The Condor 95:528–535

WINTER FORAGING AND DIET COMPOSITION OF NORTHERN SHRIKES IN IDAHO[1]

ERIC C. ATKINSON[2] AND TOM J. CADE
Raptor Research Center, Boise State University, Boise, ID 83725

Abstract. We observed color-banded and/or radio-tagged Northern Shrikes (*Lanius excubitor*) wintering in southwest Idaho and determined that foraging success of these shrikes was over 69%. Foraging success was dependent upon the type of prey attacked. Predation success upon arthropods was greater than 90%, whereas predation upon vertebrates (small mammals and passerines) was substantially lower (56% and 19%, respectively). We collected 237 pellets from 12 shrikes and identified 671 individual prey items contained in these pellets. Arthropods and small mammals were the most important prey items as measured by number (63.9% and 29.8%, respectively) and Index of Relative Importance (38.9% and 59.6%, respectively), whereas small mammals were the most important components of shrike diet by biomass contributing 83.1% of the total prey biomass. Passerines were of lesser importance in the winter diet of shrikes accounting for 11.8% of the biomass but only 1.7% of the Index of Relative Importance.

Key words: Diet breadth; Northern Shrike; Lanius excubitor; *prey choice; Index of Relative Importance; foraging success.*

INTRODUCTION

Shrikes are noted for their divergence from the more common passerine lifestyles into the predatory mode of small raptors. In North America, shrikes of the genus *Lanius* are often known by the name "butcherbird," arising from their habit of impaling large prey upon stumps, thorns, or barbed-wire. In addition to eating insects, vertebrates often make up a substantial portion of their diet (Miller 1931, Cade 1967, Scott and Morrison 1990, but see Tye 1984).

Little is known of the Northern Shrike (*Lanius excubitor*), as it is a relatively uncommon and erratic winter visitor to the continental United States (Davis 1937, 1949, 1960, 1974; Hubbard 1978; Davis and Morrison 1988). During the winter, Northern Shrikes can be observed sitting atop tall trees and powerlines and occasionally loitering around well-stocked bird feeders, where they prey upon small granivorous birds such as House Sparrows (*Passer domesticus*) and finches (*Carduelis* sp. and *Carpodacus* sp.).

With the importance of winter limitation of migratory songbird populations being realized (Terborgh 1980, Askins et al. 1990, Lymn and Temple 1991) studies of avian winter ecology have much to offer. Many passerine species spend a considerable amount of time on their wintering grounds, hence, the importance of interspecific competition, predation, and mortality during these months can not be overlooked as factors that potentially limit population size. Information on the winter diet of such poorly known species can provide the framework for studies of foraging ecology, winter territoriality, resource partitioning, and, ultimately, population regulation.

We studied the winter prey choice and foraging behavior of Northern Shrikes and present the results below.

METHODS

We performed the study in the shrub steppe of southwest Idaho during winters 1988–1989 and 1989–1990. A description of the study area and climate is found in Atkinson (1993).

TECHNIQUES

We trapped twelve Northern Shrikes on bal-chatri traps baited with either house mice (*Mus musculus*) or Zebra Finches (*Peophila guttata*). During the winter of 1988–1989, we color banded six shrikes with aluminum bands. Additionally, in the 1989–1990 season, each of six birds was outfitted with a small (<2 g) radio transmitter

[1] Received 12 August 1992. Accepted 3 February 1993.
[2] Present address: 4980 E. Baseline Rd., Belgrade, MT 59714.

(Holohil Systems, Ltd., Ontario, Canada). Foraging behavior was noted during 2–4 hr observation periods.

