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Rodent prey of the barn owl *Tyto alba* and short-eared owl *Asio flammeus* during winter in agricultural lands in southern Chile

Ricardo A. Figueroa R., Jaime R. Rau, Sonia Mayorga, David R. Martínez, E. Soraya Corales S., Andrés Mansilla & Rodolfo Figueroa M.

We compared the consumption of rodent prey by barn owl *Tyto alba* and short-eared owl *Asio flammeus* during winter in agricultural areas in southern Chile. Diets were studied on the basis of pellets collected during the winters of 1986, 1987 and 1996. Both owl species consumed a large number of different rodent prey (8-9 species), but they preyed more often on the olivaceous field mouse *Abrothrix olivaceus* (56% and 52% of all individual prey, respectively) and long-tailed pygmy rice rat *Oligoryzomys longicandatus* (12.6% and 18.6%, respectively). The diet of the two owl species largely overlapped (95%). The diet diversity of barn owls and short-eared owls was not statistically different and accordingly they showed a similar evenness in diet. The geometric mean weight of rodent prey (GMWP) for short-eared owls (33 ± 1.36 g) was significantly greater than that of barn owls (28.3 ± 1.81 g). No significant difference was found between the proportion of native and introduced rodent prey consumed by barn and short-eared owls. The high diet similarity between both owl species could be a result of convergencies in hunting modes and activity time, similar body mass, or homogeneous rodent prey distribution and abundance in the agricultural areas we studied. The higher GMWP for the short-eared owl was probably caused by the fact that it preyed on the largest rodent prey in our study sites, the Norwegian rat *Rattus norvegicus*. According to our rodent trapping in the field, barn and short-eared owls appear to be opportunistic rather than selective predators in agricultural areas in southern Chile.

Key words: agricultural lands, *Asio flammeus*, barn owl, diet overlap, rodent prey, short-eared owl, *Tyto alba*

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Dietary studies of raptors have ecological importance, because they may help understand prey distribution, abundance, behaviour and vulnerability (Fulk 1976, Marti 1987, Torre et al. 2004), energetic requirements (Bozinovic & Medel 1988) or trophic

relationships between sympatric species and raptor assemblage structures (Herrera & Hiraldo 1976, Jaksic & Braker 1983, Jaksic 1985). Factors that could influence interspecific trophic relationship and potential mechanisms of food partitioning among

coexisting raptor species are the abundance, habitat selection and body mass of prey, and feeding strategies, body size, hunting range, territoriality and activity time of raptors (Jaksic 1989, Gerstell & Bednarz 1999, Leveau et al. 2004, García & Arroyo 2005). Generally, coexisting raptor species show a low food-niche overlap when prey are in scarce supply which is assumed as the presence of competition by some authors (e.g. Lack 1946, Steenhof & Kochert 1985, García & Arroyo 2005). On the other hand, a high food-niche overlap may occur when prey resources increase, which is generally interpreted as opportunistic convergence on abundant resources (Lack 1946, Walk 1998, Leveau et al. 2004). The territoriality or agonistic behaviour may become an important factor in food-niche segregation (Jaksic 1985), but this could vanish with high food supply. The existence of different hunting modes or feeding strategies among raptors could also lead to food-niche segregation (Jaksic & Carothers 1985). If this is true, similar hunting modes among raptor birds would lead to food-niche convergency. Food partitioning by prey size might occur between species that differ in body size, with larger prey expected to be preferred with increasing body size of the raptor (Jaksic & Braker 1983, Marti 1992, Bellocq & Kravetz 1994, García & Arroyo 2005). In this case, it would be expected that raptors of similar body size take the same average prey size. Although time of activity has been demonstrated as a factor potentially involved in resource partitioning (Marti & Kochert 1995), it does not appear to be sufficiently adequate to separate food-niches of birds of prey (Jaksic 1982). Many raptors hunt during the crepuscule when both diurnal and nocturnal prey are active, reducing differences in resource partitioning.

