



Dietary ecology of two migrant flycatchers in habitats with and without cattle during the breeding season in central Argentina

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ABSTRACT

Food selection is a key aspect of a bird's life history strategy, so understanding how birds respond to variation in food abundance is relevant to evaluating their general ecology and survival, and also the potential consequences of the degradation of environments impacted by livestock. We studied the dietary ecology of Vermilion Flycatchers (VEFL) and Fork-tailed Flycatchers (FTFL), two insectivores and Neotropical austral migrants, during their breeding season. We worked in areas with and without cattle ranching in the Espinal biome of La Pampa, Argentina. We found different arthropod prey abundance for both flycatchers according to arthropod orders and/or study sites, suggesting that livestock may impact food abundance. Both consumed similar prey and positively selected for hymenopterans and coleopterans, and FTFL also positively selected for orthopterans. VEFL selected nest sites with a lower abundance of heteropterans and FTFL selected sites with a higher abundance of coleopterans. Additionally, VEFL nest survival was negatively related to the abundance of hemipterans and FTFL nest survival was positively related to the abundance of coleopterans. This study helps fill gaps on the general ecology of species that breed in rangelands, and highlights the importance of similar studies to formulate effective conservation planning for the Espinal biome.

1. Introduction

Food selection is a fundamental behaviour directly related to food availability and trophic habits, which can affect diverse aspects of a bird's life history strategy (Bairlein 1990; Carey 1996; Manly et al., 2004). On the one hand, food availability (i.e., its accessibility to the consumer), may change according to various aspects of prey ecology (e.g., prey abundance) and habitat features (Boulton et al., 2008), but is also dependent on other components of the environment, such as weather (Jahn et al., 2010) and human impacts (Benton et al., 2002). On the other hand, diet is often an evolutionarily-fixed trait that varies in specificity across a continuum from generalists to specialists (Manhães et al., 2010). Food selection may affect key traits of birds, such as body

condition (Rioux Paquette et al., 2014), breeding success (Boulton et al., 2008), as well as spatial and temporal patterns of different behaviours, including habitat use (Durst et al., 2008) and migration (Bairlein 1990).

Currently, loss of biodiversity is a pervasive pattern across the globe (MacDougall et al., 2013), including losses of insects (Lister and Garcia 2018), which represents a serious threat to insectivorous birds. Many insectivorous birds are currently in decline (Nebel et al., 2010; Bowler et al., 2019), in part due to the intensification of farming activities such as crop production and livestock (Dennis 2003; Stanton et al., 2018). Most bird studies have focused on row crop production and have dealt less with impacts of cattle ranching, probably because the former has stronger negative impacts on birds and their environments (Stanton et al., 2018). However, livestock have the potential to impact

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abundance, richness, diversity and abundance of insects (Dennis 2003; Stanton et al., 2018), although the magnitude of such effects is poorly known.

One of the largest taxonomic groups of primarily insectivorous birds are the tyrant flycatchers (Tyrannidae; Fitzpatrick 2004), which inhabit numerous New World ecosystems. The Tyrannidae is also the largest taxonomic group of Neotropical austral migrants, which breed at south-temperate latitudes of South America and migrate towards the Equator to overwinter (Chesser 1994). Migratory species have additional selection pressures than do non-migrants, since they move through a variety of ecosystems throughout the year (Wilcove and Wikelski 2008).

The Vermilion Flycatcher (*Pyrocephalus r. rubinus*; hereafter, VEFL) and Fork-tailed Flycatcher (*Tyrannus s. savana*; hereafter, FTFL) are two insectivorous, widely distributed and common Neotropical austral migrant tyrant flycatchers (Chesser 1994; Ellison et al., 2020; Jahn and Tuero 2020). In central Argentina, both species breed in the Espinal biome, which is subject to intense pressure from human activities. The Espinal is being rapidly altered by deforestation, expansion of agricultural activities, alteration of fire regimes, and overgrazing by livestock, resulting in the loss and degradation of 37% of its extent from 1973 to 2006 (Brown et al., 2006; Distel 2016). As is the case for other Neotropical austral migrants, their general ecology remains poorly understood (Faaborg et al., 2010; Jahn et al., 2020), including the food items they select across different habitats and the effects of food abundance on breeding success. Understanding the impact of human activities (e.g. extensive cattle grazing) on their trophic ecology in the Espinal is therefore relevant to evaluate the potential consequences of the degradation of the Espinal on these and other similar species.

Previous research has shown that cattle ranching has negatively impacted the diversity of insectivorous birds in Argentina (Mastrangelo and Gavin 2012; Macchi et al., 2013). Furthermore, VEFL's breeding success at our study site was lower in habitats subjected to cattle ranching (Rebollo et al., 2020). Thus, we tested two hypotheses: 1) cattle ranching impacts arthropod prey abundance, and 2) arthropod prey abundance influences breeding habitat selection and breeding success of VEFL and FTFL. We predicted that arthropod prey abundance for both species would be lower in habitats where cattle are present and that both species would selectively nest in habitats with higher arthropod prey abundance, where they would also have higher breeding success.

