Kleptoparasitism by Bald Eagles (*Haliaeetus leucocephalus*) as a Factor in Reducing Peregrine Falcon (*Falco peregrinus*) Predation on Dunlin (*Calidris alpina*) Wintering in British Columbia

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Kleptoparasitism, or food piracy, is common in a wide range of taxa, particularly among predators, with the larger species forcing smaller species to surrender their catch. The Bald Eagle (*Haliaeetus leucocephalus*) is known to rob Peregrine Falcons (*Falco peregrinus*) of just-caught prey. We present time series of kleptoparasitic interactions between eagles and peregrines hunting Dunlin (*Calidris alpina*) that were wintering at Boundary Bay in the Fraser River valley, British Columbia. In 1108 hours of observation during January, intermittently between 1994 and 2014, we recorded 667 sightings of Peregrine Falcons, including 817 attacks on Dunlin resulting in 120 captures. The population of wintering Bald Eagles in the study area increased from about 200 in 1994 to 1800 in 2014, while the rate of kleptoparasitism at the expense of peregrines increased from 0.05 to 0.20. The increase in the number of Bald Eagles coincided with a decline in January sightings of Peregrine Falcons, which suggests that some falcons may have left the study area because of interference from eagles. The decrease in Peregrine Falcon numbers can be expected to have led to reduced predation risk for Dunlins. Christmas Bird Counts conducted in the Fraser River Valley have underscored the fluctuation in eagle and peregrine numbers reported here.

Key Words: Bald Eagle; *Haliaeetus leucocephalus*; kleptoparasitism; Peregrine Falcon; *Falco peregrinus*; predation; Dunlin; *Calidris alpina*; British Columbia

Introduction

Kleptoparasitism by animals pertains to the opportunistic or habitual stealing of food from other animals. The kleptoparasite benefits by eating food that it could not have obtained itself or by saving energy by not having to search for or capture that food (Shealer *et al.* 2005). Kleptoparasitism is particularly common in waterbirds, including gulls, skuas, jaegers, and frigatebirds (Furness 1987; Calixto-Albarran and Osorno 2000), and it has been documented for numerous Falconiformes (Brockmann and Barnard 1979; Paulson 1985). Among raptors, intraguild kleptoparasitism benefits larger species over smaller species or smaller conspecifics. For instance, in Alberta and British Columbia, Peregrine Falcons (*Falco peregrinus*) were forced to surrender their prey to pursuing *Buteo* hawks, and Merlins (*Falco columbarius*) were kleptoparasitized by peregrines (Dekker 1980, 2009). Similarly, female peregrines commonly rob male peregrines, which are comparatively smaller than females (Cade 1982; White *et al.* 2002).

The inter- and intraspecific kleptoparasitic habits of the Bald Eagle (*Haliaeetus leucocephalus*) are well known (Palmer 1988; Buchler 2000). Jorde and Lingle (1998) reported that stealing fish and waterfowl from other raptors was a major food-gathering method of eagles wintering in Nebraska. On the Pacific coast of British Columbia, Bald Eagles commonly kleptoparasitized gulls and crows, as well as conspecifics, and they routinely robbed peregrines of captured seabirds (Dekker and Bogaert 1997; Dekker 1999). On Vancouver Island, eagles pirated 13 (28%) of 46 ducks captured by wintering peregrines, and, in central Alberta, Bald Eagles took four (25%) of 16 ducks from wintering Gyrfalcons (*Falco rusticolus*) (Dekker 1995; Dekker and Court 2003). On Vancouver Island and in the Fraser River Valley, peregrines lost just-caught ducks and Dunlin (*Calidris alpina*) to Gyrfalcons and Bald Eagles (Dekker *et al.* 2012).

After a numeric low in the mid-1900s, Bald Eagle populations have recovered in much of North America (Buchler 2000; Watts *et al.* 2007; Elliott *et al.* 2011; Hipfner *et al.* 2012; Elderkin 2014). Bald Eagles are year-round residents at Boundary Bay near Vancouver, British Columbia, and, in the lower Fraser River Valley, nesting territories increased from two in the 1960s to 108 in 2008 (Hancock 2003; Goulet 2009). At Boundary Bay, resident eagles are joined by migrants that begin arriving in October and reach peak numbers in January (Dekker *et al.* 2012). The wintering population has grown since 1994. In an eight-year census at the Vancouver Regional Landfill, eagles peaked at 453 in 2001 (Elliott *et al.* 2006). In an ongoing census at the same landfill, 1812 eagles were counted on 1 January 2014 (D. Hancock, personal communication).

