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# Prey Selection by Breeding and Nonbreeding Barn Owls in Argentina

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Numerous studies have focused on the foraging ecology of Barn Owls (*Tyto alba*). Food habits of Barn Owls have been described from many regions of the world (e.g. Herrera 1974, Dean 1975, Morton and Martin 1979, Jaksić et al. 1982, De Santis et al. 1983, Lenton 1984, Campbell et al. 1987, Bellocq 1990, Nores and Gutiérrez 1990). In most parts of their range, Barn Owls feed primarily on small mammals and occasionally on a variety of other vertebrates. Further studies have demonstrated that the food niche of Barn Owls varies in time and space (Marti 1988) and have established the role of the species within assemblages of vertebrate predators (Jaksić and Delibes 1987, Marti et al. 1993). Differential predation by Barn Owls on the species, size, and/or sex of small mammals has been reported in populations from both northern (Derting and Crandford 1989) and southern (Jaksić and Yáñez 1979, Dickman et al. 1991, Bellocq and Kravetz 1994) latitudes.

Differential predation by owls on rodents has been attributed primarily to differences in prey vulnerability (Longland 1987, Vassallo 1994). Selective feeding may have a more (Roberts and Wolfe 1974) or less (Errington 1956) disruptive effect on rodent populations depending on the sector of the population that is preferred, and may influence rodent behavior (Brown et al. 1988). Most previous analyses of differential predation by owls have emphasized prey vulnerability or the effects on prey populations. Here, I analyze diet composition, differential predation on rodents (by species, size, and sex), and feeding strategy of breeding and nonbreeding Barn Owls close to the southern limit of the species' distribution in Argentina.

*Study area and methods.*—The study area was established in the districts of San Andrés de Giles and Exaltación de la Cruz (province of Buenos Aires), centered in Diego Gaynor, Argentina (34°18′S, 59°14′W). At the regional scale, the area is located in the east-central zone of the country, better known as Pampas. Originally a prairie, the area has been gradually transformed into an agricultural landscape. Two main habitats are distinguished in this environment, crop fields and borders of crop fields. Crop fields occupy approximately 95% of the study area and are exposed to high levels of perturbation due to agricultural practices. Borders of crop fields are narrow habitats with natural vegetation (grasses) that occurs along fences, roads, and railways. Border habitat suffers relatively low human disturbance. The primary and secondary uses of the land are growing cereal crops (especially wheat, corn, and soya) and livestock grazing, respectively. The natural vegetation is dominated by native (*Bothriochloa* spp., *Paspalum* spp., *Stipa* spp.) and introduced (*Lolium* spp., *Briza* spp., *Bromus* spp.) grass species. Mean annual temperature is 16.0°C, and mean annual precipitation is 946 mm.

The Barn Owl diet was determined from pellet analysis, following the general procedure summarized by Marti (1987). To analyze seasonal variation in consumption of main types of prey, 860 pellets were collected from nesting and roosting sites from the fall of 1985 to the summer of 1987. Two-way ANOVA was conducted on arcsine-transformed data to test for differences in the percentage of rodents in the diet among years and seasons. Prey biomass was estimated based on records from local collections (Bellocq 1988).

Rodent species, size class, and sex were identified based on molars and innominate bones (see Bellocq and Kravetz 1983). Regressions between body mass and tooth wear allowed the prediction of size categories of rodents found in pellets (Bellocq 1988). Determination of size class and sex was not possible in some cases because the molars were absent or the pelvis broken. Size classes were established for two species of rodents following Bellocq and Kravetz (1994): (1) *Calomys laucha*, Class 1 (juveniles), <9.0 g; Class 2 (medium-sized adults), 9.1 to 15.0 g; Class 3 (large-sized adults), >15.0 g; (2) *Akodon azarae*, Class 1, <15.0 g; Class 2, 15.1 to 25.0 g; Class 3, >25.0 g. Data were pooled by fall-winter (April to September) and spring-summer (October to March) because Barn Owls breed during the fall-winter in Diego Gaynor (Bellocq and Kravetz 1993). The log-likelihood ratio was used to test the absolute frequencies of occurrence of prey categories in pellets against the hypotheses that those frequencies were similar to the relative frequencies of prey categories in the rodent populations trapped in the area.

