ABOOKIRE. 1999. Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska. Fishery Bulletin 97:962–977.
SAS INSTITUTE. 2000. SAS/STAT user's guide, version 8.1. SAS Institute Inc., Cary, NC.
SEALY, S. G. 1973. Adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. Ornis Scandinavica 4:113–121.
SONAR DATA PROPRIETARY LTD. 2000. Echoview v. 2.1. Hobart, Tasmania.
TREMBLAY, Y., AND Y. CHEREL. 2000. Benthic and pelagic dives: a new foraging behaviour in Rockhopper Penguins. Marine Ecology Progress Series 204:257–267.
VALIELA, I. 1995. Marine ecological processes. Springer, New York.
ZAR, J. H. 1999. Biostatistical analysis. Simon and Schuster, Upper Saddle River, NJ.

The Condor 106:415–419

RAPTOR PREDATION ON WINTERING DUNLINS IN RELATION TO THE TIDAL CYCLE

DICK DEKKER[1,3] AND RON YDENBERG[2]
[1]*3819-112 A Street, Edmonton, AB T6J 1K4, Canada*
[2]*Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada*

Abstract. At Boundary Bay, British Columbia, Canada, Peregrine Falcons (*Falco peregrinus*) captured 94 Dunlins (*Calidris alpina*) in 652 hunts. The two main hunting methods were open attacks on flying Dunlins (62%) and stealth attacks on roosting or foraging Dunlins (35%). Peregrines hunted throughout the day, yet the kill rate per observation hour dropped 1–2 hr before high tide and peaked 1–2 hr after high tide. The drop in kill rate coincided with the departure of the mass of Dunlins for over-ocean flights lasting 2–4 hr. The peak in kill rate occurred just after the tide began to ebb and the Dunlins returned to forage in the shore zone. The hypothesis that closeness to shoreline vegetation is dangerous for Dunlins is supported by three converging lines of evidence: (1) the high success rate (44%) of peregrine hunts over the shore zone compared to the rate (11%) over tide flats and ocean; (2) the high kill rate per observation hour at high tide; and (3) the positive correlation of kill rate with the height of the tides. Seven of 13 Dunlins killed by Merlins (*Falco columbarius*) and all five Dunlins killed by Northern Harriers (*Circus cyaneus*) were also captured in the shore zone.

Key words: Calidris alpina, *Dunlin,* Falco peregrinus, *Peregrine Falcon, raptor predation, tidal cycle.*

Depredación de *Calidris alpina* por Rapaces durante el Período Invernal con Relación al Ciclo de la Marea

Resumen. En la Bahía Boundary, Columbia Británica, Canadá, halcones *Falco peregrinus* capturaron 94 ejemplares de *Calidris alpina* en 652 horas. Los dos métodos principales de caza fueron ataques abiertos sobre individuos que estaban volando (62%) y ataques encubiertos sobre individuos que estaban posados o forrajeando (35%). *F. peregrinus* cazó a lo largo del día, pero la tasa de matanza por hora de observación disminuyó 1–2 hr antes de la pleamar y alcanzó un máximo 1–2 hr después de la pleamar. La caída en la tasa de matanza coincidió con la partida en masa de *C. alpina* para realizar vuelos sobre el océano que duraron 2–4 hr. El pico en la tasa de matanza ocurrió justo después de que la marea comenzó a menguar y de que los individuos de *C. alpina* regresaron a forrajear a la zona de playa. La hipótesis de que la cercanía de la vegetación a la línea de playa es peligrosa para *C. alpina* es apoyada por tres líneas convergentes de evidencia: (1) la alta tasa de éxito (44%) de las cacerías de *F. peregrinus* sobre la zona de playa comparada con la tasa (11%) de las cacerías sobre los planos de la marea y el océano; (2) la alta tasa de matanza por hora de observación durante la pleamar; y (3) la correlación positiva de la tasa de matanza con la altura de las mareas. Siete de 13 individuos de *C. alpina* cazados por *F. columbarius* y todos 5 individuos de *C. alpina* cazados por *Circus cyaneus* también fueron atrapados en la zona de playa.