Although barn owl *Tyto alba* and short-eared owl *Asio flammeus* are sympatric over most of their range in Chile, their diets have never been compared. The few published works on the diet of both owl species in agricultural lands of southern Chile indicate that they mainly prey upon small rodents (Rau et al. 1985, 1992, Martínez et al. 1998). Since both owl species have similar body mass (350–400 g) and hunting modes, search for prey in the same habitats, and may overlap in activity time, they should have access to similar prey species. In addition, when there is an ample supply of prey, barn owls and short-eared owls should have high dietary similarities. Here, we examine these hypotheses by evaluating rodent consumption by coexistent barn owls and short-eared owls in agricultural lands of south-

ern Chile during the period of highest seasonal rodent abundance (winter).

Study area

Our study was conducted in four agricultural areas of the Osorno province, Central Valley in southern Chile. Localities were Quirislahuén, Pilauco, Chuyaca and Chahuilco. The first three localities are very close to Osorno city (3–4 km) and the latter is located 15 km south of Osorno (40°44'S, 73°09'W). In general, the landscape is relatively homogeneous with almost all agricultural areas presenting a similar topography, vegetation and land management (Martínez et al. 1998). Topography is characterised by undulating terrains and extensive flat areas. Vegetation is composed of mainly pasturelands for livestock (e.g. cattle), croplands (e.g. wheat *Triticum aestivum*, oat *Avena sativa* and potatoes *Solanum tuberosum*), and fruit and legume gardens associated with the dispersed human settlements. Scattered small (1–4 ha) abandoned pastureland with dispersed isolated and old native trees (*Nothofagus obliqua* and *Laurelia sempervirens*) are frequent between the currently used fields. Webs of fallow vegetation strips continuously cover boundaries between agricultural fields and road borders, and some small and altered patches of the original native *Nothofagus* forest border rivers and streams. The flat terrain contains sedge-rush *Carex-Juncus* marshes (seasonal or permanent). The climate is moist-temperate with a Mediterranean influence, characterised by heavy rainfall (1500–3000 mm annually), wet, frost-free winters and short, dry summers (di Castri & Hajek 1976). Annual mean temperature is 12°C.

Material and methods

The barn owls' pellets were collected from Pilauco (May–July 1986, N=26), Quirislahuén (May–June 1987, N=42), and Chahuilco (May–July 1996, N=160). Samples were taken either under old native trees where barn owls perched or in tree cavities where they roosted. We made sure that pellets were from barn owls by direct observation of birds and permanent use of site collection. Information on short-eared owls was taken from previous works (Rau et al. 1992, Martínez et al. 1998), in which short-eared owl pellets were collected from

Quirislahuén (May-June 1986, N=46), Chuyaca (May-August 1995, N=147), and Chahuilco (May-August 1995, N=64). Samples were taken on open grounds in abandoned pastures or dried marshes, and under trees, fences and stumps used as perches. Confirmation that pellets belonged to short-eared owls was made by flushing or by using indirect signs on perches (e.g. feathers and creamy fecal waste; Holt et al. 1987). As wintering barn and short-eared owls largely depend on small mammals, other occasional prey (e.g. birds and insects) were discarded from the analysis because of low biomass contribution. We only analysed winter rodent consumption, because it was not possible to obtain pellets year-round for all localities or because samples were very small.

Rodent prey were identified and quantified on the basis of skull or dentary pairs following keys in Reise (1973) and Pearson (1995). For hair remains, we used reference collections and quantified these prey assuming the smallest possible number of individuals (e.g. hair of given a species was deemed as representing only one individual). We identified prey items to the finest possible taxonomic category in all cases. Biomass contribution of each prey species was estimated by multiplying the number of individuals in the pellets by mean body mass of each species (Marti 1987). Masses of rodent prey were taken from the unpublished database of the Ecology and Evolution Institute of the Austral University of Chile in Valdivia, Chile, and Agricultural and Livestock Service in Aysén, Chile. Body masses of rodent species not available in databases were taken from the literature. We assumed that masses of unidentified prey were similar to the mean mass of the most closely related identified taxon.