Relative abundance of rodent species, size categories within species, and sexes in the field were estimated by livetrapping within a 40-km$^2$ area that included the sites where pellets were collected. Lines of 20 or 45 Sherman traps (10 m apart) were established in 7 crop fields and 11 borders of crop fields.

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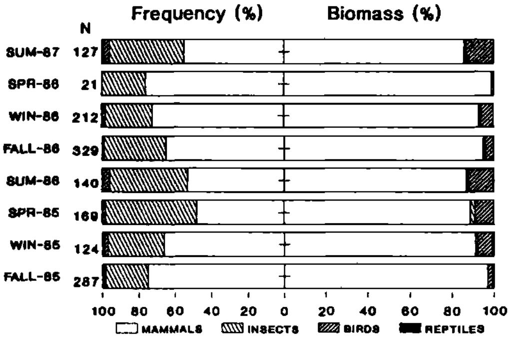

FIG. 1. Composition and seasonal variation in the diet of Barn Owls in east-central Argentina.

Traps were operated for five consecutive days, approximately once a month from April 1984 to March 1985. Captured mammals were identified, weighed, ear-tagged, classified by sex and reproductive condition, and released at the site of capture. Because crop fields occupy approximately 95% of the total study area (based on aerial photographs and site recognition), a correction for habitat heterogeneity was conducted to estimate expected frequencies of rodent species (see Bellocq 1987). Several studies on population fluctuations of rodents in central Argentina showed a synchronized pattern in the short-term dynamics and similar seasonal patterns of relative abundance, age structure, and sex ratio (Pearson 1967, Kravetz et al. 1981, Zuleta et al. 1988, Busch and Kravetz 1992). Therefore, field data obtained in 1984 to 1985 on relative abundance of rodents and their availability by size and sex were compared with data on prey consumption by owls during 1985 to 1987. I used Manly's alpha as a preference index because it is appropriate when the number of prey eaten is very small relative to the total (Krebs 1989). Manly's alpha was calculated following Chesson (1978):

$$\alpha_i = r_i n_i^{-1}\left(\sum_{j=i}^{m} r_j n_j^{-1}\right)^{-1}, \qquad (1)$$

where $r_i$ is the proportion of prey category $i$ in the diet, $n_i$ is the proportion of prey category $i$ in the wild, and $m$ is the total number of prey categories. When preference does not occur, $\alpha_i = m^{-1}$, $i = 1 \ldots m$. Prey category $i$ is preferred if $\alpha_i > m^{-1}$ and avoided if $\alpha_i < m^{-1}$.

*Results.*—In east-central Argentina, the Barn Owl is a specialist on small rodents, although occasionally it feeds on birds, insects, and reptiles. In terms of numbers, mammals were the most common prey year-round, followed by insects, birds, and reptiles (Fig. 1). In terms of biomass, however, Barn Owls fed primarily on small rodents and secondarily on birds, whereas the contribution of insects was negligible. There was no significant difference in the proportion of mammals in the diet between years ($F = 0.563$, $P > 0.5$) and seasons ($F = 0.461$, $P > 0.5$).

Barn Owls preyed on at least seven species of rodents in the study area, five species of Cricetidae, one of Muridae, and one of Caviidae (Table 1). Barn Owls exhibited differential predation on rodent species, preying more on *A. azarae* and *Oligoryzomys flavescens* and less on *C. laucha* than expected based on trapping in 1985 ($\chi^2 = 70.8$, df = 2, $P < 0.001$) and 1986 ($\chi^2 = 242.3$, df = 2, $P < 0.001$).

Predation by size (within rodent species) differed between the breeding and nonbreeding season of the owls. Frequencies of size categories of rodents in pellets differed from those expected for both *C. laucha* and *A. azarae* during fall-winter, and for *C. laucha* but not *A. azarae* during spring-summer (Table 2). In fall-winter, the owls consistently took a higher frequency of large rodents and a lower frequency of medium-sized rodents relative to the abundance of these size categories in the field. Juveniles were taken in proportion to their availability year-round. Seasonal variation in owl preference for large-sized rodents was similar for *C. laucha* and *A. azarae*, with preference increasing from summer to winter and then declining (Fig. 2).

