

A COMPARISON OF BEHAVIOR AND SUCCESS RATES OF MERLINS AND PEREGRINE FALCONS WHEN HUNTING DUNLINS IN TWO COASTAL HABITATS

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ABSTRACT.—The hunting behavior and success of raptors have been linked to prey availability, habitat conditions, and competition. In this study, I compared the behavior and hunting efficiency of wintering merlins (*Falco columbarius*) and peregrine falcons (*F. peregrinus*) that hunted dunlins (*Calidris alpina*) at coastal estuarine and beach habitats in Washington to determine whether hunting efficiency was related to differences in habitat. Flocks of up to 15,000 dunlins moved 2–15 km from estuarine sites to roost and forage at beaches during diurnal high tides. Both falcon species regularly attacked flocks of dunlins in each habitat. The success rates of hunting flights for both species (merlin: 7.8%, peregrine falcon: 12.5%) were significantly lower at beaches than previously reported for estuaries. Dunlins at the beach habitat roosted in flocks near water's edge and avoided falcons by flying out over the ocean where flocks engaged in synchronized flight in the troughs between waves. Most capture attempts by falcons occurred over water even though the likelihood of successful capture was lower there. Neither age of the hunting raptor (peregrine falcon only) nor relative density of potential kleptoparasites influenced hunting success. Several hypotheses are presented to explain differences in hunting efficiency between the two habitats.

KEY WORDS: *dunlin*; *Falco columbarius*; *Falco peregrinus*; *merlin*; *peregrine falcon*; *predation*; *Washington*; *winter*.

Comparación de conductas y tasas de éxito de *Falco columbarius* y *Falco peregrinus* en la caza de *Calidris alpina* en dos hábitats costeros

RESUMEN.—Tanto la conducta de caza como el éxito de rapaces ha sido ligada a la disponibilidad de presas, condiciones del hábitat y competencia. En este estudio, comparé la conducta y la eficiencia de caza de *Falco columbarius* y *Falco peregrinus* que capturaron *Calidris alpina* en estuarios y playas, hábitat costeros de Washington, con el fin de determinar si la eficiencia de caza estaba relacionada a diferencias en hábitat. Durante la marea alta diurna, bandadas de *C. alpina*, sobre los 15.000 individuos, se movían de dos a 15 km desde el estuario a sitios de descanso y forrajeo en playas. Las dos especies de halcones atacaron regularmente a estas bandadas (*C. alpina*) en ambos tipos de hábitats. La tasa de éxito en captura al vuelo para ambas especies (*F. columbarius* = 7.8%, *F. peregrinus* = 12.5%) fue significativamente más baja en playas que en estuarios previamente reportadas. *Calidris alpina* descansó en hábitat de playas cercanos al agua y evitaron el ataque de los halcones volando hacia el mar en sincronizadas bandadas. La mayoría de los intentos de captura por halcones ocurrió sobre el agua, donde la probabilidad de éxito era la más baja. Tanto la edad del rapaz cazador (sólo *F. peregrinus*) como la densidad de potenciales kleptoparásitos no influenciaron el éxito de captura. Presento varias hipótesis para explicar las diferencias en eficiencia de caza entre los dos hábitats.

[Traducción de Ivan Lazo]

Studies of raptor foraging ecology have identified relationships between habitat use and factors such as vegetation structure and prey abundance (Wakeley 1978a, 1978b, 1979, Baker and Brooks 1981, Bechard 1982, Toland 1987, Preston 1990). They show that raptors preferentially forage in

habitats where caloric intake is higher. These findings are consistent with the ideal free model of habitat selection (Fretwell and Lucas 1970) which holds that marginal habitats will be used by certain individuals in a population to meet some or all life requisites. Few studies have attempted to describe

foraging efficiency and examine its relationship to differing habitat conditions, prey populations, or prey behavior (Swenson 1979, Bildstein 1987, Toland 1987).

In western Washington, the merlin (*Falco columbarius*) and peregrine falcon (*F. peregrinus*) are major predators of the dunlin (*Calidris alpina*; Buchanan et al. 1986, 1988, Dobler and Spencer 1989), the most abundant winter shorebird in the region (Brennan et al. 1985, Evenson and Buchanan 1995). The behavior of hunting falcons has been described for flights directed at roosting or foraging flocks of dunlins in estuaries (Buchanan et al. 1986, 1988). Large populations of wintering dunlins occur at two coastal estuaries (Buchanan and Evenson, unpubl. data); many of these birds make short flights each day during high tide to outer beach roost sites (Buchanan 1992). Individual falcons track these movements and hunt shorebirds in both habitats. To determine whether hunting efficiency was related to habitat conditions, I observed the behavior and efficiency of merlins and peregrine falcons hunting dunlins at outer beaches to compare with earlier data collected at estuaries in western Washington (Buchanan et al. 1986, 1988).

