Demography of the Neotropical austral migrant *Elaenia albiceps chilensis* (Tyrannidae) on its breeding grounds: climate and food offer effects

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ABSTRACT: The White-crested Elaenia (*Elaenia albiceps chilensis*) is a Neotropical austral migrant that breeds in Patagonian forests and overwinter in South America tropics. We investigated White-crested Elaenia demography and the environmental conditions the specie is subjected at the northwest of Patagonia as a first attempt to elucidate its population dynamic. We studied the species abundance, individuals' body condition, survival, productivity of young and site fidelity according to changes in rainfall patterns and food supply, during three breeding seasons (2009 to 2012). We color banded 361 adult and juvenile White-crested Elaenias. During the first studied season, precipitations were remarkably above the mean and ripe fruit supply was lower than in the other seasons, whereas the abundance of arthropods remained similar along the study. The species abundance decreased 50% across the study, while adult apparent survival rate, the number of breeding females, young productivity and site fidelity were 50% lower in the first season in comparison to the following seasons. Females presented lower body condition at arrival in the first two studied periods. Site fidelity diminished after unfavorable breeding season (*i.e.* low young productivity and fruit supply), especially for males, although they were more faithful than females and had a slightly higher apparent survival rate. Our results suggest that White-crested Elaenia demography is affected by changes in its main food resource supply (fleshy fruits) during the breeding season, indicating that this part of the annual cycle could be fundamental for its population dynamic.

KEY-WORDS: body condition, breeding season, frugivory, Patagonian forest, population dynamic, site fidelity, survival, White-crested Elaenia.

INTRODUCTION

The study of demography and the factors that regulate populations are among the most important approaches to understand population trends. Birds demographic (abundance, survival and reproductive success) and behavioral features (site fidelity, space use and dispersal) are regulated by both intrinsic and extrinsic factors (*e.g.* physical and nutritional traits of individuals and food or weather variations, respectively; Martin 1996, Newton 1998). These factors interact with each other in positive and negative ways, and their implications in a population are expected to vary according to the species life history (Newton 1998).

Among demographic features, differences in life history between North and South Hemisphere birds suggest that Southern hemisphere species have lower reproductive success (as indicated by smaller clutch sizes, higher nest predation rates, more nesting attempts and

greater parental care) that is compensated with higher adult survival (see review in Martin 1996 & Russell *et al.* 2004). Throughout South America information is contrasting, with some studies indicating a higher adult survival from tropical to temperate latitudes (Martin 1996) and others pointing to a lack of such trend (Karr *et al.* 1990, França & Marini 2010), or even to variations among phylogeny and regions for tropical birds (Blake & Loiselle 2013). Although this trend has been mainly suggested for resident species, it also applies to species that perform regional or long distance migrations (Martin 1996, Russell *et al.* 2004, Blake & Loiselle 2013).

Among behavioral features site fidelity is one that can be affected by species life history as well as by environmental quality, conditioning migratory birds' abundance (Holmes & Sherry 1992). Site fidelity will be favorable if the area allows individuals to pair a previous successful partner or be more competitive because of prior territory ownership, as well as if they are able to

identify the distribution and availability of resources as food, refugees or nestling sites (Newton 2008). Contrary, site fidelity will be disadvantageous for migrants if the site diminishes in quality or represents an unpredictable habitat (Switzer 1993). In addition, site fidelity can differ according to sex, age and competitive condition, generating differences in dispersal and habitat use patterns (Latta & Faaborg 2002).

Environmental factors are relevant causes of demographic variation in resident and migratory bird populations. Food limitation can be a fundamental factor affecting body condition and, consequently, breeding success and survival (Martin 1987). Factors such as precipitation, habitat quality and resource spatial distribution, will affect food abundance and availability, affecting differently the population (Wilson *et al.* 2011). The effects of those environmental factors on the population can be quantified by measuring different external variables that indicates habitat quality (Benson & Bednarz 2010) as well as estimating the individuals' body condition by their body mass or fat deposits (Labocha & Hayes 2012). On the other hand, unusual weather conditions, sometimes related with periodic climatic events, affect the sizes of bird populations (Sillett *et al.* 2000). Some studies suggest that southern temperate birds' survival either is reduced after periods with unusual precipitation, rainy (Thomson & Estades 2012) or dry (Sagario 2010). Therefore, it is expected that climate variations also affect migratory birds' demography at southern South America.