During fall-winter, owls preyed more on female rodents and less on males than expected based on trap captures, although differences were not statis-

TABLE 1. Occurrence of rodent species (%) in the diet of Barn Owls in east-central Argentina by season, 1985 to 1987. Average body mass (g) in parentheses.

| Species | FALL-WIN 1985 | SPR 1985–SUM 1986 | FALL-WIN 1986 | SPR 1986–SUM 1987 |
|---|---|---|---|---|
| *Calomys laucha* (11.7) | 51.7 | 38.6 | 39.8 | 42.1 |
| *Akodon azarae* (20.0) | 28.7 | 39.3 | 35.7 | 34.2 |
| *Oligoryzomys flavescens* (23.0) | 7.5 | 10.0 | 19.5 | 15.8 |
| *Calomys musculinus* (13.5) | 10.9 | 11.4 | 4.9 | 2.6 |
| *Rattus* spp. | 0.4 | 0.7 | 0.0 | 5.3 |
| *Reithrodon* spp. | 0.4 | 0.0 | 0.0 | 0.0 |
| *Cavia aperea* | 0.4 | 0.0 | 0.0 | 0.0 |
| No. pellets analyzed | 92 | 77 | 155 | 28 |
| No. prey items | 265 | 140 | 344 | 38 |

TABLE 2. Frequency of size categories in pellets ($f_o$) versus availability from trapping ($f_e$) for the two main rodent species in the diet of Barn Owls in east-central Argentina. Class 1, juveniles; Class 2, medium-sized adults; Class 3, large-sized adults (see text for size intervals).

| | FALL–WIN 1985 | | | SPR 1985–SUM 1986 | | | FALL–WIN 1986 | | | SPR 1986–SUM 1987 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $f_o$ | $f_e$ | $G^a$ | $f_o$ | $f_e$ | $G$ | $f_o$ | $f_e$ | $G$ | $f_o$ | $f_e$ | $G$ |
| | | | | | | *Calomys laucha* | | | | | | |
| Class 1 | 22 | 23 | $71.18^{**}$ | 13 | 8 | $29.23^{**}$ | 37 | 32 | $60.86^{**}$ | 4 | 2 | $6.44^{*}$ |
| Class 2 | 58 | 94 | | 20 | 32 | | 58 | 95 | | 5 | 10 | |
| Class 3 | 55 | 17 | | 17 | 6 | | 47 | 15 | | 7 | 4 | |
| | | | | | | *Akodon azarae* | | | | | | |
| Class 1 | 9 | 15 | $33.46^{**}$ | 7 | 7 | $5.6^{ns}$ | 22 | 27 | $28.90^{**}$ | 2 | 2 | $1.75^{ns}$ |
| Class 2 | 40 | 52 | | 34 | 27 | | 71 | 87 | | 9 | 7 | |
| Class 3 | 25 | 7 | | 10 | 17 | | 33 | 12 | | 2 | 4 | |

$^{*}$, $P < 0.05$; $^{**}$, $P < 0.001$; ns, $P > 0.05$.

[a] G-tests comparing age classes within prey species and seasons.

tically significant in 1986 (Table 3). In contrast, more males than females were taken during spring 1985 to summer 1986. Considering the annual sex ratio in the diet of owls from fall 1985 to summer 1986, however, predation by sex was similar to expected values based on estimated sex ratios in the field ($G = 3.09$, df $= 1$, $P > 0.05$ and $G = 0.00$, df $= 1$, $P > 0.99$ for *C. laucha* and *A. azarae*, respectively).

The average number of rodents per pellet increased with increasing abundance of rodents from March to May and then declined with decreasing abundance of preferred prey (Fig. 3). The resulting curves corresponded to the increasing and declining phases of the annual fluctuation in rodent populations and approached the shape of an exponentially decelerating function. Consumption of rodents was higher during the increasing phase in the annual fluctuation of rodent populations than in the declining phase (except in September), showing differences in the pattern of consumption between the breeding and nonbreeding seasons of the owls. Pellets were not found at nesting sites in October and November when the abundance of rodents was 0.8 and 2.0 individuals per 100 traps night, respectively.

