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Do Staging Semipalmated Sandpipers Spend the High-Tide Period in Flight over the Ocean to Avoid Falcon Attacks along Shore?

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Abstract.—The interaction of aerial predators and migrant Semipalmated Sandpipers (*Calidris pusilla*) was studied at Mary's Point in the upper Bay of Fundy, New Brunswick, Canada, during August of 2009 and 2010. Peregrine Falcons (*Falco peregrinus*) were locally reintroduced and increased from one active nest site in 1989 to 27 in 2010, which coincided with a decline of sandpipers roosting at Mary's Point from an annual mean of 161,000 in 1976-1982 to 15,000 or less during this study. Mean roosting time of flocks was 33 min (range = 10 to 40 min; N = 6). Sandpipers returned to the beach 1 h:36 min after high-tide (range = 1 h:10 to 2 h:13 min; N = 5), but were soon flushed again by falcons. On ten of 19 days, during part of the high-tide period, flocks of sandpipers remained in flight over the ocean. Termed Over-Ocean Flocking (OOF), this behavior was seen on days when spring tides inundated all beach habitat, and also at lower tides, which supports the hypothesis that OOF is an antipredator strategy intended to avoid surprise attacks by falcons near the shore. Raptors sighted during 128 hours afield included 226 Peregrines, 20 Merlins (*Falco columbarius*) and two Sharp-shinned Hawks (*Accipiter striatus*). At 1.0-3.2 Peregrine sightings/h⁻¹ (mean 1.8) the level of disturbance is high and supports the hypothesis that the decline in roosting sandpipers at Mary's Point is linked to predation danger. Received 11 December 2010, accepted 17 March 2011.

Key words.—Bay of Fundy, *Calidris alpina*, migrant sandpipers, over-ocean flocking, Peregrine Falcons.

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Population estimates of Semipalmated Sandpipers (*Calidris pusilla*) migrating from arctic breeding grounds to the coast of Suriname and staging in the upper Bay of Fundy during July and August, are in the order of one to two million (Hicklin 1987; Morrison 1984; Hicklin and Gratto-Trevor 2010). During the high-tide period, when their intertidal feeding grounds are inundated, aggregations of >100,000 sandpipers were reported from traditional roosting sites in the upper Bay of Fundy. Recent estimates are lower and believed to parallel a continent-wide population decline (Morrison *et al.* 1994). However, long-term observers on the Pacific coast of Canada have suggested that census declines of migrant shorebirds on formerly traditional staging sites may be related to the return and recent increase of the Peregrine Falcon (*Falco peregrinus*) (Ydenberg *et al.* 2004).

Peregrines often hunt by stealth in attempts to take their prey by surprise (Dekker 1980, 1988; Cresswell 1996). Stealth tactics have a success rate of 24% as compared to 9% for hunts over open terrain away from

cover (Dekker 1998; Dekker and Ydenberg 2004). To avoid surprise attacks near shore, Dunlins (*Calidris alpina*) wintering at Boundary Bay in British Columbia remain in flight over the water during part or all of the high-tide period (range = 1 h:30 to 6 h:30 min; mean = 3 h:15 min). Termed Over-Ocean Flocking (OOF), these flights differ from regular transit flight or the aerial manoeuvres of sandpipers evading falcon attack (Dekker 1998; Ydenberg *et al.* 2010). At Boundary Bay, the OOF phenomenon became common after the 1990s, coinciding with the return of the Peregrine Falcon from its near disappearance due to environmental contamination. (For a video illustrating OOF see Ydenberg *et al.* 2010).

