

**FACTORS AFFECTING MOVEMENT AND HABITAT SELECTION OF
SEMIPALMATED SANDPIPERS (*CALIDRIS PUSILLA* Linnaeus) MIGRATING
THROUGH THE UPPER BAY OF FUNDY, CANADA.**

by

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Abstract

The objective of this study was to determine factors affecting habitat use by Semipalmated Sandpipers, *Calidris pusilla*, during their critical migration stopover in the upper Bay of Fundy. Using radio-telemetry, individual sandpipers were found to be highly mobile, often moving several kilometers daily between roosting and foraging sites. No direct relationship was found between the number of times a sandpiper was detected on a foraging site and the amount of their main prey, *Corophium volutator*, on that site. Using Akaike's Information Criterion model selection, the density of sandpipers foraging on mudflats around the Bay was best predicted using a single factor – density of *C. volutator* in August. This shows that sandpipers in the Bay of Fundy most often select foraging sites with high prey abundance, but will occasionally forage on sites with low prey abundance. The study points to the importance of protecting and conserving the Fundy mudflats.

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Chapter 1. General Introduction

1.1. Background - Millions of Nearctic shorebirds undertake long-distance migrations, with many species traveling between Arctic breeding grounds and wintering grounds in South America. Because long-distance migrants cannot complete the journey without periodically replenishing fat reserves, stopover sites where birds can rest and refuel become critical to the survival of individuals (Myers 1983; Piersma and Jukema 1990). In order to preserve these critical sites, conservation researchers and managers need to understand why birds use specific areas and how to maintain the underlying ecological processes that support the food base for birds using the particular sites (Elner and Seaman 2003; Butler *et al.* 2001).

1.1.2. The Semipalmated Sandpiper - The Semipalmated Sandpiper, *Calidris pusilla*, is one of North America's smallest and most abundant shorebirds (Gratto-Trevor 1992). The species inhabits a wide range of marine and freshwater areas, most commonly being found near river deltas, marshlands or inter-tidal mudflats (Gratto-Trevor 1992). A long-distance migrant, the species breeds across northern Canada and Alaska and over-winters in Northeastern South America (Gratto-Trevor 1992; Gratto-Trevor and Dickson 1994). Eastern and Western breeders follow different migratory pathways to the wintering grounds. Western populations follow a transcontinental route South, while Central and Eastern populations undertake a non-stop 3000-4000 km trans-Atlantic flight (Harrington and Morrison 1979; Gratto-Trevor 1992; Gratto-Trevor and Dickson 1994).

Semipalmated Sandpipers forage primarily on benthic invertebrates by probing into burrows or pecking on the surface to capture prey. In coastal areas, foraging is regulated by the tidal cycle, with most feeding occurring as the water recedes and at low tide (Boates and Smith 1989). When high tides inundate feeding areas, shorebirds form

dense flocks at communal roost sites to rest and preen (Colwell and Landrum 2003).

Communal roosting may provide protection against predators through increased vigilance, and flocking in large numbers may decrease an individual's risk of predation through the dilution effect (Beauchamp 1999; Michaelsen and Byrkjedal 2002).

1.1.3. The Bay of Fundy - The upper Bay of Fundy is a critical fall migratory stopover for Semipalmated Sandpipers. One to two million birds – 50% to 95% of the world's population - visit local mudflats annually, the majority from late July to late August (Mawhinney *et al.* 1993). During their 2-week stay in the area, individual sandpipers double their weight in preparation for their long southward migration by feeding on the Grammaridean amphipod *Corophium volutator*, an abundant invertebrate on mudflats in the area (Hicklin and Smith 1984). Because long-distance migrants cannot complete the journey without periodically replenishing fat reserves, stopover sites become vital to their survival (Myers 1987). The Western Hemisphere Shorebird Reserve Network has designated the upper Bay of Fundy as a site of critical importance for the species.

1.1.4. Habitat Use - It is not clear how sandpipers select foraging and roosting habitat during their time in the upper Bay of Fundy. Prior to this study, it was not known if individuals stayed on single mudflats, or used several flats around the bay. In recent years, distribution of shorebirds among feeding and roosting locations in the area has changed. Some historically important sites no longer support large numbers of birds. Given the clear importance of the Fundy region to this species, and the population decline of Semipalmated Sandpipers throughout the Western Hemisphere (Morrison *et al.* 1994), it is essential from a conservation standpoint that we understand factors influencing shorebird movements and habitat use, and protect habitat shown to be critical.

1.1.5. Population Estimates - In order to estimate accurately the number of birds using the bay, if and how birds move locally while they are in the area must be known.

Improved population estimates will facilitate accurate monitoring of population changes and will help to predict future responses of the shorebirds to human-induced changes in the ecosystem, such as the damming of tidal rivers and the subsequent removal of these barriers. Migrating shorebirds tend to concentrate with large proportions of the population occurring at only a restricted number of sites; this makes them particularly vulnerable to loss or degradation of habitat in such areas (Morrison *et al.* 1994). If birds are able to use multiple mudflats, they may be less vulnerable to localized habitat changes than if they remain on one mudflat throughout their stay. This issue is of particular importance to the Bay of Fundy region, as the removal of some intertidal causeways, which would alter surrounding mudflats, is being considered. Possible effects of this change on the population of Semipalmated Sandpipers staging in the area are unknown.

1.1.6. Research Objectives - In order to improve our understanding of shorebird habitat use and individual bird movements, an extensive field study was conducted in two key areas of the upper Bay of Fundy; the Minas Basin, Nova Scotia and Shepody Bay, New Brunswick. The objectives were to quantify shorebird habitat use and to identify some of the main factors influencing habitat selection. Habitat use was examined on two scales: first, by radio-tracking the movements of individual sandpipers, and secondly, by determining the quality of foraging sites based on sandpiper density.

The hypothesis is that movement and habitat selection are influenced by: 1) abundance and size distribution of the prey *Corophium volutator*, 2) predation threats by

Peregrine Falcons (*Falco peregrinus*) and Merlins (*Falco columbarius*) and 3) landscape characteristics of foraging and roosting locations.

1.2. Factors affecting Habitat Selection

1.2.1. Prey Abundance - *Corophium volutator* has previously been found to make up approximately 80% of Semipalmated Sandpiper diet while in the Bay of Fundy (Hicklin and Smith 1979, 1984; Gratto *et al.* 1984; Peer *et al.* 1986). Hamilton *et al.* (2003) found that populations of the energy- rich *C. volutator* have collapsed on some mudflats and suggest that the observed redistribution of shorebirds is most likely related to the decline in prey base on some sites. Semipalmated Sandpipers need to acquire extensive fat reserves in order to complete the 3000-4000 km non-stop transoceanic flight to their wintering grounds in South America (Gratto-Trevor 1992). In order to obtain the high energy requirements in a relatively short time period, birds are expected to feed only in areas that support adequate prey density.

1.2.2. Predation Risk - Another factor possibly influencing shorebird habitat selection is increased predation by raptors. Wide-spread use of chemical pesticides reduced populations of some raptor species to near extinction. Raptor populations have since made a strong recovery, due to the North American ban on DDT use in 1972 and the subsequent implementation of successful restoration programs (Noble and Elliot 1990; White *et al.* 2002).

Ydenberg *et al.* (2004) attributed changes in fall migration stopover behaviour of Western Sandpipers to the increase of Peregrine Falcon populations. The study found that sandpipers staging in the Strait of Georgia, British Columbia, have decreased body mass and length of stay periods at dangerous stopover sites. These changes may be explained by the finding that vulnerability of individual birds increases as birds gain fat reserves

necessary for long-distance migration (Piersma *et al.* 2003). Increased fat reserves could impair a bird's ability to escape from a predator due to a combination of reduced take-off ability and impaired performance in flight (Witter and Cuthill 1993). The substantial weight gain acquired by Semipalmated Sandpipers should lead heavier birds to select safer sites than the less vulnerable light-weight birds.

1.2.3. Landscape – The upper Bay of Fundy has two main branches which differ in landscape and provide a unique opportunity to examine the effects of landscape on shorebird movement and habitat use. The coastline of the Minas Basin, located in Nova Scotia, has many closely connected intertidal mudflats. The flats range in size from 3-5 km in length, and are separated by only small sections of coastline. Mudflats in Shepody Bay, New Brunswick, are much larger (10-14 km in length) and more isolated. The expectation was to find more movement in the connected landscape of Minas Basin than in Shepody Bay because a more connected landscape should allow shorebirds to exploit more feeding sites with reduced searching costs (Farmer and Parent 1997).

The study also looked at landscape features associated with different sites, such as the distance birds can forage or roost away from forested areas at each of the study sites. This is thought to be an indicator of site safety, with sites further from cover being safer, as avian predators hunt most successfully by launching surprise attacks from cover (Whitfield 2003).

1.3. Chapter Summary - The findings from this study are presented in article format. Chapters 1 and 4 are introductory and summary chapters, respectively. Chapter 2 focuses on individual bird movements which were quantified using radio-telemetry, and discusses factors influencing individual foraging and roosting site selection. Chapter 3 presents

research on factors that can predict density of foraging shorebirds. Hamilton *et al.* (2003) showed that *C. volutator* abundance and size distribution roughly predicts shorebird abundance. This relationship was examined across eight mudflats, and predicted shorebird density more accurately by using the additional factors mentioned above. Knowledge obtained from this work will help to manage and conserve critical habitat for Semipalmated Sandpipers in the upper Bay of Fundy.

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**Chapter 2. Factors affecting movements of individual Semipalmated Sandpipers
(*Calidris pusilla*) migrating through the Upper Bay of Fundy**

Abstract

Radio-telemetry was used to track movements of individual Semipalmated Sandpipers (*Calidris pusilla*) during their fall migration stopover in the upper Bay of Fundy in August of 2004 and 2005. In 2004, sandpipers from the Minas Basin, Nova Scotia and Shepody Bay, New Brunswick, were tracked, and in 2005, sandpipers were tracked only in Shepody Bay. Sandpipers were highly mobile in both the Minas Basin 2004, and Shepody Bay 2005. They were found to make daily movements of up to 20 km between foraging and roost sites, although very little movement was detected in Shepody Bay in 2004. An attempt was made to determine what factors influenced foraging and roost site selection. No clear relationship was found between the number of times sandpipers were detected on a site and the abundance of their main prey, *Corophium volutator*, or observed number of predation events by raptors at each site. Sandpipers may be selecting sites where they can roost and forage the furthest distance from cover, which they likely perceive as an indicator of site safety.

2.1. Introduction

Semipalmated Sandpipers, *Calidris pusilla*, migrate from breeding grounds in the North American arctic tundra to north-eastern South America, where they over-winter (Gratto-Trevor 1992, Gratto-Trevor and Dickson 1994). On their fall migration route, Central and Eastern breeding populations stop in the upper Bay of Fundy, where they feed and acquire essential fat reserves necessary to complete a 3000-4000 km trans-Atlantic flight to the wintering grounds. Because long-distance migrants cannot complete the journey without periodically replenishing fat reserves, stopover sites become critical to the survival of individual birds. (Skagen and Knopf 1994, Myers 1983). In order to preserve these crucial sites, researchers need to know why birds use certain areas and how to maintain the underlying ecological processes that support the food base in these areas (Elner and Seaman 2003, Butler *et al.* 2002).

The upper Bay of Fundy supports between one and two million Semipalmated Sandpipers – 50% to 95% of the world’s population- and has been designated as a site of critical importance for the species by the Western Hemisphere Shorebird Reserve Network (Mawhinney *et al.* 1993). Throughout their approximately 2-week stay in the region, individual sandpipers double their weight in preparation for their long southward migration by feeding on *Corophium volutator*, an abundant amphipod on mudflats in the area (Hicklin and Smith 1984). During high tide, when water inundates feeding areas, birds move to communal roost sites where they rest and preen until the water recedes.

It is not clear how sandpipers select foraging and roosting habitat or to what extent the birds move between 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

colour-marked shorebirds used only one mudflat for foraging and roosting. However, other sites around the Bay were not checked daily and resighting colour-marked birds can be problematic. A more quantitative approach, such as radio-telemetry, provides more detailed information on movement (Haig *et al.* 1998) and is required to address this question.

Conservation programs aimed at protecting migrant shorebirds require information on how species use habitats (Butler *et al.* 2002). Understanding how birds move within the area will help to estimate the number of birds using the bay more accurately, and help monitor any population changes. Improved population estimates will also help to 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. Migrating shorebirds tend to concentrate with large proportions of the population occurring at only a restricted number of sites, which makes them particularly vulnerable to loss or degradation of habitat in such areas (Morrison *et al.* 1994). If birds are able to use multiple mudflats, they may be less vulnerable to localized habitat changes than if they remain on one mudflat throughout their stay.

