ARTICLE

High-tide flight by wintering Dunlins (*Calidris alpina*): a weather-dependent trade-off between energy loss and predation risk

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Abstract: Migratory shorebirds wintering or staging on ocean coasts collect at high tide on roosting sites that remain above the flood line. However, some species of *Calidris* sandpipers spend the high-tide interval in flight over the ocean. In the winters of 2006–2012, the characteristics of high-tide flight by Dunlins (*Calidris alpina* (L., 1758)) were studied at Boundary Bay, British Columbia, Canada. At wind speeds of 1–6 m/s, flocks of Dunlins remained airborne over the ocean for up to 4 h at altitudes of >30 m. If winds were >10 m/s, the Dunlins coursed low over the waves. Ambient temperature was a significant determinant in the occurrence and duration of high-tide flight. In October and November, the Dunlins spent just as much time in flight before as after high tide, but in January, flight duration was 43% shorter after high tide than before high tide. The mean January temperatures were significantly lower than in October and November. The Dunlins were hunted by Peregrine Falcons (*Falco peregrinus* Tunstall, 1771), which captured 81 prey in 494 attacks. The maximum kill rate of 0.28 captures per hour of observation was recorded in the second hour after high tide, which suggests that predation risk is greatest for Dunlins that return early from high-tide flight.

Key words: Dunlins, *Calidris alpina*, high-tide flight, weather dependence, Peregrine Falcon, *Falco peregrinus*, predation risk.

Résumé : Les oiseaux de rivage migrateurs qui hivernent ou font escale sur les côtes océaniques se réunissent à marée haute dans des sites de repos qui demeurent au-dessus de la limite d'inondation. Certaines espèces de bécasseaux *Calidris* passent toutefois la période de marée haute en vol au-dessus de l'océan. Durant les hivers de 2006 à 2012, les caractéristiques du vol à marée haute de bécasseaux variables (*Calidris alpina* (L., 1758)) ont été étudiées dans la baie Boundary (Colombie-Britannique, Canada). À des vitesses du vent de 1–6 m/s, des volées de bécasseaux variables passaient jusqu'à 4 h en vol au-dessus de l'océan à des altitudes de >30 m. Si les vitesses du vent étaient >10 m/s, les oiseaux volaient à faible altitude au-dessus des vagues. La température ambiante était un important déterminant de la présence et de la durée du vol à marée haute. En octobre et novembre, les bécasseaux variables passaient autant de temps en vol avant la marée haute qu'après celle-ci, alors qu'en janvier, la durée du vol après la marée haute était de 43 % inférieure à celle du vol avant la marée haute. Les températures moyennes en janvier étaient significativement plus faibles qu'en octobre et novembre. Les bécasseaux variables étaient chassés par des faucons pèlerins (*Falco peregrinus* Tunstall, 1771), qui ont capturé 81 proies dans le cadre de 494 attaques. Le taux de capture maximum de 0,28 capture par heure d'observation a été enregistré pour la deuxième heure après la marée haute, ce qui porte à croire que les bécasseaux qui rentrent tôt d'un vol à marée haute présentent le risque de prédation le plus élevé. [Traduit par la Rédaction]

Mots-clés : bécasseaux variables, *Calidris alpina*, vol à marée haute, dépendance de la météo, faucon pèlerin, *Falco peregrinus*, risque de prédation.

