Hunting success of wintering Swainson's hawks: environmental effects on timing and choice of foraging method

J.H. Sarasola and J.J. Negro

Abstract: We examined the predatory behavior of Swainson's hawks (*Buteo swainsoni* Bonaparte, 1838) wintering in the Argentine pampas. Aerial and ground foraging were the main hunting methods employed by hawks in this region. The overall hunting success of hawks preying on insects was 50% and age-related differences in hunting success were not significant. The Swainson's hawks, however, hunted more successfully in the air (65% of prey capture attempts) than on the ground (42%). Aerial hunting while soaring was the most successful hunting method based on the number of prey captured per energy unit. Based on the analysis of prey consumed by hawks during the study period, grasshopper species with poor flight capabilities were available in the air as a consequence of the vertical air motion. With regards to daily activity patterns, the time that a hawk spent using each hunting method was not proportional to the cost ratio associated with each method. Hawks foraged in the air only during midday hours when weather conditions permitted the formation of thermals. Thus, the use of soaring flights and the availability of prey in the air were constrained by the physical environment, and hawks could only exploit airborne food sources during limited periods of the day.

Résumé : Nous avons étudié le comportement prédateur des buses de Swainson (*Buteo swainsoni* Bonaparte, 1838) qui hivernent dans les pampas d'Argentine. La chasse dans les airs et au sol sont les principales méthodes de capture utilisées par les buses dans cette région. Le succès global de la chasse des buses qui se nourrissent d'insectes est de 50 % et les différences de succès de la chasse observées en fonction de l'âge ne sont pas significatives. Cependant, les buses de Swainson chassent avec plus de succès dans les airs (65 % des tentatives de capture de proies) qu'au sol (42 %). D'après le nombre de proies capturées par unité énergétique, c'est la chasse dans les airs durant le vol plané qui est la méthode la plus efficace. L'analyse des proies consommées par les buses durant la période d'étude montre que les orthoptères à faible pouvoir de vol sont disponibles dans l'air à cause des mouvements verticaux de l'atmosphère. Les patrons d'activité journalière révèlent que le temps que les buses passent à utiliser chacune des méthodes de chasse n'est pas proportionnel au rapport des coûts associés à chaque méthode. Les buses chassent dans les airs seulement au milieu de la journée lorsque les conditions climatiques permettent la formations de courants thermiques ascendants. Ainsi, l'utilisation du vol plané et la disponibilité des proies dans les airs sont restreintes par le milieu physique; les buses ne peuvent donc utiliser les ressources alimentaires atmosphériques que durant de courtes périodes de la journée.

[Traduit par la Rédaction]

Introduction

The maximization of the net rate of energy gain provides a simple approach to understanding foraging and diet choice: an animal will forage in a manner that maximizes the rate of energy gain (McArthur and Pianka 1966; Stephen and Krebs 1986). A predator using several foraging techniques should apportion its time according to the relative cost:benefit ratios of each technique. There are, however, many contexts in which foraging behavior is constrained by the state of the animal (e.g., energetic state, age, reproductive stage) and its environment (e.g., ectothermic organisms) (Houston 1993).

In this work we examine the predatory behavior of the Swainson's hawk (*Buteo swainsoni* Bonaparte, 1838) (hereinafter also simply referred to as hawk) in its wintering range. The Swainson's hawk is a long-distance migratory raptor that breeds in North America and spends the boreal winter in southern South America, mainly in the central provinces of Argentina (England et al. 1997). A peculiar feature of this species is the many behavioral and ecological shifts exhibited between breeding and wintering areas. They are territorial and feed on small vertebrates (mammals, reptiles, and birds) in the breeding areas (for a review see England et al. 1997), whereas they become extremely gregarious, hunting and roosting in flocks of hundreds to thousands of birds, on the wintering areas (White et al. 1989; Jaramillo 1993; Woodbridge et al. 1995). Furthermore, their diet on wintering areas is almost entirely composed of insects (White et al. 1989; Jaramillo 1993; Rudolph and Fisher 1993; Canavelli et al. 2001), the most abundant source of food that is capable

