INTERANNUAL VARIATION IN FORAGING BEHAVIOR OF WHITE-CRESTED ELAENIA (*ELAENIA ALBICEPS CHILENSIS*) IN A NORTHERN PATAGONIAN FOREST

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ABSTRACT.—Avian foraging behavior may vary among years because of changes in the abundance and availability of prey. We therefore aimed to study the foraging behavior of White-crested Elaenia (*Elaenia albiceps chilensis*), a Neotropical austral migrant, in relation to interannual variation in its food resources in a mixed forest of Patagonia. During two summers of contrasting rainfall patterns, we recorded foraging maneuvers, substrate use, and use of forest microhabitat (plant species and heights) where birds capture their prey. We also evaluated the abundance of the main food items consumed by this species: ripe fruit and arthropods. The first year was very rainy, when we recorded a lower supply of ripe fruits than in the second year, whereas the abundance of arthropods was similar throughout the study. During both years, the most frequent behavior of White-crested Elaenia was searching for food items while perched, capturing them from foliage using gleaning and sally-hovering maneuvers. Nevertheless, this species notably modified the use of foraging microhabitat between years. During the first year, elaenias used the canopy of the forest and foraged mainly in *Nothofagus dombeyi* trees, whereas in the second year elaenias used the entire profile of vegetation height and increased prey capture in shrubs of *Aristotelia chilensis*. Our results demonstrate the behavioral flexibility of this Neotropical austral migrant species and highlight the importance of considering the spatio-temporal variation of resources when evaluate the foraging behavior of birds. *Received 11 September 2015. Accepted 27 February 2016.*

Key words: Argentina, behavioral flexibility, foraging behavior, frugivorous-insectivorous birds, microhabitat selection, , Neotropical Austral migrants.

Avian foraging behavior studies have greatly advanced our knowledge of how birds use the environment. Leaf arrangement on branches, leaf morphology, petiole length, and other aspects of foliage architecture influenced the ways that birds encounter and attack their prey and determine plant species selection for feeding (Robinson and Holmes 1984, Whelan 2001, Cueto and Lopez de Casenave 2002, Park et al. 2008). Moreover, these foraging patterns may vary seasonally and among years because of changes in the abundance and availability of prey (Holmes and Schultz 1988, Lovette and Holmes 1995, Murakami 2002, Newell et al. 2014). For example, interannual changes in the selection of plant species and substrates (Hejl and Verner 1990, Miles 1990, Unno 2002, Lopez de Casenave et al. 2008), and in the use of different attack maneuvers (Ford et al.1990, Szaro et al. 1990) are widely observed. These changes in bird foraging behavior associ-

ated with variations in food resources are determined by the behavioral flexibility of individuals (Greenberg 1990).

White-crested Elaenia (*Elaenia albiceps chilensis*) is the most abundant bird species during spring and summer in temperate forests of southern South America (Grigera et al. 1994, Ippi et al. 2009). This long distance migrant breeds in these forests, arriving in mid-October and remaining until late March, when it returns to the tropics to overwinter (Capllonch et al. 2011). White-crested Elaenia is a frugivorous-insectivorous species in Patagonian forests (Grigeria 1982), and has a functional role in the ecosystem as the major seed disperser for fleshy-fruited shrub species (Armesto et al. 1987, Amico and Aizen 2005). As a result, the species plays a principal role in forest regeneration (Cavallero et al. 2013, Bravo et al. 2015).

We studied the foraging behavior of the White-crested Elaenia in relation to interannual variation in its food resources in a mixed forest of *Nothofagus dombeyi* and *Austrocedrus chilensis*. Specifically, we ask whether the White-crested Elaenia changes its most frequently used maneuvers in years with different food abundances, and whether elaenias use different plant species or capture their prey at different heights in the forest.

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METHODS

Study Area.—Research was conducted during January and February 2010 and 2011 in a mixed forest of *Nothofagus dombeyi* and *Austrocedrus chilensis* (Mermoz et al. 2009) at the margins of Lake Steffen (41° 31′ S, 71° 35′ W), Nahuel Huapi National Park, northern Patagonia, Argentina. The vegetation of the area corresponds to the Subant-arctic Biogeographical Province (Cabrera and Willink 1980). The forest canopy is dominated by *Nothofagus dombeyi* and *Austrocedrus chilen-sis*, and the most representative understory species are *Aristotelia chilensis*, *Lomatia hirsuta, Schinus patagonicus* and *Berberis darwinii*.