Like raptors, shrikes regurgitate pellets containing indigestible materials including bones, hair, feathers, and arthropod exoskeletons. We collected pellets from beneath night roosts and hunting perches. We measured the length (not counting extra protrusions such as feathers or bones) and diameter of each pellet and subsequently dissected each pellet under a dissecting scope at 10×. We identified and enumerated all portions of arthropods (mandibles and exoskeleton fragments) and bones, teeth, hair, and feathers of vertebrates to the lowest possible taxon. The vertebrate collection of the Biology Department at Boise State University was used for reference. We tallied a minimum number of individuals of each taxon in each pellet by counting head capsules of insects, long bones and culmens of birds, and long bones and mandibles (or maxillae) of mammals. For each taxon, we calculated the percent frequency of occurrence (percent of pellets containing said taxon) (F), percent of the total number of prey items (N), and percent of total biomass (B). We obtained mass estimates for each taxon for the study area from the literature and from personal records (Larrison and Johnson 1981; Dunning 1984; Hayward 1985; Clark and Stromberg 1987; E. C. Atkinson, unpubl. data). We calculated an Index of Relative Importance (IRI) for each taxon following Day and Byrd (1989); IRI = F(N + B). This measure incorporates all three major diet attributes into one variable in which large IRI values indicate relatively "important" prey groups.

To compare the winter diet of Northern Shrikes to the diet of this species on its breeding grounds, we also analyzed the data presented by Cade (1967) for northern Alaska. For both data sets, we calculated several statistics: (i) Hill's numbers, which are measures of diversity, (ii) diet breadth, calculated as

$$B_j = \frac{1}{\sum_{i}^{r} p_{ij}^2}$$

where p = the proportion of the total prey items represented by each prey group (Levins 1968), and (iii) rarefaction curves, which allow comparison of data sets of different sample sizes. Hill's numbers (N1 and N2) correspond to the abundant and very abundant taxa, respectively. N1 is equivalent to e (the base of natural logarithms) with Shannon's Index as the exponent, whereas, N2 is the reciprocal of Simpson's Index (Ludwig and Reynolds 1988). To allow comparison of diet breadths of these data with those for Cade's data, we calculated standardized diet breadths by dividing breadth by the number of prey types eaten in each season (Pianka 1975). To standardize the prey groups in each sample, noncarabid beetles were classified as other beetles in the winter diet sample. Rarefaction curves and Hill's numbers were calculated with the computer package *Statistical Ecology: A Primer on Methods and Computing* (Ludwig and Reynolds 1988).

TABLE 1. Foraging attempts of wintering Northern Shrikes observed in southwest Idaho.

Prey type	Number successful	Number unsuccessful
Arthropoda (total)	(40)	(3)
Araneae	1	–
Coleoptera	13	–
Diptera	14	–
Nymphalidae	–	1
Noctuidae (larvae)	2	–
Unidentified	15	2
Mammalia (total)	(7)	(6)
Sorex sp.	1	–
Microtus sp.	6	–
Unidentified	–	6
Aves (total)	(3)	(13)
Killdeer	–	1
Horned Lark	1	1
American Robin	–	4
Red-winged Blackbird (♂)	–	1
Pine Siskin/Am. Goldfinch	1	2
Dark-eyed Junco	1	2
White-crowned Sparrow	–	2
Total	50	22
Foraging success (%)	69.44	

RESULTS

We observed a total of 72 verified foraging attempts by Northern Shrikes in the study area (Table 1). The majority (69.44%) were successful, with the shrike usually returning to its perch or alternatively flying to a butchering site to handle its prey. After unsuccessful attempts, a shrike often appeared agitated, and returned to a perch flicking its tail and scanning with quick movements of the head.

Foraging success was dependent upon the taxa

TABLE 2. Prey items of Northern Shrikes by frequency of pellets (occurrence), number, biomass, and Index of Relative Importance (IRI) wintering in southwest Idaho (n = 237 pellets).

