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Authors: Baladrón, Alejandro V., Bó, María S., and Malizia, Ana I.

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WINTER DIET AND TIME-ACTIVITY BUDGETS OF THE RED-BACKED HAWK (*BUTEO POLYOSOMA*) IN THE COASTAL GRASSLANDS OF BUENOS AIRES PROVINCE, ARGENTINA

Alejandro V. Baladrón, ¹ María S. Bó, and Ana I. Malizia Laboratorio de Vertebrados, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350, (7600) Mar del Plata, Argentina

ABSTRACT.—Food habits of the Red-backed Hawk ($Buteo\ polyosoma$) were studied in the southeastern coast of Buenos Aires Province, Argentina, during autumn and winter of 2001–03. At the study area, the Red-backed Hawk was a specialist predator. On a numerical basis, 99.5% of its prey were small mammals, and little seasonal and annual variability in diet was observed. The diet was composed of murids—mainly field mice ($Akodon\ azarae$), pampas rice rats ($Oligoryzomys\ flavescens$), and vesper mice ($Calomys\ spp.$), and by octodontids (tuco-tucos [$Ctenomys\ talarum$]). The tuco-tuco was the most important prey, representing 55% of the diet biomass. The Red-backed Hawk exhibited a sit-and-wait strategy, indicated by the high percentage of time study birds were perched (78.8%). Feeding, comfort movements, and flight were also recorded (11.6%, 4.9%, and 4.7%, respectively). We observed 61 capture attempts on tuco-tucos, of which 42.6% were successful. Hawks displayed agonistic interactions with other bird species. The main aggressor (77.5%, N=372) was the Chimango Caracara ($Milvago\ chimango$) that frequently consumed prey remains discarded by the hawks. Our work suggests a trend of preying on relatively more small mammals toward the southern end of its geographic range. The Red-backed Hawk in its wintering range seems to be a relative specialist predator mostly employing passive search as its main hunting strategy.

KEY WORDS: Red-backed Hawk; Buteo polyosoma; winter diet; time-activity budgets; coastal grasslands; Argentina.

DIETA INVERNAL Y PRESUPUESTOS DE TIEMPO Y ACTIVIDAD DE *BUTEO POLYOSOMA* EN PASTIZALES COSTEROS DE LA PROVINCIA DE BUENOS AIRES. ARGENTINA

RESUMEN.—Estudiamos los hábitos alimenticios de Buteo polyosoma en la costa sudeste de la provincia de Buenos Aires, Argentina, durante el otoño y el invierno de 2001 a 2003. En el área de estudio, B. polyosoma fue un depredador especialista. Sobre una base numérica, el 99.5% de sus presas estuvo compuesto por pequeños mamíferos y observamos poca variabilidad estacional y anual en la dieta. La dieta estuvo compuesta por múridos—principalmente ratones de campo (Akodon azarae y Oligoryzomys flavescens) y ratones del género Calomys, y por octodóntidos (Ctenomys talarum). La presa más importante fue C. talarum, representando el 55% de la biomasa de la dieta. Los individuos de B. polyosoma exhibieron una estrategia de sentarse y esperar, indicada por el alto porcentaje de tiempo que las aves estudiadas estuvieron posadas en una percha (78.8%). También registramos tiempos de alimentación, de movimientos de confort y de vuelo (11.6%, 4.9% y 4.7%, respectivamente). Observamos 61 intentos de captura de C. talarum, de los cuales el 54.5% fueron intentos exitosos. B. polyosoma mostró interacciones agonísticas con otras especies de aves. El principal agresor (77.5%) fue Milvago chimango, que frecuentemente consumió los restos de las presas descartados por B. polyosoma. Nuestro trabajo sugiere una tendencia a depredar mamíferos relativamente más pequeños hacia el límite sur de su rango de distribución. En el rango de distribución invernal, B. polyosoma parece ser un depredador relativamente especialista que utiliza principalmente una estrategia de cacería de búsqueda pasiva.

[Traducción del equipo editorial]

Predation is an important ecological and evolutionary process that affects morphology and behavior of organisms (Rytkönen et al. 1998). Theory suggests that predators make decisions which

maximize the net energy intake by choosing the most profitable prey and minimize the costs associated with searching and handling times (Marti 1987). Thus, a wide spectrum of hunting modes have been defined, which on one extreme is represented by active-search predators and, on the

¹ Email address: abaladro@mdp.edu.ar

other, passive-search (sit-and-wait) predators (Jaksic and Carothers 1985). One of the most common and important predator-prey models is that constituted by hawks and mammalian prey.