STUDY AREA

Observations were made at three beaches on the outer coast of Washington state: Copalis-North Beach (25 km in length), South Beach (23 km), and Long Beach (37 km). The beaches are contiguous, relatively flat expanses of sand backed by low dunes. Beach width during high tide ranges from 0–30 m, depending on location and tide height. The high-tide zone is characterized by open sand, varying amounts of logs, and tidal debris. Most of the length of these beaches occurs along two peninsulas situated perpendicular to the openings of Grays Harbor and Willapa Bay; only a 13 km length of South Beach is not directly across the peninsula from an intertidal area. The peninsulas are 1.5–3 km wide and are dominated on the windward side by low dunes. Dune vegetation is predominantly European beach grass (*Ammophila arenaria*) and wax myrtle (*Myrica californica*). In some areas forests of Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) occur within 150 m of the dunes.

Observations of falcon hunting behavior at estuaries (Buchanan et al. 1986, 1988) were made primarily at four sites: Samish Bay in north Puget Sound, Nisqually River delta and Totten Inlet in south Puget Sound, and Grays Harbor. These sites are described in Brennan et al. (1984, 1985). Observations at beach and estuarine sites were made under a variety of weather conditions typical of the mild, wet winters in the region.

Winter populations of dunlins at three of the estuaries ranged in size from 2000–13,000 birds (Brennan et al. 1985). Counts at Grays Harbor and Willapa Bay ranged

as high as 40,000–70,000 birds, respectively (Paulson 1993, Evenson and Buchanan, unpubl. data). Although some dunlins remained within these estuaries at high tide, quite large numbers moved to the outer beaches, densities of roosting dunlins averaged >400 birds/km on beaches (Buchanan 1992). Roosting and in-flight flocks >2000 dunlins were observed in both habitats (Brennan et al. 1985, Buchanan 1992).

METHODS

Data Collection. Field work was conducted on 38 days between Nov–Feb 1983–90 and Nov–Mar 1993–94. Observations at estuaries were made in 1979–90 (Buchanan et al. 1986, 1988, unpubl. data). I traveled a cumulative total of 894 km of shoreline conducting shorebird counts and observing falcons. Each beach was visited at least once each winter with the exception of 1993–94, when South Beach was not visited. Field work was restricted to a period 3 hr before and after high tide; high tides during field visits ranged between 2.3 and 3.2 m. High tides >2.3 m inundated all tidal flats in the adjacent estuaries under most conditions. The majority of diurnal high tides during Nov–Feb were >2.3 m and ranged as high as 3.2 m.

I made most observations from a vehicle, using 7×35 binoculars and a 25× spotting scope. Certain sections of beach were covered by foot. When falcons hunted shorebirds I recorded movement and position of the flock during attack, type of hunting flight by the falcon, and the number and type of capture attempts made.

Definitions and descriptions of falcon hunting behavior are provided by Buchanan et al. (1988), and are described here briefly. A hunting flight is a perch-to-perch flight that includes one or more capture attempts. A capture attempt is defined as an attempt to seize or knock down prey. Exploratory “feints” are not considered capture attempts. Hunting methods used by merlins and peregrine falcons included stoops, nearly vertical, rapid descents toward flocks or single birds; stealth approach, rapid, low (usually <2 m) flights toward roosting flocks; and horizontal chases, the pursuit of either flocks or single birds, often after another hunting method failed.

Data Analysis. To allow comparison with other studies, I calculated the proportion of hunting flights and capture attempts that were successful. In certain cases, I observed a sequence of hunting flights involving a single falcon. Although sequential observations are not statistically independent events (Beal and Khamis 1990), they can be used to increase sample size (Hejl et al. 1990), particularly when samples are difficult to obtain, or to minimize sampling error associated with single sampling (Morrison 1984). Recently, Leger and Didrichsons (1994) found that use of pooled observations did not cause bias if intra-subject variance exceeded between-subject variance or subject sample sizes were the same.

