VARIABILITY IN FORAGING BEHAVIOR AND IMPLICATIONS FOR DIET BREADTH AMONG SEMIPALMATED SANDPIPERS STAGING IN THE UPPER BAY OF FUNDY

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Abstract. During its fall migration stopover on mudflats in the upper Bay of Fundy, Canada, the Semipalmated Sandpiper (*Calidris pusilla*) is thought to feed primarily on the amphipod *Corophium volutator* (mudshrimp). Semipalmated Sandpipers typically use a peck-probe foraging strategy and, until recently, there had been little evidence of variability or opportunism in their foraging habits during this stopover. From 2006 to 2008 we recorded data on the sandpipers' foraging behavior and food availability at three commonly used mudflats. Behavior and food availability varied considerably at one site in one year. In 2006 at Grande Anse, where mudshrimp densities were exceptionally low and ostracod densities very high, the peck-probe strategy was almost completely abandoned for "skimming," a foraging behavior novel in this species. Because of similarities between skimming and grazing, used by Western Sandpipers (*Calidris mauri*) to consume biofilm, we hypothesized that birds switched to skimming to feed on biofilm. However, chlorophyll *a* concentration in the top 2–3 mm of sediment, an index of biofilm abundance, was not a good predictor of proportion of time spent skimming. Instead, skimming had a strong, positive relationship with ostracod density, suggesting that the sandpipers skimmed opportunistically to feed on ostracods rather than to target biofilm. Thus Semipalmated Sandpipers are capable of adapting to changes at traditional staging areas by using novel foraging mechanisms, apparently to forage opportunistically on alternative prey. If staging habitats continue to change, alternative foods and foraging modes may become increasingly important to the success of this species' migration.

Key words: Calidris pusilla, Corophium volutator, *foraging behavior, intertidal mudflats, Semipalmated Sandpiper*, *stopover ecology.*

Variabilidad en el Comportamiento de Forrajeo e Implicancias para la Amplitud de la Dieta en Individuos de *Calidris pusilla* que Paran en la Bahía Alta de Fundy

Resumen. Durante sus paradas migratorias de otoño en las planicies inundables en la bahía alta de Fundy, Canadá, se piensa que *Calidris pusilla* se alimenta principalmente del anfípodo *Corophium volutator. Calidris pusilla* usa típicamente una estrategia de forrajeo de picotazo y sondeo y, hasta hace poco, ha habido poca evidencia de variabilidad u oportunismo en sus hábitos de forrajeo durante esta parada. Desde 2006 a 2008 registramos datos del comportamiento de *C. pusilla* y de la disponibilidad de alimentos en tres planicies inundables usadas con frecuencia. El comportamiento y la disponibilidad de alimentos variaron considerablemente en un sitio en un año. En 2006 en Grande Anse, donde las densidades de *C. volutator* fueron excepcionalmente bajas y las densidades de ostrácodos muy altas, la estrategia de picotazo y sondeo fue casi completamente abandonada y reemplazada por "rozamiento," un comportamiento de forrajeo novedoso en esta especie. Debido a las similitudes entre rozamiento y pastoreo, usado por *Calidris mauri* para consumir biofilm, hipotetizamos que las aves cambiaron a usar rozamiento para alimentarse de biofilm. Sin embargo, la concentración de clorofila en los 2–3 mm superiores del sedimento, un índice de abundancia de biofilm, no predijo adecuadamente la proporción de tiempo gastado rozando. En cambio, el rozamiento tuvo una relación fuerte positiva con la densidad de ostrácodos, sugiriendo que *C. pusilla* realizó rozamientos de modo oportunista para alimentarse de ostrácodos más que para obtener biofilm. De este modo, *C. pusilla* es capaz de adaptarse a los cambios en áreas tradicionales de parada usando mecanismos novedosos de forrajeo, aparentemente para forrajear de modo oportunista presas alternativas. Si los ambientes de parada continúan cambiando, los alimentos y los modos de forrajeo alternativos pueden volverse cada vez más importantes para el éxito de la migración de esta especie.

INTRODUCTION

Because of the high energetic demands of flight, most migratory birds use stopover sites to rebuild fat stores during long-distance migration (Schaub and Jenni 2000, Schaub et al. 2008). While at these sites, migrants often rely heavily on seasonally abundant foods (Clark et al. 1993) and, in some cases, a single prey type, such as horseshoe crab eggs in Delaware Bay (Clark et al. 1993, Tsipoura and Burger 1999). If such critical foods are lost and individuals fail to adapt, their migration

may be unsuccessful (Baker et al. 2004, Morrison et al. 2004, Karpanty et al. 2006). Consequently, the ability to alter foraging habits in response to varying food availability at stopover sites is highly beneficial.

Several species of shorebirds rely on coastal stopover sites with abundant and predictable food sources, and these sites are probably the only ones in the area that provide resources adequate to ensure successful migrations (Skagen and Knopf 1993). Intertidal mudflats in the upper Bay of Fundy are an example of this, serving as critical staging areas for migrating Semipalmated Sandpipers (*Calidris pusilla*). Each year during their southbound migration to their winter range, 1.4–2.2 million Semipalmated Sandpipers (Mawhinney et al. 1993) stop on the bay's mudflats to replenish their fat reserves before migrating to South America. In these habitats, up to 90% of their diet has been thought to consist of mudshrimp, the amphipod *Corophium volutator* (Hicklin and Smith 1979, 1984). Historically, mudshrimp have been abundant on these mudflats, and their consistent availability (Peer et al. 1986), coupled with high nutritional value (Maillet and Weber 2006), is thought to be what makes these habitats such reliable stopover sites.