2. Materials and methods

2.1. Species

VEFL and FTFL breed from November to January in open savannas and dry forests, are socially monogamous and place their open-cup nests in shrubs or trees (Ellison et al., 2020; Jahn and Tuero 2020; Rebollo et al., 2020). VEFL's prey includes mostly hymenopterans, isopterans, dipterans, coleopterans, orthopterans and lepidopterans, among other insects, but also spiders (de la Peña and Salvador 2010; Ellison et al., 2020). FTFL have a similar diet as VEFL during the breeding season, although they also consume fruit during the non-breeding season (de la Peña and Salvador 2010; Jahn and Tuero 2020).

2.2. Study area

We worked in the province of La Pampa, Argentina, in the Espinal biome (Cabrera and Willink 1973, Fig. 1). The climate is semiarid, with a mean annual temperature of 15.3 °C and a mean annual rainfall of 350–550 mm (Cabrera and Willink 1973). The landscape is composed primarily of an almost monospecific forest of Caldén (*Prosopis caldenia*) interspersed with grasslands that have none to a moderate number of shrubs (Cabrera and Willink 1973; Supplementary Fig. 1S).

Specifically, we worked in Parque Luro Provincial Reserve (76.07 km², 36° 56' 00" S and 64° 14' 00" W, hereafter, "reserve") and two adjacent private ranches, Los Álamos (50.80 km², hereafter "LAR") and Giuliani (49.57 km², hereafter "GR"; Fig. 1). These sites are located along National Route 35, ~35 km south of Santa Rosa city, the capital of La Pampa Province. Most habitat features across the three study areas differed, including differences between the two areas with cattle: GR has taller Caldén plants with larger trunks and crowns than the other two areas; the reserve has greater species richness of woody plants and a higher percentage of mid-level plant stratum coverage (shrubs and saplings combined) than do both ranches. Additionally, GR has lower percent bare soil than LAR and lower percent herb cover than the reserve (Rebollo et al., 2020). The reserve is the largest protected area of Caldén forest in the Espinal and is an Important Bird Area (Maceda 2005). Activities such as agriculture, livestock, and hunting have been banned in the reserve since 1967 (González-Roglich et al., 2012). Both LAR and GR are rangelands that are used by their respective owners principally

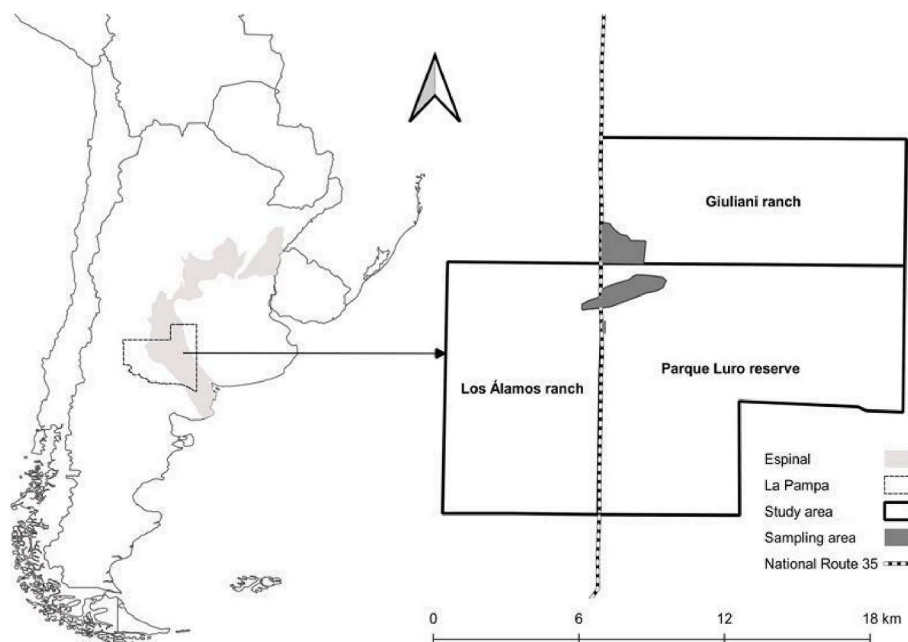


Fig. 1. Location of Parque Luro Provincial Reserve, Giuliani and Los Álamos ranches, and our sampling areas in the Espinal biome, La Pampa Province, Argentina.

for raising cattle, but also for some low impact agricultural and hunting activities. The average stocking rate in the region is $\sim 5\text{--}15\text{ hm}^2$ (i.e. $1\text{ hm}^2 = 10,000\text{ m}^2$) per cattle equivalent and the production per hm^2 is $\sim 14\text{--}41\text{ kg}$, and both vary according to rangeland conditions (Morris and Ubici 1996).