The primary objective of this study was to quantify individual shorebird movements around the upper Bay of Fundy using radio-telemetry. The study attempted to identify the main factors that contribute to individual movements and habitat selection during the migration stopover. It was hypothesized that the degree of movement may be influenced by three main factors; 1) the abundance and size distribution of *C. volutator*, 2) predation threats by raptors and 3) landscape composition.

It was predicted that birds will forage primarily on sites with abundant adult *C. volutator* and avoid sites with low *C. volutator* density. *C. volutator* makes 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). Sandpipers are known to be size-selective predators, preferring large adults over juvenile (Boates and Smith 1979; Peer *et al.* 1986; Wilson 1990).

We predicted that shorebirds would avoid sites with the highest predation risk. The main predators of shorebirds in the Bay of Fundy are Peregrine Falcons (*Falco peregrinus*) and Merlins (*Falco columbarius*). These raptors altered shorebird stopover behaviour elsewhere (Ydenberg *et al.* 2002). Mudflat area, shape and composition of surrounding landscape are indicators of site safety. Some sites are thought to be safer because of the distance a bird can forage away from cover, which is often the source of predator attacks (Whitfield 2003). Therefore, smaller sites surrounded by forest may be perceived by the birds as being more dangerous than large open sites.

The substantial weight gain by Semipalmated Sandpipers during their time in the Bay of Fundy may influence their vulnerability to predation and as a result their perception of danger associated with feeding and roosting areas. Predation risk may increase as birds increase their fuel load because the increased fat reserves could impair a bird's ability to escape from a predator, both through a reduced take-off ability and through impaired performance in flight (Whitfield 2003). Newly arriving, low weight birds may be more likely to feed on the more dangerous sites, because they are less vulnerable to predation (Ydenberg *et al.* 2002).

Further, to quantify the general relationship between movement and sandpiper mass, the hypothesis was tested that birds reduced distances moved as they gain weight during their stopover in the Bay of Fundy. It was predicted that, upon arrival, light birds should be able to move greater distances in search of available prey. Over the course of their stopover, as the birds gain weight by building fat reserves in preparation to continue migration, the energetic cost of moving between sites should increase and so birds should move less.

A few studies have examined how wetland connectivity affects avian movements (Farmer and Parent 1997; Haig 1998), but none have examined the effects of mudflat connectedness on individual movements. The upper Bay of Fundy has two main branches which differ in landscape and provide a unique opportunity to examine the effects of landscape on shorebird movement and habitat use. The coastline of the Minas Basin is composed of several small, closely connected mudflats. Shepody Bay has fewer mudflats, all larger in area and more isolated (See Figures 2.1 and 2.2). More movement was expected among sites in the Minas Basin, where neighbouring mudflats are close together, than on the more separated flats of Shepody Bay because a more connected landscape should allow shorebirds to exploit more feeding sites with reduced searching costs (Farmer and Parent 1997).

2.2. Materials and methods

2.2.1. Study Area - The study was conducted in two areas of the upper Bay of Fundy; Nova Scotia's Minas Basin (45° 00' N, 64° 20' W) and New Brunswick's Shepody Bay (45° 40' N, 64° 20' W). The tides in the upper Bay of Fundy rise and fall 12-15 meters

(36-45 feet) twice daily; at mean low water about 5000 ha of salt marsh and 35,000 ha of mud and sand flats are exposed (Hicklin 1987).

Eight mudflats in the upper Bay of Fundy were selected (Johnson's Mills, Daniel's Flat, Peck's Cove, Mary's Point, and Minudie in Shepody Bay, and Avonport, Evangeline Beach, and Cheverie in the Minas Basin) to monitor throughout the study (Figures 2.1, 2.2 and 2.3). All sites except Daniel's Flats have beach exposed at high tide where shorebirds can roost. The two areas of the Bay differ in landscape composition. The Minas Basin consists of several mudflats (3-5 km in length) which tend to be separated by only a small area of coastline. Shepody Bay has fewer mudflats which are larger (10-14 km in length) and more isolated, with several kilometers separating the flats.

2.2.2. Radio-tracking - Large numbers of adult Semipalmated Sandpipers were captured at high tide roost sites using pull traps (following the technique of Peter Hicklin, Canadian Wildlife Service). In 2004, 19 sandpipers from Johnson's Mills, Shepody Bay and 20 from Blue Beach, Minas Basin were fitted with 0.9-g BD-2 radio transmitters (Holohil Systems Ltd.). In 2005, an additional 45 sandpipers were tagged from three sites in Shepody Bay (20 from Hopewell Rocks, 15 from Johnson's Mills and 10 from Slack's Cove). 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 its feathers. Light birds (21.9-29.2g), were selected, as low weights indicate recent arrival in the area. In the Minas Basin, birds were caught at Blue Beach on 6 August 2004. In Shepody Bay, birds were caught at Johnson's Mills on 10 and 11 August 2004. In 2005, birds were caught on 2 August at Johnson's Mills, 3 August at Hopewell Rocks, and 4 August at Slack's Cove.

Tagged birds were tracked using a Cessna 172 airplane with H-style antennas mounted on the plane's struts. In 2004, flights followed the coastline along both Shepody Bay and the Minas Basin during high and low tide, in attempts to locate all tagged birds. Seven flights of 2 to 4 hours duration (21 total flight hours) were conducted between August 10 and August 19, 2004. In 2005, we conducted 26 hours of flights covering the Shepody Bay coastline between August 6 and 15. 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.

2.2.3. Prey abundance -To assess prey base accurately, stratified random sampling of sediment (21 samples per mudflat) was carried out along three transects on each of the study flats in late July, and again in late August. In 2004, a total of seven mudflats were sampled, Cheverie, Avonport and Evangeline Beach in the Minas Basin and Johnson's Mills, Daniel's Flats, Mary's Point and Minudie in Shepody Bay. In 2005, Johnson's Mills, Daniel's Flats, Mary's Point and Peck's Cove were sampled in Shepody Bay.

Samples were collected using an 80-cm² 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 the samples were sorted, *C. volutator* were placed in 2-mm size classes, dried, and weighed. This provided data for estimates of numbers and size distributions of *C. volutator* at each mudflat.

2.2.4. Predation risk – Our 8 focal mudflats were visited regularly at low tide. During each visit, 4 continuous hours of observations were conducted, and roosts were observed

during 2-hour periods around high tide. During each observation period, observers scanned continuously for predators. When one was detected, the predator was identified along with 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 and were measured directly from local maps.

2.2.5. Statistical analyses – Analysis of variance (ANOVA) was conducted to assess differences in mean distances moved by individual birds. ANOVA was also used to assess differences among the fixed factors; tide levels ('High', 'Low') and years ('2004', '2005') in predation events ('Number of predators per observation hour', 'Number of attacks per observation hour'). Regression analysis was used to determine the relationship between percent of total radio-tracking detections at each site and prey density, and to determine the relationship between distances moved and weight gained by individual birds over time. The number of days since a bird was tagged was used as an indicator of weight gain, as birds were building fat reserves throughout their stay. Graphical analysis showed that assumptions of normal distribution and homogeneity of variance were met.

2.3. Results

2.3.1. 2004 Movement: Minas Basin - All 20 birds tagged at Blue Beach were located between 1 and 7 times. Birds were generally found to use multiple roosting and foraging sites. A total of 34 radio-tracking detections were made during low tide and Cheverie was found to be the most frequently visited of 6 foraging sites (50% of detections, Table 2.1). During high tide, a total of 39 detections were made on 6 roost sites of which Summerville was the most frequently used site (33% of detections). The mean (\pm SE)

distance moved between radio-tracking detections was 6.97 ± 0.5 km ($n = 79$) (Figure 2.4). The greatest distance a bird moved between radio-tracking detections in the Minas Basin was 21.8 km. Individual sandpipers moved significantly greater distances in Minas Basin 2004 and Shepody Bay 2005, than in Shepody Bay 2004 ($F_{2,378} = 21.98$, $p = 0.001$, Figure 2.4). No birds moved between Minas Basin and Shepody Bay in 2004.

2.3.2. 2004 Movement: Shepody Bay - In 2004, very little movement was observed with sandpipers tagged at Johnsons's Mills. The birds were located between 1 and 9 times, with 3 birds never being found. Of 34 low tide detections, 83% were of birds foraging at Johnson's Mills (Table 2.1). The birds used a total of 3 different foraging sites. During high tide, all 44 detections were at Johnson's Mills; radio-tagged birds were not found roosting at any other site. The mean distance moved between detections ($n = 80$) was 2.99 ± 0.5 km (Figure 2.4). The greatest distance a bird moved between subsequent detections was 15.1 km.

2.3.3. 2005 Movement: Shepody Bay - In 2005, the 45 sandpipers tagged at three different roost sites were much more mobile than birds tagged in Shepody Bay in 2004, regardless of where they were originally tagged. The birds were located between 1 and 14 times, and 6 birds were never found. Sandpipers were found foraging on 6 different mudflats. 129 detections were made during low tide, most frequently at Daniel's Flat (67% of detections, see Table 2.1). Birds also used a total of 6 different roost sites. Of 112 high tide detections, 58% were of birds roosting at the Hopewell Rocks. Site of tagging had no effect on the distance moved by individual birds (ANOVA, $F_{2,33} = 0.39$, $p = 0.67$, see table 2.2). The overall mean distance birds moved between detections was

6.23 ± 0.28 km (Figure 2.4), and the greatest distance moved between radio-tracking detections was 17.8 km.

2.3.4. Effects of Prey on Movements – *C. volutator* density was higher at both Mary's Point and Daniel's Flat, and was lower in Johnson's Mills, between 2004 and 2005 (Figure 2.5). There was no relationship between the number of times birds were located foraging on a site and the August density of *C. volutator* at each site ($R^2 = 0.003$, $F_{1,8} = 0.019$, $p = 0.89$; Figure 2.6.). *C. volutator* were present on all mudflats used by shorebirds, although occasionally tagged birds were located feeding on sites with extremely low *C. volutator* densities. Further, 25% of sandpipers tagged in the Minas Basin and 15% of birds tagged in Shepody Bay 2005, were found feeding on sites with low *C. volutator* density after previously foraging on a site with high *C. volutator* density. In 2004, the majority of birds tagged at Johnson's Mills remained on the site throughout the stopover period, despite a low *C. volutator* density at the site.

2.3.5. Effects of Predation on Movements - There were significantly more predators observed per hour (ANOVA, $F_{1,53} = 14.5$, $p = 0.0001$) and more attacks per hour observed during high tide than low tide in both years (ANOVA, $F_{1,53} = 16.57$, $p = 0.0001$; Figure 2.7).

There was no evidence to support the hypothesis that sandpipers would avoid sites with the highest predation risk. In the 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 attacks per hour. In Shepody Bay, 2005, Daniel's Flats was the site most used by foraging sandpipers and also had the highest observed predation risk of all sites in the area over both years. Hopewell Rocks

had more predators per hour (ANOVA, effect of site, $F_{7,32} = 2.34$, $p=0.069$) and significantly more attacks per hour (ANOVA, effect of site, $F_{7,32} = 4.20$, $p = 0.006$, Figure 2.8.) than any roost site in either year, but was still the most frequented high tide site in 2005.

2.3.6. Movements and weight gain – There was no evidence to suggest that individual birds moved less distance over time, as they gained weight (Figure 2.9). This result is somewhat surprising given that costs associated with movement should increase as body mass increases.

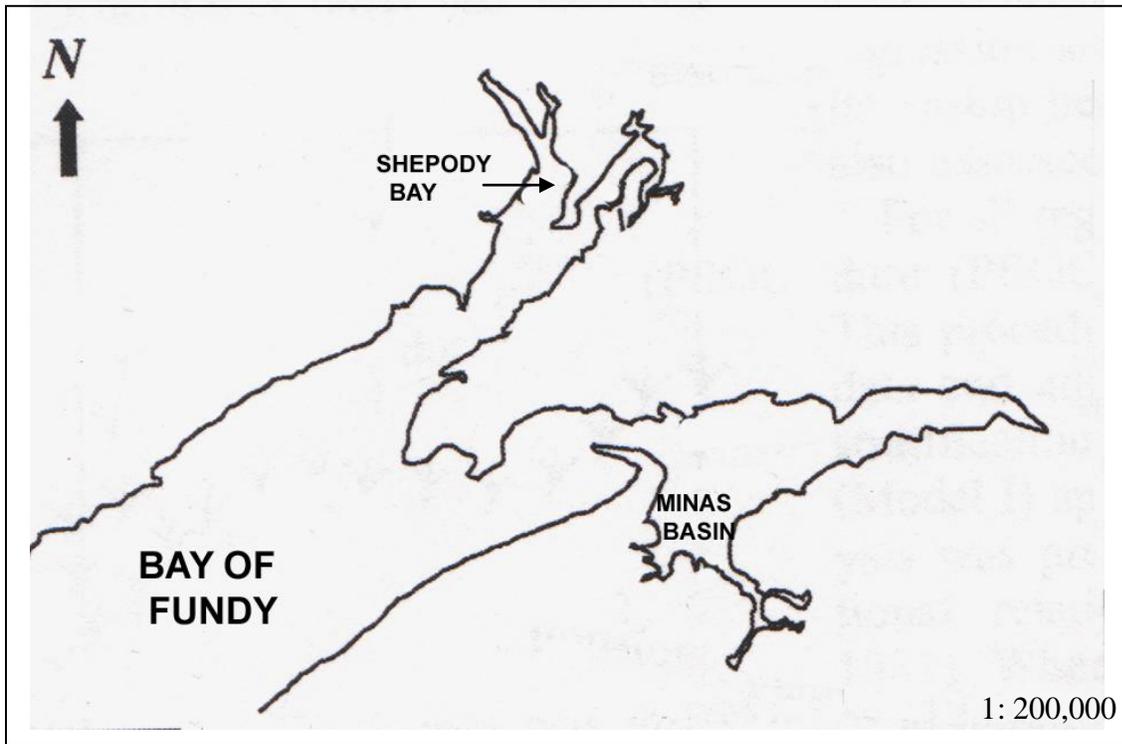


Figure 2.1. Map of the Bay of Fundy, showing Shepody Bay and Minas Basin.

