SELECTION OF PREY BY SIZE IN SCREECH OWLS

CARL D. MARTI AND JANET G. HOGUE[1]
Department of Zoology, Weber State College, Ogden, Utah 84408 USA

ABSTRACT.—Five wild-caught Screech Owls (*Otus asio*) were tested for preference of prey by size. Testing was done in flight cages where owls were allowed to select from three alternate regimens of white laboratory mice (*Mus musculus*). These regimens contained either 4 or 8 mice in 4 weight categories (10–19 g, 20–29 g, 30–39 g, 40–49 g). The owls were tested 10 times on each regimen, both when they had eaten as much as they desired the day before and when they were fasted 36 h before testing. Smaller mice were taken in numbers greater than larger ones in all regimens on both hunger levels. Larger mice were taken at higher frequencies by fasted than by fed owls when choice was less, but when greater numbers of mice were available even fasted owls took significantly more smaller mice. Selectivity indices show that the smallest mice were taken above their availability and the largest mice below their availability in every regimen. No significant differences were found between mean individual weights of mice taken by fed or fasted owls but fasted owls did consume a significantly greater total weight of mice per day. Very little variation was found among the owls with respect to size of prey captured, nor was much variation apparent within each owl over all tests. *Received 3 April 1978, accepted 6 December 1978.*

PREDATORS that detect and capture prey individually must do so with enough efficiency that they do not expend more energy than they obtain. Certain prey must exist that are more efficiently found, captured, or killed by predators (Emlen 1968), Schoener 1969). Size of prey is most likely an important factor in this efficiency. Our objective was to determine preferred size of prey and the effect of moderate food deprivation on size selected by the Screech Owl (*Otus asio*) under controlled conditions. Major variables in selection of prey by size include hunger level, experience and size of the predator, prey defenses, and prey densities. We attempted to reduce the variables of predator size, experience, prey defense, and density as much as possible.

Much interest has focused on prey selection since Ivlev (1961) and yet a great deal is still unknown about why a certain predator takes a particular individual prey. Predator-prey relationships are not simple. A host of interacting variables must be considered to understand these relationships fully, but before the interactions of variables can be evaluated, the effect of each must be known. Numerous papers present models that attempt to simplify and/or predict predator-prey relationships (for example, see MacArthur and Pianka 1966, Emlen 1968, Schoener 1971). Additionally, experimental studies have shown predator selection to be based on several aspects of prey vulnerability, i.e. lack of protective coloration (Dice 1947, Kaufman 1974a), oddity (Mueller 1971), and prey activity (Kaufman 1974b). The roles of experience (Mueller and Berger 1970), specific searching image (Tinbergen 1960), and hunger (Mueller 1973) of the predator have also been investigated. Selection of prey by size has been studied in robberflies (Powell and Stage 1962), fish (Werner and Hall 1974, O'Brien et al. 1976), storks (Ogden et al. 1976), and shrikes (Slack 1975), but only to a limited extent in raptors (Storer 1966, Mueller and Berger 1970, Snyder and Wiley 1976).

METHODS AND MATERIALS

Owls used in out tests were wild-caught as adults and thus had experience in hunting under natural conditions. The Screech Owl was chosen because of the wide range of prey it takes and also because its

[1] Present address: 11805 Southwest Butner Road, Portland, Oregon 97225 USA.

The Auk 96: 319–327. April 1979

small size allowed use of prey sizes that could be obtained in sufficient quantities. Based on body weight and wing measurements the owls we used were four males and one female. All prey were white laboratory mice (*Mus musculus*) in 4 size categories: A, 10–19 g; B, 20–29 g; C, 30–39 g; and D, 40–49 g. These sizes cover the range of prey most often taken by races of Screech Owls feeding largely on vertebrates. Three regimens of mice were used. Regimen 1 consisted of one mouse from each size category. This group forced owls to take mice from more than one category if a single mouse did not satisfy their hunger. Regimen 2 had two mice from each size, thus providing more choice within a size category. Regimen 3 contained four mice each from the smallest and largest size categories, thus insuring that an owl could be fully satiated from one or the other of the two extreme prey sizes.