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of sustaining large concentrations of hawks (England et al. 1997). In accordance with this dietary shift, foraging behavior described for the hawks during winter differ from those in the breeding areas and are typical of insect-eating birds. The aerial method consists of stooping, thrusting out their talons, and grabbing flying insects (e.g., dragonflies). Hawks immediately transfer the captured prey to their bill and ingest it whole (Jaramillo 1993). The ground foraging method involves hawks pouncing at and running down grasshoppers and crickets (England et al. 1997; Canavelli et al. 2003). Although these hunting methods are described along with reports on food habits of the species during winter, no attempts have been made to evaluate the success of these foraging displays. Recent reports on daily activity patterns of wintering Swainson's hawks have shown a relationship between foraging behavior and time of day. Canavelli et al. (2003) reported that hawks were ground foragers more often during early morning and late afternoon, whereas they were frequently involved in aerial foraging during midday. If Swainson's hawks forage in an optimal manner, then its foraging behavior should be predictable. However, the pattern of hunting behavior of wintering Swainson's hawks has not been studied in depth.

We compared hunting success of wintering Swainson's hawks preying on insects on the ground and in the air. We examined age-specific hunting success and the effect of weather variables on hunting rates and success. To test the prediction of balance between success and the time devoted to each method, we also estimated the energy cost of each of the foraging methods. We also provide first evidence of insect species with poor flight capabilities being used as prey by Swainson's hawks during aerial foraging bouts. Related to this finding we propose a thermal-dependence hypothesis to explain the relationship between foraging behavior and the time of day. According to this hypothesis, Swainson's hawks would prefer to hunt while soaring in thermals, because this would be the most energy-saving way to capture their insect prey. However, as thermals are limited to central hours of the day, Swainson's hawks have to resort to other hunting methods to cover all their food requirements.

Material and methods

Study area

The field site was located about 15 km east of the town of Santa Rosa (36°33′S, 64°07′W), La Pampa province, central Argentina. The region has a flat topography that contains a mosaic of crops, including sunflowers, corn, and soybeans, as well as patches of implanted pastures and natural habitats, such as grasslands of the genus *Stipa* L. The study was conducted between 26 January and 18 February 2004 in fields near a grove of *Eucalyptus* L'Hér. trees (range 500–4000 m), where ca. 2000 Swainson's hawks were roosting. According to early-morning and late-afternoon estimates, the number of hawks roosting in this grove remained the same throughout the study. The abundance of hawks could be due in part to a population outbreak of grasshoppers at the site that provided enough food for all hawks to remain in the area during the entire observation period.

Foraging success

Observations of focal individuals were recorded to assess foraging success (Altmann 1974). We first conducted field surveys for Swainson's hawks involved in foraging activities. When a flock was found, we scanned with 10× binoculars starting at a randomly selected point on the ground (for ground foraging groups of birds) or in the air (for aerial foraging flocks). Then, using a 20×–60× spotting scope, we began observing a single, focal individual for a 5-min sampling period. Shorter observation periods were obtained in cases in which the hawk flew away or out of sight. Once the 5-min sampling interval was finished, we searched for a new focal individual and began a new sampling period. We continued in this manner up to a maximum of six observations of focal individuals per flock or foraging group to minimize sample dependence. We continued field surveys until a different foraging group was found and we could start a new set of observations.

For each observation we recorded start time and time at successive prey-capture attempts. Each attempt was classified as successful or unsuccessful according to whether or not Swainson's hawks captured and ate the prey. Individual hawks were classified as juvenile or adults based on plumage characteristics (Wheeler and Clark 1995), with immature birds grouped along with juveniles. For each individual observation we recorded the hawk's foraging behavior (aerial or ground), prey type (when identification was possible through the spotting scope), ground substrate (for ground-foraging hawks), estimated flight altitude (for flying hawks), air temperature, and average wind speed. These latter variables were measured using a portable weather monitor (Brunton Company, Riverton, Wyoming). To ensure that the focal hawk was actually foraging, only individual records with at least one capture attempt were used to compute foraging rates and success.

