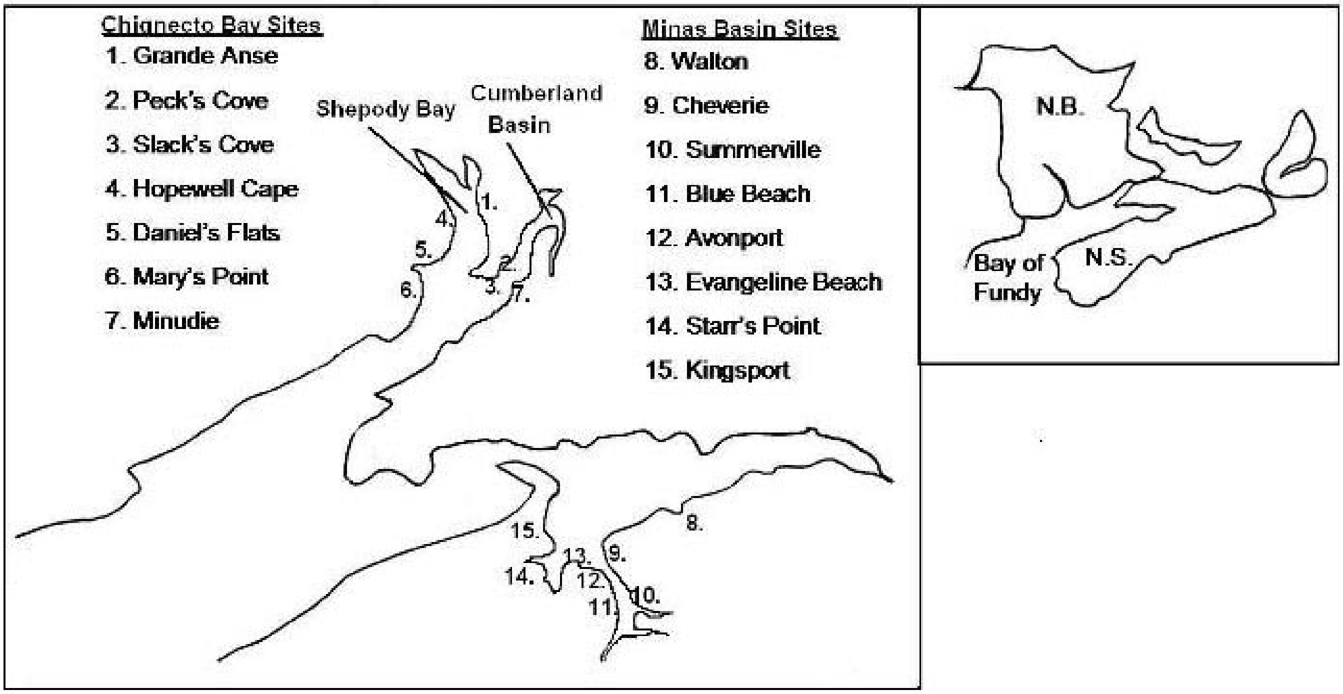
Large numbers of adult Semipalmated Sandpipers were captured at high tide roost sites using the Fundy Pull Trap (Hicklin et al. 1989). In 2004, 19 sandpipers from Grande Anse in Chignecto Bay and 20 from Blue Beach, Minas Basin were fitted with 0.9-g BD-2 radio transmitters (Holohil Systems Ltd.). In Chignecto Bay, birds were caught at Grande Anse on 10 and 11 August 2004. In the Minas Basin, sandpipers were caught at Blue Beach on 6 August 2004. In 2005, we restricted our study to Chignecto Bay and tagged 45 sandpipers from three sites (20 from Hopewell Cape, 15 from Grande Anse, and 10 from Slack's Cove). In 2005, birds were captured on 2 August at Grande Anse, 3 August at Hopewell Cape, and 4 August at Slack's Cove in New Brunswick. The radios were glued to a clipped area of lower back feathers following the method of Warnock and Takekawa (2003). This attachment method allows the transmitter to fall off when the bird molts. Light birds (21.9–29.2g) were selected, as low body mass indicates recent arrival in the area (P. W. Hicklin, pers. comm.). Plumage and timing of migration indicated that all birds captured and tagged were adults. Sex of birds was not determined and, therefore, could not be considered as a factor in this study. Although bill length is often used to distinguish between sexes, it also differs between Eastern and Central Arctic breeders, with average bill length increasing from east to west. As both populations migrate through the Bay of Fundy (Gratto-Trevor and Dickson 1994), it was impossible to separate sexes.

Tagged birds were tracked using a Cessna 172 airplane, flying at an altitude of between 150 and 300 m, with H-style antennas mounted on the plane's struts. In 2004, flights followed the coastline along both Chignecto Bay (Shepody Bay and Cumberland Basin) and the Minas Basin during high and low tides in attempts to locate all tagged birds. Seven flights of 2 to 4 h duration (21 total flight hours) were conducted between 10 and 19 August 2004. In 2005, we conducted eight flights (26 total flight hours) covering the Chignecto Bay coastline between 6 and 15 August. Birds were also tracked regularly from the ground at communal roost sites in both areas. Once a tagged bird was detected, its GPS location was recorded and the bird was assumed to be on the beach where the signal was strongest. GPS locations were usually confirmed visually by noting position of flocks. Locations were typically quite accurate for high-tide tracking, as birds were localized in tight roosting groups usually covering less than 200 m. At low tide, birds spread out over approximately a 1- to 2-km area. In these situations, several passes were made over the mudflat to pinpoint the location of the bird as accurately as possible.

Prey Abundance

To assess the prey base accurately, in 2004, seven mudflats were sampled: Cheverie, Avonport, and Evangeline Beach in the Minas Basin and Grande Anse, Daniel's Flats, Mary's Point, and Minudie in Chignecto Bay. In 2005, Grande Anse, Daniel's Flats, Mary's Point, and Peck's Cove were sampled in Chignecto Bay. At each site, stratified random sampling of sediment was carried out along three 250-m transects (seven samples per transect for a total of 21 samples per mudflat) running parallel to shore on each of the study flats in late July and again in late August. Transects were located approximately 150, 300, and 450 m from shore, except at Evangeline Beach where they were 650, 750, and 850 m from shore. Samples were collected using an 80-cm^2 corer pushed into the sediment to the bottom of the aerobic layer (the region in which invertebrates are found). Samples were then rinsed through a 250-µ sieve (Crewe et al. 2001) to remove mud and preserved in 95% ethanol. During fall 2004 and 2005, the contents of samples were sorted, *C. volutator* were placed in 2-mm size classes, dried, and weighed. These data provided estimates of numbers and size distributions of *C. volutator* at each mudflat. Only the adult size classes (>4 mm) of *C. volutator* were used for analyses as these are the prey preferred by sandpipers (Peer et al. 1986).

Fig. 1. Map of the Bay of Fundy, showing study sites in Chignecto Bay and Minas Basin.



