

OBSERVATIONS ON THE COMPARATIVE BEHAVIORAL ECOLOGY OF HARRIS' HAWK IN CENTRAL CHILE

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ABSTRACT.—Throughout one year we observed the behavioral ecology of Harris' Hawks (*Parabuteo unicinctus*) in central Chile. The hawks' activity period lacked diel or annual variation. Their most common flight mode was soaring in thermals and wind updrafts, rarely using flapping flight, and never hovering. Harris' Hawks appeared to select physiographic features that favored the presence of updrafts, particularly north- and west-facing slopes and ridgetops, but were also commonly seen flying over ravines (where they perched frequently). Prey were primarily small- and medium-sized mammals, and secondarily medium-sized birds. Although not aggressive, Harris' Hawks were nonetheless attacked by two other sympatric raptors, Black-chested Eagles (*Geranoaetus melanoleucus*) and Red-backed Hawks (*Buteo polyosoma*). These three species, which were studied over the same period and with the same techniques, were similar in activity and behavior, although Harris' Hawks were slightly more different than the latter were between themselves.

Observaciones sobre la ecología conductual comparativa de peucos en Chile central

RESUMEN.—Por un año observamos la ecología conductual del peuco (*Parabuteo unicinctus*) en Chile central. El período de actividad de los peucos no difirió ni dentro del día ni a lo largo del año. Su modo de vuelo más común fue el planeo en corrientes térmicas y de obstrucción, raramente usando el vuelo batido y nunca el revoloteo. Los peucos parecieron seleccionar características fisiográficas que favorecían la presencia de corrientes ascendentes, particularmente las laderas de exposición norte y oeste y las cimas, pero también se los veía volando sobre quebradas (en donde también se posaban). Sus presas eran principalmente mamíferos de tamaños pequeño y mediano, y secundariamente aves de tamaño mediano. Aunque los peucos eran poco agresivos, eran atacados por otras dos especies simpátricas de rapaces, el águila (*Geranoaetus melanoleucus*) y el aguilucho (*Buteo polyosoma*). Estas tres especies, que fueron estudiadas en el mismo período y con las mismas técnicas, eran similares en actividad y conducta, aunque los peucos eran ligeramente más diferentes que las otras dos entre ellas.

[Traducción Autores]

The Harris' Hawk, *Parabuteo unicinctus*, is distributed from the southwestern United States in the north through Central and South America to central Chile and Argentina (Brown and Amadon 1968). The species has been relatively well studied in North America (e.g., Mader 1975a, Bednarz et al. 1988 and references therein). By contrast, little has been published about the species elsewhere in Central and South America. To our knowledge, the only reports come from Chile and cover its diet (Jaksic et al.

1980), food-niche relationships with other sympatric predators (Jaksic et al. 1981), and conservation status (Jaksic and Jiménez 1986). Here we report on aspects of the behavioral ecology of the Harris' Hawk near its southernmost distributional limit. This study is based on one year of observations made in central Chile concurrent with those made on two other sympatric raptors: Black-chested Eagle (*Geranoaetus melanoleucus*; Jiménez and Jaksic 1989) and Red-backed Hawk (*Buteo polyosoma*; Jiménez and Jaksic 1991). Because this is the last report of this series, we take the opportunity to make comparisons between the behavioral ecology of the Harris' Hawk and the two other species.

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STUDY SITE AND METHODS

The study site is described in Jiménez and Jaksic (1989). Briefly, San Carlos de Apoquindo (33°23'S 70°31'W) is a rugged area 20 km E of Santiago in the Andean foothills with elevations ranging from 1050–1915 m. The physiography includes both flat areas and numerous ridges dissected by deep ravines. The climate is mediterranean, with cool, rainy winters and dry, hot summers. The wind blows westwardly from the valley to the mountains during the daytime. The dominant vegetation is an evergreen scrub (very similar to the California chaparral) that changes physiognomy depending on topography and orientation.

