

## ARTHROPOD PREY AVAILABILITY AND BREEDING OF THE THREATENED STRANGE-TAILED TYRANT (*ALECTRURUS RISORA*)

Paula F. Zermoglio<sup>1,3</sup> · Adrián S. Di Giacomo<sup>2</sup> · Alejandro G. Di Giacomo<sup>2</sup> · Marcela K. Castelo<sup>1</sup>

<sup>1</sup>Departamento de Ecología, Genética y Evolución, Instituto IEGEBA (CONICET-UBA), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. Pabellón II, Ciudad Universitaria, C1428EGA Buenos Aires, Argentina.

<sup>2</sup>Departamento de Conservación, Aves Argentinas/Asociación Ornitológica del Plata, Matheu 1246, C1249AAB Buenos Aires, Argentina.

E-mail: Paula F. Zermoglio · pzermoglio@ege.fcen.uba.ar

**ABSTRACT** · The Strange-tailed Tyrant (*Alectrurus risora*) is an insectivorous flycatcher (Tyrannidae) endemic to the natural tall grasslands of northern Argentina and southern Paraguay. *Alectrurus risora* has a polygynous mating system and the abundance of arthropods could be a major factor determining the establishment of male breeding territories and the extent of the breeding season, which is shorter than in most other reported tyrant flycatchers. To investigate this hypothesis, we examined the abundance of arthropods in upland and lowland breeding habitats. Upland habitats seem to be preferred for breeding, and usually harbour more nests. Data from one year showed that, for both grasslands, the beginning of the breeding season coincides with a greater availability of arthropods, and that the short reproductive season of *A. risora* coincides with a general lower availability of prey during February and March in the year we conducted the study. In upland territories, males attracted more females and had more active nests than males holding territories in lowland grasslands. However, the abundance and biomass of total arthropods and of potential prey were higher in lowland than in upland grasslands, with the exception of the abundance of Orthoptera, which was higher in upland habitat and could represent one of the major prey items. Therefore, we conclude that 1) female preference for males in upland grasslands cannot be explained by higher arthropod prey availability, and 2) the availability of arthropod prey may be important in determining the extent of the breeding season, although further, multiannual studies are required to corroborate this hypothesis.

**RESUMEN** · Disponibilidad de artrópodos presa asociados a territorios de reproducción de un ave en peligro de extinción, el Yetapá de Collar (*Alectrurus risora*)

El Yetapá de Collar (*Alectrurus risora*) es un tiránido insectívoro endémico de los pastizales altos naturales del norte de Argentina y sur de Paraguay, que posee una temporada reproductiva más corta que aquella reportada para la mayoría de los tiránidos. *Alectrurus risora* posee un sistema de apareamiento poligínico, y la abundancia de artrópodos podría representar un factor determinante en el establecimiento de los territorios de los machos y en la duración de la temporada reproductiva. Con el fin de investigar esta hipótesis examinamos la abundancia de artrópodos en hábitats reproductivos de pastizales altos y bajos. Los pastizales altos parecen ser más utilizados durante la época reproductiva y usualmente albergan un mayor número de nidos activos. Los datos de un año de muestreo mostraron que el inicio de la temporada reproductiva coincide con el pico de abundancia de artrópodos en ambos pastizales, y que su corta duración coincide, para el área en estudio durante el año analizado, con una menor disponibilidad de presas durante los meses de febrero y marzo. En los territorios ubicados en el pastizal alto los machos atrajeron más hembras y tuvieron más nidos activos que en los territorios de pastizal bajo. Sin embargo, la abundancia y biomasa de artrópodos totales y de presas potenciales fueron mayores en el pastizal bajo, con la excepción de la abundancia de Orthoptera, que podría representar uno de los tipos principales de presa. A partir de estos resultados, concluimos que 1) la preferencia de las hembras por machos en el pastizal alto no puede ser explicada por una mayor disponibilidad de artrópodos presa, y 2) la disponibilidad de artrópodos presa podría representar un factor importante en la determinación de la extensión de la temporada reproductiva, pero se requieren estudios adicionales, plurianuales, para corroborar esta hipótesis.

**KEY WORDS:** Arthropods · Grasslands · Insectivorous birds · Tyrannidae · Wetlands

Receipt 25 May 2016 · First decision 25 June 2016 · Acceptance 10 November 2016 · Online publication 18 November 2016

Communicated by Kaspar Delhey © The Neotropical Ornithological Society

## INTRODUCTION

The Strange-tailed Tyrant, *Alectrurus risora* (Passeriformes: Tyrannidae), is a globally threatened species (Vulnerable) that currently inhabits grasslands in northern Argentina and southern Paraguay (Birdlife International 2013). The populations of *A. risora* have declined due to the conversion of grasslands into agricultural lands and today the distributional range of the species represents 10% of its historical range (Di Giacomo & Di Giacomo 2004). This species is an obligate insectivorous bird that depends exclusively on natural grasslands for nesting and feeding (Vickery et al. 1999, Fitzpatrick 2004).