Predator Activity

Focal mudflats were each visited four times at low tide. During each low-tide visit, 4 h of continuous observation were conducted, and roosts were observed during 2-h periods for 1 h on either side of high tide. During each observation period, observers scanned continuously for predators. When one was detected, the predator was identified and the observer recorded whether or not an attack occurred and the outcome of the attack. The escape response of the shorebirds was also noted. Mudflat area and the distance birds could forage away from cover were considered as possible indicators of site safety (Pomeroy et al. 2006) and were measured directly from local maps.

Predation events per hour may be a poor measure of predation risk experienced by birds when feeding at particular sites because it does not take sandpiper densities into account. To address this, we used low-tide shorebird count data to determine shorebird density and then measured predation risk as number of successful attacks $\cdot$ h^{-1} $\cdot$ bird density^{-1} measured over 4 ha. We did not obtain accurate flock size data at high-tide roost sites; therefore, this approach was used only to assess predation risk experienced by birds at low tide.

Statistical Analyses

Data were analyzed using SYSTAT version 9 and SPSS version 15. Before analysis, the assumption of normality was assessed visually using normal probability plots (Tabachnick and Fidell 2007), and Cochran's test was used to test for homogeneity of variance (Underwood 1997). When violations were detected, they were managed through transformation or use of non-parametric techniques.

Analysis of variance (ANOVA) was conducted to assess differences among locations and years in mean distances moved by individual birds. ANOVA was also used to assess differences among tide levels ("High," "Low") and individual roost sites in predation events ("Number of predators per observation hour," "Number of attacks per observation hour"). When significant main effects were found, the post-hoc Tukey's Test was used to isolate differences between levels of factors. Predators and attacks per hour at high tide and predation risk at low tide were compared between the 2 years using the non-parametric Kruskal-Wallis test. Data from Minas Basin in 2004 were not compared with the two Chignecto Bay data sets because effects of location and year are confounded.

Because birds were tagged at three different sites in Chignecto Bay in 2005, preferences of birds for various roosting and foraging sites were assessed using a two-stage process for that year's data. We restricted our analysis to birds that were detected at least twice to ensure that preference could be evaluated. First, preferences were ranked for each bird, i.e., the site at which an individual bird was most frequently detected was ranked most highly, etc. Ties were ranked as such. This procedure avoided the potential bias associated with using raw numbers of detections, given that different birds were detected varying numbers of times (two to eight times at high tide and two to seven times at low tide). Second, effect of tagging location on site preference was tested using a repeated measures ANOVA, with rank preference as the response variable, bird as the subject, detection site as a within-subjects factor, and location of tagging as a between-subjects factor. Multivariate results were evaluated using Pillai's Trace, the most robust of available multivariate tests (Scheiner 2001). Univariate results were evaluated with the Huyn-Feldt correction factor applied to control for mild deviations from sphericity (Potvin et al. 1990). When significant main effects were detected, post-hoc testing to isolate differences was conducted using the Bonferroni correction for multiple comparisons.

Multiple regression combined with Akaike's information criterion (AIC) model selection (Burnham and Anderson 2002) was used to determine the suite of factors that best predicted habitat use by tagged sandpipers, measured as arcsine square root transformed proportion of detections within each day of tracking. We chose to use proportion rather than number of birds because number detected varied among days, and therefore, proportion was a better indicator of preference independent of our success in tracking birds. This approach was used only for 2005 data, because in 2004 virtually all birds in Chignecto Bay used only one mudflat, and there were too few successful tracking days in the Minas Basin to allow us to generate the models. For low-tide detections, variables considered included prey abundance, distance to cover (an index of relative site safety), predator abundance, and predator attacks. For high tide, we examined distance to cover, predator abundance, and predator attacks. Variables to be included were selected using a sequential multiple regression approach. Issues with multicollinearity were assessed by examining condition indices (with a cutoff of 30 indicating a problem) and correlations between independent variables (Tabachnick and Fidell 2007). Mudflat at which birds were detected could not be included in either model because there was only a single measure of each of the variables listed above for each mudflat. Furthermore, days since tagging was not useful to include in the main model because on each day values of the dependent variable (proportion detected) summed to a constant, so data points were not independent.

Instead, to test the hypothesis that birds may have altered site selection over time in response to increased mass and, therefore, perhaps shifted priority from gaining food to avoiding predators, we compared mean number of days since being tagged that birds were detected at each site using a two-way fixed factor ANOVA, with both site at which birds were located and site of tagging as independent variables. Analyses were conducted separately for low- and high-tide trackings. To ensure that the results of this analysis were not confounded with differential retention of birds tagged at different sites, we used a Kruskal-Wallis test to compare last day of tagging (i.e., the number of days since being tagged that a bird was located for the last time) among tagging sites.

RESULTS

Individual Shorebird Movements

The distances moved by individual sandpipers varied among locations and years ($F_{2, 63} = 8.68$, $p < 0.001$, Fig. 2). Individuals moved significantly greater distances in Minas Basin in 2004 and Chignecto Bay in 2005 than in Chignecto Bay in 2004 (Tukey's test). In Minas Basin, 2004, all 20 birds tagged at Blue Beach were located one to seven times. The sandpipers were generally found to use multiple roosting and foraging sites. A total of 34 radio-tracking detections were made during low tide and, of six foraging sites, Cheverie, Minas Basin, was the most frequently visited (50% of detections, Table 1). During high tide, a total of 39 detections were made on six roost sites, of which Summerville was the most frequently used (33% of detections). The greatest distance a bird moved between radio-tracking detections in the Minas Basin was 21.8 km. No marked sandpipers moved between Minas Basin and Chignecto Bay in 2004.

In Chignecto Bay, 2004, very little movement was observed among sandpipers tagged at Grande Anse. Tagged birds were located between one and nine times, and three birds were never found. Of 34 low-tide detections, 83% were of birds foraging at Grande Anse (Table 1). The sandpipers used a total of three different foraging sites at low tide. During high tide, all 44 detections were at Grande Anse. During aerial surveys, other potential roosting sites (Mary's Point, Hopewell Cape, and Slack's Cove) were searched and no radio-tagged birds were detected. Neither were tagged birds found roosting on Mary's Point during ground-tracking periods in that year. The greatest distance a bird moved between successive detections was 15.1 km.

In 2005, the 45 sandpipers tagged at three different roost sites in Chignecto Bay were much more mobile than birds tagged at Grande Anse in 2004, regardless of where they were originally tagged. Individual birds were located between one and 14 times, and six birds were never found. The marked sandpipers foraged on six different mudflats in that year. During low tide, 129 detections were made, most frequently at Daniel's Flats (67% of detections, see Table 1). These birds also used a total of six different roost sites. Of 112 high-tide detections, 59% were of birds roosting at Hopewell Cape. Site of tagging had no effect on the distance moved by individual birds (ANOVA, $F_{2, 33} = 0.39$, $p = 0.67$, see Table 2). The greatest distance moved between radio-tracking detections was 17.8 km.

