Wilson Bull., 100(1), 1988, pp. 108–118

MERLIN PREDATION ON WINTERING DUNLINS: HUNTING SUCCESS AND DUNLIN ESCAPE TACTICS

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ABSTRACT.—Interactions between Merlins (*Falco columbarius*) and Dunlins (*Calidris alpina*) were studied at estuarine areas in western Washington during winter, 1979 to 1985. Twenty-five of 111 hunting flights by Merlins were successful (22.5%). Five of seven capture attempt techniques were used successfully with a success rate of 4.9%. The most common capture techniques were the stoop at a flock and the chase of an individual isolated from the flock. Most hunting flights (54%) lasted less than 1 min, but hunts of over 5 min were observed (10%). Hunting success rates varied little with the duration of the hunting flight or the size of the Dunlin flock initially targeted. Success rates for hunting flights by Merlins were much higher in Washington (22.5%) than reported from California (12.5%); these higher rates may be the result of a functional response by Merlins in Washington. Dunlins exhibited three distinct types of synchronized predator evasion flights. Dunlins isolated from flocks were often pursued and captured. The most common evasive measure used by isolated birds was a lateral dodge executed while in linear flight away from the flock. *Received 5 June 1987, accepted 15 Oct. 1987.*

The Dunlin (*Calidris alpina*) is the most abundant Calidridine sandpiper wintering at estuaries along the Pacific coast of North America (e.g., Page et al. 1979). Throughout much of this range, the Merlin (*Falco columbarius*) may be its most common diurnal predator (see Page and Whitacre 1975). Shorebirds are an important source of prey for Merlins (Cade 1982). Previous studies of predation by Merlins have concentrated on hunting success rates and mortality of prey species (Rudebeck 1951, Page and Whitacre 1975, Kus et al. 1984). Only Kus (1985) has given more than cursory attention to behavioral interactions between predator and prey. Published descriptions of the flocking behavior of Dunlins (Major and Dill 1978, Davis 1980, Potts 1984) also lack quantitative accounts of behavioral interactions between predator and prey. Because of this, we examined the behavioral relationship between Merlins and Dunlins during winter. Our objectives were: (1) to describe and quantify hunting and capture techniques used by Merlins in pursuit of Dunlins, and (2) to describe techniques used by flocks and individual Dunlins to evade Merlins.

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STUDY AREA AND METHODS

The data were collected at sites in four estuaries in western Washington. Three study sites, Samish Bay, Nisqually River delta, and Kennedy Creek delta are located in Puget Sound. Bowerman Basin is located in Grays Harbor on the outer Pacific coast. Site descriptions are provided in Brennan et al. (1985). Additional observations were also made at Eld Inlet, in southern Puget Sound, and at North Bay and Ocosta in Grays Harbor (Herman and Bulger 1981).

Field work began at Bowerman Basin and Samish Bay during winter 1979. Between December 1980 and March 1981 all four sites (Samish, Nisqually, Kennedy, Bowerman) were visited weekly. Subsequent visits were made to Bowerman Basin through 1982 and Kennedy Creek delta through 1985.

During each visit to a site, we observed movement patterns of foraging flocks of Dunlins throughout the tidal cycle. Direct counts or estimates of shorebird numbers were made as the birds foraged on exposed tidal flats. During hunting flights by Merlins, we recorded the method of attack used, the locations of hunts, predator avoidance behavior exhibited by Dunlins, and, if possible, the size of the flock being attacked. Hunting flight duration was usually determined using a watch, but it occasionally was estimated if several hunts occurred in succession. In some cases an exact determination of duration was impossible, because a hunt was in-progress when first observed. In these cases, we recorded duration from the time the Merlin was first observed hunting. All observations were made during winter (November–March), using binoculars and spotting scopes.

Because more than one Merlin hunted at several of the sites, and because individual Merlins often could not be distinguished, our results represent a composite sample rather than information about the hunting of specific individuals.