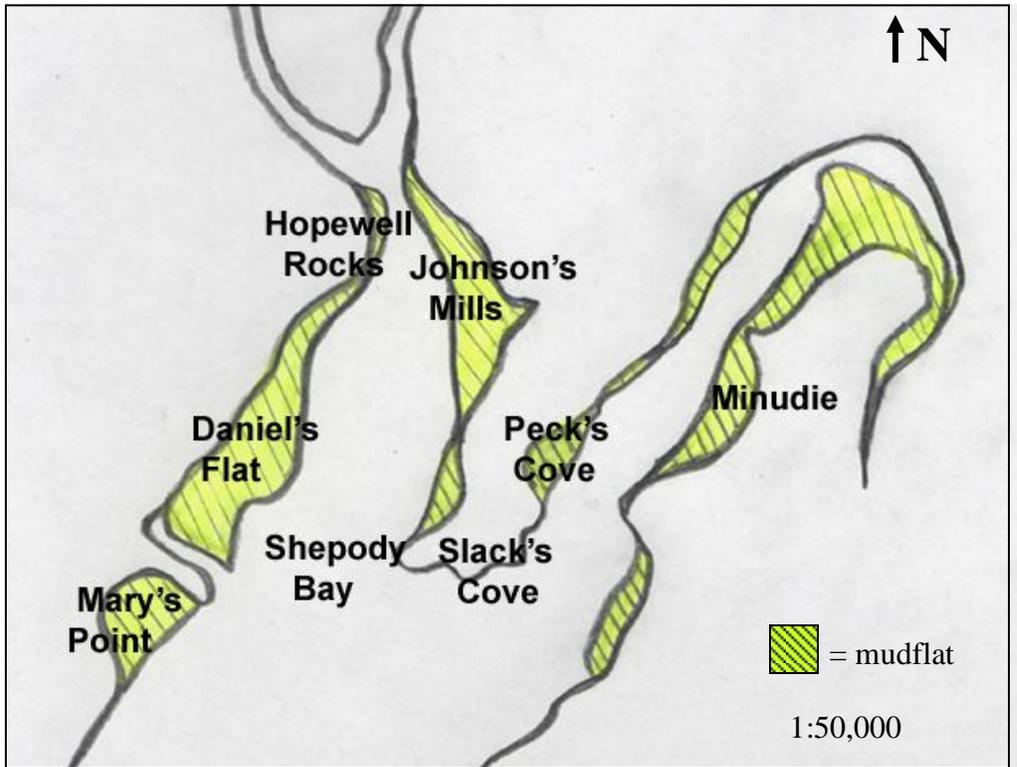


Figure 2.2. Map of study sites in Shepody Bay, upper Bay of Fundy.

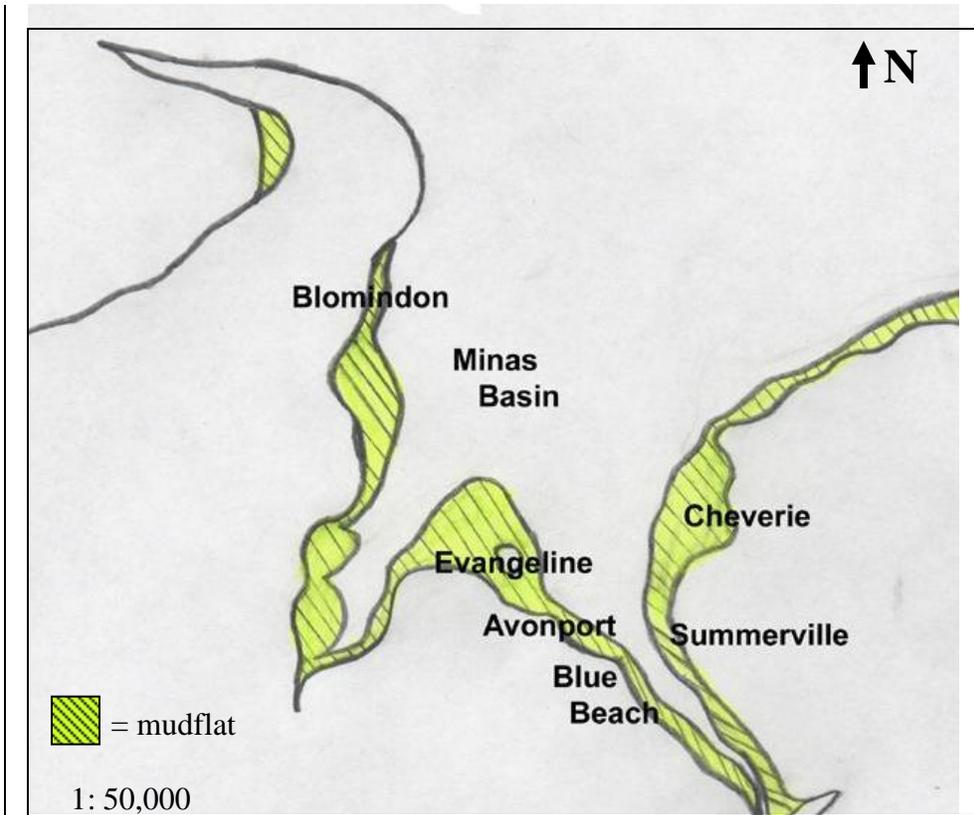


Figure 2.3. Map of study sites in the Minas Basin, upper Bay of Fundy.

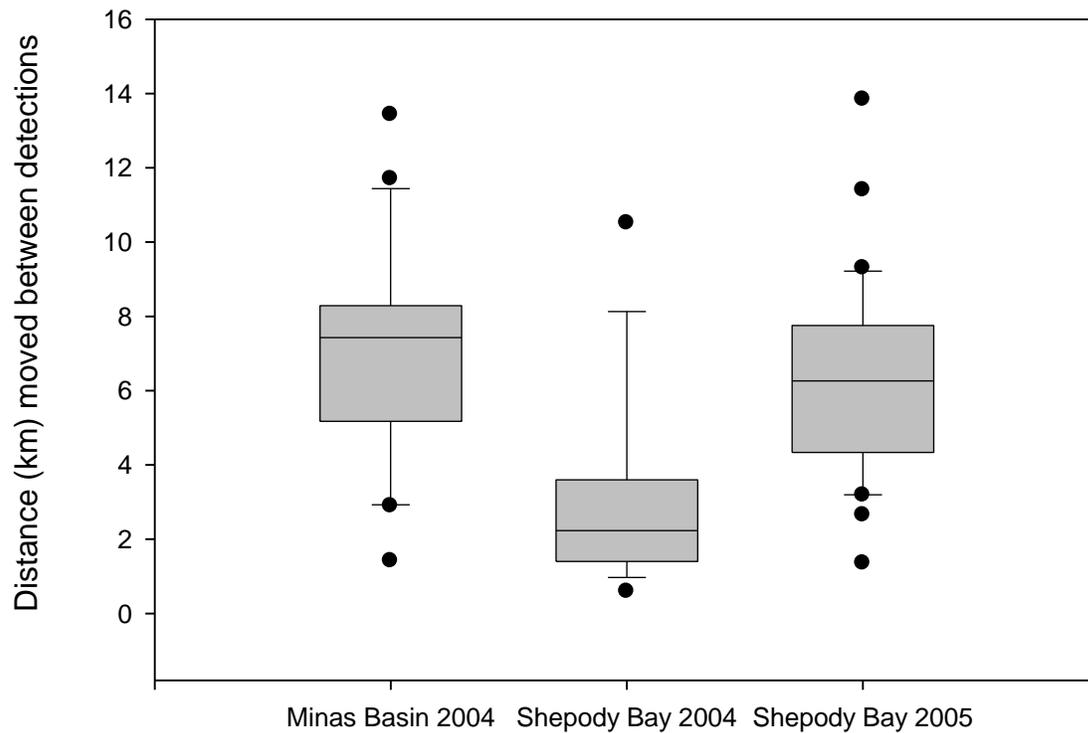


Figure 2.4. Distance moved between radio-tracking detections, averaged for individual birds at two locations in 2004 and 2005. The boundary of the box closest to zero indicates the 25th percentile, the line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Error bars above and below the box indicate the 90th and 10th percentiles.

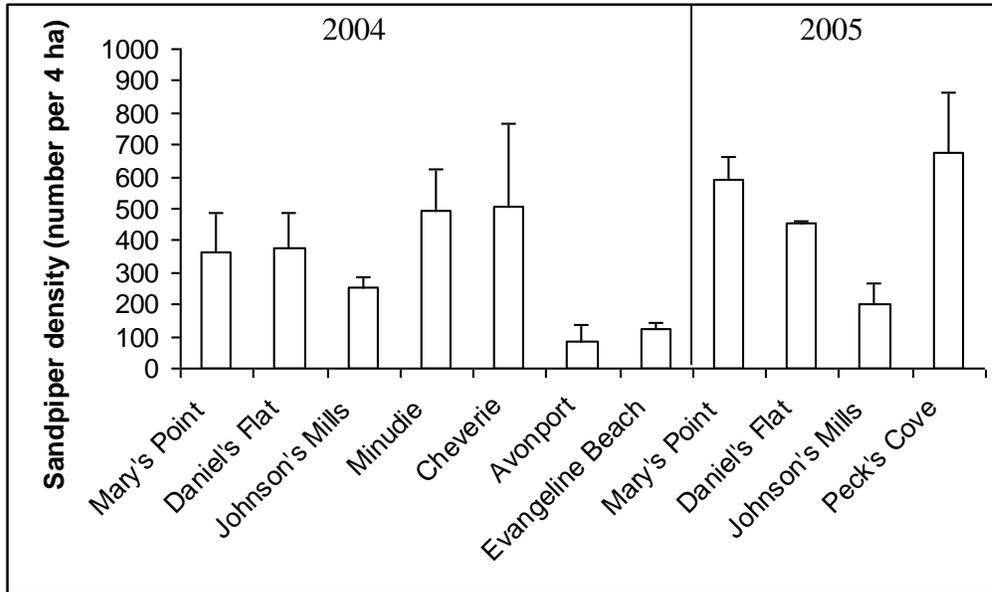


Figure 2.5. Mean number of adult *C. volutator* (≥ 4 mm in body length) per sampling core in August. Bars indicate one standard error.