In testing, individual owls were allowed to select prey overnight from regimens of mice in indoor flight cages (2 × 2 × 2.5 m) with temperature maintained at 20–22°C. Mice were given food and water but no shelter from the owls. Photoperiod was automatically controlled on a 12-h light schedule; all tests were done during the owl's normal activity period under light judged subjectively to be about that of a full moon. Two cages had one-way glass for observation of the owl's behavior. Each owl was tested on two hunger levels. Under level 1 the owl was allowed to eat as much as it desired the day before testing. Owls on level 2 were fasted 36 h before testing to simulate wild owls that may not always feed to satiation every night due to adverse weather or low prey populations. Owls were accustomed to the flight cages for at least a week before testing and then left in the cages continuously. Regimens of mice were introduced and left overnight. In the morning they were checked and mice taken by the owls were recorded. Each owl was tested on each regimen for 10 days at each hunger level. This resulted in a total for five owls of 300 tests. Owls were not tested while molting because of the added energy required in growing feathers.

Prey selection indices were calculated using Ivlev's (1961) formula:

$$E = (r - p)/(r + p)$$

where r is the proportion of a mouse weight category taken by the owls and p is the proportion of a mouse weight category available to the owls. Ivlev's index ranges from +1 to −1, with values close to +1 indicating consumption at much greater proportions than availability, those near −1 indicating capture considerably below availability. Indices were calculated for each prey population at each owl hunger level.

RESULTS

Pooled data from five owls show selection on smaller prey over larger in all regimens (Fig. 1). These data were subjected to analysis of variance for repeated measures on rank (Freidman test, Sokal and Rohlf 1969). Regimens 1 and 2 on hunger level 1 produced significant selection on smaller mice ($P < 0.05$). However, when fasted the owls on the same 2 regimens showed more individual variability (Fig. 2) and, although more small mice were taken than large, the difference was not significant ($P > 0.25$). Hunger proved not to be a factor in size selection in regimen 3: the selection patterns for the two hunger levels were very similar (Fig. 1, 2). Selection was not significant in either ($P > 0.10$) because the size of prey taken by one owl was the reverse of the trend for the other birds. When that individual was eliminated from the analysis, significant selection on smaller mice was evident at both hunger levels ($P < 0.05$). The same owl selected prey against the trend in regimens 1 and 2 when fasted. Analysis of these data without that individual showed significant selection on smaller mice in regimen 2 ($P < 0.005$) but not in regimen 1 ($P > 0.10$).

Figure 3 gives Ivlev indices of owl selection in relation to prey availability. Size A mice were selected above their availability in every case while C and D mice were selected below their availability in every situation and greatly below in several.

Overall, no significant difference ($t = 1.11$, $P > 0.05$) was found in the mean weight of individual mice taken between fed and fasted owls, but fasted owls did consume a significantly greater total weight of mice per day (52.7 g vs 29.4 g; t-tests, all $P < 0.001$). Fasted owls took larger numbers of smaller mice when they were

