

Time-activity budgets and hunting behavior of the Roadside Hawk (*Rupornis magnirostris*) and the Long-winged Harrier (*Circus buffoni*)

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ABSTRACT: We conducted a study aimed to evaluate and compare the behavioral patterns of the Roadside Hawk (*Rupornis magnirostris*) and the Long-winged Harrier (*Circus buffoni*), two common but poorly known Neotropical raptors. From 2005 to 2008, we quantified the time-activity budgets of both raptors at the Pampas region of Argentina in order to determine their allocation of time to different activities, their foraging strategies and hunting modes, and whether their behavioral patterns change in different habitats and seasons. The Roadside Hawk and the Long-winged Harrier showed dissimilar activity patterns. Hawks devoted more time to perching (45.5% of total time) than harriers (13%), whereas harriers devoted more time to foraging (45%) than hawks (13%). No differences were found in the time they devoted to fly. In addition, both species differed in the use of flying modes, perching sites, and habitat types. Hawks preferably used cruising flights, perched on tall poles or trees, and were found in woodlands and urban areas. Harriers preferably used soaring and circle flights, perched on the ground, and were found in grasslands and agroecosystems. Notwithstanding, the most obvious difference between these raptors were their hunting modes: the Roadside Hawk behaved as a sit-and-wait predator and the Long-winged Harrier as a wide-foraging predator. These patterns seem to be consistent in different habitat contexts and showed certain differences between seasons. Our results suggest that these species may segregate spatially by utilizing different hunting habitats as well as behaviorally, by using different hunting modes.

KEY-WORDS: behavioral patterns, Neotropical raptors, Pampas region, sit-and-wait predator, wide-foraging predator.

INTRODUCTION

Time-activity budgets quantify how birds apportion time to various activities (Paulus 1988). These may reveal critical aspects of their use of the spatial and temporal dimensions, and are important to understand the niche partitioning among sympatric species (Schoener 1971). This approach has been extensively used in birds, showing that patterns of daily activity can vary widely between species and that they are important to determine the life history and ecological adaptations of birds (Hamilton *et al.* 2002). However, the study of behavioral patterns of raptorial birds is often difficult, because the seemingly limited repertoire of behaviors displayed and the long periods of inactivity typically attributed to these predators (Gaibani & Csermely 2007). For this reason, behavioral studies of raptors have been often overlooked.

The most diverse and detailed information on time-activity budgets of diurnal raptors (Falconiformes and Accipitriformes) that eat vertebrates in the Americas comes from studies conducted on Nearctic species. For example,

Osprey (*Pandion haliaetus*; Stinson 1978, Levenson 1979, Jamieson *et al.* 1982), Ferruginous Hawk (*Buteo regalis*; Wakeley 1978), Red-tailed Hawk (*B. jamaicensis*; Soltz 1984), Peregrine Falcon (*Falco peregrinus*; Palmer *et al.* 2001), and Bald Eagle (*Haliaeetus leucocephalus*; Warnke *et al.* 2002). Comparatively, this kind of research has been much less developed in the Neotropics. The bulk of information available comes from Argentina and Chile and is limited to a few species: the Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*) (Jiménez & Jaksic 1989, de Lucca & Saggese 2012), the Variable Hawk (*G. polyosoma*) (Jiménez & Jaksic 1991, Baladrón *et al.* 2006), and the Harris Hawk (*Parabuteo unicinctus*) (Jiménez & Jaksic 1993, Santander *et al.* 2014). Thus, data on time-activity budgets is lacking for most Neotropical diurnal raptors.