Taxon	Occurrence		Number		Biomass		IRI	
	n	%	*n*	%	g	%	Total	%
Arthropoda								
Araneae	2	0.84	2	0.30	0.04	<0.01	0.25	<0.01
Insecta								
Orthoptera								
Acridadae	19	8.02	60	8.94	54.00	0.73	77.58	2.01
Unid. grasshopper	5	2.11	6	0.89	5.40	0.07	2.04	0.05
Dermaptera	1	0.42	1	0.15	0.05	<0.01	0.06	<0.01
Hemiptera	2	0.84	2	0.30	0.10	<0.01	0.25	<0.01
Homoptera	1	0.42	1	0.15	0.05	<0.01	0.06	<0.01
Coleoptera								
Carabidae	55	23.21	140	20.86	126.00	1.71	523.85	13.60
"tiger beetles"	9	3.80	9	1.34	0.90	0.01	5.13	0.13
Scarabaeidae	9	3.80	10	1.49	8.00	0.11	6.08	0.16
Staphylinidae	16	6.75	35	5.22	33.25	0.45	38.27	0.99
Tenebrionidae	2	0.84	2	0.30	1.88	0.03	0.28	<0.01
Curculionidae								
Rhynchophorinae	2	0.84	3	0.45	0.03	<0.01	0.38	<0.01
Unid. beetle	81	34.18	153	22.80	137.7	1.87	843.22	21.89
Unid. insect	5	2.11	5	0.75	0.50	<0.01	1.60	0.04
Reptilia								
Sceloporus sp.	2	0.84	2	0.30	7.00	0.09	0.33	<0.01
Unid. lizard	1	0.42	1	0.15	3.50	0.05	0.08	<0.01
Passeriformes								
Horned Lark	3	1.27	3	0.45	92.40	1.25	2.16	0.06
Black-capped Chickadee	2	0.84	2	0.30	21.60	0.29	0.50	0.01
European Starling	1	0.42	1	0.15	79.90	1.08	0.52	0.01
Brewer's Sparrow	1	0.42	1	0.15	20.0	0.27	0.18	<0.01
White-crowned Sparrow	6	2.53	6	0.90	153.00	2.08	5.51	0.14
Dark-eyed Junco	17	7.17	17	2.53	319.60	4.34	49.26	1.28
Pine Siskin	1	0.42	1	0.15	14.60	0.20	0.15	<0.01
House Sparrow	1	0.42	1	0.15	27.4	0.37	0.22	<0.01
Unid. bird	7	2.95	7	1.04	140.70	1.91	8.70	0.23
Mammalia								
Insectivora								
Sorex vagrans	1	0.42	1	0.15	8.00	0.11	0.11	<0.01
Rodentia								
Reithrodontomys megalotis	18	7.59	18	2.68	252.00	3.42	46.30	1.20
*Peromyscus maniculatus**	36	15.19	36	5.37	756.00	10.26	237.42	6.16
*Microtus longicaudus***	6	2.53	6	0.90	240.00	3.26	10.52	0.27
Microtus pennsylvanicus	1	0.42	1	0.15	45	0.61	0.32	<0.01
Microtus sp.	66	27.85	66	9.84	2,838.00	38.51	1,346.55	34.96
Mus musculus	25	10.55	25	3.73	537.5	7.29	116.26	3.02
Unid. rodent	47	19.83	47	7.00	1,445.25	19.61	527.68	13.70
Total			671		7,369.35		3,851.80	

* Possibly some *P. crinitus*.
** Possibly some *M. montanus*.

of the prey (log-likelihood ratio test [Sokal and Rohlf 1981]; G = 42.98, df = 2, $P < 0.001$). Success was much higher when shrikes were taking arthropods than when they were hunting for small mammals (G = 9.67, df = 1, $P < 0.005$). Mammal-hunting in turn was more successful than pursuing birds (G = 3.98, df = 1, $P < 0.05$).

For diet analysis, we collected a total of 237 pellets regurgitated by 12 Northern Shrikes. One hundred eighty-five intact pellets ranged in length from 10.00 to 37.10 mm and in diameter from 7.40 to 14.50 mm ($\bar{x}$ = 22.93, SD = 5.71 and $\bar{x}$ = 11.18, SD = 1.07, respectively). On average, each pellet contained portions of 2.8 prey items.