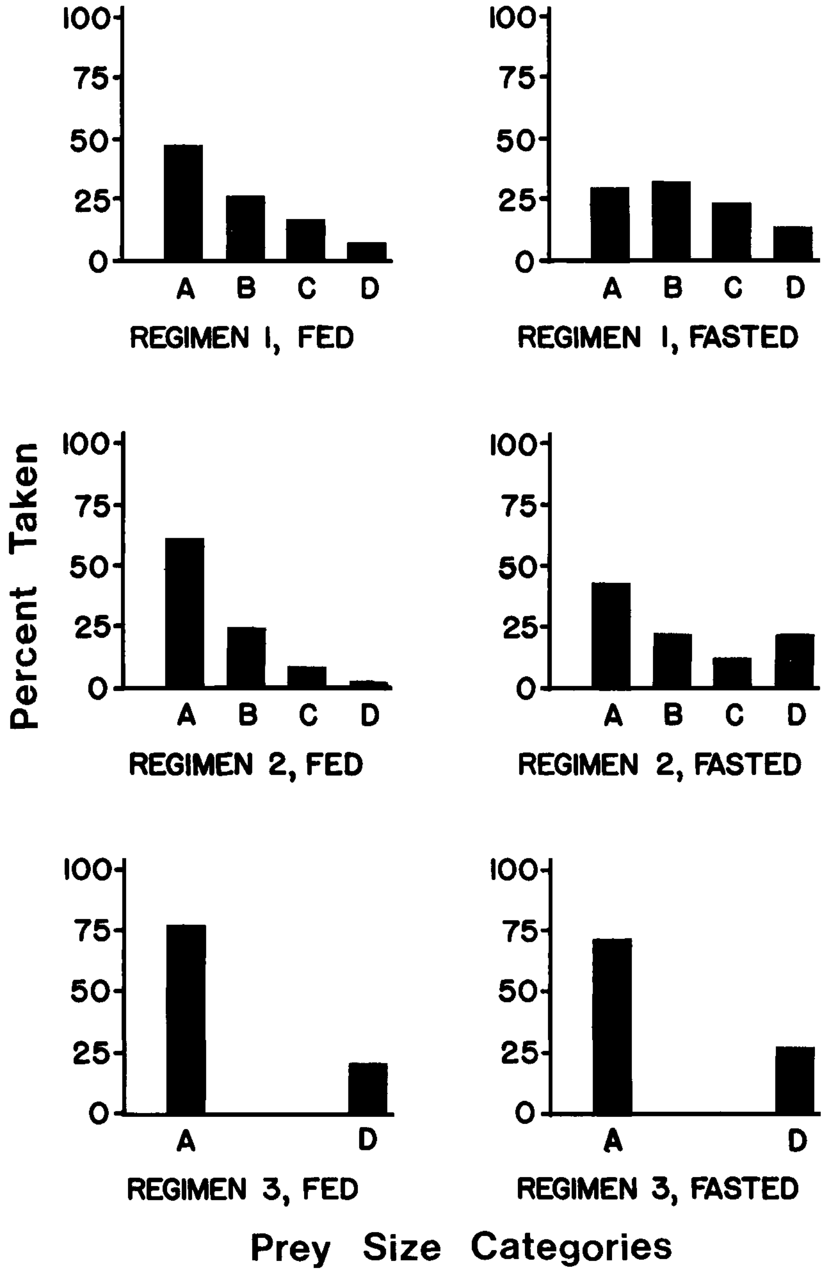

Fig. 1. Prey selection by Screech Owls from prey regimens of varying composition. Data are pooled from five owls. Prey category A = 10–19 g, B = 20–29 g, C = 30–39 g, D = 40–49 g.

available instead of fewer larger ones to achieve an equivalent food intake. We found the owls were consistent in the mean weight of mice they killed per day, i.e. none of the five owls had significant variation in the total weight they killed per day among all three prey populations (F-tests, all $P > 0.05$) when fed daily and only one had significant variation when fasted ($F = 38.17$, $P < 0.005$). No significant