All these theories about the factors controlling population dynamics remain slightly evaluated in passerine birds of South America, been mainly studied in tropical species (Karr *et al.* 1990, Martin *et al.* 2000, Parker *et al.* 2006, Blake & Loiselle 2013). Thus, there is still little information for temperate latitudes of South America and migratory birds of the Neotropical austral system, despite some advances for different passerine families in survival (Willson & Pendleton 2008, Sagario 2010, Thomson & Estades 2012), site fidelity (Jahn *et al.* 2009) and life history traits (*e.g.* parental care, Llambías *et al.* 2015).

The White-crested Elaenia (*Elaenia albiceps chilensis*) is the most abundant Neotropical austral migrant passerine at the Patagonian forest (Grigera *et al.* 1994, Ippi *et al.* 2009). This tyrant flycatcher arrives up to mid-October to breed and start its migration to the tropics between mid-February and March (Fitzpatrick 2004, Bravo *et al.* 2017). It is a frugivorous-insectivorous species with an important role as the main disperser of seed of endemic plants of the Patagonian forest (Armesto *et al.* 1987, Amico & Aizen 2005) and as a controller of herbivorous insects of *Nothofagus* trees (Mazia *et al.* 2009). There are studies of White-crested Elaenia

abundance (Brown *et al.* 2007), diet (Grigera 1982, Brown *et al.* 2007), foraging behavior (Chust *et al.* 2012, Cueto *et al.* 2016a), functional role (Mazia *et al.* 2009, Cavallero *et al.* 2013, Bravo *et al.* 2015), and migration routes (Marini & Cavalcanti 1990, Capllonch *et al.* 2011, Cueto *et al.* 2016b, Bravo *et al.* 2017), but its survival has never been studied, as well as the relationship between its demographic parameters with environmental factors.

The aim of our study was to analyze the demography of the White-crested Elaenia through the analysis of changes in abundance, productivity of young, survival, site fidelity and body condition, related with food offer and precipitation variability during the breeding season. We aim to improve our knowledge about the factors affecting its population at temperate latitudes of South America.

METHODS

Study site

We conducted our study from October to March of three consecutive breeding seasons (2009/10, 2010/11 and 2011/12) in a Patagonian mixed forest of *Nothofagus dombeyi* (Coihue) and *Austrocedrus chilensis* (Ciprés de la Cordillera) at Steffen Lake (41°30'S; 71°35'W, 550 m a.s.l). This is a representative and well protected area of the temperate forest of southern South America inside Nahuel Huapi National Park, at the northwest of Argentinean Patagonia (Mermoz *et al.* 2009). At the study site, the forest is characterized by a canopy above 20 m of height and an understory (< 10 m) with fleshy fruit shrubs, mainly *Aristotelia chilensis* (Maqui) and *Schinus patagonicus* (Laura).

The climate is cold-temperate with precipitations concentrated in autumn and winter (April–September). Annual mean precipitation in the study area is 1264 mm (for 1993–2012 period) and annual mean temperature is 9.1°C (for 2000–2012 period), with a maximum mean temperature of 15°C (January) and a minimum of 3.5°C (July) (data from Station N° 2300 "Lago Steffen", *Red Hidrológica Nacional, Subsecretaría de Recursos Hídricos de la Nación*).

We established two permanent plots on the northern margin of the lake, separated 1000 m by a small bay. The plots area were 4 ha (Plot 1) and 7 ha (Plot 2) and we gridded them in 25 x 25 m squares, for bird and food resource surveys (68 squares for P1 and 109 squares for P2). Both plots had the same vegetation composition and structure, representing a well-preserved mixed forest with three types of patches: open areas, young forest and old forest (see Bravo *et al.* 2015), therefore we pooled the data for the analysis.

Bird surveys

Scientific nomenclature and common name follow the recommendation by the South American Checklist Committee (Remsen-Jr. *et al.* 2018). To get demographic data of the White-crested Elaenia we used capture-mark-recapture method. We captured birds using 24 mist nets of 12 m × 3 m, 38 mm mesh size (12 per plot). Nets were distributed along the area separated at least 50 m from each other, arranged in fixed places at every capture session to register the mist net of every captured and recaptured bird in order to study site fidelity. During every breeding season, nets were opened for two consecutive days per month in both plots (in similar month dates along every session), since sunrise and for at least five hours.