Definitions of hunting behavior.—In this paper we discriminate between two different types of hunting behavior: the hunting flight and the capture attempt. We define a hunting flight as a single flight involving any number of capture attempts at suitable prey in *any number* of different flocks. A capture attempt is an attempt to seize or knock down a specific prey individual during a hunting flight; this seems to correspond with the term *attack* used by Kus (1985). We used this modified definition of the hunting flight for two reasons: First, Merlins occasionally followed moving Dunlin flocks for great distances (up to 1000 m) and attacked the flock at widely separated locations without perching in the interim. These hunts were directed at the same prey, although at different locations after several minutes had elapsed. Second, hunting flights involving multiple capture attempts often occurred when Dunlin flocks were either splitting into smaller units or in the process of rejoining other flocks, thus causing confusion as to whether the focus of attack had changed to such an extent that classification as an additional hunt was warranted. This apparently was the intent of Page and Whitacre's definition (G. Page, pers. comm.), and our definition is identical to it.

Chi-square analysis was used to test for differences in behavior described here. Because some data on hunting flight duration were inexact, hunting flights were grouped into interval classes of one minute for purposes of analysis (e.g., <1 min, 1–2 min). We used Yates' correction for continuity (Zar 1984) to improve the approximation of the chi-square distribution in all tests with df = 1.

RESULTS

Populations of Dunlins and Merlins.—Winter numbers of Dunlins ranged from ca 700 at Eld Inlet to ca 13,000 at Bowerman Basin (Table 1) (see

TABLE 1

MAXIMUM COUNTS OF DUNLINS AND INDIVIDUAL MERLINS AT STUDY AREAS IN WESTERN WASHINGTON, 1979–85

Year	Site	Maximum Dunlin count	Number of known individual Merlins[a]
1979–80	Samish	7,000	1
	Bowerman	15,000	1
	North Bay	1,000	1
1980–81	Samish	10,500	3
	Nisqually	2,500	1
	Kennedy	2,400	1
	Bowerman	15,000	1
	North Bay	4,000	2
	Ocosta	3,000	2
1981–82	Eld	700	1
	Kennedy	4,100	1
	Bowerman	11,500	2
1982–83	Kennedy	2,450	3
1983–84	Kennedy	2,030	1
1984–85	Kennedy	4,400	2

[a] Based on individual plumage characteristics.

Brennan et al. [1985] for census details for winter 1980–1981 at the four primary sites). We believe that at least 12 different Merlins were observed during this study (Table 1). We identified individuals of the subspecies *columbarius* and *suckleyi* (Brown and Amadon 1968).

Descriptions of hunting activities.—We observed seven distinguishable methods used by Merlins to capture Dunlins: (1) nearly vertical stoops at or into flying flocks, originating at heights 10–30 m above water; (2) stoops directed at single Dunlins, originating at heights 5–15 m; (3) a low-angle glide-stoop, directed at flocks or individuals, and initiated from a brief burst of powerful flapping while in descent flight; (4) a low stealth attack, by which the Merlin would approach a flock, either on the ground or in flight, using a low and rapid flight in which surprise seemed important; (5) the flock chase, a horizontal pass through a flying flock, invariably initiated after the failure of other techniques; (6) the low chase attack of a single Dunlin isolated from a flock; and (7) ringing, which occurred when the Merlin attempted to seize the Dunlin from below or above as a solitary Dunlin circled upward in an attempt to remain above the Merlin.

An additional behavior exhibited by Merlins, the feint stoop, merits description here. The feint stoop is a shallow, incomplete stoop which terminates above the in-flight flock of Dunlins. It is not a capture attempt technique as defined here, and it is not considered such in this discussion. The feint stoop may be a method used by Merlins to test cohesiveness in a Dunlin flock. An alternative hypothesis, however, is that the Merlin merely miscalculated its stoop and terminated descent to prepare for another stoop.