Predation risk has been implicated by many researchers as an important determinant in the feeding behavior of a wide variety of prey species (Lima et al. 1985, Milinski 1986). According to theory, avian prey species balance predation risk with foraging needs. For instance, in a trade-off between relative safety from predators and optimal caloric gain, forest passerines tend to forage close to the protective cover of trees and bushes, whereas open-country birds stay well

Manuscript received 29 May 2003; accepted 12 November 2003.
[3] E-mail: tj_dick_dekker@hotmail.com

away from vegetation that could conceal raptors (Valone and Lima 1987, Lima 1988). In estuarine habitats, shorebirds frequent open expanses of mudflats which allow for the timely discovery of approaching raptors. Raptors that hunt shorebirds, such as the Peregrine Falcon (*Falco peregrinus*) and the Merlin (*Falco columbarius*), commonly use stealth methods to take their prey by surprise (Page and Whitacre 1975, Dekker 1980, 1988, Palmer 1988, Cresswell 1996, White et al. 2002). If rising tides inundate the mudflats and force the shorebirds close to the vegetated high-tide line, most leave and fly to roosting sites in adjacent country. In some locations, shorebirds roost in habitats they do not normally frequent, such as agricultural lands (Butler 1994) or wave-swept beaches (Buchanan 1996). On the northwest Pacific coast of North America, and probably elsewhere in its extensive wintering range, Dunlin flocks fly out over the ocean and remain in flight for 2–4 hr until the tide turns. This behavior was interpreted as a possible antipredator strategy by Brennan et al. (1985) and first documented as such by Dekker (1998). Hotker (2000) saw the same phenomenon on the north coast of Germany and termed it "airborne roosting." Staying in flight over the water far offshore makes sense if roosting sites close to the high-tide mark are dangerous. Ydenberg et al. (2002) found that the choice of stopover sites by migrating Western Sandpipers (*Calidris mauri*) in British Columbia, Canada, could best be explained by a hypothesis that sandpipers are more vulnerable to raptor predation on small feeding sites than on wide expanses of open mudflats.

In this article, we examine a large data set of observed hunts and kills by Peregrine Falcons to test the hypothesis that proximity to shoreline vegetation is dangerous for Dunlins, and that Dunlins tend to avoid risk when they are satiated, but are more willing to take risk when hungry. As additional evidence for that hypothesis, we also report on Dunlin kills by Merlins (*Falco columbarius*) and Northern Harriers (*Circus cyaneus*).

METHODS

The study area was at Boundary Bay, on the southern edge of the Fraser River estuary (49°05′N, 123°00′W) in British Columbia, Canada. The bay is 16 km across and the intertidal zone is roughly 4 km wide at the lowest ebb. The tidal rhythm includes two flood tides, one usually higher than the other, per 24-hr period. During winter the highest tides almost always occur during daylight hours and inundate all intertidal mudflats and most of the narrow strip of saltmarsh, which is covered with low vegetation. A dyke protects low-lying agricultural fields inland. Boundary Bay is a major stopover for migratory waterbirds and a wintering location for circa 50 000 Dunlins and 1000 Black-bellied Plovers (*Pluvialis squatarola*). Birds of prey are common (Butler and Campbell 1987). In winter, the bay is hunted over by at least six peregrines and one or more Merlins (Dekker 2003).

Between early November and early February, 1994–2003, DD spent part or all of 151 days (940 hr) in the study area, walking the dyke or sitting in a parked vehicle. Flocks of Dunlins were monitored for alarm behavior such as sudden flushing. Hunting raptors were also discovered by frequently scanning the area through 8× wide-angle binoculars. Perched peregrines and Merlins were often kept under surveillance for periods of up to 2 hr in the hope of seeing them hunt. We use the term "hunt" to mean a completed attack of which the outcome was known. A hunt could include one or more passes or swoops at the same Dunlin. An attack on a flock and subsequent pursuit of a single Dunlin fleeing that flock were counted as one hunt. However, if the falcon abandoned the pursuit and again attacked the same or a different flock, it was tallied as another hunt. This definition of a hunt was also used by Dekker (1980, 1988, 2003) and is the equivalent of the term "attack" as formulated by Cresswell (1996). In this paper, both terms are used interchangeably.