The climate is cold-temperate, and precipitation is concentrated in autumn and winter (Apr–Sept). Annual mean precipitation in the region of Lake Steffen is 1274 mm (1993–2011, Nro. 2300 Station "Lago Steffen", Red Hidrológica Nacio-nal, Subsecretaría de Recursos Hídricos de la Nación). Annual mean temperature is 8.5 °C, with a maximum mean temperature of 16.2 °C (Jan) and a minimum of 2.2 °C (Jul) (2000–2010, Nro. 2300 Station "Lago Steffen", Red Hidrológica Nacio-nal, Subsecretaría de Recursos Hídricos de la Nación).

Bird Sampling.—Foraging behavior of elaenias was recorded in two plots of 6 ha and 4 ha, separated by 1000 m, and occupying deltas of the two biggest streams at the northern margin of Lake Steffen. Plots were divided into 25 × 25 m squares, each of which was sampled on foot at approximately the same time during every visit, depending on weather conditions, from 4 January to 26 February, in each year of the study. Birds were followed in the field and observed with binoculars as long as they remained in sight (usually well less than a minute, which was considered a foraging sequence, see below). When a bird was observed foraging, we recorded foraging maneuver, the substrate from which food was taken or towards which the attack was directed, height above the ground (to the nearest m), plant species, and when possible, prey taken. Following Remsen and Robinson (1990), bird foraging maneuvers were defined as: (1) gleaning: when a perched or walking bird took prey items from the surface of a nearby substrate; (2) sally-hovering: when a flying bird took prey items from the surface of a substrate; and (3) sally-strike:

when a flying bird pursued aerial prey items. Substrate types considered were foliage (including leaves and twigs), branches, trunk, and air. We considered the following categories for foraging height: 0.5–2.0 m, 2.1–5 m, 5.1–9 m and >9 m, following Chust et al. (2012), and we considered the following plant species: *Nothofagus dombeyi*, *Austrocedrus chilensis*, *Aristotelia chilensis*, and *Lomatia hirsuta*, because they are the most abundant plant species in the two plots (Bravo et al. 2015), and >95% of our observations were on individuals of those species. *Nothofagus dombeyi* and *Austrocedrus chilensis* are canopy trees that can reach >20 m high. *Lomatia hirsuta* is an understory tree <10 m high. While, *Aristotelia chilensis* is a shrub that reaches no more than 5 m in height.

Consecutive observations of the same individual were taken into account, because they provide a more complete description of the behavioral repertoire of the species (e.g., Morse 1990) despite their statistical dependence (Hejl et al. 1990). In order to avoid the problem of data dependence, we followed the guidelines in Airola and Barrett (1985), considering each sequence of foraging observations of an individual (instead of single observations of foraging maneuvers) as a single datum when determining the frequency of use of feeding categories. When n consecutive observa-tions from the same individual were recorded, each observation contributed to the species' total frequency by a value of $1/n$, and all observations from the same individual contributed $\Sigma 1/n = 1$ to the species' frequencies (Airola and Barrett 1985). Using this procedure, we incorporated all of our observations into the analysis (thus diminishing the conspicuousness bias) without biasing the species' frequencies. Following the sample size recommendations of Morrison (1984), we record-ed >30 independent observations per year and per plot. Because we did not observe notable differ-ences in foraging behavior and microhabitat use between plots, we pooled the observations from the two plots.

