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INTERACTIONS OF PEREGRINE FALCONS (*FALCO PEREGRINUS*) AND DUNLIN (*CALIDRIS ALPINA*) WINTERING IN BRITISH COLUMBIA, 1994–2015

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ABSTRACT.—Contemporary declines of shorebirds have been linked to environmental causes, but the role of predation in shorebird declines is not clear. From 1994 to 2015, we observed the interactions of Peregrine Falcons (*Falco peregrinus*) and Dunlin (*Calidris alpina*) wintering on the Pacific coast of British Columbia. Peregrine sightings per hour of observation declined on a seasonal basis from October to February, but increased chronologically from 0.36/hr in 1994 to 1.24/hr in 2015. Peregrines captured 205 Dunlin in 1369 attacks. Hunting success rates increased from 10.8% in October to 15.0% in the winter months. During high tide, when the intertidal zone was flooded, some Dunlin flocks spent up to 315 min in sustained flight over the ocean, apparently as an antipredator strategy, but other flocks roosted on the foreshore, or sat out the high-tide interval on agricultural fields inland. This study suggests that these antipredator behaviors allow the Dunlin population to persist at Boundary Bay as predator numbers increase.

KEY WORDS: *Peregrine Falcon*; Falco peregrinus; *Dunlin*; Calidris alpina; *antipredator behavior*; *prey capture*.

INTERACCIONES ENTRE INDIVIDUOS DE *FALCO PEREGRINUS* Y *CALIDRIS ALPINA* INVERNANDO EN LA COLUMBIA BRITÁNICA ENTRE 1994 Y 2015

RESUMEN.—La disminución actual de las poblaciones de aves limícolas ha sido relacionada con causas ambientales, pero no está claro el papel de la depredación sobre dicha disminución. Desde 1994 hasta 2015 observamos las interacciones entre individuos de *Falco peregrinus* y *Calidris alpina* invernando en la costa pacífica de la Columbia Británica. El avistamiento de ejemplares de *F. peregrinus* por hora de observación disminuyó durante la misma temporada de octubre a febrero, pero aumentó cronológicamente de 0.36/hora en 1994 a 1.24/hora en 2015. Los halcones capturaron 205 individuos de *C. alpina* en 1369 ataques. Las tasas de éxito de caza aumentaron de 10.8% en octubre a 15.0% en los meses de invierno. Durante la marea alta, cuando la zona intermareal estuvo inundada, algunas bandadas de *C. alpina* se mantuvieron hasta 315 minutos en vuelo sostenido sobre el océano, aparentemente como una estrategia antidepredador, pero otras bandadas pasaron la noche en la zona costera o se posaron afuera del intervalo de la marea alta, en campos de cultivo tierra adentro. Este estudio sugiere que estos comportamientos antidepredadores permiten la persistencia de la población de *C. alpina* en Boundary Bay a medida que el número de depredadores aumenta.

[Traducción del equipo editorial]

Population declines of migratory shorebirds have been of increasing concern to researchers and conservation agencies (Warnock and Gill 1996, Brown et al. 2001, Gratto-Trevor et al. 2011, Andres et al. 2012). The probable causative factors are environmental deterioration and wetland loss in addition to hunting on wintering grounds (Morrison et al. 1994). Ydenberg et al. (2004) found that

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length of stay at one stopover site in British Columbia declined as falcon populations increased, and postulated that perceived census declines of shorebirds at traditional staging sites may be linked to disturbances by Peregrine Falcons (*Falco peregrinus*), which have made a strong population recovery after the 1970s when the use of toxic chemicals (DDT) in agriculture was banned (Cade and Burnham 2003).