Introduction

When flood waters inundate their intertidal feeding grounds, flocks of sandpipers wintering or staging on ocean shores are known to assemble on roosting sites that remain above the high-tide mark (Hicklin 1987; Rogers 2003; Conklin et al. 2008). However, if safe roosting sites are distant from the foraging location, the metabolic cost of flying back and forth twice daily can be high (Piersma 1994). Instead of sitting out the high-tide interval on land near their foraging grounds, some species of sandpiper abandon the shoreline and remain airborne over the water until the tide has turned. Such high-tide flight by Dunlins (*Calidris alpina* (L., 1758)) wintering along the Pacific coast of British Columbia was termed over-ocean flocking by Dekker (1998). Hotker (2000) observed wintering Dunlins in high-tide flight off the north coast of Germany and called it airborne roosting. During their fall migration, Semipalmated Sandpipers (*Calidris pusilla* (L., 1766)) staging in the upper Bay of Fundy engaged in high-tide flight when all beach habitat had been flooded (Dekker et al. 2011). Western Sandpipers (*Calidris mauri* (Cabanis, 1857)) staging at Boundary Bay in British Columbia flew out over the ocean in high-tide flight formations in August of 2011 (D. Dekker and N. Hentze, personal observation).

The hypothesis that high-tide flight is a strategy to reduce predation risk was tentatively suggested by Brennan et al. (1985). To test the hypothesis, Dekker (1998) presented a large data set of attacks on Dunlins by falcons. In flight, the sandpipers were less vulnerable to surprise attacks by Peregrine Falcons (*Falco peregrinus* Tunstall, 1771) and Merlins (*Falco columbarius* L., 1758), which commonly hunt low over the ground or water and hide their approach behind shoreline vegetation (Page and Whitacre 1975; Dekker 1980, 1988; Cresswell 1996). Dunlins that did not engage in high-tide flight and instead remained on shore were subject to the highest rate of raptor predation. Peregrines hunting Dunlins over the salt marsh had a success rate of 44%, compared with 10%–11% for falcons attacking Dunlins over the tide flats or ocean away from the shore (Dekker 1998, 2003).

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High-tide flight by Dunlins wintering at Boundary Bay has been timed at a maximum duration of 6 h (Ydenberg et al. 2010). Assuming that flood waters rise at the same speed as the ebb subsides, the width of tide flat before and after high tide should be equal, which suggests that Dunlins can be expected to stay airborne just as long before as after high tide. However, flight requires energy and energy loss rises as the temperature drops. The purpose of this study is to test the following three hypotheses: (1) wind speed and ambient temperature are critical determinants in the occurrence and duration of high-tide flight; (2) high-tide flight lasts just as long before as after high tide; and (3) Dunlins that do not engage in high-tide flight or return early from such flights are subject to the highest rate of predation danger. This study enlarges the database of Dunlins killed by peregrines reported in similar research projects at Boundary Bay (Dekker 1998, 2003; Dekker and Ydenberg 2004). A long-term objective of these field studies has been to test the hypothesis that the primary objective of high-tide flight is to reduce predation risk for wintering Dunlins.

Materials and methods

The study was conducted at Boundary Bay in southwestern British Columbia (49°5′N, 123°0′W). The bay is 16 km across and the intertidal zone is approximately 4 km wide at the lowest ebb. The tide flats are bordered by a 0–150 m strip of salt marsh. A gravelled road on a 2 m high dike separates the coastline from low-lying agricultural fields and meadows inland. Dunlins begin arriving in October and are estimated at circa 40 000 (Ydenberg et al. 2010). The only other shorebird to winter in numbers (circa 1000) is the Black-bellied Plover (*Pluvialis squatarola* (L., 1758)). Bald Eagles (*Haliaeetus leucocephalus* (L., 1766)) and other diurnal raptors occur year-round. Migrating and wintering Peregrine Falcons are common from August to April (Dekker 1998). For a detailed description of the Fraser delta and its avifauna, see Butler and Campbell (1987).

Between January 2006 and January 2012, the study area was visited on 65 days for a total of 488 observation hours divided over five periods with high daytime tides: 9–28 January 2006 (128 h), 19–24 October 2008 (42 h), 8–21 November 2009 (88 h), 16–30 January 2011 (110 h), and 8–22 January 2012 (120 h). Tide height predictions for the southwest coast of British Columbia were obtained for Point Atkinson (http://tides.mobilegeographics.com). Actual high-tide levels were checked using a 1 m measuring stake set up at the edge of the salt marsh. Mean high and low temperatures for the study period and daytime hourly wind speeds were taken from Environment Canada's Web site (http://www.weatheroffice.gc.ca) as recorded at the Vancouver International Airport, which is 15 km northwest of Boundary Bay. Wind speeds (m/s) on the dike at the time of high tide in January 2012 were measured using a Kestrel anemometer (Neilsen-Kellerman, Boothwyn, Pennsylvania, USA).