Predator evasion flocking behavior.—Dunlins exhibit three distinct types of predator evasion flocking behavior in response to hunting Merlins. In *flashing* flight, Dunlins gather in dense, cohesive spherical or elliptical aerial flocks. Their highly synchronized movement results in "flashing," when the birds' dark-colored dorsal and light-colored ventral surfaces are alternately exposed. Flashing appears to result from one of two different movements: (1) a very rapid change in flight direction which appears synchronous among flock members, although the maneuver seems to be initiated by a single bird (Potts 1984) or (2) a tilt in body position relative to the bird's longitudinal axis. Dunlins regularly exhibited *flashing* behavior when foraging during rising tides, as well as in response to the presence of hunting raptors. We discuss *flashing* only in terms of its effectiveness as a predator evasion mechanism.

The second flocking behavior, *rippling* flight, resembles *flashing* but does not involve a change in flight direction by the flock. A seemingly localized synchronous movement, caused by a delayed timing of flock members as they shift body axis position, passes through the flock in one or more waves, producing a rippling effect. These waves of movement always start at one side of the flock and sweep completely through the flock, either horizontally or vertically.

In the third type of flocking, *columnar* flight, Dunlins coalesce into a towering tornado-like vertical column which often undulates throughout its length. Rippling and flashing movements commonly occur in *columnar* flocks. Intergradation between *flashing* and *rippling* flocks is common.

Success rates.—We observed 111 Merlin hunting flights with known outcomes. Twenty-five were successful, for a success rate of 22.5%. The success for hunting flights did not vary significantly among the four primary study sites (Samish 16.7%, N = 30; Nisqually 14.3%, N = 7; Kennedy 18.4%, N = 49; and Bowerman 25.0%, N = 16; $\chi^2 = 0.48$, df = 3, $P > 0.75$). During the 1980–81 winter, when all four primary sites were visited with nearly equal frequency, we did not detect monthly differences in success rates when all sites were combined (December 20%, N = 5; January 25%, N = 8; February 21%, N = 14; and March 24%, N = 17; $\chi^2 = 0.06$, df = 3, $P > 0.99$).

Nine hunting flights were successful on the initial capture attempt; this represented 8% of all hunts with known outcomes and 36% of successful

TABLE 2
FREQUENCIES OF CAPTURE ATTEMPT TECHNIQUES USED BY MERLINS IN WESTERN WASHINGTON

Capture attempt technique	Number of attempts	Success rate
Stoop at flock	151	5.3
Stoop at single Dunlin	50	2.0
Low chase of single Dunlin	149	5.4
Flock chase	32	0.0
Ringing flight	16	6.2
Low stealth attack	48	8.3
Low-angle glide-stoop	2	0.0
Totals	448	4.9

flights. Of these nine hunts, six utilized the stoop at the flock and three were by the low stealth attack (see below).

The success rate for all capture attempts was 4.9% and ranged from 2.0 to 8.3% for the five successful techniques (Table 2). The flock chase and the low-angle glide-stoop were never successful. Success rates were not significantly different ($\chi^2 = 1.89$, df = 4, $P > 0.75$) among successful capture attempt techniques. There were, however, significant differences in the frequency of occurrence of those five techniques ($\chi^2 = 190.5$, df = 4, $P < 0.001$).

General hunting behavior.—The most frequent initial capture attempt technique was the stoop, usually preceeded by a conspicuous high elevation approach flight (53% of observed initial capture attempts). A low stealth attack was used 47% of the time. Of the unsuccessful hunting flights which initially used the low stealth attack and later incorporated stoops, 9 were successful (20%). A stoop through the flock was included in 59% of the flights (N = 65). Feint stoops were noted in 20% of the hunting flights. Merlins often made several feint stoops before stooping down through a flock. Feints, however, did not improve the success rate for hunting flights (9%), suggesting that this activity was not an adaptation to improve hunting efficiency.

Merlins isolated Dunlins from flocks by using stoops, horizontal pursuits, or feint stoops (93% of instances with known cause of isolated bird; N = 26). Of the flights which included any kind of stoop (including feint stoop), 27% (N = 18) succeeded in splitting the flock into at least two subflocks. Split flocks were the most common source of isolated birds (43%), followed by stoops which failed to split the flock (25%), horizontal pursuit (21%), lack of flock synchronization (7%), and feint stoop (4%).