I evaluated the dataset to determine whether inclusion of all sequential observations in the analysis was appropriate. First, I randomly selected three hunting flights per falcon and recorded the number of capture attempts per flight and calculated both intra-subject variance and between-subject variance (Leger and Didrichsons 1994). The calculated ratio of intra-subject variance to between-subject variance was 1:0.95 (i.e., intra-subject variance ex-

ceeded between-subject variance). I next calculated the number of different merlins and peregrine falcons seen hunting in each habitat. For this calculation I assumed that birds tallied between years were different birds. The numbers of falcons observed hunting in each habitat were nearly identical. At least 17 and 23 merlins hunted shorebirds at beaches and estuaries, respectively, and 11 different peregrine falcons were observed hunting in each habitat. Finally, observations at beach sites were spatially and temporally independent from those made at estuaries. For these reasons, I felt justified to use all sequential observations.

To determine whether falcons hunted with similar relative frequencies in the two habitats, I compared mean indices of hunting activity (number of flights/hr/yr) at each habitat using a Mann-Whitney test. I combined both species for this analysis because the only two estuarine sites that supported peregrine falcons were not visited all years (Buchanan et al. 1986). To test the null hypothesis that there was no difference in the efficiency of falcons hunting dunlins in different habitats, I assessed hunting efficiency in three ways. First, I compared success rates by hunting flight and by individual capture attempt for merlins and peregrine falcons at beaches and estuaries with a 2×2 chi-square contingency analysis (Zar 1984), with a correction for continuity ($df = 1$). Second, I compared the number of capture attempts per hunting flight in each habitat using the Mann-Whitney test. Finally, I compared the number of capture attempts made per flight over land and over water for both species using the Wilcoxon test.

I assessed the effects of two factors, age of falcons and presence of kleptoparasites, on hunting efficiency. Age is known to influence hunting efficiency in birds and younger, inexperienced birds generally are less successful at securing prey than adults (Burger 1988). My sample size was too small to fully evaluate the relationship between age and hunting success. However, for the peregrine falcon I used chi-square analysis to compare the proportions of hunting flights involving subadults in each habitat to determine whether differences in success rate might be explained simply by the age ratio of the birds I observed hunting in the two habitats. This analysis was not conducted for merlins because it was not always possible to determine age of hunting merlins. Because previous studies found that merlin hunting behavior varied significantly in the presence of kleptoparasites (Buchanan 1988), I attempted to determine whether the presence of known potential kleptoparasites (Brockmann and Barnard 1979) influenced the success rates of hunting flights in the two habitats. For this analysis I compared mean density indices (birds/hr/yr) of potential kleptoparasites at beach and estuarine sites using a one-tailed *t*-test.

RESULTS

Behavior of Dunlins at Beaches. Dunlins responded to attacks from falcons by flying directly over the ocean where flocks engaged in rapid, highly synchronized evasive movements. All predator evasion flights occurred over the water. Flocks nearly always flew very low over the water, and as-

cended and descended in an undulating motion with the passing of each cresting wave. All evasive flights at beaches occurred within 20 m of the water, and in most cases the bottom of the flock was < 1 m above water.

Behavior of Falcons. All 75 hunting flights by falcons at beaches were directed at dunlins. Hunting flights were directed at single birds and flocks ranging in size up to 12,000 dunlins. All three captures made by peregrine falcons were brief (1–2 capture attempts/flight) pursuits of solitary dunlins that had split (or were forced) away from flocks; captures made by merlins were of birds taken directly from in-flight flocks of about 4000 and 60 dunlins. Both species occasionally continued to chase birds they isolated from a flock, but no such extended pursuits were successful. Two of seven prey captures occurred over water.

Falcons were equally likely to be observed hunting in either habitat. The index of hunting incidence (hunts/hr/yr) was the same at beach ($\bar{x} = 0.64$, $SD = 0.89$) and estuarine sites ($\bar{x} = 0.55$, $SD = 0.44$; $U = 46$, $P > 0.20$).

I observed hunting flights by merlins (51) and peregrine falcons (24) directed at flocks of dunlins at beach habitat and found the success rates for hunting flights at beach sites were significantly lower than at estuaries for both species (merlin: 8 vs. 23%, $\chi^2_c = 4.17$, $P = 0.043$; peregrine falcon: 13 vs. 47%, $\chi^2_c = 4.00$, $P = 0.046$). The success rates for capture attempts were also lower at beach sites, but the differences were not significantly different (merlin: $N = 176$ capture attempts, 2 vs. 6%, $\chi^2_c = 2.42$, $P = 0.13$; peregrine falcon: $N = 52$ capture attempts, 6 vs. 15%, $\chi^2_c = 2.26$, $P = 0.15$).

