AGE-RELATED MORTALITY IN A WINTERING POPULATION OF DUNLIN

BARBARA E. KUS,[1] PHILIP ASHMAN,[2] GARY W. PAGE,[3] AND LYNNE E. STENZEL[3]

[1]*Division of Environmental Studies, University of California, Davis, California 95616 USA;*
[2]*1242 East Dayton Street, Madison, Wisconsin, 53703 USA; and*
[3]*Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970 USA*

ABSTRACT.—Despite considerable evidence that juvenile shorebirds experience significantly higher annual mortality rates than adults, identification and quantification of the sources of mortality have received little attention. We found that the proportion of juvenile Dunlins (*Calidris alpina*) in the kills of a Merlin (*Falco columbarius*) one winter at Bolinas Lagoon, California was greater than the proportion of juveniles in the lagoon's winter population. This is evidence that raptor predation may be one of the factors contributing to the age differences in annual mortality rates of shorebirds. We suggest that the greater vulnerability of juveniles to predation by the Merlin may be caused by age-related differences in Dunlin flocking behavior. *Received 23 March 1983, accepted 6 September 1983.*

STUDIES of the population dynamics of shorebirds (Charadrii) indicate that, in general, juveniles experience higher annual mortality rates than adults (Goss-Custard 1980). This differential mortality has been reported for a wide range of European (Boyd 1962 and references therein) and North American species (e.g. Holmes 1966, Myers 1980, Page et al. 1983). Although a difference in survivorship between age-classes appears to be widespread among shorebird populations, little attention has been directed toward identifying and quantifying specific sources of mortality and evaluating their contribution to this pattern. Heavy mortality among first-year birds is generally thought to be the result of their relative inexperience in dealing with such selective pressures as predation, feeding efficiency, and extremes in environmental conditions (see references above); these hypotheses have not been tested empirically in shorebirds, however.

Here, we report the results of a study in which we attempted to determine the extent to which predators are responsible for age-related differences in the mortality rates of Dunlins (*Calidris alpina*). Specifically, we compare the age ratio of Dunlins in predator kills with the age ratio of Dunlins in a population wintering at Bolinas Lagoon, California in order to evaluate whether or not the mortality rate due to predation is higher for juveniles than for adults.

Predation by raptors is one of the major causes of winter mortality for Dunlins at Bolinas Lagoon, reducing the population by as much as 21% over a 5-month period (Page and Whitacre 1975). Northern Harriers (*Circus cyaneus*), American Kestrels (*Falco sparverius*), Short-eared Owls (*Asio flammeus*), Peregrine Falcons (*Falco peregrinus*), and Merlins (*Falco columbarius*) are among the more frequent predators of small shorebirds at the lagoon, and attacks by Red-tailed Hawks (*Buteo jamaicensis*), Cooper's Hawks (*Accipiter cooperii*), and Great Horned Owls (*Bubo virginianus*) also occur occasionally. We confined our analysis of the effect of predators on mortality rates to an examination of Dunlins killed by a female Merlin present at the lagoon during the fall and winter of 1979–1980. Merlins are the most significant of the Dunlins' diurnal predators at Bolinas Lagoon; during one winter (1972–1973) a single Merlin was responsible for approximately half of the observed predation on Dunlins by all raptors (Page and Whitacre 1975). Unlike many other shorebird predators at the lagoon, the Merlin we studied was relatively predictable in her hunting patterns. This enabled us regularly to observe her hunting and eating sandpipers and to collect the remains from a large portion of her kills. We were therefore able to base our examination of age-related mortality rates on direct observation of the effect of a single, known predator.

STUDY SITE AND METHODS

Study site.—Bolinas Lagoon is a shallow 570-ha estuary on the central California coast, approximately

24 km northeast of San Francisco. This study area and its shorebird population have been described by Page et al. (1979). It is a major over-wintering site for large numbers of shorebirds that forage on the expansive mudflats. Dunlins are present at the lagoon from late September through early May. During 1979–1980, Dunlin numbers increased to approximately 2,000 by November and remained at this level until the onset of migration in early April (Fig. 1).