From these pellets we identified prey items representing 671 individuals of 33 taxa or prey groups (Table 2).

Arthropods were the most numerous prey item and were found in 153 of the pellets dissected. Beetles were by far the most preyed-upon arthropod accounting for over 82% of the insects taken. Of the beetles found in pellets, nearly one-half were carabids. Even though arthropod prey were very small (usually weighing less than one gram), they had a high IRI value owing to the large number taken. In fact, arthropods comprised over one-third of the total IRI and were second only to small mammals.

One hundred ninety-one different pellets contained portions of small mammals. Small mammals made up the bulk of the diet measured by both biomass and IRI (83.1% and 59.6%, respectively). The majority of the rodents eaten by shrikes were voles, although deermice (*Peromyscus maniculatus*), harvest mice (*Reithrodontomys megalotis*), and wild housemice were also taken.

Songbirds were a significant contributor to shrike diet by biomass (11.8%) but less so by either percentage of total number of prey items or percent of total IRI (5.8% and 1.7%, respectively).

Standardized diet breadths and values for Hill's numbers (N1 and N2) for wintering shrike diet and breeding shrike diet (Cade 1967) are presented in Table 3. Hill's numbers, N1 and N2, correspond to the number of abundant taxa (or prey groups) and to the number of very abundant taxa, respectively.

TABLE 3. Hill's numbers and standardized diet breadth for Northern Shrikes wintering in Idaho (this study) and Northern Shrikes breeding in Alaska (from Cade 1967).

	Hill's numbers		Standardized diet breadth
	N1	N2	
Winter	11.8	7.9	0.2144
Adjusted winter	8.7	5.9	0.2180
Breeding	6.3	4.0	0.1742

DISCUSSION

The foraging success of wintering Northern Shrikes was quite high and is similar to estimates for breeding and wintering Loggerhead Shrikes (*L. ludovicianus*) in California (66%, 65%, and 64%) and for both Loggerhead Shrikes and American Kestrels (*Falco sparverius*) (55% and 58%, respectively) wintering in Arizona (Craig 1978, Mills 1979, Morrison 1980, Scott and Morrison 1990). All three of these species hunt in similar manners by drop-pouncing from elevated perches, hawking, hunting while in hovering flight, and occasionally by chasing small passerines. Northern Shrikes maintain winter territories (Atkinson 1991, 1993) and, similar to the situation observed in Loggerhead Shrikes (Miller 1931, Craig 1978), they can simultaneously advertize their territory-occupancy, survey for trespassers, and search the surrounding area for prey; however, in contrast to Craig (1978) and in agreement with Morrison (1980), we believe that the prey-searching behavior of shrikes is not without energetic cost above and beyond simple perching. Alert perching by Black-billed Magpies (*Pica pica*), as opposed to rest perching, can increase energetic costs to approximately 1.7 times basal metabolic rate (BMR) (King 1974, Mugaas and King 1981). Wakely (1978) estimated that when Ferruginous Hawks (*Buteo regalis*) were engaged in sit-and-wait hunting, a behavior characterized by occasional perch changes and short foraging attempts, that costs increased to 2.5 times BMR. The energetic cost of rest perching, on the other hand, has been estimated at 1.27 times BMR (King 1974, Mugaas and King 1981). Cunningham (1979) noted that Loggerhead Shrikes exhibit a lower than expected basal metabolic rate which he correlated with this species' mode of hunting: long periods of sitting, waiting for movements of prey. This lower BMR would translate into considerable savings especially during periods of low prey activity. However, when searching for prey, Northern Shrikes actively scan the surrounding area, often perching in an upright and alert posture, and more importantly, change perches an average of once every two minutes (Atkinson 1991, 1993). Long periods spent at one location are relatively rare.