Field data were recorded in diary form and entered into an annotated table of hunts and kills, divided over three zones. Zone 1 represented the saltmarsh shore including a 5–10 m strip of wrack and sparsely vegetated mud beyond the ragged marsh edge. To investigate whether peregrine hunting success was influenced by distance from shore, we arbitrarily split the intertidal zone in two: zone 2 extended roughly 0.5 km from the saltmarsh; zone 3 lay beyond zone 2. Depending on the tide height, zones 2 and 3 could consist of mudflats and ocean. Although a hunt or pursuit might cross over from one zone into the next, the position of the prey at the start of the attack defined the zone in which the hunt was considered to have taken place. In a few borderline cases, the choice amounted to a judgment call or best guess. Details on Peregrine Falcon characteristics and hunting methods, and Dunlin behavior when avoiding raptors were given in Dekker (2003).

We recorded the zone (1, 2, or 3) in which each hunt took place and the time until or since the nearest high tide. From this summary, we derived the kill rate per observation hour in relation to the time of day (intervals of 1 hr) and the time of the nearest high tide, based on the tide tables published for Point Atkinson, British Columbia. In a separate data analysis, RY compared the kill rate to the height of the tide (grouped into 40-cm intervals) at the time of the kill, using the algorithm available at XTide (Flater 1998). The result was tested for significance by standard regression procedures. The peregrine hunting success rate over the shore zone (zone 1) was compared statistically to zones 2 and 3 by a G-test of independence (Sokal and Rohlf 1981).

No attempt was made to record the number of Dunlins present in the attack zone when hunts and kills took place. Large numbers of Dunlins do not necessarily translate into a high kill rate. On the contrary, singletons or small, isolated flocks of prey were reported to be more vulnerable to stealth attacks by peregrines than large or multiple flocks spaced out over a wide area (Dekker 1980, 1998, Thiollay 1982).

RESULTS

A total of 652 peregrine hunts directed at Dunlins was observed. Of these, 94 ended in kills. Hunts and kills took place throughout daylight hours at average rates

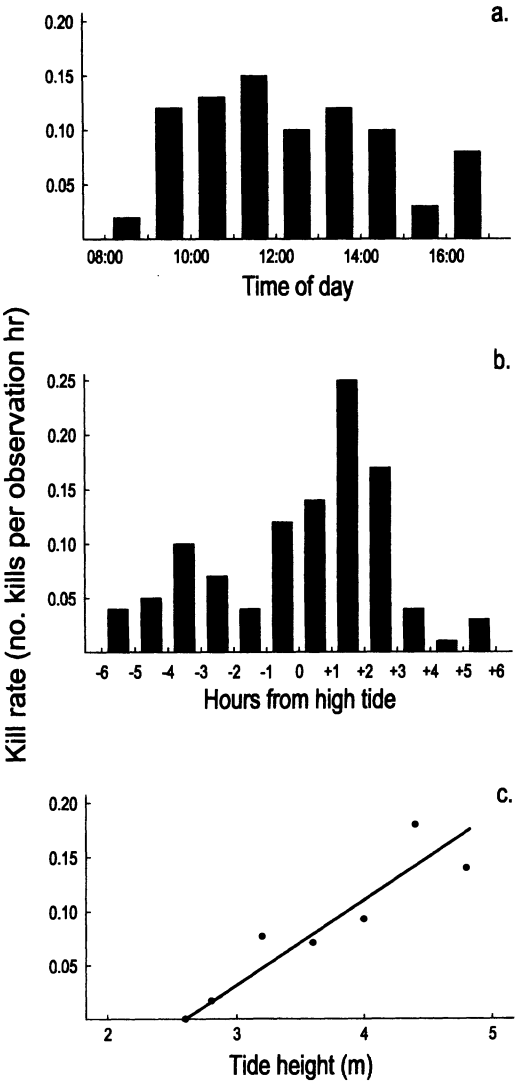

FIGURE 1. Temporal and tidal patterns of Peregrine Falcon predation on Dunlins wintering at Boundary Bay, British Columbia, Canada. (a) Kill rate (no. captures per observation hr) in relation to the time of day. Number of kills and observation time (hr) in the successive intervals were 1/49, 11/95, 15/117, 19/128, 13/136, 15/126, 13/127, 3/110, 4/52. (b) Kill rate relative to the crest of the nearest high tide. Number of kills and observation time (hr) in the successive intervals were 2/49, 3/55, 6/62, 5/75, 4/87, 12/100, 13/106, 25/104, 18/90, 3/79, 1/69, 2/58. (c) Correlation between kill rate and height of the tide. The regression equation is *kill rate* = 0.068 × *tide height* (m) − 0.16 (r^2 = 0.86, $F^{1,5}$ = 29.8, $P < 0.001$). Number of kills and observation time (hr) for the successive points were 0/25, 1/58, 8/104, 16/224, 26/279, 36/199, 7/50.