Age-composition of the population.—We trapped Dunlins at approximately 2-week intervals throughout the winter in order to determine the ratio of juveniles to adults in the Bolinas Lagoon population. For each period, our estimate of the proportion of juveniles in the lagoon population is derived through direct extrapolation from the age ratio of the corresponding sample of trapped birds. We captured birds by two methods and compared the results to evaluate the possibility that our sampling technique, and therefore our population estimates, were biased toward a particular age-class. Although it is difficult to determine the nature and extent of biases associated with different trapping techniques, there is some evidence (Pienkowski and Dick 1976, Goss-Custard et al. 1981) that the composition of catches made by mist-nets, which we used extensively, may be biased in favor of juveniles. In November and December, we caught four samples with mist-nets and four with noose-mats. The mist-nets were positioned at dusk over channels that the Dunlins followed as they flew into the salt marsh to roost for the night. The noose-mats were hidden beneath the sand during the day in areas where large flocks of Dunlins were feeding or roosting. Noose-mat traps have the advantage of eliminating any age-related differences in flying expertise, which has been suggested as a reason for the potential bias associated with the use of mist-nets (Pienkowski and Dick 1976). We regressed the proportion of juveniles in each trapped sample against date for each method, compared the resultant lines, and found no statistical differences in either the slopes ($P = 0.29$) or the Y-intercepts ($P = 0.18$). While this evidence suggests that our estimates of the age structure of the population were not differentially biased by the two methods, it does not refute the possibility that both trapping techniques might be similarly biased toward catching juveniles. However, any bias that resulted in our overestimating the proportion of juveniles in the population would only make the experiment a conservative test of our hypothesis by making a selective preference by Merlins for juveniles more difficult to detect.

Each bird was banded with a unique color combination for individual recognition and was aged by plumage characteristics. Birds were considered to be immature if they had buffy edges on their innermost tertials or inner middle-wing coverts and adult if these feathers were white- or grey-tipped. Age can also be determined by the shape of the outermost primary, the juvenile feather being more pointed, worn, and narrower than the more bluntly tipped feather of the adult. Because this characteristic is more variable than the first, we tested the reliability of the primary-shape method by determining the age of each bird we captured independently by both criteria and comparing the results. We found that we were able to age birds by primary feather characteristics alone with 97% accuracy. Although it was not necessary for aging live birds, we relied heavily on the feather-shape technique for aging prey from feather remains, which often did not include the key coverts (see below).

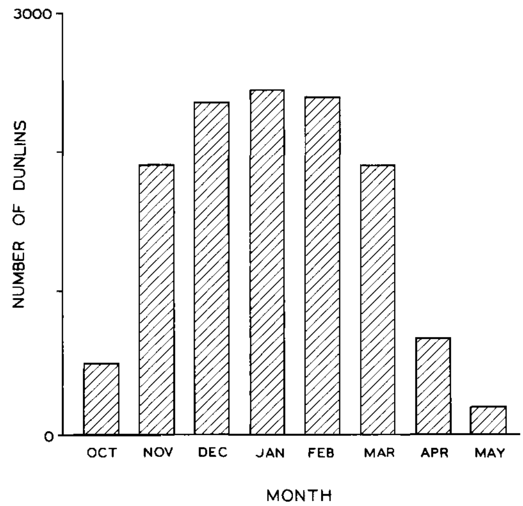

Fig. 1. Number of Dunlins at Bolinas Lagoon, October 1979–May 1980.