Based on the number and duration of sightings, the Black-chested Eagle was the most common raptor at the site, having been sampled (timed with a stopwatch) for nearly 93 hr over a calendar year (Jiménez and Jaksic 1989); the second most common raptor was the Red-backed Hawk, observed for nearly 29 hr timed (Jiménez and Jaksic 1991). Harris' Hawk ranked third in this respect, having been monitored for 13 hr over the same sample period.

Following the same protocol used for the other two species, for each Harris' Hawk observed we recorded: 1) time of observation and duration of activity, 2) activity type, and 3) habitat beneath bird. We recognized the following activity types (cf. Jiménez and Jaksic 1989 for detailed description): thermal soaring, wind soaring, cruising, hovering, harassing, perching, and miscellaneous behavior. We recognized the following habitat types (cf. Jiménez and Jaksic 1989 for detailed description): flatlands, ravines, ridgetops, and slopes (east-, west-, south-, and north-facing). We mapped these habitats and calculated their surface areas (slope-corrected) with a digital planimeter from a high-resolution aerial photograph. The physiognomy of each habitat type, in terms of the vegetative cover represented by trees, shrubs, herbs, bare ground, and rocks, as well as estimated prey numbers, were reported in Jiménez and Jaksic (1989).

We made observations with binoculars from the top of a hill, from dawn to dusk, with the day divided into six equal-time intervals (see Jiménez and Jaksic 1989). Observations took place during one entire day every other week between 1 August 1984 and 1 August 1985. We pooled a total of 780 min of sampling into four seasons: spring (1 August to 30 October), summer (1 November to 31 January), fall (1 February to 30 April), and winter (1 May to 31 July). We used one- or two-way ANOVA for unequal sample sizes (Sokal and Rohlf 1981:210, 360), with PROC GLM in SAS (1985), and the Student-Newman-Keuls test for *a posteriori* contrasts (SAS 1985:444). For analyzing frequency data, we used the *G* statistic (Sokal and Rohlf 1981:695). It should be noted that the assumption of independence of data is violated in behavioral studies, because what a bird does one minute is very likely to influence what it will be doing the next minute. However, this should affect more strongly comparisons made within a season than between seasons. Still, the *P*-values calculated should be considered imprecise and our interpretations of differences and similarities taken cautiously.

We identified prey remains found under perches and one nest, and from regurgitated pellets. Prey were iden-

tified with standard procedures (Marti 1987), as exemplified by Jiménez and Jaksic (1989) and Pavez et al. (1992) for sympatric Black-chested Eagles.

RESULTS AND DISCUSSION

Activity levels (measured in minutes) did not differ among times of the day ($F = 1.74$, $df = 5$, $P > 0.12$), nor with season ($F = 1.73$, $df = 3$, $P > 0.16$); the interaction between these variables was significant ($F = 1.91$, $df = 15$, $P < 0.03$). Indeed, Harris' Hawks were observed throughout the day with no clear peaks of activity in any interval of the day, or in any particular season. Thus, Harris' Hawks differed from sympatric Black-chested Eagles, which had a bimodal activity period throughout the year, and from Red-backed Hawks, which were more active during summer and least active during winter.

Thermal soaring was the most common flight mode throughout the year, ranging from 47% (winter) to 16% (summer) of the observed time (Table 1). Wind soaring was the second most prevalent flight mode, accounting for 37% (fall) to 16% (summer) of the activity time. Harris' Hawks spent most of their time perched during summer (64%), but very little during winter (4%). The remaining activities (Table 1) accounted at the most (during winter) for 19% of the daily activity period, and for less than 7% during the remaining seasons. It should be noted that our sampling technique (observing from a hilltop) may have biased our detections toward soaring birds and away from perching Harris' Hawks and those making short low flights. Unlike sympatric Black-chested Eagles (Jiménez and Jaksic 1989) and Red-backed Hawks (Jiménez and Jaksic 1991), Harris' Hawks apparently did not hover, and spent little time in agonistic interactions (Table 1).