The growing number of Bald Eagles on the coast of British Columbia and their increasing kleptoparasitic pressure on Peregrine Falcons was investigated by Dek-

ker (1999, 2003), who reported that wintering falcons had stopped hunting ducks and, instead, concentrated on smaller prey such as Dunlin (*Calidris alpina*), which could be carried away out of reach of pursuing eagles. In 2006–2011, as eagle numbers continued to grow, the falcons increased their kill rate of Dunlin by 72% to compensate for prey losses. Given a further increase in kleptoparasitic pressure from eagles, Dekker *et al.* (2012) predicted a decline in peregrine numbers on the intertidal coast. This paper presents time series of peregrine counts and behavioural observations of hunts by peregrines on Dunlin wintering in Boundary Bay between 1994 and 2014. Empirical data (peregrine sightings per hour and hunting success) are combined with Christmas Bird Count (CBC) numbers to evaluate temporal trends in abundance of Dunlin and raptors and test the hypothesis that kleptoparasitism by Bald Eagles on Peregrine Falcons has reached a "tipping point," leading some peregrines to depart coastal hunting grounds in the Fraser River Delta.

Study Area

The study area is at Boundary Bay 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 tide flats are bordered by a strip of salt marsh up to 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 is a major stopover for migratory waterbirds. Dunlin begin arriving in October and stay until April. Estimated at about 40 000 birds, the Dunlin population can be substantially higher in late November or temporarily absent during periods of low temperatures when the bay freezes over (Ydenberg *et al.* 2010; Dekker 2013; Drever *et al.* 2014). The only other shorebird to winter in appreciable numbers (about 1000) is the Black-bellied Plover (*Pluvialis squatarola*). Mallards (*Anas platyrhynchos*), Northern Pintails (*A. acuta*), American Wigeon (*A. americana*), and Green-winged Teal (*A. crecca*) congregate in late summer and stay well into March. Bald Eagles and other diurnal raptors, including Peregrine Falcons, occur year-round. For a more detailed description of the delta and its avifauna, see Butler and Campbell (1987).

Methods

Behavioural observations

Although visits to the study area took place in all months of the year, only January visits were considered for the analysis of changes in peregrine sightings and kleptoparasitic events because the number of locally wintering eagles was at its peak in January (Dekker *et al.* 2012). During January of 11 winters between 1994 and 2014, DD spent 1108 hours in the study area. Observations were conducted from a vehicle parked on the dike at locations with an unobstructed view of the tide flats or during short walks on the dike to remain in view of the largest Dunlin concentrations. Methods for recording peregrine attacks on waterbirds and kleptoparasitic interactions by eagles have been described in previous studies (Dekker 2003, 2013).

Christmas Bird Counts

Observations were augmented with annual counts of wintering Bald Eagles, Peregrine Falcons, and Dunlin obtained from the CBC. The CBC is a survey administered by the National Audubon Society and conducted annually by volunteer birdwatchers on a single day from December 14 to January 5. Counts are restricted to a "count circle" with a diameter of 24 km in which more than 10 volunteers follow assigned routes counting every bird they see. Data were obtained from the count circle at Ladner, Delta, British Columbia (BCLA), 1994 to 2013 (Audubon 2013*). The BCLA includes Boundary Bay and the Vancouver Regional Landfill site. One year, 1996, was excluded from our analyses because of low participation in the CBC and continuing heavy snowfall on count day.

Statistical methods

Three measures of peregrine abundance and hunting success were derived from behavioural observations: (i) peregrine sightings, calculated 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, (ii) kleptoparasitism rate, defined as the proportion of observations in each field season during which eagles chased peregrines carrying prey, and (iii) hunting success, measured as the proportion of hunts by Peregrine Falcons in each field season that resulted in successful capture of prey.

Temporal trends in peregrine sightings, kleptoparasitism, and hunt success were estimated using generalized linear models (GLMs) in R 3.2.0 (R Foundation for Statistical Computing, Vienna, Austria). Each response variable was modeled as a function of relation to year from 1994 to 2014, with the year value reset, such that 1994 had a value of 1. Peregrine sightings were modeled as a Poisson-distributed variable suitable for count data, and the model included log-transformed number of observation hours as an offset to account for variable effort over time. Kleptoparasitism and hunt success were modeled as probabilities using a binomial distribution. To allow for non-linear trends over time, trend models included both a linear and a quadratic term for year. If the quadratic term was not significant, it was removed and inference was drawn from the simpler linear model.