Age composition of Merlin kills.—A female Merlin was observed hunting sandpipers at Bolinas Lagoon between 12 October 1979 and 14 March 1980. The Merlin generally spent the entire day on the lagoon, resting or hunting birds on the mudflats by launching attacks from low perches in the adjacent salt marsh. Following a successful hunt, she returned to one of these perches where she ate the entire prey except for the body feathers and parts of the wings, which were discarded at the base of the perch. We checked the Merlin's perches regularly and collected the feather remains of any kills we found. We aged all Dunlin kills in the manner described above, except for seven for which there were insufficient remains.

Statistical analyses.—We used a multiple linear regression model to quantify the proportion of juveniles in the population and in the Merlin's kills (dependent variables) as a function of period during the winter season (independent variable). Because our samples of trapped birds were larger in size than our samples of prey remains, we used a weighted least

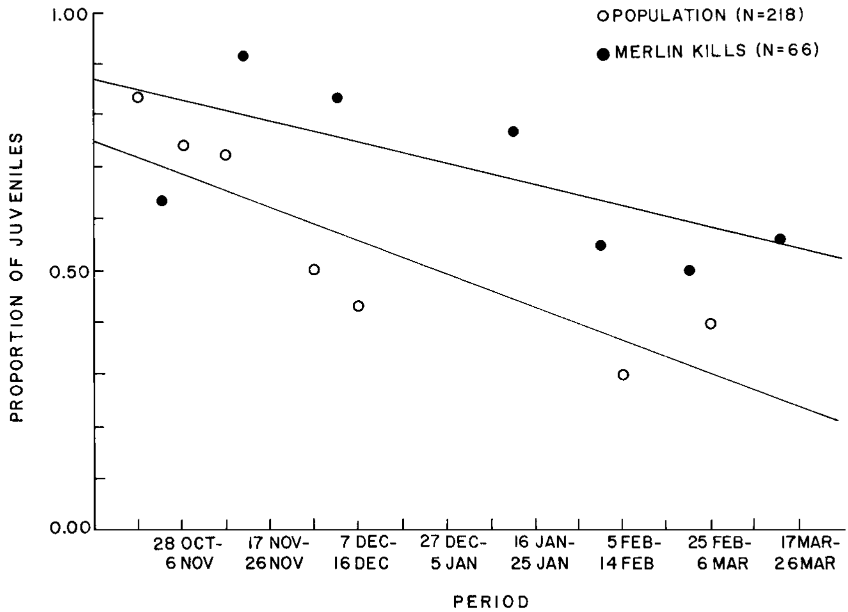

Fig. 2. Proportion of juvenile Dunlins in the population and in the Merlin's diet at Bolinas Lagoon in winter, 1979–1980.

squares analysis (Dixon 1981) to compare the slopes and Y-intercepts of the two lines. This technique weights each point in the regression according to its associated sample size and thus corrects for any inequalities in error variance that might exist between cases. All significance levels presented are for two-tailed tests.

Results

We caught a total of 218 Dunlins during seven sampling periods spanning the winter season. During these and four additional periods, we collected 146 of the Merlin's prey remains, 73 of which were Dunlins. Of the Dunlin remains, 40% ($n = 29$) were collected after actual observation of the Merlin eating the bird. Of the 73 Dunlin kills, 9% ($n = 7$) were excluded from our analysis because not enough material was present to determine age.

We believe that our sample of prey remains was a good indicator of the Merlin's diet on the lagoon throughout the winter. For the winter of 1972–1973, Page and Whitacre (1975) estimated that the Merlin at Bolinas Lagoon ate an average of 2.2 prey per day. Based on this estimate, our sample of prey remains represents 43% of the Merlin's prey for the 155 days she was known to be on the lagoon.

Figure 2 illustrates the proportion of immature Dunlins in the total population ($Y = 75.19 - 3.26x$) and in the Merlin's diet ($Y = 86.67 - 2.08x$) at different periods throughout the winter. As has been previously reported by Page (1974), juveniles arrive earlier than adults at Bolinas Lagoon, which accounts for the initial predominance of immature birds in the population. The subsequent arrival of adult Dunlins causes the proportion of young birds in the population to decrease. The age ratio stabilizes by midwinter, although in Fig. 2 it appears to continue to decline because of the linear function used to describe the data.