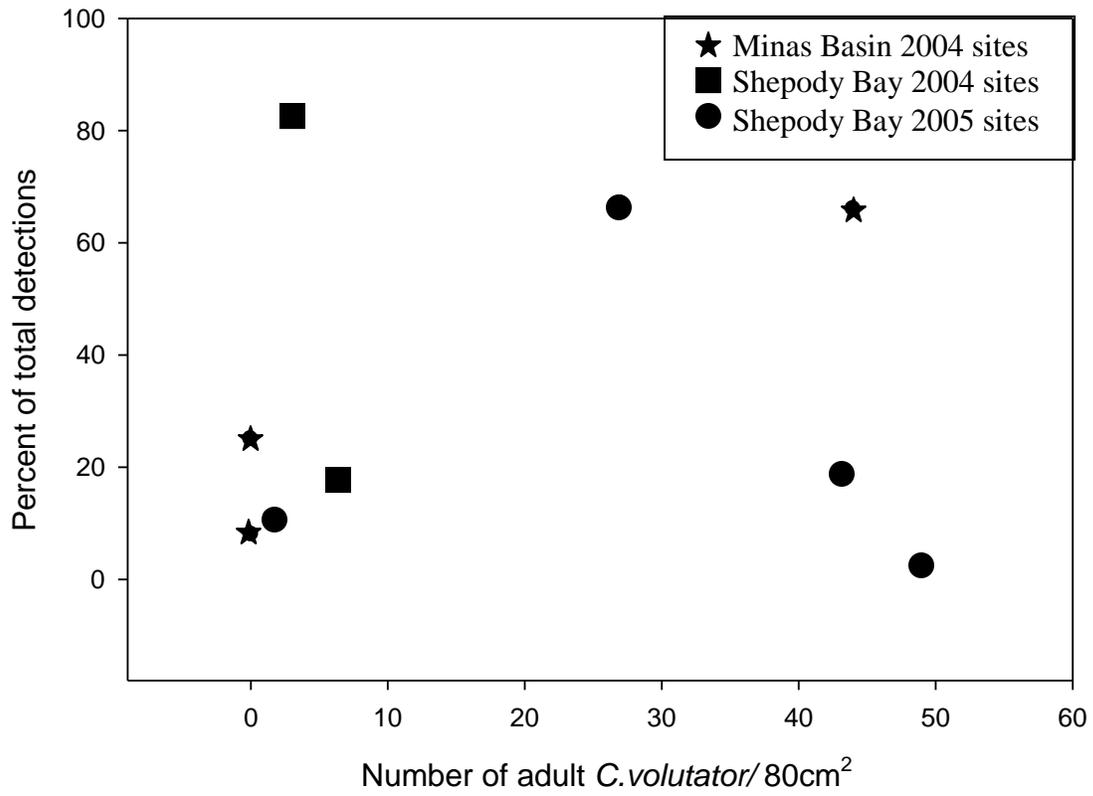


Figure 2.6. Number of detections (presented as percent) that a site was used by radio-tracked sandpipers versus mean number of *C. volutator* at that site. Total number of detections was 79, 80 and 241 for Minas Basin 2004, Shepody Bay 2004 and Shepody Bay 2005, respectively.

|

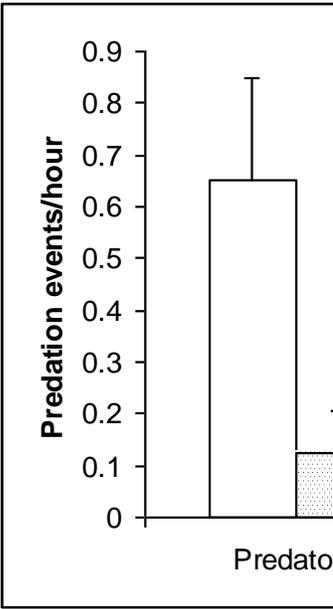
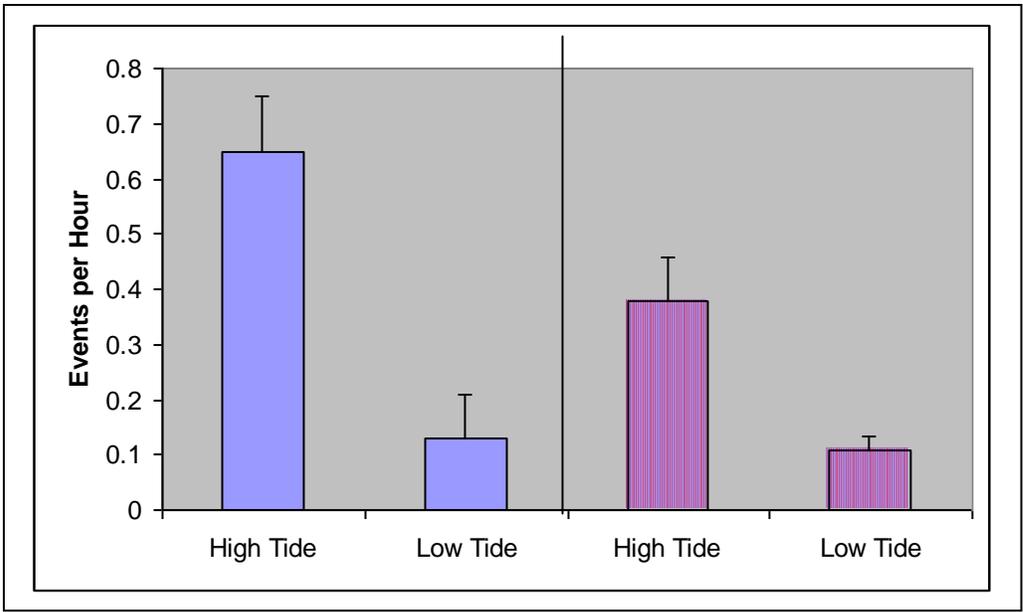


Figure 2.7. Mean number of predators and attacks per hour for each 4-h observation period at low tide (on foraging sites) and 2-h observations period at high tide (on roosting sites) on sites in the upper Bay of Fundy. Data pooled over regions and years. Bars indicate one standard error.

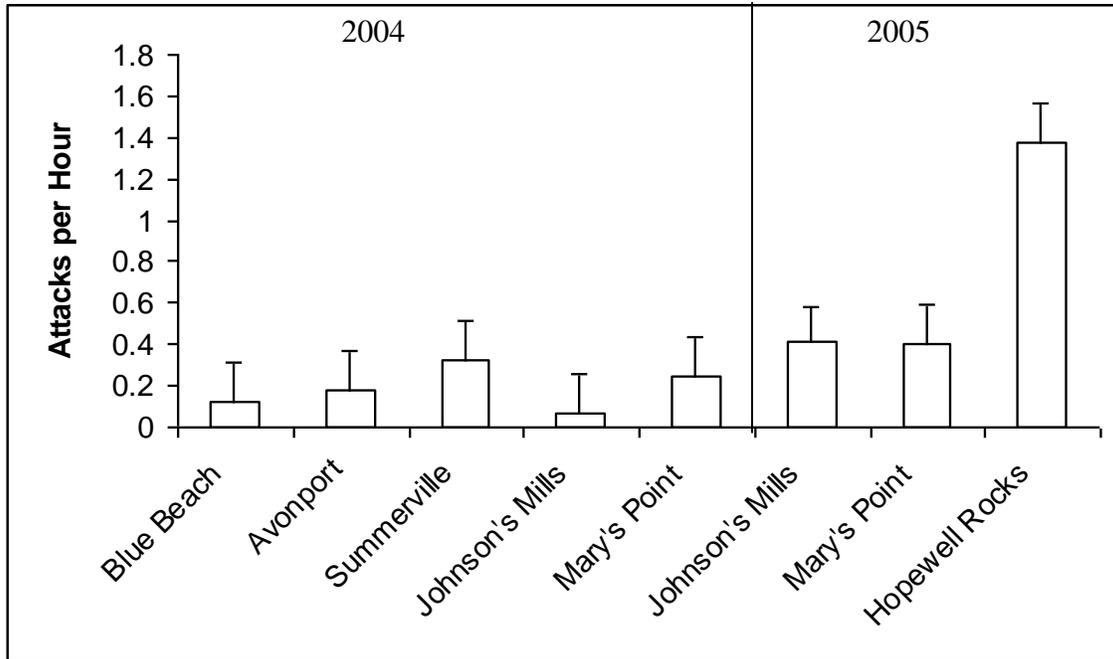


Figure 2.8. Number of attacks per hour observed during each observation period at each site and year of the study (n = 4). Bars indicate one standard error.

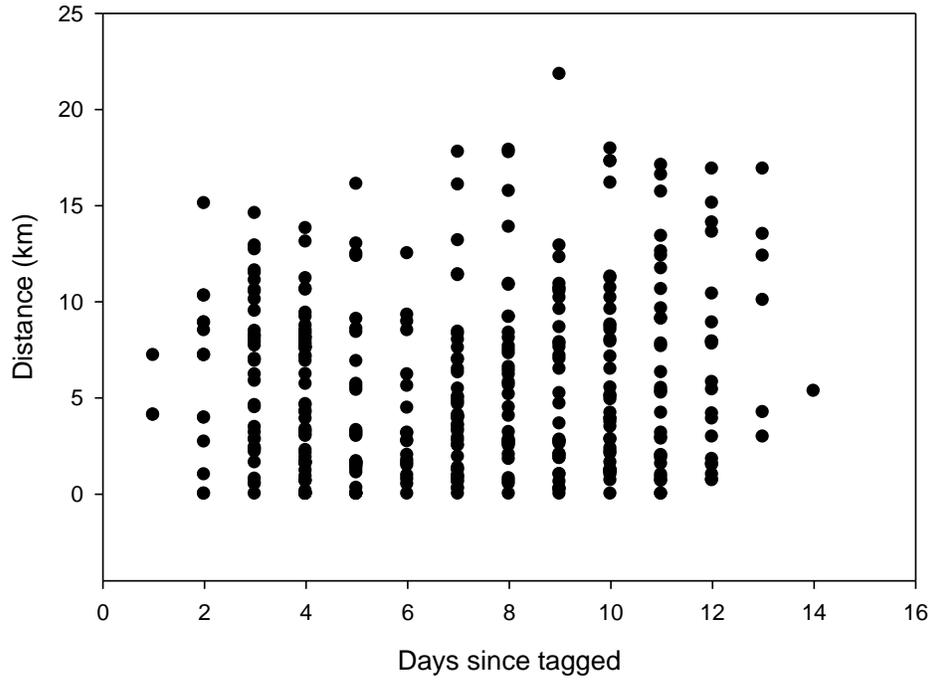


Figure 2.9. Distance moved by individual birds in New Brunswick and Nova Scotia as they gained weight over time in 2004 and 2005.

Table 2.1. Percent of total radio-tracking detections that birds were found on each site at low tide and high tide for 2004 and 2005.

Tide	Minas Basin 2004		Shepody Bay 2004		Shepody Bay 2005	
	Site	% Use	Site	% Use	Site	% Use
Low	Cheverie	50.0	Johnson's Mills	83.0	Daniel's Flat	67.3
	Evangeline Beach	19.0	Daniel's Flat	11.0	Johnson's Mills	18.7
	Kingsport	9.5	Hopewell Rocks	6.0	Mary's Point	10.0
	Starr's Point	9.5			Hopewell Rocks	3.8
	Avonport	6.0			Peck's Cove	3.2
	Walton	6.0			Minudie	1.5
High	Summerville	33.0	Johnson's Mills	100.0	Hopewell Rocks	58.9
	Avonport	26.0			Johnson's Mills	23.2
	Blue Beach	21.0			Mary's Point	9.8
	Cheverie	15.0			Pink Rock	3.6
	Evangeline	2.5			Slack's Cove	2.7
	Hantsport	2.5			Daniel's Flat	1.8

Table 2.2. Mean (\pm SE) distance that individual sandpipers moved from the original tagging site in Shepody Bay 2005. Number of observations is indicated in parenthesis.

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

2.4. Discussion

Semipalmated Sandpipers migrating through the upper Bay of Fundy used multiple intertidal sites to roost and forage throughout their 2-week stay in the region. Some sites were used only as either foraging or roosting sites, and others were used at both high and low tides. It might be expected that birds prefer to forage on mudflats either with a roost site or close to a roost site in order to reduce the energy expenditure of traveling (Goss-Custard *et al.* 1992) and to maximize feeding time. However, the birds did not select sites where they could both forage and roost over sites where they could do only one or the other. For example, 58% of all roosting detections in Shepody Bay (2005) were at the Hopewell Rocks, a site which has a very small intertidal mudflat associated with it and therefore is used only at high tide. Birds selected this site over other roosts in 2005, and were observed to make daily flights of over 15 km to roost at this site, even though this site had the highest predation risk of any roost site observed in either year.

In 22% of all consecutive radio-tracking detections made in Shepody Bay 2005 and 17% of all detections made in Minas Basin 2004, birds moved a distance of 10 km or greater. Several of these movements were between a foraging and roost site on a single day. This suggests that movements of 5-20 km were not overly energetically demanding for the birds, even after they had acquired a significant fuel load.

2.4.1. 2004 Movements- Movements and habitat site use by individual Semipalmated Sandpipers differed between the Minas Basin and Shepody Bay in 2004 (See Figure 2.4). We predicted that birds would move greater distances and use multiple sites in the Minas Basin because the landscape consists of many smaller mudflats which are separated by small sections of coastline. Farmer and Parent (1997) found that landscape connectivity

affected the movements of Pectoral Sandpipers, *Caladris melatonos*, during a mid-continental spring migration stopover. They showed that as the distance between wetlands decreased, individual birds moved between wetlands more frequently and moved longer distances from their release site. This suggests that a more connected landscape allows shorebirds to exploit more feeding sites with reduced searching costs. Our 2004 results supported this hypothesis and agreed with Hicklin's (1987) findings that sandpipers migrating through Shepody Bay show little movement and tend to remain on one site.