The upper Bay of Fundy mudflat system has been changing in recent years; at some sites mudshrimp densities have become highly variable (Hamilton et al. 2003, Sprague et al. 2008), sandpiper populations are declining (Morrison et al. 1994, Bart et al. 2007), and use of some mudflats has dropped significantly. How sandpipers cope with these changes is important in determining the success of their migration. The Grande Anse mudflat in New Brunswick, Canada (45° 48′ N; 64° 30′ W), experienced a severe collapse of mudshrimp during the 1990s (Shepherd et al. 1995) that continued until recently (Hamilton et al. 2003, Ginn 2009). During the period when mudshrimp were largely absent from Grande Anse, some sandpipers continued to use the mudflat and even returned to it to feed after visiting other sites (Sprague et al. 2008), suggesting that they have some flexibility in prey choice.

How flexible sandpipers are in their foraging strategy depends on how they choose their prey. If they select foods on the basis of nutrient content they may continue to search for preferred prey such as the mudshrimp, rich in polyunsaturated fatty acids (Maillet and Weber 2006), even when densities are low. However, if birds feed opportunistically according to relative abundance (Davis and Smith 2001), they may be less likely to choose a previously preferred food as its abundance becomes more variable. If sandpipers are flexible in their food choices, they may shift their diet in response to unpredictable availability and/or localized declines of their preferred prey (e.g., Steenhof and Kochert 1988, Beukema 1993, Baillie and Jones 2004). If available, polychaete worms as well as other invertebrates are also potential prey items for sandpipers in this region (Hicklin and Smith 1984).

During summer 2005, a period when mudshrimp populations at Grande Anse were extremely low, anecdotal observations (N. Robar, pers. comm.) suggested that Semipalmated Sandpipers foraged at this site by a technique novel for this species in the upper Bay of Fundy. We have termed this behavior "skimming," which is characterized by sustained contact between the bill tip and sediment surface. When skimming, birds move much more slowly than when pecking or probing, as do Western Sandpipers (*Calidris mauri*) grazing on surficial biofilm in British Columbia, Canada (Elner et al. 2005, Kuwae et al. 2008). Thus we hypothesized that Semipalmated Sandpipers may be using this novel foraging technique to ingest biofilm as an alternate food. Flexibility in prey use may thus translate into variability in foraging behavior.

Our primary objective in this study was to determine the extent to which Semipalmated Sandpiper foraging behavior varied at three commonly used sites in the Bay of Fundy. If we detected variability, our second objective was to understand what was driving these differences. From 2006 to 2008 we quantified foraging behavior and the prey base at three mudflats. We expected that if the birds' foraging behavior varied we should see a difference in proportion of time devoted to each behavior by site and/or year. Once this differing allocation of behavior was established, we could examine specific prey–behavior relationships to determine what was driving this variability. We hypothesized that, if the novel skimming behavior was used for feeding on biofilm, skimming activity should be predicted by chlorophyll *a* concentration, an index of biofilm abundance (Underwood and Smith 1998). Additionally, if the birds were responding to variation in availability of their preferred prey, mudshrimp, they should use the novel skimming behavior more often in areas where mudshrimp were scarce and alternative foods that are effectively obtained by skimming were plentiful.

METHODS

STUDY SITES

Our field work took place from 2006 to 2008 on three intertidal mudflats that are traditional staging areas for migrating Semipalmated Sandpipers. Grande Anse (45° 48′ N, 64° 30′ W), Mary's Point (45° 43′ N, 64° 40′ W), and Peck's Cove (45° 45′ N; 64° 37′ W) are located in Shepody Bay and Cumberland Basin, respectively, of the upper Bay of Fundy, New Brunswick (Fig. 1). Extremely high tidal fluctuation in this region generates intertidal mudflats that extend approximately 2 km from shore at Grande Anse and Mary's Point and 800 m at Peck's Cove.

SAMPLING PROTOCOL

We recorded sandpipers' foraging behavior with camcorders (Sony Handycam DCR-HC90 and Sony HD Handycam HDR-HC5) mounted on a tripod, elevated approximately 2 m above the ground. We began filming approximately 2 hr after high
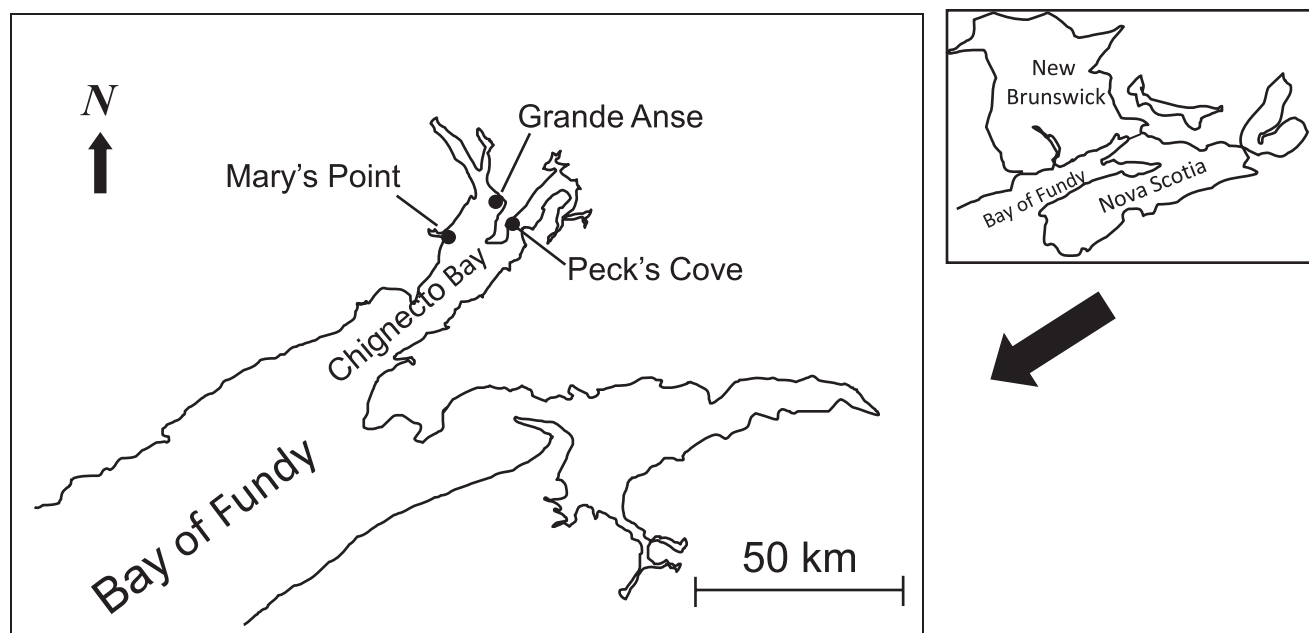
FIGURE 1.   Three intertidal mudflats in Chignecto Bay, upper Bay of Fundy, sites of video recording of foraging Semipalmated Sandpipers: Mary's Point, Grande Anse (both in Shepody Bay), and Peck's Cove (in Cumberland Basin).