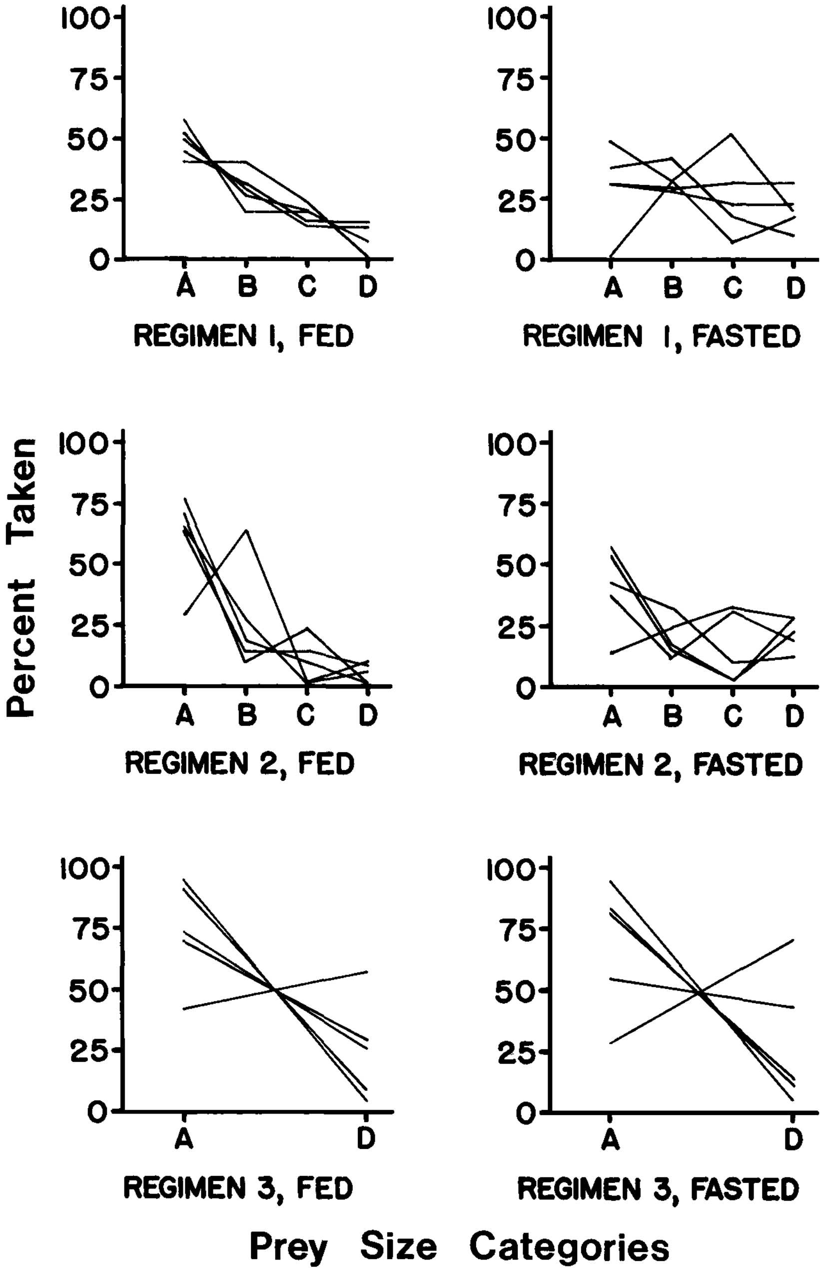

Fig. 2. Selection of prey by five individual Screech Owls from prey regimens of varying composition.

variation among owls in weight of mice killed per day appeared in any regimen when the owls were fed daily (F-tests, all $P > 0.05$). When fasted, significant variation in weight killed per day was found only in regimen 1 ($F = 9.47$, $P < 0.05$).

Our owls very seldom killed mice that they did not at least partially eat. In only one series (fasted owls on regimen 2) was there a significant difference between mean

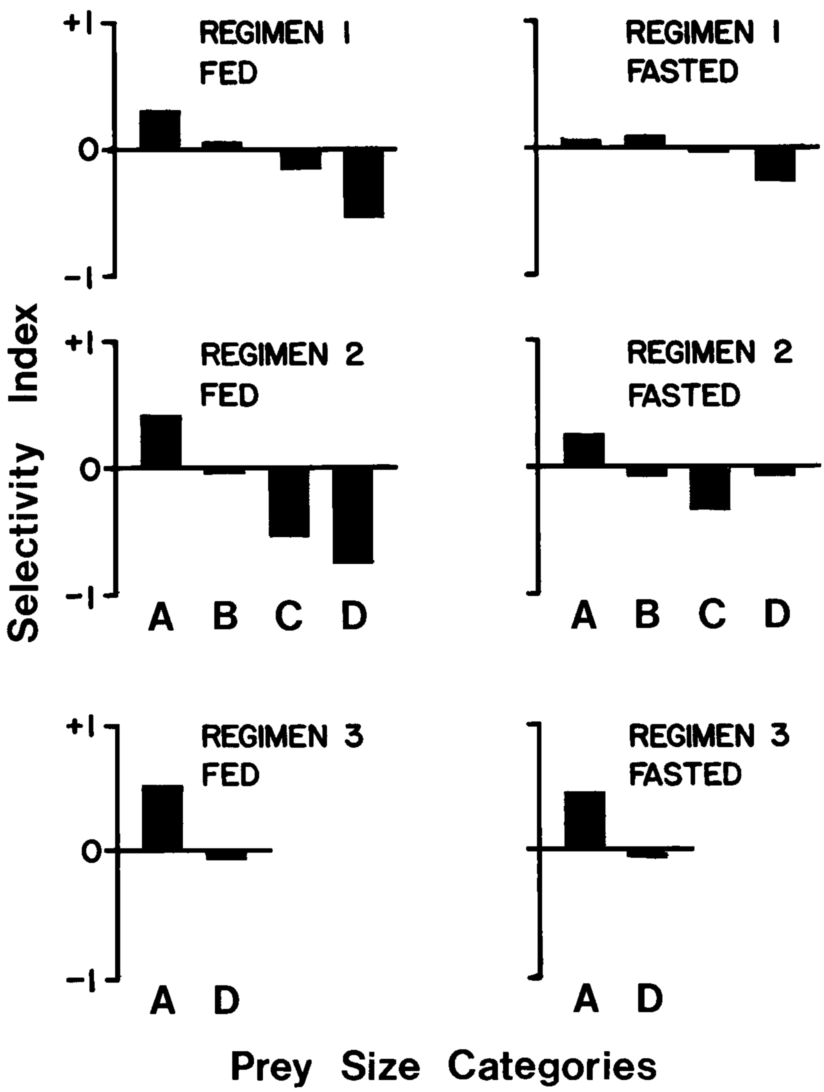

Fig. 3. Selectivity (see text) of Screech Owls under varying prey regimens.