Diet of owls were compared utilising food-niche estimators (Marti 1987). The diet diversity (food-niche breadth) was estimated by use of the Shannon-Wiener Index (H' ; Krebs 1989) and statistically compared by the Hutcheson t-test (Zar 1996). Complementarily, we evaluated how similar the frequencies of individual prey in diet were by using the index of evenness based on the Shannon-Wiener function: $J' = H'/\log S$; where S is the number of species in the sample (Krebs 1989). The J' index ranges from 0 (no prey item is equally represented) to 1 (all prey items are equally represented). The diet similarity (food-niche overlap) was estimated by using the Horn index (R_o ; Krebs 1989). This index ranges from 0 (no similarity) to 1 (complete similarity). The geometric mean weight of prey (GMWP) was calculated fol-

lowing Marti (1987): $GMWP = \text{antilog}(\sum n_i \log w_i / \sum n_i)$, where n_i is the number of individuals of the i th species, and w_i is the mean weight. Although some authors have suggested that geometric means tend to underestimate mean weight of prey (Walker et al. 2007), we preferred using GMWP, because it made comparisons with previous studies on owls diet possible. In addition, differences in consumption of introduced (Murinae) versus native (Sigmodontinae) rodents were evaluated with χ^2 -tests using contingency tables (Fowler & Cohen 1986).

Except for Chuyaca, we were unable to obtain concurrent data on the field abundance of rodent prey in our study localities. In Chuyaca, we evaluated the relative abundance of rodents by live-trapping transects using medium Sherman traps in abandoned pastures located inside the owls' hunting area (see Martínez et al. 1998 for details). Because this trapping was locally restricted and only a small fraction of owls's prey was captured, we combined results from Chuyaca with data collected from three other vegetationally similar agricultural areas by using the same trapping method to obtain a coarse estimate of the rodent field abundance (Fig. 1). Trapping was made either in pasture, marshes or

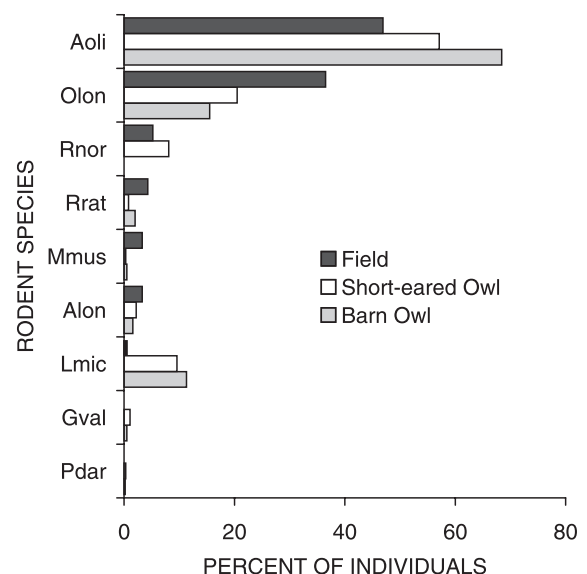


Figure 1. Comparison of the proportion of rodent prey in the winter diet of barn and short-eared owls versus the winter rodent abundance in the field estimated by live-trapping transects in agricultural areas of southern Chile. Alon = *Abrothrix longipilis*, Aoli = *A. olivaceus*, Gval = *Geoxus valdivianus*, Mmus = *Mus musculus*, Olon = *Oligoryzomys longicaudatus*, Lmic = *Loxodontomys micropus*, Rnor = *Rattus norvegicus*, Rrat = *R. rattus* and Pdar = *Phyllotis darwini*.

forest edges to better represent the prey availability on the owls' hunting areas. However, because most abundance estimates were obtained five or six years after pellet collections or from areas where owls did not hunt, no statistical comparisons were made.

Results

In all localities, the barn owls mostly preyed upon the olivaceous field mouse *Abrothrix olivaceus* and secondarily upon the southern big-eared mouse *Loxodontomys micropus* or the long-tailed pygmy rice rat *Oligoryzomys longicaudatus* (Table 1). The remaining rodent prey account for less than 8% by number for all localities (see Table 1). The olivaceous field mouse also accounted for the higher contribution of biomass, followed by the southern big-eared mouse and introduced rats (*Rattus* spp., see Table 1). The barn owl diet was highly similar among localities with $R_o=0.90$ for Pilauco and Quirislahuén, $R_o=0.89$ for Pilauco and Chahuilco, and $R_o=0.89$ for Quirislahuén and Chahuilco. The diet of short-eared owls was also highly similar among localities (symmetrical niche overlap=91.8%; Martínez et al. 1998). Thus, we combined results from all localities for comparisons between both owl species.