The high success of preying upon insects accounted for much of the overall success rate. A substantial amount of energy can be gained by preying upon insects without expending inordinate amounts of energy through chasing, overpowering, and handling this type of prey. In fact, Craig (1978) calculated that Loggerhead Shrikes obtained 10–30 times more energy/minute foraging on insects than while foraging on mice, which require substantial handling time. This is in spite of the fact that insects are quite small and contain only a fraction of the energy contained within a small mammal or passerine. There does not appear to be any significant difference in the apparent metabolizable energy contents between arthropod and vertebrate prey (Karasov 1990).

In the winters of southwest Idaho, arthropods are active through much of the season. Even on days when the temperature did not rise above 0°C, spiders, carabids, and dipterans were available on south-facing slopes and near rimrock outcroppings. Sun-warmed rocks may increase the availability of arthropods during the winter, a relationship which may partially account for the importance that Northern Shrikes apparently place on these habitats (Atkinson 1991, 1993). Year-round insect activity apparently provides an important food source for wintering Northern Shrikes; nearly 40% of the total IRI was made up of arthropods. Forty percent may be a slight underestimate of the IRI for arthropods since small dipteran parts were not identified in pellets and shrikes were observed to take flies on warm days (Table 1).

Ground beetles (Carabidae), dung beetles (Scarabaeidae), rove beetles (Staphylinidae), and darkling beetles (Tenebrionidae) can attain large sizes and are active through much of the winter in shrub steppe and mesic areas. The former three families contributed substantially to the overall diet of Northern Shrikes; however, only two of the 352 beetles contained in pellets were tenebrionids (*Eleodes* sp.). This is surprising in light of how visible and easily approached darkling beetles are in sagebrush communities in early spring. On the other hand, shrikes may not prey upon these beetles because of the noxious chemicals they emit when disturbed (Slobodchikoff 1978).

Like the wintering population of Northern Shrikes (Great Grey Shrike) in southeastern Sweden studied by Olsson (1984b), the most important dietary components as measured by both biomass and Index of Relative Importance were small mammals. In this study, nearly one-half (48%) of the identified mammals were voles (*Microtus* spp.) with deermice contributing nearly one-fourth (24%) of the mammals by number. Voles are the staple of the Swedish population accounting for over one-half of the prey items taken. In that area, winters were more severe than in southwestern Idaho and, hence, insects were more scarce; however, similar to the Idaho situation, Olsson (1984a) reported that many of the insects taken were beetles.

The foraging success while preying upon small mammals was over 50%, or greater than twice the success rate while foraging upon songbirds. Small mammals, especially *Microtus* spp., probably represent very high quality prey items for Northern Shrikes. Voles are large-bodied, are active through all seasons and at all portions of the day, and are less agile than small birds; however, preying upon voles is not without risk. A shrike may spend several minutes dancing about and dodging the defensive behavior of the vole before subduing it with bites to the nape.

Northern Shrikes in southwest Idaho relied upon passerines for a relatively minor portion of their winter diet during the two years of the study. The most commonly taken avian species were Dark-eyed Juncos (*Junco hyemalis*) followed by White-crowned Sparrows (*Zonotrichia leucophrys*). Shrikes took birds as small as Black-capped Chickadees (*Parus altricapillus*) and Pine Siskins (*Carduelis pinus*) and as large as European Starlings (*Sturnus vulgaris*). Starlings, in addition to weighing approximately 10 g more than Northern Shrikes, are powerful fliers. We suspect that such prey were probably taken by surprise. Cade (1962, 1967) reported that most birds that fall prey to shrikes are taken by surprise and rarely while in flight. Medium-sized passerines such as Red-winged Blackbirds (*Agelaius phoeniceus*), although sometimes attacked by Northern Shrikes, can easily out-fly their pursuer (pers. observ.).