Based on ranked preferences of each bird, tagging location did not affect site selection at either low or high tide (multivariate RM-ANOVA: low tide low tide $F_{6, 44} = 1.4$, $p = 0.24$; high tide $F_{4, 40} = 0.50$, $p = 0.74$). However, as described above, individual sandpipers did display overall preferences in site selection (univariate RM-ANOVA: low tide $F_{3, 75} = 16.9$, $p < 0.001$; high tide with Huynh-Feldt correction applied: $F_{1.6, 35.5} = 7.58$, $p = 0.003$). At low tide, birds preferred Daniel's Flats over all other sites, and Grande Anse was preferred over Peck's Cove (Fig. 3). At high tide, Hopewell Cape was preferred over Mary's Point and Grande Anse (Fig. 3). Overall, individuals did not range widely in the Bay of Fundy but instead tended to roost and feed in discrete areas.

Prey Base

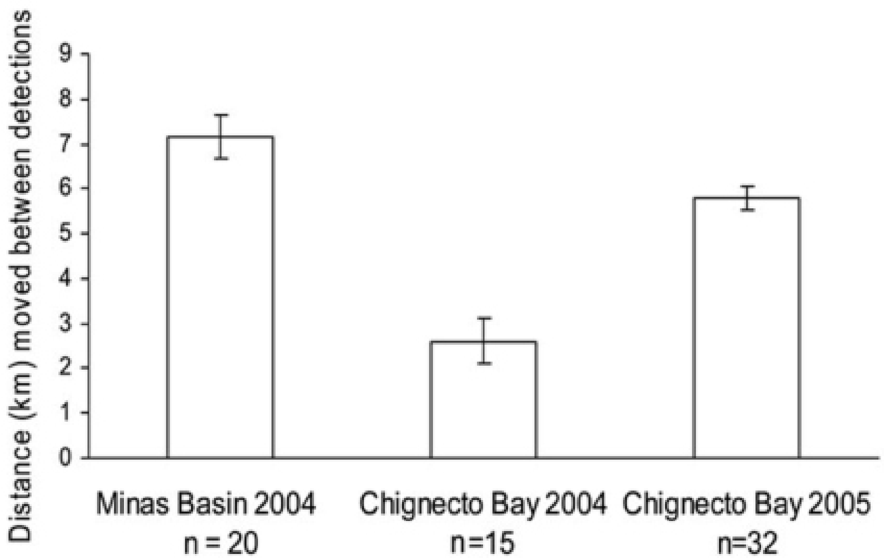
In Minas Basin in 2004, the prey base was highly variable, with extremely high densities of adult *C. volutator* at Cheverie, and extremely low values at Avonport and Evangeline Beach (Fig. 4). In Chignecto Bay, *C. volutator* density varied both among sites and among years (Sprague 2006). Grande Anse exhibited consistently lower prey densities than the other sites, and between 2004 and 2005, *C. volutator* density increased at both Mary's Point and Daniel's Flats and declined at Grande Anse (Fig. 4).

Effects of Predation on Movements

There were significantly more sandpiper predators observed per hour (ANOVA, $F_{1, 53} = 14.5$, $p < 0.0001$) and more attacks per hour (ANOVA, $F_{1, 53} = 16.57$, $p < 0.0001$) observed during high tide than low tide in both years and in both locations (Fig. 5a). The low-tide predation rate in Chignecto Bay did not differ between 2004 and 2005 for predators per hour per bird (Krusal-Wallis $X^2_1 = 0.86$, $p = 0.36$) or attacks per hour per bird (Krusal-Wallis $X^2_1 = 0.12$, $p = 0.73$; Fig. 5b). Predation risk at high-tide sites could not be quantified on a per bird basis because accurate roost counts were not possible. However, although predators and attacks per hour seemed higher in 2005, they did not differ significantly between years in Chignecto Bay (predators: Kruskal-Wallis $X^2_1 = 1.77$, $p = 0.18$; attacks: Kruskal-Wallis $X^2_1 = 1.26$, $p = 0.26$) (Fig. 5a). Given the extremely high densities of birds typically found at roosts (often ≥ 10 000), it is unlikely that failing to correct for the number of birds present would substantially affect perceived risk on a per bird basis.

Sandpipers did not avoid sites with the highest predator activity, especially if that site had high prey availability. In Minas Basin, birds selected Cheverie over the other mudflats at low tide throughout their stay. This site had the highest number of observed predators per hour, attacks per hour, and successful

Fig. 2. Distance moved between radio-tracking detections, averaged for individual birds at two locations in 2004 and 2005. Number of birds observed at each location is provided under the location. Error bars are ± 1 SE.



attacks per hour. In Chignecto Bay, 2005, Daniel's Flats was the site most used by foraging sandpipers and also had the highest observed predator activity of all sites in the area over both years. However, both these sites had relatively high prey availability (Fig. 4) and offered foraging areas with large distances from cover (Table 3), which may have offered some measure of safety from predators. Therefore, it is not possible to completely decouple predation risk and food availability, although the relative avoidance by birds of food-rich Peck's Cove (Fig. 4), with very little distance from cover (Table 3), allows some interpretation (see Discussion). It is probable that predators responded to shorebird abundance, and notable that sandpipers did not disperse substantially to other mudflats in response to elevated predation levels, suggesting a benefit to selecting the current site. Among roost sites, Hopewell Cape had more predators per hour, although not significantly so, (ANOVA, $F_{7,\ 32}$ = 2.34, p = 0.07, Fig. 6a) and had significantly more attacks per hour (ANOVA, $F_{7,\ 32}$ = 4.20, p = 0.006, Fig. 6b) than any other site in either year, but was still the most frequented high-tide site in 2005. Again, it offered a greater distance from cover than the other roost sites (Table 3).

Factors Influencing Site Selection

Although *C. volutator* were present on all the mudflats used by shorebirds, tagged birds were sometimes located feeding on sites with extremely low *C. volutator* densities. Furthermore, 25% of sandpipers tagged in Minas Basin and 15% of birds tagged in Chignecto Bay in 2005 were found feeding on sites with low *C. volutator* density after previously foraging on a site with high *C. volutator* densities. In 2004, most birds tagged at Grande Anse remained on the site throughout the stopover period, despite a low *C. volutator* density at this site.

When assessing the relative importance of multiple factors in predicting site selection by shorebirds foraging at low tide in 2005, we found that a model containing distance from cover of the foraging site and *C. volutator* density was the best choice (Table 4). Number of predator attacks per hour was unimportant (linear regression $F_{1,\ 38}$ = 2.1, p = 0.15, r^2 = 0.05), and number of predators present could not be included because it was too correlated with distance from cover (statistical condition index = 33.0). Habitat use by sandpipers increased with distance from cover, which was by far the more

Table 1. Number and percentage of total radio-tracking detections for low tide and high tide during each site and year combination.