Diet composition

To analyze the diet of the Swainson's hawks, we collected regurgitation pellets under roost trees. Collected pellets were hydrated and broken apart by hand, and remains of prey items were separated for identification. Arthropods were identified using mandibles, heads, femurs, tarsus, elytra, and any other parts that allowed identification to the species level (for Acrididae prey) and the subfamily level (for the remaining prey items) using reference collections and keys (Salto and Bletrame 1999). To estimate the minimum number of individual prey in each sample, whole heads, feet, elytra, and mandibles were counted.

Relative abundance of grasshoppers was estimated for perennial pastures and plowed fields used by ground-foraging hawks. We used an net to capture insects at 10 points distributed every 5 m along a linear transect that was 45 m long. This transect was replicated five times in each sampled plot. The mean number of orthopterans captured in the five transects was used to compare abundance among plots from the above pastures and fields.

Energy cost of foraging

A comparison of foraging methods necessarily requires not only an analysis of their success ratios and capture rates,

Table 1. Diet of wintering Swainson's hawks (*Buteo swainsoni*) on the study area (*N* is the number of individual preys identified in the pellets).

Prey	*N*	Percent frequency
Orthoptera (subtotal)	3222	97.8
Dichroplus pratensis Bruner, 1900	1416	43
Dichroplus elongatus Giglio-Tos, 1894	726	22
Dichroplus vittatus Bruner, 1900	67	2
Dichroplus punctulatus (Thunberg, 1824)	95	2.9
Dichroplus sp.	254	7.7
Rhammatocerus pictus (Bruner, 1900)	362	11
Staurorhectus longicornis Giglio Tos, 1897	187	5.7
Dipontus sp.	26	0.8
Scyllina sp.	23	0.7
Xyleus laevipes Stål, 1878	4	0.1
Allotruxalis strigata (Bruner) Rehn, 1944	10	0.3
Acrididae unidentified	49	1.5
Tettigoniidae	2	0.1
Gryllidae	1	0
Coleoptera (subtotal)	55	1.7
Scarabidae	32	1
Carabidae	17	0.5
Curculiunidae	1	0
Coleoptera unidentified	5	0.2
Mantodea		
Mantidae	6	0.2
Hymenoptera		
Formicidae	7	0.2
Hemiptera		
Cicadidae	4	0.1
Arachnids		
Aranae	1	0
Total prey items	3295	

but also of the energetic cost associated with each hunting method. However, although information on basal metabolic rates (BMRs) for several falconiform species is available (Wasser 1986), little is known about the energetic costs for most raptor activities (e.g., walking, preening). Because of this lack of knowledge of energetic demands, our assessment of energetic costs of hunting activities is based on the estimated increase in metabolic rates resulting from the hunting method used the hawks.

The energetic cost of flight foraging for the Swainson's hawk using soaring flights was assumed to be two times the BMR (Smith et al. 1986; Baudinette and Schmidt-Nielsen 1974). Schmidt-Nielsen (1972) and Fedak et al. (1974) estimated the cost of running to be three times the cost of active flight for 900-g birds, such as the Swainson's hawk. However, hawk activity during ground foraging included also short flights. For this reason it was more appropriate to use values obtained by Nudds and Briant (2000) for short flights in birds (27.8 BMR) to estimate the cost of ground foraging for the Swainson's hawk.

The capture:cost ratios for each of the hunting methods employed by wintering Swainson's hawks was calculated by dividing the capture rate (prey/hour) for each hunting method by its respective cost index. Because the use of hunting method was correlated with time of day (Canavelli et al. 2003; this work), the skewness in the distribution toward the afternoon might have resulted in a biased estimate of the amount of time devoted to each of the foraging methods. For this reason, we compared capture costs for each of the hunting techniques with more detailed data on time-budget and daily-activity patterns previously reported for the Swainson's hawk in our study area (Canavelli et al. 2003).