2.4.2. 2005 Movements – Sandpipers were radio-tracked in Shepody Bay again in 2005 to test whether the lack of movement observed in birds using Johnson's Mills in 2004 was consistent across years and at different sites. Surprisingly, regardless of where birds were trapped, they were much more mobile, using several sites to roost and feed and moving greater distances between radio-tracking detections. The birds did not remain on one site, as seen in 2004, so prey composition and predation risk was examined at the different sites in an effort to determine why differences in individual bird movement and habitat use were observed between years. This finding casts doubt on 2004 support of landscape connectivity hypothesis and Hicklin's (1987) results.

2.4.3. Effects of Prey on Movements- In Shepody Bay 2005, prey abundance was more concentrated, with significantly higher *C. volutator* densities in Mary's Point and Daniel's Flat and lower *C. volutator* densities in Johnson's Mills (Figure 2.5). Wilson (1990) found that within a flat, birds are likely to forage where *C. volutator* abundance is above a threshold density and areas below this threshold are avoided. The lower abundance of *C. volutator* at Johnson's Mills may have caused birds roosting on that site

to leave and forage on a more energetically profitable site. This could account, at least in part, for the increase in movement detected in Shepody Bay in 2005.

Boates (1980) suggested that, in order to maintain a positive energy budget, birds would have to feed primarily on *C. volutator* larger than 4.0 mm. Hamilton *et al.* (2003) found evidence that shorebirds' choice of foraging areas is influenced by abundance of adult prey, but not juveniles. No clear relationship was found between the density of adult *C. volutator* at a site and the number of times a bird visited that site (Figure 2.6). In both years, at least a few marked birds returned to sites with low *C. volutator* density, even after sampling high *C. volutator* density sites. This could be explained in at least two ways. First, sandpipers may have not have spent the entire low tide feeding on the low *C. volutator* density site, but may have just sampled the site and then moved to a more profitable mudflat to continue feeding for the remainder of the low tide. No evidence was found to confirm this because birds were usually located only once during a low tide foraging bout and individual bird movements were not monitored throughout a tidal cycle. However, in 2005, one bird was located feeding at Johnson's Mills early in the low tide cycle and then was located feeding at Daniel's Flat, a site with high *C. volutator* density, later in the same tidal cycle.

The second explanation for why birds were located foraging on sites with low *C. volutator* density is that sandpipers may not be feeding as exclusively on adult *C. volutator* while in the Bay of Fundy as is currently thought, and that they may not incorporate knowledge from a previous low tide foraging bout to select where to feed the following day. Polychaetes and other invertebrates are a known food source for the species (Gratto and Gratto 1984; Hicklin and Smith 1984) and could possibly be an

important alternate food source for the birds during the stopover. Elner et al (2005) found that biofilm on the mudflat surface makes up a significant portion of the diet of migrating Western Sandpipers. Biofilm has not been investigated as a food source for Semipalmated Sandpipers in the Bay of Fundy; however, personal observation of foraging methods on sites with low *C. volutator* densities suggests that the shorebirds in the Bay of Fundy are able to and are likely feeding on biofilm when no *C. volutator* is available.

2.4.4. Effects of Predation on 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 predation risk throughout their stay in the upper Bay of Fundy; instead the highest abundance of raptors was on sites with the highest sandpiper density, suggesting that raptor distribution is influenced by shorebird distribution, rather than the reverse. The sites with the highest invertebrate densities attracted the highest shorebird densities, therefore attracting the most predators, making the most profitable sites for the shorebirds also the most risky.

However, the shorebirds may perceive some sites as being less risky due to their 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). In Shepody Bay 2005, we located sandpipers feeding and roosting most frequently on Daniel's Flats and the Hopewell Rocks which are sites with the highest number of predators observed per hour. Both Daniel's Flats and the Hopewell Rocks are bordered by a 500-m marsh field, instead of being surrounded by dense forest as are

many of the other sites. It is possible that the birds perceive these sites as less risky, because they have a higher chance of detecting a predator as it flies over the marsh before attacking, allowing the sandpipers to increase their chances of survival by launching an escape flight to avoid being caught.

The Hopewell Rocks was the most frequently used roost site in 2005, with flocks of over 200,000 birds observed daily during early-mid August. The high densities of sandpipers likely attracted Peregrine Falcons and Merlins to the beach causing twice the number of predators, attacks and successful attacks observed per hour as at any other roost site in either year (Figure 2.8). Predation from raptors increased at both low and high tide in 2005. This extra predation pressure may have caused the birds to move to form larger flocks to increase individual chance of survival (Parrish and Edelstein-Keshet 1999), which is a possible explanation for the increased movement in Shepody Bay in 2005. Cresswell (1996) found that flocking reduced the probability of an individual Redshank, *Tringa totanus*, being killed by Sparrowhawks, *Accipiter nisus*, and Peregrines. Larger flocks were attacked more often but were less likely to be successful than attacks on smaller flock sizes.

2.4.5. Interaction of Predation and Weight Gain - It was predicted that heavier birds would select safer sites, because the increased fat reserves decrease the bird's maneuverability in flight, leaving them more susceptible to predation (Piersma *et al.* 2003; Witter and Cuthill 1993). No evidence was found to support this hypothesis because sandpipers were often located using sites with the most observed predation events per hour, even late in the stopover period when significant weight had presumably been gained. Butler *et al.* (2002) suggested that the risk of predation might be too great to

leave a familiar site for an unfamiliar site. However, the sandpipers were also often located using new, possibly unfamiliar sites, again, even after significant weight had been gained.

Birds at a wide range of stages of migration feed and roost together while in the Bay of Fundy. Because weight gain did not affect the distance birds were moving between roosting and feeding areas (Figure 2.9), it seems unlikely that heavy birds are making decisions independent of the rest of the flock. The heavy birds seem more likely to move to a site where a large flock of birds has already chosen to roost or feed, even if the high density of shorebirds attracts more predators to the site.

2.5. Conclusions

Other studies have looked at post-breeding or over-wintering movements of shorebirds (Warnock *et al.* 1995; Plissner *et al.* 2000; Ruiz *et al.* 1989), this study is one of the first to examine shorebird movements during migration stopovers, and the first to detect large scale movements. Farmer and Parent (1997) also found that Pectoral Sandpipers were very localized in their movements during spring migration stopovers in the Great Plains, with 90% of radio-tagged birds moving less than 10 km from original release site. Similarly, Butler *et al.* (2002) radio-tracked Western Sandpipers, *Caladris mauri*, during their fall migration stopover in the Fraser River Delta, British Columbia. He found that individual birds tended to remain on one site, moving only 4-6 km following the tide up and down the beach. Hence, the pattern of behaviour of Semipalmated Sandpipers in the Bay of Fundy, as shown by this study, appears to be different from that of other related species.

This study provided the first solid evidence of large-scale movements and habitat use of shorebirds migrating through the upper Bay of Fundy, and identified important feeding and roosting sites in the Minas Basin and Shepody Bay. Because the birds were clearly mobile, they may be able to adapt to human-induced changes to the system that might affect single mudflats. However, to ensure conservation of this essential stopover site, populations of shorebirds migrating through the Bay of Fundy need to be closely monitored. Because the shorebirds are highly mobile and selection of both foraging and roost sites is variable throughout their time in the Bay of Fundy, accurately estimating numbers of shorebirds migrating through the area is very difficult. To improve population estimates and to account for variation in shorebird abundance at roost sites, multiple surveys synchronized across known roosts around the Bay should be conducted as in Colwell and Landrum (1993). This would improve our ability to monitor possible population changes of migrating shorebirds in this critical coastal region.

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Chapter 3. Predicting foraging site selection by Semipalmated Sandpipers, *Calidris pusilla*, migrating through the upper Bay of Fundy.

Abstract

The objective of this study was to identify factors which best predict density of foraging Semipalmated Sandpipers on different mudflats around the upper Bay of Fundy.

Semipalmated Sandpipers stopover in the area for approximately two weeks to build fat reserves necessary to complete their southward migration. The following factors were tested: density of their main prey, *Corophium volutator*; predation risk; date in August and landscape features of the foraging sites. Using Akaike's Information Criterion model selection, sandpiper density was best predicted using a single factor, namely density of *C. volutator* in August.

3.1. Introduction

The upper Bay of Fundy is a key fall migratory stopover point for Semipalmated Sandpipers (*Calidris pusilla*), a small shorebird which breeds in the North American low arctic and winters in northern South America. One to two million birds – between 50% and 95% of the world's population - visit local mudflats annually (Mawhinney *et al.* 1993). The majority of sandpipers arrive in late July, with numbers peaking in early August and declining gradually throughout the month (Hicklin 1987). During their approximately two-week stay in the Bay of Fundy, sandpipers double their weight from about 20 to 40 g, in preparation for the final leg of their migration - a 4000-km non-stop trans-Atlantic flight to their wintering grounds (Wilson 1990; Gratto-Trevor 1992). During this time, Semipalmated Sandpipers feed almost exclusively on the energy-rich amphipod *Corophium volutator*, the most abundant macroinvertebrate found on intertidal mudflats in the area (Hicklin and Smith 1984).

During their critical refueling stopover in the Bay of Fundy, it is not clear how birds select foraging habitat. Distribution of shorebirds among mudflats appears to have changed in recent years. Some sites which historically reported high densities of foraging sandpipers no longer support large numbers of birds (Hamilton 2003). This change may be due to changes in mudflat sedimentation causing alterations in the prey base, or increased predator disturbance, or to unknown factors. In order to properly manage and conserve this vital habitat for Semipalmated Sandpipers, there is a need to understand why birds forage in a given place at a given time and how to maintain the underlying ecological processes that support the food base for particular birds (Elner and Seaman 2003; Butler *et al.* 2001). A variety of factors may influence habitat selection by sandpipers in the Bay of Fundy. These include food abundance and availability, perceived

predation risk and inter/intraspecific competition (Lima and Dill 1990; Elchuk and Wiebe 2002).

3.1.1. Factors Influencing Foraging Site Use - *Corophium volutator* makes up 80-100% of the diet of Semipalmated Sandpipers while in the Bay of Fundy (Hicklin and Smith 1979, 1984; Gratto *et al.* 1984; Peer *et al.* 1986). Sandpipers are size-selective predators, preferring large adult prey over juvenile *C. volutator* (Boates and Smith 1979; Peer *et al.* 1986; Wilson 1989), and they tend to forage in larger numbers on mudflats where *C. volutator* densities, especially those of adult amphipods, are highest (Hicklin and Smith 1984; Hamilton *et al.* 2003). Hamilton *et al.* (2003) found that abundance and size distribution of *C. volutator* roughly predicts shorebird abundance across mudflats.

Peregrine Falcons (*Falco peregrinus*) and Merlins (*Falco columbarius*) are the main predators of shorebirds in the Bay of Fundy. Recent population increases of these raptors may pose increased threats to migrating shorebirds and affect where shorebirds choose to roost and feed. In addition to predation risk and prey abundance, features of the landscape that affect foraging site selection were examined. The mudflat area exposed at low tide and the proximity to roost sites were included in the model. The distance from cover that birds are able to forage is also an indicator of site safety, because raptors often hunt using surprise attacks launched from cover (Page and Whitacre 1975; Dekker 1988; Cresswell 1996; Whitfield 2003). Therefore a large, open mudflat may be perceived as less dangerous than a smaller mudflat where birds have to forage closer to cover.

3.1.2. Research Objective- The primary objective of this study was to determine mudflats that were preferred foraging sites for sandpipers, based on bird density, and to identify factors that contribute to foraging site selection. The effects of predation risk, prey abundance, date and mudflat area on foraging site selection were examined.

However, competition was excluded from this study, because aggressive interactions between foraging shorebirds in the Bay of Fundy are seldom observed, suggesting that foraging success is not influenced by sandpiper density (personal observation, Wilson 1990).

3.2. Materials and Methods

3.2.1 Study Area- The study was conducted in two areas of the upper Bay of Fundy; Nova Scotia's Minas Basin (45° 00' to 45° 20' N - 64° 00' to 64° 20' W) and New Brunswick's Shepody Bay (45° 40' to 45° 60' N - 64° 20' to 64° 40' W). The tides in the upper Bay of Fundy rise and fall over 12-15 meters, twice daily, exposing large intertidal mudflats which are feeding grounds for migrating shorebirds. In 2004, 7 mudflats were monitored (Johnson's Mills, Daniel's Flat, Mary's Point, and Minudie in Shepody Bay, and Avonport, Evangeline Beach, and Cheverie in the Minas Basin). In 2005, 4 mudflats were monitored in Shepody Bay (Johnson's Mills, Daniel's Flats, Mary's Point and Peck's Cove). Refer to Figures 2.1, 2.2 and 2.3 for maps of the area.