The number of capture attempts per flight at beach sites (merlin: $\bar{x} = 3.45$, $SD = 3.52$; peregrine falcon: $\bar{x} = 3.47$, $SD = 2.92$) were the same as at estuarine sites (merlin: $\bar{x} = 3.81$, $SD = 4.77$, $Z = 0.04$, $P > 0.50$; peregrine falcon: $\bar{x} = 2.75$, $SD = 2.4$; $U = 152.5$, $P > 0.20$). Both falcons made fewer capture attempts per flight over land (merlin: $\bar{x} = 0.69$, $SD = 0.68$; peregrine falcon: $\bar{x} = 0.5$, $SD = 1.06$) than over water (merlin: $\bar{x} = 2.78$, $SD = 3.6$, $T_- = 248$, $P < 0.001$; peregrine falcon: $\bar{x} = 2.5$, $SD = 2.25$, $T_- = 3$, $P < 0.001$). All four prey captures by merlins occurred over the beach. Two of three captures of prey by peregrine falcons occurred over the water when single birds were captured away from flocks; the third capture occurred when a single bird was taken above the beach after leaving a flock out over the water. The success rates of

capture attempts made over beaches by merlins and peregrine falcons were 11.4 and 8.3%, respectively. Only 5% of capture attempts by peregrine falcons over water were successful.

When attacking a flock over the beach, both species always used low stealth approaches above land; there were no initial approaches over water. In some cases, the flock saw an approaching falcon ≈ 250 m away and moved to a position over the breakers where much of the hunting activity occurred. In such cases, the falcon either continued the attack directly or circled to a position above the breakers (merlins: 20–50 m, peregrine falcons: 40–80 m), from where they initiated stoops or discontinued the attack. For merlins, 17 flights occurred exclusively over the beach, 12 were initiated over the beach and moved to water (e.g., capture attempts were made above beach and water during a hunting flight), and 22 occurred exclusively over water (e.g., the capture attempt occurred over water). This pattern of hunting location differed slightly for peregrine falcons, where three flights occurred exclusively over beach, four were initiated over beach and moved to water, and 17 occurred exclusively over water (2×3 contingency test; $\chi^2 = 5.42$, $P = 0.07$). Low attacks occurred in 38 (75%) and 10 (42%) of the hunting flights by merlins and peregrine falcons, respectively; most low approaches were stealth flights, but some flights over water (merlin = 10, peregrine falcon = 5) also included low pursuit of single birds. All stoops by both species were made over water and occurred in most flights that were exclusively above water (merlin: 16 of 22, 73%, peregrine falcon: 15 of 17, 88%).

Influences on Hunting Efficiency. Nine of 24 hunting flights by peregrine falcons at beaches (38%) were made by subadult birds. This is similar to the proportion of flights by subadults observed at estuaries (33%; $\chi^2_c = 0.08$, $P = 0.78$).

I observed six raptor species in the two habitats that are known to steal prey from other raptors: bald eagle (*Haliaeetus leucocephalus*), northern harrier (*Circus cyaneus*), red-tailed hawk (*Buteo jamaicensis*), rough-legged hawk (*B. lagopus*), gyrfalcon (*F. rusticolus*), and peregrine falcon. As a group, these species were observed at a much lower frequency (birds/hr/yr) at beaches ($\bar{x} = 0.34$, $SD = 0.22$) than at estuaries ($\bar{x} = 1.42$, $SD = 0.4$; $t = 6.6$, $df = 14$, $P < 0.0005$). I observed only one instance of attempted kleptoparasitism at beach sites

(a gyrfalcon attempted to take prey from a peregrine falcon immediately after capture).

DISCUSSION

Merlins and peregrine falcons hunted less efficiently, in terms of the success rate of hunting flights, at beaches (8 and 13%, respectively) than at estuarine sites (23 and 47%, respectively). Both species had similar success rates for capture attempts at beach sites (2 and 6%, respectively) and estuaries (6 and 15%, respectively) but peregrine falcons were more successful than merlins at capturing dunlins. Although peregrine falcons are often far more successful at securing prey (Ratcliffe 1980), relatively low rates of success have been documented (Bertochi et al. 1984, see review by Roalkvam 1985). The variation in rates of successful hunting flights by peregrine falcons and merlins have been attributed to factors such as age, experience, degree of intent, and energy requirements (Ratcliffe 1980, Treleaven 1980, Sodhi et al. 1993); factors associated with the hunting success rates of other raptor species include the behavior and vulnerability of prey and vegetation structure (Swenson 1979, Bildstein 1987, Toland 1987).