As an open-habitat tyrant flycatcher, its main hunting strategies are “aerial hawking” and “perch to ground sallying”, although it can also hunt on the ground or among the grasses (Fitzpatrick 1980). From focal observations of feeding individuals, it is known that prey items include mostly caterpillars, mayflies, mantises, small dipterans and beetles, dragonflies, and orthopterans, which are captured from high perches in the grassland (Di Giacomo & Di Giacomo 2004). They have also been observed capturing arthropods, mostly Orthoptera, on or near the ground, taking advantage of the disturbance caused by armadillos in the grass (Di Giacomo & Di Giacomo 2006).

In El Bagual Ecological Reserve, Formosa, Argentina, *A. risora* nests are built near the ground on the base or among the leaves of tall grasses in both well-drained upland grasslands and in floodable lowland grasslands (Di Giacomo et al. 2011a). The modal clutch size consists of three eggs, and successful nests fledge on average 2.3 chicks, with an overall nest survival of 0.23 on average over the entire cycle. Most females breed in the same area for two or three consecutive years. In contrast, males are rarely seen in the same area for more than one year, suggesting sexual differences in mortality rates (Di Giacomo et al. 2011a). *Alectrurus risora* has a polygynous mating system, in which parental care is provided exclusively by the females, who build the nest, incubate the eggs, and brood and feed the chicks. Males are territorial and defend contiguous territories of 2–2.5 ha that include the territories of up to four females each (Di Giacomo et al. 2011a). In upland territories, males have more females and active nests than in lowland grasslands (AS Di Giacomo, pers. observ.), even though upland grasslands represent only 1.5% of the total habitat available for breeding in the reserve (values estimated from Maturo et al. 2005).

Most tropical and subtropical passerines have long breeding seasons, with several nesting attempts and second broods in the same breeding season (Stutchbury & Morton 2001). The breeding season for *A. risora* in subtropical grasslands of Formosa, however, only extends from mid-September to mid-January (four months), and females have a single brood per year (Di Giacomo et al. 2011a). Furthermore, the breeding season is two months shorter in comparison

with that of other passerine birds breeding in the same grasslands, such as Sharp-tailed Tyrant (*Culicivora caudacuta*), Tawny-bellied Seedeater (*Sporophila hypoxantha*), Grassland Sparrow (*Ammodramus humeralis*), and Wedge-tailed Grass-finch (*Emberizoides ypiranganus*), which have a breeding season that lasts up to six months (Maturo et al. 2005).

The energy budget of birds during reproduction should cover not only adult maintenance but also reproductive activities such as nest building and parental care (King 1974). Because energy expenses in birds increase over 50% during the reproduction peak in some temperate biomes, there is a great correspondence between the occurrence of the breeding season of birds and food availability (Ricklefs 1974, Walsberg 1985). Despite its importance, relationships between food availability and the timing of breeding in Neotropical (tropical and subtropical) grassland passerines have received little attention (Vickery et al. 1999, Azpiroz et al. 2012). Focusing on such relationships can be of particular interest for the conservation of species that nest in low areas, as food availability can be critically affected by periodical floods.

In order to investigate if the abundance of arthropod prey is one of the determinants of the establishment of the male breeding territories and of the extent of the breeding season in *A. risora*, we evaluated: 1) whether occupied territories in upland grasslands have higher abundance or biomass of arthropods than occupied territories in lowland grasslands; and whether 2) richness, abundance, and biomass of arthropods increase during spring and summer (i.e., nesting period). We expected abundance and biomass of arthropods to be higher during the breeding season, and, during that period, to be higher in upland grasslands, in agreement with the higher number of *A. risora* observed in this habitat.

## METHODS

**Study area.** We conducted the study at “Reserva El Bagual” (hereafter REB), in the province of Formosa, Argentina (26°18'23"S, 58°49'2"W). REB is a 3,300 ha private protected area located in the ecoregion of the Humid Chaco (Cabrera & Willink 1980) where livestock grazing and agriculture have been excluded since 1985 (Di Giacomo & Krapovickas 2005). The main habitat of REB is grassland, which in well-drained or upland areas is dominated by pyrogenic tall grasses, such as *Imperata brasiliensis*, *Elionurus muticus*, or *Andropogon lateralis*, while *Paspalum intermedium* dominates in the lowland floodable grasslands.

**Breeding data: male territories and nests.** We collected data on *A. risora* breeding from September 2007 to January 2008 in upland and lowland grasslands. From 2004 to 2006 we captured males and females both during the non-breeding and the breeding season using mist-nets. We banded males,

females, and chicks (at the nest, as described below) with a numbered aluminium ring and a unique combination of coloured plastic bands. We delimited the territories of banded males and females with a grid system using the territory mapping technique (Bibby et al. 1992). We put poles (2 m high) every 100 m forming two 30 ha grids (30 squares of 100 x 100 m) within our study area (see Di Giacomo et al. 2011a for details). We placed one grid in the upland grassland and another grid in the lowland grassland, where males of *A. risora* maintained breeding territories each year. All individuals observed in the grids were mapped every 7–14 days during the entire breeding season (from early September to January). We considered that a male had a territory when it was recorded during at least four weeks in the same habitat area and exhibited display behaviour (Vickery et al. 1992). The nests were located but not followed for reproductive success to avoid disturbance and potential clutch losses, given the conservation status of the species.

We found nests by observing female nest building behavior (Martin & Geupel 1993) or by flushing females during systematic nest searching within the 30 ha study area every 7–14 days. We are confident that we found the majority of the nests, as there were no observed fledglings from a female whose nest had not been previously discovered.