The Pacific coast from southern British Columbia to Mexico serves as both an important migration route and a wintering range for the *pacifica* subspecies of Dunlin (*Calidris alpina*; Warnock and Gill 1996). The Fraser River delta in British Columbia, Canada, supports a wintering population of approximately 30,000 Dunlin, which appears to have been stable over the last 50 yr despite industrial expansion along the waterfront of metropolitan Vancouver (Butler and Vermeer 1994, Shepherd 2001, Drever et al. 2014). A review of Christmas Bird Count data from across North America found that although neither the western nor the eastern populations of migratory Dunlin have declined over the long term, they show large and irregular fluctuations; however, the role of predation in these fluctuations is unknown (Xu et al. 2015).

An observational field study of peregrine predation on Dunlin wintering at Boundary Bay in the Fraser River Delta was begun in 1994 and continued periodically until 2015. The objective of the study was exploratory, to gain insight into the dynamic interaction of peregrines and Dunlin. Here we review a large sample of empirical data collected on peregrine abundance and hunting success rates within individual winters and seasonally from October to February (Dekker 1998, Dekker et al. 2012, Dekker and Drever 2015).

When the intertidal zone floods, Dunlin collect on the waterline along the salt marsh, but the birds often flush and shift to other points. False alarms are frequent (Beauchamp 2010). If attacked by a peregrine, roosting Dunlin fly out over the bay in an apparent antipredator strategy termed over-ocean flocking, later renamed high-tide flight (Dekker 1998, 2013). The strategy is explained by the premise that predation risk is lower for individual Dunlin that take part in the aerial maneuvers of a dense flock than the predation risk for Dunlin roosting or foraging on the ground or in shallow water. The hunting success rate of peregrines attacking Dunlin over the open tide flats or ocean was 9.1%, compared to 23.6%, in surprise attacks near the salt marsh (Dekker 2003).

The timing and altitude of high-tide flight depend on the height of the tide and wind speed. To reduce energy expenditure, the mode of flight includes moments of sailing on lateral airflows (Hentze 2012), and the duration of flight is asymmetrical around high-tide time, i.e., longer before the high-tide time than after it (Dekker 2013).

The purpose of this report is to consolidate two decades of information on the interactions of Peregrine Falcons and Dunlin wintering at Boundary Bay, British Columbia. We also augment the results with comparative data for December 2015.

METHODS

Study Area. Our study area is at Boundary Bay, a Ramsar Wetland in the Fraser River estuary of southwestern British Columbia (49°05′N, 123°00′W). The bay is 16 km across and the intertidal zone is roughly 5 km wide at the lowest ebb. The tidal flats are bordered by a strip of salt marsh of 0–150 m wide. A gravel road on a 2-m-high dike separates the coastline from low-lying agricultural fields and meadows inland. Boundary Bay serves as a major stopover and important wintering area for migratory waterbirds. Dunlin begin arriving in October and stay until April. The local wintering population is estimated at approximately 30,000 (Butler and Vermeer 1994, Shepherd 2001, Drever et al. 2014), with highest numbers observed in late November and temporary declines during periods of low temperatures when the bay freezes over (Dekker 2013). Wintering Black-bellied Plovers (*Pluvialis squatarola*) number around 1000. Mallards (*Anas platyrhynchos*), Northern Pintails (*A. acuta*), American Wigeons (*A. americana*), and Green-winged Teals (*A. crecca*) congregate in late summer and stay well into March. Bald Eagles (*Haliaeetus leucocephalus*) and other diurnal raptors, including Peregrine Falcons, occur year-round. For a detailed description of the delta and its avifauna, see Butler and Campbell (1987).

Observations. Over a 22-yr period from 1994 to 2015, we monitored the study area for 1811 hours from a vehicle parked on the Boundary Bay dike at pull-outs with an unobstructed view of the shoreline and the ocean. Our methodology was unchanged over the years and consisted of frequently scanning the coast through 8× magnification wide-angle binoculars. A useful clue for finding peregrines is alarm behavior by Dunlin, which, at the approach of a falcon, rise into the sky and form dense formations

Table 1. Hours of observation, sightings of Peregrine Falcons, sightings/hr, hunts, hunts/hr, captures of Dunlin, and percent hunting success at Boundary Bay, British Columbia, 1994–2015. Rows in bold represent summaries for each month.