Observed occurrences of Harris' Hawks (in minutes) differed both among habitat types ($F = 18.06$, $df = 6$, $P < 0.0001$) and among seasons ($F = 3.53$, $df = 3$, $P < 0.02$); there was a significant interaction between these variables ($F = 2.13$, $df = 18$, $P < 0.004$). Throughout the year, Harris' Hawks flew more often over north-facing slopes (from 59% in summer to 19% in winter), secondarily over west-facing slopes, ravines, and ridgetops (from 35% to 3% in different seasons), and very little over flatlands, south- and east-facing slopes (Table 2). Except for the latter three, there were clear seasonal shifts in the use of the remaining four habitat types (SNK *a posteriori* test, $P < 0.05$ in all cases). West-facing slopes were used more during fall and winter

Table 1. Time (in minutes) spent by Harris' Hawks in different activities in central Chile, 1984–1985.

ACTIVITY	SPRING ^a N = 12 d	SUMMER N = 12 d	FALL N = 6 d	WINTER N = 7 d
Thermal soaring	8.3 ± 4.8 ^b	3.5 ± 1.9	8.4 ± 7.7	5.2 ± 3.9
% time	34.4	15.8	34.3	47.3
Wind soaring	5.8 ± 3.3	3.5 ± 2.1	9.1 ± 4.1	3.3 ± 1.9
% time	24.2	15.8	37.1	30.0
Cruising	1.5 ± 1.0	0.8 ± 0.5	1.3 ± 1.0	2.1 ± 1.3
% time	6.2	3.6	5.3	19.1
Hovering	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
% time	0.0	0.0	0.0	0.0
Harassing	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0
% time	0.0	0.4	0.4	0.0
Perching	8.3 ± 5.9	14.3 ± 14.5	5.4 ± 8.1	0.4 ± 0.5
% time	34.4	64.4	22.1	3.6
Other	0.2 ± 0.2	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
% time	0.8	0.0	0.8	0.0
Total time/period	24.1 ± 10.6	22.2 ± 13.9	24.5 ± 16.0	11.0 ± 5.2
Total time/season	289.2	266.4	147.0	77.0

^a See Methods section for periods involved.

^b Mean number of minutes this activity was observed per day ± two standard errors.

than in other seasons, while the reverse happened with regard to north-facing slopes (Table 2).

Jiménez and Jaksić (1989) showed that the areal representation of different habitat types in the study site was as follows: north-facing slope (26%), south-

facing slope (19%), ridgetop (18%), west-facing slope (14%), flatland (9%), ravine (7%), and east-facing slope (7%). Harris' Hawks thus appeared to avoid flying over south-facing slopes and flatlands, while they concentrated on ravines (Table 2). The near

Table 2. Time (in minutes) spent by Harris' Hawks on seven habitat types in central Chile, 1984–1985.

ACTIVITY	SPRING ^a N = 12 d	SUMMER N = 12 d	FALL N = 6 d	WINTER N = 7 d
Flatland	0.1 ± 0.2 ^b	0.4 ± 0.5	0.4 ± 0.5	0.7 ± 1.3
% time	0.4	1.8	1.6	6.4
Ravine	7.9 ± 3.9	4.7 ± 4.3	3.5 ± 2.6	0.7 ± 0.6
% time	32.8	21.2	14.3	6.4
Ridgetop	4.0 ± 3.7	2.1 ± 2.1	5.6 ± 5.8	1.8 ± 2.2
% time	16.6	9.4	22.9	16.3
North slope	9.2 ± 5.5	13.1 ± 14.9	4.8 ± 4.9	2.1 ± 1.6
% time	38.2	59.0	19.6	19.1
South slope	0.5 ± 0.4	1.2 ± 1.2	2.9 ± 1.9	1.1 ± 1.8
% time	2.1	5.4	11.8	10.0
East slope	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.8 ± 1.0
% time	0.0	0.0	0.4	7.3
West slope	2.4 ± 3.1	0.7 ± 0.8	7.2 ± 9.9	3.8 ± 2.6
% time	9.9	3.2	29.4	34.5
Total time/period	24.1 ± 10.6	22.2 ± 13.9	24.5 ± 16.0	11.0 ± 5.2
Total time/season	289.2	266.4	147.0	77.0

^a See Methods section for periods involved.