3.2.2. Bird Counts- Four 1-ha quadrats were set up on each of the focal mudflats by placing colored posts every 50 m along the edge of the quadrats (Figure 3.1). The quadrats were set up between 100 and 450 m from shore, in areas where birds were observed to be feeding. Evangeline Beach was an exception as only two quadrats 700 m from shore were set up on this site because the substrate closer to shore was sandy and not appropriate habitat for *C. volutator*. Each site was visited four times throughout the month of August (Table 3.1). During each visit, an observer was positioned between the quadrats for 4-hour observation periods and would count the number of shorebirds within each 1-ha quadrat every hour using a telescope (15-45 magnification).

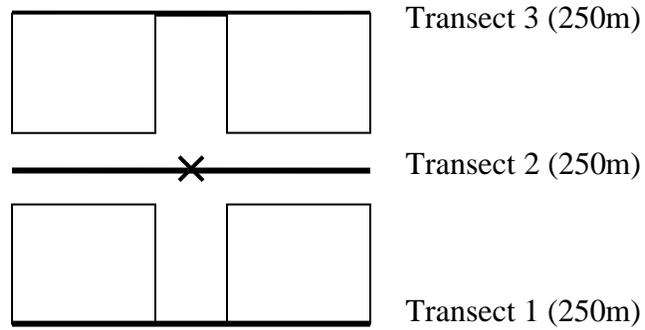


Figure 3.1. Layout of four 1-ha quadrats and three invertebrate sampling transects set up on each mudflat to count shorebird densities. The X represents the position of the observer.

3.2.3. Prey Abundance- To assess the prey base accurately, stratified random sampling of sediment (21 samples per mudflat) was carried out along three transects on each of the seven study flats in late July, and again in late August (Figure 3.1). Samples were collected using an 80-cm² corer, then rinsed through a 0.25-mm sieve (Crewe *et al.* 2001) to remove mud. Remaining contents were preserved in 95% ethanol. At a later date, samples were sorted, and *C. volutator* were placed in 2-mm size classes. This provided numbers and size distributions of *C. volutator* at each site.

2.2.4. Statistical Analysis- To assess differences in foraging bird densities at each site, multi-factorial analysis of variance (ANOVA) was used. Density of adult *C. volutator* was analyzed using a 3-way mixed model ANOVA with the fixed factor ‘Site’ and ‘Time of sampling’ (July and August) and the random factor ‘Transect (nested within site)’. A separate analysis was conducted for the data collected in 2004 and 2005. Multiple comparisons on significant fixed effects were made using Tukey’s test. The sites Avonport and Evangeline Beach were not included in the 2004 analysis because no adult *C. volutator* were found at the sites during the August sampling period, therefore there was no variance. The assumptions of homogeneity of variances and normal distributions were not met for this analysis and no transformations could correct the problem. However, the analysis should be robust against violations of assumptions due to the large number of treatments and a relatively large sample size (Underwood 1997).

Linear regressions were used to determine the relationship between mean density of foraging birds at each site and the mean number of adult *C. volutator* found in July and August at each site, and the relationship between mean bird density and the different size classes of *C. volutator*. It was determined using an analysis of covariance (ANCOVA)

that the relationship between shorebirds and density of adult *C. volutator* did not differ significantly between years (df = 1, 9, F = 0.22, p = 0.97); therefore we combined data from 2004 and 2005 in the regressions.

Akaike's Information Criterion (AIC) was used to determine how other variables would influence our model (Burnham and Anderson 2002). To do this, shorebird count data from each of four visits at each study site was used, instead of using mean density at each site. This allowed testing the effect on individual shorebird abundance estimates of mean density of adult *C. volutator* in July, mean density of adult *C. volutator* in August, mudflat area exposed at low tide and date of count in August. As demonstrated in Chapter 2, predation risk from raptors is positively correlated with shorebird abundance. This indicates that raptors are able to move to areas with the highest shorebird density, and therefore predation risk was not included as a factor in predicting foraging shorebird density. The variables distance from cover and proximity to roost had very low predictive power and were removed from the model (Table 3.2)

AIC model selection evaluates the relative fit of all possible models from the data set and identifies the model that accounts for the most variation with the least number of variables. A second order AIC, AICc, was used to account for small sample sizes and takes into account the number of parameters included in the model (K) and the sample size (n). The model with the best fit will have the lowest AICc value.

$$AICc = AIC + \frac{2K(K+1)}{n-K-1}$$

Two measures were used to compare models, the delta AIC and the Akaike weights, which are calculated using the formulae below.

$$\text{Delta AIC } (\Delta_i) = AIC_i - \min AIC$$

AIC_{*i*} is the value for model *i* and min AIC is the lowest (or best) AIC value for the set. A delta AIC value of < 2 indicates substantial evidence for the model, values of 3-7 indicate considerably less support and values of > 10 indicate the model is very unlikely (Burnham and Anderson 2002).

$$\text{Akaike weight} = w_i = \frac{\exp(-0.5*\Delta_i)}{\sum_{r=1}^R \exp(-0.5*\Delta_r)}$$

Akaike weights indicate the probability that the model is the best among the whole set of possible models. Akaike weights were compared to give an evidence ratio (w_j/w_i), that indicates how much more likely model *j* is to be the most appropriate model than model *i*. When no single model was overwhelmingly supported by the data ($w_{\text{for best model}} < 0.9$), model averaging was used to calculate the relative importance of each parameter in the model (Johnson and Omland 2004).

$$\text{Model-average estimate} = \hat{\theta} = \sum_{r=1}^R w_r \hat{\theta}_r$$

3.3. Results

3.3.1. Density of Shorebirds- In the Minas Basin 2004, Cheverie had higher densities of foraging sandpipers than Evangeline Beach or Avonport, though the difference was not significant (ANOVA, $F_{1,11} = 2.94$, $p = 0.15$). In Shepody Bay, sandpiper densities increased at both Daniel’s Flats and Mary’s Point and decreased at Johnson’s Mills in 2005 relative to 2004 (Figure 3.2.). Peck’s Cove had the highest mean density (673 birds per 4-ha) of any site in either year and Avonport had the lowest overall density (83 birds per 4-ha).

3.3.2. Prey Abundance – Because ANOVA results found a significant interaction between ‘Site*Month’ in both 2004 and 2005, the main effects of ‘Site’ and ‘Month’

were not examined (Tables 3.3 and 3.4). In July 2004, there was a significantly higher density of adult *C. volutator* on Minudie than on any other site and Mary's Point had a significantly higher *C. volutator* density than Johnson's Mills. In August 2004, there was a significantly higher density of adult *C. volutator* in Cheverie than in Daniel's Flat and Johnson's Mills. The density of adult *C. volutator* decreased significantly from July to August on Mary's Point, Daniel's Flat and Minudie in 2004. Adult *C. volutator* density decreased on Johnson's Mills, and increased in Cheverie between July and August, though not significantly (Figure 3.3). In the Minas Basin 2004, density of adult *C. volutator* on Evangeline Beach was zero for both July and August and was extremely low on Avonport (0.027 adults/80cm² and 0.04 adults/80cm² for July and August respectively).

In July 2005, Daniel's Flat had significantly higher densities of adult *C. volutator* than both Peck's Cove and Johnson's Mills. Peck's Cove also had significantly higher densities than Johnson's Mills. In August 2005, Peck's Cove had significantly higher densities of adult *C. volutator* than Daniel's Flat and Johnson's Mills. Daniel's Flat also had significantly higher densities than Johnson's Mills. All sites decreased significantly between July and August except for Johnson's Mills (Figure 3.4.).

The density of *C. volutator* in August explained a higher proportion of variation of mean bird density at each site ($R^2 = 0.88$, Figure 3.5.) than density of adult *C. volutator* in July ($R^2 = 0.61$) in both years. The R^2 values were obtained using the density of foraging shorebirds averaged over four low tide observation periods at each site. Adult *C. volutator* in the size class 4-6mm explained the most variation in foraging bird density ($R^2 = 0.81$) than any other adult size class (6-8mm $R^2 = 0.35$, 8-10mm $R^2 = 0.31$, 10mm+

$R^2 = 0.182$). There was a strong relationship between the number of adult *C. volutator* and the mean density of foraging birds found on each site (Figure 3.5).

3.3.3. Predicting Foraging Site Use - Using AICc, we found that the best model to predict foraging bird density in 2004 had the following parameters: density of adult *C. volutator* in July, density of adult *C. volutator* in August, date in August and mudflat area ($R^2 = 0.425$). This model has an Akaike weight of 0.39, indicating that it has a 39% chance of being the best model among all models considered in the set. The evidence ratio indicates that this model is 1.465 times more likely to be the best model than the second best model (density = August adult *C. volutator* + July adult *C. volutator* + date), and is 12.33 times more likely to be the best model than the weakest model in the set (density = July adult *C. volutator*). In all models, date in August was negatively correlated with shorebird density (Table 3.5).

From the 2005 data, the density of adult *C. volutator* in August was found to be the single best predictor of sandpiper density ($R^2 = 0.483$). The associated Akaike weight, W_i , of this model was 0.542. The second best model (density = August adult *C. volutator* + July adult *C. volutator*) was 1.99 times less likely to be the best model and the least fitting model for the data set included all four variables and was 13.87 times less likely to be the best model.

The density of adult *C. volutator* in August was also found to be the best single predictor variable when using data from both 2004 and 2005 combined. The W_i of this model was 0.454 and the evidence ratio indicates that this model is 2.15 more likely to be the best model than the second best model (density = August adult *C. volutator* + July adult *C. volutator*).

In all three cases, $W_{\text{best model}}$ was < 0.9 , indicating that there is not overwhelming support for any one model. However, there is substantial support for several of the models within the set. Therefore, model averaging was used to determine the relative importance of each parameter in the model (Table 3.6.). In all cases, density of adult *C. volutator* in August was found to be the most important factor. There was the least support for this in 2004, with the weight for August *C. volutator* being 0.329, indicating that it has only a 33% chance of being the most important parameter in the model. In 2005, August *C. volutator* had a weight of 0.44 and with both years combined August *C. volutator* had the most predictive strength with a weight of 0.49. In both cases this parameter had double the predictive weight of the next most likely parameter.

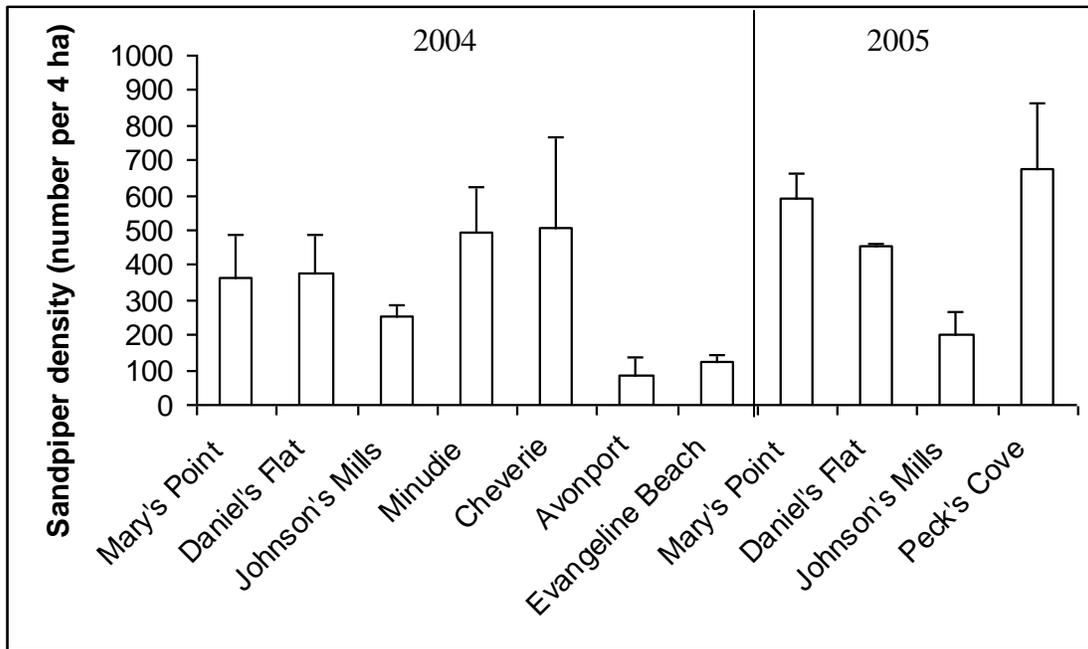


Figure 3.2. Mean density of Semipalmated Sandpipers foraging within 4 1-ha quadrats (4 ha total). Error bars are 1 SE, n=4 observation periods.