MONTH/YR	HOURS	SIGHTINGS	SIGHTINGS/HR	HUNTS	HUNTS/HR	KILLS	% SUCCESS	DUCKS
Oct 1999	4	10	2.50	5	1.25	1	25.0	0
Oct 2006	40	44	1.10	26	0.65	2	7.7	5
Oct 2008	42	61	1.50	34	0.80	4	11.8	0
October	**86**	**115**	**1.34**	**65**	**0.76**	**7**	**10.8**	
Nov 1998	14	8	0.57	0	0	0	0	2
Nov 2002	179	149	0.83	215	1.20	37	17.2	0
Nov 2003	103	89	0.86	45	0.44	2	4.4	6
Nov 2009	88	74	0.84	44	0.50	4	9.1	1
November	**384**	**320**	**0.83**	**304**	**0.79**	**43**	**14.1**	
Dec 2002	65	39	0.60	81	1.25	12	14.8	0
Dec 2015	90	112	1.24	40	0.44	14	35.0	0
December	**155**	**151**	**0.97**	**123**	**0.80**	**26**	**16.3**	
Jan 1994	14	5	0.36	4	0.28	1	25.0	0
Jan 1995	91	32	0.35	25	0.27	5	20.0	0
Jan 1997	118	93	0.79	167	1.42	14	8.4	0
Jan 1998	126	47	0.37	89	0.71	6	6.7	1
Jan 2000	89	38	0.43	36	0.40	8	22.2	0
Jan 2002	144	74	0.51	53	0.37	11	20.7	0
Jan 2003	89	62	0.70	62	0.70	10	16.1	1
Jan 2006	123	114	0.93	117	0.90	17	14.5	0
Jan 2011	110	114	1.04	185	1.68	33	17.8	0
Jan 2012	120	57	0.48	57	0.48	14	24.6	0
Jan 2014	84	31	0.37	22	0.26	1	4.5	0
January	**1108**	**667**	**0.60**	**817**	**0.74**	**120**	**14.7**	
Feb 2008	**78**	**44**	**0.56**	**60**	**0.77**	**9**	**15.0**	**0**
Totals	**1811**	**1297**	**0.71**	**1369**	**0.76**	**205**	**15.0**	**16**

that swoop back and forth until the danger is past (Dekker 2003, 2013).

The time period for all observations was chosen to occur when daytime high tides for Point Atkinson, British Columbia (http://tides.mobilegeographics.com) were predicted to be >4.0 m, which results in the flooding of the intertidal zone up to or over the edge of the salt marsh. If the daytime ebb retreated <2 km, foraging flocks of Dunlin could be kept in view all day, including at low tide.

Statistical Analyses. We used the behavioral observations during each field season to calculate two measures: (1) peregrine sightings, defined as the total number of peregrines detected over the field season divided by the number of observation hours to derive an average number of sightings per hour of observation, (2) hunting success, measured as the proportion of hunts in each field season that resulted in a successful capture of Dunlin. Temporal trends and seasonal variation in peregrine sightings and hunting success were estimated using generalized linear models (GLMs) in R (R Core Team 2014). Each response variable was modeled as a function of Year from 1994 to 2015 (with the year value reset from 1994, which was assigned a value of 1), and Winter Month (assigned a value relative to January; i.e., October = –2, November = –1, December = 0, January = 1). Both measures were modeled using the numerator as a Poisson-distributed variable and the denominator as a log-transformed offset to account for variation in survey effort or peregrine hunts over time.

RESULTS

Between 1994 and 2015, 1297 peregrines were sighted in 1811 hr of observation (0.71/hr; Table 1). The sighting frequency declined seasonally from 1.34/hr in October to 0.56/hr in February ($\beta_{month} = -0.18$, SE = 0.026, t = –7.20, $P < 0.001$). Peregrine sightings increased over time from 0.36/hr in 1994 to 1.24/hr in 2015 ($\beta_{winter} = 0.026$, SE = 0.005, t = 5.19, $P < 0.001$; Fig 1).