Observations were conducted from a vehicle parked on the dike at pullouts with an unobstructed view of the tide flats and salt marsh shore. With the twin objective of timing the duration of high-tide flights and recording falcon attacks, the observer stayed within viewing distance of the largest aggregation of Dunlins, either foraging, roosting, or in flight over the bay. If high-tide flight was ongoing when the observer arrived on the dike, that particular sequence was not used in subsequent calculations of flight duration because the start of the flight had not been seen. Only complete sessions, timed from beginning to end, were used to determine minutes spent in flight before and after high tide. On windy days, measuring flight duration at Boundary Bay was complicated by the fact that only a portion of the local Dunlin population might remain in flight while others returned to the shore early or had not engaged in the flight at all. However, as long as one or more flocks (>100 birds) stayed over the ocean and well offshore, the high-tide flight was deemed to have continued until all flocks had landed.

Alarm reactions by Dunlin flocks, such as sudden flushing, were a key to the approach of raptors. Methods in recording peregrine attacks were the same as in previous research (Dekker 1998, 2003; Dekker and Ydenberg 2004). An attack was defined as one completed attempt by a peregrine to seize a prey of which the outcome became known to the observer. The attack was considered successful if the falcon seized a Dunlin or forced it into the water, even though some of these prey were lost to kleptoparasitic Bald Eagles and Gyrfalcons (*Falco rusticolus* L., 1758) (Dekker et al. 2012). The timing of each Dunlin kill was compared with the tidal scale, and the number of captures seen per observation hour was calculated for the respective time slots on either side of the high-tide mark.

Statistical analysis

The relationship between duration of high-tide flight and mean temperature was statistically tested using linear regression. To normalize the distribution of residual values, the flight duration was transformed using logarithm base 10 of each value plus one. The differences between the mean temperatures of January and October and November were compared with a Student's *t* test for equal variances (Sokal and Rohlf 1995).

Results

High-tide flight was recorded on 45 of the 65 observation days divided over five periods (Table 1). Total flight time was 114:25 h with a mean of 2:32 h/day (*n* = 45, range 0:10–5:30 h/day). On 27 days, high-tide flight occurred before high tide, and on 40 days after high tide. Overall, mean duration around high tide was not symmetrical, with 2:03 h/day in the before high-tide period and 1:29 h/day in the after high-tide period, a difference of 34 min (28%). However, high-tide flights were temporally symmetrical in October and November with a near equivalent duration of 1:51 h before and 1:53 h after high tide (Fig. 1).

Dunlins in typical high-tide flight formations continually changed direction and generally stayed over the upwind part of the bay. They flew at slower speeds than during transit flight and frequently stopped beating their wings for a brief moment of sailing against lateral airflows. Turning downwind, they gained speed and lost altitude until the flock swung back upwind again to roughly repeat the same sedentary circuit.

The start of high-tide flight tended to be abrupt, with separate flocks leaving the shore almost simultaneously and flying out over the bay, although the number of Dunlins taking part in the flights varied. On days with light winds (1–5 m/s) and moderate temperatures, all Dunlins flew out over the ocean, and flock sizes could be >10 000. By contrast, if wind speeds were >10 m/s, part of the population stayed behind, and flying flocks often broke up when small groups separated and returned to shore. Landing on floating debris or vegetation at the outer edge of the salt marsh, these early returning birds frequently flushed again in false alarms. Actual attacks by peregrines triggered the flock's departure to resume high-tide flight over the water.