tide and followed flocks of Semipalmated Sandpipers across the mudflat. Birds commonly feed at the water's edge, following the tide out as it recedes. Tidal recession is quite rapid as a result of a large tidal range and shallow slope, so new mudflat is continually exposed, and once birds select a foraging spot they can feed without being forced back by incoming waves. When a flock settled and began to forage, we filmed the birds for the duration of feeding in that area. We defined these "feeding bouts" as the time between the flock's landing in an area and taking off to forage elsewhere; they ranged from 30 sec to approximately 20 min. After each feeding bout, without moving the camera, we entered the field of view and marked out a temporary plot in the sediment indicating where the birds had been feeding. These plots (size range 4–25 m^2) were appropriately sized to fill the field of view and varied with how close the camera was to the flock.

Immediately following filming, we collected from each plot two core samples of sediment for assessing densities of invertebrates and two samples for assessing presence of biofilm on the sediment surface. We collected core samples by inserting a piece of PVC pipe (diameter 5.8 cm) into the sediment to the well-defined point where the mud changes color and becomes firm and compact and in which few invertebrates are found. Depth of this layer varies both among and within mudflats, with typical ranges as follows (presented as mean ± SD): Grande Anse = 7.2 ± 2.0 cm; Mary's Point = 4.9 ± 2.7 cm; Peck's Cove = 4.1 ± 1.4 cm (T. Gerwing, unpubl. data). Bill lengths (exposed culmen) of sandpipers foraging in the upper Bay of Fundy range from approximately 16 to 23 mm (Ginn

2009), so birds should be able to reach prey in the upper 2 cm of the sediment. At a wide range of mudflats across the Bay of Fundy, including our study sites, mudshrimp typically inhabit the top 3 cm of sediment (Oake 2010, Coulthard and Hamilton 2011), and most polychaete species are also primarily in the upper sections of the sediment (T. Gerwing, pers. comm.). Therefore the majority of animals sampled should reflect those available to birds. Furthermore, these animals reside in vertical burrows and can move up and down, so while sampling to the depth of the compacted layer may overestimate availability of prey at any particular time, it ensures that we did not miss potentially available prey.

We collected biofilm samples from within the foraging areas with a 10-cm^3 syringe with the top cut off. We drew sediment into the syringe, inverted the plunger, forcing the top layer of sediment out through the end of the syringe, and scraped the top 2–3 mm of sediment into scintillation vials for further processing.

DATA PROCESSING

We obtained data from the video by scan sampling (Altmann 1974). We superimposed the temporary plot area over each frame of each clip and stopped the video at 10-sec (2006 and 2007) and 15-sec (2008) intervals to record the behavior (pecking, probing, skimming, or nonforaging) of each individual in the plot. We determined the proportion of time devoted to each behavior by dividing the total number of individuals using a particular behavior by the total number of individuals scanned in the clip.

We rinsed sediment samples through a 250-μm mesh (Crewe et al. 2001) and stored the retained invertebrates in 95% ethanol. Within each sample, we counted mudshrimp, polychaetes, and ostracods. Additionally, we dried and weighed mudshrimp to obtain biomass and measured all individuals from rostrum to telson, classifying them as adults (≥4 mm) or juveniles (<4 mm). We assessed polychaetes in terms of abundance (number) rather than biomass because with multiple species involved the range of sizes was extreme, and a single large polychaete, which would benefit only a single bird, would strongly skew results. Furthermore, many samples contained too few polychaetes to yield accurate weights, and pooling them to estimate an average weight would be inappropriate given the large size range. We counted ostracods in each sample because these animals are extremely small (< 2 mm long) and difficult to remove from samples, and we could not weigh small samples accurately. However, we estimated ostracod biomass available to birds in each sample by drying and weighing a known number of ostracods together and then calculating biomass from this number (possible because all individuals were of similar size).

We extracted chlorophyll *a* (Chl *a*) from biofilm samples with a buffered acetone solution (90% acetone containing 10% saturated aqueous magnesium carbonate). We added 3 mL of solution to each sample and refrigerated samples for 20–22 hr. Samples were then held at room temperature for 2 hr. We centrifuged the acetone–Chl *a* solution (at 2400 revolutions min^{-1} for 15–20 min) to remove suspended sediment. Using a spectrophotometer (GENESYS 10vis, ThermoFisher Scientific), we measured absorbencies of the supernatant at 664 and 750 nm, the former to detect Chl *a*, the latter to control for turbidity. To correct for phaeophytin (previously degraded chlorophyll) and thus ensure that we were measuring primary production of living cells only, we added 0.10 mL of 3.5% hydrochloric acid to each sample to degrade intact chlorophyll and remeasured absorbencies after 90 sec. We calculated Chl *a* concentration (mg m^{-2}) from absorbance values by the equations in Eaton et al. (1995). Additional detail on this method and calculations is provided in Coulthard and Hamilton (2011).