The Roadside Hawk (*Rupornis magnirostris*) and the Long-winged Harrier (*Circus buffoni*) are two common, but little known raptor species of the Neotropics. These species are sympatric for the greater part of their distributions (del Hoyo & Collar 2014). The Roadside

Hawk (269 g; Dunning-Jr. 2008) is widespread from northern Mexico to Río Negro Valley in central Argentina (Thiollay 1994), where it inhabits woodlands and forest margins and, to a lesser extent, open fields near woodlands (Canevari *et al.* 1991). The Long-winged Harrier (420 g for males and 613 g for females; Dunning-Jr. 2008) is endemic of South America, ranging from Venezuela to Patagonia, occasionally reaching as far south as Tierra del Fuego in Argentina (Thiollay 1994). This raptor is found throughout open areas of central Argentina, Uruguay and Brazil, being common in grasslands, agricultural fields, savannas, marshes, and wetlands (Canevari *et al.* 1991, de la Peña 1992).

In the Pampas region of Argentina, these two raptor species belong to the same trophic guild, as both are considered major predators of small vertebrates. Previous studies performed at that region indicate that the Roadside Hawk consumes almost exclusively small mammals during winter, but also incorporates insects in its diet during summer (Baladrón *et al.* 2011), whereas the Long-winged Harrier consumes birds and small mammals, although seems to specialize in birds during the breeding season (Bó *et al.* 1996). Thus, it is expected that some degree of interference competition between them occurs. The use of different hunting habitats and/or hunting behaviors may help to reduce the interference among sympatric predators (Jaksic 1985). In this sense, the Roadside Hawk has been characterized as a passive search predator (Panasci & Whitacre 2000) and the Long-winged Harrier as an active search predator (Isacch *et al.* 2001). Notwithstanding, if these raptors are in fact segregated through the spatial, temporal, or behavioral dimensions is difficult to assert, as no quantitative studies on their behavioral patterns have been performed.

We conducted a study aimed to evaluate and compare the behavioral patterns of the Roadside Hawk and the Long-winged Harrier. Our specific objectives were: (1) to quantify time allocation of both species to daily activities, (2) to determine their foraging strategies and hunting modes, and (3) to assess whether their behavioral patterns change in different habitat contexts and between breeding and non-breeding seasons.

METHODS

The study was carried out in Mar Chiquita County, southeast Buenos Aires Province, Argentina (37°32'–37°45'S; 57°19'–57°26'W), which is located in the Pampas region. The landscape includes zones of native vegetation such as marshes and grasslands, and zones highly modified by the development of agriculture (Cabrera 1971, Bilenca & Miñarro 2004). Most of the land in the study area is devoted to grazing fields and

pastureland and, to a lesser extent, to cropland which is cultivated for corn, soybean, and wheat production (Isacch 2008). Small villages and periurban areas, native woodlands, and tree plantations complete the landscape of the study area. This habitat heterogeneity supports a high faunal diversity, which represents a wide spectrum of potential prey for raptors (Iribarne 2001).

From 2005–2008, we registered raptors' activities during daylight by quantifying their time-activity budgets (Martin & Bateson 1993). Firstly, we looked for raptors by vehicle through paved and unpaved roads of the study area, and on foot in areas where species were previously registered. Once the bird was spotted, the individual was observed with 10 × 50 binoculars and all its activities registered in a digital voice recorder until it was lost from sight (continuous recording method; Gaibani & Csermely 2007). These recordings were later analyzed to determine the duration of all behaviors (Martin & Bateson 1993). The sampling was conducted in an opportunistic manner throughout the period and the search effort was evenly distributed across seasons (breeding and non-breeding) and habitat types. Habitat types were grouped in four categories: agroecosystems (crops, pastures and grazing fields), woodlands (native forests, groves at agroecosystem margins, and forestations), urban (small villages and periurban areas), and grasslands (tallgrass prairies, marshes, and psammophytic grasslands). No surveys were conducted in bad weather conditions.

The behavior of both raptors was classified into three basic categories: flying, foraging, and perching (Table 1). Flying activities included all moves between hunting areas, changes of perching site, and high-altitude flights. Foraging included all those behaviors involved in prey capture, searching (active or passive), transporting, handling, and feeding. Perching activities included all behaviors made on perch except those related to foraging. In addition, we quantified the number and frequency of discrete events, such as capture attempts, vocalizations and other occasional behaviors. To standardize observation days and interval durations, time-activity budgets were expressed as the proportion of time spent in each activity respect to the total time registered (Martin & Bateson 1993). Given the limited observation time, the time-activity budgets of each species were calculated by pooling data of different ages (juveniles and adults) and sexes. Since the use of different hunting modes would be, at first, the most contrasting behavior of these species, we performed a more detailed description of their foraging activities with emphasis on the hunting technique used by each raptor (Jaksic & Carothers 1985). Values are reported as means ± standard error (SE).