^b Mean number of minutes this activity was observed per day ± two standard errors.

Table 3. Prey of Harris' Hawks in central Chile, based on prey remains and pellets found under several perches and one nest, 1984–1985. Integer numbers are the absolute numerical representation of each prey item; numbers in parentheses are the percent numerical representation of major prey classes. Prey weights in grams.

PREY	WEIGHT	PELLETS	REMAINS	TOTAL
Mammals	—	(67.4)	(66.7)	(67.3)
Rodentia				
<i>Abrocoma bennetti</i> (Bennett's chinchilla rat)	231	5	1	6
<i>Akodon longipilis</i> (Hairy field mouse)	63	1	0	1
<i>Akodon olivaceus</i> (Olivaceous field mouse)	44	1	0	1
<i>Octodon degus</i> (Fence degu rat)	184	20	3	23
<i>Oryzomys longicaudatus</i> (Long-tailed rice rat)	36	3	0	3
Lagomorpha				
<i>Oryctolagus cuniculus</i> (European rabbit) ^a	1300	18	12	30
Mammals unidentified	—	47	0	47
Birds	—	(19.8)	(29.1)	(21.2)
Tinamiformes				
<i>Nothoprocta perdicaria</i> (Chilean Tinamou)	400	1	1	2
Columbiformes				
<i>Zenaida auriculata</i> (Eared-dove)	125	0	1	1
Galliformes				
<i>Callipepla californica</i> (California Quail)	200	0	1	1
Piciformes				
Unidentified	100	1	0	1
Passeriformes				
<i>Mimus thenca</i> (Chilean Mockingbird)	65	1	2	3
<i>Curaeus curaeus</i> (Austral Blackbird)	90	1	1	2
<i>Sturnella loyca</i> (Red-breasted Meadowlark)	110	1	0	1
<i>Anairetes parulus</i> (Tufted Tit-tyrant)	11	1	0	1
Birds unidentified	—	21	1	22
Bird egg	—	1	0	1
Reptiles	—	(7.8)	(4.2)	(7.3)
Sauria				
<i>Liolaemus</i> sp. (Unidentified lizard)	15	4	0	4
<i>Callopistes palluma</i> (Chilean racerunner)	65	4	1	5
Serpentes				
<i>Philodryas chamissonis</i> (Long-tailed snake)	150	3	0	3
Insects		(5.0)	(0.0)	(4.2)
Coleoptera				
Buprestidae	<1	1	0	1
Scarabaeidae	<1	5	0	5
Insects unidentified	<1	1	0	1
Total number of prey	—	141	24	165

^a Both adults and juveniles; the weight indicated is for adults.

proportional use of north-facing slopes and ridgetops may be explained because these habitat types receive more direct solar radiation, and thus probably generate more thermal drafts. Similarly, west-facing slopes receive radiation from the setting sun, and are

swept by the prevailing westerly wind (Jiménez and Jaksic 1989). In contrast, south-facing slopes and flatlands received relatively low amounts of incident radiation and were sheltered from prevailing winds. Harris' Hawks behaved similarly to Black-chested

Eagles (Jiménez and Jaksic 1989) and Red-backed Hawks (Jiménez and Jaksic 1991), except for flying much more often over the cool and windless ravines.