weight of mice killed per day and mean weight of mice eaten per day ($t = 2.22$, $P < 0.05$). However, when mice were only partially consumed all five owls cached the remains, presumably to be eaten later. We removed such cached mice each morning. Caching of food has been reported in several species of owls and other raptors (see Mueller 1974, Collins 1976). Phelan (1977) documented food caching and later consumption of hidden prey by a wild Screech Owl.

Discussion

We found in our tests that fed Screech Owls took smaller prey above its availability in every prey regimen. Increased hunger coupled with low prey density reduced preferential selection of prey by size. However, in regimens that gave greatest choice of prey, the effect of hunger was eliminated and selection of prey by size was essentially the same for fed and fasted owls.

Although few data are yet available, it appears that greater prey abundance increases selection of preferred prey in predators as diverse as insects (Powell and Stage 1962), fish (Ivlev 1961, Werner and Hall 1974), and birds (this study).

If Screech Owls are capable of killing mice weighing 50 g and larger (VanCamp and Henny 1975), why do they not conserve energy used to search for and capture prey by selecting one larger mouse than several smaller ones? Several reasons alone or, more likely, collectively may favor selection of smaller prey. First, more small prey species are available, and within a prey species smaller individuals would likely be younger and less experienced, and thus more vulnerable to predators. Evidence that younger prey may be more vulnerable to owls was given by Lay (1974). Second, energy expended in catching and killing large prey may not be worth risking, as Slack (1975) theorized, if the prey escape more often because they are larger, stronger, or more experienced. Wilson (1975) summarized available evidence to show that within the overall size-range of prey a predator reaches a peak of capture success very rapidly from smallest to larger prey, followed by a broad plateau and then a gradual decline in success with further increases in prey size. Third, risk of injury to the owl may be greater with larger prey. Fourth, Screech Owls are sit-and-wait predators and do not expend much energy in searching for prey, so they may be able to afford to take smaller and thus easier prey. Schoener (1969) predicted that predators that pursue prey over shorter distances should eat smaller prey than wide-ranging predators. Finally, total food consumption for a night may be achieved in two or more widely separated meals, each fully satisfied by smaller prey individuals.

Interpreting results to explain what is occurring in nature should always be a goal of laboratory studies on wild animals. This is often difficult because nature cannot be duplicated in the laboratory and, in fact, most laboratory studies attempt to isolate and measure only one or a few variables. In this study several artificial factors were necessary to ensure equal opportunities for the owls to select various prey sizes. Wild owls would rarely, if ever, be able to select simultaneously from so many potential prey, nor would they often have so long to evaluate prey. We observed our owls many times following the introduction of prey. The birds appeared to carefully inspect prey before attacking; even fasted owls did not immediately attack. First captures rarely occurred in less than 15 min and often not before 30 min following introduction of prey. Wild owls would normally have to make these decisions much faster. Two possible reasons may explain the slower decisions in our captives. The large number of prey simultaneously available might have caused confusion requiring more evaluation, or the owls may have learned that prey would remain available and quick captures were not necessary. Another possible bias in our results could have come from differential activity of certain sizes of mice, since increased activity of prey has been shown to make prey more vulnerable to raptors (Kaufman 1974b). However, subjective observation failed to reveal noticeable differences in level of activity between small and large mice within the test cages. Additionally, mice from each category were tested objectively by counting line-crossing activity in a box with gridded floor. No significant correlation between size and activity was found ($r = 0.25$, $P > 0.05$). Smaller mice did move more quickly than larger ones, but it is not known if this made them more vulnerable. Spiegel et al. (1974) thought that the rapid and erratic movements of wild Norway rats (*Rattus* *norvegicus*) might have made them more vulnerable to owl attack than more sluggish domestic strains.