Every captured bird was banded with numbered aluminum and a unique combination of color bands. We weighted birds to the nearest 0.1 g with a 30 g spring scale in every capture occasion and measured their tarsus length to estimate their arrival and departure body condition (details below). We aged individuals by the presence (adult) or lack (juvenile) of the characteristic white crown (Schulenberg 2009). To determine the sex and reproductive status of birds, we registered the development of the incubation patch (females) and cloacal protuberance (males) following Ralph *et al.* (1993), and used the differences in wing and tail length between females and males for sexing non-breeding birds following Cueto *et al.* (2015). When an individual did not match with those criteria of sexing it was classified as "unsexed adult".

From November to February, after net sampling, we surveyed each plot to relocate those banded birds that remained at the study site to complete their capture history for survival and site fidelity estimates. Searches were carried out systematically by walking through the study area during five hours after sunrise and three hours before sunset, at least once per day for a mean of 10 days or until no new banded birds were seen after searching for 10 h. We registered the identity of each banded bird found and its location on the grid. The position of every relocated bird was recorded estimating the distance and angle respecting a reference point of the grid, using a compass. We also recorded eventual encounters while collecting environmental data.

Arthropods and fruit abundance

Arthropod abundance was estimated using blue sticky traps (Young 2005). We used blue because it is neutral in terms of attracting or repelling insects (Ausden & Drake 2006). Each trap was of 10 × 20 cm, attached inside a plastic transparent cylinder of 15 cm diameter to prevent that leaves, branches and rain affect its capture efficiency. We used 28 blue sticky traps (14 per plot) that were randomly placed, tided horizontally on an exposed branch of a shrub or tree, two meters above the ground, operated for an average of 15 days per month depending on weather conditions. After the survey, we counted the number of captured individuals at each trap.

We evaluated fruit production of *Aristotelia chilensis* (Elaeocarpaceae), the main fleshy-fruited shrub consumed by White-crested Elaenia at the study site (Bravo *et al.* 2015). We randomly selected 10 individuals in each plot and counted the number of ripe fruits every 15 days from November to March. We used a semi-quantitative index from 0 to 5 (Saracco *et al.* 2004), where 0: no fruits, 1: 1–10 fruits, 2: 11–50 fruits, 3: 51–100 fruits, 4: 101–500 fruits, and 5: 501–1000 fruits.

Precipitation patterns

To assess the potential effect of climate on the White-crested Elaenia's demography and their food abundance, we analyzed the variations on precipitation at the study site. Precipitation data were available from the weather station N° 2300 - "Lago Steffen" (*Red Hidrológica Nacional, Subsecretaría de Recursos Hídricos de la Nación*), for the period 1993–2012. We considered wet or dry months to be those with monthly rainfall above or below one standard deviation of the average monthly rainfall for a 20-years period of climatic data (Ropelewski & Folland 2000).

Data analysis

Bird abundance and productivity of young: In order to compare bird abundance among breeding seasons, we calculated the season capture rate for each bird category (female and male in breeding and non-breeding conditions; and juveniles) as the total number of captures per 100 h of net effort. We used the data from November to February, and excluded from the analysis birds captured in October and March that did not remain in the study site in the summer (*i.e.* those individuals that were just passing through). Juveniles capture rate in every season was used as a measure of productivity of young (du Feu & McMeeking 1991).

Relative body condition: We generated an index of body condition using the residuals of the linear regression between every bird tarsus length and their body mass (Labocha & Hayes 2012). Positive residuals indicated that birds were in relatively good condition, *i.e.* they were heavy for their size, and negative residuals indicated relatively poorer condition. We used a two-way ANOVA to examine the differences of body condition between breeding seasons, arrival from spring migration (October–November) and departure from the breeding study site (February–March) of females and males. Given the unequal sample sizes, we used Type III method to

compute the sum of squares (Shaw & Mitchell-Olds 1993). Comparisons of treatments after ANOVA were performed using the Kramer modification of Tukey's test (Day & Quinn 1989) using the free software InfoStat (2014).