2.3. Field work

During four consecutive breeding seasons (between October and February, starting in October 2015 and ending in February 2019), we searched for and monitored nests according to methods described in Ralph et al. (1993) across a sampling area of 3.22 km^2 (Fig. 1). We sampled nestling flycatchers 12 days after hatching and also captured flycatchers using polyester mist nets ($3 \times 12\text{ m}$ or $3 \times 18\text{ m}$, 32 mm mesh size; NABC 2001). We placed the nets 2–20 m from nests and to attract flycatchers to the net, we placed a live captive Southern Caracara (*Caracara plancus*) next to the net or used a speaker playing conspecific calls, between 4:30–14:00 h and 17:00–21:00 h. We marked the captured birds with individually numbered metal bands and three Darvic color bands, using unique combinations. We aged them as juveniles (with juvenile plumage), immature adults (having molt limits, i.e. contrasting between the more recently replaced and older retained feathers, having formative plumage but before the second prebasic molt), or mature adults (without molt limits, having uniform plumage after the second prebasic molt) and sexed them using plumage criteria in Pyle (1997) and 1998. When we could not distinguish between immature and mature adult birds, we aged them as “after juvenile” age. We sexed nestlings and juveniles, which are not dimorphic, using molecular techniques (see below), obtaining DNA from blood samples collected during banding by puncture of the brachial vein. Blood was stored in absolute ethanol. We also held each bird in a clean cloth bag for 20–30 min for collection of a fecal sample that was stored in 70% ethanol (Rosenberg and Cooper 1990). We then returned them to their nest (in the case of nestlings) or released them at the site of capture (NABC 2001).

We evaluated food abundance by capturing arthropods using aerial net bags (BioQuip 7318NA), doing 35 sweeps 0.50–2.00 m above the ground along transects (hereafter, “sweep transects”) that were 25 m in length (Cooper and Whitmore 1990), located in the reserve ($n = 59$), GR ($n = 13$), and LAR ($n = 33$). To describe food selection, we sampled arthropods along sweep transects located 20–200 m from each nest site where we had captured birds and collected fecal samples (within which we always attempted to sample arthropods as close to the nest as possible). We fixed these distances at 20–200 m because, although in the field we observed VEFL foraging up to $\sim 350\text{ m}$ from their nest and FTFL up to $\sim 500\text{ m}$ from their nest, they usually foraged near their nest (i.e., within 25 m). The direction of the sweep transect from the nest was chosen randomly. Sweep transects were also located 20 m in a random direction from control sites used to evaluate breeding site selection, which was done by comparing used (nest sites) and unused (control) sites, as described in Rebollo et al. (2020). All environments were easily sampled despite the presence of the mid-level plant stratum. Arthropod samples were stored in 70% ethanol. Each sweep transect was sampled once by the same person (MER) and all samples were collected between 7:30–11:30 a.m. during non-rainy days, with temperatures of $20\text{--}27\text{ }^\circ\text{C}$, and with winds of up to 15 Km.h^{-1} .

2.4. Laboratory work

We extracted DNA from blood samples following the protocol suggested by Butler (2009), using Chelex® 100 (Bio Rad Laboratories, CA, EEUU). We sexed birds following the methodology suggested by Griffiths et al. (1998), employing PCR with P2/P8 primers and Phusion Blood Master Mix polymerase (Thermo Fisher, MA, EEUU) to amplify the CHD1 and CHD-Z genes. We conducted an initial denaturing step at $98\text{ }^\circ\text{C}$ for 5 s that was followed by 35 cycles at $98\text{ }^\circ\text{C}$ for 1 s, $48\text{ }^\circ\text{C}$ for 5 s

and $72\text{ }^\circ\text{C}$ for 20 s. We completed this with a final run at $72\text{ }^\circ\text{C}$ for 2 min. We then separated PCR products by electrophoresis.

We identified arthropod fragments from fecal samples and individual arthropods from sweep transects to the lowest taxonomic level possible using a dissecting microscope (Olympus SZ2-ILST). We classified holometabolous insects (lepidopterans and coleopterans) as ‘larvae’ or ‘adults’. To aid in identification, we consulted reference material deposited at the MHNLP (Museo de Historia Natural de La Pampa), as well as the literature (Manhães et al., 2010). Moreover, to aid in identifying taxa that were represented by fragments in the fecal samples, we dissected some of the collected arthropods to compare with the fecal sample fragments. We estimated the minimum number of arthropod items per fecal sample by summing pairs of matching body parts and by counting unique body parts for a given arthropod. We recorded non-identified fragments as “undetermined arthropods” and disregarded fragments too small to analyze (Manhães et al., 2010). We calculated the percentages of frequencies (counts of all arthropod items) and occurrence (number of samples in which a particular arthropod item was present) in the fecal samples and in abundance samples collected along sweep transects (Rosenberg and Cooper 1990; Manhães et al., 2010). Finally, we deposited all samples in the MHNLP collection.

2.5. Data analysis

We analyzed overall arthropod abundance (Fig. S2) by modelling the total number of arthropods per netted sample according to year (2016–17, 2017–18 and, 2018–19), site (reserve, LAR or GR) and date (number of days since October 31, because that was the first date we captured birds) using a Generalized Linear Model (GLM; Crawley 2015). We then separately modeled the frequency of hymenopterans, coleopterans, hemipterans and orthopterans in netted samples using GLMs. We used these arthropod orders because they were the most frequent items in each species’ diet (see 3. Results section; Table 1), so we considered them potential prey.