We evaluated the agreement in the activity patterns between species, habitats (agroecosystems, woodlands, urban, and grasslands), and seasons (breeding and non-

TABLE 1. Ethogram showing the activities and sub-activities used to describe the time-activity budgets of the Roadside Hawk (*Rupornis magnirostris*) and the Long-winged Harrier (*Circus buffoni*).

Activity	Sub-activity	Definition
Flying	Circular flight	The individual flies in circles at elevated positions.
	Soaring/gliding	The individual flies helped by wind or heat currents, reduced wing movements.
	Cruising flight	The individual flies by only beating or combined with short soaring.
Foraging	Passive search	The individual regularly scan the patches from perches.
	Active search	The individual scan the patches on the wing, often diving.
	Feeding	The individual feeds on prey.
	Handling	The individual manipulates, plucks, or transports prey.
Perching	On perch	The individual rests or remains inactive on utility poles, fence posts or trees.
	On ground	The individual rests or remains inactive on the ground.
	Comfort	The individual performs maintenance activities (cleaning, grooming, preening).

breeding) using the Kendall's Coefficient of Concordance (W; Zar 2010). This coefficient examines the intensity of the association (*i.e.* agreement) among variables based on rank correlation. Kendall's W statistic ranges from 0 to 1, with higher values indicating higher concordance. The null hypothesis states that there is no agreement among variables. A Friedman's test is then made to determine the significance of W value in terms of the F-distribution. If P value is ≤ 0.05 , then the null hypothesis is rejected, and it is accepted that there is association among variables (Zar 2010). In addition, differences in the percent of time devoted to each particular sub-activity were compared using Mann-Whitney U-tests (Zar 2010). All statistical analyses were carried out using R software (R Core Team 2015).

Furthermore, we compared the time-activity budgets between species through the similarity percentage (SIMPER) procedure (Clarke & Warwick 1994). This procedure examines the contribution of each activity category to the average dissimilarity between species, and the contribution to similarity within each species. Afterwards, we constructed a dissimilarity matrix (Bray-Curtis distance) with time-activity budgets of both raptor species in order to compare the similarity of their activity

patterns. Time percentage data were transformed by taking square roots in order to diminish the influence of extreme values (Quinn & Keough 2002). Finally, we used non-metric multidimensional scaling analysis (nMDS) to represent dissimilarities between both raptor species. We used statistical software PRIMER v. 5 for all analyses (Clarke & Warwick 1994).

RESULTS

General activity patterns

In total, we registered 472 min of daily activity of the Roadside Hawk through 25 observation days (mean duration: 18.9 ± 5.4 min), and 323 min of activity of the Long-winged Harrier through 30 observation days (mean duration: 10.8 ± 3.4 min). Both species showed different daily patterns in their general activities ($W = 0.55$, $F_{8,8} = 1.26$, $P = 0.376$). The most important differences were the percentage of time they allocated to perching (45.5% for the Roadside Hawk and 13.0% for the Long-winged Harrier; $U_{25,30} = 192$, $P = 0.004$) and foraging (13% and 45%, respectively; $U_{25,30} = 197$, $P = 0.006$; Figure 1).

