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DIET SHIFTS OF BLACK-CHESTED EAGLES (*Geranoaetus melanoleucus*) FROM NATIVE PREY TO EUROPEAN RABBITS IN CHILE

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ABSTRACT.—For two years we studied the feeding ecology of Black-chested Eagles (*Geranoaetus melanoleucus*) in San Carlos de Apoquindo, central Chile. We estimated the diet of eagles using three different methods and evaluated the abundance of introduced European Rabbits (*Oryctolagus cuniculus*) throughout one year. Eagles preyed in decreasing order of frequency on mammals, reptiles, insects and birds. The biomass component of insects in the diet was negligible. At the species level, the European Rabbit was the most frequently consumed prey (43.9% by number and 81.7% by biomass). The diet composition changed only slightly throughout the year. During non-breeding seasons birds and insects were not consumed. Depending on the technique used, we found differences in the estimated diet. Birds were underestimated and insects were overestimated by direct observations of prey captures and transportations. In contrast, insects were underestimated by the analysis of prey remains. At the class level, the analysis of regurgitated pellets seems to represent the diet of eagles better. European Rabbits were present throughout the year in the study site, peaking during the eagles' breeding season, when kittens were abundant. Eagles preyed preferentially on small rabbits and apparently avoided large individuals. Eagles have increased their consumption of European Rabbits over time as did foxes in the study area.

Cambio en la dieta del Águila Chilena (*Geranoaetus melanoleucus*) de presas nativas a Conejos Europeos en Chile.

EXTRACTO.—Durante dos años estudiamos la ecología trófica de Águilas Chilenas (*Geranoaetus melanoleucus*) en San Carlos de Apoquindo, en Chile central. Estimamos la dieta de las águilas usando tres métodos diferentes y evaluamos la abundancia de Conejos Europeos (*Oryctolagus cuniculus*) introducidos a lo largo del año. Las águilas depredaron en orden de frecuencia decreciente sobre mamíferos, reptiles, insectos y aves. El componente de biomasa de insectos en la dieta fue insignificante. Al nivel de especie, el Conejo Europeo fue la presa más frecuentemente consumida (43.9% en número y 81.7% en biomasa). La composición de la dieta solo cambió ligeramente a lo largo del año. Durante la estación no reproductiva aves e insectos no fueron consumidos. Dependiendo de la técnica usada, encontramos diferencias en la estimación de la dieta. Las aves fueron subestimadas y los insectos sobreestimados mediante observaciones directas de capturas y transportes de presas. En contraste, los insectos fueron subestimados por los análisis de restos de presas. Al nivel de clase, los análisis de egagrópilas parecían representar mejor la dieta de las águilas. Los Conejos Europeos estuvieron presentes a lo largo de todo el año en el sitio de estudio, alcanzando máximos durante la estación reproductiva de las águilas, cuando los conejos pequeños eran abundantes. Las águilas depredaron preferentemente sobre conejos pequeños y aparentemente evitaron a los adultos. Las águilas, al igual que los zorros, han aumentado el consumo de Conejos Europeos en el tiempo en el sitio de estudio.

The Black-chested Eagle, *Geranoaetus melanoleucus*, is broadly distributed in South America, from Venezuela to Tierra del Fuego (Brown and Amadon 1968). It is found throughout Chile (Goodall et al. 1951), especially in open habitats, from sea level up to 2200 m (Barros 1967). Information on the feeding ecology of this eagle is scarce (Jiménez and Jaksić 1989). Most authors report only qualitative and anecdotal information on its diet (see review by Jiménez and Jaksić 1990). In general, previous au-

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thors concur that these eagles prey in decreasing frequency on birds, rodents, young rabbits, and reptiles. Results differ among localities, however (Jiménez and Jaksić 1990). This implies that the eagles show considerable plasticity, opportunistically capturing and consuming the most abundant prey.