Statistical analysis

Chi-square tests using Yates' correction for continuity (Zar 1998) were used to compare success rates among hunting methods and age classes. Pearson's correlation coefficient (Zar 1998) was used to examine the relationship among hunting rates and success with weather variables, and among the percentage of observations of Swainson's hawks foraging in the air (arcsine-transformed) with mean ambient temperature. We used an analysis of variance (ANOVA) to examine between-substrate differences in hunting success and striking rate for ground-foraging hawks. A two-way ANOVA

Fig. 1. Pattern of daily hunting used by Swainson's hawks (*Buteo swainsoni*) in La Pampa and mean air temperature. Bars in each 2-h time period denote the fractions in which hawks were recorded either foraging (on the ground or in the air) or involved in other activities.

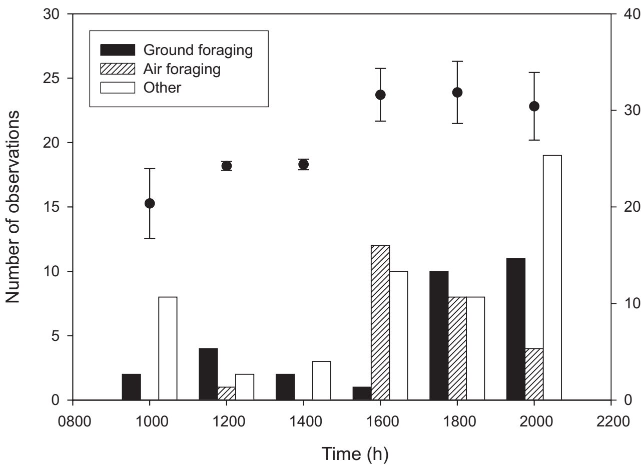
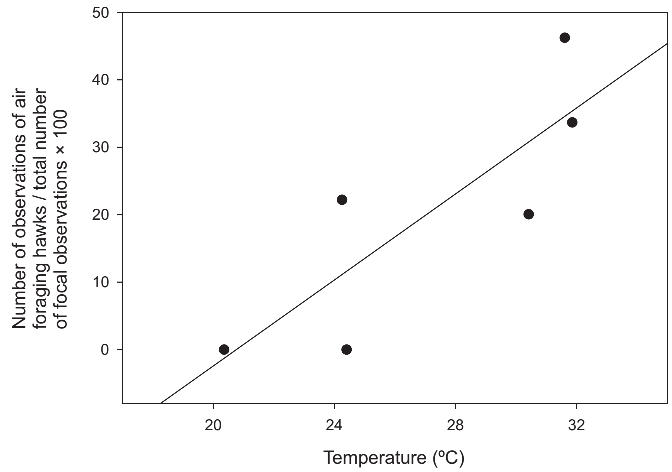


Fig. 2. Relationship between the number of observations of air foraging Swainson's hawks per total number of focal observations (%) and mean air temperature for each of the six 2-h block periods.



was used to analyze differences in striking rates related to age and hunting mode. All variables met the assumption of normality (Kolmogorov–Smirnov test, $P > 0.10$ for all the variables) and were suitable for parametric testing. Values reported are means ± 1 SD.

Results

Prey type and foraging behavior

A total of 120 observations of focal individuals were recorded representing 236 capture bouts. Of these bouts, 145 (61%) corresponded to ground foraging and the remaining 91 (39%) to aerial foraging. Swainson's hawks are known to hunt from perches in their breeding grounds (England et al. 1997) and we have captured them in Argentina using bal-chatri traps baited with mice near fence posts (Sarasola and Negro 2004; Sarasola et al. 2004). However, only one prey-capture attempt from a perch was recorded during the observation of 15 focal hawks perched on fence posts. This single attempt was made on a grasshopper on the ground. After the strike, the hawk returned to the same post and ate the prey.