We used two-way log-likelihood contingency tests of independence (*G-tests*; Agresti 2002) to analyze yearly variations of foraging maneuvers, foraging substrate, foraging height, and plant species where individuals were foraging. When the null hypothesis of independence among cells in the two-way table was rejected, we used standard-
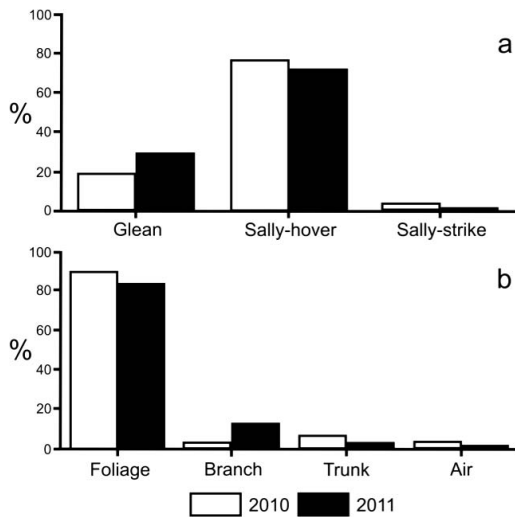
FIG. 1. Percentage of maneuvers employed (a) and substrate used (b) by White-crested Elaenias (*Elaenia albiceps chilensis*) to catch food in mixed forests of *Nothofagus dombeyi* and *Austrocedrus chilensis* of Patagonia during the summers of 2010 ($n = 96$) and 2011 ($n = 85$).

ized Pearson residuals (SPR) to evaluate the nature of the association (Agresti 2002). A SPR that exceeds 2 (in absolute value) indicates lack of fit for that cell, meaning that more or less subjects (depending on the SPR signal) were at these combinations than the null hypothesis of independence predicts (Agresti 2002).

Fruit and Arthropod Abundance.—We only evaluated fruit production of *Aristotelia chilensis,* because this species is the most abundant fleshy-fruit species at our study site (Bravo et al. 2015), and because its fruit is the most important in White-crested Elaenias' diet (Bravo et al. 2015). Fruit abundance of *Aristotelia chilensis* was evaluated during February, because this is when its fruit ripens (Bravo et al. 2015). We randomly selected 20 individual shrubs (10 per plot), and estimated once a week, during the 2 years of the study, the quantity of ripe fruits. 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. To compare the maximum abundance of ripe fruit between years, we used the highest index recorded for each individual during the month, and calculated the proportion of individuals that offered no ripe fruits (index 0),

that offered <50 ripe fruits (indexes 1 and 2), and that offered >50 ripe fruits (indexes 3 to 5). For each category, we evaluated the difference in abundance of ripe fruit between years using a test for difference of two proportions (Zar 2010).

Arthropod abundance was estimated using blue sticky traps (Young 2005). We used the color blue because it is neutral in terms of attracting or repelling insects (Ausden and Drake 2006). The size of each trap was 200 cm^2 (10 × 20 cm), and traps were attached to a plastic transparent cylinder 15 cm in diameter and 20 cm long, to prevent leaves from falling in and affecting the trap's capture efficiency. During the 2 years of the study, we installed 28 traps (14 per plot) in January and February. Traps were located in the foliage of *Aristotelia chilensis* ~2 m above ground level, and were operated from 5–21 days, depending on weather conditions. Abundance of arthropods per trap was assessed by calculating a relative abundance index (RAI = number of caught individuals / number of trapping days). We evaluated the difference between years in the average RAI using a two-tailed paired sample *t*-test, because we trapped arthropods in the same location during both years of the study (Zar 2010).

Rainfall Patterns.—Precipitation data were available from the weather station No. 2300 "Lago Steffen" (Red Hidrológica Nacional, Subsecretaría de Recursos Hídricos de la Nación) for the period of 1993–2011. We considered two variables when analyzing rainfall patterns during January and February: monthly precipitation and number of rainy days per month. We considered wet or dry months to be those with monthly rainfall and number of rainy days above or below one standard deviation of the average monthly rainfall and number of rainy days, respectively, during the 18-year period of climatic data (Ropelewski and Folland 2000).

RESULTS

During the two study years, White-crested Elaenias used the same foraging maneuvers ($G = 2.87$, $df = 2$, $P = 0.24$), capturing prey mainly by sally-hover (Fig. 1a). Elaenias also used the same foraging substrate in both years ($G = 2.96$, $df = 3$, $P = 0.39$), using foliage on which to find and capture prey (Fig. 1b).
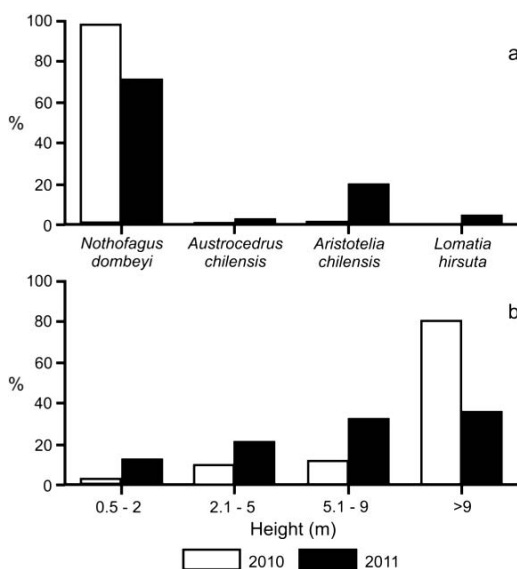
FIG. 2.   Percentage of plant species (a) and heights (b) used by White-crested Elaenias (*Elaenia albiceps chilensis*) to catch food in mixed forests of *Nothofagus dombeyi* and *Austrocedrus chilensis* of Patagonia during the summers of 2010 ($n = 96$) and 2011 ($n = 85$).