The relative decline in availability of immature Dunlins during the winter is reflected in the Merlin's diet; yet, a comparison of the two regression lines reveals that young birds consistently incurred a higher rate of predation than did adults (comparison of Y-intercepts, $P = 0.012$; comparison of slopes, $P = 0.44$). Inspection of the data for each sampling period in Fig. 2 shows that during the 28 October–6 November period, the Merlin's diet included a substantially lower proportion of juvenile Dunlins relative to their occurrence in the population than during any other period of the winter. We are unable to explain this in either a methodological or biological context and on these bases have no reason to exclude the observation from the data presented here. Statistically, however, it can be demonstrated that this particular point does not fall within the confidence interval of the regression line calculated when the point is excluded ($P = 0.02$; Snedecor and Cochran 1967: 157). Comparison of this second line ($Y = 103.17 - 3.47x$) with that representing the population composition shows that they differ significantly ($P = 0.006$) in their Y-intercepts.

DISCUSSION

The results of this study indicate that Dunlin mortality due to predation is age related, juveniles experiencing a higher rate of predation than adults. Although we examined the diet of only one predator, we suspect that these results may apply to other predators as well. An analysis of kills made by Short-eared Owls during the study at Bolinas Lagoon also showed a preponderance of juveniles among the Dunlin remains (73% juveniles, $n = 18$). More complete information concerning the hunting methods and diets of specific predators will be required before the generality of our results can be ascertained.

The composition of the Merlin's diet at various stages of the winter appears to be determined, in part, by the relative availability of adult and juvenile Dunlins on the lagoon, as evidenced by the nearly parallel decline in the two regression lines in Fig. 2. Dunlins are clearly not selected at random from the population, however.

Several aspects of the distribution and behavior of Dunlins on the lagoon may contribute to this age difference in vulnerability (Kus 1980, in prep.). Dunlins associate in highly cohesive flocks, both on the ground and in the air. Flocking in Dunlins appears to facilitate early detection of approaching predators and is particularly important in thwarting attacks by the Merlin, whose success in hunting is determined, in large part, by its ability to surprise flocks on the ground (Page and Whitacre 1975, Kus 1980). Additionally, the synchronous maneuvers of airborne flocks appear to hinder the Merlin's ability to single out a particular individual for attack. Moreover, individual vulnerability is inversely related to flock size and is increased with greater proximity to the flock periphery (Kus in prep.). Differences between age-classes with respect to these determinants of risk could explain, in part, the high level of juvenile mortality that we observed in the present study (Kus unpubl. data). Additionally, juvenile vulnerability may be enhanced by a general inexperience in avoiding attacks by predators. Young birds may fail to respond appropriately to flock alarm calls or may be less coordinated in maintaining synchrony with the rest of the flock during an attack, thereby increasing their vulnerability even further.

ACKNOWLEDGMENTS

We are grateful to the many PRBO volunteers who helped us capture, band, and count Dunlins on Bolinas Lagoon. Michael Miller contributed invaluable assistance with statistical analyses. David Ainley, Joel Berger, Robert Boekelheide, John Bulger, David DeSante, Jan Mendelson, Tom Miller, J. P. Myers, Matthew Rowe, Steve Smith, David Winkler, and an anonymous reviewer provided helpful comments on the manuscript. William J. Hamilton III lent support and helpful comments throughout this study. Margaret Greene provided essential logistic support. This study was funded in part by grants to the senior author from the U. C. Davis Jastro-Shields Research Scholarship Fund, the Frank M. Chapman Memorial Fund, and Sigma Xi, the Scientific Research Society. This is contribution number 254 of Point Reyes Bird Observatory.