To analyze prey consumption, we relied on data from fecal samples (Fig. S3). In the case of VEFL, we separately modeled the frequency of hymenopterans, coleopterans and hemipterans in the fecal samples, using GLMs. In the case of FTFL, we ran the same analysis but considered

Table 1

Results of General Linear Models to evaluate the variation of item frequency as a measure of food abundance in Vermilion Flycatcher (VEFL) and Fork-tailed Flycatcher (FTFL) diets, in La Pampa, Argentina. Values are χ^2 , df, P.

Prey item	Abundance	VEFL	FTFL
Hymenoptera			
Age		7.44, 4, 0.11	0.05, 1, 0.83
Sex		2.92, 1, 0.09	
Year	24.75, 2, <0.001	8.02, 3, 0.048	31.68, 2, <0.001
Site	74.75, 2, 0.002	7.50, 2, 0.02	1.73, 2, 0.42
Date	9.61, 1, 0.002	30.87, 1, <0.001	1.62, 1, 0.20
Coleoptera			
Age		2.16, 4, 0.71	0.62, 1, 0.43
Sex		0.34, 1, 0.56	
Year	5.87, 2, 0.05	0.67, 3, 0.88	1.85, 2, 0.40
Site	3.17, 2, 0.21	2.13, 2, 0.35	2.76, 2, 0.25
Date	10.72, 1, 0.001	6.07, 1, 0.01	0.01, 1, 0.92
Hemiptera			
Age		6.27, 4, 0.18	
Sex		0.36, 1, 0.55	
Year	31.22, 2, <0.001	5.91, 3, 0.12	
Site	44.10, 2, <0.001	2.42, 2, 0.30	
Date	27.07, 1, <0.001	14.78, 1, <0.001	
Orthoptera			
Age			3.6, 1, 0.06
Year	2.17, 2, 0.34		3.35, 2, 0.19
Site	3.23, 2, 0.2		3.7, 2, 0.16
Date	9.12, 1, 0.003		0.74, 1, 0.39

the frequency of hymenopterans, coleopterans and orthopterans. Explanatory variables were: age ('nestling', 'juvenile', after 'juvenile', 'immature adult' or 'mature adult' for VEFL, and 'nestling' or 'after juvenile' for FTFL), sex (only for VEFL because we determined sex for only a few FTFL; see 3. Results section), year (2015–16, 2016–17, 2017–18 and 2018–19 for VEFL, 2015–16, 2016–17 and 2017–18 for FTFL), site (reserve, LAR or GR), and date.

To evaluate food selection, we used GLMs comparing prey consumption vs. abundance during 2016–17, 2017–18 and 2018–19 breeding seasons for VEFL, and 2016–17 and 2017–18 for FTFL, as these are the years for which we had both fecal samples and abundance samples of each flycatcher throughout each breeding season. We also used GLMs to measure breeding habitat selection, comparing used and unused nest sites (Manly et al., 2004; Crawley 2015) during the 2016–17 breeding season at the reserve, GR and LAR (Fig. S4). The response variables for food selection were binomial: (1) fecal samples or (0) samples in the sweep transect nearest to where the bird was captured. The response variables for habitat selection were also binomial: (1) sample in the sweep transect nearest to a nest site or (0) samples in the sweep transect nearest to the control site. We used frequency of hymenopterans, coleopterans, hemipterans as explanatory variables in VEFL selection models, and hymenopterans, coleopterans and orthopterans in the FTFL models.

To quantify breeding success, we compared the probability of a nest surviving to fledging at least one nestling for each breeding attempt, based on the total number of exposure days and daily survival rate of egg and nestling periods (Dinsmore et al., 2002), obtained for both species by Rebollo et al. (2020). We used Linear Models (LMs; Crawley 2015) to model the probability of nest survival of VEFL according to the frequency of abundance of hymenopterans, coleopterans and hemipterans and total arthropods, and evaluated the frequency of abundance of hymenopterans, coleopterans and, orthopterans and total arthropods when modeling nest survival for FTFL. We ran these models only for the end of the 2016–17 breeding season (VEFL: January 16 - February 7; FTFL: January 25 - February 7) to exclude the effect of year and date.

For all flycatcher GLMs, we employed the Binomial distribution and "logit" link function, except for hymenopterans in the FTFL diet model and in both food selection models, for which we used a Quasibinomial error distribution to correct for overdispersion (dispersion parameter >1.3 ; Crawley 2015). We used a Quasibinomial distribution for all food abundance models, except for the total abundance model, in which we employed a Quasipoisson distribution and a "log" link. We evaluated collinearity of numerical variables using a Pearson correlation and multicollinearity using variance inflation factors (VIF). None of the GLMs had collinearity ($r < 0.7$) or multicollinearity, except for all food abundance models, in which date was independently modeled (VIFs >3.5). We simplified all models following a backward stepwise selection, using hypothesis tests and removing non-significant terms until we

obtained the simplest model. We employed Tukey Contrasts *a posteriori* to conduct multiple comparisons of the means of the categorical variables selected in the GLMs. We calculated model explanatory capacity using adjusted R^2 for LMs or deviance parameters for GLMs (Crawley 2015). We used a Chi-square Test to compare VEFL and FTFL diets. We conducted all analyses in program R v.3.4.1 (R Core Team 2017), using a significance level of 0.05.