Prey captured in all observations of focal ground-foraging Swainson's hawks were orthopterans. We were unable to visually identify the prey captured by hawks during aerial foraging. Nonetheless, analysis of 51 regurgitation pellets collected beneath hawk roosts showed that 98% of prey (n = 3295 prey items) were orthopterans, mostly grasshoppers of the genera *Dichroplus* Stål, 1873 (77%) and *Rhammatocerus* Saussure, 1861 (11%) (Table 1). These data suggest that grasshoppers were also consumed by hawks when foraging in the air, because neither dragonflies nor any other flight-capable prey were recorded in the diet.

Which hunting methods was used by Swainson's hawks depended on the time of the day ($\chi^2_{[6]} = 18.3$, $P = 0.005$). Ground foraging was observed most often in the morning and late in the afternoon compared with aerial foraging, which was observed most often early in the afternoon (Fig. 1). Furthermore, the percentage of the total number of observations in which hawks were recorded foraging in the air for 2-h time blocks was correlated with mean air temperature of each time block ($r = 0.83$, $P = 0.02$, $n = 6$; Fig. 2). Hawks were recorded foraging in the air when air temperature was >24 °C, mostly between 1400 and 1800 (Figs. 1, 2). The percentage of aerial-foraging hawks declined toward late afternoon.

Ground-foraging behavior exhibited by Swainson's hawks included short runs following prey, but also short flights in which hawks landed directly on prey. Attacks using only bills also were observed, but this prey-capture method was conditional on the close proximity of the prey. Hawks foraged in the air using soaring and circling flights, capturing prey with only their talons and delivering it to their bills. Wing beating and hovering flights, flight options used by foraging hawks during the breeding season (England et al. 1997), were not recorded in our study.

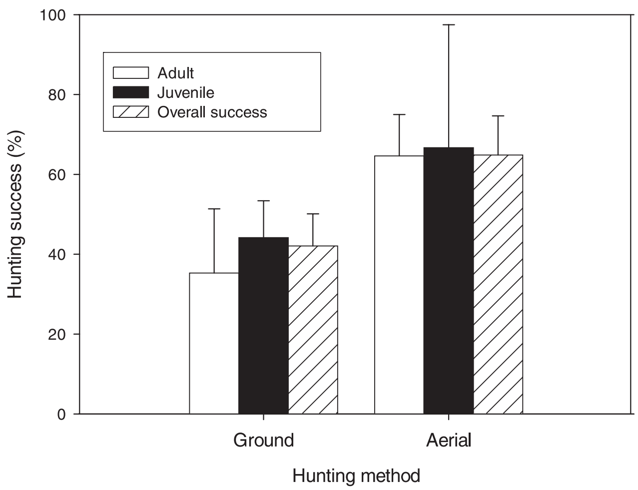
Hunting rates and success

Overall success across hunting methods was 50.8%. Swainson's hawks were significantly less successful in capturing prey when foraging on the ground (42.1%) than in the air (64.8%) ($\chi^2_{[1]} = 4.4$, $P = 0.03$). Age-related differences in hunting success (Fig. 3) were not significant for aerial foraging ($\chi^2_{[1]} = 0.01$, $P = 0.93$) or for ground foraging ($\chi^2_{[1]} = 0.8$, $P = 0.38$). The striking rates (number of attempts/min) did not differ for hunting mode ($F_{[1,51]} = 0.09$, $P = 0.76$) or for age classes ($F_{[1,51]} = 0.03$, $P = 0.85$), but the interaction of these factors was statistically significant ($F_{[1,51]} = 6.70$, $P = 0.01$) (see also Table 2). For aerial foraging, striking rate was negatively correlated with air temperature ($r = –0.50$, $P = 0.02$, $n = 25$) but was not correlated with wind speed ($r = 0.12$, $P = 0.58$, $n = 25$). Striking rate for ground foraging was negatively correlated with wind speed ($r = –0.39$, $P = 0.03$, $n = 30$). Hunting success was not correlated with weather variables for ground foraging or for aerial foraging ($P > 0.10$ for all tests). Ground foraging was recorded in three land-use types that had a gradient in vegetation height and canopy cover: plowed fields (no vegetation), harvested

Table 2. Rates of prey-capture attempts and successes of wintering Swainson's hawks by age and hunting method.