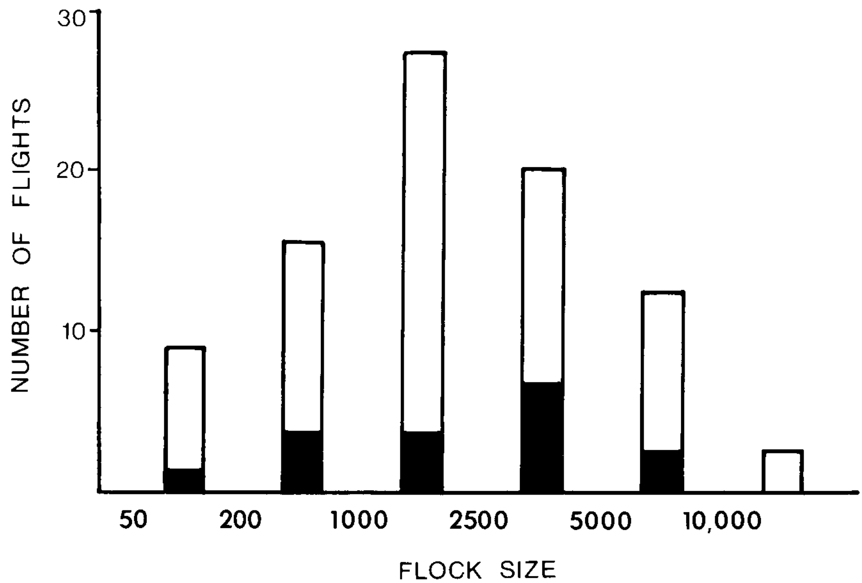

FIG. 1. Size of Dunlin flocks initially attacked by hunting Merlins. Solid bars represent number of successful hunting flights. Success rates for flights at each flock size are as follows: 22%, 25%, 15%, 35%, 25%, and 0%.

Prey was captured in flight during all but two successful hunting flights. The two exceptions occurred when Dunlins were knocked into or landed in water and were retrieved by the Merlin.

The size of Dunlin flocks initially targeted by Merlins was quite variable (Fig. 1), ranging from 50 to 10,000. Flocks tended to separate into smaller groups when pursued, although flocks smaller than 50 birds were rarely seen. Because flocks often split or rejoined during hunts, we were occasionally unable to monitor the size of flocks being targeted. Success rates of hunting flights in relation to flock size during the initial attack are presented in Fig. 1.

Most hunting flights by Merlins lasted less than 6 min (Fig. 2). Hunts lasting longer than one minute (46% of all hunts) typically involved combinations of stoops, feint stoops, flock splitting, or chases of individual Dunlins. We found no difference in success rates per hunt between hunts which lasted less than 1 min and all other hunt durations up to 6 min ($\chi^2 = 0.96$, df = 5, $P > 0.95$), although hunts which lasted less than 1 min were significantly more common than those lasting 2 min ($\chi^2 = 21.6$, df = 1, $P < 0.001$).

Evasive responses.—Dunlins exhibited *flashing* or *rippling* flocking be-

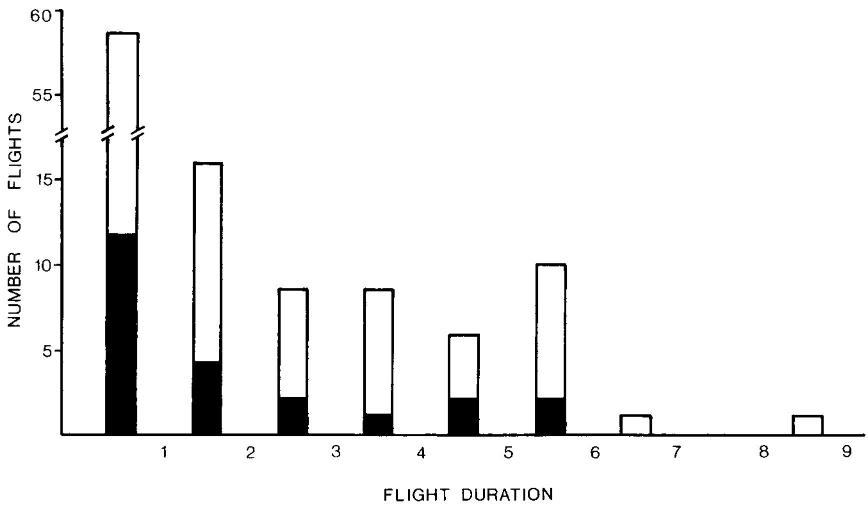

FIG. 2. Duration (min) of hunting flights by Merlins. Solid bars represent number of successful hunting flights.