Here, we compare sandpiper numbers at one traditional roosting site in the Bay of Fundy to pre-Peregrine days, and discuss their high-tide behavior and antipredator tactics in light of similar observational studies at Boundary Bay, British Columbia. We test the hypothesis that migrant Semipalmated Sandpipers staging in the upper Bay of

Fundy have abandoned traditional roosting sites because of a high level of disturbance by aerial predators, which was suggested by MacKinnon *et al.* (2008). Piersma *et al.* (2006) correlated shorebird avoidance of near-shore roosting sites with the presence of nocturnal avian predators. The importance of avoiding surprise attacks by aerial predators is a basic tenet of much research on the feeding habits of prey species (Lima 1987; Cresswell 1996; Ydenberg *et al.* 2002; Lank *et al.* 2003; Stephens *et al.* 2007). In this paper, we pose a related hypothesis linking the return of the Peregrine to a change in high-tide behavior of the sandpipers, which now, instead of roosting on shore, may spend part or all of the high-tide period in flight.

METHODS

Study Area

Mary's Point is a 1,200 hectare coastal wetland in the upper Bay of Fundy, New Brunswick, Canada (Fig. 1). During 1976-1982, it contained the largest traditional sandpiper roost in the upper Bay of Fundy (Hicklin 1987). Mary's Point includes a mostly wooded peninsula with a maximum elevation of 10 m. Rimmed with beaches, the Point extends east from the coastline and curves southward for a distance of 2.3 km. Adjacent mudflats contain high densities of Mud Shrimps (*Corophium volutator*), an abundant food resource for migrating shorebirds (Hicklin and Smith 1984; Hicklin 1987; Gratto-Trevor 1992). Shorebird surveys began in 1974 (Gratto *et al.* 1984; Sprague *et al.* 2008; Beauchamp and Ruxton 2008; Beauchamp 2010).

Tide schedules for August 2009 and 2010 were obtained from Environment Canada for Hopewell Rocks, 15 km north of Mary's Point. During the study period,

high-tide ranged from 10.5 to 13.8 m. Tides of over 13.0 m inundate all beach and saltmarsh habitat. At ebb time, the mudflats extend to or just beyond the rocky headland of the Mary's Point peninsula, 1.75 km across from the beach at the base of the Point.

Over 21 consecutive days, DD and ID in association with DC spent 128 observation hours in the study area (67.5 before high-tide and 60.5 after high-tide). From a stationary and slightly elevated viewpoint near the base of the Point, we continually monitored the shore and the intertidal zone through binoculars. Each day, we roughly estimated the number of roosting sandpipers and timed their arrival and departure. Alerted by alarm behavior, such as sudden flushing or the tightening of airborne flocks, we scanned the area for falcons, which were kept in focus for as long as they remained visible. The number and timing of sightings were recorded in an annotated field diary. We purposely focussed our observations on the densest sandpiper aggregations because Peregrines generally show a tendency to attack large flocks (Beauchamp 2010).

Information on past and recent surveys of Peregrine nest sites in the upper Bay of Fundy was obtained from government wildlife departments in Nova Scotia and New Brunswick. After their extirpation half a century ago due to environmental contamination, Peregrine Falcons were reintroduced into the Bay of Fundy by the release of 178 captive-reared juveniles in 1982-1993 (Amirault 2003). Breeding in the wild was first recorded in 1989, and active nest sites increased from five in 1993, to eleven in 2001, 16 in 2005 and 27 in 2010. Without artificial restocking, Merlins (*Falco columbarius*) have also become common.

Assuming that falcon activity was constant during the day, we tested whether the pattern of falcon sightings per hour deviated significantly from an even rate. We used a χ^2 test comparing observed numbers of falcons with that expected (on the basis of the overall sighting rate and the observation hours) in each hour interval. To test whether the pre- and post-high-tide peaks differed, we compared sighting rates in matching intervals before and after high-tide using two sample t-tests with unequal variances.

RESULTS

At low tide, the number of sandpipers foraging on the mudflats south of Mary's Point peaked at 75,000-150,000 on 14 August 2010. As the tide rose, flocks of sandpipers began leaving the intertidal zone 3 h:20 min before high-tide (mean departures were 2 h:29 min before high-tide, $N = 5$). On sunny days with good visibility, departing flocks could be followed through binoculars for several km. Coursing low over the ocean against the predominantly southerly winds, the flocks showed up as white vibrating lines against the dark water. On dull days, they soon vanished from sight. Other flocks continued to pass by the rocky tip of the peninsula, evidently coming from farther north in