**Arthropod sampling.** We used sweep net sampling to estimate monthly relative abundances of arthropods throughout the year in upland and lowland grasslands (from October 2007 until September 2008). February 2008 was quite atypical, as there was heavy precipitation and flooding in the grasslands, and the number of samples taken in that month was limited for both grasslands. Due to logistical problems, samples from July 2008 were not taken ( $N = 22$ , 11 months for each grassland). In each of the grids used for bird sampling (upland and lowland), we randomly selected ten cells every month and sampled arthropods as follows. A sweep net (40 x 75 cm) (Cooper & Whitmore 1990, Hutto 1990) was swept 20 times within each grid cell between 1 and 1.5 m above the ground along a transect of 25 m, where the birds typically feed (Di Giacomo & Di Giacomo 2006). We took a total of 220 samples of arthropods throughout the year in both grasslands, preserving the content of the net in 80% alcohol (Buffington & Redak 1998) for further analysis in the laboratory.

Arthropod specimens were separated from plant remains and identified to the level of order (Biaggini et al. 2007) using general insect identification keys (Invertebrados II, DBBE-FCEN-UBA 2007). We determined the number of orders present and their abundance per grassland and per month (mean number of individuals). In the samples, we only counted large arthropods (hereafter “total arthropods”), and we excluded the mesofauna (Acari and Collembola) since these are never taken by the study species (AG Di Gia-

como, pers. observ.). Among large arthropods we identified potential prey items. We considered as potential prey those arthropods belonging to Coleoptera, Diptera, Lepidoptera, Ephemeroptera, Odonata and Orthoptera orders, following Di Giacomo & Di Giacomo (2004).

**Data analyses.** We expected that breeding season duration and the number of nests in each grassland should be correlated with the abundance of potential prey or of arthropods with certain minimum size. Hence, we analyzed differences in arthropod abundance, size, and taxonomic identity separately. We determined the taxonomic richness as the number of orders present in a sample, and we determined relative abundance as the number of individuals present in each sample.

We measured the body length of arthropod specimens with a digital calliper to the nearest 0.1 mm and assigned them to one of four size categories: < 2 mm, 2–5 mm, 5–10 mm, and > 10 mm. We considered body length from the clypeus to the abdomen tip, not taking ovipositors, wings or stiles into account (Granihar 1997, Hódar 1997, Brady & Noske 2006). We indirectly calculated arthropod biomass from individual lengths using a generic insect regression equation (Brady & Noske 2006), which follows a power model, where the weight is a direct function of the body length.

To test for differences in arthropod abundance and composition between grasslands we performed Mann-Whitney *U*-tests, because data did not meet parametric tests assumptions even when transformed. We compared: 1) the number of orders of arthropods present in each grassland; 2) the mean abundance and biomass of arthropods in each grassland per month; and 3) the mean abundance and biomass of potential prey in each grassland per month. For the first variable, we considered that an order was present if we found at least one individual belonging to it in any of the samples taken for a given month in that environment.

To evaluate differences in food availability between grasslands specifically during the period of nesting activity (i.e., October through January), we compared abundance and biomass of total arthropods and of potential prey by means of Mann-Whitney *U*-tests. In each case, we pooled the four months data for each grassland.

Finally, in order to determine whether the short breeding season of *A. risora* could be influenced by decreased food availability as summer progresses, we evaluated insect community during two periods: spring and summer months with and without nesting activity (i.e., October through January vs. February through March). For this, we pooled data from both grasslands for each period and we performed Mann-Whitney *U*-tests on total arthropods and potential prey abundance and biomass. All analyses were performed using R software (R Development Core Team 2008).

## RESULTS

**Breeding data: male territories and nests.** During the breeding season 2007–2008, from October to January, we identified 5 male territories in upland grasslands and 5 territories in lowland grasslands. Males in upland grasslands had a mean of 2.4 females (range 1–4), totalling 23 active nests. In lowland grasslands, males had a mean of 1.8 females (range 1–3), with a total of 14 active nests (40% fewer than in upland grasslands). The monthly distribution of active nests during the breeding season is shown in Figure 1.

**Arthropod availability: comparison between grasslands.** We collected a total of 21,161 arthropods belonging to 14 different orders: Araneae, Coleoptera, Dictyoptera, Diptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, Odonata, Orthoptera, Planipennia, Pseudoscorpionida, Psocoptera, and Thysanoptera. We did not find significant differences in the number of orders of arthropods between grasslands ( $U = 47$ ;  $N = 22$ ;  $P = 0.395$ ).

The most represented order was Hymenoptera, followed by Homoptera and Heteroptera, while Pseudoscorpionida, Planipennia, and Odonata were the least represented. The orders Araneae, Coleoptera, Diptera, Heteroptera, Homoptera, Hymenoptera, and Thysanoptera were found every month in both grasslands. Orthoptera were found in both grasslands during the whole year, except in lowland grassland in August.