STATISTICAL ANALYSES

For analyses we used SPSS version 16.0 (SPSS 2008) and SAS version 9.1 (SAS Institute 2005). To correct violations of statistical assumptions, we arcsine-square-root transformed all proportion data (Zar 1999), and in other instances when necessary we applied log or square root transformations. If transformations did not correct failed assumptions, we applied nonparametric techniques if available; otherwise, we interpret results with caution. We evaluated results at a significance level of $\alpha = 0.05$.

We used multivariate analysis of variance (MANOVA) with canonical analysis (following Scheiner 2001) to assess differences in both foraging behavior and prey by site and year. This allowed us to determine if, at a population level, Semipalmated Sandpipers' behavior varied as well as the extent to which prey availability varied. Year and site were fixed independent factors. For behavior, time spent pecking and probing were dependent variables. For prey, dependent variables were mudshrimp biomass, polychaete abundance, and Chl *a* concentration. Site × year interactions in both data sets led to additional analyses. For behavior, we recoded the categorical variables year and site into a composite variable that included nine levels of site–year combinations (Leech et al. 2008) and reran the analysis. For prey, we split the data set by year and restricted additional analyses to 2006, the year in which we observed unusual foraging behavior. In both cases, we assessed the individual factors that contributed most to the overall multivariate result with univariate Kruskal–Wallis tests. We used Mann–Whitney *U* tests with alpha-level corrections for multiple comparisons (adjusted $\alpha = 0.0125$) to obtain relevant pairwise comparisons with Grande Anse 2006. Skimming and ostracods occurred only at Grande Anse, so we tested for differences by year separately for that site with Kruskal–Wallis tests.

We attempted to use ANCOVA to generate overall models to predict foraging behavior. However, interactions between site and prey, coupled with weak relationships for some prey–behavior combinations made such models impossible. Food availability and behavior at Grande Anse in 2006 differed substantially from all other site–year combinations (Fig. 2 and 3), so we investigated prey–behavior relationships in that specific case. We used hierarchical multiple regression coupled with AIC model selection (Burnham and Anderson 2002) to determine the best predictors (from mudshrimp, Chl *a*, and ostracods, on the basis of our a priori hypotheses) of skimming behavior at Grande Anse in 2006. Independent variables were log-transformed to meet or minimize violations of model assumptions. Models that fell outside the acceptable range of collinearity (tolerance <0.2) (Menard 1995) were not included in the overall result. AIC values <2 indicated substantial evidence in support of a particular model (Burnham and Anderson 2002). This analysis revealed a single prey variable as the best predictor of skimming. After visually inspecting this relationship, we refined the model by using a one-slope, straight broken-line analysis (Robbins et al. 2006) on the untransformed data.

RESULTS

BEHAVIOR

Over the three years, we obtained 121 video clips (24 in 2006, 34 in 2007, 63 in 2008). Foraging birds fed by three main mechanisms; pecking—shallow penetration of the bill (¼ or less of the bill length) into the sediment (Baker and Baker 1973), probing—deeper penetration of the bill (greater than ¼ of its length) into the sediment (Baker and Baker 1973), and, skimming—prolonged, direct contact between the substrate and bill tip, often with slow side-to-side movements.
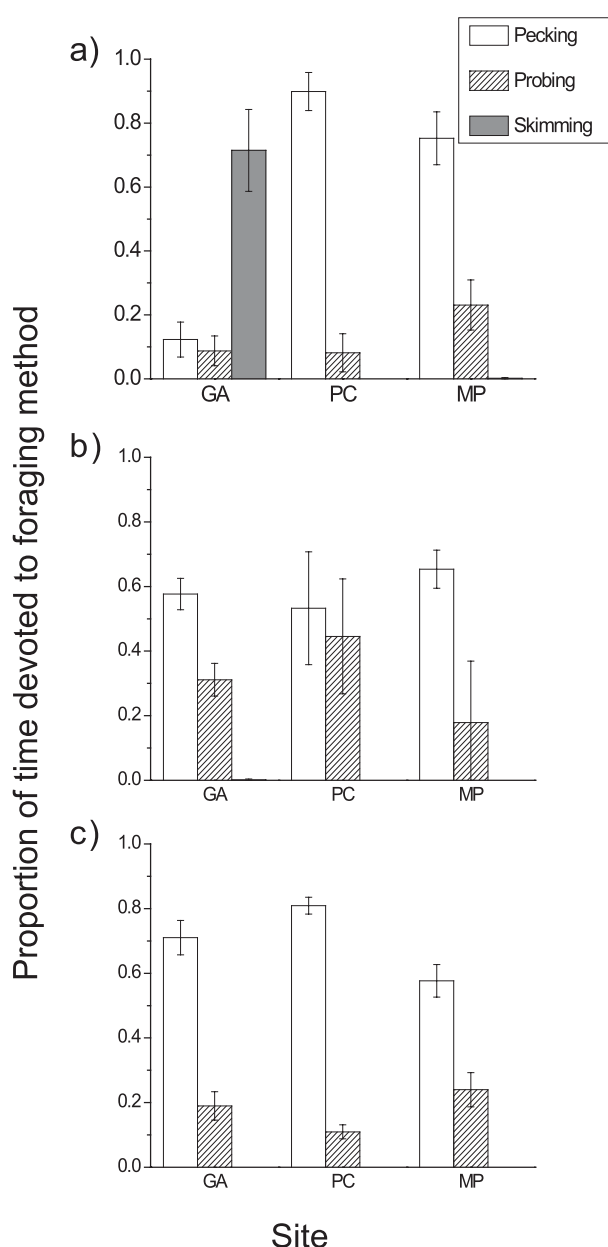
FIGURE 2.   Mean (± SE) proportion of total time in foraging patches that Semipalmated Sandpipers spent using three methods of foraging at each study site in (a) 2006, (b) 2007, and (c) 2008. GA= Grande Anse; PC = Peck's Cove; MP= Mary's Point. Proportions do not sum to 1, as other nonforaging behaviors are not included. For results of statistical analyses, see text.