Quantitative studies in central Chile report that the Black-chested Eagles prey primarily on rodents, especially on *Octodon degus* (75.9%, 53.8%, and 43.4% by number of total prey, according to Schlatter et al. 1980, Jiménez and Jaksić 1989, 1990, respectively), and secondarily on European Rabbits (*Oryctolagus cuniculus*; 18.8%, 13.8%, according to Schlatter et al. 1980, and Jiménez and Jaksić 1989, respectively). The relatively low incidence of European Rabbit in the diet of the eagles, and in those of other sympatric predators, has been attributed to the "lack of behavioral adjustment" of native predators to hunt "for this recently introduced prey" (Jaksić and Soriguer 1981).

Here, we analyze the seasonal variation in the diet of eagles using three different techniques, and compare the results with the estimated abundance of rabbits in the field. We show that since earlier studies, eagles have markedly increased their consumption of introduced rabbits.

STUDY AREA AND METHODS

We studied Black-chested Eagles in a 900-ha area located in San Carlos de Apoquindo (33°23'S 70°31'W), at the foothills of the Andes (1200 m elevation), 20 km east of Santiago, Chile. The study site has rugged topography, with high ridges, deep ravines, and few flat areas. The climate is of the Mediterranean type with vegetation composed primarily of evergreen shrubs. Additional information on the study site can be found in Jiménez and Jaksić (1989). Eagles remained in the study site the year round. Two pairs nested in 1987 and three in 1988.

We studied the diet of the eagles using pellets (e.g., Marti 1987), prey remains, and observations of kills and prey carried. We analyzed 236 regurgitated pellets, and 158 prey remains collected under 5 nests and 11–15 roosting places every other week between December 1987 and March 1989. We recorded the capture and transport of prey by eagles during an entire day at least every other week from August 1987 to September 1988. These observations were conducted from 0800–1900 H from vantage points that provided good visibility over the entire area, using binoculars (16 × 50) and a spotting scope (20–40 × 60). We divided the year into two periods: the non-breeding season, from March through August, and the breeding season, from September through February (see Jiménez and Jaksić 1989). Prey were identified at least to class.

We assessed the abundance of European Rabbits in the area by counting all the individuals observed within a 70-m-wide and 6-km-long transect while walking between 0800-1000 H and between 1800–2000 H. We surveyed the rabbits during 27 transects between November 1987 and October 1988. Both the observed rabbits and those captured and transported by the eagles were assigned to three size classes: large, medium, and small. These size classes corresponded roughly to the weight classes determined by Zunino and Vivar (1983–85; larger than 1100 g, between 800 and 1100 g, and smaller than 800 g, respectively).

RESULTS

Diet. The 624 prey items were composed of mammals (78.2%), reptiles (11.4%), insects (7.8%) and birds (2.6%; Table 1). The most frequently consumed prey was the European Rabbit (43.9%), followed by the rodent *Octodon degus* (18.9%) and in turn by the snake *Philodryas chamissonis* (9.5%). Insects were primarily coleopterans, which were captured by juvenile eagles during their early hunting flights.

By biomass, the bulk of the eagle's diet was composed of mammals (95.8%), 81.7% of the total biomass were European Rabbits (Table 1). In decreasing frequency eagles preyed on reptiles (3.4%) and birds (0.8%). Insects added a small amount of biomass (0.02%).

Diet by Season. Prey classes were similar for the four seasons of this study (Table 1). At the species level, the rank order in frequencies of prey eaten by the eagles was positively correlated between the 1987 and 1988 breeding seasons (Spearman rho = 0.882, $P < 0.001$), as well as with that of the 1988 non-breeding season (rho = 0.951 and 0.852, $P < 0.001$, respectively). The 1987 non-breeding season showed the same trend, but we did not use statistics due to the small sample. Neither European Rabbits, nor reptiles were consumed during the 1987 non-breeding season. Birds and insects were apparently not consumed during the non-breeding seasons (Table 1). During breeding seasons, the number of different prey taken by the eagles increased, as birds and insects were incorporated in the diet (Table 1).