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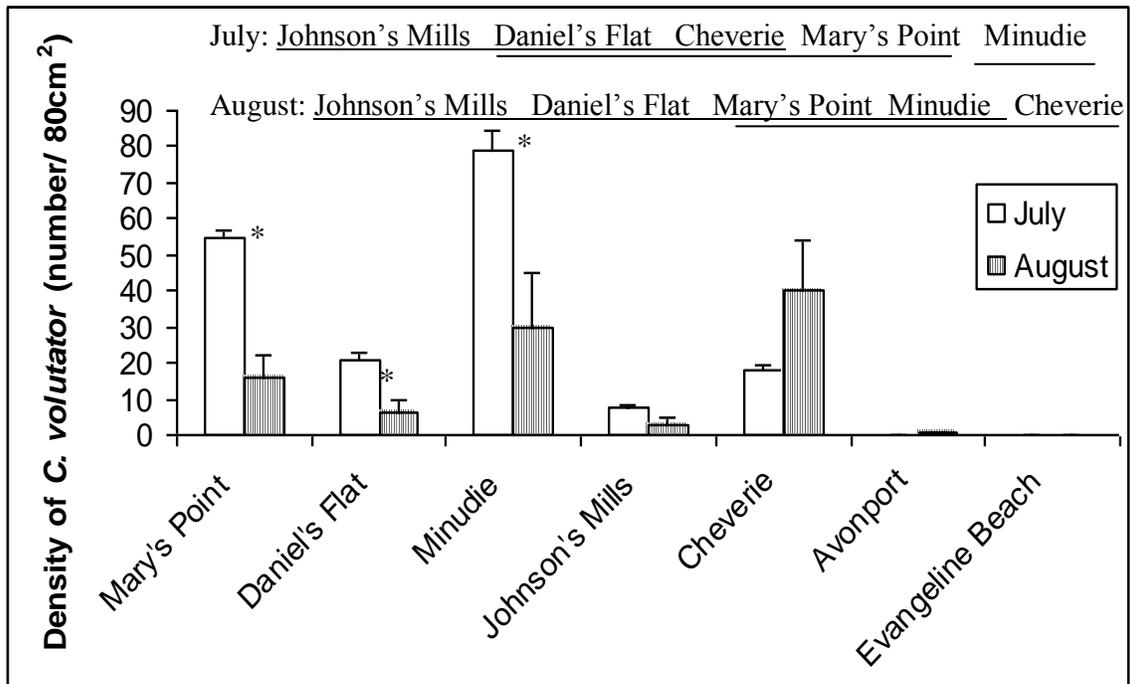


Figure 3.3. Mean number of adult *C. volutator* (≥ 4 mm body length) per sampling core measured in July and August 2004. Error bars are 1 SE, n = 30 samples/site. Stars above bars indicate significant differences between months. Site names sharing a common line indicate sites that are not significantly different.

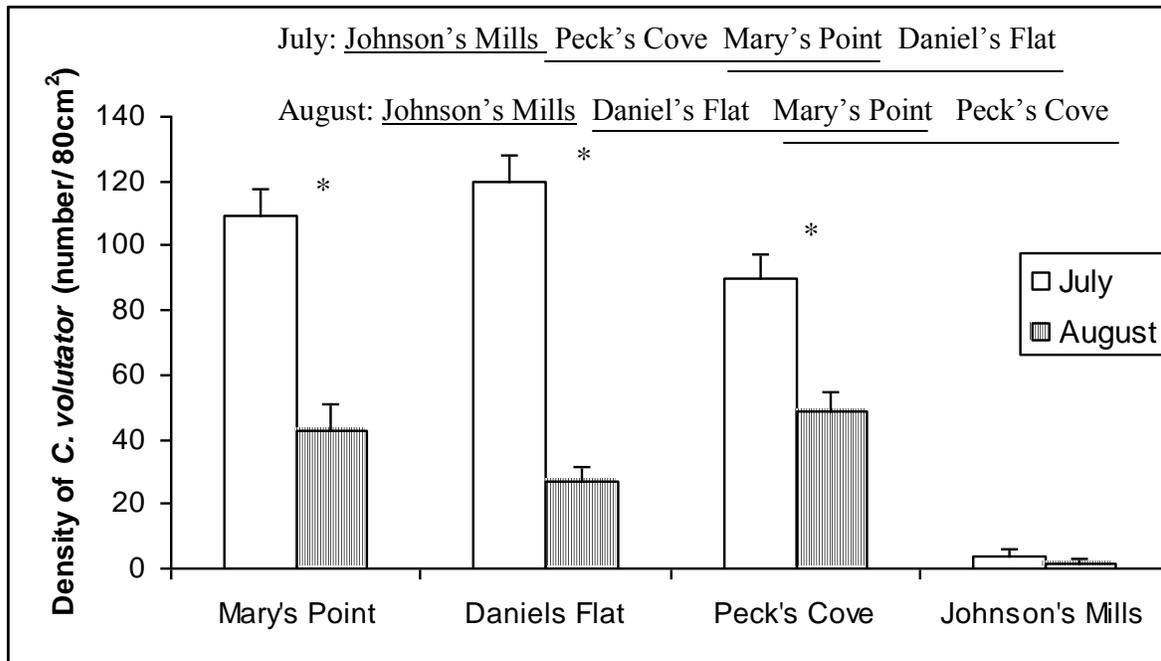


Figure 3.4. Mean number of adult *C. volutator* (≥ 4 mm body length) per sampling core measured in July and August in 2005. Error bars are 1 SE, $n = 21$ samples/site. Stars above bars indicate significant differences between months. Site names sharing a common line indicate sites that are not significantly different.

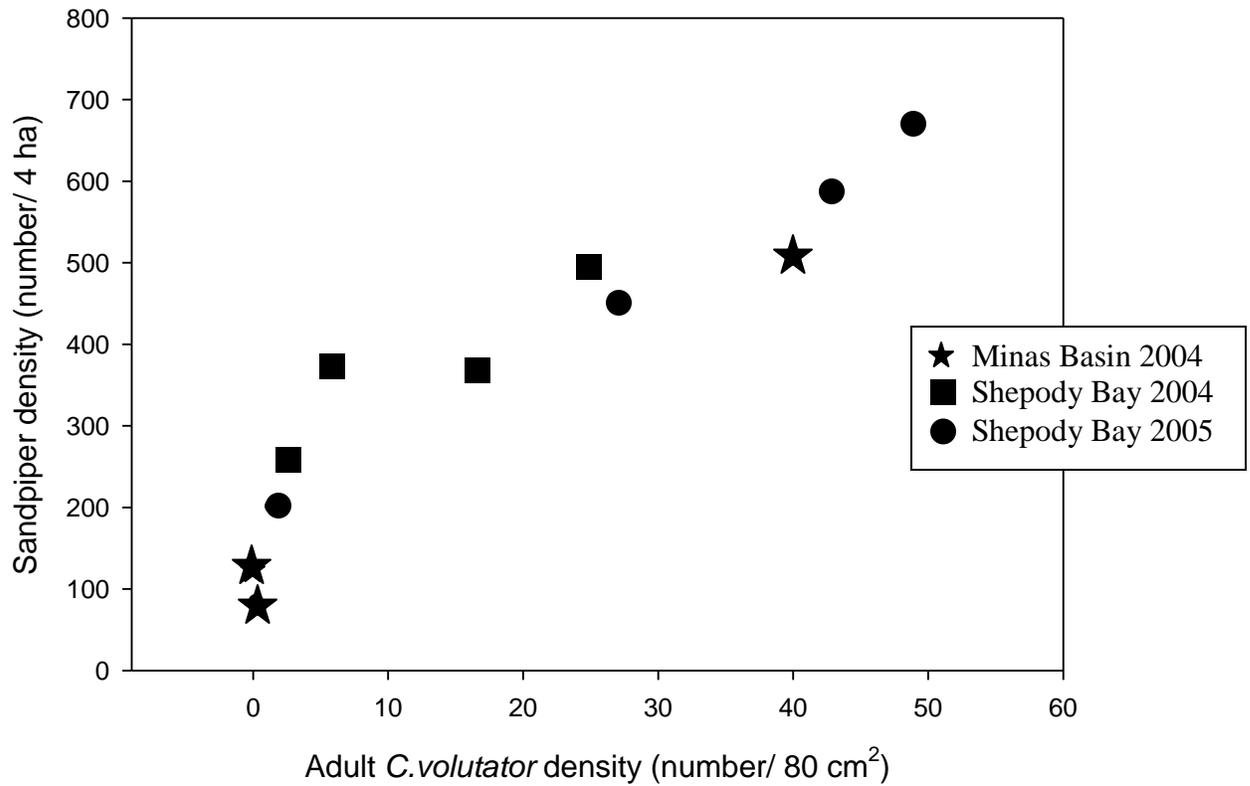


Figure 3.5. Relationship between density of shorebirds foraging within 4-ha and density of adult *C. volutator* (≥ 4 mm body length) per sampling core, in August 2004 and 2005 combined. $R^2 = 0.88$.

Table 3.1. Dates of low tide observation periods in 2004 and 2005.

Site	Dates of observation in August
Minas Basin 2004	
Cheverie	8, 11, 20, 21
Avonport	4, 9, 10, 19
Evangeline	15, 16, 17, 18
Shepody Bay 2004	
Daniel's Flat	11, 12, 18, 19
Mary's Point	11, 12, 18, 19
Minudie	5, 16, 20, 21
Johnson's Mills	4, 9, 10, 13, 15
Shepody Bay 2005	
Daniel's Flat	8, 9, 12, 16
Mary's Point	8, 9, 12, 16
Peck's Cove	7, 8, 10, 13
Johnson's Mills	7, 8, 14, 18

Table 3.2. Values used in AICc analysis. Mudflat area is the area exposed at low tide. Distance to cover is the furthest distance a bird can forage away from a wooded area at low tide. Distance to roost is the distance from the center of the mudflat to the nearest roost site, sites which birds can forage and roost were given the value 0.3 km.

Site	Mudflat area (km²)	Distance to cover (km)	Distance to roost (km)
Mary's Point	3.0	2.5	0.3
Daniel's Flat	7.3	3.75	8.5
Johnson's Mills	5.25	3.0	0.3
Minudie	2.4	1.75	0.3
Peck's Cove	2.6	2.0	4.5
Cheverie	3.75	3.0	0.3
Avonport	3.5	2.5	0.3
Evangeline Beach	1.5	1.5	0.3

Table 3.3. Results of ANOVA to determine effects of site and sampling period on density of adult *C. volutator* in 2004.

Dependent Variable = Density of Adult <i>C. volutator</i> (≥ 4 mm body length)					
Source of Variation	Df	MS	Denominator	F-ratio	p-value
Site	4,10	13297.7	Transect(Site)	4.35	0.014
Month	1,10	13816.1	Month*Transect(Site)	9.08	0.013
Site*Month	4,10	8148.6	Month*Transect(Site)	5.35	0.014
Transect(Site)	10,10	2485.2	Month*Transect(Site)	1.63	0.22
Month*Transect(Site)	10,170	1520.6	Error	1.31	0.22

Table 3.4. Results of ANOVA to determine effects of site and sampling period on density of adult *C. volutator* in 2005.

Dependent Variable = Density of Adult <i>C. volutator</i> (≥ 4 mm body length)					
Source of Variation	Df	MS	Denominator	F-ratio	p-value
Site	3,8	71579.1	Transect(Site)	13.84	0.0015
Month	1,8	144857.8	Month*Transect(Site)	92.27	0.000001
Site*Month	3,8	21973.3	Month*Transect(Site)	13.99	0.0015
Transect(Site)	8,8	5171.8	Month*Transect(Site)	3.29	0.056
Month*Transect(Site)	8,214	1569.8	Error	1.47	0.166

Table 3.5. Results of model selection analysis using information theoretic models and Akaike Information Criterion for 2004, 2005 and both years combined to determine predict the density of foraging sandpipers in the upper Bay of Fundy. 2004 results are Minas Basin and Shepody Bay combined, 2005 results are Shepody Bay only. The best model in each data set is in bold print. C.v. indicates density of adult *C. volutator* (≥ 4 mm body length), AICc indicates Akaike Information Criterion adjusted for small sample size and Wi is the Akaike weight associated with each model.

2004 Results					
Variables in Model	AICc	Delta AICc	R²	Wi	Evidence Ratio
August C.v.	322.010	2.096	.239	.137	2.852
July C.v.	324.939	5.025	.153	.031	12.33
August C.v. + July C.v.	323.016	3.102	.265	.083	4.715
August C.v. + July C.v. + Date	320.678	.764	.368	.266	1.465
August C.V. + July C.v. + Area	322.797	2.883	.319	.092	4.23
August C.V. + July C.v. + Area + Date	319.914	0	.425	.39	
2005 Results					
Variables in Model	AICc	Delta AICc	R²	Wi	Evidence Ratio
August C.v.	174.129	0	.483	.542	
July C.v.	179.175	5.047	.292	.043	12.47
August C.v. + July C.v.	176.129	2.000	.483	.199	2.7
August C.v. + July C.v. + Date	177.508	3.379	.503	.100	5.4
August C.V. + July C.v. + Area	178.078	3.949	.485	.075	7.2
August C.V. + July C.v. + Area + Date	179.389	5.260	.506	.039	13.87
Both Years Combined					
Variables in Model	AICc	Delta AICc	R²	Wi	Evidence Ratio
August C.v.	489.383	0	.379	.454	
July C.v.	496.995	7.611	.264	.010	44.95
August C.v. + July C.v.	490.917	1.534	.385	.211	2.15
August C.v. + July C.v. + Date	491.842	2.458	.408	.133	3.41
August C.V. + July C.v. + Area	492.042	2.659	.397	.120	3.78
August C.V. + July C.v. + Area + Date	493.095	3.712	.410	.071	6.40

Table 3.6. Relative importance of each parameter in the model calculated using model averaging. The most important parameter in each data set is in bold print. C.v. indicates *C. volutator* density, date indicates date of observation in August and area is the mudflat area exposed at low tide.