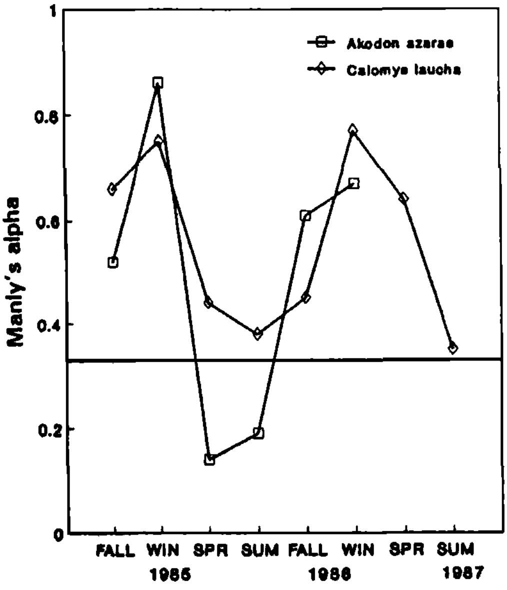

FIG. 2. Seasonal variation in preference of Barn Owls for large-sized rodents in east-central Argentina. The horizontal line indicates no preference, values higher than 0.3 indicate preference, and lower values indicate avoidance.

*Discussion.*—Annual and seasonal variations in the consumption of small rodents were not statistically significant in Diego Gaynor, in contrast to studies conducted in the United States (Marti 1974) and Spain (Veiga 1981). Close to the southern limit of their distribution in South America, Barn Owls occasionally feed on small marsupials (Massoia 1983), bats (Nores and Gutiérrez 1990), lizards (De Santis and Pagnoni 1989), and frogs (Soncini et al. 1985), in addition to the prey items reported in this study. Barn Owl predation on arthropods was negligible in this study as well as in other areas in Argentina (Faverín 1989, Nores and Gutiérrez 1990) and around the world (Jaksić et al. 1982, Marti 1988).

Differential predation by owls on rodent species has been attributed to differences between owl hunting habitat and habitat selected by prey (Pearson and Pearson 1947), activity levels of prey (Fulk 1976), prey morphology as it influences vulnerability to predators (Kotler 1985), and size of prey (Marti and Hogue 1979, Vassallo 1994). In this study, differential predation on rodent species was consistent with the selection of borders of crop fields for hunting habitat. Consumption of *A. azarae* and *O. flavescens* by owls was higher than expected based on trap captures, whereas *C. laucha* was taken by owls at a lower frequency than its availability. The most common ro-

TABLE 3. Frequency of males and females in pellets ($f_o$) versus availability from trapping ($f_e$) for the two main rodent species in the diet of Barn Owls in east-central Argentina.

| | FALL-WIN 1985 | | | SPR 1985-SUM 1986 | | | FALL-WIN 1986 | | | SPR 1986-SUM 1987 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $f_o$ | $f_e$ | $G^a$ | $f_o$ | $f_e$ | $G$ | $f_o$ | $f_e$ | $G$ | $f_o$ | $f_e$ | $G$ |
| ***Calomys laucha*** | | | | | | | | | | | | |
| Males | 42 | 55 | $11.05^{***}$ | 17 | 12 | $4.91^{*}$ | 57 | 61 | $1.14^{ns}$ | 6 | 4 | $2.09^{ns}$ |
| Females | 31 | 18 | | 5 | 10 | | 21 | 17 | | 2 | 4 | |
| ***Akodon azarae*** | | | | | | | | | | | | |
| Males | 8 | 14 | $4.95^{*}$ | 16 | 10 | $5.46^{**}$ | 23 | 30 | $2.71^{ns}$ | 3 | 3 | $0.00^{ns}$ |
| Females | 23 | 17 | | 11 | 17 | | 41 | 34 | | 4 | 4 | |

$^{*}$, $P < 0.05$; $^{**}$, $P < 0.02$; $^{***}$, $P < 0.001$; ns, $P > 0.05$.

[a] G-tests comparing sex classes within prey species and seasons.

dents in the study area are segregated by habitat; *A. azarae* and *O. flavescens* are largely restricted to borders of crop fields, and *C. laucha* occurs mostly in open fields (Busch and Kravetz 1992). Borders of crop fields have advantages over open fields as hunting habitat for raptors. Standing crops provide difficult access to aerial predators. In contrast, borders are readily accessible and often support high densities of rodents (Busch and Kravetz 1992). Differences in prey size also may be a factor in differential predation because *A. azarae* and *O. flavescens* are, on average, heavier than *C. laucha* (Table 1). Prey selection on rodent species probably did not result from differences in activity time between predator and prey because small rodents in the study area are primarily nocturnal (Crespo 1966). Moreover, the small mammal species that occur in the study area do not possess morphological characteristics that could result in interspecific differences in vulnerability to aerial predation, such as bipedal locomotion or inflated auditory bullae.