We reduced the variability of predator size by using a single species. The Screech Owl is a species with a low index of sexual dimorphism in size (Earhart and Johnson 1970). We found no correlation between the mean weights of the owls we used and the mean mouse weight each owl selected when fed daily, when fasted, or all combined ($r = -0.31$, $P > 0.05$). The heaviest bird took prey averaging very nearly the same as two smaller birds. The results of these experiments predict that Screech Owls take vertebrate prey by size without their own body weight being a significant variable. This is in contrast to the much more dimorphic accipiters, especially the Sharp-shinned Hawk (*Accipiter striatus*) (Storer 1966, Snyder and Wiley 1976).

The variability of prey defense was reduced by using a single prey species of one color. We observed no indication that the domestic mice of any size or age used recognized potential threat from the owls. The only apparent variability in prey defense was that larger mice may be more formidable to experienced owls and thus avoided when a choice is available. We used only adult owls experienced in hunting in the wild since Mueller and Berger (1970) and Sparrowe (1972) showed that inexperienced raptors often attempted to take inappropriate prey. We found no evidence that prey selection by individual owls varied significantly among the five birds used.

For such a widespread and abundant species, an unexpectedly small amount of data is available on the diets of wild Screech Owls. We combined 12 studies to obtain a sample of 3,524 prey (Allen 1924, Cahn and Kemp 1930, Errington 1932, Kelso 1938, Wilson 1938, Craighead and Craighead 1956, Eaton and Grzybowski 1969, Stewart 1969, Smith and Wilson 1971, VanCamp and Henny 1975, L. J. Korschgen pers. comm., D. G. Smith pers. comm.). These data were used to estimate a mean prey weight of 38.1 g for wild Screech Owls, which is considerably greater than the mean of 23.1 g for prey of owls in our experiments. However, this apparent discrepancy may not in reality be as great. Weights of prey of wild owls used to estimate the mean prey weight were averages of adult animals (Marti 1976). Wild Screech Owls may have selected smaller individuals of some species, thus inflating our estimate.

More detailed prey information, admittedly very difficult to obtain, is needed on individual wild owls for better comparisons. Screech Owls take a wide diversity of prey; Errington (1932) termed them opportunistic predators. This versatility may have survival advantages if preferred prey decline and may be especially important to a nonmigratory raptor. Some races feed heavily on arthropods (Ross 1969). We included in our analysis only studies of races feeding primarily on vertebrates to compare with our experimental results. Voles (*Microtus* spp.) were by far the most abundant prey of wild Screech Owls. These mice exist in very much the same range of weights we offered to our birds. However, the relative abundance and vulnerability of different weights of voles in the wild are not known.

It must be remembered that size of prey is only one of the important parameters in prey selection. Furthermore, interaction with other factors may affect the size of prey that will be taken. We have shown that both predator hunger and prey availability alter size selection.

ACKNOWLEDGMENTS

Support for this study came from a Weber State College Faculty Research and Development Grant to the senior author. Special thanks go to Kathryn W. Denne for help in numerous aspects of this project.

Thanks also to Gary G. Bogue, James A. Mosher, and Charles J. Henny for supplying the Screech Owls used, and to Wayne I. Jensen who contributed mice used as prey. Joseph R. Murphy and Clayton M. White read an earlier draft and supplied helpful suggestions. James H. Foster and Kimbal L. Wheatley gave valuable statistical assistance. We are grateful to Leroy J. Korschgen and Dwight G. Smith for unpublished data on prey of wild Screech Owls.

LITERATURE CITED

ALLEN, A. A. 1924. A contribution to the life history and economic status of the Screech Owl (*Otus asio*). Auk 41: 1–16.

CAHN, A. R., & J. T. KEMP. 1930. On the food of certain owls in east-central Illinois. Auk 47: 323–328.

COLLINS, C. T. 1976. Food caching behavior in owls. Raptor Res. 10: 74–76.

CRAIGHEAD, J. J., & F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Harrisburg, Pennsylvania, Stackpole.

DICE, L. R. 1947. Effectiveness of selection by owls of deer-mice (*Peromyscus maniculatus*) which contrast in color with their background. Contrib. Lab. Vert. Biol. Univ. Michigan, Ann Arbor. 34: 1–20.

EARHART, C. M., & N. K. JOHNSON. 1970. Size dimorphism and food habits of North American owls. Condor 72: 251–264.