2004 Data	Parameter Weight
August C.v.	.329
July C.v.	.288
Date	.251
Area	.191
2005 Data	
August C.v.	.440
July C.v.	.199
Date	.174
Area	.186
2004-2005 Combined	
August C.v.	.479
July C.v.	.152
Date	.185
Area	.185

3.4. Discussion

3.4.1. Density of Foraging Shorebirds - The distribution of Semipalmated Sandpipers around the foraging sites in the upper Bay of Fundy has changed in recent years. In this study conducted in 2004 and 2005, low densities of shorebirds were found using the Johnson's Mills, Evangeline Beach and Avonport mudflats, sites which have historically supported high densities of shorebirds (Hicklin 1987). The most dramatic decrease has been observed at Avonport, where Hicklin and Smith (1984) reported a mean density of 412 shorebirds foraging per 1 ha plot in 1977; only 21 birds per ha were estimated at this site in 2004.

The changes in sandpiper distribution and density most likely reflect changes in abundance of *C. volutator*, which was the most significant factor in predicting foraging site selection by Semipalmated Sandpipers in the Bay of Fundy in this study (Table 3.5). In 2000, Hamilton (unpublished data) calculated mean densities at Avonport to be over 120,000/m². In 2004, Avonport *C. volutator* densities were only 90/m² (Figure 3.3). Shepherd *et al.* (1995) also reported a collapse in *C. volutator* densities at Johnson's Mills between the late 1970's and 1994. The decreases are likely explained by changes in mudflat sedimentation around the Bay (Hamilton *et al.* 2003). Variations in environmental factors, such as particle substrate size and composition, have been shown to strongly influence the abundance and availability of invertebrate prey, which in turn, affects habitat use by shorebirds feeding in intertidal habitats (Myers *et al.* 1980; Grant 1984).

3.4.2. Predicting Foraging Site Use – In 2004, the density of foraging shorebirds in the Bay of Fundy was predicted best from the amount of adult *C. volutator* in July and

August, the mudflat area exposed at low tide and the date in August. In 2005 and in 2004-2005 combined, the density of foraging shorebirds was predicted best using only a single variable, density of adult *C. volutator* in August. Unlike the 2004 models, date in August and mudflat area were not strong predictive parameters in 2005. In 2004, sandpiper counts were spread over a larger time period, beginning on August 4th and ending on August 21st. In 2005, sandpiper counts were compressed into a shorter time period, beginning August 7th and ending Aug 18th. It is likely that the difference in observation timing may have led to date in August being significant in 2004, because the observations would have begun during peak migration and continued until shorebird numbers in the Bay of Fundy had declined significantly. Observations in 2005 may have missed the peak migration numbers and therefore the overall decline throughout the month would not have been detected clearly.

Using model averaging, the density of adult *C. volutator* in August had higher predictive strength than the density of adult *C. volutator* in July (Table 3.6). The largest size classes of *C. volutator* become depleted between July and August in the Bay of Fundy partially as a result of predation, by the high numbers of shorebirds migrating through the area (Peer *et al.* 1986; Hilton *et al.* 2002). However, declines in populations of large adult *C. volutator* have also been noted on mudflats that are not used by migrating shorebirds, which Gratto (1979) attributed to natural mortality of the largest individuals. This trend was evident on all sites in Shepody Bay in both 2004 and 2005, but not on Cheverie in the Minas Basin where the density of adult *Corophium* increased between July and August (Figure 3.3). This increase can be attributed to an increase in the smallest adult size class, 4-6mm, while all other adult size classes decreased in

August, consistent with observations at the other sites. The significant depletion in prey observed in Shepody Bay may lead to the shorebirds becoming more concentrated on fewer sites later in the season in order to build essential fat for their southward migration. This could explain why the best model for 2005, using only August *C. volutator* densities, had the most predictive strength ($W_i = 0.54$) of all models in either year.

Evans (1976) and Kersten and Piersma (1987) suggest that shorebird distributions in the non-breeding season may be influenced strongly by food, especially when prey abundance decreases and energetic costs associated with migration increase. Colwell and Landrum (1993) found that invertebrate prey density explained a high percent of variation in the abundance of Least Sandpipers, *Calidris minutilla*, and Western Sandpipers, *Calidris mauri*, during the non-breeding season in the Mad River estuary, California ($r^2 = 0.53$ and 0.40 , respectively). The density of *C. volutator* alone was also weakly positively correlated with abundance of both species ($r^2 = 0.36$ and 0.31 , respectively). This relationship was not as strong as the correlation between mean densities of Semipalmated Sandpipers in the Bay of Fundy and *C. volutator* abundance ($r^2 = 0.61$ in July and 0.88 in August) found during 2004 and 2005.

In this study, variation in the mean density of foraging sandpipers was best explained by density of *C. volutator* in the 4-6 mm size class ($R^2 = 0.80$), than with densities of larger size classes of adult *C. volutator*. This agrees with Gratto *et al.* (1984) who found that Semipalmated Sandpipers in the Bay of Fundy were underusing the largest *C. volutator* (7-10 mm), and stomach content analysis showed that the sandpipers were selectively feeding on *C. volutator* between 3.3-6 mm. They suggested that the energetic cost of handling and ingesting the large *C. volutator* outweighs the energy they

provide. However, two observations were made in 2005 of a sandpiper consuming a large polychaete, which was at least four times its bill length (Sprague, personal observation). This indicates that sandpipers in the area will feed on very large prey items, although not frequently.

3.4.3. Conclusions – The objective of this study was to identify key factors that influence densities of foraging Semipalmated Sandpipers in the Bay of Fundy. Shorebird density was found to strongly correlate with densities of the main prey, *C. volutator volutator*, especially with August *C. volutator* densities within the size class 4-6 mm. Correlations between shorebird abundance and density of their main invertebrate prey have been shown in other studies, but the relationships were not as strong as demonstrated here. This energy-rich food source provides the fuel necessary for the sandpipers to complete the transoceanic flight to the wintering grounds in South America. Other factors may also play a less significant role in predicting shorebird densities, such as the date in August and the mudflat area. It was also predicted that predation risk would be negatively correlated with shorebird abundance; however, the number of predation events observed per hour was correlated positively with sandpiper abundance. This relationship is the opposite of what was expected, as the aim was to determine factors that the shorebirds were responding to when selecting habitat, not factors that were responding to the presence of shorebirds. Therefore, predation risk was not included as a factor in the AICc model to predict foraging shorebird density.

Changes in *C. volutator* densities at some sites are altering shorebird distributions, with some historically important sites being currently unable to support large numbers of shorebirds. Because the world's largest population of Semipalmated Sandpipers depends

upon the upper Bay of Fundy mudflats, both shorebird distribution and prey distribution should continue to be studied and monitored in order to protect and conserve this critical site. The protection of stopover resources is critical to the survival of populations of migrating shorebirds (Myers 1983).

3.5. Literature Cited

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Chapter 4. General Discussion

4.1. Summary

The objective of this study was to determine factors affecting habitat use by Semipalmated Sandpipers migrating through the upper Bay of Fundy. This area is a critical migration stopover for the shorebirds, and understanding what influences habitat selection is crucial in order to preserve this site and this species. Habitat selection was studied in two ways; first, by radio-tracking the movements of individual sandpipers, and second, by determining the quality of foraging sites based on sandpiper density.

4.2. Individual Bird Movements

Using radio-telemetry, important roost and foraging sites were identified for migrating shorebirds in both Shepody Bay and the Minas Basin. Semipalmated Sandpipers used multiple sites to forage and roost during their approximately two-week stay in the upper Bay of Fundy. In the Minas Basin, Cheverie was the preferred foraging site and Summerville was the preferred roost site.

Differences in individual bird movement patterns were found in Shepody Bay between 2004 and 2005. In 2004, little movement was detected with the majority of birds tagged at Johnson's Mills remaining on that site to roost and forage. In 2005, the birds were tagged at three different roost sites (including Johnson's Mills) and were more mobile, regardless of where they were tagged. Daniels' Flat was the most frequented foraging site and shorebirds were most often located roosting at the Hopewell Rocks. The increase in movement may be attributed to an increase in raptor predation and a change in prey abundance around the Bay in 2005. Hopewell Rocks, 2005, had significantly more predation events than any other roost site in either year. Large flocks of over 200,000 shorebirds were observed roosting regularly at Hopewell Rocks, throughout August 2005.

The numbers at the Hopewell Rocks are much higher than observed at other roost sites in either year, indicating that increased predation pressure is likely causing shorebirds to move to form large roosts and hence increase chances of individual survival.

Prey abundance also changed between 2004 and 2005 in Shepody Bay. *C. volutator* density decreased at Johnson's Mills, and shorebirds no longer remained on the site to forage. Prey abundance at this site has decreased in 2005 to a level no longer supporting large numbers of foraging shorebirds, likely forcing the birds to move elsewhere in search of food.

4.3. Predicting Density of Foraging Sandpipers

Foraging sandpiper density was very strongly correlated with abundance of their main prey, *C. volutator*. Density of *C. volutator* in August, especially in the 4-6-mm size class, was the best single predictor of shorebird density. As the prey becomes depleted through intense predation, the shorebirds become concentrated at fewer sites that can support the high numbers of foraging birds.

Sandpipers did not avoid sites with highest observed predation rates. More predation events were observed on sites with the highest shorebird densities, suggesting that raptor distribution is highly influenced by shorebird density. However, in Shepody Bay 2005, radio-tagged individuals were detected most frequently on sites where they could forage and roost the furthest distance from cover. These sites are likely perceived as being less risky, because the shorebirds have more time to detect and respond to an approaching predator.

4.4. Further Work

Several additional questions arose during the study. In particular, sandpipers were frequently observed foraging on mudflats with very low *C. volutator* densities, such as Avonport, Evangeline Beach and Johnson's Mills. The prey of birds at these sites is unknown. In order to answer this question, blood samples were collected from 15 birds foraging on Johnson's Mills in 2005. Samples of possible prey, including *C. volutator*, three polychaete species (*Nereis sp.*, *Heteromastus sp.* and *Nephtys sp.*) and biofilm containing diatoms on the mudflat surface were also collected. These samples will be used to conduct a stable isotope analysis in order to determine diet composition of birds feeding on low-*C. volutator* sites.

One problem encountered in the field was that not every bird was located during each radio-tracking period. Some birds were not located for one or two days, then would reappear at a later date. It is unknown if these birds left the area that was being covered during radio-tracking flights, or if they remained in the area and their signals were not detected. However, there was no movement between Minas Basin and Shepody Bay in 2004, suggesting that the shorebirds are not likely to leave one bay to forage in the other. The use of satellite transmitters would solve this problem, as all tags are constantly sending a signal to a satellite receiver. Although the transmitters are currently too large to attach to a sandpiper, in the future, this equipment could address several questions that still remain about shorebird habitat use. For example, this technology would permit following daily movements of individuals in order to determine how much time that a bird spends foraging and roosting at each site. It would be very interesting to see if birds feeding on low *C. volutator* density sites remained there for the entire low tide cycle, or if

they only remained on that site for a short time before moving to feed on a more profitable site. It could also be determined if birds were leaving the area covered by radio-tracking flights to use other, possibly important, foraging and roost sites.

4.5. Conservation Implications

Because shorebird movements were highly variable between areas in the upper Bay of Fundy and between years, monitoring populations of shorebirds migrating through the area can be difficult. It is essential to improve population estimates and shorebird survey techniques in order to accurately monitor any changes in the world's largest population of Semipalmated Sandpipers. This could be achieved by conducting multiple, synchronized surveys across all known roosts around the Bay (Colwell and Landrum 2003). High mobility of birds also indicates that the sandpipers would likely be able to adapt to human induced changes to the system that might affect single mudflats. The impact of cumulative changes to mudflats remains unknown.

To ensure conservation of this essential stopover site, continued radio-tracking is recommended to monitor movements over a larger area of the Bay of Fundy. Because movements, predation risk and prey abundance are highly variable on a small scale, such as a single mudflat, monitoring and conservation management plans need to incorporate all foraging and roost sites of the sandpipers around the upper Bay of Fundy.

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