Overall, barn owls preyed on at least eight rodent species with olivaceous field mouse being the most important prey by both number and biomass (Table 2). Taking into account both number and biomass, the southern big-eared mouse and long-tailed pygmy rice rat were the secondary prey of barn owls (see

Table 2). Although introduced rats were less consumed, their biomass contribution was similar to that of southern big-eared mice (see Table 2). Short-eared owls preyed upon nine rodent species with olivaceous field mouse being the most important by number and second by biomass (see Table 2). In spite of the fact that the number contribution of the Norwegian rat *Rattus norvegicus* was low, it accounted for the highest biomass contribution (see Table 2). As with barn owl, the southern big-eared mouse and long-tailed pygmy rice rat were the secondary prey both in terms of number and biomass (see Table 2). The diets of both owl species overlapped considerably ($R_o=0.95$). The diet diversity of barn owl and short-eared owl was not statistically different ($t_{200}=0.94$, $P>0.05$), and accordingly, they showed a similar evenness (see Table 2). The GMWP for short-eared owls (33 ± 1.36 g) was significantly greater than that of barn owls (28.3 ± 1.81 ; $t_{745}=-4.32$, $P<0.01$). No significant difference was found between the proportion of native and introduced rodents in barn owl diet from different localities ($\chi^2=0.3$, $P>0.05$), or for barn versus short-eared owls' diet ($\chi^2=1.1$, $P>0.05$).

A total of 211 individuals, including seven different rodent species, were captured in 1664 trap nights. The most captured species were the olivaceous field mouse and long-tailed pygmy rice rat which accounted for 47% and 36% of all individual rodents, respectively. The southern big-eared mouse was the least captured species (<1% of all individual rodents). In general, the ranking of prey species in the diet of barn and short-eared owls reflected the

Table 1. Winter diet of the barn owl *Tyto alba* in three agrosystems in southern Chile. Rodent mass is given as mean \pm SE. N%= number percentage and B%= biomass percentage.

Species	Mass (g)	Quirislahuén		Pilauco		Chahuilco	
		N%	B%	N%	B%	N%	B%
<i>Abrothrix longipilis</i>	33.4 \pm 0.26	1.1	0.9	7.3	6.8	0.3	0.3
<i>Abrothrix olivaceus</i>	24.8 \pm 0.28	43.2	24.6	60.0	41.6	58.5	39.2
<i>Geoxus valdivianus</i>	29.1 \pm 2.5	0.0	0.0	0.0	0.0	0.6	0.5
<i>Loxodontomys micropus</i>	50.7 \pm 1.4	16.0	18.5	10.9	15.5	7.1	9.8
<i>Oligoryzomys longicaudatus</i>	27.8 \pm 0.25	4.5	3.0	7.3	5.6	15.8	11.8
<i>Phyllotis darwini</i>	66 ^a	1.1	1.7	0.0	0.0	0.0	0.0
<i>Rattus rattus</i>	107.5 \pm 16.9	4.5	11.2	5.4	16.4	0.0	0.0
<i>Rattus</i> spp.	150 ^b	1.1	3.9	0.0	0.0	5.0	20.1
<i>Mus musculus</i>	14.6 \pm 1.37	0.0	0.0	0.0	0.0	0.6	0.2
Unidentified rodents	55.5 ^c	28.5	36.2	9.0	14.1	12.1	18.1
Total prey items		88		55		323	
Total biomass (g)		3830.3		1967.4		11956.4	
Total pellets		42		26		160	

^a Mass obtained from Jaksic et al. 1986.

^b Mean mass of the two *Rattus* species inhabiting study areas (*R. rattus* and *R. norvegicus*).

^c Mean mass of all identified rodent prey.

Table 2. Rodent prey of the barn owl and short-eared owl during winter in agrosystems in southern Chile. Rodent mass is given as mean \pm SE. N% = number percentage and B% = biomass percentage.