As observed from the dike, high-tide flights could be divided into two different modes. If winds were light, the Dunlins flew >30 m high and stayed within 1 km from shore. By contrast, when the winds were >10 m/s, the flocks coursed very low over the water and often ranged >1 km from shore. These low-level flights could only be discovered by scanning the bay through binoculars.

Tide-height prediction tables for the 5 months of the study period ranged from 4.41 m in January 2006 to 4.71 m in October 2008 (Table 1). As indicated by the measuring stake, flood levels on all days rose high enough to inundate the entire width of tide flat. Mean daily temperature was 7.3 °C for October 2008 and November 2009 combined, and 4.4 °C for the three January months of 2006, 2011, and 2012. The difference was highly significant (Student's *t* = 3.4, *P* = 0.001). There was a positive and statistically

Table 1. Occurrence of high-tide flight by Dunlins (*Calidris alpina*) wintering at Boundary Bay, British Columbia, and environmental conditions during the study periods.

	Jan. 2006	Oct. 2008	Nov. 2009	Jan. 2011	Jan. 2012
Observation days	19	5	13	14	14
Occurrence of high-tide flights	14	5	10	12	4
Tide height (m; mean ± SD)	4.41 ± 0.21	4.70 ± 0.016	4.52 ± 0.21	4.51 ± 0.28	4.49 ± 0.31
Daily temperature (°C; mean ± SD)	5.9 ± 1.05	9.6 ± 1.24	6.7 ± 1.77	5.8 ± 2.46	1.0 ± 3.70
Wind speed (m/s; mean ± SD)	4.4 ± 5.18	3.3 ± 5.77	5.8 ± 8.91	3.3 ± 5.24	4.4 ± 8.74

Fig. 1. Mean duration (min) of high-tide flight before and after high tide (0) by Dunlins (*Calidris alpina*) wintering at Boundary Bay, British Columbia. The flight was temporally symmetrical around the high-tide mark in October and November when ambient temperatures were moderate, but during the colder weather of January, the Dunlins spent more time in flight before high tide than after. Early return to shore increased their vulnerability to avian predators. The duration of high-tide flight before and after high tide for the five periods are respectively—January 2006: 167 min (*n* = 7) and 87 min (*n* = 13); October 2008: 94 min (*n* = 5) and 101 min (*n* = 5); November 2009: 122 min (*n* = 8) and 121 min (*n* = 8); January 2011: 115 min (*n* = 6) and 73 min (*n* = 11); January 2012: 10 min (*n* = 1) and 48 min (*n* = 3).
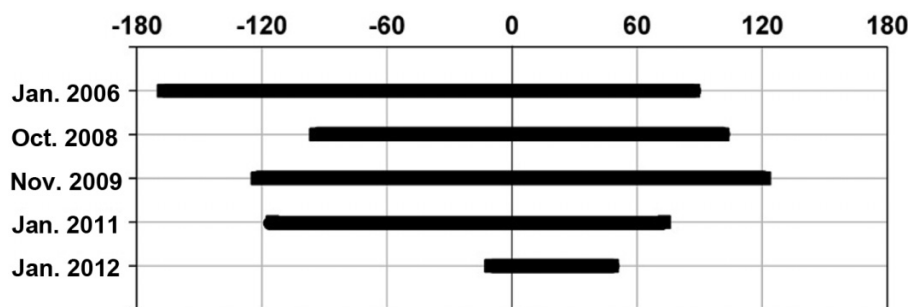
significant relationship between log duration of high-tide flight and mean temperature (β (SE): 0.17 (0.024); $F_{[1,52]}$ = 48.1, P < 0.0001; R^2 = 0.48; Fig. 2).

High-tide flight did not occur on 9 days in January of 2012 when the temperature was between –2 and –9 °C, and the daily mean ranged from 2.2 to –5.7 °C. The mean temperature of January 2012 was 1.0 °C, the lowest monthly mean recorded during the study (Table 1). On days when shore ice formed, the Dunlins sat out the high-tide interval on the ice 300–500 m away from the snow-covered salt marsh.