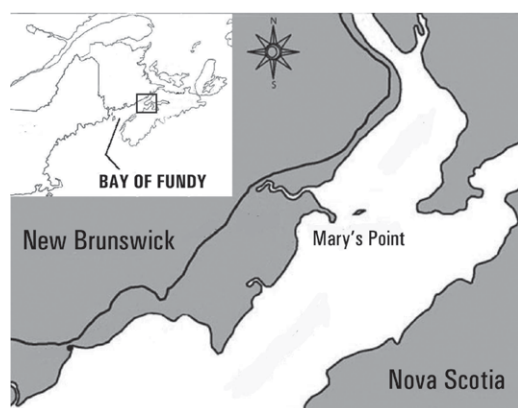


Figure 1. Location of Mary's Point in the upper Bay of Fundy.

Shepody Bay and travelling in the same southerly direction as the others.

During the two-hour high-tide period (from 1 h before to 1 h after high-tide) sand-piper presence in the area was low. On five of 18 days in August 2010 there were no sand-pipers roosting on the beach, and on seven of these 18 days we counted between 50 and 200 birds, most of them in the wrack washed up by preceding tides (Table 1). The majority of these roosting birds were Semipalmated Plovers (*Charadrius semipalmatus*) and Least Sandpipers (*Calidris minutilla*). The highest roosting aggregations of 2,000-15,000 Semi-palmated Sandpipers occurred on four days between 14 and 18 August 2010.

Roosting flocks did not stay on the beach for the entire high-tide period. The longest time spent roosting, interrupted by false alarms, was 1 h:45 min. On six days, the birds left after 10-40 min (mean = 33 min), and each time their departure was triggered by an attacking Peregrine or Merlin.

Flocks of sandpipers returning from distant roosts or OOF flight began landing at Mary's Point 1 h:10 min after high-tide. Mean arrival time was 1 h:36 min after high-

tide (range = 1 h:10 to 2 h:13 min; N = 5). Waiting for the waters to ebb, the birds assembled in packed ranks on the edge of the beach closest to the water line. In this end phase of the roosting interval, estimated numbers could briefly grow to >30,000, but they frequently flushed, and falcon attack caused them to fly away or split up, with part of the flock leaving the Point and going out of sight across the peninsula.

Falcon Sightings

If undisturbed for some time, foraging shorebirds at Mary's Point tended to spread out quite evenly over the intertidal zone, but Peregrine attacks led to the temporary abandonment of large sections of mudflat. Moving some distance away, the flocks then became more concentrated. We sighted 226 Peregrines, all of them in flight over the shore, mudflats or ocean. The overall mean sighting rate was 1.8/h⁻¹ and ranged from 1.0 to 3.2/h⁻¹ over the twelve hours of the tide cycle (Table 2). The sighting rate relative to high-tide is portrayed in Fig. 2. The low rates six and five h before high-tide may in part be due to poor viewing conditions, but regardless of whether these intervals are included or not, the difference between the pre- and post-high-tide peaks is highly significant ($\chi^2 = 35.9$, 11 df, $P < 0.001$, $\chi^2 = 31.9$, 9 df, $P < 0.001$).

Table 1. Estimated number of sandpipers roosting at Mary's Point in the two hours around high tide (-1 to +1) from 2 to 19 August 2010. (By way of comparison, annual maxima of roosting sandpipers at Mary's Point varied from 100,000 to 350,000 (mean 161,000) in 1976-1982 (Hicklin 1987)).

Date	Estimate of roosting sandpipers
2 August	n/a
3 August	0
4 August	0
5 August	60
6 August	40
7 August	50
8 August	150
9 August	200
10 August	0
11 August	0
12 August	100
13 August	0
14 August	5,000
15 August	15,000
16 August	200
17 August	2,000
18 August	4,000
19 August	2,000

Table 2. Sightings of Peregrines per observation hour in the six hours before (-) high-tide and the six hours after (+) high-tide at Mary's Point, New Brunswick, Canada, in August of 2009 and 2010.