TABLE 1. Success rates of Peregrine Falcons hunting Dunlins at Boundary Bay, British Columbia, Canada. Zone 1 represents the ocean shore–saltmarsh edge; zone 2 extends 0.5 km beyond zone 1; zone 3 begins 0.5 km from the saltmarsh. Depending on tide height, zones 2 and 3 could consist of mudflats and ocean.

Zone	No. hunts	No. kills	Success rate (%)
Zone 1	75	33	44
Zone 2	299	33	11
Zone 3	278	28	10
Total	652	94	14

of 0.69 hunts per hr and 0.10 kills per hr. The kill rate per observation hour was quite consistent throughout the day except for declines in early morning (08:00–09:00) and late afternoon (15:00–16:00; Fig. 1a).

The kill rate showed a strong association with the tidal cycle, rising with the flooding tide and falling with the ebbing tide (Fig. 1b). The kill rate peaked 1–2 hr after high tide. The only anomaly in this pattern was a marked low in kill rate beginning 2 hr before high tide. The rate during this 1-hr interval was nearly one-half of the previous interval and one-third of the next. The kill rates also showed a strong and significant linear relation with the height of the tide, rising steadily to 0.14–0.18 kills per hr at tide heights over 4.2 m (Fig. 1c).

The success rate of hunts differed substantially between zones and apparently as a function of the type of attack. In zone 1 all attacks were aimed at Dunlins roosting or feeding near the saltmarsh, and peregrines always attacked using stealth, approaching very low (<1 m) over the shoreline vegetation or rushing up over the dyke. Surprise could be near complete, resulting in the capture of a Dunlin the moment the flock flushed in alarm. In zone 1, peregrines had a success rate of 44% (33 kills in 75 hunts; Table 1). If a stealth hunt in this zone was not immediately successful, peregrines rarely gave chase.

The success rate of all hunts in zone 2 was nearly the same as in zone 3 (11% vs. 10%). Combined, the success rate of stealth hunts in these two zones was 14% (21 kills in 154 hunts), significantly lower than in zone 1 (G = 14.2, $P < 0.001$). Most (70%) hunts in zones 2 and 3 did not use stealth, but were open attacks on Dunlins in flight or of birds that had flushed well ahead of the falcon. These open attacks on flying Dunlins had a success rate of 9% (37 kills in 406 hunts). The success rate of all peregrine attacks over zones 2 and 3 (11%) was significantly lower than all hunts over zone 1 (44%; G = 29.4, $P < 0.001$).

Other raptors also attacked Dunlins. Harriers frequently attempted to approach roosting Dunlins by stealth. Of an estimated 300 harrier attacks only five were successful and all of these took place in zone 1. Probably reflecting the low risk posed by harriers, Dunlins showed minimal avoidance response. If flushed by harriers, the Dunlins returned to the same place as soon as the raptor had passed by. Merlins were

far less common than harriers, but more adept hunters of Dunlins; 7 of 23 stealth attacks on flocks roosting in zone 1 were successful (30%). Merlins also hunted over zones 2 and 3, using stealth as the initial strategy in 28 attacks on flocks. After the stealth approach failed, six captures were made by persistent pursuit of single Dunlins that had left the flock (21%).

Attacks by Merlins and peregrines always caused Dunlin flocks to move to another location or to begin their over-ocean flights, which generally started 1–2 hr before the rising tide inundated all mudflat habitat.

DISCUSSION

The hypothesis that raptor predation risk for small shorebirds increases with closeness to vegetation is supported in this study by three converging lines of evidence: (1) the high success rate of peregrines hunting over the saltmarsh zone; (2) the relatively high kill rate per observation hour when Dunlins are in the saltmarsh zone; and (3) the positive correlation of kill rate with the height of the rising tide. The results of this study also lend additional support for the hypothesis that the over-ocean flocking of Dunlins during high winter tides is an antipredator strategy (Dekker 1998, Hotker 2000). Flying far from shore, at varying altitudes depending on weather conditions, the Dunlins are safe from the most dangerous type of raptor attack: a stealth approach concealed behind vegetation.