Peregrines launched 494 attacks on Dunlins, of which 81 (16%) ended in capture. The respective number of kills made before and after high tide was 34 and 47. Correlating kill times over the 6 h on either side of the high-water mark showed a prominent peak of 0.28/h during the second hour after high tide (Fig. 3).

During a cold spell in January of 2012, the Dunlins roosted on shore ice >300 m away from vegetation. Peregrines attacked these flocks on two occasions, each resulting in the immediate capture of one of the Dunlins. The roosting flock flushed in a moment of panic, but instead of flying away, the birds at once descended again onto the same spot.

Discussion

Migratory sandpipers staging or wintering in coastal habitats can be expected to spend as little energy as possible to wait out the high-tide interval, and there can be no doubt that the metabolic cost of high-tide flight is greater than it is for birds roosting on land. However, as reported above, in the interest of minimizing energy loss, flocks of Dunlins fly at lower speeds than during transit flight and use lateral airflows for brief moments of sailing (Dekker 1998; Ydenberg et al. 2010). Hentze (2012) analyzed the flight kinematics of Dunlins wintering at Boundary Bay and reported that sailing took up 14% of high-tide flight compared with 1% or less in transit flight.

An important finding of the present study is that there was a significant relationship between ambient temperature and Dunlin behaviour. The colder the weather, the less time the flocks spent in flight over the ocean, which supports hypothesis 1 to the

Fig. 2. Duration of high-tide flight by Dunlins (*Calidris alpina*) wintering at Boundary Bay, British Columbia, in relation to mean daily temperature. There were no flights on nine additional days when daily lows ranged from –2 to –9 °C.
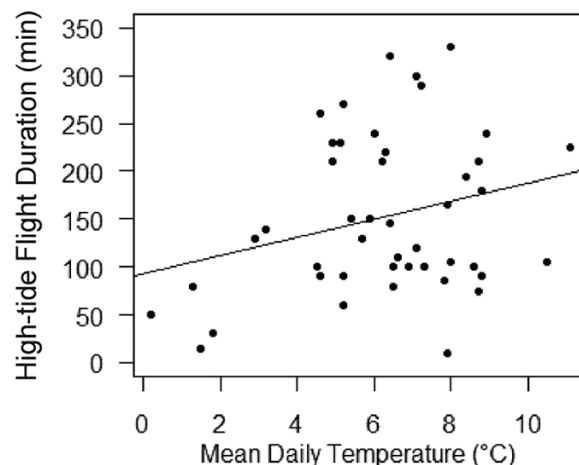
effect that ambient temperature is a crucial determinant in flight duration. The results do not support hypothesis 2, which poses that the Dunlins should stay airborne just as long in the before high-tide period as in the after high-tide period. The explanation for the lack of temporal symmetry in overall flight duration is again related to ambient temperature. During January, the mean temperature was significantly lower than in October and November. Mean flight duration in January was 2:14 h before high tide and 1:17 h after high tide, a difference of 57 min (27%). By contrast, in October and November when the mean temperature was 7.3 °C, the before and after high-tide flight durations were nearly identical at 1:51 and 1:53 h, respectively (Fig. 1).

Tired and hungry sandpipers can be expected to shorten their flight and land as soon as the tide begins to turn. Early returning flocks typically touched down in a hesitant manner, and false