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Dr. Robert E. Bleiweiss was appointed Chapman Fellow for the period September 1983 through August 1984. He will study the systematics and speciation in Andean hummingbird genera. Dr. Robert M. Zink, also appointed a Chapman Fellow for September 1983 through August 1984, will study the systematic and biogeographic relationships of thrashers (*Toxostoma*) and the Brown Towhee complex (*Pipilo*) in the aridlands of North America.

Chapman grants during 1983, totalling $34,623 with a mean of $533, were awarded to: Marianne G. Ainley, American women ornithologists: their contributions to science 1900–1950; Peter Arcese, correlates and consequences of dominance behavior in the Song Sparrow (*Melospiza melodia*) on Mandarte Is., B.C.; Christopher Paul Lyman Barkan, risk sensitive foraging behavior of Black-capped Chickadees; James C. Bednarz, ecological study of the cooperatively breeding Harris' Hawk; Paul S. Bencuya, parental role partitioning in the Merlin and its adaptive significance; Craig W. Benkman, food availability, foraging efficiency and the regulation of Crossbills (*Loxia*) in eastern North America; David E. Blockstein, reproductive behavior and parental investment in the Mourning Dove (*Zenaida macroura*); Jeffrey D. Brawn, effects of density on the breeding biology of Western Bluebirds; Mark Andrew Brazil, winter distribution and comparative ecology of Steller's and White-tailed Sea Eagles in north-east Hokkaido, Japan; Charles R. Brown, costs and benefits of coloniality in Cliff Swallows in Nebraska; Angelo Paul Capparella, effects of riverine barriers on gene flow in Amazonian forest undergrowth birds; Peng Chai, factors affecting prey selection of various insect taxa by the Rufous-tailed Jacamar (*Galbula ruficauda*); Jeffrey D. Cherry, interaction of magnetic, stellar, and sunset cues in the orientation of nocturnal restlessness of migratory sparrows; Bruce A. Colvin, Barn Owl nesting, population dynamics, and dispersion in southwest New Jersey; Nonie Coulthard, White-throated Bee-eater (*Merops albicollis*): cooperative breeding in relation to ecological factors; Janice R. Crook, helping and infanticide in the Barn Swallow; Thomas A. Davis, water balance and incubation physiology of avian eggs in wet nests; William James Davis, acoustic communication in the Belted Kingfisher (*Megaceryle alcyon*); John Merrit Emlen and R. Cary Tuckfield, ecological and evolutionary determinants of song variation in Black-throated Sparrows: R. Todd Engstrom, geographic variation in clutch size in birds; Susan Evarts, test of the incidence of multiple paternity in Mallard (*Anas platyrhynchos*) clutches; Anthony David Fox, summer feeding ecology of the Greenland White-fronted Goose, with particular emphasis on pre-nesting behaviour; Thomas L. George, density compensation on Baja California islands: the role of predation; J. Christopher Haney, selection pressures and the evolution of sociality in the White-throated (*Cyanolyca mirabilis*) and Silver-throated (*C. argentigula*) Jays; Lise A. Hanners, influences of parent/offspring behavior on Laughing Gull (*Larus atricilla*) reproductive success; Sara M. Hiebert, control of torpor in hummingbirds; A. M. Hindmarsh, vocal mimicry of starlings on Fair Isle; Peter W. Houde, Lithornithidae of North America; David Hutchinson, Discovery Park Anna's Hummingbird project and the range expansion of Anna's Hummingbirds in the Pacific northwest; Victoria Ingalls, avian predator strategies to insect startle defences: the habituation of blue jays to successive presentations of startling stimuli; Paul A. Jones, breeding biology of a founding colony of California Gulls (*Larus californicus*), Alviso, California; Jan Kalina, socioecology of Black-and-White Casqued Hornbills (*Bycanistes subcylindricus*) and their role as seed dispersers for tropical rainforest trees; Chris Kellner, predation ecology of American Kestrels wintering in central Kentucky; Douglas J. Levey, seed size and the

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