havior in 76 of 83 (92%) hunting flights (Table 3). Dunlin flocking behavior was difficult to monitor because flocks usually separated into smaller units which may have exhibited different evasive tactics. For this reason, we combined *flashing* and *rippling* for this analysis, although *flashing* was clearly more common. *Columnar* flocking was observed only seven times during hunting flights by Merlins.

There was a tendency for evasion flights to move away from salt marsh, often several hundred m from exposed mud flats or salt marshes. Significantly more flocking took place over water than over mud flats immediately prior to chases of isolated birds ($\chi^2 = 5.8$, df = 1, $P < 0.025$). Consequently, more chases of isolated birds occurred over water than over any other substrate (e.g., mud flats, salt marsh) ($\chi^2 = 12.6$, df = 1, $P < 0.001$).

When separated from a flock, Dunlins flew out over open water in zigzagging flight, rarely more than 0.3 m above the water. Isolated birds moved linearly away from the flock when pursued by a Merlin. The most frequent evasion technique used was a quick lateral dodge (N = 44) executed at the last possible moment to evade a Merlin approaching from behind. Other evasion techniques were landing on water (N = 7), ringing flight (N = 6), and landing on mud or salt marsh (N = 2). The lateral dodge technique was significantly more common than any other (χ^2 = 78.3, df = 3, $P < 0.001$).

TABLE 3
DUNLIN FLOCKING TYPES IN RESPONSE TO HUNTING FLIGHTS BY MERLINS

Flock type	Number of flights	Dunlin evasion success	Merlin attack success
Flashing	53	85%	15%
Flashing, rippling	23	91%	9%
Flashing, rippling, columnar	7	71%	29%

Landing in water seemed to be used as a last resort, after repeated lateral dodges failed to discourage the attacking Merlin. Dunlins using this method resumed flight after the Merlin passed overhead. Twice Dunlins were knocked into the water by Merlins. On one occasion the Merlin returned quickly and captured the Dunlin before it regained flight.

DISCUSSION

Hunting by Merlins.—Our observed success rate for hunting flights of 22.5% was significantly higher than the 5% success rate reported by Rudebeck (1951) or the 12.8% reported by Page and Whitacre (1975) (χ^2 = 14.0, df = 1, $P < 0.001$, and $\chi^2 = 4.38$, df = 1, $0.025 < P < 0.05$, respectively). Also, Kus (1985) reported a success rate of 10.0% in a three-year study in California, but she used a different definition of the hunting flight, making it difficult to compare the two studies. Toland (1986) reported a success rate of 25% from 8 hunting flights in Missouri. The low success rate noted for migratory Merlins by Rudebeck (1951) involved hunts directed at passerines. Highest success rates for Merlins (Page and Whitacre 1975, Kus 1985, Toland 1986, this study) were recorded at wintering sites where falcons hunted on a regular basis for several months. Familiarity of territory and resident prey species during extended wintering periods may enhance success.

We do not know why hunting success rates are higher in Washington than in California. Perhaps these success rates reflect different energetic demands experienced by Merlins and Dunlins in these two regions, although this seems unlikely. Our study area is over 1000 km north of Bolinas Lagoon, California, where Page and Whitacre (1975) made their observations, and lies within 250 km of the northern extent of the common winter range of the Dunlin. The winter shorebird guild in Washington exhibits less diversity than in California (Pitelka 1979), and the Dunlin is by far the most abundant shorebird in this region. The Merlin's greater reliance on this species is likely a functional response, and this may explain the higher success rate for hunting flights (Murdoch and Oaten 1975).