Survival: We estimated apparent annual survival rate between two breeding season intervals (2009/10 to 2010/11 and 2010/11 to 2011/12) as the probability of an individual survive and return to the same breeding area. This is an approximation of the real survival rate, because it does not account for permanent or temporal emigration (Lebreton *et al.* 1992). We used captures, recaptures and relocation data of 269 birds, considering only adult birds as we never recaptured or relocated any marked juvenile. We excluded from the analysis the individuals that were captured just once and were not relocated during the season (*i.e.*, likely transient individuals). We fitted Cormack-Jolly-Seber (CJS) mark-recapture models to assess apparent annual survival rate and capture probability (Lebreton *et al.* 1992). We confirmed models goodness-of-fit and lack of over-dispersion using the median $\hat{c}$ procedure (Burnham & Anderson 2002). We modeled apparent survival probability (φ) as constant, varying in time (years) and between sexes, and examined the influence of these two covariates together, as additive and interactive effects. We considered capture-recapture-relocation probability (p) constant in time and equal among sexes. We based our decision on sampling effort as we systematically sampled the plots with mist nets and active search since the arrival of the birds till their departure, compensating possible differences in detection caused by changes in females and males behavior during their breeding period (as incubation and territorial defense). The relative importance of each model was compared using: Akaike›s Information Criterion adjusted for small sample size (AICc), the difference of AICc between models (ΔAICc), their weights (wi) and deviance (Burnham & Anderson 2002). Models with a ΔAICc < 2 of the top model were considered to have equal support, so we model-averaged survival estimates (Burnham & Anderson 2002). Model averaging generated an annual mean apparent survival rate for each sex and breeding period, with their standard errors and confidence intervals. We performed this analysis in R (version 3.1.1 2014, The R Foundation for Statistical Computing) using the RMark package (version 2.1.8; Laake & Rexstad 2008) that provides an interface to the software MARK (version 7.2; White & Burnham 1999).

Site fidelity: We analyzed it as the percentage of adult birds banded in a previous field season that were recaptured or relocated in a subsequent field season. We compared the differences in annual return rates between breeding seasons (2009/10 to 2010/11 *vs.* 2010/11 to 2011/12)

for all returning White-crested Elaenias individuals and by sexes, through a difference of proportions test (Agresti 2002). We used a Bonferroni correction to adjust α when more than one test was performed on related data. We considered the data from November to March for the analysis and used the free software InfoStat (2014).

We estimated the displacement distance between the first capture and the first recapture or relocation of individuals in every breeding season. For this, the position of the mist nets and relocation position of every bird were georeferenced in a metric coordinate system, using the free software Quantum Gis 1.8.0-Lisboa (QGIS Development Team, 2012). We performed a T test (Agresti 2002) to compare the displacement distance between sexes and between returning periods: 2009/10 to 2010/11 versus 2010/11 to 2011/12, and 2009/10 to 2010/11 versus 2009/10 to 2011/12 displacement.
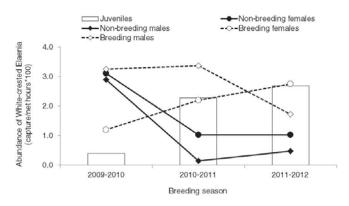
Arthropods and fruit variations: Abundance of arthropods was assessed by calculating a relative abundance index per trap (*RAI* = number of caught individuals / number of trapping days) and then estimated the average of all traps for the season. We evaluated differences in arthropod abundance among seasons by using one factor Analysis of Variance with Repeated Measures (Winer 1971), because we counted arthropods in the same points at every season. We used the Tukey multiple comparison test for comparing means when season factor was significant (Winer 1971). We tested equality and symmetry of covariance matrices (Winer 1971). Data violated the symmetry assumption, so we used the Greenhouse-Geiser procedure (Lower Bound Epsilon correction = 0.5) to adjust the degrees of freedom of within-subject effects (Winer 1971). For ripe fruit offer, we calculated the proportion of individuals that offered no ripe fruits (index 0), less than 50 ripe fruits (indexes 1 and 2), and those that offered more than 50 ripe fruits (indexes 3 to 5). For each category, we evaluated the difference in abundance of ripe fruit between seasons using a test for difference of proportions (Zar 2010). ANOVAs, the Tukey comparisons and all assumption tests were performed on the free software InfoStat (2014).