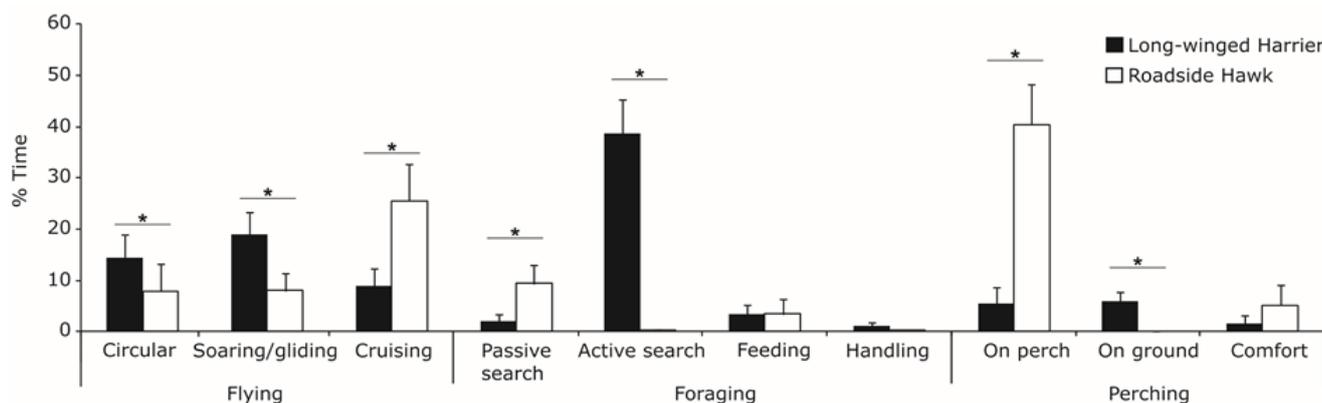


FIGURE 1. Time-activity budgets of the Roadside Hawk (*Rupornis magnirostris*) and the Long-winged Harrier (*Circus buffoni*), showing the general pattern of activities and sub-activities. Asterisks (*) indicate significant differences at $P < 0.05$ (see text for details).

Even though the Roadside Hawk and the Long-winged Harrier did not differ in the time they devoted to fly (41.5% and 42.0%, respectively; $U_{25,30} = 317.5$, $P = 0.59$), they differed in the use of flying modes: the Roadside Hawk used more often the cruising flight (> 64% of time devoted to fly) and the Long-winged Harrier used more frequently the circular flight and soaring/gliding (> 80% of the time). We also found differences between both species in relation to their preference by perching sites, since the Roadside Hawk used preferentially tall

poles or trees as perching sites whereas the Long-winged Harrier used almost exclusively the ground (Figure 1). Notwithstanding, the most evident difference between both species was found during foraging activities, since the Roadside Hawk used preferentially the passive searching mode and the Long-winged Harrier the active searching (Figure 1). These different patterns of activity were evidenced by the limited overlap in their daily time-activity budgets in the SIMPER procedure (Table 2), as well as in the nMDS ordination analysis (Figure 2).

TABLE 2. Contribution of each sub-activity to similarity/dissimilarity in the time-activity budgets of the Roadside Hawk (*Rupornis magnirostris*) (RH) and the Long-winged Harrier (*Circus buffoni*) (LWH), according to SIMPER analysis. Sub-activities were arranged in decreasing order according to their contribution to dissimilarity.

Sub-activity	% Similarity		% Dissimilarity RH vs. LWH	
	RH	LWH	Contribution	Cummulative
Active search	0.02	48.75	20.63	20.63
On perch	50.5	0.89	19.18	39.81
Cruising flight	34.81	7.69	14.8	54.62
Soaring/gliding	5.04	22.45	12.8	67.42
Circular flight	0.88	11.96	11.31	78.72
Passive search	7.34	0.34	6.95	85.67
On ground	0	7.25	5.7	91.37
Comfort	1.21	0	3.89	95.26
Feeding	0.2	0.51	3.64	98.9
Handling	0	0.16	1.1	100
Average similarity	34.6	37.1		
Average dissimilarity			84.1	