Time	Observation hours	Peregrine sightings	Sighting rate
-6	8	8	1.0
-5	9.5	10	1.1
-4	8.5	27	3.2
-3	14.5	24	1.7
-2	12.5	23	1.8
-1	13.5	15	1.1
+1	14	14	1.0
+2	14.5	28	1.9
+3	14.5	40	2.8
+4	6.5	12	1.8
+5	6	18	3.0
+6	4	7	1.8
Total	128	226	1.8

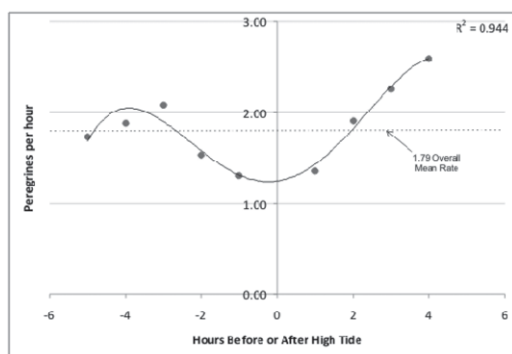


Figure 2. The sighting rate of Peregrines relative to the time of high tide (occurs at '0'). Points are the sighting rates in successive, overlapping 3 h intervals. For example, the leftmost point is the sighting rate 6-4 h before high-tide, the next 5-3 h, etc. The overall average sighting rate is 1.79 h^{-1} . The fitted line (4th degree polynomial: $R^2 = 0.94$) is used to illustrate that the rate is lowest around high-tide – which coincides with sandpiper departure from Mary's Point – and peaks 3 h before and after high-tide. The post high-tide peak, when sandpipers return from distant roost sites or OOF, is greater.

Using two sample t-tests with unequal variances, we compared sighting rates in matching intervals before and after high-tide to test whether the pre- and post-high-tide peaks differed. The rates cannot be distinguished statistically in the 1 h ($P = 0.097$) or 2 h ($P = 0.039$) intervals, but differed significantly in the 3 h ($P < 0.0001$) and >3 h ($P < 0.0001$) intervals. Overall, the post-high-tide sighting rate is significantly greater ($P < 0.0001$). The dip around the high-tide mark coincides with the departure of sandpipers from Mary's Point at that time.

Hunting falcons generally flew low, flushing the shorebirds ahead of them and singling out individuals for one or more attempts at capture. If viewed against an open background of sea and sky, flying falcons could be followed in the binoculars at distances of 2-3 km. Although surprise attacks by Peregrines are significantly more successful than open attacks, it does not follow that Peregrines always rely on stealth methods, on the contrary (Dekker 1980, 1999, 2003). The majority of hunting at Mary's Point took place over mudflats and ocean far from shore. Visibility against the treed background of the Point was poor, and many chases either became lost to view or carried

on out of sight across the peninsula. Falcons in persistent pursuit of fleeing prey were commonly joined by one or two conspecifics, also swooping at the same dodging target. We saw Peregrines capture 17 small shorebirds. Eight of these were caught in 15 hunts by adult falcons, which could be distinguished by grey dorsal coloration and white chests (Palmer 1988). As shown by their overall brown plumage, the vast majority of Peregrines were immatures, and their success rate was less than five percent.

We sighted 20 Merlins in flight over the shore or intertidal zone. Like Peregrines, they caused widespread alarm reactions. Merlins captured two sandpipers after long pursuits. Sharp-shinned Hawks (*Accipiter striatus*) made two low surprise attacks on sandpipers roosting at Mary's Point and grabbed one of them just after it flushed from the beach.