In comparison of breeding vs. winter diet of Northern Shrikes we used data from Cade (1967) who described the diet of Northern Shrikes during the breeding season in northern Alaska. These data show much similarity with the wintering diet of shrikes in Idaho. Of 807 prey items identified in that study, over 75% were insects, primarily bumblebees (*Bombus* spp.) (357 individuals) and carabids (137 individuals). At 17% (by number), the carabid component of the summer diet is very similar to their importance in winter (22%).

Birds contributed slightly more by number to the breeding season diet than to the winter diet (8% vs. 5%) whereas microtines were twice as common by number as winter prey than as summer prey (30% vs. 16%).

The diversity of wintering shrike diet is slightly greater than that of breeding Northern Shrikes as measured with Hill's diversity numbers. The breeding shrikes studied by Cade (1967) rely upon

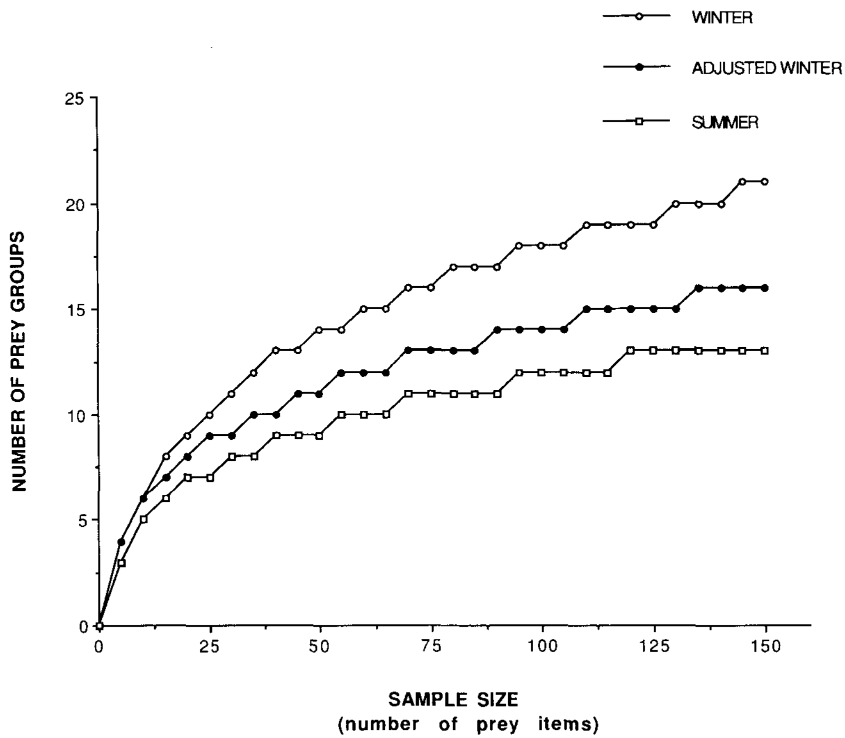

FIGURE 1. Rarefaction curves of Northern Shrike winter diet (this study) and breeding season diet (from Cade 1967).

approximately seven-tenths of the number of abundant and very abundant prey groups to make up their diet than do the wintering shrikes in the present study.

The standardized diet breadth for breeding shrikes in Alaska was approximately 80% of that of wintering shrikes in Idaho, reiterating the fact that the latter take a somewhat larger array of prey items.

The plot of summer and winter rarefaction curves give indications of both evenness and diversity of the diet during each season (Fig. 1). Evenness can be compared by examining the slopes of the rarefaction curves: a steeper slope indicates greater evenness in the sample or community. The proportions of the various prey groups are slightly more equably distributed in the winter diet than in the diet of breeding shrikes.

Diversity is indicated by the height to which the curve rises at given sample sizes. By examining the curves it is apparent that the adjusted diet of wintering Northern Shrikes in Idaho is only slightly more diverse than the diet of breeding shrikes in Alaska.