Temporal trends in CBCs were estimated using generalized additive models (GAMs) by modeling response variables in relation to year, from 1994 to 2014, using package mgcv in R. The GAM approach is an extension of the GLM in which predictors are smoothed functions rather than linear relationships (Wood 2006), and it allows the fitting of non-linear trends over time. For eagles, the total number of birds was used as it provided a better representation of eagle abundance,

and eagle detection is not heavily influenced by the number of observers (Elliott *et al.* 2011). For peregrines and Dunlin, the number of birds was divided by the total party-hours to account for variable survey effort, and this variable was used as the response variable in trend models that fit a smooth curve as a function of year. For peregrines and eagles, the response variables were log-transformed to normalize residuals.

Results

At Boundary Bay, peregrine sightings during January increased over time and then decreased sharply in the last two years (2012, 2014) of observation (Table 1, Figure 1); the trend model included a significant quadratic term (Table 2). Beginning with 0.36/h in 1994, peregrine sightings increased over time, nearly tripling to reach peak values of 0.93/h and 1.04/h in 2006 and 2011, then declining to 0.37/h in 2014.

During 1108 hours of observation in January 1994–2014, eagles attempted to interfere with hunting peregrines 101 times. On 48 occasions, prey-carrying falcons managed to stay ahead of pursuing eagles, but in 17 cases eagles succeeded in securing a Dunlin dropped or struck down by peregrines. In 36 instances, one or more eagles (range 1–12 eagles) left their perches to approach falcons attacking Dunlin some distance away. If the falcon was unsuccessful in catching prey or aborted its hunt, the eagles turned back. In 10 of these instances, the peregrine swooped aggressively at the eagles. Over the years, the frequency of kleptoparasitic events increased and subsequently declined again, roughly in parallel with the fluctuation in peregrine sightings (Figure 1).

Peregrines were observed hunting Dunlin 817 times, resulting in 120 captures, representing an overall hunt success rate 14.7.0%. Hunt success varied over time, and the trend model showed a significant increase in mean hunt success from 1994 to 2014 (Table 2, Figure 1), although hunt success of 4.5% in 2014 was the lowest recorded

Christmas Bird Counts

The number of eagles counted in the Ladner CBC circle ranged from 200 to 210 between 1994 and 2004,

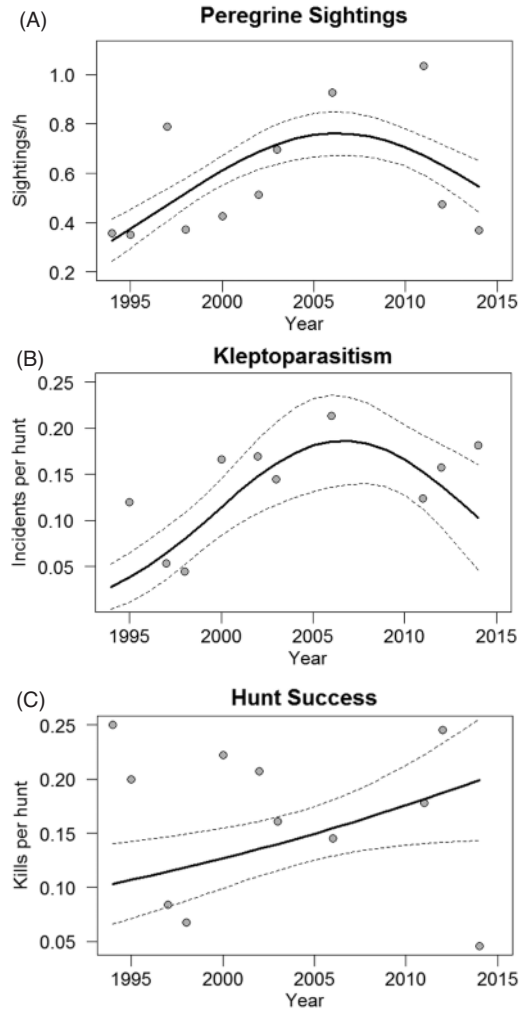

FIGURE 1. Temporal trends in Peregrine Falcon (*Falco peregrinus*) (A) sightings, (B) kleptoparasitism rate, and (C) hunt success observed during Januarys at Boundary Bay, Delta, British Columbia, 1994 to 2014. Solid line shows estimated trend; dashed lines indicate 95% confidence interval.

TABLE 1. Observations of Peregrine Falcons (*Falco peregrinus*) hunting Dunlins (*Calidris alpina*) during January of 11 years between 1994 and 2014 at Boundary Bay, British Columbia.