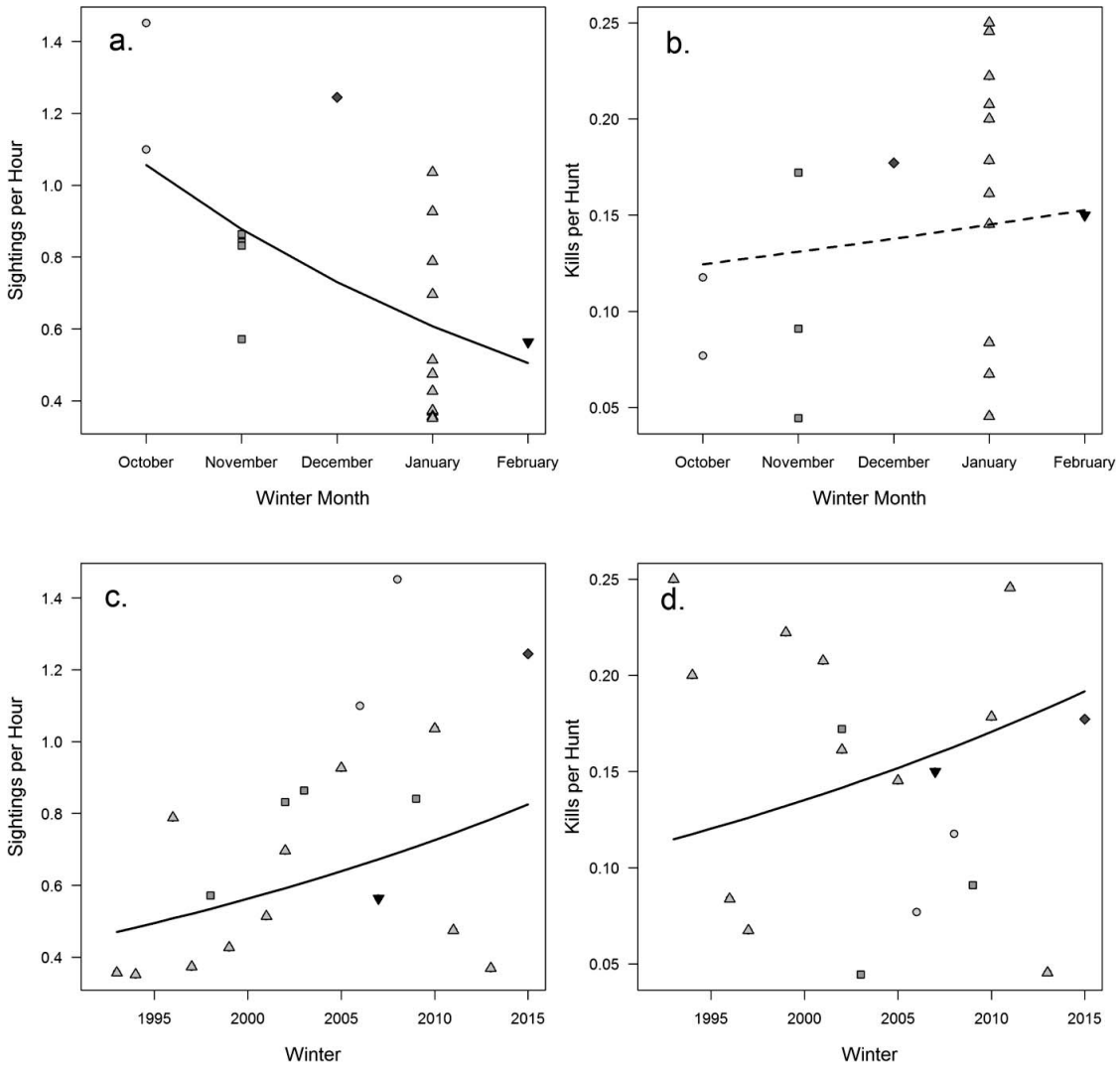

Figure 1. (a) Abundance and (b) hunting success of Peregrine Falcons (*Falco peregrinus*) in October–February at Boundary Bay, British Columbia. Lines indicate predicted values from General Linear Models representing peregrine sightings and hunting success as a function of month. (c) Abundance and (d) hunting success of Peregrine Falcons (*Falco peregrinus*), 1994 to 2015. Lines indicate predicted values from General Linear Models representing peregrine sightings and hunting success as a function of year (predicted values calculated at median values for parameters not shown in each panel). Different symbols indicate month of observations, as shown in the upper panels.

Over the duration of the study, we observed peregrines launch 1369 hunts aimed at Dunlin, with a capture rate of 15.0% (Table 1). The hunting success rate increased from 10.8% in October to 15.0% in February, although this increase was not statistically significant ($\beta_{month} = -0.051$, SE = 0.071, t = 0.71, P = 0.46; Fig.1).

The Dunlin reacted to the flooding of the intertidal zone with different strategies (Table 2). These strategies included: (1) high-tide flight over the water at various altitudes; (2) roosting in dense aggregations on the foreshore; (3) alighting on driftwood logs or floating debris well offshore; and (4) flying inland to roost or forage on muddy fields

Table 2. High-tide behavior of Dunlin, 6–19 December 2015.

DATE (TIME)	HIGH-TIDE FLIGHT	FORESHORE ROOST	INLAND FLIGHT
6 Dec (13:33 H)	yes	yes	yes
7 Dec (14:06 H)	yes	yes	yes
8 Dec (14:39 H)	yes		
9 Dec (15:11 H)	yes	yes	
10 Dec (15:45 H)	yes	yes	yes
11 Dec (15:45 H)	yes	yes	
12 Dec (07:00 H)	yes	yes	
13 Dec (07:35 H)	yes	yes	yes
14 Dec (08:14 H)	yes	yes	
15 Dec (08:53 H)	yes	yes	
16 Dec (09:34 H)	yes	yes	
17 Dec (10:15 H)	yes		
18 Dec (10:57 H)	yes	yes	