The overall percentage of stealth hunts by peregrines in this study (35%) is nearly equivalent to the 36% reported in 233 shorebird hunts on the coast of Scotland (Cresswell 1996). By contrast, the percentage of stealth flights in 569 shorebird hunts recorded at a large marshy lake in Alberta was 77% (Dekker 1988). The explanation for these dissimilar values is that the habitat in these two areas was quite different. At the lake, reedy shorelines created suitable cover for stealth hunts. Open attacks on flying shorebirds were uncommon at the lake except when drought had caused the shallows to recede well away from shore (Dekker 1991, 1999). By the same token, the high proportion of open hunts at Boundary Bay (62%) reflected the lack of opportunities for surprise over zones 2 and 3. Once the Dunlins were >10 m from the saltmarsh (the boundary between zones 1 and 2), the distance from shore had no significant bearing on the hunting success rate of peregrines (i.e., kill rates for zones 2 and 3 were nearly equivalent).

While peregrines evidently hunt and capture prey throughout the day, the fact that they killed much less often just before and much more often just after high tide cannot be related to habitat. If that were so, the kill rate per observation hour 1–2 hr before and 1–2 hr after high tide should be the same, which is clearly not the case. The most plausible reason for the observed difference is related to the behavior of the Dunlins. Well before the cresting tide, often when the floodwaters are still >50 m from the saltmarsh, the great majority of Dunlins depart on their over-ocean flights, while others fly inland especially during or after heavy rain. The drop in kill rate during this period reflects the decreased vulnerability of the birds during over-ocean flights. (The kill rate at inland roosting sites outside the study area was not recorded.)

The peak in kill rate immediately after high tide is probably due to the Dunlins' need to compensate for energy expended during 2–4 hr of over-ocean flying. Returning Dunlins are likely to be hungry, more intent on foraging and less vigilant than at other times during the tidal cycle. Consequently, the trade-off temporarily shifts toward increased risk.

A second and complementary reason for the high kill rate just after high tide is that some peregrines, particularly the adults, spend most of the day perching and may not start hunting until flocks of Dunlins begin to congregate near the saltmarsh. Adult peregrines are significantly more successful in the use of stealth than juveniles. Only 25% of all hunts were by adults, yet they accounted for 47% of kills (Dekker 2003).

PREY SELECTION

Based on the examination of prey remains, a relatively high percentage of shorebirds caught by raptors are known to be juveniles (Kus et al. 1984, Whitfield 1985, Warnock 1994). The mechanics of age-related prey selection seem simple if we assume that juveniles are on the outsides of flocks, either on the ground or in flight (Ydenberg and Prins 1984, Ruiz et al. 1989, Newton 1998). In this study, at least 69% of captured Dunlins were taken by peregrines directly from the outside or tail end of flocks (Dekker 2003). Furthermore, the percentage of juveniles may be high in small, isolated flocks that render themselves vulnerable to stealth attacks during the high tide. Such risky behavior includes (1) late departure on over-ocean flocking flights; (2) persistence in roosting or foraging along the high-tide line; (3) early return to shore after over-ocean flocking; and (4) a switch to inland roosts or feeding sites. The proportion of juveniles in flocks in such high-risk situations, and their physical condition compared to conspecifics that flock over the ocean, might present an interesting avenue for further research.

This study was privately financed by DD. During the last year, travel expenses were partially reimbursed by the Centre for Wildlife Ecology at Simon Fraser University, British Columbia. Accommodation in 2000–2003 was provided by D. Leach. Occasional co-observers were I. Dekker, D. Hancock, R. Swanston, and P. Thomas. G. Court did the *G*-tests. I. Gordon assisted with the data analysis for Figure 1c. R. Dekker prepared the graphs. Referees J. Buchanan and R. Butler made helpful comments on the first draft of this paper.

LITERATURE CITED

BRENNAN, L. A., J. B. BUCHANAN, S. G. HERMAN, AND T. M. JOHNSON. 1985. Interhabitat movements of wintering Dunlins in western Washington. Murrelet 66:11–16.

BUCHANAN, J. 1996. A comparison of behavior and success rates of Merlins and Peregrine Falcons when hunting Dunlins in two coastal habitats. Journal of Raptor Research 30:93–98.

BUTLER, R. W. 1994. Distribution and abundance of Western Sandpipers, Dunlins, and Black-bellied Plovers in the Fraser River estuary, p. 18–23. *In*

R. W. Butler and K. Vermeer [EDS.], The abundance and distribution of estuarine birds in the Strait of Georgia, British Columbia. Canadian Wildlife Service Occasional Paper No. 83, Ottawa, ON, Canada.