Comparison between both grasslands pooling data for the whole year did not show significant differences in the abundance of total arthropods ( $U = 82$ ;  $N = 22$ ;  $P = 0.150$ ). However, month-by-month analysis showed that arthropods are significantly more abundant in lowland grassland in January ( $U = 105$ ;  $N = 21$ ;  $P < 0.001$ ), March ( $U = 107$ ;  $N = 21$ ;  $P < 0.001$ ), April ( $U = 103$ ;  $N = 21$ ;  $P < 0.001$ ), May ( $U = 100$ ;  $N = 21$ ;  $P = 0.002$ ), June ( $U = 92.5$ ;  $N = 21$ ;  $P = 0.009$ ) and December ( $U = 84$ ;  $N = 21$ ;  $P = 0.044$ ), which mainly correspond to summer and autumn (Figure 1). No significant differences were found for October and November ( $U = 62$ ;  $N = 19$ ;  $P = 0.177$  and  $U = 56$ ;  $N = 20$ ;  $P = 0.674$ ; respectively, Figure 1). Total arthropod biomass across the entire year was greater in lowland grassland ( $U = 91$ ;  $N = 22$ ;  $P = 0.050$ ), and analyses month-by-month showed there are significant differences between grasslands during January ( $U = 95$ ;  $N = 21$ ;  $P = 0.005$ ), March ( $U = 90$ ;  $N = 21$ ;  $P = 0.015$ ) and May ( $U = 98$ ;  $N = 21$ ;  $P = 0.010$ ; Figure 1).

Comparison between lowland and upland grasslands within the four months of reproduction (October to January) revealed that total arthropod availability is greater in lowland grassland (abundance:  $U = 1043$ ,  $N = 81$ ,  $P = 0.036$ ; biomass:  $U = 1096$ ,  $N = 81$ ,  $P = 0.004$ ). Similarly, during the breeding season, potential prey abundance and biomass were greater in lowland grassland (Table 1; abundance:  $U = 1197.5$ ,  $N = 81$ ,  $P < 0.001$ ; biomass:  $U = 1160$ ,  $N = 81$ ,  $P = 0.001$ ). However, prey abundance

classified by size showed no differences between grasslands (Table 1). Analysis of each type of potential prey item showed that abundance of Diptera and Lepidoptera was greater in lowland grasslands, while abundance of Orthoptera was greater in upland grasslands (Table 2).

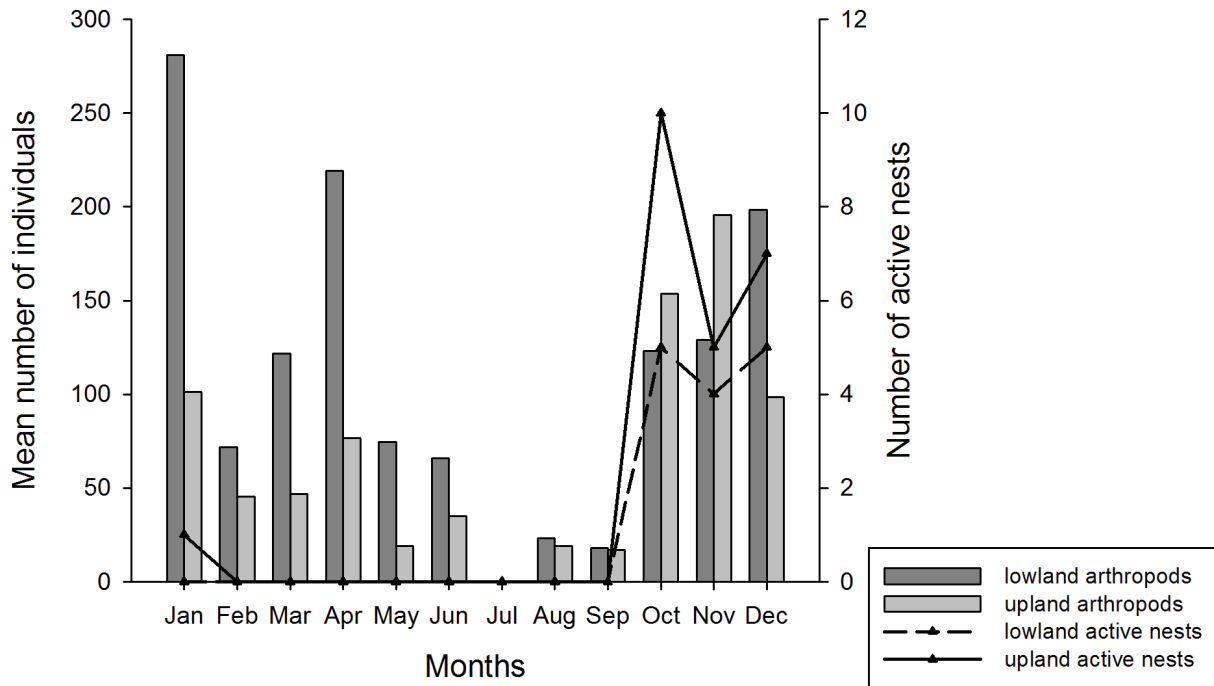
**Arthropod availability over time.** Abundance of total arthropods increased in coincidence with the beginning of the breeding season and reached a maximum in January (Figure 1). During February, we observed a sharp decrease in total arthropod abundance in both grasslands (Figure 1). Comparison between the spring–summer periods with and without nests showed a lower abundance of arthropods during February and March, compared to the period from October to January (total arthropod abundance:  $U = 628$ ,  $N = 116$ ,  $P < 0.001$ ; potential prey abundance:  $U = 497.5$ ,  $N = 116$ ,  $P < 0.001$ ). However, we found no significant differences between these periods with respect to arthropod biomass (total arthropod biomass:  $U = 1199$ ,  $N = 116$ ,  $P = 0.447$ ; potential prey biomass:  $U = 1249$ ,  $N = 116$ ,  $P = 0.313$ ).