Wintering Northern Shrikes in Idaho, as well as breeding birds in Alaska (Cade 1967), do not concentrate their foraging efforts on a limited number of prey types. On the contrary, breeding and nonbreeding shrikes take a variety of prey ranging in size from small insects to medium-sized passerines and are, thus, quite diverse and probably very opportunistic in their choice of prey.

Foraging theory predicts that low availability of prey should act to increase diet breadth through the inclusion of less acceptable foods of low value (Emlen 1966, MacArthur 1972, Pulliam 1974). In times of abundant resources (i.e., arctic summers) shrikes should narrow their use of the prey types available and diet breadth should decrease. Wintering shrikes, on the other hand, in response to low overall prey availability, should increase the number of suitable prey taxa contained in their diet. Additionally, thermoregulatory costs associated with low ambient temperatures (Root 1988) should also act to increase diet breadth. This, in fact, appears to be the case in this system; albeit, the diet diversity of wintering shrikes is only slightly greater than that of breeding birds. This may be partially accounted for by differences in actual prey diversity, density, and availability between Idaho and Alaska. For example, Hegazi (1981) reported that Northern Shrikes in the harsh environment of the Egyptian western desert preyed upon arthropods in direct relation to their availability, rarely taking vertebrates. Further studies of Northern Shrikes in areas characterized by harsh winters where arthropods are unavailable may provide insight into the prey selection and the factors that ultimately influence the diet breadth of these predatory songbirds.

ACKNOWLEDGMENTS

We thank James Munger, Alfred Dufty, Marc Bechard, Viking Olsson, and Reuven Yosef for reviewing this manuscript. Charles Baker was very helpful with identification of arthropods. Funding was provided by the Raptor Research Center and the Idaho Department of Fish and Game. Melonie Atkinson was especially helpful and supportive through all portions of the study.

LITERATURE CITED

ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America, p. 1–57. *In* D. M. Power [ed.], Current ornithology. Plenum Press, New York.

ATKINSON, E. C. 1991. Winter ecology of Northern Shrikes (*Lanius excubitor*) in Idaho: foraging, territories, and niche overlap with American Kestrels (*Falco sparverius*). M.Sc.thesis, Boise State Univ., Boise, ID.

ATKINSON, E. C. 1993. Winter territories and night roosts of Northern Shrikes in Idaho. Condor 95: 515–527.

CADE, T. J. 1962. Wing movements, hunting, and displays of the Northern Shrike. Wilson Bull. 74: 386–408.

CADE, T. J. 1967. Ecological and behavioral aspects of predation by the Northern Shrike. Living Bird 6:43–86.

CLARK, T. W., AND M. R. STROMBERG. 1987. Mammals in Wyoming. Museum of Natural History, Univ. of Kansas, Lawrence, KS.

CRAIG, R. B. 1978. An analysis of the predatory behavior of the Loggerhead Shrike. Auk 95:221–234.

CUNNINGHAM, K. G. 1979. Bioenergetics of the Loggerhead Shrike: relation between lifestyle and metabolism. M.Sc.thesis, Univ. of California, Irvine, CA.

DAVIS, D. E. 1937. A cycle in Northern Shrike emigrations. Auk 54:43–49.

DAVIS, D. E. 1949. Recent emigrations of Northern Shrikes. Auk 66:293.

DAVIS, D. E. 1960. Recent emigrations of Northern Shrikes. Auk 77:347–348.

DAVIS, D. E. 1974. Emigrations of Northern Shrikes 1959–1970. Auk 91:821–825.

DAVIS, D. E., AND M. L. MORRISON. 1988. Changes in cyclic patterns of abundance in four avian species. Am. Birds 41:1341–1343, 1345–1347.

DAY, R. H., AND G. V. BYRD. 1989. Food habits of the Whiskered Auklet at Buldir Island, Alaska. Condor 91:65–72.