Minas Basin 2004			Chignecto Bay 2004			Chignecto Bay 2005		
Site	N	% of total	Site	N	% of total	Site	N	% of total
Low Tide								
Cheverie	16	50.0	Grande Anse	28	83.0	Daniel's Flats	91	70.5
Evangeline Beach	6	19.0	Daniel's Flats	4	11.0	Grande Anse	24	18.7
Kingsport	3	9.5	Hopewell Cape	2	6.0	Mary's Point	13	10.0
Starr's Point	3	9.5				Peck's Cove	4	3.2
Avonport	2	6.0				Minudie	2	1.5
Walton	2	6.0						
High Tide								
Summerville	13	33.0	Grande Anse	44	100.0	Hopewell Cape	66	58.9
Avonport	11	28.5				Grande Anse	30	26.8
Blue Beach	8	21.0				Mary's Point	11	9.8
Cheverie	6	15.0				Slack's Cove	3	2.7
Evangeline Beach	1	2.5				Daniel's Flats	2	1.8

important variable of the two in the model (Table 4, standardized beta coefficients). *C. volutator* density had relatively little effect on habitat use, although when considered with distance to cover there was a slight positive relationship (Table 4). This lack of response by birds to prey availability may be because the preferred site (Daniel's Flats) had the second-lowest *C. volutator* density (Fig. 4), but also a much greater distance from cover than the other sites. Hence, birds appear to be selecting the safest site with at least a moderate prey density. For roosting birds, the three variables considered—predators per hour, attacks per hour, and distance from cover—could not be incorporated into the same model because they were highly correlated (statistical condition index = 55.0). Evaluated separately, predators and attacks per hour produce slightly stronger models than distance from cover (Table 5). Birds selected sites at which there were more predators and attacks per hour, although it is likely that in this instance predators were responding to prey, not the reverse. More importantly, birds preferred roost sites that were far from cover, in particular Hopewell Cape.

Habitat Selection Over Time

Sandpipers did appear to select roosting sites based, in part, on their body masses. In 2005, birds detected at Grande Anse at high tide had been tagged more recently, and were presumably lighter, than those detected elsewhere (ANOVA $F_{2, 99} = 12.16$ $p < 0.0001$ and Tukey's test) (Fig. 7a). Location of tagging did not affect results ($F_{2, 99} = 0.64$, $p = 0.53$).

The relationship between time since tagging and foraging site use varied with location of tagging (ANOVA interaction term $F_{4, 110} = 3.46$, $p = 0.011$). For birds tagged at Hopewell Cape and Slack's Cove, there was no relationship between days since tagging and mudflat use (HC: $F_{2, 58} = 0.15$, $p = 0.86$; SC: $F_{2, 26} = 1.07$, $p = 0.36$). However, sandpipers tagged at Grande Anse were detected on the Grande Anse mudflat earlier in their stay than on the other mudflats ($F_{4, 26} = 3.87$, $p = 0.014$, and Tukey's test) (Fig. 7b). None of these results is an artifact of biased detectability of birds tagged at the three sites. There were no differences among tagging sites in the length of time after tagging that the sandpipers were first detected (Krusal-Wallis $X^2_2 = 1.27$, $p = 0.53$).

Table 2. Mean distance moved by birds tagged at each of the three capture sites in Chignecto Bay 2005. Number of observations is indicated in parentheses.

Site of Tagging	Distance moved (km)	
	Mean	Standard error
Slack's Cove	6.9	0.6 (n = 59)
Hopewell Cape	6.0	0.4 (n = 122)
Grande Anse	5.8	0.6 (n = 60)

DISCUSSION

Semipalmated Sandpipers migrating through the upper Bay of Fundy in late summer appear to be highly flexible in their use of foraging and roosting habitats and their movement between these habitats. In two of three year–location combinations, the sandpipers did not remain on one mudflat, but instead used multiple roost sites and intertidal foraging areas throughout their 2-week stay in the region. Some sites were used only for either foraging or roosting, and others were used during both high and low tides. It might be expected that sandpipers prefer to forage on mudflats with associated roosting sites, or on mudflats that were relatively close to a roost site in order to reduce the energy expenditure of traveling (Goss-Custard et al. 1992), assuming that travel for sandpipers is not "free" (van Gils et al. 2006). It is also assumed that sandpipers would maximize their feeding time while the intertidal zone is exposed during the receding, low, and rising tidal periods. However, radio-tracked birds did not select sites where they could both forage and roost over sites where they could do only one or the other. In 2005, 58% of all roosting detections in Chignecto Bay occurred at Hopewell Cape, a site used only during the high-tide periods. Birds selected this site over other roosting sites in 2005, and were observed to make daily flights of over 15 km in order to roost at this site.

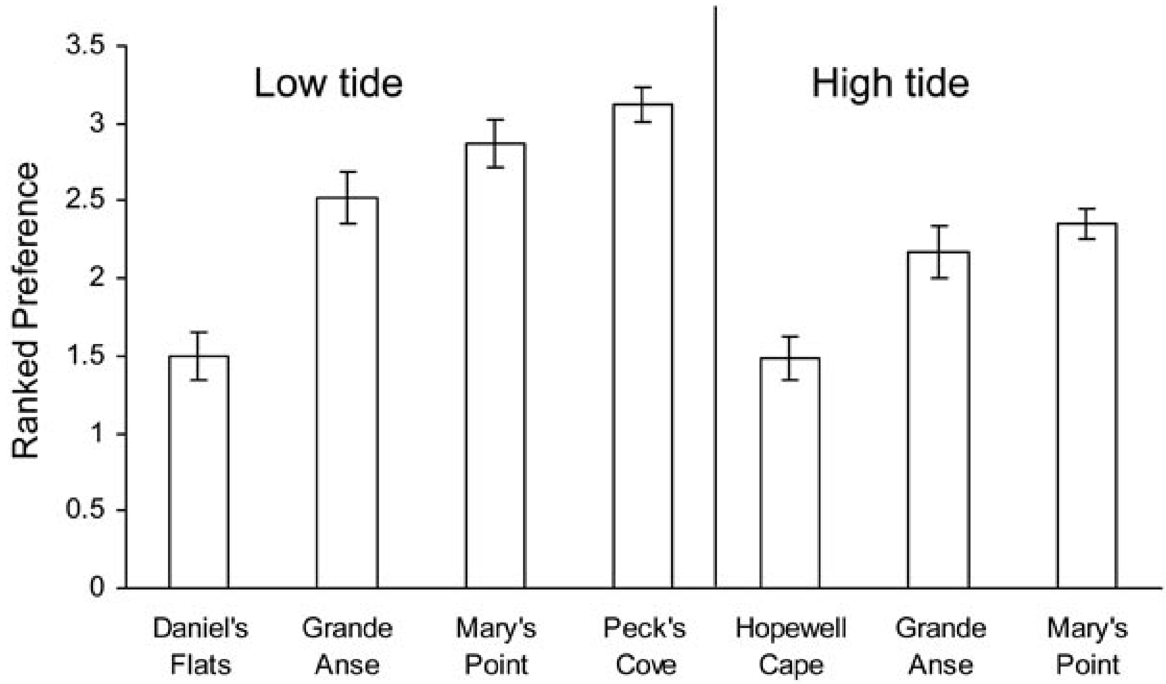
In 22% of all consecutive radio-tracking detections made in Chignecto Bay in 2005 and 17% of detections made in Minas Basin in 2004, the marked sandpipers moved a distance of 10 km or more. Several of these movements were between a foraging and roosting site in a single day. This suggested that the energetic costs of flights of 5–20 km, even after the birds had acquired a significant fuel load, were outweighed by the benefits of sampling new sites.