The Red-backed Hawk (*Buteo polyosoma*) is a medium-sized raptor exclusively distributed in South America. In Argentina, it is resident in a broad area along Los Andes mountain range, to the sea level in Patagonia (Canevari et al. 1991). During winter, hawks migrate to the lowland plains of north and central Argentina (Fjeldså and Krabbe 1990), reaching the coastal dunes area and natural grasslands of Buenos Aires Province, where they are considered a rare species (Narosky and Di Giácomo 1993). Migrations of Red-backed Hawks into Chile and Peru have also been reported (Zalles and Bildstein 2000).

Despite its wide geographic distribution, there is little information known about this raptor. Studies mainly involving the hawks' diet in a comparative framework with other raptors species were performed in Chile (Schlatter et al. 1980, Jaksic and Carothers 1985, Bozinovic and Medel 1988, Jiménez and Jaksic 1991). In reference to both its hunting mode and feeding habits, the Red-backed Hawk is considered an active searcher and a generalist predator (Jaksic and Carothers 1985, Thiollay 1994). Although rodents are the dominant prey item in the diet of this raptor, latitudinal variations in its composition have been found (Jiménez 1995). Thus, a higher consumption of birds has been recorded near its northern distributional limit (i.e., El Cauca Colombia), but the hawks' diet progressively diversifies, being mainly composed of birds, lagomorphs, reptiles and amphibians, as one moves south within its range. At the southern extreme of its distribution, the diet is composed exclusively of small mammals (i.e., Tierra del Fuego, Argentina; Jiménez 1995).

We have analyzed Red-backed Hawk's diet and time-activity budgets on its wintering range in natural coastal grasslands of central Argentina. This study represents the first quantitative analysis of the feeding ecology of the Red-backed Hawk in Argentina.

METHODS

We conducted our study in the vicinity of Mar de Cobo (Partido de Mar Chiquita, Buenos Aires Province, Argentina; 37°58′S, 57°34′W). This area comprises a small coastal village (<10 m above sea level) with a mixture of coastal dunes and natural grasslands, the typical habitat arrangement along the coast of central Argentina. Dominant vegetation is characterized by grasses (*Panicum racimosum, Distichlis scoparia* and *Bromus unioloides*) and forbs (*Ambrosia tenuifolia*; Malizia 1994). Pasture fields,

cultivated areas, and tree plantations surround the study area. This environmental heterogeneity supports a diversity of small mammals, mainly murids such as the field mouse (Akodon azarae) in grasslands, and the pampas rice rat (Oligoryzomys flavescens) and the vesper mouse (Calomys spp.) in cultivated areas and its borders (Reig 1965, Dalby 1975, Mills et al. 1992, Comparatore et al. 1996). The tucotuco (Ctenomys talarum) is an unique rodent that is subterranean (Malizia 1998).

Dietary Analysis. Weekly, we collected Red-backed Hawk's pellets and prey remains from May–August 2001–02. Preliminary surveys on the study area allowed us to identify the foraging areas of five Red-backed Hawks. We also identified perches, both posts and trees, where hawks were observed feeding. These sites were located in similar environments and were <300 m away from each other. Mammalian preys were identified by using skull taxonomic keys (Bellocq and Kravetz 1983) and collections of Laboratorio de Vertebrados (Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata). Preys were identified to the finest taxonomic level possible.

To describe the diet of the Red-backed Hawk, we calculated the numeric frequency of prey items and the biomass contribution (percent) of each prey type in the diet as the number of individuals in the samples multiplied by the mean body mass of each species. Furthermore, we estimated the numeric mean mass of prey. Mean body mass of murids and octodontids were obtained from Redford and Eisenberg (1992) and A. Malizia (unpubl. data), respectively. Food-niche breadth (FNB) was estimated using Levins' (1968) index: FNB = $1/(\Sigma p_i^2)$, where p_i was the proportion of prey taxon i in the diet. A standardized niche breadth value (FNBst) was then calculated, which ranged from 0–1: $FNB_{st} = (FNB - 1)$ (n-1), where n was the total number of prey categories (Colwell and Futuyma 1971). Frequencies among years and seasons were compared by using chi square and binomial tests, respectively. Items with frequencies ≤5 were grouped for these analyses (Zar 1984).