			No of attempts/min		No. of successes/min	
Hunting method	Age class	Total strikes	Mean	Maximum	Mean	Maximum
Aerial	Juvenile	9	0.62±0.49	1.5	0.52±0.57	1.5
	Adult	82	1.23±0.85	3.2	0.79±0.61	1.9
	Total	91	1.06±0.80	3.2	0.45±0.38	1.9
Ground	Juvenile	111	1.25±0.84	2.8	0.56±0.43	1.6
	Adult	34	0.73±0.44	1.8	0.28±0.14	0.6
	Total	145	1.06±0.76	2.8	0.71±0.60	1.6

Fig. 3. Age-specific and overall hunting success of wintering Swainson's hawks by hunting methods. Error bars represent 95% confidence intervals.



wheat (canopy <25 cm, cover <30%), and perennial pastures (canopy 40–50 cm, cover 30%–50%). Striking rate significantly differed along this vegetation-height and canopy-cover gradient ($F_{[2,27]} = 3.8$, $P = 0.03$). Hawks were more active in more densely covered fields (e.g., perennial pastures) (Tukey test, $P = 0.03$). However, no significant differences in hunting success were observed among the three land-use types ($F_{[2,27]} = 0.3$, $P = 0.71$). The mean abundance of orthopterans was higher in perennial pastures (36.3 ± 14.9, $n = 3$ plots) than in plowed fields (4.3 ± 2.6, $n = 4$).

Energy efficiency

Standardizing by unit energy cost, the number of prey captured by aerial foragers was 21 times higher than the number of prey captured on the ground (21.3 vs. 1.0 captures/energy unit, respectively), despite the fact that Swainson's hawks used both hunting strategies equally (48% vs. 52% for aerial foraging and ground foraging, respectively; Canavelli et al. 2003). The balance between energetic cost and time devoted to each hunting method could only be achieved if soaring is assumed to be a 58% more costly activity than walking (i.e., 44 BMR). Even using our gross estimation of energetic costs associated with each of the foraging methods, such a relationship between soaring and running or short flights is incongruous with previous studies of the energetics of animal locomotion (Schmidt-Nielsen 1972; Fedak et al. 1974; Nudds and Bryant 2000).

Discussion

Aerial foraging during soaring flight and ground foraging with running and short flights were the most commonly foraging behaviors observed in wintering Swainson's hawks. Perch hunting was rarely carried out, even though the hawks often perched in fence posts, power poles, and trees. Although observations were made opportunistically on foraging hawks, the daily distribution of the use of hunting methods agreed with that reported by Canavelli et al. (2003). Wintering hawks were more active aerial hunters during early afternoon (1400–1600) and spent more time hunting on the ground during morning and late afternoon.

Most research aiming to assess age-related differences in hunting success of raptors reported that adults were better hunters. Toland (1986), for example, found differences in hunting performance between immatures and adults in eight out of nine raptor species, including the Swainson's hawk. Surprisingly, we did not observe a similar relationship in our study. This lack of difference might be due in part to a small number of records of air-foraging juveniles but also to the relative high abundance of the prey consumed and the fact that insects are easy prey that are not harmful to the predator. Swainson's hawks did not require special flight and ground-walking skills, or any special prey-manipulation ability, because the time elapsed between prey capture and consumption was short. On the other hand, our method for aging birds into only two age classes could have led to the inclusion of subadults with immature birds, thereby affecting the final estimate of age-specific hunting performance.

Large concentrations of hawks are common in wintering grounds and are necessarily linked to a local, high prey availability and insect population outbreaks as observed in our study area. For that reason our results could be considered to accurately reflect the foraging behavior and hunting success of Swainson's hawks in their wintering grounds.