19 Dec (11:40 H)	yes	yes	

and flooded meadows. For weather-dependent variability and duration of each strategy, see Dekker (2013).

In December 2015, high-tide flight was observed everyday, but only a portion of the population took part and the length of time the birds stayed airborne varied greatly. High-tide flight of large flocks (>100 birds) was routine on days when wind speeds were 1–5 m/s). When wind speeds were >10 m/s, the flocks flew low (1–5 m) over the waves, often >1 km from shore, where they could easily escape detection by observers because the flock only occasionally rose high enough above the waves to make them visible through binoculars. Light rain or showers did not stop the flights, but heavy rain did. The longest time that some flocks remained airborne over the water was recorded on 18 December 2015 and included 183 min before the high-tide time and 132 min after, for a total time of 315 min.

DISCUSSION

Given the low chance and high amount of time involved in actually witnessing the split-second action of a falcon seizing a sandpiper in flight, the sample size of most visual studies of peregrine predation on shorebirds is very small (Buchanan et al. 1986, Cresswell 1996). The results presented herein constitute the largest number of shorebird kills observed directly in the field.

The seasonal decline in peregrine sightings from 1.34/hr in October to 0.60/hr in January was to be expected because some or all first-year immature peregrines migrate away for the winter. The fall departure of the inexperienced immature birds and the proportional increase in adult falcons would explain the observed rise in hunting success rate from 10.8% in October to 16.3% in December (Table 1). The capture rate of adult peregrines hunting Dunlin at Boundary Bay was 26.8%; the comparative rate for first-year immature birds was 9.0% (Dekker 2003).