EATON, S. W., & J. A. GRZYBOWSKI. 1969. Food habits of owls on the Niagra frontier. Kingbird 19: 135–138.

EMLEN, J. M. 1968. Optimal choice in animals. Amer. Natur. 102: 385–389.

ERRINGTON, P. L. 1932. Food habits of southern Wisconsin raptors. Part 1. Owls. Condor 34: 176–186.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. New Haven, Connecticut, Yale Univ. Press.

KAUFMAN, D. W. 1974a. Adaptive coloration in *Peromyscus polionotus*: experimental selection by owls. J. Mammal. 55: 271–283.

———. 1974b. Differential predation on active and inactive prey by owls. Auk 91: 172–173.

KELSO, L. H. 1938. A study of the Screech Owl (*Otus asio*). Unpublished M.S. thesis, Ithaca, New York, Cornell Univ.

LAY, D. M. 1974. Differential predation on gerbils (*Meriones*) by the Little Owl, *Athene brahma*. J. Mammal. 55: 608–614.

MACARTHUR, R. H., & E. R. PIANKA. 1966. On optimal use of a patchy environment. Amer. Natur. 100: 603–609.

MARTI, C. D. 1976. A review of prey selection by the Long-eared Owl. Condor 78: 331–336.

MUELLER, H. C. 1971. Oddity and specific searching image more important than conspicuousness in prey selection. Nature 233: 345–346.

———. 1973. The relationship of hunger to predatory behavior in hawks (*Falco sparverius* and *Buteo platypterus*). Anim. Behav. 21: 513–520.

———. 1974. Food caching behavior in the American Kestrel (*Falco sparverius*). Z. Tierpsychol. 34: 105–114.

———, & D. D. BERGER. 1970. Prey preferences in the Sharp-skinned Hawk: the roles of sex, experience and motivation. Auk 87: 452–457.

OGDEN, J. C., J. A. KUSHLAN, & J. T. TILMANT. 1976. Prey selectivity by the Wood Stork. Condor 78: 324–330.

O'BRIEN, W. J., N. A. SLADE, & G. L. VINYARD. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57: 1304–1310.

PHELAN, F. J. S. 1977. Food caching in the Screech Owl. Condor 79: 127.

POWELL, J. A., & G. I. STAGE. 1962. Prey selection by robberflies of the genus *Stenopogon,* with particular observations on *S. engelhardti* Bromley (Diptera: Asilidae). Wasmann J. Biol. 20: 139–157.

ROSS, A. 1969. Ecological aspects of the food habits of insectivorus Screech Owls. Proc. West. Found. Vert. Zool. 1: 301–344.

SCHOENER, T. W. 1969. Models of optimal size for solitary predators. Amer. Natur. 103: 277–313.

———. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369–404.

SLACK, R. S. 1975. Effects of prey size on Loggerhead Shrike predation. Auk 92: 812–814.

SMITH, D. G., & C. R. WILSON. 1971. Notes on the winter food of Screech Owls in central Utah. Great Basin Natur. 31: 83–84.

SNYDER, N. F. R., & J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20: 1–95.

SOKAL, R. R., & F. J. ROHLF. 1969. Biometry. San Francisco, W. H. Freeman Co.

SPARROWE, R. D. 1972. Prey-catching behavior in the Sparrow Hawk. J. Wildl. Mgmt. 36: 297–308.

SPEIGEL, R., E. PRICE, & U. W. HUCK. 1974. Differential vulnerability of wild, domestic, and hybrid Norway rats to predation by Great Horned Owls. J. Mammal. 55: 386–392.

STEWART, P. A. 1969. Prey in two Screech Owl nests. Auk 86: 141.

STORER, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83: 423–436.

TINBERGEN, L. 1960. The natural control of insects in pinewoods. 1. Factors influencing the intensity of predation by songbirds. Arch. Neerl. Zool. 13: 265–343.

VANCAMP, L. F., & C. J. HENNY. 1975. The Screech Owl: its life history and population ecology in northern Ohio. U.S. Fish Wildl. Serv., N. Amer. Fauna No. 71.

WERNER, E. E., & D. J. HALL. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042–1052.

WILSON, D. S. 1975. The adequacy of body size as a niche difference. Amer. Natur. 109: 769–784.

WILSON, K. A. 1938. Owl studies at Ann Arbor, Michigan. Auk 55: 187–197.