Age composition of tuco-tuco individuals was inferred from large bones and cranial ossification patterns. We assigned each individual to one of these age categories: young, sub-adult, or adult (Malizia 1994). The number of tuco-tuco individuals for each age category was compared with demographic data obtained on previous studies performed at the same study area (A. Malizia unpubl. data) by using the Kolmogorov-Smirnov test (Zar 1984). Tuco-tuco abundance was determined through capture-mark-release trapping. In this 2-yr survey, 25 live traps were set during 5-d sample period. Sex, mass, and reproductive condition were recorded for all animals (A. Malizia unpubl. data).

Time-activity Budgets. From May–August 2002–03, we evaluated Red-backed Hawk's daily activity by quantifying its time budgets during foraging periods. We used a continuous recording method (Martin and Bateson 1993), by means of direct observation with 8×50 binoculars, at ≥100 m distance. Daily, hawks were followed from their arrival to the study area until they departed.

Each day was divided in four intervals (morning = 1000–1200 H, midday = 1200–1400 H, afternoon = 1400–1600 H, sunset = 1600–1800 H). The activities were classified into one of the following behavioral categories: perching (considered as passive searching), feeding (in-

Table 1. Numeric and percent frequency (in parentheses) of prey items consumed by the Red-backed Hawk during autumn and winter in southeastern Buenos Aires Province, Argentina.

Prey Item	Frequency N (Percent)									
	Autumn 2001		Winter 2001		Autumn 2002		Winter 2002		Total	
Mammalia										
Rodentia										
Muridae										
Field mouse (Akodon azarae)	11	(27.5)	10	(31.3)	14	(23.3)	25	(30.9)	60	(28.2)
Verper mouse (Calomys spp.)	15	(37.5)	10	(31.3)	16	(26.7)	13	(16.05)*	54	(25.4)
Pampas rice rat (Oligoryzomys										
flavescens)	3	(7.5)	5	(15.6)	10	(16.7)	19	(23.5)	37	(17.4)
Long-nosed mouse (Oxymycterus rufus)	1	(2.5)	0	(0.0)	0	(0.0)	4	(4.9)	5	(2.3)
Marsh rat (Holochilus brasiliensis)	0	(0.0)	0	(0.0)	1	(1.7)	4	(4.9)	5	(2.3)
Unidentified murids	3	(7.5)	0	(0.0)	5	(8.3)	3	(3.7)	11	(5.1)
Octodontidae										
Tuco-tuco (Ctenomys talarum)	7	(17.5)	6	(18.7)	14	(23.3)	13	(16.05)	40	(18.8)
Aves										
Passeriformes	0	(0.0)	1	(3.1)	0	(0.0)	0	(0.0)	1	(0.5)
Total	40		32		60		81		213	
N pellets	19		15		20		26		80	
N prey remains	2		1		11		7		21	

^{*} P < 0.05.

cluding capturing, handling, and ingesting prey), comfort movements (including cleaning and grooming), and flight (considered as active searching when longer than 30 sec). We considered a perched hawk as passive searching, given that individuals regularly scanned the ground for potential prey when perched. To standardize observation day and interval durations, time budgets were expressed as the proportion of time spent in each activity respect to the total time registered. These data were analyzed by using the Kruskall-Wallis test and Dunn's multiple comparison method (Zar 1984). The capture, handling, and ingesting prey times were also calculated.

Furthermore, we distinguished two kinds of events: agonistic interactions (recording aggressor species and the activity of hawks during each event) and prey capture attempts (recording the number of failed and successful captures, type of prey, and hunting mode). The capture efficiency was calculated as the ratio of successful captures divided by the number of total capture attempts. We considered that an attempt began when hawks made a direct flight toward the ground, and it was completed when hawks returned to the perch. The duration of successful and failed captures was compared by using the student *test.* Frequencies of event categories were analyzed by using chi-square test (Zar 1984). Values are given as means (±SD).

RESULTS

Diet. We collected 80 pellets and 21 prey remains from which we identified 213 individual prey (Table 1). Rodents were the most common prey type in the hawks' diet. Murids, including field

mice, vesper mice, and pampas rice rats, were the most abundant prey type (80%; N=161), representing 45% of the diet biomass. The tuco-tuco comprised the remaining 20% (N=40) and contributed 55% of the biomass consumed by the hawks (Table 2). Only one Passeriform bird was identified in winter 2001 (Table 1). The mean body mass of all prey was 44.8 g (± 45.3).