Month	Hours of observation	Sightings	Sightings/h	Hunts	Hunts/h	Kills	% success
Jan. 1994	14	5	0.36	4	0.29	1	25.0
Jan. 1995	91	32	0.35	25	0.27	5	20.0
Jan. 1997	118	93	0.79	167	1.42	14	8.4
Jan. 1998	126	47	0.37	89	0.71	6	6.7
Jan. 2000	89	38	0.43	36	0.40	8	22.2
Jan. 2002	144	74	0.51	53	0.37	11	20.8
Jan. 2003	89	62	0.70	62	0.70	10	16.1
Jan. 2006	123	114	0.93	117	0.95	17	14.5
Jan. 2011	110	114	1.04	185	1.68	33	17.8
Jan. 2012	120	57	0.48	57	0.48	14	24.6
Jan. 2014	84	31	0.37	22	0.26	1	4.5
Total	1108	667	0.60	817	0.74	120	14.7

TABLE 2. Estimates for trend models of behavioural observations of hunting Peregrine Falcons (*Falco peregrinus*) at Boundary Bay, Delta, British Columbia, 1994–2014, with 1994 set to a value of 1.

Parameter	Estimate	SE	*Z*-value	*P*
Peregrine sightings				
Intercept	−1.114	0.133	−8.40	< 0.001
Yr	0.137	0.029	4.74	< 0.001
Yr^2	−0.006	0.001	−4.29	< 0.001
Kleptoparasitism				
Intercept	−3.537	0.456	−7.75	< 0.001
Yr	0.326	0.098	3.32	< 0.001
Yr^2	−0.013	0.004	−2.88	< 0.001
Hunt success				
Intercept	−2.160	0.204	−10.57	< 0.001
Yr	0.039	0.016	2.35	0.02

Note: SE = standard error.

and then increased from 2005 to 2013 to more than 1000 (Figure 2). The GAM model indicated that this pattern was statistically significant (estimated df = 3.1, residual df = 3.9, $F = 16.3$, $P < 0.001$).

The Ladner CBC data indicate that peregrines were also relatively scarce at the beginning of the time series, with 0.02–0.05 birds per party-hour observed between 1994 and 2000. Peregrine counts then increased from 2001 onward, reaching the highest value of 0.11/party-hour in 2011 (Figure 2), but then declining to 0.05/party-hour in 2014. This pattern was statistically significant (GAM model: estimated df = 5.2, residual df = 6.2, $F = 11.3$, $P < 0.001$). The high recorded in 2011 coincided with the year in which we observed the greatest number of falcons per hour at Boundary Bay (Table 1).

Dunlin counts from the Ladner CBC also increased over time, ranging from 23 to 148/party-hour from 1994 to 1999, and then increasing and leveling off at 118–290/party-hour from 2010 to 2014. The GAM model indicated that this pattern was statistically significant (estimated df = 1.9, residual df = 2.4, $F = 3.7$, $P = 0.04$).

Discussion

Although Bald Eagle counts over the Strait of Georgia are reported to have shown no region-wide trend over the past decade from 1999 to 2011 (Crewe *et al.* 2012), the steep increase in the number of eagles in the Boundary Bay study area is remarkable. The causative explanation is related to three factors: (1) Boundary Bay offers a rich food base for eagles that hunt waterfowl and habitually kleptoparasitize gulls (Dekker 1999); (2) the regional landfill 3 km inland attracts masses of scavenging eagles (Elliott *et al.* 2006) that disperse to Boundary Bay at low tide; and (3) declining spawning runs of Chum Salmon (*Oncorhynchus keta*) in southwestern British Columbia force eagles to abandon inland rivers and switch to coastal foraging locations (Elliott *et al.* 2011).

Crewe *et al.* (2012) reported no region-wide trend in Peregrine Falcon sightings, whereas our behavioural observations at Boundary Bay and the Ladner CBC