The amount of time perching in different habitat types was not related to their relative availability ($G = 20.0$, $df = 4$, $P < 0.001$). In 42% of 45 sightings, Harris' Hawks were perched in north-facing slopes, 33% were perched in ravines, 11% in ridgetops, 9% in west-, and 5% in south-facing slopes. We never saw Harris' Hawks perching in flatlands or east-facing slopes. These findings are similar to those reported for Black-chested Eagles (Jiménez and Jaksic 1989) and Red-backed Hawks (Jiménez and Jaksic 1991), except for perching in ravines. Note that order of preference for habitat types used for perching by Harris' Hawks was the same as for flying over. The apparent preference for perching on north-facing slopes may be because they afford easy access to updrafts. The preference for perching in ravines may be associated to the higher densities of mammalian prey in those areas (cf. data in Jiménez and Jaksic 1989).

Perch substrates were not used homogeneously ($G = 48.0$, $df = 8$, $P < 0.001$). In decreasing order, perches used were standing dead trees (33%), live trees of *Quillaja saponaria* (29%), live trees of *Lithraea caustica* (16%), boulders (9%), standing dead bromeliads (7%), live trees of *Kageneckia oblonga* (2%), of *Porlieria chilensis* (2%), and live columnar cacti (2%). Sympatric Black-chested Eagles (Jiménez and Jaksic 1989) and Red-backed Hawks (Jiménez and Jaksic 1991) displayed roughly the same perching preferences. All these structures were above the general level of the scrub canopy, and probably provided good visibility and easy access to updrafts.

Aggressive encounters (harassment) were observed only during summer and fall, and occupied less than 1% of the Harris' Hawks' time (Table 1). Red-backed Hawks (weight = 975 g) initiated 53 attacks on Harris' Hawks and received 48 attacks (Jiménez and Jaksic 1991), Black-chested Eagles (weight = 2378 g) perpetrated 49 and received 62 attacks (Jiménez and Jaksic 1989), and conspecifics (weight = 876 g) initiated 13 and received 7 attacks throughout the same observation period. Black-chested Eagles were about as frequently harassed by conspecifics as by other species (49% of attacks on Black-chested Eagles were allospecific; cf. Jiménez and Jaksic 1989), whereas Red-backed Hawks were slightly more frequently harassed by other species than by conspecifics (55% of allospecific attacks; cf.

Jiménez and Jaksic 1991). Harris' Hawks were infrequently harassed by conspecifics (23% of the attacks) and primarily by Red-backed Hawks (46%) and Black-chested Eagles (31%) which are larger. None of these agonistic encounters involved prey, unlike the situation reported by Bildstein (1987) for sympatric Red-tailed Hawks (*Buteo jamaicensis*) and Rough-legged Hawks (*B. lagopus*) in Ohio.

Because pellets found under perches and remains found under the one nest sampled were collected in the same habitat and time of the year, a comparison is warranted. Mammalian prey were equally represented among pellets and nest remains, avian prey were comparatively underrepresented among pellets, and the reverse occurred with both reptilian and insect prey (Table 3). Overall, the differences in prey composition were not dramatically different between pellets and nest remains. Harris' Hawks in this locality consumed primarily small- (rodents) and medium-sized mammals (rabbits), and secondarily medium-sized birds (several orders). Lizards and snakes were minor components of their diet, and insects were almost insignificant in biomass. No comparable data are available for sympatric Red-backed Hawks (Jiménez and Jaksic 1991), but for Black-chested Eagles Jiménez and Jaksic (1989) and Pavez et al. (1992) showed that their diet in the same locality is similar to that reported here for Harris' Hawks. Major differences are the lack of insect consumption by the eagles, the relatively higher consumption of reptiles, and the lower consumption of birds.

It is noteworthy that throughout the study period, no evidence was observed of cooperative breeding and/or hunting, as is common in North America (Mader 1975b, 1979, Bednarz 1987, 1988).

In summary, Harris' Hawks were slightly more different in terms of activity and behavior than were Black-chested Eagles and Red-backed Hawks. Among the most remarkable differences between Harris' Hawks and the others were: (a) they lacked diel or annual differences in activity levels, (b) they did not use hovering as a flight mode, (c) they spent more time flying over ravines, (d) they used perches in ravines more often, and (e) they showed lesser aggressiveness.

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