RESULTS

Bird abundance and productivity of young: We banded 361 adult and juvenile White-crested Elaenias and recaptured 44 individuals during 5394 mist netting hours (Table 1). Complementary we relocated 25 adults that were not recaptured in nets but detected by active search. We did not recapture or relocate any marked juvenile after its hatching year. Male capture during October-November represented 69% of all captures. The latest captured individuals towards the end of the breeding

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season (March) were mainly juveniles. Captures of new individuals decreased almost 50% between the first and last studied seasons (Table 1). During 2009/10 we registered the lowest percentage of breeding females (28%) and the lowest productivity of young, while for the following seasons the percentage of breeding females exceeded that of non-breeders (68% for 2010/11 and 73% for 2011/12) and the productivity of young increased (Fig. 1).

Relative body condition: White-crested Elaenias arrived in relatively good condition only during the 2011/12 breeding season ($F_{2,169}$ = 3.42, P < 0.001; Fig. 2A), presenting the lowest condition during 2009/10, especially females. The condition for the departure period did not present a statistical different variation between breeding seasons ($F_{2,66}$ = 1.72, P = 0.187; Fig. 2B) or sexes ($F_{1,169}$ = 21.58, P = 0.060).

Survival: The best fitted model indicated a variation in apparent annual survival rate between breeding seasons, being 50% lower for 2009/10–2010/11 interval in relation to 2010/11–2011/12 (0.41 ± 0.07 *vs.* 0.80 ± 0.15). Models that considered survival vary among seasons and sexes had a great support following AICc and

ΔAICc criterion (Table 2). Results from model averaging revealed that the mean apparent annual survival rate was equally low for females and males for the first interval but males tended to increase its survival more than females towards the following breeding season (Table 3).

Site fidelity: From 231 banded and sexed adult White-crested Elaenias, 69 individuals returned the following breeding seasons. Within those faithful birds, 14 individuals returned all the studied seasons and 12 skipped from the first season (2009/10) to the third (2011/12), not being recapture or relocated during the second season (2010/11). Annual return rate varied significantly between breeding seasons, being higher for 2010/11 to 2011/12 period (Zc = -0.13, P = 0.028) in

Figure 1. Abundance by sex reproductive status and juvenile productivity of the migratory White-crested Elaenia along three breeding seasons, at Nahuel Huapi National Park, Patagonia, Argentina. *Total adults*, includes all captured individuals with more than one year old (*i.e.* breeding and non-breeding individuals). *Breeding birds* were defined by the presence of developed incubation patch (female) and cloacal protuberance (male) and *Juveniles* by the lack of the white crown.

Figure 2. Body condition variation of the migratory White-crested Elaenia females and males, during: **a**) arrivals and **b**) departures in three breeding seasons, at Nahuel Huapi National Park, Patagonia, Argentina. Boxes represent the mean condition in every period (± SE - Standard Error). Condition was derived as the residuals of a linear regression between body mass and tarsus length. Positive residuals indicate better condition. Asterisk indicates the statistically different season.

Table 1. Captures and recaptures of the migratory White-crested Elaenia by sex and age, in three breeding seasons (October to March) at Nahuel Huapi National Park, Patagonia, Argentina. Individuals that did not match with the criteria of sexing were left as "unsexed adults".

Breeding seasons	Total banded birds	Females	Males	Juveniles	Unsexed adults	Total captures and recaptures
2009–2010	152	61	85	3	3	152
2010–2011	136	55	68	27	4	154
2011–2012	73	46	33	23	2	104
Total	361	162	186	53	9	410

Table 2. Models results for the apparent annual survival rate (φ) and recapture (p) probability of the migratory White-crested Elaenia in three breeding seasons at Nahuel Huapi National Park, Patagonia, Argentina (*n* = 269). Models are arranged by Akaike's Information Criterion adjusted for sample size (AICc). (.) Parameter is constant; k: number of parameters; wi: model weight.

Model	*k*	AICc	ΔAICc	w_i	Deviance
φ (time) p (.)	3	373.38	0.00	0.49	4.75
φ (time * sex) p (.)	5	374.54	1.16	0.27	1.77
φ (time + sex) p (.)	4	374.86	1.48	0.23	4.17
φ (.) p (.)	2	382.42	9.04	0.01	15.84
φ (sex) p (.)	3	383.60	10.22	0.00	14.97

Table 3. Apparent annual survival rate and capture probability estimates (measured as capture, recapture and relocation) for the migratory White-crested Elaenia in three breeding seasons at Nahuel Huapi National Park, Patagonia, Argentina. Estimates correspond to model averaging of the best-fitted models that indicated that survival varied by time and sex-class.