The frequency of plant species used by elaenias in which to forage changed between study years ($G = 12.71$, $df = 3$, $P = 0.005$, Fig. 2a). The main shift was the increased use of *Aristotelia chilensis* and the decreased use of *Nothofagus dombeyi* during 2011 (Table 1).The foraging height at which elaenias captured their prey varied between the study years ($G = 20.85$, $df = 3$, $P < 0.001$, Fig. 2b). The shift between years was related to a strong decrease in the use of higher vegetation strata during 2011 (Table 1).

Fruit production on shrubs of *Aristotelia chilensis* showed notable changes between years. The proportion of individuals with no ripe fruits was higher in 2010 than in 2011 (0.75 and 0,

respectively), and plants with <50 ripe fruits tended to be higher in 2011 (2010 = 0.05 and 2011 = 0.28, Test for two proportions, $Zc = 1.52$, $P = 0.064$). Plants with >50 ripe fruits were also higher in the second year (2010 = 0.20 and 2011 = 0.72, Test for two proportions, $Zc = 3.00$, $P = 0.001$).

Arthropod abundance was similar between years. Average ± SD RAI in 2010 was 2.8 ± 1.9 individuals/day, while during 2011 it was 1.9 ± 3.1 individuals/day. The difference between years was not statistically significant (two-tailed paired sample *t*-test, $t_{26} = 1.24$, $P = 0.11$).

During the two study years, January precipitation (2010 = 60.2 mm, 2011 = 63.0 mm) and the number of rainy days (2010 = 7 days, 2011 = 7 days) were similar to historical variation for this month (Fig. 3). In contrast, February precipitation (2010 = 77.5 mm, 2011 = 14.6 mm) and the number of rainy days (2010 = 9 days, 2011 = 2 days) were very different. February 2010 was very wet compared to the historical record, and 2011 was similar to the historical variation for this month (Fig. 3).

DISCUSSION

The two years of the study had contrasting climatic conditions, with the first year having a strong increase in rainfall and number of rainy days during February compared to 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. Climatic conditions during February 2010 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 and Proebsting 1986, Spayd

TABLE 1.   Standardized Pearson residuals (SPR) to evaluate the nature of the association after the null hypothesis of independence among cells in the two-way table was rejected (Agresti 2002), for vegetation species and strata used by White-crested Elaenias (*Elaenia albiceps chilensis*) to catch food in mixed forests of *Nothofagus dombeyi* and *Austrocedrus chilensis* in Patagonia during the summers of 2010 and 2011. See Methods for details on SPR interpretation.

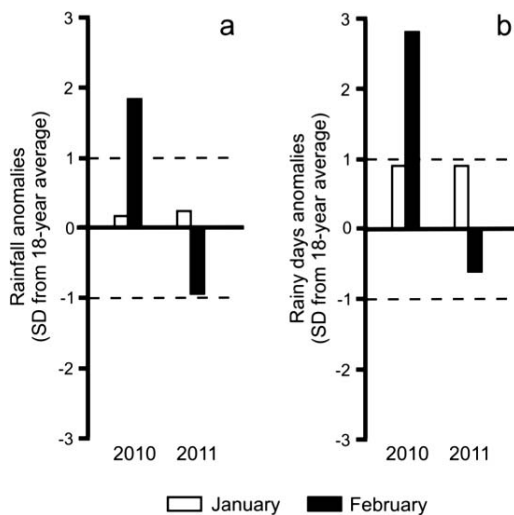|	Vegetation Species				Vegetation Stratum			
	Nothofagus dombeyi	*Austrocedrus chilensis*	*Lomatia hirsuta*	*Aristotelia Chilensis*	0.5–2 m	2.1–5 m	5.1–9 m	>9 m
2010	4.6	−0.7	−1.6	−4.6	−2.9	−2.5	−3.6	6.2
2011	−4.6	0.7	1.7	4.3	3.0	2.5	3.6	−6.2