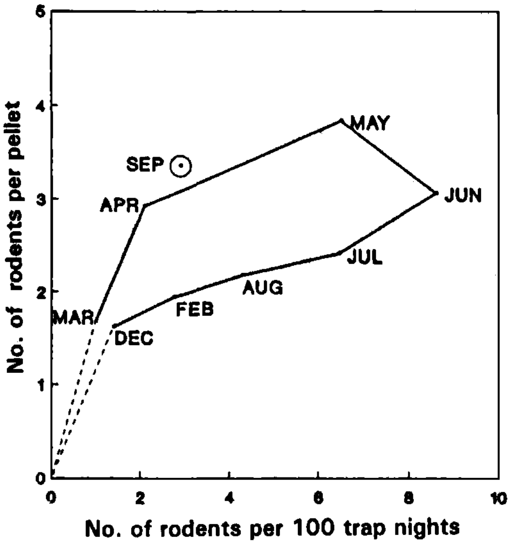

FIG. 3. Relationship between number of rodents per Barn Owl pellet and rodent abundance in east-central Argentina.

Differential predation by owls based on the sex of rodents has been attributed to behavioral and morphological (body mass) differences between sexes of prey (Longland 1987, Vassallo 1994). In this study, differential predation by sex of rodents likely resulted from behavioral differences because the rodents occurring in the study area are not sexually dimorphic. Rodents reproduce during spring-summer, and the highest recruitment occurs during fall (Zuleta et al. 1988, Busch and Kravetz 1992). Breeding female rodents are more territorial than males and spend time near the nest during lactation (Zuleta et al. 1988). Because the level of locomotive activity influences predation risk (Kaufman 1974), this may explain why owls took fewer female rodents than expected in spring-summer. During the nonbreeding season of rodents (fall-winter), males tend to be more territorial than females, decreasing their vulnerability to aerial predation.

Breeding Barn Owls selectively fed on large rodents (within species). This result supports the predictions of Emlen's (1966) hypothesis that predators will feed selectively when food is abundant. The choice of large rodents by breeding Barn Owls may result from a maximization of net energy intake, supporting the criterion of selective feeding behavior. The abundance of preferred prey during the fall seemed to be high enough to make selection of large rodents a profitable strategy to fulfil energetic requirements during reproduction. Furthermore, the availability of food resources during breeding was unlikely to be a limiting factor for Barn Owl population growth, because no starvation of the youngest chicks (common in owls) was recorded in nest boxes in the study area (Bellocq and Kravetz 1993). Differences in rodent vulnerability by age or social behavior may provide an alternative explanation for prey selection by size (Longland 1988, Vassallo 1994). Socially dominant rodents display territorial behavior that reduces their risk to predation through increased knowledge of their home range (Metzgar 1967). Moreover, adult rodents may use more microhabitats with dense vegetation (Dickman et al. 1991) and move shorter distances (Vassallo 1994) than dispersing juveniles and hence face a lower predation risk. In contrast, juveniles and older individuals would be more vulnerable to predation than younger adults. If differences in prey vulnerability were the primary cause of prey selection by size in this study, then selection would be most apparent during the breeding season in spring-summer when rodents display strong territorial behavior. However, the owls did not consistently select larger individuals during spring-summer.

The observed differences in the pattern of consumption of rodents by Barn Owls may be explained by differences in the energetic requirements and population structure of owls in the breeding and nonbreeding season. Given the same abundance of rodents, prey consumption by owls was higher during the breeding season. The amount of food required by chicks to attain a relatively stable body mass of 450 to 500 g in 30 to 35 days (Bellocq and Kravetz 1993), and the energetic demands of breeding adults, are higher than the energy required to simply maintain body condition under usual environmental conditions.

In conclusion, close to the southern limit of their distribution in Argentina, the Barn Owl is a specialist on small rodents and occasionally takes a wide variety of vertebrates. It also feeds selectively on large rodents when prey abundance is high during the breeding season, but not consistently when prey abundance is low during the nonbreeding season. The pattern of prey consumption differs between the breeding (higher consumption of food) and nonbreeding seasons.

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