## DISCUSSION

In the present study, we investigated arthropod availability in two grassland habitats and its potential relationship with *A. risora*'s nesting preference for one of those environments. Our results show that the upland grassland, which is the preferred habitat for breeding, has lower prey availability than the lowland grassland. In addition, we found an association between the beginning of the breeding season and the abundance and biomass of arthropods available in these habitats. We discuss below the implications and new hypotheses derived from our findings.

We found an association between abundance and biomass of arthropods at the beginning of the breeding season of *A. risora*. Arthropods are much more abundant during the spring, they decline in autumn (May) and reach lowest values during the winter (August and September). During our sampling period the abundance of arthropods decreased sharply in February. This could probably be due to unusual floods, which occurred during that month, although it could also be linked to the annual period of water stress during January, which in turn inhibits vegetation growth for a few weeks (Gorleri 2005).

It is generally accepted that birds in temperate regions have shorter breeding seasons and larger clutch sizes than birds in tropical regions (Snow & Snow 1964, Skutch 1985, Martin 1996). For instance, the clutch size of the Fork-tailed Flycatcher (*Tyrannus savana*) is larger in tropical than in temperate regions (Jahn et al. 2014), and in the Amazon, the breeding seasons of tyrants may extend from seven months to year-round (Johnson et al. 2012, Stouffer et al. 2013; for review on further examples of tropical and temperate birds see Russell et al. 2004). However, reproductive traits of subtropical birds seem not to fit into



**Figure 1.** Monthly mean total arthropod abundance (number of individuals) and total number of Strange-tailed Tyrant (*Alectrurus risora*) active nests in upland and lowland grasslands at Reserva El Bagual, Formosa, Argentina, from October 2007 to September 2008.

the classical view of tropical vs. temperate life history paradigm, and it has been widely accepted that southern birds do not necessarily follow these trends, which were originally identified in northern birds (see Russell et al. 2004). In a recent review on the breeding birds of the Cerrado (Brazilian tropical savanna), Marini et al. (2012) indicate that medium to large size tyrants breed between September and December, rendering the breeding season shorter than in other non-temperate biomes despite their latitude. However, these authors note that clutch size is small in the Cerrado birds, as is expected for tropical latitudes where long breeding seasons favor small clutches.

Our study in the REB is consistent with the results of Marini et al. (2012) for the Cerrado, since *A. risora* has a short breeding season and small clutch size (see Di Giacomo et al. 2011a). We observed that towards the end of the season (i.e., during February and March) arthropod availability was low, and this could have some effect on the extent of the reproductive season of *A. risora*. However, February was an atypically rainy month, and hence the link between prey availability and the extent of the breeding season remains weak. In any case, if arthropod availability was the major determinant of the duration of the breeding season in insectivorous birds, we would expect other insectivorous species to be similarly affected and also have short breeding seasons. This is not the case for at least some of the insectivorous species inhabiting the REB (e.g., Lesser Grass-finch *Emberizoides ypiranganus*, Di Giacomo & Krapovickas 2005), and therefore more studies are needed to sup-

port this idea. The Chaco region presents a highly seasonal climatic pattern, with alternating periods of floods and droughts, and is subject to frequent seasonal fires, which are known to affect the settlement of reproductive groups of *A. risora* (Di Giacomo et al. 2011b). However, little is known about how climate affects the population dynamics of arthropods in this area. It is possible that the seasonality in arthropod availability due to weather conditions could limit the reproductive season of insectivorous birds.

Our data did not support the hypothesis that the difference in abundance of breeding *A. risora* between grasslands is linked with differences in arthropod availability. As observed in other years (AG Di Giacomo pers. observ.), during the 2007–2008 breeding season, males in upland grasslands had more females and nests in their territories than males from lowland grasslands, despite the higher abundance and biomass of arthropods in the latter. Nevertheless, analyses by arthropod order showed that Orthoptera had a higher abundance in upland grasslands. Insects belonging to this order can represent the most abundant prey item in the diet of many insectivorous birds (Wiens & Rotenberry 1979, Kaspari & Joern 1993, Asokan et al. 2009). This agrees with observations made of *A. risora* individuals carrying food to nestlings (AGDG, pers. observ.) and of prey captures of birds following armadillos (Di Giacomo & Di Giacomo 2006). These facts are not surprising, since orthopterans and mantids are usually among the largest grassland insects, and it has been suggested that prey size rather than taxonomic identity might be important for tyrannid flycatchers' diet

**TABLE 1.** Mean abundance by size class, mean total abundance, mean biomass, and taxonomic richness (mean number of Orders) of potential arthropod prey of the Strange-tailed Tyrant (*Alectrurus risora*) at Reserva El Bagual, Formosa, Argentina during the breeding season 2007–2008 (mean  $\pm$  SD). Arthropod prey orders considered were Coleoptera, Diptera, Odonata, Orthoptera and Lepidoptera. Mean values were calculated from samples taken in upland (N = 29) and lowland (N = 30) grasslands from October to December 2007.