Parameter	Breeding seasons interval	Sex	Estimate	SE	95% Confidence Interval	
					lcl	ucl
Survival (φ)	2009–2010 to 2010–2011	Female	0.40	0.09	0.25	0.58
		Male	0.41	0.08	0.28	0.56
	2010–2011 to 2011–2012	Female	0.74	0.17	0.34	0.94
		Male	0.84	0.17	0.30	0.98
Capture probability (p)	Constant in time	-	0.49	0.09	0.32	0.66

relation to the first interval (Table 4). Considering the birds that returned across the entire study and those that skipped the second studied season, site fidelity of 2011/12 season increased from 33% to 49% (54 individuals), increasing the above-mentioned difference with the first interval. Fidelity did not vary significantly between sexes (*Zc* = -0.11, *P* = 0.084), but males tended to return in greater proportion than females towards 2011/12 (Table 4).
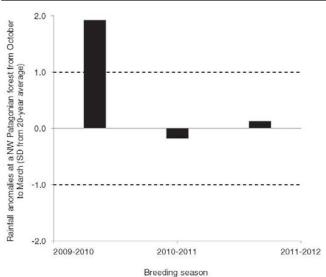
With respect to territory fidelity, only three males moved between plots along the study, less than 1500 m. The mean displacement between seasons was: 94 ± 100 m for 2009/10 to 2010/11 seasons, 85 ± 71 m between 2010/11 to 2011/12 , and 102 ± 84 m for birds that were banded in 2009/10 and only relocated in 2011/12. There were no significant differences between the mean displacement of the first and second period (*t* = 0.42, *P* = 0.676), neither between the first and the third (*t* = -0.29,

P = 0.772). Females tended to displace more than males when they returned (*n* = 30, 118 m ± 86 m *vs.* *n* = 54, 76 ± 78 m on average, respectively. *t* = 2.25, *P* = 0.027).

Precipitation variability: The first study year was an unusual rainy year, with an important input during the October–March period (638 mm) that was almost two standard deviations above the historical record (371 mm). At the following breeding seasons, precipitation was close to average (347 and 390 mm, respectively; Fig. 3).
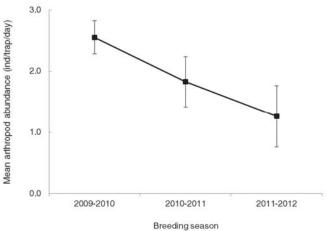
Arthropods and fruit offer. Arthropod abundance was similar among seasons ($F_{2, 27}$ = 3.027; *P* = 0.093; Fig. 4) but ripe fruit production varied notably between seasons. The proportion of plants without ripe fruits was higher in the first study season than the two following breeding seasons (Fig. 5, test for more than two proportions, *Zc* = 22.86, *P* = 0.003), while plants with more than 50 ripe fruits were higher in the second and third seasons (*Zc* = 6.94, *P* = 0.031; Fig. 5).

Table 4. Site fidelity (annual return rate) of the migratory White-crested Elaenia in three breeding seasons at Nahuel Huapi National Park, Patagonia, Argentina. Estimation is presented as the percentage and number of adult birds that returned from a previous banding season, by sex-class and for the complete studied population. Total estimation includes birds captured at 2009/10 that returned at 2011/12, not being recaptured or relocated during 2010/11. Returns include both recaptures in nets and relocations of color-banded individuals.
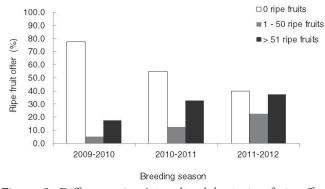
Banding and returning seasons	Returning individuals		
	All	Females	Males
2009/2010 to 2010/2011	20% (29)	20% (12)	20% (17)
2010/2011 to 2011/2012	33% (28)	19% (9)	50% (19)
Total	30% (69)	24% (26)	35% (43)

Figure 3. Rainfall anomalies during three breeding seasons of the migratory White-crested Elaenia at Steffen Lake, Nahuel Huapi National Park, Patagonia, Argentina. Values are expressed in standard deviations from an average climatic data of a 20-year period. Wet and dry years were those with annual rainfall respectively above and below one standard deviation (dashed lines) from the mean.