3. Results

3.1. Food abundance and diet

We collected 6577 arthropods (62.64 ± 47.0 arthropods/sample), corresponding to 11 Insecta and 2 Arachnida orders (Supplementary Table S1). Hemipterans, spiders, and dipterans dominated by frequency (Fig. 2) and hemipterans, dipterans and spiders dominated by occurrence (Supplementary Table S1). VEFL consumed eight Insecta orders and two Arachnida, while FTFL consumed eight Insecta orders and one Gastropoda (Supplementary Table S1). VEFL consumed mainly hymenopterans, coleopterans and hemipterans in terms of frequency (Fig. 2) and coleopterans, hymenopterans and hemipterans in terms of occurrence (Supplementary Table S1). FTFL consumed mainly hymenopterans, coleopterans and orthopterans in terms of frequency (Fig. 2) and coleopterans, orthopterans and hymenopterans in terms of occurrence (Supplementary Table S1).

The total abundance of arthropods per sample differed by year, with 2018–19 being lower than 2017–18 (Estimate \pm s.e. = -0.76 ± 0.30 , $z = -2.50$, $P = 0.03$), and by site, with the reserve being higher than LAR (Estimate \pm s.e. = 0.44 ± 0.14 , $z = 3.17$, $P = 0.004$; Fig. 3a). Total abundance was negatively related with date (Estimate \pm s.e. = -0.01 ± 0.003 , $\chi^2 = 4.94$, $df = 1$, $P = 0.03$). This model explained 24.26% of variation of the total abundance of arthropods.

The abundance of hymenopterans differed by year and by site, with the reserve being lower than LAR and GR but also with LAR being lower than GR (Table 2; Supplementary Table S2; Fig. 3b). This model explained 55.07% of variation of the abundance of hymenopterans. The abundance of hymenopterans was also positively related with date (Table 1; Supplementary Table S3), explaining 9.08% of the variation. The abundance of coleopterans was negatively related with date (Table 1; Supplementary Table S3), explaining 14.83% of the variation. The abundance of hemipterans differed by year and by site, with the reserve being higher than LAR and GR, but also with LAR being higher than GR (Table 1; Supplementary Table S2; Fig. 3c). This model explained 47.58% of variation of the abundance of hemipterans. The abundance of hemipterans was also negatively related to date (Table 1; Supplementary Table S3), explaining 19.62% of the variation. The abundance of orthopterans was positively related with date (Table 1; Supplementary Table S3), explaining 9.76% of the variation.

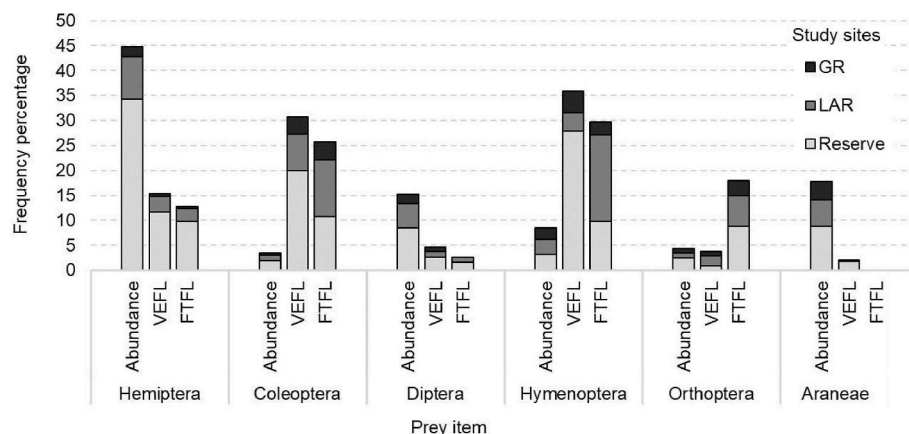


Fig. 2. Frequency percentage of prey items obtained from 108 abundance samples from sweep transects, 81 fecal samples of Vermilion Flycatchers (VEFL) and 52 fecal samples of Fork-tailed Flycatchers (FTFL). Each frequency percentage is shown by study site: Parque Luro Provincial Reserve ("Reserve"), and two cattle ranches: Giuliani ranch (GR) and Los Álamos ranch (LAR). All samples come from La Pampa Province, Argentina, and were obtained during four breeding seasons (three breeding seasons for food abundance: 2016–17, 2017–18 and 2018–19; four breeding seasons for VEFL: 2015–16, 2016–17, 2017–18 and 2018–19; three breeding seasons for FTFL: 2015–16, 2016–17 and 2017–18).