Sandpipers tracked in the Minas Basin in 2004 were highly mobile (Fig. 2). Conversely, sandpipers using Chignecto Bay in 2004 remained largely on one site. This latter result agreed with Hicklin's (1987) finding that most sandpipers migrating through Chignecto Bay showed high site fidelity. However, the Semipalmated Sandpipers tracked in Chignecto Bay in 2005 displayed a very different pattern. Regardless of where the birds were trapped, they were much more mobile; they used several sites to roost and feed and they moved greater distances between radio-tracking detections. Hicklin's (1987) findings appear, therefore, to not be generalizable across years; there is substantial interannual variation in habitat use by sandpipers foraging in Chignecto Bay.

Effects of Prey on Movements

In Chignecto Bay in 2005, prey abundances were more concentrated than in the previous year, with significantly higher *C. volutator* densities at Mary's Point and Daniel's Flats and lower *C. volutator* densities at Grande Anse (Fig. 4, Sprague 2006). Wilson (1990) found that within a mudflat, birds foraged where *C. volutator* abundances were above a threshold density, which was estimated at between 625 and 3838 adult *C. volutator*/m^2, and areas below that threshold were avoided. Abundance of *C.*

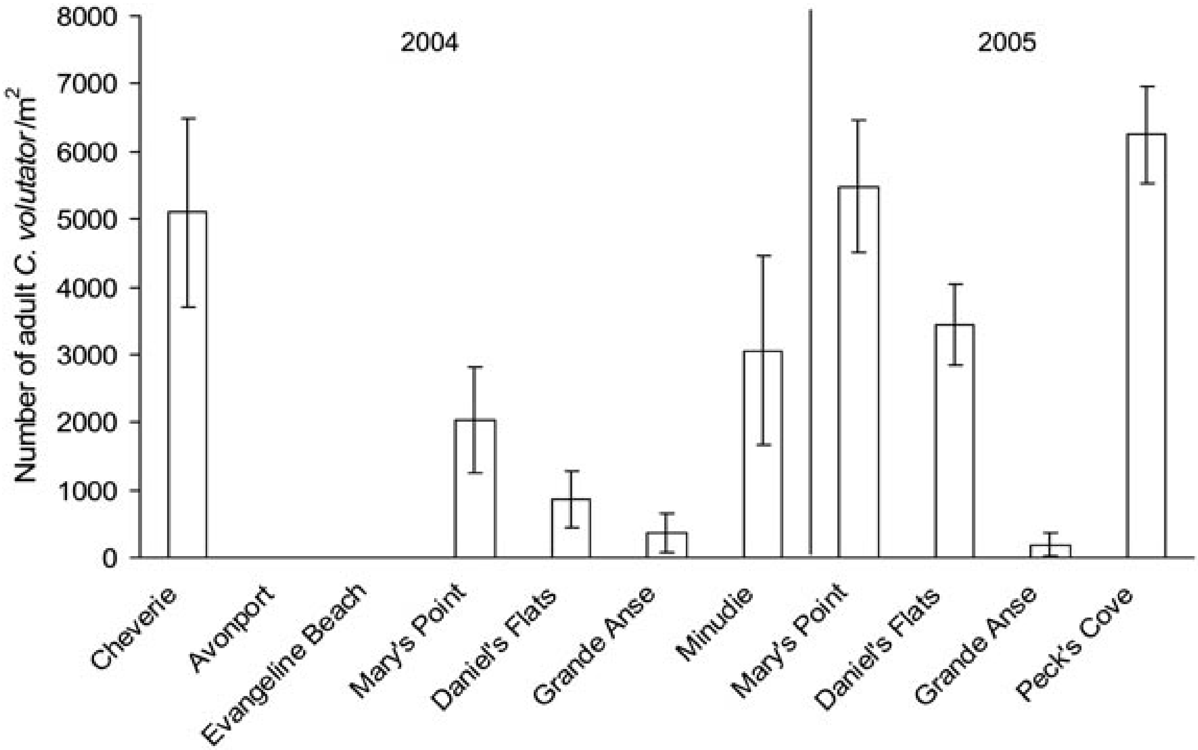
Fig. 3. Ranked preference of site usage by sandpipers in Chignecto Bay for low and high tides in 2005. Lower numbers indicate stronger site selection; i.e., the rank closest to 1 indicates the preferred site. Error bars are ± 1 SE.



volutator at Grande Anse in 2005 was well below this range (Fig. 4), and may have caused birds roosting on that site to leave and forage on a more profitable site. This could account, in part, for the increased movement detected in Chignecto Bay in 2005. *C. volutator* abundance at Grande Anse in 2004 was also low, but may still have been adequate to cause the sandpipers to remain in this traditionally frequented site.

Sandpipers in both years and locations were periodically detected on sites with low prey availability. However, birds detected on a site with low *C. volutator* density may not have spent the entire low tide feeding there, but may have just sampled the site before moving to a more profitable mudflat for the remainder of the low tide. Animals often sample potential foraging sites before selecting the most profitable area to feed (Kushlan 1981, Stephens and Krebs 1986). Furthermore, in this situation where birds are present in an area for a short time, the sandpipers may continue to sample sites throughout their stay. In a review of decision-making strategies used by animals (primarily birds) when assessing environmental parameters, Valone (2006) concluded that food patch distributions can be learned in approximately 1 to 3 weeks. This roughly matches the amount of time foraging sandpipers spend in the Upper Bay of Fundy. We found no evidence to confirm sampling within a single foraging bout because birds were usually detected only once during a low tide, and individual bird movements were not monitored throughout a complete tidal cycle. However, in 2005, one bird was located feeding at Grande Anse early in the low-tide cycle and was later found foraging at Daniel's Flats, a site with high *C. volutator* density, later in the same tide cycle, suggesting that movements within a single tide cycle do occur.

Fig. 4. Mean density of adult *C. volutator* (≥4 mm in body length) in August. Error bars are ± 1 SE.



It is also notable that in both years at least a few marked birds returned to foraging sites with low *C. volutator* density, even after sampling sites with high *C. volutator* density. Possible explanations for this behavior are that sandpipers may not be feeding as extensively on adult *C. volutator* while in the Bay of Fundy as is currently thought, that they may not incorporate knowledge from a previous low-tide foraging bout in order to select where to feed the following day, or that the sandpipers are searching for safety. Polychaetes and other invertebrates are also a known food source for Semipalmated Sandpipers (Gratto et al. 1984, Hicklin and Smith 1984) and could possibly be an important alternative food source for the birds during the stopover, especially in sites with low *C. volutator* abundances. Kuwae et al. (2008) found that biofilm on the mudflat surface makes up a substantial portion of the diet of migrating Western Sandpipers. As our study was focused on the known primary food source of Semipalmated Sandpipers, we did not measure biofilm abundance. However, recent work in the Bay of Fundy indicates that although biofilm is also a component of the diet of Semipalmated Sandpipers foraging in this area, there is no evidence that birds are selecting foraging sites based on biofilm abundance (M. G. Ginn, pers. comm.).