Variable	Upland	Lowland	Mann-Whitney Test	
			U	P value
Size class abundance				
0–2 mm	8.28 $\pm$ 8.46	12.23 $\pm$ 12.57	308	0.054
2–5 mm	15.14 $\pm$ 14.92	16.17 $\pm$ 9.72	353.5	0.217
5–10 mm	4.59 $\pm$ 4.06	7.10 $\pm$ 6.76	339	0.148
>10 mm	3.00 $\pm$ 3.28	3.6 $\pm$ 3.15	362	0.268
Total abundance	30.03 $\pm$ 23.68	39.13 $\pm$ 23.23	296.5	0.036
Biomass (g)	8.23 $\pm$ 9.17	15.44 $\pm$ 14.89	300	0.041
Taxonomic richness	9.03 $\pm$ 1.61	8.90 $\pm$ 1.16	415.5	0.767

**TABLE 2.** Mean abundance and biomass of potential arthropod prey of the Strange-tailed Tyrant (*Alectrurus risora*) discriminated by order, sampled in grasslands at Reserva El Bagual, Formosa, Argentina during the breeding season 2007–2008. Mean values were calculated from samples taken in upland (N = 29) and lowland (N = 30) grasslands from October to December 2007.

Prey taxa	Variable	Upland	Lowland	Mann-Whitney Test	
				U	P value
Coleoptera	Mean abundance	13.48 $\pm$ 14.90	11.53 $\pm$ 7.82	382	0.421
	Mean biomass	0.46 $\pm$ 0.39	0.70 $\pm$ 1.17	405	0.649
Diptera	Mean abundance	9.21 $\pm$ 9.18	19.40 $\pm$ 13.71	208	< 0.001
	Mean biomass	0.15 $\pm$ 0.14	0.85 $\pm$ 0.89	109	< 0.001
Lepidoptera	Mean abundance	1.00 $\pm$ 1.56	4.20 $\pm$ 7.25	287.5	0.025
	Mean biomass	1.44 $\pm$ 3.08	1.74 $\pm$ 2.77	334	0.126
Odonata	Mean abundance	0.14 $\pm$ 0.44	0.90 $\pm$ 1.42	311.5	0.061
	Mean biomass	0.72 $\pm$ 2.25	4.69 $\pm$ 7.56	314.5	0.068
Orthoptera	Mean abundance	6.21 $\pm$ 5.77	3.10 $\pm$ 5.20	258	< 0.001
	Mean biomass	5.46 $\pm$ 7.06	6.76 $\pm$ 8.93	413.5	0.744

(i.e., birds capture bigger prey regardless of their identity, Hespeneide 1971).

Temperature and humidity constrain insect development, feeding, and reproduction (Chown & Nicolson 2004, Harrison et al. 2012), and hence their distributions are limited by those environmental factors. The higher abundance of most arthropod orders in lowland grasslands may be due to increased water availability during most of the year. Presence of water assures a greater availability of resources for herbivorous insects and a greater microhabitat heterogeneity, which in turn offers more refuges and breeding sites (Jedlikowsky et al. 2016, Lenhart et al. 2015, Marini et al. 2009). However, as mentioned above, little is known about how weather conditions affect arthropod communities in the study area.

We found no evidence that greater availability of arthropods favours the establishment of *A. risora* females. It should be taken into consideration that sampling methods greatly influence estimates of food

availability, and that the probability of an insect being sampled does not necessarily match its probability of being captured by a bird (Poulin & Lefebvre 1997). In this sense, several authors have pointed out the need of using different simultaneous sampling methods to estimate arthropod community composition and abundance (Cooper & Whitemore 1990, Hutto 1990, Wolda 1990, Buffington & Redak 1998). The present work was conducted using a single method, meant to be suitable to sample for potential prey of *A. risora*, but which could have introduced some bias in prey availability estimation. For instance, some flying insects, such as those of Odonata order, spend most of the time in the air rather than on the vegetation, and could have been underrepresented in our samples. Other characteristics of insects, aside from their identity and size, might as well influence bird foraging behavior, such as life stage, palatability, nutritive value, coloration, and activity patterns (Cooper & Whitmore 1990). These traits, which we did not con-

sider in the present work, should be taken into consideration in future studies.

Although the availability of prey was lower in upland grasslands, it might be high enough for the birds to meet energetic requirements in both habitats. Therefore, it is possible that, besides prey preferences, other factors may influence habitat selection. These include nest predation risk, competition with conspecifics, polygyny, and historical and current distribution in relation to habitat loss (Di Giacomo et al. 2010c). For instance, *A. risora* occupies upland and lowland grasslands in the REB, an area that was utilized for livestock grazing and agriculture until recently (Di Giacomo & Krapovickas 2005). These activities might have pushed the species to use non-optimal habitats, forcing it to choose breeding sites following their availability rather than their relative quality. For tyrant flycatchers in general, one important aspect is the availability of perches that allow observation and capture of their preys (Fitzpatrick 1980). In the REB, the upland grassland has a greater availability of high perches due to the greater diversity of tall grasses and shrubs (data extracted from Maturo et al. 2005), which are usually not present in lowland grasslands because they are annually flooded. Future studies should compare foraging and the reproductive success of *A. risora* between these different types of grassland to test this hypothesis.