FIG. 3.   Anomalies in January and February rainfall (a) and number of rainy days (b) at Lake Steffen, Nahuel Huapi National Park, northern Patagonian, Argentina, during 2010 and 2011. Values are expressed in standard deviations from the average of the 18-year period of climatic data at the weather station Nro. 2300 Station "Lago Steffen", Red Hidrológica Nacional, Subsecretaría de Recursos Hídricos de la Nación. Wet or dry months were those with January or February rainfall or number of rainy days above or below one standard deviation (dashed lines) from the mean, respectively.

et al. 2002). These changes in resource abundance had different effects on foraging behavior of White-crested Elaenias. Elaenias did not change foraging maneuvers or the substrate in which they captured prey. During the 2 years, the most frequent behavior that we observed was searching and detecting prey while perched, and capturing prey on foliage using gleaning and sally-hovering maneuvers. Nevertheless, elaenias notably modified the use of foraging microhabitats. During the summer of 2010, they used the forest canopy, foraging mainly in foliage of *Nothofagus dombeyi*; while in the summer of 2011, White-crested Ealenias used the entire profile of vegetation height, and increased their capture of prey in shrubs of *Aristotelia chilensis*. In particular, this change was because of increased consumption of fruits, because across all records for which we could identify prey captured, in 2010, only 1% were fruit, while in 2011, 21% of the records were *Aristotelia chilensis* fruits.

White-crested Ealenias used the same capture maneuvers during the 2 years, even though we recorded changes in the main food resources of this species. We also observed a similar stereotyped behavior in the use of foraging maneuvers in different habitat types where the ealenias used the same foraging maneuvers in Patagonian forests that have undergone structural alterations by human activities (Chust et al. 2012) and in shrubby and open forest habitats of the Monte Desert (Blendinger 2005, Lopez de Casenave et al. 2008). However, in our study White-crested Elaenias showed a context-dependent use of plant species and foraging heights. Those changes in microhabitat use could be related to interannual variation in fruit abundance of *Aristotelia chilensis*, the main producer of fleshy-fruits in our study area (Bravo et al. 2015). Changes in forest microhabitat use demonstrated the behavioral flexibility in the feeding ecology of White-crested Elaenias. Foraging flexibility is commonly observed in Nearctic-Neotropical and Palaearctic-Afrotropical migrant species (e.g., Martin and Karr 1990, Salewski et al. 2003), and is suggested to be a behavior for coexistence with resident species (Salewski and Jones 2006). Our results are the first description of foraging flexibility in a Neotropical austral migrant species, and a more detailed study is necessary to identify its role in interspecific coexistence with resident species in both its breeding and wintering areas.

The context-dependent response of White-crested Elaenias in foraging microhabitat use may have implications for its functional role in temperate forests of Patagonia. The White-crested Elaenia is the most abundant bird species during spring and summer (Grigera et al. 1994, Ippi et al. 2009), and is the main seed disperser of fleshy-fruited shrub species in Patagonia forest (Armesto et al. 1987, Amico and Aizen 2005, Cavallero et al. 2013, Bravo et al. 2015). Although years of low fruit production *per se* would likely lead to reduced sapling recruitment, the change in foraging microhabitat use of White-crested Elaenias during those years may be generating more drastic negative effects on forest regeneration. The role of a single bird species in ecosystem services has been studied by other researchers. For example, Lemon-bellied White-eyes (*Zosterops chloris*) are responsible for pest control in cacao agroforestry in Indonesia (Maas et al. 2015). Since Patagonian forests are ecosystems of low redundancy, and biological interactions depend on very few species

(Aizen and Ezcurra 1998), the effects observed in our study in the foraging behavior of White-crested Elaenias could have important negative effects in the ecosystem services that this migratory species provides when visiting the austral temperate forest of South America.

ACKNOWLEDGMENTS

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