Throughout the study, Semipalmated Sandpipers spent the majority of their time in foraging areas pecking (Fig. 2). However, at Grande Anse in 2006, skimming replaced pecking as the most commonly used behavior (Fig. 2a). It was essentially nonexistent in other years and locations, resulting in substantially more skimming at Grande Anse in 2006 than in other years (Kruskal–Wallis, $\chi^2_2 = 36.1$, $P < 0.001$; Fig. 2).

Differences among sites in the proportion of time spent pecking and probing varied with year (MANOVA, year × site interaction: $F_{8,224} = 12.7$, $P < 0.001$). When site and year were taken into account simultaneously, the behaviors differed among the nine site–year combinations (MANOVA, $F_{16,224} = 9.7$, $P < 0.001$). The canonical analysis generated two significant roots ($P < 0.001$ and $P = 0.001$, respectively). The first root explained 86% of the explainable variation and was driven more strongly by pecking than by probing (standardized discriminant function coefficients: pecking = 1.24, probing = 0.88). Pecking varied by year–site combination (Kruskal–Wallis, $\chi^2_8 = 45.5$, $P < 0.001$); it was less common at Grande Anse in 2006 than in 2007 ($Z = -3.8$, $P < 0.001$) or 2008 ($Z = -4.2$, $P < 0.001$; Fig. 2) and less common than at Peck's Cove ($Z = -3.7$, $P < 0.001$) or at Mary's Point ($Z = -3.1$, $P = 0.002$) in 2006 (Fig. 2).

RELATIONSHIPS BETWEEN BEHAVIOR AND
PREY ABUNDANCE

Over the three years, four potentially important (on the basis of previous information on this species and related shorebirds) foods were present: mudshrimp, biofilm, ostracods, and polychaetes. Mudshrimp and biofilm were generally abundant in all years at all sites (with the exception of low mudshrimp densities at Grande Anse in 2006) (Fig. 3a, b). Ostracods were present only at Grande Anse, with a large spike in biomass occurring in 2006 (Fig. 3c). Polychaete densities were high only at Mary's Point in 2008 (Fig. 3d).

Differences among sites in the overall prey community varied by year (MANOVA, site × year interaction, $F_{12,321} = 6.7$, $P < 0.001$). Sites differed in 2006 ($F_{6,38} = 4.2$, $P = 0.002$); the canonical analysis generated one significant root ($P = 0.001$, explaining 87% of variance), and mudshrimp was the only prey variable contributing to the response (standardized discriminant function coefficients: mudshrimp = 1.02, Chl a = 0.08, polychaetes = 0.00). Mudshrimp biomass differed by site in 2006 (Kruskal–Wallis, $\chi^2_2 = 13.8$, $P = 0.001$), with biomass at Grande Anse less than that at Peck's Cove ($P < 0.001$) and similar to that at Mary's Point ($P = 0.31$, Mann–Whitney U tests, Fig. 3a).

At Grande Anse, ostracod biomass varied with year (Kruskal–Wallis, $\chi^2_2 = 15.9$, $P < 0.001$) and was significantly higher in 2006 than in 2007 ($P < 0.001$) or 2008 ($P < 0.001$, Mann–Whitney U tests, Fig. 3c).