Dekker and Drever (2015) linked a 2006–2014 decline in peregrine sightings/hr at Boundary Bay to kleptoparasitic pressure from Bald Eagles, which increased from circa 200 in 1994 to 1800 in 2014 (Elliott et al. 2006, Dekker et al. 2012). Eagles were also common in December 2015. In 11 instances, we observed one or more eagles interfering with hunting peregrines, resulting in the loss of two Dunlin prey. High eagle presence near the high-tide line may well explain why the majority (80%) of peregrine hunts observed in December 2015 took place far out over the ocean, often >1 km from shore. Due to distance and poor visibility, we could not determine the outcome of 36 of 76 (46%) peregrine attacks on Dunlin recorded in December 2015. Nevertheless, the observed capture rate of 35% in 40 hunting sequences was more than double the 15% overall rate. To help determine whether a distant hunt was successful or not successful, we watched the reaction of eagles. After failed hunts, falcons flew away and were not chased by eagles. Conversely, if a Dunlin had been captured, the successful peregrine was pursued by one or more eagles for varying distances.

Because of their limited skill at capturing Dunlin, usually involving multiple swoops at fleeing prey, immature peregrines were particularly vulnerable to pursuing kleptoparasitic Bald Eagles. By comparison, adult peregrines often caught a Dunlin at the first attack, which allowed the falcon sufficient time to get away from eagles (Dekker and Drever 2015). Frequent harassment and prey loss to eagles presumably drove immature peregrines away from the coast, resulting in a proportional increase in adult falcons, which would explain the observed rise in overall hunting success rate in December 2015 (Fig. 1).

At inland locations where eagles were less common than along the coast, wintering and migrating peregrines routinely hunted ducks such as wigeon and pintails (Dekker 1987, 1995). The rarity of duck kills reported after 2000 at Boundary Bay further

supports the contention, first posed in 2003, that prey losses to Bald Eagles forced peregrines to stop hunting ducks because they were too heavy to be carried away at the approach of eagles. Thus, kleptoparasitic pressure from Bald Eagles tended to force peregrines to concentrate on lightweight prey such as Dunlin at Boundary Bay.

Peregrine sightings in December 2015 were relatively high at 1.24/hr, which may have been associated with weather conditions. The ambient temperature during December 2015 did not drop below 0° C. By contrast, in winters when the bay became temporarily covered with ice, Dunlin left the area, followed by the departure of some or perhaps most of the peregrines (Out 2010, Dekker 2013).

A noteworthy behavior of the local Dunlin was their different reaction to high tide. While a portion of the population engaged in prolonged high-tide flight, other flocks roosted on the foreshore of the salt marsh or departed for inland fields (Table 2). This variation in high-tide behavior might be related to dissimilar age or physical condition, such as body mass or fat reserves, of the birds in question. Another possible differentiating factor might be the birds' geographic origin. Dunlin wintering at Boundary Bay most likely originated from populations that breed at different latitudes and each group may have its own method of coping with intertidal flooding. Such questions were outside the scope of this study and might be a subject for future research.

The results of this long-term study suggest that the interactive dynamics of Peregrine Falcons and Dunlin wintering at Boundary Bay did not change in a significant way over 22 yr. Peregrine attacks on sandpipers, whether lethal or not, constitute a powerful and sustained disturbance to the foraging needs of sandpipers, perhaps forcing them to shorten their stay on migration stopovers and jeopardizing their chances of accumulating enough fat to complete their migrations (Lank et al. 2003). The information presented herein suggests that Dunlin in winter expend much time and energy in predator avoidance. Yet, despite this energetic cost and the reported increase in the number of peregrines at Boundary Bay, the local Dunlin population does not appear to have declined in size over a 22-yr period, suggesting that the anti-predator strategies adopted by these Dunlin may allow population maintenance despite increasing predator numbers.

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