Fig. 3. Temporal and tidal pattern of Peregrine Falcon (*Falco peregrinus*) predation on Dunlins (*Calidris alpina*) wintering at Boundary Bay, British Columbia, as expressed in kill rate per observation hour. Panel A represents 94 Dunlins kills made over 940 h in 1994–2003 (Dekker and Ydenberg 2004). Panel B represents 81 Dunlins kills observed over 595 h in the same study area from 2006 to 2012. Number of kills and observation hours in the successive time intervals are from left to right: 1/29, 4/42.5, 5/47.5, 7/55, 7/57.5, 10/60, 11/57.5, 18/64, 9/55, 7/49, 0/44.5, 2/33.5.
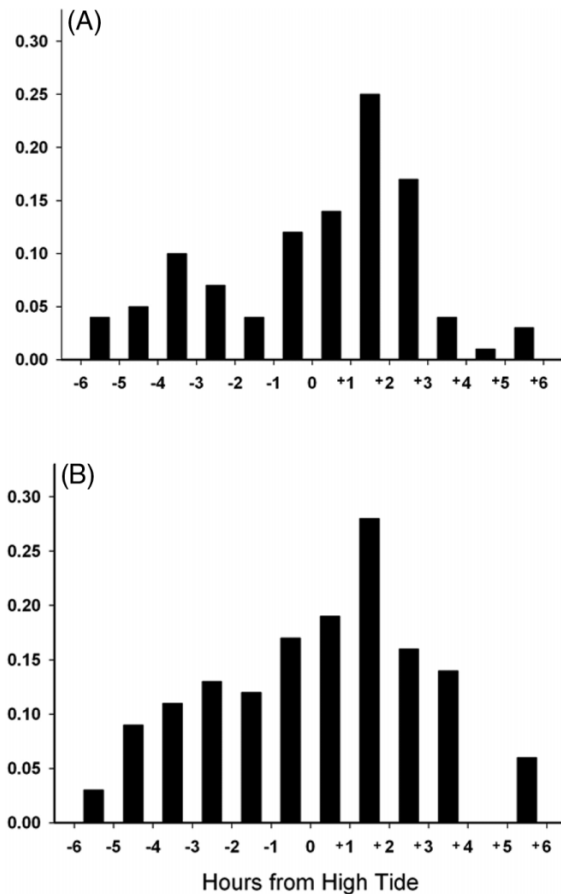
alarms were frequent (Beauchamp 2010). At Boundary Bay, an incentive for early landing was that the invertebrate prey base is most abundant closest to the salt marsh shore (Pomeroy et al. 2006). However, there is a critical trade-off with predation risk. The hunting success rate of peregrines, using typical stealth tactics, is four times higher over the salt marsh than it is in open attacks over the mud flats or ocean (Dekker 1998, 2003). Furthermore, as reported in this study, the capture rate of Dunlins per hour of observation increased to a peak of 0.28/h in the second hour after high tide, and dropped to 0.16 and 0.14/h in the third and fourth hours after high tide, respectively (Fig. 3). Thus, Dunlins that returned to the shore in the second hour after high tide, instead of staying airborne for another hour or two, were the most vulnerable to peregrine predation, which supports hypothesis 3.

During the coldest days of January 2012, the Dunlins did not engage in high-tide flight at all, and showed a minimal defensive reaction to falcon attack, which might be explained by their energy-stressed condition. As reported above, a large flock (estimated at 1000 birds) roosting on the ice 300–500 m offshore, briefly flushed when one of them was seized by peregrines, but the flock landed again at once on the same spot. A similarly reluctant response to hunting falcons was reported during freezing weather in January 1995. Then, a peregrine attacked a flock of

circa 200 Dunlins just after they had begun to spread out on the emerging mud flats. Only those Dunlins directly in line with the low-flying falcon flushed while the others continued to forage (Dekker 1998).

The normal reaction of roosting or foraging Dunlins to the approach of falcons is to instantaneously flush and gain attitude. If a peregrine or Merlin flies above them, the birds draw together into dense globular or elliptical formations that twist and turn in attempts to ward off direct attack (Buchanan et al. 1988; Dekker 2003). Such violent and erratic manoeuvres are in great contrast to the relaxed movements of flocks in typical high-tide flight. Frequent flushing of roosting flocks that are panicked by real or perceived raptor attacks probably wastes more energy than high-tide flight and can even lead to collisions and accidental fatalities (Dekker et al. 2012).