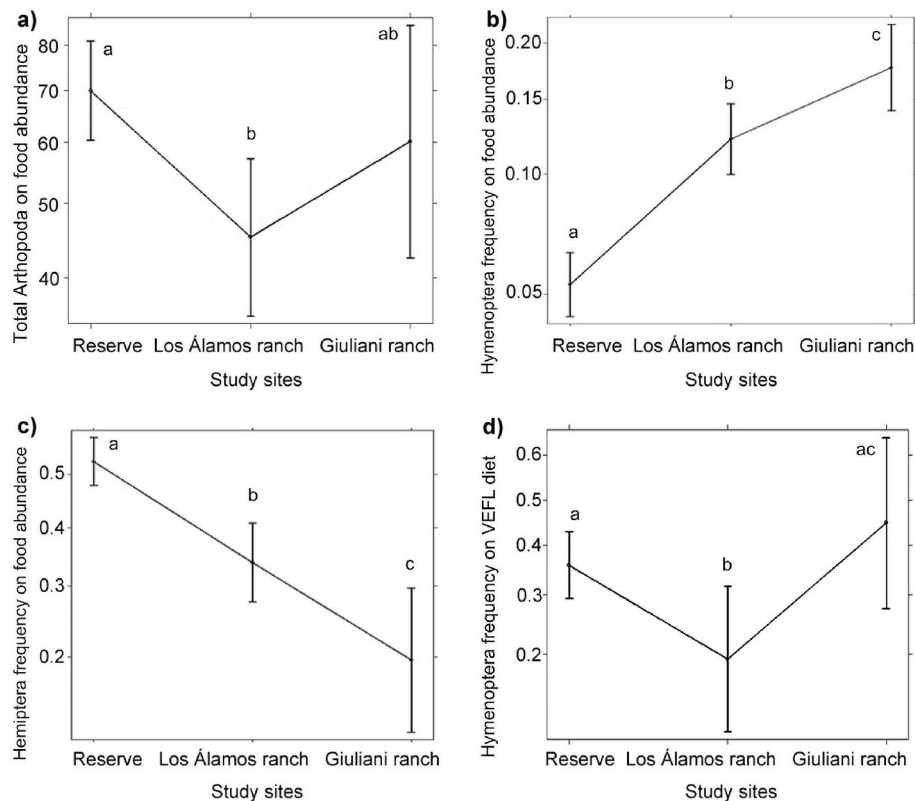


Fig. 3. Significant results of Generalized Linear Models to evaluate the variation of a) total arthropods, b) hymenopteran frequency and c) heteropter frequency as a measure of food abundance, and d) hymenopteran frequency in Vermilion Flycatcher (VEFL) diet, comparing study sites (reserve without cattle ranching and two cattle ranches) in La Pampa, Argentina. Different letters indicate significant differences. Values are estimates and bars are \pm s.e.

Table 2

Results of Generalized Linear Models to describe food selection (prey consumed vs. abundance) and habitat selection (prey abundance in habitats used for nesting vs. unused habitat for nesting) for Vermilion Flycatchers (VEFL) and Fork-tailed Flycatchers (FTFL) in La Pampa, Argentina. Values are Estimate \pm s.e., χ^2 , df, P.

Prey item	VEFL food selection	VEFL habitat selection	FTFL food selection	FTFL habitat selection
Hymenoptera	12.24 \pm 5.22, 16.48, 1, <0.001	1.19 \pm 5.38, 0.05, 1, 0.83	8.22 \pm 4.01, 7.46, 1, 0.006	4.21 \pm 5.52, 0.59, 1, 0.44
Coleoptera	20.3 \pm 6.66, 39.28, 1, <0.001	-10.15 \pm 17.16, 0.35, 1, 0.55	17.78 \pm 6.36, 20.42, 1, <0.001	27.17 \pm 12.44, 7.9, 1, 0.005
Hemiptera	-1.32 \pm 3.26, 0.17, 1, 0.68	-3.36 \pm 1.59, 5.05, 1, 0.02		
Orthoptera			8.12 \pm 4.22, 5.41, 1, 0.02	-7.56 \pm 5.85, 1.8, 1, 0.18

The frequency of hymenopterans in VEFL diet differed by site, with LAR being lower than the reserve and GR, and was related with year and positively with date (Table 1; Supplementary Table S2; Supplementary Table S3; Fig. 3d). This model explained 29.29% of variation of Hymenoptera frequency in VEFL diet. The frequency of coleopterans in VEFL diet was negatively related with date (Table 2; Supplementary Table S3), explaining 8.10% of the variation. The frequency of hemipterans in VEFL diet was negatively related with date (Table 2; Supplementary Table S3), explaining 18.19% of the variation.

The frequency of hymenopterans in FTFL diet differed by year (Table 2; Supplementary Table S2), explaining 42.31% of the variation. The frequency of coleopterans and orthopterans in FTFL diet did not

differ by either age, year, site or date (Table 2; Supplementary Table S2). The frequency of hemipterans in FTFL diet differed by year (Table 2; Supplementary Table S2) and was negatively related with date (Table 2; Supplementary Table S3), explaining 36.82% of the variation.