Several studies on raptor foraging behavior have found that striking rate, instead of hunting success, better indicated prey abundance (Donazar et al. 1993; Redpath et al. 2002). Consistent with this finding, we found orthopteran abundance in perennial pastures to be related to striking rate but not to hunting success. Furthermore, weather variables affected the availability of prey by improving prey mobility. Wind speed could increase the escape distance of orthopterans on the ground, whereas an increase in air temperature could indicate an acceleration of the ascending air, which leads to a spatial dispersion of insects on the thermal. Thus, the significance of the interaction effects between age and hunting mode in the striking rates does not have a unique and plausible explanation and could be the result of a multiplicity of factors affecting insect abundance (wind, time of day, and vegetation cover), as well as the low number of field observations that covers all possible combinations between these factors.

Prey captured during aerial foraging were not visually identifiable. However, we found strong evidence supporting our contention that orthopteran species with little or no flight capabilities were also available in the air because of thermals. Members of the genus *Dichroplus*, for example, include small grasshopper species (3 cm long) that jump 1–2 m off the ground (J.H. Sarasola, personal observation). Previous reports of aerial hunting by wintering Swainson's hawks have been related to the presence of dragonflies (Jaramillo 1993; Rudolph and Fisher 1993), but this potential prey type was not observed in the area during the study. The analysis of pellets collected in the roost used by hawks during the study period determined that grasshoppers, mainly *Dichroplus* sp., were the main prey consumed by hawks and that there were no remains of dragonflies or similar high flying-capable prey (e.g., butterflies). For the breeding grounds, Woffinden (1986) also reported pre-migratory flocks of Swainson's hawks preying on grasshoppers flying from the ground or vegetation and "ascending to considerable heights" on the air. Although this author did not provide estimates of altitude, the mean altitude for our focal observation on air-foraging hawks was 76.4 ± 40.7 m, a considerable height that non-flying prey can only reach with the help of columns of warm rising air. Furthermore, studies on insect abundance and distribution in the air using radar techniques have also stated the importance of vertical air movements in the vertical distribution of insects in the atmosphere (Farrow 1986). In the pampas of southern Buenos Aires province, airplane pilots have reported that Swainson's hawks soar as high as 900–1200 m (L.M. Santiago, personal communication), whereas another pilot reported grasshoppers impacting on a glide plane at an altitude of 1500 m in La Pampa province (C. Alliaga, personal communication).

Aerial hunting was the most efficient method used by Swainson's hawks in terms of hunting performance and energetic expenditure when compared with ground foraging. Solar radiation and temperature resulted in thermal formation (Ballam 1984) that was linked to the time of day. In optimal weather conditions, hawks become aerial hunters, switching to ground foraging only when thermals are absent. Because different hunting techniques could result in the capture of different prey, the analysis of the cost:benefit ratios for each foraging technique required the assumption of equal caloric returns per successful attempt. That is, we must assume that the same or similar prey types were captured in the air and on the ground. In other raptors, for example, predatory behavior reflected a balance between the energetic cost of the hunting method and the size (energy content) of the prey (Collopy and Koplin 1983). In the case of Swainson's hawks, the assumption that similar prey types were captured by the two hunting methods was ascertained by visual identification of prey and by the analysis of pellets. Thus, the conditions that allowed hawks to use the most efficient foraging method arose as the most important factor in the balance between costs and benefits. We suspect that the time that hawks devoted to aerial foraging did not allow them to meet all their daily energetic requirements and that they needed the additional prey captured on the ground. Individual time-budget analysis with radio-tagged birds should be conducted to address this question.

Evidence supporting aerial encounters between grasshopper and hawks as a consequence of thermals might help to explain the mechanisms of habitat selection by wintering hawks at regional and landscape scales. Soaring flight was the most energy-efficient method of flight possible (Pennycuick 1975) and was probably the only way that Swainson's hawks could cover the 10 000 km of their migratory trip (Fuller et al. 1998). In addition, the availability of grasshoppers in thermals as a result of their abundance on the ground could allow hawks to develop a prey-searching strategy to exploit this scattered food source on their wintering grounds at a low cost.

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