At Grande Anse in 2006, pecking was almost entirely replaced by skimming, and mudshrimp densities were very low but ostracod densities were extremely high. Multiple regression using AIC model selection indicated that a lone predictor, ostracod density, best predicted proportion of time spent skimming (Table 1). That model was at least six times more likely to be the best than any model containing Chl a (Table 1). Following this, and upon visual inspection of the nonlinear positive relationship between skimming and ostracods, we refined it with a one-slope, straight broken-line analysis of the raw data ($F_{2,7} = 11.4$, $P = 0.006$, $r^2 = 0.92$, Fig. 4a). Skimming also appeared
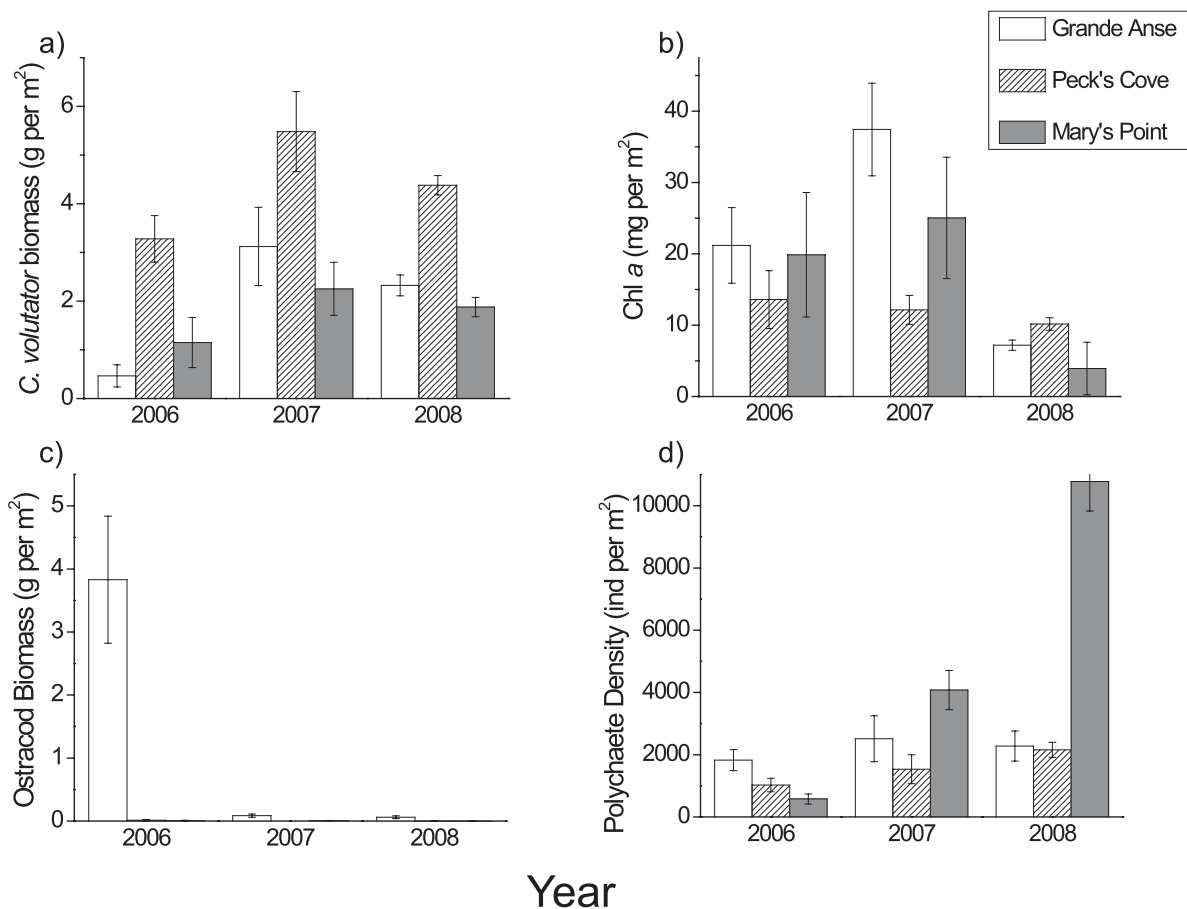
FIGURE 3.   Mean (± SE) availability of the four main potential food items by site and year; (a) *Corophium volutator* (mudshrimp) biomass, (b) Chl *a* concentration, (c) ostracod biomass, (d) polychaete density. For statistical comparisons, see text.

to decline nonlinearly with mudshrimp density (Table 1), though heterogeneity of variance that was only partially corrected by transformation (Fig. 4b) made it difficult to assess the independent functional relationship between the two. Overall, though, there was more skimming in plots in which mudshrimp were absent than in those in which they were present (Mann–Whitney *U* test: $Z = -2.6$, $P = 0.01$). Finally, Chl *a* concentration showed a positive but nonsignificant nonlinear relationship with skimming at Grande Anse in 2006 (Table 1, Fig. 4c).

DISCUSSION

Migrating birds that rely on a single staging area are particularly vulnerable to changes in habitat or food availability, and consequences of such changes can be severe. For example, Red Knots dependent on horseshoe crab eggs in Delaware Bay have suffered substantial population declines in recent years as their food supply has diminished (Baker et al. 2004), either because other suitable prey are unavailable,

or because they are unable to take advantage of them (Niles et al. 2009). Thus flexibility and ability to forage opportunistically may make a substantial difference for species facing such habitat changes.

Throughout their annual cycle, Semipalmated Sandpipers consume a wide variety of prey (Skagen and Oman 1996). However, while staging in the upper Bay of Fundy they are traditionally considered to rely very heavily on the amphipod *Corophium volutator* (mudshrimp) (Hicklin and Smith 1979, 1984). Until recently, there has been little evidence to suggest that individuals feeding on mudflats in this area are variable or opportunistic with respect to their diet and behavior. Our study demonstrates that sandpipers staging in the upper Bay of Fundy are capable of both behavioral and dietary flexibility in response to changing resources. We found evidence of a novel foraging mechanism seemingly used to take advantage of a spike in abundance of an alternate prey. As staging areas continue to change and food availability becomes less predictable, alternate behaviors and foods will likely become increasingly important if sandpipers are to continue to rely on these habitats.

TABLE 1.   Results of multiple regression and AIC model selection of factors predicting proportion of time spent skimming by Semipalmated Sandpipers during foraging at Grande Anse in 2006 ($n = 10$). Independent variables were log-transformed. K is the number of parameters in each model, β is the standardized beta coefficient for each parameter, ΔAIC_c is the difference in Akaike's information criterion from the top model and AIC_w is the likelihood that a particular model is the best of the options available.

Model[a]	K	P	r^2	β_{Ost}	$\beta_{C.vol.}$	$\beta_{Chl\,a}$	ΔAIC_c	w_i
Ost [b]	2	0.02	0.55	0.74	—	—	0	0.48
C. vol.	2	0.04	0.47	—	−0.69	—	1.49	0.23
Ost + *C. vol.*	3	0.06	0.61	0.52	−0.32	—	3.15	0.10
Chl *a*	2	0.11	0.32	—	—	0.57	3.71	0.08
Ost + Chl *a*	3	0.09	0.55	0.70	—	0.06	4.26	0.06
Chl *a* + *C. vol.*	3	0.09	0.55	—	−0.54	0.32	4.28	0.06
Ost + *C. vol.* + Chl *a*	4	0.16	0.61	0.44	−0.33	0.09	9.06	0.005

[a]Abbreviations for model parameters: Ost = ostracod density (individuals m^{-2}); *C. vol.* = density of adult mudshrimp (individuals m^{-2}); Chl *a* = Chl *a* concentration (mg m^{-2}).
[b]AIC_c of top model = −16.3.