Figure 4. Variation in arthropods abundance between three breeding seasons of the migratory White-crested Elaenia, at Nahuel Huapi National Park, Patagonia, Argentina. Values represent the mean arthropods abundance index (number of individuals captured per sticky trap per survey days, ± SE - Standard Error) for every season.

Figure 5. Differences in *Aristotelia chilensis* ripe fruit offer between three breeding seasons of the migratory White-crested Elaenia, at Nahuel Huapi National Park, Patagonia, Argentina. The percentage of *Aristotelia chilensis* plants within every fruit offer score is shown for each season.

DISCUSSION

Our results suggest that the demography of migratory White-crested Elaenia is affected by environmental changes on its breeding grounds. The three seasons of our study had contrasting climatic conditions, with the first season having a remarkable increase in rainfall respecting the historical average for the study area. This climatic variation was reflected in changes in the supply of ripe fruits of *Aristotelia chilensis*, but not in the abundance of understory arthropods. The increase in rainfall during the first season resulted in few days of full sun, likely leading to the inability of *Aristotelia chilensis* shrubs to produce ripe fruits, a relationship widely documented for others species (Aalders *et al.* 1969, Patten & Proebsting 1986, Spayd *et al.* 2002). During that first season a lower proportion of females became reproductive (28%), which was reflected in a low productivity of young. Besides, birds' relative body condition tended to be lower than the following seasons and both survival and site fidelity diminished by 50% after that period.

Previous studies have shown the impact of food limitation in reproductive status and success of resident and migratory birds, as birds adapt their reproductive cycle according to food availability (Martin 1987, Sherry & Holmes 1995, Marshall *et al.* 2002, Jahn *et al.* 2014). For example, females of *Parus major* are able to modify their laying date so it coincides with periods of higher caterpillar abundance (their main food item) and higher temperatures, promoting nesting success (van Noordwijk *et al.* 1995). With respect to the influence of arthropods supply on White-crested Elaenias demography, we found that slightly variations in foliage arthropods abundance did not affect bird's reproductive status and productivity of young, neither body condition or survival. Similar results were reported for Nearctic-Neotropical migrants (*Vireo olivaceus*, Marshall *et al.* 2002, and *Seiurus aurocapilla*, Vernouillet *et al.* 2014) and for White-crested Elaenias breeding at central Chile (González *et al.* 2004). Consistent with Cueto *et al.* (2016a) that found changes in the species foraging behaviour related with fruit offer variations at the same study site, we conclude that fruit is the main food resource affecting White-crested Elaenia reproductive success and demography during the breeding period. Our work represents a primary approximation of the effect of food limitation in White-crested Elaenia demography and reinforces the importance of more detailed study for a complete understanding of the role of food resources on the species population dynamic.

Decrease in new individuals capture rate along our study years could be considered as an indirect measure of low immigration rate, caused by a poor influx of new birds to the population (Newton 1998). This could be due to events of lower reproductive success (as in the first studied season), or higher mortality during the non-breeding period. As White-crested Elaenia present high migratory connectivity between their non-breeding and breeding areas (Bravo *et al.* 2017), the decrease in their captured rate could also be related with environmental variations at their wintering sites on the Brazilian Cerrado and Atlantic Forest (for example, see Wilson *et al.* 2011).

Our study represents the first survival estimation for a Neotropical austral migrant species and revealed that survival varied across seasons. For Nearctic-Neotropical migrants breeding at temperate latitudes of North America and wintering in the tropics, the temporal variation in survival has been attributed to weather anomalies across the areas used by birds along their life cycle (Mazerolle *et al.* 2005), as they promote decreases in food availability diminishing survival and productivity of young (Sillett *et al.* 2000, Mazerolle *et al.* 2005). Our results are consistent with those studies, as survival of White-crested Elaenia decreased after years with rainfall anomalies that affected ripe fruit supply. Unfortunately, there are not similar studies at the species wintering sites that allows linking the entire annual cycle survival process. Nevertheless,

recent studies revealed White-crested Elaenias returns to their wintering areas in the Brazilian Cerrado and Atlantic Forest by routes with different habitat structure and refueling opportunities (Bravo *et al.* 2017), indicating that a good body condition at departure could be fundamental to survive the journey between breeding and wintering sites. According to that, the poor relative body condition of birds during arrival and departure of the first season could enhance birds' mortality during autumn migration, diminishing survival values between breeding seasons. This relationship between rainy breeding seasons with the reduction in the species departure body condition has also been reported by previous studies (González *et al.* 2004). Our results reinforce the need of demographic studies across the entire annual cycle to improve our knowledge of White-crested Elaenia population dynamic.