Effects of Predation on Sandpiper Movements

It has been suggested that sandpipers on migration stopovers avoid sites or habitat types that are especially dangerous (Lindstrom 1990), even if those sites are richer in food (Ydenberg et al. 2002). Semipalmated Sandpipers did not avoid the sites with the highest observed predator activity throughout their stay in the upper Bay of Fundy. Instead, the highest abundances of raptors were on sites with the highest sandpiper densities,

Fig. 5. (a) Mean number of predators and attacks per hour for each 4-h observation period at low tide (on foraging sites) and 2-h observation period at high tide (on roosting sites) on sites in the upper Bay of Fundy. (b) Mean number of predators and attacks per hour at low tide on a per sandpiper basis in the same areas. Error bars are ± 1 SE. Statistical comparisons reported in the text do not include Minas Basin data.

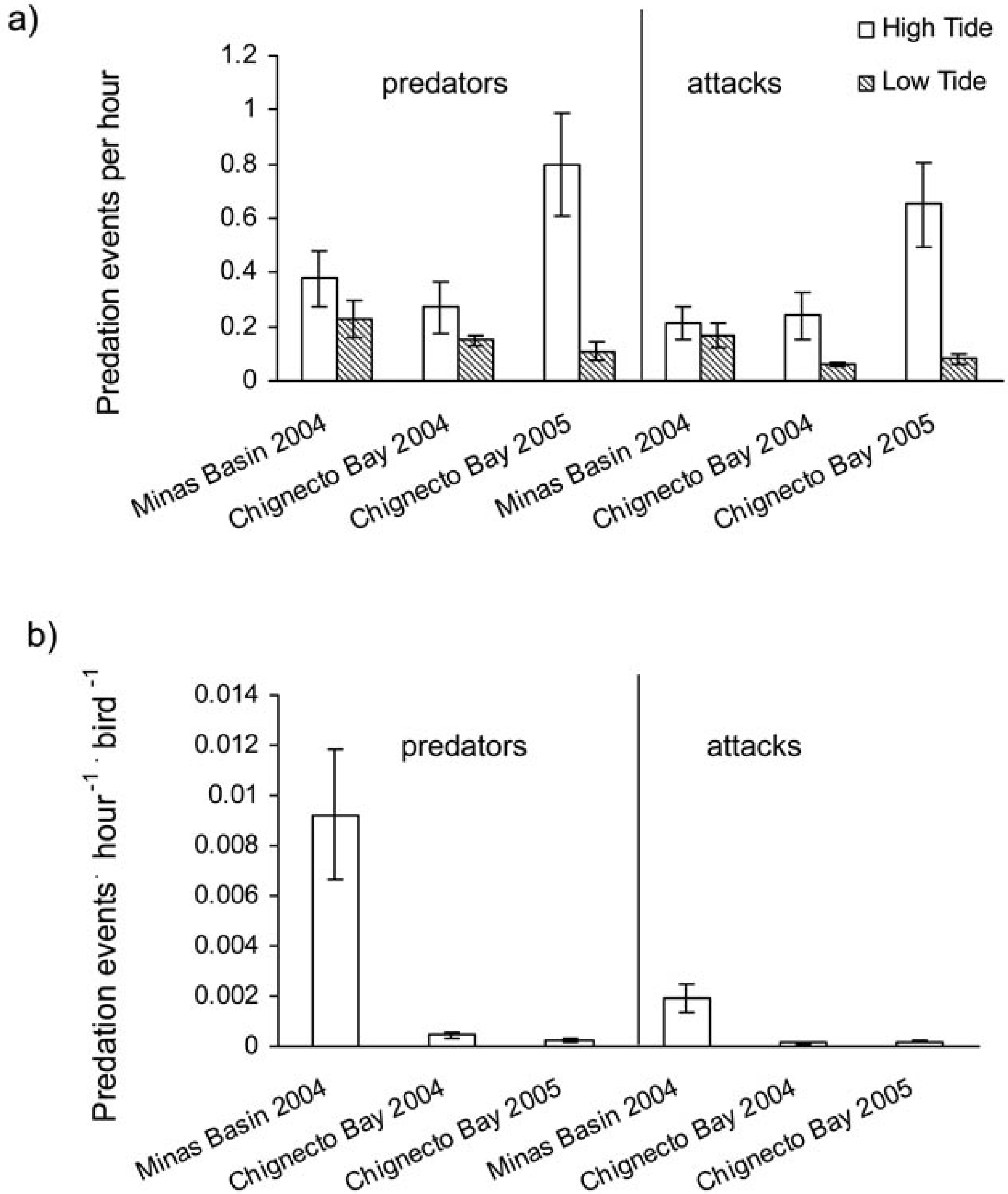


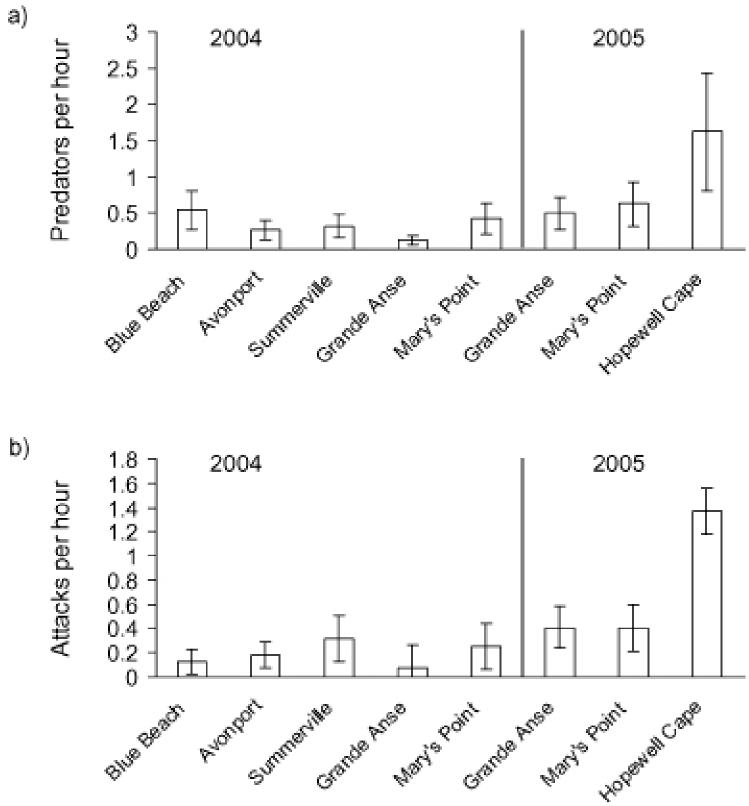
Table 3. Greatest distance (km) from cover that birds can forage or roost at each site in Chignecto Bay and Minas Basin.