For the whole sampling period, comparisons among numeric frequencies of prey showed significant differences ($\chi^2 = 80.36$, df = 6, P < 0.0001), which were attributed to infrequent prey items (Table 1). However, no significant differences between years were found ($\chi^2 = 7.44$, df = 4, P =0.112). When seasonal variations in frequencies for each rodent species were analyzed, an inverse trend between vesper mouse and pampas rice rat was observed (Table 1). The former evidenced a decreasing trend, although it was only significant in winter 2002 ($\chi^2 = 8.07$, df = 3, P < 0.05). The latter showed increasing frequencies that were not significant ($\chi^2 = 4.71$, df = 3, P = 0.194). Field mice and tuco-tucos did not vary significantly among seasons (P > 0.65). Long-nosed mice (O. rufus) showed low frequencies during all seasons, whereas marsh rats (H. brasiliensis) were present in hawks' diet exclusively during 2002 (Table 1). Food-niche breadth

Table 2. Body mass, numeric frequency and percent biomass of prey items in the winter diet of the Red-backed Hawk in southeastern Buenos Aires Province, Argentina.

Prey	Mass (g)	Frequency (N)	BIOMASS (%)
Mammalia			
Rodentia			
Muridae			
Akodon azarae	21	60	14.0
Calomys spp.	15	54	9.0
Oligoryzomys flavescens	23	37	9.4
Oxymycterus rufus	70	5	3.9
Holochilus brasiliensis	147	5	8.2
Octodontidae			
Ctenomys talarum	125	40	55.5
Total		201	

indices were: FNB = 4.28~(N=7) and FNB_{sta} = 0.55 for the whole sampling period. However, seasonal values were higher, showing a peak during autumn 2002 (FNB_{sta} = 0.76).

Comparisons between age composition of tucotucos in the diet and the availability of individuals of each age class in the field indicated an overestimation of young individuals in the raptor's diet (45.5% in samples vs. 13.9% in field samples; Kolmogorov-Smirnov test: $D=11,\ N=33,\ P<0.001$). Frequencies of subadult and adult tuco-tucos in the samples and in the field did not show significant differences (36.4% vs. 41.7% and 18.2% vs. 44.4%, respectively; P>0.35).

Time-activity Budgets. We quantified time budget data for Red-backed Hawks for 71 hr over 21 observation d (12 d and 27 hr in 2002 and 9 d and 44 hr in 2003). Perching was the most common activity exhibited by the Red-backed Hawk (78.8%) and constituted the dominant activity witnessed in all time intervals (Fig. 1). Perching differed significantly from all other recorded categories (H = 66.0, df = 3, P < 0.0001). Feeding was the second most prevalent activity exhibited by hawks (11.6%). Both flight and comfort activities exhibited were infrequent during all observation days and time intervals (4.9% and 4.7%, respectively; Fig. 1).

Prey capture activity was low during the morning, increased significantly during midday ($\chi^2 = 38.7$, df = 3, P < 0.0001), and decreased during afternoon and sunset periods (Fig. 2). We recorded 61 capture attempts all directed toward tuco-tucos ($\bar{x} = 2.44$ per observation d, range = 1–6), of which 26

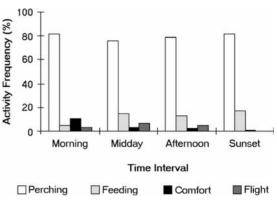


Figure 1. Time-activity budgets (percent) of the Red-backed Hawk in daily time intervals, during autumn and winter 2002–03 in southeastern Buenos Aires Province, Argentina. Morning = 1000–1800 H, midday = 1200–1400 H, afternoon = 1400–1600 H, and sunset = 1600–1800 H.

(42.6%) were successful. However, efficiency was highly variable among days ranging from 0–100%.

Mean duration of successful and failed captures was 32 sec (± 10) and 22 sec (± 18), respectively. These durations were not statistically different (t=1.5, df = 17, P>0.229). All successful captures consisted of a direct flight from a perch toward the prey, followed by prey capture on the ground and a flight back to the perch. Prey handling took place immediately after capture, and consisted of struggling with and killing the prey by squeezing with

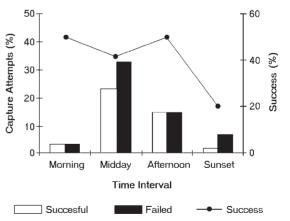


Figure 2. Frequency of capture attempts (percent) and success ratio of the Red-backed Hawk in each time interval, during autumn and winter 2002–03, in southeastern Buenos Aires Province, Argentina. Morning = 1000–1800 H, midday = 1200–1400 H, afternoon = 1400–1600 H, and sunset = 1600–1800 H.

talons (3 \pm 2.6 min; N=11) followed by consumption (18.2 \pm 6.8 min; N=23). In all cases, the Red-backed Hawk consumed mainly body muscular mass, discarding prey's head and viscera.