The Merlin observed by Page and Whitacre (1975) directed 81% of its hunts at sandpipers on the ground, and it failed in all 82 flights or stoops at flying sandpipers. Kus (1985) found that 55% of the hunts were directed at birds on the ground. In Washington, however, the stoop at flying flocks was the most frequent capture attempt technique observed (34%); low stealth flights were common (11%) but never resulted in the capture of prey on the ground.

Page and Whitacre (1975:82) found that, as the shorebirds decreased in number, success rate also decreased. In Washington, we did not observe this decline in hunting efficiency. Populations of Dunlins at the four primary study sites remained fairly stable throughout the 1980–81 winter (see Brennan et al. 1985), and during this period hunting success rates for Merlins changed very little (see Results).

Kus (1985) found that Merlins in California directed most hunts at solitary birds or large flocks even though the success rate of attacks (=capture attempts) and hunts declined with increasing flock size. This is slightly different from the findings of Page and Whitacre (1975) whose success rates were high for hunts directed at single birds (25.6%) and large flocks (21.4%) but low for smaller flocks (6.9–8.3%). In arriving at these figures, they considered only those hunts directed at birds on the ground. Of the ground-oriented attacks, less than half were directed at flocks larger than 50 birds. Our data are not comparable since less than 4% of the hunts in Washington were initially directed at flocks smaller than 50 birds. Although our data on the frequency of hunting flights directed at various flock sizes are otherwise inconclusive, the success rates of hunts did not decline with increasing initial flock size (Fig. 1). This was probably a result of the high proportion (24%) of hunting flights (N = 6) which were successful on the initial stoop into a flock.

Evasive responses.—Once a flock of Dunlins is in flight, the primary defense mechanism appears to be flock cohesion. This is common to all three flocking types. An additional mechanism in *flashing* flight is the highly synchronous nature of flock movements. In *rippling* and *columnar* flights, the occurrence of ripple movements might be more confusing to the falcon than simple *flashing* because some of the flock would be made up of birds whose bodies are tilted in one of two extreme positions. There would also be birds in various positions between these extremes, including birds in the level flight position. A Dunlin positioned with the wings held vertically may represent a more elusive target for a Merlin attacking from above than one in the normal horizontal flight position, because the upper wing may serve to impede contact by the falcon (see Webb 1986). Of the captures we saw clearly, Dunlins appeared to be captured while in a fairly level flight position. Rippling flight may thus serve as a means of evasion for a constantly changing subgroup of the flock.

In *columnar* flight, flock surface area necessarily increases to produce the vertical column. The surface areas of the flock which expand, however, are the sides, which are less susceptible to attack. The surface exposed to attack, the top, is reduced in size. The top surface of a columnar flock actually tracks a Merlin circling above, and this creates much of the undulation effect. Flashing, rippling, increased column height, decreased area of frequent attack, and irregular undulations make this the most complex flocking behavior and potentially the most confusing to a predator.

All three types of defensive flocking behavior may be used during one Merlin hunt, suggesting that these tactics are used in response to a changing set of stimuli. The decreasing frequency of occurrence of the three flocking types (flashing, rippling, columnar) seems puzzling; however, if the probability of flock asynchronization is higher during *columnar* flight (because it is more complex), this could explain the rarity of this behavior.

In contrast to Boyce's findings in California (1985), we did not observe that flocks retrieve isolated birds. When a Dunlin becomes isolated the Merlin appears to force it farther away from the flock. Such behavior by the Merlin probably reduces the likelihood of the Dunlin's quickly rejoining the flock, thereby increasing the Merlin's potential for success.

ACKNOWLEDGMENTS

We thank A. M. Cahall, M. A. Finger, T. M. Johnson, J. Peard, and T. A. Stierhoff for assistance in the field during 1980–81. C. M. Anderson and C.-J. Pei provided stimulating discussion and insight. The manuscript has been improved by comments from J. C. Bednarz, C. R. Blem, D. A. Boyce, P. G. Connors, B. E. Kus, G. W. Page, and an anonymous reviewer. Funding during 1980–81 was provided by NSF-SOS Grant SPI80-04760.

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