Influence of Technique Used. Estimates of the eagle's diet at the class level were influenced by study technique (Table 2; $\chi^2 = 39.39$, df = 6, $P < 0.005$). Although we found significant differences only for total prey and for insects, some trends were evident among the other prey classes. Direct observations of capture and transport of prey by eagles apparently overestimated consumption of insects and underestimated birds and reptiles (Table 2). On the other

Table 1. The diet, in percentage of items, of Black-chested Eagles in a central Chilean site during sucessive breeding (Bree.) and non-breeding (Non-Br.) seasons. For the entire study period, the percent biomass is also shown. Subtotals for class are in parentheses.

PREY	WEIGHT[1]	NON-BR. 1987	BREE. 1987	NON-BR. 1988	BREE. 1988	TOTAL BY NUMBER	TOTAL BY BIOMASS
Mammals		(100.0)	(74.5)	(95.2)	(82.2)	(78.2)	(95.80)
Oryctolagus cuniculus	800	0.0	47.5	47.6	39.0	43.9	81.69
Octodon degus	184	44.4	21.5	33.3	11.7	18.9	8.05
Abrocoma bennetti	231	0.0	1.1	4.8	4.7	2.4	1.29
Phyllotis darwini	62	0.0	0.5	0.0	0.5	0.5	0.07
Unidentified rodent	159	44.4	3.1	9.5	10.3	6.4	0.18
Unidentified mammal	319	11.2	0.8	0.0	16.0	6.1	4.52
Birds		(0.0)	(2.6)	(0.0)	(2.8)	(2.6)	(0.78)
Zenaida auriculata	137	0.0	0.3	0.0	0.0	0.2	0.05
Metriopelia melanoptera	125	0.0	0.0	0.0	0.9	0.3	0.10
Unidentified bird	131	0.0	2.3	0.0	1.9	2.1	0.63
Reptiles		(0.0)	(12.9)	(4.8)	(9.9)	(11.4)	(3.40)
Philodryas chamissonis	150	0.0	10.8	4.8	8.0	9.5	3.30
Callopistes palluma	65	0.0	0.5	0.0	0.5	0.5	0.07
Unidentified iguanid	9	0.0	1.6	0.0	1.4	1.4	0.03
Insects		(0.0)	(10.0)	(0.0)	(5.1)	(7.8)	(0.02)
Unidentified scarabaeid	1	0.0	2.2	0.0	0.0	1.3	0.00
Unidentified coleopteran	1	0.0	1.8	0.0	4.2	2.5	0.01
Unidentified insect	1	0.0	6.0	0.0	0.9	4.0	0.01
Total prey items[2]		9	381	21	213	624	100.00
Pellets		0	266	4	112	382	
Prey remains		0	53	4	101	158	
Transport and capture		9	62	13	0	84	

[1] Weights (in g) were taken from Zunino and Vivar (1983–85) for *Oryctolagus*, from J. E. Jiménez (unpublished data) for *Zenaida*, and from Jiménez andJaksić (1989) for the other taxa. Weights for unidentified prey are the average weight of the most related identified taxa, except for Iguanidae, for which we averaged the weights of the species that occur at the study site. We assumed that insects weighed 1 g.

[2] The totals may be overestimated because some prey may have been counted more than once.

hand, pellets and prey items yielded similar results, except for a relative underestimation of insects using prey items.

Abundance of European Rabbits and Their Consumption by Eagles. The estimated abundance of rabbits in San Carlos de Apoquindo varied throughout the year. The number of rabbits observed on transects ($N = 56$) was greater during the eagle's breeding (74.1%) than non-breeding season (25.9% of the monthly average count). Counts peaked in December and January. A similar pattern applied to both large and small rabbits (2.51 and 1.12 vs. 1.04 and 0 daily average count for breeding and non-breeding seasons, respectively; Fig. 1). Medium-sized rabbits were more common during the non-breeding season (0.28 vs. 0.17 daily average count, for non-breeding and breeding seasons, respectively).