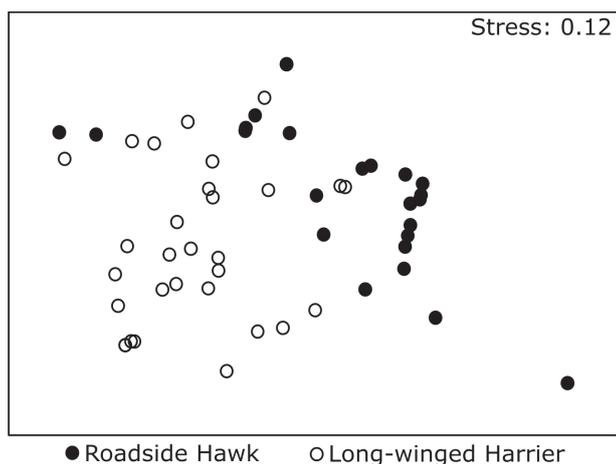


FIGURE 2. Non-metric Multidimensional Scaling ordination analysis (nMDS) based on dissimilarities in the time-activity budgets of the Roadside Hawk (*Rupornis magnirostris*) and the Long-winged Harrier (*Circus buffoni*).

Foraging activity and hunting modes

The quantification of foraging activities of the Roadside Hawk and the Long-winged Harrier evidenced their

different hunting modes and techniques. The Roadside Hawk behaved as a passive search predator. This species used almost exclusively the sit-and-wait technique, searching for prey from tall perches in bouts of $9.46 \text{ min} \pm 2.9 \text{ min}$ ($n = 12$), interrupting this activity to make rapid changes of perch ($8.25 \pm 1.9 \text{ s}$), or more rarely for comfort behaviors. We observed only two events of prey capture by hawks, one of them on a small rodent and other on a passerine; no failed attempts were registered.

The quantification of foraging activities of the Long-winged Harrier showed that this species behaved as a wide-foraging predator, searching for prey on the wing in intervals of $1.29 \text{ min} \pm 0.18 \text{ min}$ ($n = 46$). The technique was characterized by slow quartering over the vegetation ($15.5 \pm 1.8 \text{ s}$), which alternated with low flights and dives ($15.8 \pm 3.0 \text{ s}$). We registered 16 capture attempts, in which the harrier suddenly swoops onto the vegetation to catch prey. From total attempts, we registered three successful captures (efficiency: 19.0%), and only in one case we could determine the prey, a young Brown Hare (*Lepus europaeus*).

Spatial and seasonal variability

The Roadside Hawk was mostly registered at periurban areas (62.4% of total time), whereas the remaining time this species was found in woodlands. Even though perching activity (on perch) was more frequent in woodlands than in urban areas ($U_{8,17} = 6$, $P = 0.001$), the general behavior pattern did not differ between habitat types ($W = 0.83$, $F_{8,8} = 4.89$, $P = 0.018$). The Long-winged Harrier was registered mainly in grasslands (73.3% of total time), and agroecosystems in a lesser extent. The general pattern of activity did not vary according to habitat type for this raptor ($W = 0.80$, $F_{8,8} = 4.04$, $P = 0.032$), and median tests did not reveal differences between both habitats for any sub-activity (all $P > 0.250$).

The activity patterns of both species showed certain variability between breeding and non-breeding seasons (Roadside Hawk: $W = 0.72$, $F_{8,8} = 2.67$, $P = 0.093$; Long-winged Harrier: $W = 0.44$, $F_{8,8} = 0.80$, $P = 0.620$). In this sense, hawks used more frequently cruising flights during the breeding season than during the non-breeding season ($U_{10,15} = 38.5$, $P = 0.04$), whereas harriers devoted more time to active searching, feeding and handling during the non-breeding season than during the breeding season ($U_{8,22} = 44$, $U_{8,22} = 55$, and $U_{8,22} = 55$, respectively, all $P < 0.008$).

Vocalizations

Vocalizations were common for the Roadside Hawk, being registered in 68% of observation days, but they were quite uncommon for the Long-winged Harrier (< 17% of observation days). Hawks vocalized mainly during perching (87% of total vocalization events, $n = 275$), less frequently during flying (12.3%) and rarely during foraging (0.7%). Frequency of vocalizations averaged 4.1 ± 0.7 vocalizations per min in such events. Harriers vocalized mainly while flying (74% of total vocalization events, $n = 42$), and less frequently during perching (26%). Frequency of vocalizations of harriers averaged 1.2 ± 0.3 vocalizations per min.