Site	Distance to Cover (km)
Chignecto Bay Foraging Sites	
Daniel’s Flats	3.25
Mary’s Point	1.875
Grande Anse	3.0
Peck’s Cove	1.75
Minudie	2.0
Chignecto Bay Roosting Sites	
Hopewell Cape	0.5
Grande Anse	0.01
Mary’s Point	0.02
Slack’s Cove	0.01
Minas Basin Foraging Sites	
Cheverie	2.75
Avonport	1.5
Evangeline Beach	2.5
Minas Basin Roosting Sites	
Cheverie	0.02
Summerville	0.01
Blue Beach	0.01

suggesting that raptor distribution is influenced by shorebird distribution, rather than the reverse. Sites with adequate prey densities attracted the most shorebirds, and consequently, the most predators, thus making profitable sites for the shorebirds also potentially the most risky.

However, although sandpipers cannot control the numbers of predators at sites they frequent, they can base their selection of sites on habitat characteristics that may minimize risk, such as distance from cover. Several studies have shown that raptors hunt most successfully when using surprise attacks launched from cover (Page and Whitacre 1975, Dekker 1988, Cresswell 1996, Pomeroy 2006). Distance from tall cover has been shown to significantly affect roost site selection of overwintering Red Knots and Great Knots (*Calidris tenuirostris*) (Piersma et al. 1993, Rogers et al. 2006). In Chignecto Bay in 2005, we located sandpipers feeding and roosting most frequently at Daniel’s Flats and Hopewell Cape, respectively. Although they attracted the most

Fig. 6. Number of (a) predators per hour and (b) attacks per hour noted during each high-tide observation period at each site in each year of the study (*n* = 4). Error bars are ± 1 SE.



predators, both Daniel's Flats and Hopewell Cape were bordered by a 500-m marsh field, instead of being near a forested area, as are many of the other sites. It was possible that birds selected these sites because they had a greater chance of detecting and escaping from a predator if it flew over the marsh before attacking. Peck's Cove, on the other hand, had the highest *C. volutator* density of any of the sites, but is bordered by dense forest, and was largely avoided by birds. Such a trade-off between safety and food has also been noted in habitat selection by Western Sandpipers both between (Ydenberg et al. 2002, Pomeroy et al. 2008) and within sites (Pomeroy 2006). Lind (2004) concluded that the ability to detect a predator is paramount in determining survival during an attack. Thus, although birds fed where predators were abundant, like many other species (Lima and Dill 1990) they may have selected foraging and roosting habitats, in part, to minimize perceived risk.

In 2005, birds tended to be detected at Grande Anse earlier in their stay (therefore, when lighter) than at the other sites, particularly at high tide when they were most vulnerable. This suggests that birds were avoiding Grande Anse later in their stay after they had presumably gained weight and were possibly more susceptible to predation, as a result of decreased maneuverability in flight (Witter and Cuthill 1993, Burns and Ydenberg 2002, Piersma et al. 2003). Pomeroy et al. (2008) found that heavier Western Sandpipers were more likely to avoid dangerous sites than were lighter individuals. Observations made in 2007 further support this

Table 4. Results of multiple regression and AIC model selection for factors predicting habitat use by sandpipers foraging at low tide. Note that other factors, including predators and attacks per hour and mudflat area had to be excluded from these models because of multicollinearity. C. v. density refers to August density of *C. volutator*. Dist from cover refers to maximum distance from cover that a bird can forage on a mudflat. AIC model likelihood was calculated from AICc values.

Model	df	F	*p*	R^2	AIC likelihood	Independent variables	Standardized beta coefficient
1	1,38	3.84	0.057	0.09	<0.0001	C. v. density	-0.30
2	2,37	22.9	<0.001	0.55	0.696	C. v. density	0.30
						Dist from cover	0.91
3	1,38	38.3	<0.001	0.50	0.304	Dist from cover	0.71

view. Birds roosted extensively at Grande Anse early in the season, however, later in the season they continued to feed at the site (which then hosted a healthy *C. volutator* population) but they were also observed crossing Chignecto Bay to roost at Hopewell Cape (D. J. Hamilton, pers. obs.; M. G. Ginn, pers. comm.). The forested area surrounding Grande Anse may have been less safe for the heavier birds, as they would have had less time to detect predators launching surprise attacks from the trees.

Predation events by raptors were more frequent in 2005 than 2004 at both low and high tide. This extra predation pressure may have caused birds to move to form larger flocks in order to increase their individual chances of survival (Parrish and Edelstein-Keshet 1999). If so, this would offer another possible explanation for the increased movements of sandpipers in Chignecto Bay in 2005. Cresswell (1996) found that flocking reduced the probability of an individual Redshank (*Tringa tetanus*) being killed by Sparrowhawks (*Accipiter nisus*) and Peregrines, and that larger flocks were attacked more often, but the predatory attacks on the larger flocks were less likely to be successful. Dietz et al. (2007) found that Red Knots compensated for reduced escape flight ability due to body mass gain by forming large flocks in order to minimize the risk of predation. Hopewell Cape was the most frequently used roost site in 2005, when flocks of over 200 000 birds were observed daily from early to mid-August. The high densities of sandpipers likely attracted Peregrine Falcons and Merlins to the beach, resulting in a doubling of the number of predators, attacks, and successful attacks per hour relative to any other site in either year (Fig. 5a). The low-tide predation risk (predation events$\cdot h^{-1}\cdot$bird density^{-1}) was similar in Chignecto Bay between years (Fig. 5b). Therefore, increased movement in 2005 may have been due to increased predation activities during high-tide periods, which may have caused the sandpipers to form large flocks at the roosting sites but then disperse to forage at low tide.

Combined Factors Influencing Site Selection

We found that overall sandpiper foraging habitat use in 2005 was best predicted by a combination of distance to cover and prey availability, with distance to cover being by far the more important variable. This is consistent with the analysis of Pomeroy et al. (2008), who also found that the best predictive models incorporated both food and safety. As expected, a larger distance to cover led to more sandpipers in our study. However, somewhat surprisingly, shorebird habitat use was only slightly positively affected by *C. volutator* density after distance to cover was accounted for (Table 4). This does not imply that food availability is not important. Rather, the result is probably an artifact of high prey densities at most sites. Daniel's Flats, the foraging site most often selected by tagged

Table 5. Results of regressions for factors predicting habitat use by sandpipers roosting at high tide. Note that none of these variables could be combined into a single model because of problems of multicollinearity.