In this study, we evaluated the relationship between the arthropod availability and the establishment of *A. risora* male breeding territories in two natural grasslands used for breeding. Our results show that, although there is a relationship between the abundance of arthropods and the beginning of the breeding season, arthropod abundance does not explain the distribution of females and nests of *A. risora*. Still lacking is a characterization of the nutritional requirements of *A. risora*, which could provide further information on the potential effects that the arthropod community composition could have in a given habitat. To better understand the reproductive biology of this threatened species, future analyses should be performed on a multi-year basis, and simultaneously including and comparing other variables, such as perch availability (specially in relation to the occurrence of periodical floods) and predation rates in each grassland. Additionally, climatological variables, namely temperature and water availability regimes, together with seasonal flood-drought episodes, should be taken into consideration to better understand both the bird and its prey population dynamics.

#### ACKNOWLEDGMENTS

The authors would like to thank Alparamis S.A. and Aves Argentinas for allowing us to conduct this study at REB. ASDG was supported by a Canon National Park Science Scholarship from the American Association for Advance of Science (AAAS). ASDG and MKC are Research fellows of CONICET. We would also like

to thank the editor and the anonymous reviewers for their thorough critiques, which have helped us to greatly improve our manuscript.

#### REFERENCES

- Asokan, S, AM Samsoor ALI & R Manikannan (2009) Diet of three insectivorous birds in Nagapattinam District, Tamil Nadu, India – a preliminary study. *Journal of Threatened Taxa* 1: 327–330.
- Azpiroz, AB, JP Isacch, RA Dias, AS Di Giacomo, CS Fontana & CM Palarea (2012) Ecology and conservation of grassland birds in southeastern South America: a review. *Journal of Field Ornithology* 83: 217–246.
- Biaggini, M, R Consorti, L Dapporto, M Dellacasa, E Paggetti & C Corti (2007) The taxonomic level order as a possible tool for rapid assessment of arthropod diversity in agricultural landscapes. *Agriculture, Ecosystems and Environment* 122: 183–191.
- Bibby, CJ, ND Burgess & DA Hill (1992) *Bird census techniques*. Academic Press, London, UK.
- Birdlife International (2013) Species factsheet: *Alectrurus risora*. Available from <http://www.birdlife.org> [Accessed 13 April 2013].
- Brady, CJ & RA Noske (2006) Generalised regressions provide good estimates of insect and spider biomass in the monsoonal tropics of Australia. *Australian Journal of Entomology* 45: 187–191.
- Buffington, ML & RA Redak (1998) A comparison of vacuum sampling versus sweep-netting for arthropod biodiversity measurements in California coastal sage scrub. *Journal of Insect Conservation* 2: 99–106.
- Cabrera, AL & A Willink (1980) *Biogeografía de América Latina*. Serie de Biología 13. Organization of American States, Washington, DC, USA.
- Chown, SL & SW Nicholson (2004) *Insect physiological ecology: mechanisms and patterns*. Oxford Univ. Press, Oxford, UK.
- Cooper, RJ & RC Whitmore (1990) Arthropod sampling methods in ornithology. Avian foraging: theory, methodology and applications. *Studies in Avian Biology* 13: 29–37.
- Di Giacomo, AS & AG Di Giacomo (2004) Extinción, historia natural y conservación de las poblaciones del Yetapá de Collar (*Alectrurus risora*) en la Argentina. *Ornitología Neotropical* 15 (Supplement): 145–157.
- Di Giacomo, AS & AG Di Giacomo (2006) Observations of Strange-tailed Tyrants (*Alectrurus risora*) and other grassland birds following army ants and armadillos. *Journal of Field Ornithology* 77: 266–268.
- Di Giacomo, AG & SF Krapovickas (2005) *Historia natural y paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina. Inventario de la fauna de vertebrados y de la flora vascular de un área protegida del Chaco Húmedo*. Temas de Naturaleza y Conservación 4. Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- Di Giacomo, AS, AG Di Giacomo & JC Reboreda (2011a) Male and female reproductive success in a threatened polygynous species: the Strange-tailed Tyrant, *Alectrurus risora*. *Condor* 113: 619–628.
- Di Giacomo, AS, AG Di Giacomo & JC Reboreda (2011b) Effects of grassland burning on reproductive success of globally threatened Strange-tailed Tyrants *Alectrurus risora*. *Bird Conservation International* 21: 411–422.
- Fitzpatrick, JW (1980) Foraging behavior of Neotropical tyrant-flycatchers. *Condor* 82: 43–57.
- Fitzpatrick, JW (2004). Family Tyrannidae (tyrant-flycatchers). Pp 170–462 in del Hoyo, J, A Elliott & DA Christie (eds).