DISCUSSION

In this study, we found that the Roadside Hawk and the Long-winged Harrier showed contrasting behavioral patterns in the Pampas region of Argentina. The analysis of their time-activity budgets revealed that the Roadside Hawk devoted most of its daily activity to perching and passive searching, whereas the Long-winged Harrier allocated most of its daily time to active searching and flight activities. These patterns seem to be consistent in different habitat contexts and showed certain differences

between breeding and non-breeding seasons. In addition, these raptors differed in their hunting modes: the Roadside Hawk behaved mainly as a sit-and-wait predator whereas the Long-winged Harrier behaved as a wide-foraging predator, which coincides with previous descriptions for both species (Panasci & Whitacre 2000, Isacch *et al.* 2001). These contrasting patterns seem to represent opposite ends of the spectrum of hunting modes proposed for raptors (Jaksic 1985), which ranges from those that maximize prey encounter rates to those that minimize costs of searching, by waiting the most profitable prey (Jaksic & Carothers 1985).

The use of different hunting modes and the characteristics of the main prey of each raptor, *i.e.* rodents for the Roadside Hawk (Baladrón *et al.* 2011) and birds for the Long-winged Harrier (Bó *et al.* 1996), may determine their preference by different habitats. The Roadside Hawk used mainly periurban areas and woodland edges which provide fundamentally perching sites adequate to passive searching. From such elevated positions, hawks may have a broad vision of the hunting patches and enhance their chance of prey detection, especially rodents that thrive in periurban areas and field margins (Bilenca *et al.* 2007). The Long-winged Harrier showed affinity by open habitats, such as grasslands and agroecosystems, where this species may display more efficiently the active hunting mode. This may respond to the fact that this raptor usually displays the tactic of slow quartering flights over the vegetation surface to capture flushed birds (Simmons 2000, Isacch *et al.* 2001). Thus, it may be exploiting the broad offer of small birds that use grasslands and agroecosystems as refuge in the study area (Pretelli *et al.* 2013, Spinazzola 2013).

Although the time-activity budgets of both raptors did not vary according to habitat type, we did find some differences in their activity patterns between the breeding and non-breeding seasons. Such differences may be related to two main factors: (1) different energy demands and time allocation due to reproductive tasks (courtship, nest attendance, territoriality) during the breeding season and (2) changes in prey abundance and availability between both seasons (Newton 1979). The Roadside Hawk, for instance, used cruising flights more frequently during the breeding season. This may be linked to directional moves to change of hunting patches, but also with an increase in its territoriality and nest vigilance behaviors. This hawk has been characterized as opportunist (Beltzer 1990, Panasci & Whitacre 2000) and, in the study area, it may experience changes in its diet between the non-breeding season (mainly rodents; Baladrón *et al.* 2011) and the breeding season (more insects; Author's unpub. data). This may influence the foraging behavior through modulating the duration of hunting bouts and the extension of hunting areas. The Long-winged Harrier

used soaring/gliding flights more frequently during the non-breeding season than during the breeding season. This may be due to the expansion of its hunting ranges as a result of the decrease in the availability of its main prey (birds; Bó *et al.* 1996, Pretelli *et al.* 2013), as well as to a reduction of its home range due to nest vigilance and territoriality during the breeding season (Simmons 2000).

We report for the first time on the time-activity budgets of two common, but poorly known species, the Roadside Hawk and the Long-winged Harrier. These raptors showed similarities in their sizes, food habits, and geographic distributions, but differed in their behavioral patterns. Our results suggest that they may segregate spatially by utilizing different hunting habitats as well as behaviorally by using different hunting modes. Such segregation may determine a low degree of interference competition between both raptors (Jaksic 1985), and may also explain the lack of aggressive encounters between them (Baladrón & Pretelli 2013). Although based on a modest amount of data, our study highlights the importance of quantifying the time-activity budgets of Neotropical raptor species in order to know how these predators segregate through different niche dimensions.

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