In addition, our mean apparent annual survival estimate (60%) is higher than the mean reported for other migratory Flycatchers of comparable size and behavior, breeding at temperate North America (50%; Karr *et al.* 1990, Koronkiewicz *et al.* 2006) but similar to tropical resident flycatchers (Johnston *et al.* 1997, França & Marini 2010, Blake & Loiselle 2013). Our results reinforce the hypothesis of higher survivorship of southern hemisphere tropical and temperate birds respecting to northern hemisphere ones (Martin 1996). Nevertheless, this trend requires more research including the hypothesis of reproduction cost, nest predation rate and adult mortality, that have been mainly verified for North American and tropical birds (Martin *et al.* 2000, Martin 2015).

Regarding migratory behavior, the higher capture rate of White-crested Elaenia males comparing to females at the beginning of the breeding season suggest that males could be arriving earlier, a behavior that is expected in territorial birds as a manner of territory acquisition (Kokko *et al.* 2006). The later departure of juveniles than of adults was also reported in studies at the austral extreme distribution of the species (Brown *et al.* 2007), and is usual in immature birds without prior migration experience (Whitaker & Warkentin 2010). Concerning site fidelity, comparisons between seasons showed a tendency for greater dispersal after breeding periods with low reproductive success, suggesting that White-crested Elaenias could be more predisposed to relocate after seasons with low productivity, as were reported for Nearctic-Neotropical migrants (Haas 1998).

On the other hand, our results of site fidelity are higher than previous studies that just considered recaptured birds on its estimations reporting returning rates only up to 11% (*e.g.* Espinosa & Egli 1997, Amico & Aizen 2005, Brown *et al.* 2007), even in long term studies (Rozzi & Jiménez 2013). Include data of relocations prevent underestimations of returning rates and improves apparent annual survival estimation (Martin *et al.* 2017).

However, if we considered only recaptured birds our result of site fidelity remains higher for Steffen's Lake (19% at 41°S) comparing to the estimation of a long term study at the species austral distribution in Navarino Island (10% at 56°S). The lower faithfulness at Navarino could respond to its habitability conditions, as summer precipitations and temperatures are lower than our study area, the vegetation structure varies widely in short distances and the main fruit item consumed by elaenias (*Drymis winteri* fruits) are available in autumn during their departure (Rozzi & Jiménez 2013). These factors could be promoting higher replacement rates of birds breeding at that higher latitude, indicating that Navarino Island could be a marginal habitat for the species.

Conclusions and future perspectives

Previous studies have emphasized the importance for species with low reproductive success to compensate this demographic feature with higher adult and juvenile survival (Martin 1996, Stahl & Oli 2006). However, migratory individuals face variable conditions along their life cycle that will impact on their survival indicating that there must be other mechanisms acting in their demographic dynamics. White-crested Elaenia has a diet and foraging behavior plasticity that allows them to adapt their food consumption to what is available according to the environment and rainfall variations, all along their geographical distribution (Johnson 1967, Grigera 1982, Celis-Diez 2002, Cueto *et al.* 2016a). Therefore, the compensation to a low productivity of young with a higher survival rate could be mediated by the White-crested Elaenia feeding plasticity, allowing the species to live in diverse and changing habitats.

Nevertheless and beyond the species plasticity, there is a connectivity between breeding and wintering areas as well as migratory routes (Bravo *et al.* 2017) that can force changes in the species demography, as those areas are being negatively affected by climatic change and human activities affecting the annual cycle of the birds. For example, the species' main wintering and stopover biomes (Atlantic Forest, Yungas and Cerrado, respectively) are highly threatened by deforestation for agricultural purposes (Malizia *et al.* 2012, Ferreira *et al.* 2014). Therefore to improve our knowledge of White-crested Elaenia population dynamic it is essential to promote long term studies that connect studies in demography, behavior, habitat use and food supply, with processes developed in wintering areas and throughout the routes the species uses during migration.

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