Over-Ocean Flocking

On days of poor visibility and strong winds, flocks of sandpipers leaving Shepody Bay and Mary's Point flew low over the water and soon became lost to sight, making any OOF—if it occurred—impossible to see. However, we recorded OOF on one day in 2009 and nine days in 2010, all of which were characterized by fair to good visibility and light winds. During 13-16 August 2010, large flocks remained airborne over the ocean for 25-85 min, continuously changing shape, altitude and direction. On these four dates, spring tides resulted in the complete inundation of all shoreline beach habitat. We also noted OOF during tides of 10.6-11.5 m, which left >100 m of beach above the floodline. The respective dates were 3 August 2009 and 2, 7, 9, 10 and 19 August 2010. Low-level OOF was seen on 16 August 2010 with moderate winds and overcast skies. Through the binoculars, we watched a flock of circa 1,000 sandpipers coursing just above the waves at an estimated distance of 3 km from our vantage point. Evidently, the birds were not travelling to a roosting destination for they reversed direction at least eight times, flying back and forth over the bay. Eventually, after 35 min of continuous observation they faded away into the distance.

DISCUSSION

The results reported support the hypothesis that the roosting habits of sandpipers in the upper Bay of Fundy have changed following the reintroduction of the Peregrine Falcon to the region. The change has been particularly noticeable at Mary's Point, where the birds used to roost predictably, arriving well before high-tide. Collecting in dense aggregations of 100 birds per m² (Mawhinney *et al.* 1993), they stayed until the waters began to ebb with few if any disturbances. Then, the only raptor occasionally seen to attack the roosting birds was the Sharp-shinned Hawk (DC). Peregrines were not reported until after 1982. Annual maxima at the Mary's Point roost used to vary from 100,000 to 350,000 birds (mean 161,000), which constituted the largest estimates recorded at 34 roosting sites surveyed in the Bay of Fundy in 1976-1982 (Hicklin 1987). By contrast, during the two-hour period from one hour before to one hour after high tide, we estimated the largest roosting aggregation at Mary's Point at 15,000, and we saw no roosting birds at all on the beach on five of 19 days. Further, during the end phase of the roosting interval, when the sandpipers returned to Mary's Point from distant roosts or from OOF, they appeared to be restless, flushing frequently. Beauchamp (2010) reported false alarms at the rate of one for every minute spent roosting. After false alarms, the birds soon returned to the same spot, but they usually abandoned the site after falcon attacks.

Additional evidence for the hypothesis that raptor presence has resulted in the abandonment of traditional sandpiper roosting sites in the upper Bay of Fundy derives from Hopewell Rocks Provincial Park, 15 km north of Mary's Point. In 2004-2005, Hopewell was the most frequented sandpiper roost in Shepody Bay, sometimes exceeding 100,000 birds (Sprague *et al.* 2008). This was rarely the case in 2009 and not at all in 2010, when park staff estimated the largest roosts at 1,000-2,000 birds. They also noted that some flocks remained airborne over the bay, flying back and forth for two hours instead of landing (Paul Gaudet, manager of

interpretation, Hopewell Rocks Provincial Park, pers. com.). A pair of Peregrines first nested at Hopewell in 2009. In 2010, the pair produced three young, which were on the wing by the time the migrant sandpipers began arriving.

Hicklin and Gratto-Trevor (2010) wrote that flocks of Semipalmated Sandpipers staging in the Bay of Fundy "can remain in the air throughout the high-tide periods when attacks by aerial predators are frequent." Although they did not provide details, their statement and this paper constitute the first published records of OOF in the upper Bay of Fundy. Our observations at Mary's Point concur with those from Boundary Bay, British Columbia (Dekker 1998; Ydenberg *et al.* 2010). However, while the timing of the Boundary Bay flights could be precisely measured from start to finish, this was not possible at Mary's Point, due to poor visibility and the far wider expanse of ocean.

An important aspect of OOF that remains to be investigated is its energetic cost. Compared to ground-based roosting, OOF can be expected to be expensive in terms of energy with crucial impacts on the length of the fall staging period when fat has to be stored to fuel the long non-stop flight from the Bay of Fundy to wintering grounds in Suriname (Hicklin 1987; Morrison *et al.* 1994). However, as described in Dekker (1998) and Ydenberg *et al.* (2010), flocks of Dunlins engaged in OOF fly in a manner quite different from direct transit flight or the twists and turns typical of sandpipers panicked by aerial predators. Moving against the wind, with fluttering wingbeats, flocks in OOF expend as little energy as possible, using lateral airflows to stay airborne.