Agonistic interactions between the Red-backed Hawk and other bird species were recorded frequently (N = 480). The most frequent aggressor was the Chimango Caracara (Milvago chimango; 77.5% of events; $\chi^2 = 708.3$, df = 3, P < 0.0001) followed by Southern Lapwing (Vanellus chilensis; 9.8%), gulls (*Larus* spp.; 8.1%), and others (4.6%; i.e., Passeriformes, Crested Caracara [Caracara cheriway], and pigeons [Columba spp.]). In addition, the Chimango Caracara exhibited a mean rate of 6.1 (±6.9) interactions/hr. A maximum frequency of 30 attacks/min was reached when two chimangos attacked one hawk simultaneously. The interactive episodes with chimangos occurred mainly when the Red-backed Hawk was perched (66%) and were much less frequent when hawks were in flight or feeding (20% and 14%, respectively; $\chi^2 = 42.44$, df = 2, P < 0.0001).

DISCUSSION

During the autumn and winter seasons, in the vicinity of Mar de Cobo, the Red-backed Hawk behaved as a specialist predator, preying almost exclusively upon small mammals. On a numerical basis, field mice, vesper mice, tuco-tucos, and pampas rice rats made a similar contribution to hawks' diet (Table 1). Food-niche breadth values were intermediate to high, reflecting the evenness in numeric frequencies of most representative prey. On the other hand, tuco-tucos were the most important prey based on biomass (Table 2). Therefore, tuco-tucos play a very important role as a food item for the Red-backed Hawk in our study area.

Our results on diet composition are partly in agreement with that of Schlatter et al. (1980) from central Chile. These authors also reported a high proportion of rodents in the Red-backed Hawk's diet (89%), but documented the presence of other items such as lagomorphs, birds, marsupials, and reptiles. In addition, our data differ from that of Jiménez (1995) from northern Chile, who reported 45% of small mammals and a higher proportion of amphibians, reptiles, and birds in the diet. Our work at a southern location of Argentina indicated a diet of 99.5% rodents. These results support the report of a trend toward an increase of small mammal consumption from north to south within the geographic range of this raptor (Jiménez 1995). Finally,

mean body mass (44.8 g) of prey taken by Red-backed Hawks was considerably lower than that reported for Chile (213 g; Schlatter et al. 1980); the heavy mass of prey in Chile is related with a numeric prevalence of fence degu-rat (*Octodon degus*) in that area.

Predation pressure on some specific age classes is clearly evident for tuco-tucos because the young individuals showed a significantly higher occurrence in hawks' diet compared to their field availability. Moreover, given that younger individuals of tuco-tuco are less active above ground than older ones (Kittlein et al. 2001), the bias toward juveniles is likely more extreme than indicated by our data. This could be related to the handling constraints of larger prey, as well as the higher susceptibility of younger individuals due to their lack of experience in avoiding predators (Malizia 1994, Malizia et al. 2001).

Several factors may promote a close trophic association between hawks and tuco-tucos. First, hawks may have preyed heavily upon this rodent, because it was the most profitable prey in terms of energy available and handling costs. Second, capture attempts by raptors peaked in midday hours, which is in accordance with primary daily activity of tuco-tucos (pers. observ.). Third, efficiency of Redbacked Hawks in capturing this rodent was quite high (42.6%), and similar to that as reported for other mammal-eating buteonines (46% for Swainson's Hawks [B. swainsoni] to 60% for Red-tailed Hawks [B. jamaicensis]; Toland 1986).

The high percentage of total time devoted to perching activity and the fact that all capture attempts were initiated from perches suggests that the Red-backed Hawk is primarily a sit-and-wait predator in our study area. This conclusion differed from that of Jaksic and Carothers (1985), who stated that this raptor is mainly an active searcher.

Agonistic interactions between the Red-backed Hawk and the Chimango Caracara were very common ($\bar{x}=6.1$ attacks/hr). We observed chimangos consuming prey remains left from the hawks, indicating a possible commensalist association, although those aggressive interactions suggest a cost to Red-backed Hawks. Alternatively, the fact that the Red-backed Hawk was often attacked by chimangos while they were feeding may suggest kleptoparasitism. A similar relationship between the Chimango Caracara and other bird species in the same study area has also been observed (e.g., Copello and Favero 2001).

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