Prey species	Mass (g)	Barn owl		Short-eared owl	
		N%	B%	N%	B%
<i>Abrothrix longipilis</i>	33.4 \pm 0.26	1.3	1.1	2.0	1.5
<i>Abrothrix olivaceus</i>	24.8 \pm 0.28	56.0	36.3	51.7	28.8
<i>Geoxus valdivianus</i>	29.1 \pm 2.5	0.4	0.3	1.0	0.6
<i>Loxodontomys micropus</i>	50.7 \pm 1.4	9.2	12.3	8.7	9.9
<i>Oligoryzomys longicaudatus</i>	27.8 \pm 0.25	12.6	9.2	18.6	11.6
<i>Phyllotis darwini</i>	66 ^a	0.2	0.4	0.3	0.4
<i>Rattus norvegicus</i>	201 ^b	0.0	0.0	7.4	33.6
<i>Rattus rattus</i>	107.5 \pm 16.9	1.5	4.2	0.7	1.8
<i>Rattus</i> spp.	150 ^c	3.6	14.4	0.0	0.0
<i>Mus musculus</i>	14.6 \pm 1.37	0.4	0.2	0.2	0.1
Unidentified rodents	41.7 ^d	14.8	21.6	9.4	11.7
Total prey items		466		404	
Total biomass (g)		17754.1		17968.4	
Total pellets		228		257	
Food-niche breadth (H')		0.495		0.557	
Evenness (J')		0.519		0.584	
Geometric mean weight (g)		28.3		33	
Simple mean weight (g)		44.2		61.6	

^a Mass obtained from Jaksic et al. 1986.

^b Mass obtained from Martínez et al. 1998.

^c Mean mass of the two *Rattus* species inhabiting study areas (*R. rattus* and *R. norvegicus*).

^d Mean mass of all identified rodent prey.

ranking of prey species in the field (see Fig. 1). Only the southern big-eared mouse and the olivaceous field mouse appeared to have been consumed in a higher proportion than those estimated in the field (see Fig. 1).

Discussion

Barn owls and short-eared owls in our study area had very similar diets as they virtually preyed on the same rodent species in the same proportion. Convergence in hunting modes, activity time and body mass of owls, and prey abundance could be acting together. Both the barn and short-eared owl hunt individually, mainly by active searching and secondarily by sit-and-wait or perching (Jaksic & Carothers 1985). They are both very active flyers with cruising or quartering habits (Marti 1974, Jaksic & Carothers 1985). In this way, both owl species could have access to rodent prey with similar behaviour and microhabitat utilisation which should be mirrored in a high dietary similarity. However, some authors have suggested that the hunting modes are not steady predictors of food-niche metrics (e.g. Jaksic & Carothers 1985).

Even though barn and short-eared owls utilise similar habitats in our study area, hunting could have

taken place within defended territories (Korpimäki 1987, Holt & Leasure 1993). However, mean size of owls' territory may be particularly small in areas with very high small mammal abundance (Lockie 1955, Village 1987, Shaw 1995). Because the higher seasonal rodent abundance in agricultural areas of southern Chile occurs during late autumn and winter (R.A. Figueroa, unpubl. data), it is probable that barn and short-eared owls shared the same habitats, and therefore the same prey species, by reduction of hunting range when they concurrently searched for prey. Rodents may have provided an abundant food resource and thus made the level of exploitation competition insignificant (Jaksic 1985, Walk 1998), consequently leading to a high food-niche overlap (Lack 1946). Dietary similarities between barn owl and short-eared owl could also be due to the fact that their mean body masses are similar: 350–400 g and 400–500 g, respectively (Clark 1975, Marti 1992). This would guarantee access to prey species with similar body size. However, even though raptors' body mass has been demonstrated to be a good predictor of the size of their prey, it does not appear to influence diet breadth and overlap (Jaksic 1989).