OOF by Dunlins was also observed on the north coast of Germany (Hotker 2000), but less regularly than at Canada's Boundary Bay. Dunlins wintering along the Wadden Sea in The Netherlands rarely reverted to OOF because adjacent fields and meadows constituted suitable wide-open spaces for ground-based roosting away from vegetative cover (Dekker and Ferwerda 2008; Dekker 2009).

As theorized by Dekker (1998), prior to European settlement of British Columbia's

Fraser Delta, OOF must have been a routine habit of saltwater shorebirds to wait out the high-tide period. Then, the intertidal zone was likely covered with dense vegetation, discouraging migrant sandpipers from landing there. However, after the lowlands were dyked and drained for agriculture, the sandpipers had the option of sitting out high-tide inland. Roosting of wintering Dunlins on wet meadows and ploughland used to be routine in the lower Fraser Delta (Butler and Campbell 1987), but became less common by the mid 1990s after the return of the Peregrine Falcon (Ydenberg *et al.* 2010). However, during rain, a few flocks still fly inland or remain behind on the edge of the salt marsh while the majority are engaged in OOF. The reasons why some sandpipers do not depart on OOF remain to be investigated.

Roosting sites other than the known traditional locations may exist in unexpected places. Distances of up to 20 km between feeding and roosting sites were reported by Sprague *et al.* (2008), who monitored the movements of radio-tagged Semipalmated Sandpipers from the air. On 15 August 2011, one of us (DC) observed a roost of 30,000-40,000 birds on a stony shelf at Brae Beach, 13 km south of Mary's Point. In the Bay of Fundy region as well as in British Columbia, flocks of migrant sandpipers have also been reported roosting inland on roads, airport runways, the causeway of a ferry terminal and in a gravel pit (Dekker 1998; MacKinnon *et al.* 2008). A natural substrate used by inland-roosting Semipalmated Sandpipers is the bare islets and rocky shores of Black River Lake, 10 km south from the mudflats of Minas Basin in the upper Bay of Fundy. Flocks of up to 5,000 birds began using this roosting site after 1995, when the first pair of Peregrines was recorded nesting in Nova Scotia after an absence of 40 years (Mark Elderkin, wildlife biologist, Government of Nova Scotia, pers. com.). For a rare photograph of several hundred Semipalmated Sandpipers roosting on a seaside cliff well above the waterline see MacKinnon *et al.* (2008).

Compared to the Pacific coast of Canada, predation pressure at Mary's Point is exceptionally high. Peregrine sightings recorded

in this study were twice as numerous as at Boundary Bay (288 sightings in 324 hours, mean $0.9/h^{-1}$; D. Dekker, unpublished data). The reason is not that the number of falcons at Mary's Point is greater than during winter on the Pacific coast, on the contrary. As far as is known, there was only one pair of falcons nesting near the study area, and breeding Peregrines are highly territorial, chasing intruders away. However, the falcons doing most of the hunting at Mary's Point were the pair's progeny. In both 2009 and 2010, the local pair raised three young. Initially, just-fledged juveniles follow their parents, but within one or two weeks they hunt independently and together with siblings (Dekker and Taylor 2005). During their first fall, Peregrines are significantly less successful at hunting than mature falcons on breeding territory (2-5% vs. 22-46%; see Dekker 2009), and spend more time in flight than do adults. Assuming that the majority of prey caught are Semipalmated Sandpipers, weighing 25-50 g, active young Peregrines would have to catch and eat four or five sandpipers each day to make up their daily food requirements (Palmer 1988; White *et al.* 2002).

In conclusion, during the time when migrating Semipalmated Sandpipers are staging in the upper Bay of Fundy, hunting activity by locally fledged young Peregrines - in addition to their parents, Merlins and Sharp-shinned Hawks—causes a very high degree of predator disturbance, which supports the hypothesis that the sandpipers have been discouraged from using formerly safe, traditional roosting sites. For the same reason, our results suggest that the sandpipers spend more time in OOF flights than formerly so as to escape raptor harassment along shore.

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