BEHAVIORAL DIFFERENCES AND LINKS WITH PREY CONSUMPTION

Semipalmated Sandpipers varied their foraging behavior by site and year. Individuals used a peck-probe foraging strategy, alternating between frequent pecks and less frequent probes, as is typical of many calidrid sandpipers (Baker and Baker 1973, Sutherland et al. 2000). Except at Grande Anse in 2006, pecking was the predominant behavior, as previously observed in this species (Baker and Baker 1973).

We observed a drastic switch in behavior at Grande Anse in 2006, where sandpipers fed despite very low densities of their historically major prey, mudshrimp. Here, the common peck-probe foraging strategy, observed in all years and at all sites, was almost completely abandoned for skimming. The skimming behavior used by Semipalmated Sandpipers in this region was described anecdotally in years leading up to our study and was thought to be similar to biofilm grazing by Western Sandpipers (Elner et al. 2005, Kuwae et al. 2008). Behavioral, morphological, and isotopic evidence clearly suggests that Western Sandpipers graze on biofilm (Elner et al. 2005, Kuwae et al. 2008), and gut-content analysis of both this species and Dunlins (*Calidris alpina*) has confirmed that biofilm can be a major food source for these birds (Mathot et al. 2010). However, we found little support for our hypothesis that Semipalmated Sandpipers adopted skimming to feed on biofilm. The positive relationship between skimming and Chl *a* concentration was weak and nonsignificant, and multiple regression models including Chl *a* as a predictor were substantially weaker than those without. Furthermore, biofilm was present at all sites in all years, and levels were not exceptional at Grande Anse in 2006 (Fig. 3b).
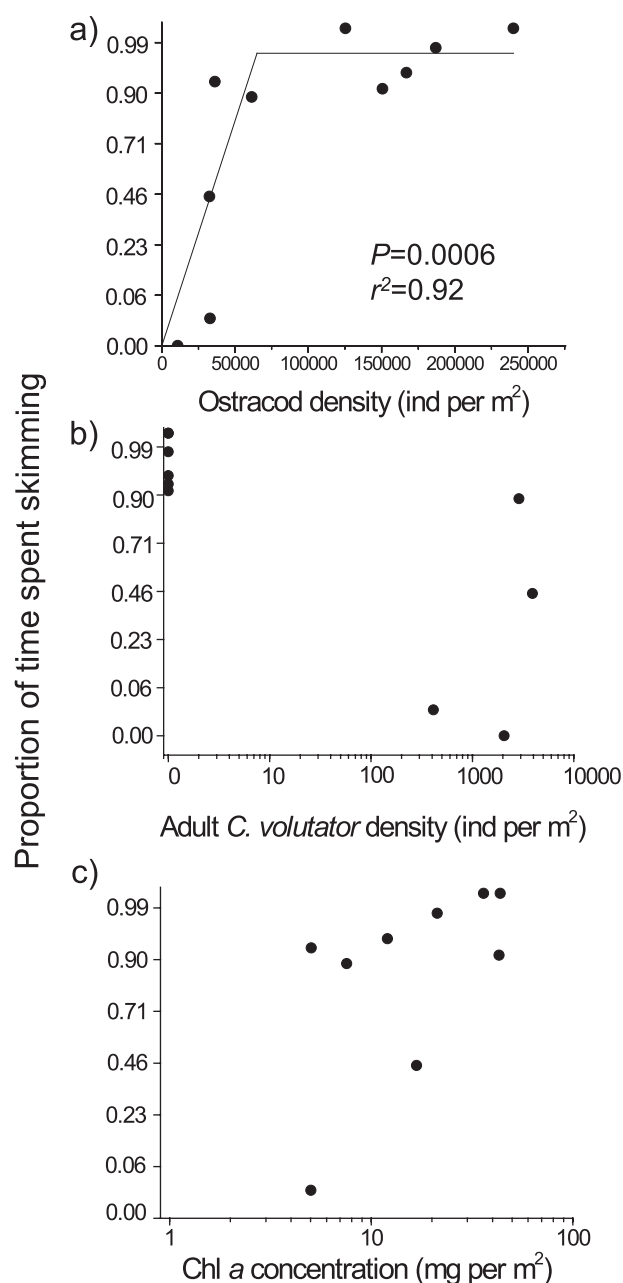

FIGURE 4.   Relationship between proportion of time spent skimming and (a) ostracod density (individuals m^{-2}), (b) log-transformed density of adult *Corophium volutator* (mudshrimp) (individuals m^{-2}), (c) log-transformed Chl *a* concentration (mg m^{-2}), at Grande Anse 2006 ($n = 10$). The line in panel (a) represents the relationship generated from the one-slope, straight broken-line analysis. For details of multiple regression models, see Table 1.

Conversely, skimming had a very strong relationship with ostracod abundance. Biomass of mudshrimp was severely depressed in 2006, and this was coupled with a spike in ostracod abundance, resulting in a nearly 8-fold difference between the two in biomass available. Our data suggest that Semipalmated Sandpipers shifted their foraging strategy opportunistically in response to this alternative food source. Proportion of time

spent skimming increased linearly with ostracod density to a breakpoint of approximately 65 000 ostracods m^{-2} (95% CI ≈ 34 000–96 000), at which point skimming approached 100% and leveled off. In 2007 and 2008, ostracod densities were substantially lower, mudshrimp rebounded, and no skimming was observed, even in plots that contained high biofilm levels and very few mudshrimp (80% of plots contained fewer than 4000 adult mudshrimp m^{-2} at Grande Anse in 2007, $n = 15$). This provides further evidence that sandpipers are targeting ostracods rather than biofilm when skimming. The nonsignificant trend toward a positive, nonlinear relationship between skimming and Chl a (Fig. 4c) was probably driven by the fact that ostracods are frequently found on the surface of dense concentrations of biofilm, and, in fact, ostracod density is correlated with Chl a concentration ($F_{1,7} = 8.0$, $P = 0.03$, $r^2 = 0.53$). Stable-isotope analysis indicates that biofilm was part of the diet in 2006 (Ginn 2009), and more recent work supports this conclusion (Quinn 2011). However, we argue it was probably obtained as a by-product of ostracod consumption, rather than as a target food source.