Although differences in activity patterns between predators and prey generally could explain differential predation on rodent species, for the owl

species studied here, this does not appear to be the case. Barn owls are mostly nocturnal (Smith et al. 1974, Marti 1974), but occasionally hunt during day (e.g. Harte 1954, Haverschmidt 1970). Short-eared owls are also primarily nocturnal or crepuscular during winter (Clark 1975, Bosakowski 1989, Holt & Leasure 1993), but they may largely extend hunting activities to daylight hours (Clark 1975, Village 1987). In fact, on several occasions, we observed them searching for prey at midday and in the afternoon during winter. A similar daily activity pattern was observed in South Scotland by Village (1987). In this manner, it would be expected that the diet of both owl species did not overlap considerably, because they could access rodent prey with different daily cycles. However, most rodent prey species in southern Chile may extend their activity period largely into the day during winter (Muñoz et al. 1990), thus being available to owls both during the day and during the night. The diurnal activity of rodents during winter could have been accentuated by the shortening of daylight hours. Possibly, diurnal activity of short-eared owls avoided interference interactions with barn owls during night to a certain extent (Walk 1998, Leveau et al. 2004), but it could not be sufficient to cause marked differences in proportion of consumed rodent prey. Finally, the high homogeneity of the agricultural landscape in our study area would explain the high diet similarity among barn and short-eared owls from distinct localities, because this factor could determine relatively similar rodent prey assemblages on the most sites (Martínez et al. 1998, Bosè & Guidali 2001).

Our results suggest that barn and short-eared owls were opportunistic rather than selective predators in agricultural areas of the Osorno province, i.e. they appeared to prey more on the most abundant rodent prey species, the olivaceous field mouse and long-tailed pygmy rice rat (see Fig. 1). Various authors have claimed that barn owls show no food preferences, and that their diet is a reflection of the abundance of small mammals species within their hunting territories (Glue 1971, Bunn et al. 1982, Torres-Mura & Contreras 1989, Scheibler & Christoff 2004, Begall 2005). Similarly, short-eared owls also take whatever prey is most abundant or vulnerable to them (Martínez et al. 1998). However, in some studies, the proportion of consumed rodents by barn owls differed from those obtained by trapping in the field, suggesting prey selection (Perrins 1982, Bellocq 1998, Baxter & Matshili 2003). In addition, computer simulations have shown that barn owl pellets

could not truly mirror the proportion of prey in the field (Yom-Tov & Wool 1997). We recognise that our interpretation regarding prey selection could be erroneous, because most rodent trapping was not carried out concurrently with the collection of pellets. Moreover, results of live trapping are affected by sampled area, trap type and bait used, and could fail to capture all small mammal species present in the local community (Blem et al. 1993, Torre et al. 2004).

In addition to prey abundance, it is probable that activity level (Kaufman 1974) and microhabitat preference (Trejo & Guthmann 2003) could also explain the high proportion of long-tailed pygmy rice rat in the diets of both owls. This rat is a highly mobile species with a wider home range (0.032–0.480 ha) than the olivaceous field mouse (0.073–0.253 ha; Murúa et al. 1986) which would make it more vulnerable to predation. Moreover, the long-tailed pygmy rice rat in agricultural lands preferentially utilise dense shrubs mixed with pastures on fence borders (R.A. Figueroa unpubl. data), which increases the probability of encounters with owls, because fence posts are favourite perches (Martínez et al. 1998). In the case of the olivaceous field mouse, the occupation of more open habitat (e.g. abandoned pastures) could have increased its vulnerability (Dickman et al. 1991, Trejo & Guthmann 2003). Possibly, southern big-eared mouse was 'selected' because of its larger body size (51 g) relative to the remaining native rodents (≤ 30 g). We believe that higher GMWP for the short-eared owl was caused by the fact that it preyed on the largest rodent prey in our study sites, the Norwegian rat. Because it was not possible to identify most *Rattus* spp. remains from pellets at the species level, we did not know if Norwegian rats were eaten, and to what extent, by barn owls. Since GMWP may vary locally for the barn owl (Alvizatos & Goutner 1999, Pillado & Trejo 2000, Lekunze et al. 2001, Scheibler & Christoff 2004) and short-eared owl (Jaksic 1983, Cirignoli et al. 2001), our results may reflect the local body size distribution of the rodent community in agricultural areas of southern Chile.

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