Dunlins do not start high-tide flight if the flood does not inundate the entire intertidal zone. Then the birds roost on the remaining strip of tide flats well away from the marsh vegetation. Neither do Dunlins engage in high-tide flight if the winds are completely calm or during continued heavy rain. On very wet days, some flocks fly inland to roost or forage on flooded meadows and fields (Dekker 1998; Dekker and Ydenberg 2004; Shepherd and Lank 2004). Inland shifts by Dunlins occur commonly in localities where the tide flats border on extensive open agricultural lands (Conklin et al. 2008; Dekker and Ferwerda 2008). In the past, before coastal salt marshes were drained and cultivated, open ground suitable for roosting was probably very scarce. Then, high-tide flight can be expected to have been the natural and only recourse of staging sandpipers when the intertidal zone was flooded (Dekker et al. 2011).

The question of whether or not Dunlins wintering at Boundary Bay routinely engage in high-tide flight at night was investigated by Hentze (2012). Using radar, he reported that all high-flying flocks descended at sundown; however, his equipment was unable to detect distant flocks flying very low over the ocean >1 km from shore, a behaviour often noted during the present study if winds were >10 m/s. In January of 2011 and 2012, when high-tide occurred between 06:00 and 08:00, long lines of birds were coursing very low over the waves at first light, 30–35 min before sunrise. Similar nocturnal flights could easily escape detection by researchers. Zharikov et al. (2009) noted that Dunlins wintering in the Fraser Estuary of British Columbia avoided feeding at night near shore when Snowy Owls (*Bubo scandiacus* (L., 1758)) were present. Adding to night-time danger, peregrines routinely forage in crepuscular light and have been known to be active nocturnally (Dekker 1999; White et al. 2002).

It might have been interesting to compare peregrine hunting success and kill rates between the fall months and January. Although such data are available from this and previous studies, the results would be biased because predation pressure on Dunlins wintering at Boundary Bay is uneven. During fall, the peregrine's major prey are ducks, but falcons stop hunting ducks later during the winter when Bald Eagles become numerous on the coast. Prey loss to pursuing eagles forces falcons to concentrate on Dunlins, which are light enough to be carried away out of reach of potential kleptoparasites (Dekker et al. 2012).

To sum up, as an antipredator strategy, high-tide flight does not free the species from falcon attacks. On the contrary, flocks of Dunlins flying over the open ocean do not escape detection by predators, and peregrines routinely attack prey over water (Dekker 1999, 2009; White et al. 2002). However, on the individual level, open-country birds that assemble in large flocks dilute their risk of being captured (Lima and Dill 1990). Upon the approach of falcons, airborne flocks of sandpipers become denser by the striving of their members to seek the safety of the centre of the flock. Conceivably, Dunlins in the centre may be the stronger birds, whereas outside birds are the weaker ones and the most vulnerable to attacking falcons. Peregrines tend to direct their stoops at

the edges or bottom of Dunlin flocks (Dekker 2003). Based on prey remains found, researchers have collected evidence that first-year shorebirds indeed make up the largest percentage of raptor kills (Whitfield 1985; Warnock and Gill 1996).

The results of this study support the hypothesis that the occurrence and duration of high-tide flight is contingent upon weather conditions, as well as tide height. Regarding the second hypothesis to the effect that flight duration is symmetrical around high-tide, this too is dependent upon local weather conditions. The overall mean flight duration of 2:32 h/day found here is lower than the 3:20 h/day reported by Dekker (2009) and Ydenberg et al. (2010), a disparity which may well be related to a difference in wind speed, ambient temperature, and tide height during those respective studies.

In addition to lending support for the general principle that flocking in prey species is an antipredator strategy, this study presents evidence, based on an unprecedented large sample of Dunlins seen to be captured by peregrines, that staying airborne for as long as the metabolic cost allows is a trade-off with predation risk.

Acknowledgements

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