3.2. Diet comparison between bird species

VEFL and FTFL consumed mainly the same arthropod items, although VEFL also consumed spiders and mites and FTFL also consumed gastropods (Supplementary Table S1). Both species consumed insects, such as hymenopterans and coleopterans, but also hemipterans were important in the VEFL diet and orthopterans were important in the FTFL diet (Supplementary Table S1; Fig. 2). The frequency of hymenopterans ($\chi^2 = 0.68$, df = 1, $P = 0.41$), coleopterans ($\chi^2 = 0.52$, df = 1, $P = 0.473$), and hemipterans ($\chi^2 = 0.40$, df = 1, $P = 0.53$) consumed did not differ between the two bird species, but FTFL consumed more orthopterans than VEFL ($\chi^2 = 24.27$, df = 1, $P < 0.001$).

3.3. Food and habitat selection

VEFL positively selected hymenopterans and coleopterans (Table 2), explaining 77.52% of the variation. FTFL positively selected hymenopterans, coleopterans, and orthopterans (Table 2), explaining 61.26% of the variation. VEFL only selected breeding habitat with lower abundance of hemipterans (Table 2), explaining 7.5% of the variation; FTFL only selected nest sites with higher abundance of coleopterans (Table 2), explaining 11.14% of the variation.

3.4. Breeding success

VEFL nest survival was negatively related to the abundance of hemipterans at the breeding site (Table 3), explaining 30.25% of the

Table 3

Results of Linear Models to describe breeding success according to food abundance of Vermilion Flycatchers (VEFL) and Fork-tailed Flycatchers (FTFL), in La Pampa, Argentina. Values are Estimate \pm s.e., F, df, P.

Prey item	VEFL	FTFL
Hymenoptera	0.6 \pm 0.8, 0.57, 1, 13, 0.47	1.16 \pm 0.84, 1.93, 1, 16, 0.18
Coleoptera	1.92 \pm 4.37, 0.19, 1, 13, 0.67	1.38 \pm 0.51, 7.32, 1, 16, 0.02
Hemiptera	-1.08 \pm 0.41, 7.07, 1, 13, 0.02	
Orthoptera		0.08 \pm 1.01, 0.01, 1, 16, 0.94
Total	-0.003 \pm 0.002, 1.37, 1, 13, 0.26	-0.004 \pm 0.003, 2.29, 1, 16, 0.15

variation. FTFL nest survival was positively related to the abundance of coleopterans at the breeding sites (Table 3), explaining 27.1% of the variation. We found no other significant associations between prey abundance and breeding success.

4. Discussion

In the study area of central Argentina, the total food abundance for VEFL and FTFL was higher in the reserve than in one of two rangelands sampled and also, abundance of some arthropod prey types varied according to study site. The two bird species positively selected hymenopterans and coleopterans, and FTFL also positively selected orthopterans. VEFL selected nest sites with a lower proportion of hemipterans and FTFL with a higher proportion of coleopterans. VEFL's breeding success was negatively associated with hemipteran frequency, while FTFL's breeding success was positively associated with coleopteran frequency. These results suggest that livestock may impact food abundance for both insectivorous species, as reported in other environments (Dennis 2003; Stanton et al., 2018). We also found an association between the abundance of some arthropods and breeding habitat selection and breeding success of both, as is also found in other passerines (Martin 1995).

We found the highest food abundance for flycatchers at the reserve, with a higher total arthropod abundance at the reserve than at one of the ranches (Los Álamos Ranch), but the reserve did not differ relative to the other ranch (Giuliani Ranch) and both ranches did not differ from each other. Hymenopterans, which were positively selected by both bird species, were less abundant in the reserve than in both private rangelands and their abundance was positively related with date and study year, whereas abundance of hemipterans showed a totally opposite pattern. Coleopterans and orthopterans did not differ among sites. This suggests that prey abundance of both bird species varies according to arthropod composition and at least partially between sites with and without cattle ranching.

That livestock affect the arthropod community, specifically their distribution and abundance, is a pattern that has also been reported in other rangelands across habitats and biomes (Dennis 2003; Stanton et al., 2018). It is not clear what mechanisms mediate the influence of livestock on the arthropod community, but they are most likely indirect effects through modifications in plant composition and structure (Siemann et al., 1999; Dennis 2003). Indeed, in a previous study, we found that habitat features differed among the three study areas addressed in this study, where for example the reserve had greater woody plant richness and percent cover of shrubs and saplings than both ranches (Rebollo et al., 2020). Nevertheless, the responses of different arthropods and birds to livestock activity is likely related to species-specific characteristics such as feeding behaviour, trophic level, life history, size and mobility (Dennis 2003). So, further research would allow further insights into the positive, negative or neutral impacts of livestock practices, ways to improve them to mitigate impacts on focal species and ultimately achieve sustainable land use practices in the Espinal.