- Handbook of the birds of the world. Volume 9: Cotingas to pipits and wagtails.* Lynx Edicions, Barcelona, Spain.
- Gorleri, MC (2005) Caracterización climática del Chaco Húmedo. Pp 13–25 in Di Giacomo, AG & SF Krapovickas (eds). *Historia natural y paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina.* Temas de Naturaleza y Conservación 4. Aves Argentinas. Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- Granihar, SR (1997) Biomass estimates of terrestrial arthropods based on body length. *Journal of Biosciences* 22: 219–224.
- Harrison, JF, HA Woods & SP Roberts (2012) *Ecological and environmental physiology of insects.* Oxford Univ. Press, Oxford, UK.
- Hespenheide, HA (1971) Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* 113: 59–72.
- Hódar, JA (1997) The use of regression equations for estimation of prey length and biomass in diet studies of insectivore vertebrates. *Miscellanea Zoologica* 20: 1–10.
- Hutto, RL (1990) Measuring the availability of food resources. Avian foraging: theory, methodology and applications. *Studies in Avian Biology* 13: 20–28.
- Invertebrados II (2007) *Claves para la determinación de ordenes de insecta.* Cátedra de invertebrados II (Artrópodos). Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Univ. de Buenos Aires. Buenos Aires, Argentina.
- Jahn, AE, DT Tuero, AM Mamani, V Bejarano, DA Masson & E Aguilar (2014) Drivers of clutch-size in Fork-tailed Flycatchers (*Tyrannus savana*) at temperate and tropical latitudes in South America. *Emu* 114: 337–342.
- Jedlikowski, J, P Chibowski, T Karasek & M Brambilla (2016) Multi-scale habitat selection in highly territorial bird species: exploring the contribution of nest, territory and landscape levels to site choice in breeding rallids (Aves: Rallidae). *Acta Oecologica* 73: 10–20.
- Johnson, EI, PC Stouffer & R Bierregaard JR (2012) The phenology of molting, breeding and their overlap in central Amazonian birds. *Journal of Avian Biology* 43: 141–154.
- Kaspari, M & A Joern (1993) Prey choice by three insectivorous grassland birds: reevaluating opportunism. *Oikos* 68: 414–430.
- King, J (1974) Seasonal allocation of time and energy resources in birds. Pp. 4–85 in Paynter, Jr RA (ed). *Avian energetics.* Publications of the Nuttall Ornithological Club 15, Cambridge, Massachusetts, USA.
- Lenhart, PA, MD Eubanks & ST Behmer (2015) Water stress in grasslands: dynamic responses of plants and insect herbivores. *Oikos* 124: 381–390.
- Marini, L, P Fontana, A Battisti & KJ Gaston (2009) Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland-forest mosaic: a multi-scale approach. *Insect Conservation and Diversity* 2: 213–220.
- Marini, MA, FJA Borges, LE Lopes, NOM. Sousa, DR Gressler, LR Santos, LV Paiva, C Duca, LT Manica, SS Rodrigues, LF Franca, PM Costa, LC França, NM Heming, MB Silveira, ZP Pereira, Y Lobo, RCS Medeiros & JJ Roper (2012) Breeding biology of birds in the Cerrado of Central Brazil. *Ornitología Neotropical* 23: 385–405.
- Martin, TE & GR Geupel (1993) Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64: 507–519.
- Martin, TE (1996) Life history evolution in tropical and south temperate birds: what do we really know? *Journal of Avian Biology* 27: 1–10.
- Maturo, HM, LJ Oakley, & DE Prado. (2005) Vegetación y posición geográfica de la Reserva El Bagual. Pp 59–73 in Di Giacomo AG & SF Krapovickas (eds). *Historia natural y paisaje de la Reserva El Bagual, Provincia de Formosa, Argentina. Inventario de la fauna de vertebrados y de la flora vascular de un área protegida del Chaco Húmedo.* Temas de Naturaleza y Conservación 4. Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- Parisi, V, C Menta, C Gardi, C Jacomini & E Mozzanica (2005) Microarthropod communities as a tool to assess soil quality and biodiversity: a new approach in Italy. *Agriculture, Ecosystems and Environment* 105: 323–333.
- Poulin, B & G Lefebvre (1997) Estimation of arthropods available to birds: effect of trapping technique, prey distribution, and bird diet. *Journal of Field Ornithology* 68: 426–442.
- R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Ricklefs, RE (1974) Energetics of reproduction in birds. Pp 152–297 in Paynter, Jr RA (ed). *Avian energetics.* Publications of the Nuttall Ornithological Club 15, Cambridge, Massachusetts, USA.
- Russell, EM, Y Yom-Tov & E Geffen (2004) Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology* 15: 831–838.
- Skutch, AF (1985) Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithological Monographs* 36: 575–594.
- Snow, DW & BK Snow (1964) Breeding seasons and annual cycles of Trinidad landbirds. *Zoologica* 49: 1–39.
- Stouffer, PC, EI Johnson & RO Bierregaard Jr (2013) Breeding seasonality in central Amazonian rainforest birds. *The Auk* 130: 529–540.
- Stutchbury, BJ M & ES Morton (2001) Behavioral ecology of tropical songbirds. Academic Press, London, UK.
- Vickery, PD, ML Hunter JR & JV Wells (1992) Is density an indicator of breeding success? *The Auk* 109: 706–710.
- Vickery, PD, PL Tubaro, JMC Silva, BG Peterjohn, JR Herkert & RB Cavalcanti (1999) Conservation of grassland birds in the western hemisphere. *Studies in Avian Biology* 19: 2–26.
- Walsberg, GE (1985) Physiological consequences of microhabitat selection. Pp. 389–413 in Cody, ML (ed) *Habitat selection in birds.* Academic Press, Orlando, Florida, USA.
- Wiens, JA & JT Rotenberry (1979) Diet niche relationships among North American grassland and shrubsteppe birds. *Oecologia* 42: 253–292.