Ostracods are consumed by Semipalmated Sandpipers in small amounts in other areas (Duffy et al. 1981, Gratto et al. 1984, Skagen and Oman 1996). They have also been noted in the droppings of Broad-billed Sandpipers (*Limicola falcinellus*) near the Black Sea (Verkuil et al. 2006) and of Redshanks in Spain (Perez-Hurtado et al. 1997), and in the stomachs of wintering Dunlins in Washington (Brennan et al. 1990). Other meiofaunal prey are also important components of the diets of Western Sandpipers in the Fraser River estuary, British Columbia (Sutherland et al. 2000), of Red-necked Phalaropes (*Phalaropus lobatus*) in the Bay of Fundy (Mercier and Gaskin 1985), and of various waders in Mauritania (Zwarts et al. 1990). It is therefore not surprising that Semipalmated Sandpipers appear to have taken advantage of this unusual abundance of ostracods. Furthermore, our data suggest that meiofaunal prey, when present in high abundance, may be a more important food source in this system than previously recognized.

Mudshrimp, although not as strong a predictor as ostracod abundance, still affected time spent skimming at Grande Anse in 2006; birds skimmed more when adult mudshrimp were completely absent from their foraging areas. We therefore cannot completely exclude the possibility that the low density of mudshrimp at Grande Anse alone led birds to switch to the more tactile skimming behavior. However, the strong link with ostracod abundance makes that seem very unlikely. Biomass was also low at Mary's Point in 2006, and we observed no skimming there. We suggest that the observed change in behavior was a result of the joint changes in the abundance of both prey items (see below).

Although we observed skimming only in one year and at one site of this study, it has also been observed regularly at the Bay of Fundy by Semipalmated Sandpipers foraging at night (Hebert 2011, Quinn 2011; E. MacDonald, unpubl. data). It is

a more tactile technique than pecking or probing and so may be a more efficient means of foraging at night. Notably, skimming at night occurs regardless of prey availability (Hebert 2011), so we speculate that birds use it routinely to capture a range of prey when tactile foraging is necessary, but they can also switch to it during the day when dictated by prey availability. A more complete understanding of all prey obtained by this method during day and night is required to clarify its contribution to fattening during migratory stopover. However, the flexibility with which birds appear to use this method suggests that it may already be of general importance through night foraging, and that its importance may grow if the abundance of foods obtained by traditional daytime foraging methods continue to fluctuate.

BENEFITS OF FLEXIBILITY AND OPPORTUNISM

An opportunistic foraging strategy, in which individuals take prey in proportion to their availability (Davis and Smith 2001), appears to be very important for some shorebird species. At stopover sites on the Great Plains, Davis and Smith (2001) found that American Avocets (*Recurvirostra americana*) and Long-billed Dowitchers (*Limnodromus scolopaceus*), both larger shorebirds capable of handling larger, more profitable prey, chose smaller prey that were more abundant. At each of four sites in Washington, Brennan et al. (1990) found that wintering Dunlins chose prey by their abundance; polychaetes were the main prey chosen at the three sites where they were most abundant, and amphipods were chosen at a fourth site where their densities were highest.

Behavioral flexibility is also an important foraging strategy in other shorebirds. Western Sandpipers forage in a highly variable manner, pecking for epifaunal prey, probing for infaunal prey (Sutherland et al. 2000, Nebel et al. 2005), and grazing for biofilm (Kuwae et al. 2008, Mathot et al. 2010). At the Wash estuary in England, in recent years Ruddy Turnstones (*Arenaria interpres*) have used nonintertidal habitats in response to insufficient food supplies during winter (Smart and Gill 2003). By flexibility and opportunism in habitat use, foraging styles, and diet, these birds can cope with changes to their prey base.

Until now, there has been little evidence to suggest that Semipalmated Sandpipers in the Bay of Fundy are flexibile or opportunistic in feeding. The flexible and opportunistic behavior we observed suggests that these birds may be able to continue to use traditional staging areas when their preferred prey is less available, provided that an alternate prey takes its place. Ostracods sometimes occupy the sediment surface at high densities and thus may offer an alternative to mudshrimp when the latter are scarce. At lower densities, however, the small size of ostracods may limit their usefulness as a prey item, for the same reasons that adult mudshrimp are preferred over juveniles (Peer et al. 1986). As in other shorebird–prey interactions (Piersma et al. 1994, Desholm 2000), there may be a threshold density above which ostracods become a profitable

food item. This is the case for Semipalmated Sandpipers foraging on mudshrimp (Hicklin and Smith 1984, Wilson 1990). Thus, it may be that a combination of ostracods exceeding a critical abundance and mudshrimp falling below their threshold of profitability led to the switch in foraging behavior and probable prey consumption we observed in 2006. Our data also point to the possibility that the Semipalmated Sandpiper's assumed preference for mudshrimp may be more related to that prey's historically broad availability than to preference per se. In the future, it will be interesting to see how birds respond when mudshrimp and ostracods are equally abundant or equally scarce.

ACKNOWLEDGMENTS

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