We found that the diet of VEFL and FTFL during their breeding season consisted mainly of hymenopterans, coleopterans, hemipterans, orthopterans, and dipterans, which is consistent with some previous

studies (de la Peña and Salvador 2010; Ellison et al., 2020; Jahn and Tuero 2020). Both flycatchers consume similar prey, irrespective of their age, although some insectivorous passerines show a difference in diet according to age, since nestlings require food to fuel accelerated growth (Wiesenborn and Heydon 2007; Durst et al., 2008). Male and female VEFL consume similar prey, as in Southwestern Willow Flycatcher (*Empidonax traillii extimus*; Wiesenborn and Heydon 2007; Durst et al., 2008). However, because different prey offer different nutrients (Bairlein 1990; Carey 1996), further studies are necessary to understand if there are sex or age differences in diet using alternative techniques; for example, stomach flushing is more accurate than fecal analysis to analyze diet at lower taxonomic levels, such as family or species. Alternative methods may also help to overcome a potential drawback of our approach, since differential fragmentation and digestibility of prey items may affect its description using fecal analysis (Rosenberg and Cooper 1990).

We found a strong positive selection for hymenopterans and coleopterans by both flycatchers, and also for orthopterans in the case of FTFL. In contrast, both species consumed hemipterans according to their abundance. VEFL consumed more hymenopterans and less coleopterans and hemipterans and FTFL consumed less hemipterans at the end of breeding season, even as they became more abundant. Nutritional requirements of both flycatchers, provided by different kinds of prey, may thus vary across their breeding season, as has been found in other insectivores, whose nestlings consume different insect orders as they grow (Mitrus et al., 2010). In addition, prey size varied approximately from 2 mm to 7 cm and may provide differential prey biomass, which was not evaluated in our study. This may also help explain food selection of VEFL and FTFL in central Argentina, as proposed for other insectivorous passerines (Marchetti et al., 1998; Wiesenborn and Heydon 2007). Finally, the fact that FTFL is considerably bigger than VEFL (Ellison et al., 2020; Jahn and Tuero 2020) may make orthopterans, which are usually relatively large prey items, a more suitable prey for the former.

Heteropteran abundance negatively explained nest site selection of VEFL, while coleopteran abundance positively explained FTFL nest site selection, although only weakly in both cases. VEFL selected nest sites with low heteropteran abundance, the kind of prey that they consume according to their abundance. Note, however, that coleopterans showed low abundance, in sixth place after other taxa in terms of frequency. So, both bird species weakly selected habitats to nest in according to prey abundance, as is found in other bird species (Martin 1995). Nevertheless, nest site selection of both flycatchers is likely additionally influenced by factors not evaluated in this study (e.g., food abundance according to biomass, predation, brood parasitism; Martin 1995; Larison et al., 1998; Rebollo et al., 2020).

That VEFL had lower nest survival at sites with a higher proportion of hemipterans may be because hemipterans are the most abundant group in our study site. Although VEFL consumed hemipterans in relation to their abundance, they selectively nested in sites with lower abundance of this group of arthropods. In comparison, FTFL showed higher nest survival when breeding at sites with a higher proportion of coleopterans, the second most common prey that they positively selected according to food and nest habitat. These patterns might be a consequence of different prey offering different nutrients and having different biomass (Bairlein 1990; Carey 1996; Marchetti et al., 1998; Wiesenborn and Heydon 2007), as mentioned previously, given that type and abundance of food is a limitation for breeding birds (Martin 1995). On the other hand, nest survival may be affected by traits not evaluated in our study, such as habitat characteristics (Rebollo et al., 2020), risk of predation (Martin 1995), brood parasitism (Rebolledo et al., 2003), and food availability (Boulton et al., 2008). We detected nest failure as a result of nest predation, brood parasitism and weather conditions, but we did not detect nest failure as a result of starvation, so in the future it will be necessary to quantify each cause of nest failure to understand how each is affected by food abundance and parental foraging behaviour. Thus, we cannot exclude the possibility that range management also affected

predator or brood parasite abundances, subsequently affecting nest survival.

We conclude that cattle ranching has the potential to impact food abundance of two Neotropical austral migrants and that abundance of some arthropod prey types may influence their breeding habitat selection and breeding success. These findings contribute to fill gaps on the general ecology of and threats to Neotropical austral migrants (Faaborg et al., 2010; Jahn et al., 2020), particularly in the context of current declines of insects and migratory and insectivorous birds around the world (Wilcove and Wikelski 2008; Nebel et al., 2010; Lister and Garcia 2018; Bowler et al., 2019). Although the two studied species are classified as “least concern” (BirdLife International 2021), they breed in environments under substantial pressure from human activities, such as the Espinal (Brown et al., 2006; Distel 2016). We call for similar studies with a greater number of sites and across years and seasons, which will allow a deeper understanding of whether the selection pressures evaluated here are impacted by cattle ranching and how protected areas can preserve the biodiversity of this biome. Finally, we call for further studies on Neotropical austral migrants and other bird species that are affected by increasing impacts of human activities in central Argentina (Brown et al., 2006; Distel 2016).

CRedit authorship contribution statement

María Emilia Rebollo: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Alex E. Jahn:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **César Adrián Stella:** Conceptualization, Methodology, Investigation, Resources. **Lorenzo Pérez-Rodríguez:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Fernando Gabriel López:** Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **José Hernán Sarasola:** Conceptualization, Methodology, Resources, Writing – original draft. **Joaquín Cereghetti:** Conceptualization, Investigation, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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