Data for rabbits captured by eagles during years when the rabbit abundances were estimated, showed that of 21 observed captures, 68.2% were made during the breeding season and 31.8% during the non-breeding season (Fig. 1). Of the rabbits captured 57.1% were small, and all of these were taken during the breeding season.

Comparing the abundances of different rabbit size classes in the field with those captured by eagles shows that eagles preyed on rabbits primarily when kittens were available (Fig. 1). Eagles did not capture rabbits independently of their body sizes ($\chi^2 = 18.27$, df = 2, $P < 0.001$). When kittens were not

Table 2. Diet of Black-chested Eagles in a central Chilean site based on pellets, prey items, and direct observation of transport and capture of prey. Percent of prey in the diet of eagles at the class level and for *Oryctolagus cuniculus*, and statistics for the independence tests are shown.

	Pellets	Items in Nests	Items Carried	Total %	Total Number	χ^2	df	*P*
Mammals	75.9	84.8	76.2	78.2	488	1.15	2	>0.25
Oryctolagus cuniculus	45.5	45.6	33.3	43.9	274	2.67	2	>0.25
Birds	3.4	1.9	0.0	2.6	16	5.47	2	>0.05
Reptiles	12.3	12.7	4.8	11.4	71	4.49	2	>0.1
Insects	8.4	0.6	19.0	7.8	49	27.43	2	<0.005
Total items	382	158	84		624	39.39	6	<0.005

available (non-breeding season), eagles seemed to prey on medium-sized rabbits (Fig. 1).

Discussion

Our results concur with those of previous studies on the diet of eagles, by showing that the eagles prey primarily on mammals (>70% by number; see Schlatter et al. 1980, Jiménez and Jaksić 1989, 1990). We also found that reptiles were their second most frequent prey. However, unlike previous work, we found that insects were more frequent in the diet than were birds. Former studies recorded no insect prey. These results may reflect differences in prey availability, different prey (Jiménez and Jacksić 1990), or different food study techniques (but see below).

Mammals were the staple prey of eagles during the two years and during breeding and non-breeding seasons. There were seasonal differences in the other prey classes. Birds and insects were prey only during breeding seasons, when reptiles also tended to be more commonly eaten. Although European Rabbits were present during the 1987 non-breeding season, they were not detected as a component of the eagles' diet, perhaps because of the small sample. A seasonal difference in diet reported by Jiménez and Jaksić (1990) for several eagle populations, was also observed in this population, suggesting that eagles prey opportunistically on the most abundant prey available.

In other raptor studies, the results of dietary estimation with different techniques are controversial. Whereas Collopy (1983) found no differences in dietary estimates by using different techniques, others have found differences. Unlike our findings, the use of prey remains as diet estimators has been reported to overestimate the vertebrate prey taken, especially for those prey for which only the bones are found, and to underestimate invertebrate prey (Errington 1932, Snyder and Wiley 1976, Simmons et al. 1991). In contrast, pellet analysis has been