BUTLER, R. W., AND R. W. CAMPBELL. 1987. The birds of the Fraser River delta: populations, ecology and international significance. Canadian Wildlife Service Occasional Paper No. 65, Ottawa, ON, Canada.

CRESSWELL, W. 1996. Surprise as a winter hunting strategy in Sparrowhawks, Peregrines, and Merlins. Ibis 138:684–692.

DEKKER, D. 1980. Hunting success rates, foraging habits, and prey selection of Peregrine Falcons migrating through central Alberta. Canadian Field-Naturalist 94:371–382.

DEKKER, D. 1988. Peregrine Falcon and Merlin predation on small shorebirds and passerines in Alberta. Canadian Journal of Zoology 66:925–928.

DEKKER, D. 1991. Prairie water: wildlife at Beaverhills Lake, Alberta. University of Alberta Press, Edmonton, AB, Canada.

DEKKER, D. 1998. Over-ocean flocking by Dunlins (*Calidris alpina*) and the effect of raptor predation at Boundary Bay, British Columbia. Canadian Field-Naturalist 112:694–697.

DEKKER, D. 1999. Bolt from the blue—wild peregrines on the hunt. Hancock House Publishing, Surrey, BC, Canada.

DEKKER, D. 2003. Peregrine Falcon predation on Dunlins and ducks and kleptoparasitic interference from Bald Eagles wintering in British Columbia. Journal of Raptor Research 37:91–97.

FLATER, D. [ONLINE]. 1998. Xtide: harmonic tide clock and tide predictor. <http://www.flaterco.com/xtide/> (1 December 2003).

HOTKER, H. 2000. When do Dunlins spend high tide in flight? Waterbirds 23:482–485.

KUS, B. E., P. ASHMAN, G. W. PAGE, AND L. E. STENZEL. 1984. Age-related mortality in a wintering population of Dunlin. Auk 101:69–73.

LIMA, S. L. 1988. Vigilance and diet selection: a simple example in the Dark-eyed Junco. Canadian Journal of Zoology 66:593–596.

LIMA, S. L., T. L. VALONE, AND T. CARACO. 1985. Foraging efficiency—predation risk trade-off in the grey squirrel. Animal Behavior 33:155–165.

MILINSKI, M. 1986. Constraints placed by predators on feeding behaviour, p. 236–252. *In* T. L. Pitcher [ED.], The behaviour of teleost fishes. Croom Helm Ltd., London.

NEWTON, I. 1998. Population limitation in birds. Academic Press, San Diego, CA.

PAGE, G., AND D. F. WHITACRE. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

PALMER, R. S. 1988. Handbook of North American birds. Vol. 5. Diurnal raptors, part 2. Yale University Press, New Haven, CT.

RUIZ, G. M., P. G. CONNORS, S. E. GRIFFIN, AND F. A. PITELKA. 1989. Structure of a wintering Dunlin population. Condor 91:562–570.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Freeman and Co., New York.

THIOLLAY, J. M. 1982. Les ressources alimentaires facteur limitant la reproduction d'une population insulaire de Faucun Pelerins (*Falco peregrinus brookei*). Alauda 50:16–44.

VALONE, T. J., AND S. L. LIMA. 1987. Carrying food items to cover for consumption: the behavior of ten bird species feeding under the risk of predation. Oecologia 71:286–294.

WARNOCK, N. D. 1994. Biotic and abiotic factors affecting the distribution and abundance of a wintering population of Dunlin. Ph.D. dissertation, University of California, Berkeley, CA.

WHITE, C. M., N. J. CLUM, T. J. CADE, AND W. G. HUNT. 2002. Peregrine Falcon (*Falco peregrinus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 660. The Birds of North America, Inc., Philadelphia, PA.

WHITFIELD, D. P. 1985. Raptor predation on wintering waders in southeast Scotland. Ibis 127:544–558.

YDENBERG, R. C., R. W. BUTLER, D. B. LANK, C. G. GUGLIELMO, M. LEMON, AND N. WOLF. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. Journal of Avian Biology 33:47–55.

YDENBERG, R. C., AND H. H. T. PRINS. 1984. Why do birds roost communally?, p. 123–239. *In* P. R. Evans, J. D. Goss-Custard, and W. G. Hale [EDS.], Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, UK.