Independent variable	df	F	*p*	R^2	Standardized beta coefficient
Distance from cover	1,42	6.96	0.012	0.14	0.38
Predators per hour	1,42	7.35	0.01	0.15	0.39
Attacks per hour	1,42	10.15	0.003	0.18	0.44

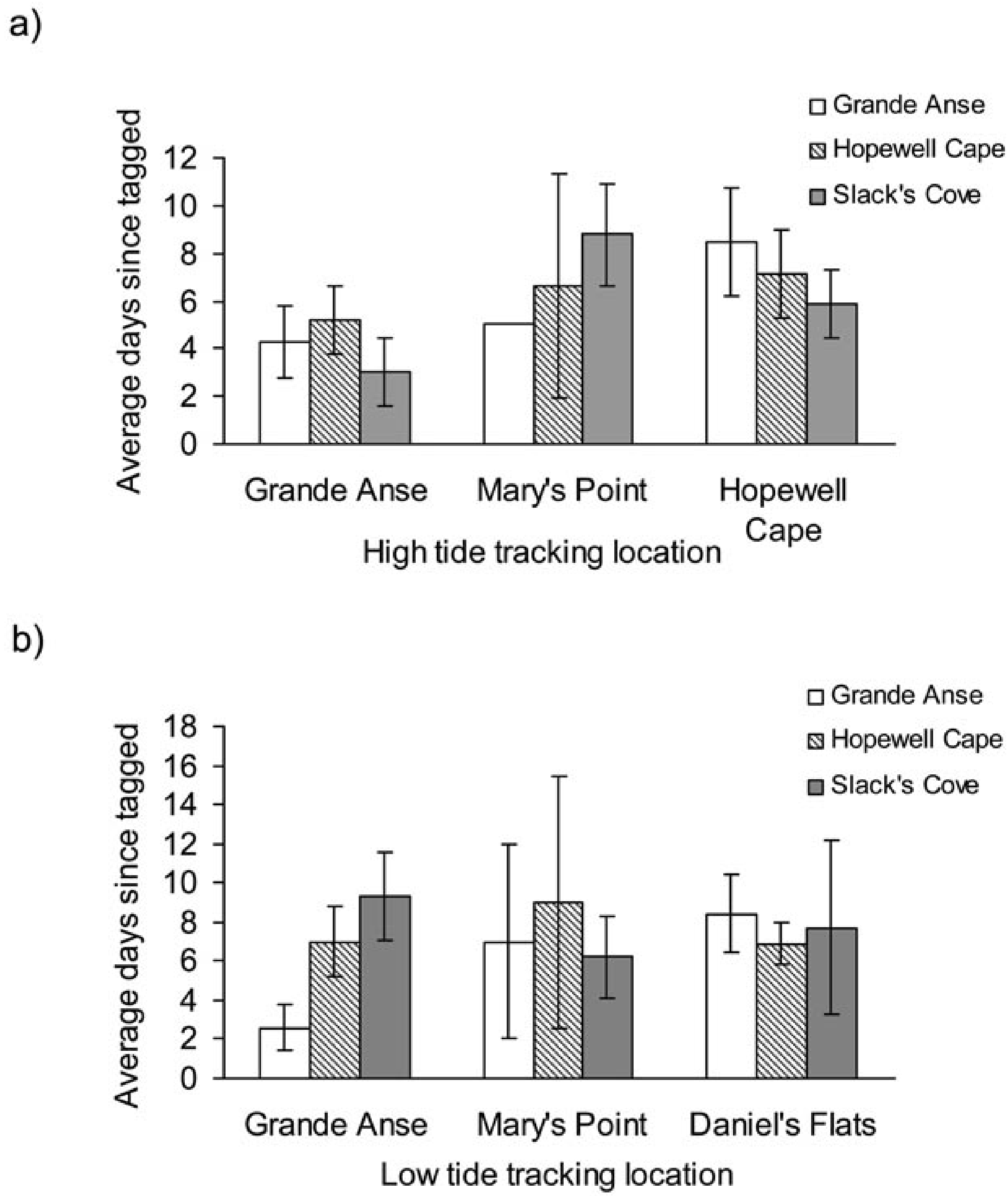
sandpipers in 2005, had the safest predator landscape (greatest distance to cover), but also had the second-lowest *C. volutator* density of Chignecto Bay sites used at low tide (Fig. 4). Sandpipers were likely selecting Daniel's Flats because of the safer predator landscape it provided, but also because the *C. volutator* density was above the threshold that makes it energetically profitable to use (Wilson 1990). The density of adult *C. volutator* at Daniel's Flats reached this critical threshold range in both 2004 and 2005 (Fig. 4). Hence, we infer that site safety may be of paramount importance provided that food availability is adequate. The same appears to hold true for roosting sandpipers. Distance from cover again predicted site selection, with increased roosting at the one site (Hopewell Cape) that was farthest from cover.

CONCLUSION

This study provides the first evidence of large-scale movements of and habitat use by shorebirds migrating through the upper Bay of Fundy, and identified important feeding and roosting sites in Minas Basin and Chignecto Bay. Other studies have examined the post-breeding or overwintering movements of shorebirds (Ruiz et al. 1989, Warnock et al. 1995, Plissner et al. 2000, Leyrer et al. 2006, Rogers et al. 2006), but very few studies have examined movements during migration stopovers. Of those that have, very limited movement seems to be the norm for small shorebirds (Farmer and Parent 1997, Butler et al. 2002), although greater movement was reported in larger Red Knots (van Gils and Piersma 1999). Hence, the observed movements by Semipalmated Sandpipers staging in the Bay of Fundy during our study suggest that they may differ from other calidrine species in this respect.

Habitat use by Semipalmated Sandpipers staging in the upper Bay of Fundy is dictated by site safety and food. Also notable is the interannual variation in selection of and movements between roosting and foraging areas that we documented in Chignecto Bay between 2004 and 2005. This capacity to modify their movement patterns when necessary suggests that Semipalmated Sandpipers can at least to some degree adapt to natural variations in mudflat community dynamics and perhaps to human-induced changes in this system. However, given the importance of upper Bay of Fundy mudflats and roost sites to this species (Hicklin and Smith 1984, Hicklin 1987, Hamilton et al. 2003), the flexibility displayed by these birds should not be viewed as reason to reduce efforts to conserve critical habitats for these migrant sandpipers. Rather, it should be viewed as incentive to ensure that this important ecosystem is maintained, such that migrant shorebirds continue to have foraging and roosting options available to them when natural changes occur. Furthermore, in view of the mobility of migrant shorebirds over short staging periods, to obtain accurate population estimates, simultaneous surveys of known roosts around the Bay should be conducted as described in Colwell and Landrum (1993). This would improve our ability to monitor possible population changes of migrating shorebirds in this critical coastal region.

Fig. 7. Average number of days since being tagged that birds were located at each site in Shepody Bay 2005 for (a) high tide and (b) low tide. Separate bars represent birds tagged from the three capture sites, as indicated in the legend. Error bars are ± 1 SE.



Finally, relative safety of sites should be incorporated in future studies on a landscape scale (Butler et al. 2003, Lank et al. 2003, Ydenberg et al. 2007, Pomeroy et al. 2008). Our results suggest that sites that provide a safer predator landscape are being selected by migrating sandpipers, and that site safety may under some circumstances be more important than food availability in determining foraging habitat. Therefore, in agreement with Pomeroy et al. (2008), we conclude that in a highly dynamic system where food can be variable, landscape features such as distance to cover are important to consider when selecting candidate sites for shorebird conservation measures.

Responses to this article can be read online at:
http://www.ace-eco.org/vol3/iss2/art4/responses/

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