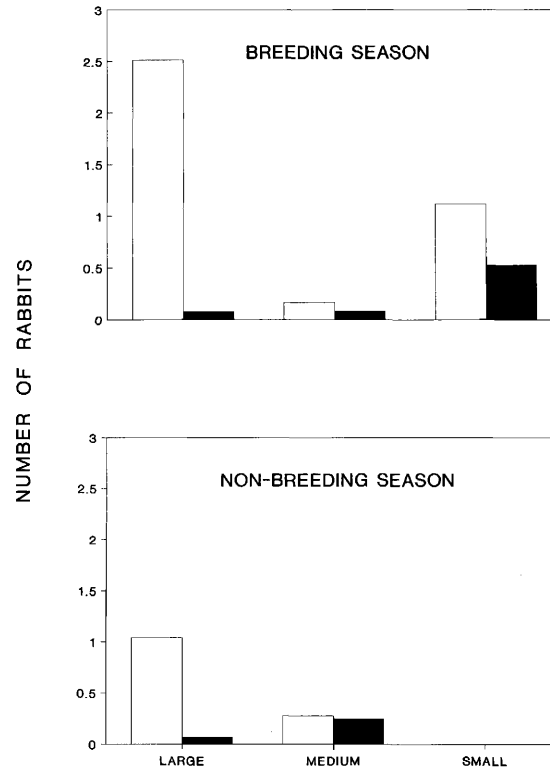

Figure 1. Daily average number of large-, medium-, and small rabbits observed on transects (N = 56, open bars) and captured by Black-chested Eagles (N = 21, closed bars) during breeding and non-breeding seasons in central Chile.

reported to underestimate the occurrence of vertebrate prey (Errington 1932).

At the prey species level, we found some differences with previous work. Our data show that the most important mammal in the eagle's diet was the European Rabbit. Despite working in the same study site during 1984–85, Jiménez and Jaksić (1989) found that rabbits were only the second most important prey item, comprising 13.8% of the Black-chested Eagle's diet. Schlatter et al. (1980), working in a nearby site during 1973–74, also reported a low incidence of rabbits in the diet (18.8% of prey items). It appears, then, that eagles are now eating more rabbits than they used to.

Interestingly, studies on the diet of foxes (*Pseudalopex culpaeus*) in the same study site also showed a substantial increase in rabbit consumption over time: from 19.7% in 1976 to 37.0% in 1983, and to 48.0% in 1984 (Jaksić et al. 1980, Simonetti 1986, Iriarte et al. 1989b, respectively).

The increase in European Rabbits in the diet of some central Chilean predators over time may be due to an increase in the number of rabbits. Unfortunately there are no previous density estimates available for our study site. The habitat conditions in San Carlos de Apoquindo seem to have remained the same during the past 15 years according to our casual observations. Therefore, an increase of rabbits owing to the clearing of brush, as suggested by Fuentes and Jaksić (1980), is probably not the case. Rabbits have been present at the site for more than 50 years according to local residents. This observation refutes the hypothesis that rabbits are still arriving from elsewhere into the site.

The human presence in the area seems to have increased in recent years (pers. observation, P. Ramírez, pers. comm.). People come to the area mainly to hunt and trap rabbits. Consequently, if humans have some influence on rabbit abundances, their increased activities in San Carlos de Apoquindo should have been detrimental rather than favorable for the rabbit populations. The explanation of Simonetti (1986), that the diet shift of foxes toward more consumption of rabbits in the study area "may relate to artificial causes, such as increased human trapping of rabbits," does not apply to eagles, as we have never seen them capturing rabbits caught in snare traps. As Simonetti (1986) pointed out, the hypothesis of a dietary shift toward rabbits because the relative abundance of native rodents may have decreased (Jaksić and Soriguer 1981), does not explain the change observed, since native rodents are now at least as abundant as before judging from rodents per trap per day encountered by Jaksić et al. (0.03; 1981), Simonetti (0.06; 1986), Iriarte et al. (0.10; 1989a), and Jiménez and Jaksić (0.14; 1989).

To our knowledge, so far only Iriarte et al. (1989a) attempted to estimate the abundance of rabbits in central Chile over time. Although they were able to capture only kittens and subadults, their density estimates throughout a year concur roughly with our estimates. As in our findings, Zunino and Vivar (1983–85) documented that European Rabbits increased in numbers as they reproduce between August and February. The number of rabbits taken by eagles showed the same trend as rabbit abundance along the year. The fact that eagles prey more on rabbits when they are more abundant in the field implies that Black-chested Eagles exhibit a functional response to this prey.

The apparent avoidance of adult rabbits by eagles may be explained by their size. Adult rabbits were abundant throughout the year in our study site. They are probably too large to be captured and successfully handled by eagles. This may explain why adult rabbits behaved as if they were immune from predation (see also Jaksić et al. 1979a, 1979b, Jaksić and Ostfeld 1983).

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