Solitary shorebirds can be more vulnerable to predation than birds in flocks (Kus 1985). Species reliant upon synchronized flocking when threatened by predators perhaps benefit from this behavior by reducing the probability of predation (Kus 1985), by confusing the predator (Davis 1980). In this study I found that five of seven prey captures were of single birds isolated from flocks. Most captures occurred above beaches with only two captures occurring over water. There were no successful captures made through attacks on large flocks over water. This was in striking contrast to hunting behavior at estuaries where 43 and 32% of all prey captures by peregrine falcons and merlins, respectively, occurred during stoops at flocks of dunlins (Buchanan et al. 1986, 1988). In both habitats, attacks at flocks resulted in single birds becoming isolated from the flock and these were most successful when dunlins were not flying over waves.

Shorebirds are known to evade predators by flying over water (Hunt et al. 1975, Bertochi et al. 1984, Boyce 1985, Buchanan et al. 1988). The height of dunlin evasive flights I observed at beaches was lower than at estuaries (e.g., 50 m; Buchanan et al. 1988), suggesting an adaptive advantage of dunlins flying low over the water to evade fal-

cons. There are several possible reasons why shorebirds evade predators by flying over water and why falcons are less effective when hunting shorebirds in beach habitat. First, shorebirds are capable of safely landing in water to escape capture (Hunt et al. 1975, Buchanan et al. 1991). Although both peregrine falcons and merlins are known to retrieve floating or swimming birds from water (Dekker 1980, Boyce 1985, Buchanan et al. 1991), they may not be able to do so in turbulent water (e.g., the breaker zone). If falcons are reluctant to retrieve such birds, perhaps they must attempt more difficult captures of prey in mid-air. This is an unlikely explanation because falcons typically secure shorebirds in flight. Second, despite the fact that merlins and peregrine falcons occasionally hit the water at the terminus of stoops during hunting flights (three observations for each species at estuaries; J.B. Buchanan, unpubl. data), the risk of hitting a wave during a stoop, or of being inundated by a cresting wave may influence a falcon's ability to capture prey so close to the water. It is difficult to assess the potential importance of this factor. Third, falcons may simply be confused by the contrasting movements of individuals within the flock relative to the movement of the waves and may have difficulty tracking target birds. Predator confusion is one reason why prey species evade predators by assembling in large flocks capable of cohesive movements (Curio 1976, Davis 1980). Falcons in this study were unsuccessful in all attempts to capture dunlins during stoops over cresting waves even though stoops over calm water were commonly made and often successful at estuaries (Buchanan et al. 1988). Successful captures over water occurred during horizontal pursuit of birds isolated from flocks; it is likely that any confusion effect is negligible during horizontal pursuit of a single bird. These results appear to support a predator-confusion hypothesis. Finally, the lower rate of hunting success at beaches did not appear to be related to density of potential kleptoparasites, which were more abundant at estuarine sites.

According to the ideal free model of habitat selection (Fretwell and Lucas 1970), both dunlins and falcons should attempt to spend as much time as possible in habitats that serve to maximize inclusive fitness. This means that shorebirds should forage in habitats where invertebrate prey is available at a level that offsets physiological costs associated with roosting, vigilance, and predator avoidance. Similarly, merlins and peregrine falcons

should hunt in areas where prey is abundant and available enough to offset costs associated with foraging. Falcons may hunt in beach habitat, where they are less efficient predators, in order to meet their high energetic costs. A merlin, for example, requires about 70–75 g food each day (Page and Whitacre 1975), and in western Washington would need to consume about 3 dunlins (Brennan et al. 1984) or similar-sized prey every 2 days to meet this intake requirement. Owing to the short daylength and very high diurnal tides during winter, shorebirds may spend as much or more time at beach sites than at estuaries on certain days. Therefore, a merlin may need to hunt shorebirds in less optimal conditions to meet its average daily energy requirement, unless other prey are available. This expended effort may be offset by the greater success rate for hunting flights at estuaries, and the fact that falcons can more easily track flock movement between habitats (e.g., search time is reduced). However, it is unknown whether the lower success rate of hunting flights at beaches represents a significant physiological stress to falcons and whether other potentially suitable prey are available during the periods when dunlins are roosting at outer beaches. These issues must be addressed to better understand these predator-prey relationships.

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