DUNNING, J. B. 1984. Body weights of 686 species of North American Birds. Western Bird Banding Assoc. Monograph 1.

EMLEN, J. M. 1966. The role of time and energy in food preference. Am. Nat. 100:611–617.

HAYWARD, G. D. 1983. Resource partitioning among six forest owls in the River of No Return Wilderness, Idaho. M.Sc.thesis, Univ. of Idaho, Moscow, ID.

HEGAZI, E. M. 1981. A study of the amount of some invertebrates that are eaten by wild birds in the Egyptian western desert. J. Agric. Sci., Cambridge 96:497–501.

HUBBARD, J. P. 1978. The status of the Northern Shrike in New Mexico. Western Birds 9:159–168.

KARASOV, W. H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. *In* M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. [eds.], Avian foraging: theory, methodology, and applications. Stud. Avian Biol. 13:391–415.

KING, J. R. 1974. Seasonal allocation of time and energy resources in birds, p. 4–85. *In* R. A. Paynter [ed.], Avian energetics. Publ. Nuttall Ornithol. Club 15:1–334.

LARRISON, E. J., AND D. R. JOHNSON. 1981. Mammals of Idaho. Univ. Press of Idaho, Moscow, ID.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ.

LUDWIG, J. A., AND J. F. REYNOLDS. 1988. Statistical ecology: a primer on methods and computing. Wiley-Interscience Publications, New York.

LYMN, N., AND S. A. TEMPLE. 1991. Land-use changes in the Gulf Coast region: links to declines in midwestern Loggerhead Shrike populations. Passenger Pigeon 53:315–325.

MACARTHUR, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York.

MILLER, A. H. 1931. Systematic revision and natural history of the American shrikes (*Lanius*). Univ. Calif. Pubs. in Zool. 38:11–242.

MILLS, G. S. 1979. Foraging patterns of kestrels and shrikes and their relation to an optimal foraging model. Ph.D.diss., Univ. of Arizona, Tucson, AZ.

MORRISON, M. L. 1980. Seasonal aspects of the predatory behavior of Loggerhead Shrikes. Condor 82: 296–300.

MUGAAS, J. N., AND J. R. KING. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie. Stud. Avian Biol. 5:1–78.

OLSSON, V. 1984a. [Winter habits of the Great Grey Shrike *Lanius excubitor*. I. Habitat.] Var Fagelvarld 43:113–124.

OLSSON, V. 1984b. [The winter habits of the Great Grey Shrike *Lanius excubitor*. III. Hunting methods.] Var Fagelvarld 43:405–414.

PIANKA, E. R. 1975. Niche relations of desert lizards, p. 292–314. *In* M. L. Cody and J. M. Diamond

[eds.], Ecology and evolution of communities. Harvard Univ. Press, Cambridge, MA.
PULLIAM, H. R. 1974. On the theory of optimal diets. Am. Nat. 108:59–74.
ROOT, T. L. 1988. Energy constraints on avian distributions and abundances. Ecology 69:330–339.
SCOTT, T. A., AND M. L. MORRISON. 1990. Natural history and management of the San Clemente Loggerhead Shrike. Proc. West. Found. Vertebr. Zool. 4(2):23–57.
SLOBODCHIKOFF, C. N. 1978. Experimental studies of tenebrionid beetle predation by skunks. Behaviour 66:313–322.
SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman, San Francisco, CA.
TERBORGH, J. W. 1980. The conservation status of neotropical migrants: present and future, p. 21–30. *In* A. Keast and E. S. Morton [eds.], Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Inst. Press, Washington, DC.
TYE, A. 1984. Attacks by shrikes *Lanius* spp. on wheatears *Oenanthe* spp: competition, kleptoparasitism or predation? Ibis 126:95–101.
WAKELY, J. S. 1978. Activity budgets, energy expenditures, and energy intakes of nesting Ferruginous Hawks. Auk 95:667–676.