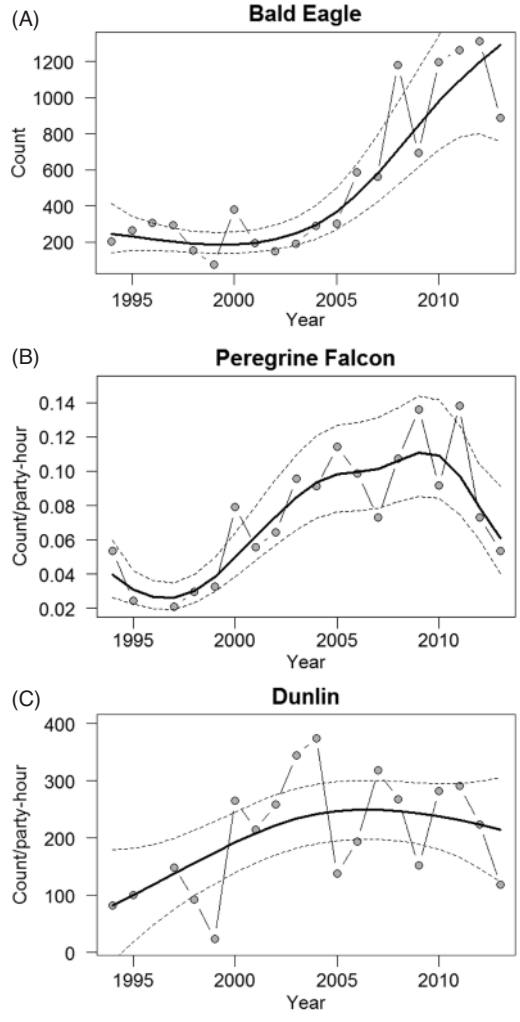

FIGURE 2. Temporal trends in numbers of (A) Bald Eagles (*Haliaeetus leucocephalus*), (B) Peregrine Falcons (*Falco peregrinus*), and (C) Dunlins (*Calidris alpina*) in the Ladner circle of the Audubon Christmas Bird Count, British Columbia, conducted in December from 1994 to 2013. Solid line shows estimated trend; dashed lines indicate 95% confidence interval.

data indicate that the local peregrine population increased over time, and subsequently declined at Boundary Bay in 2012–2014. Dunlin numbers increased during 1994–2014, as did hunt success of peregrines, indicating that prey sources remained available over this period (Drever *et al.* 2014). Bald Eagles also increased during this period and became persistent kleptoparasites of hunting peregrines, taking 10–20% of captured Dunlin. These results support the prediction made by Dekker *et al.* (2013) that continued interference by eagles would result in the abandonment of the shoreline study area by some peregrines.

Although this study focused on kleptoparasitism, eagles may affect hunting peregrines in other ways. Over the course of this study, a routine method for surveying falcons was to drive the dike road and check driftwood logs. In 2014, one or more eagles — as many as 17 in one case — took up all prominent driftwood logs at high tide, leaving no room for falcons. This apparent competition for shoreline perches may in itself have been a reason why some falcons left the coast.

The success rate of falcons hunting Dunlin shows a slight increase over time from 14.4% in 1994–2003 to 16.9 % in 2006–2014 (Table 1; Figure 1). We hypothesize that the increase in success rate is linked to the growing pressure from kleptoparasites, because, after eagles began to dominate the coast, the only falcons that managed to cope were the better hunters, which were able to catch a Dunlin quickly, allowing enough time to escape before the arrival of kleptoparasites. Therefore, the increasing proportion of experienced hunters would have resulted in higher hunt success over time.

Hunting success rates differ between immature and adult peregrines (Dekker 1980, 2009). At Boundary Bay, immature peregrines made a catch in 9% of 399 Dunlin hunts, significantly less than the 27% success of adult peregrines in 164 hunts (Dekker 2003). After their initial attack fails, first-year falcons commonly persist with long pursuits and multiple swoops at their intended prey (Dekker 1988, 1999). In contrast, adults sometimes take a Dunlin by surprise at the first pass. By virtue of their expertise as hunters, adult peregrines often have time to carry their prey away before potential kleptoparasites approach. Conversely, because of the extended time a young falcon may need to secure its prey, interference from eagles can become a serious hindrance. Harassed by kleptoparasites, immature falcons probably depart the coast for inland regions where eagle numbers may be lower.

The findings of this study support the hypothesis that the increase in the population of kleptoparasitic Bald Eagles has resulted in a local decline in Peregrine Falcon numbers at Boundary Bay between 2005 and 2014. The decline was most pronounced, in both our counts and the CBCs, during a limited number of years from 2012 to 2014, and it remains to be seen whether these low peregrine counts represent the "new normal" given the continuing high abundance of Bald Eagles. Peregrines are important predators of shorebirds (Ydenberg *et al.* 2010), and, therefore, a continuing lower abundance of peregrines should result in a reduction of predation risk to wintering Dunlin, indicative of the cascading effect that can occur when top predators return to an ecosystem.

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