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Bird mixed-species flock formation is driven by low temperatures between and within seasons in a Subtropical Andean-foothill forest

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ABSTRACT

According to both the predation avoidance and foraging efficiency hypotheses, birds within mixed flocks increase their foraging efficiency and/or can spend more time feeding and less time looking out for predators. These hypotheses predict that birds in mixed flocks obtain benefits. Thus, mixed flock formation could serve as a strategy to cope with difficult conditions imposed on birds such as climatic conditions that ultimately result in a change in predation pressure or food resources. We evaluate the hypotheses that forming part of a flock confers benefits to its members and the associated prediction that birds will take advantage of these benefits and flock more often under cold and dry weather conditions between and within seasons to cope with such conditions. We surveyed the presence of mixed flocks, flocking propensity, number of species and individuals in mixed flocks in the Subtropical Yungas foothill of Argentina, to examine seasonality, flocking behavior of birds and their responses to two climatic variables: temperature and humidity. Bird species presented a higher flocking propensity and mixed flocks occurred more frequently during the dry and cold seasons than during the more benign seasons, and lower values of temperature within seasons triggered the flocking behavior. Although effects between seasons were expected, birds also showed a short-term response to small changes in temperature within seasons. These results strengthen the ideas proposed by the foraging hypothesis. Although benefits derived from flocking have yet to be determined, whatever they are should be understood in the context of seasonal variation in life-history traits.

Abstract in Spanish is available with online material.

Key words: bird behavior; Northwest Argentina; seasonality.

Mixed-species flocks are interspecific groups of birds that forage in close association. Species in these flocks actively maintain a bond over time by making contact calls and by moving together while looking for food (Greenberg 2000). In South American tropical rain forests, mixed flocks occur throughout the year. The weather is mild, the average monthly temperatures are above 18°C, and forests never lose their foliage cover. These tropical flocks retain the same species and individuals that share a stable territory year-round (Munn & Terborgh 1979, Powell 1979, Terborgh *et al.* 1990, Jullien & Thiollay 1998). On the contrary, in temperate forests of North America there is marked seasonality in weather and ecological conditions and mixed flocks tend to form outside the breeding season, during the fall and winter. Mixed flocks in these forests do not seem to have stable territories, and the number of species and individuals changes throughout the year (Morse 1970, 1977). These differing seasonal patterns of mixed flocks indicate that birds are responding to seasonal changes in climatic and ecological conditions. In fact, it is widely recognized that birds behave differently across seasons, while features of mixed flocks vary geographically and with climate (Moynihan 1962, Morse 1970, Buskirk 1972, Munn & Terborgh 1979, Powell 1979, Terborgh *et al.* 1990 Jullien & Thiollay 1998, Hino 2000). Nevertheless, can birds also respond to short-term changes in climatic and ecological conditions within seasons? To explain why birds form mixed flocks, two (not necessarily mutually exclusive) hypotheses have been proposed: the predation avoidance and the foraging efficiency hypotheses. The predation avoidance hypothesis argues that birds forming mixed flocks diminish their probability of being predated in comparison with solitary birds (Miller 1922, Buskirk 1976, Goldman 1980, Jullien & Clobert 2000). The foraging efficiency hypothesis posits that birds in mixed flocks have greater foraging success than solitary birds (Moynihan 1962, Buskirk 1972, Krebs 1973, Morse 1977, Berner & Grubb 1985, Sridhar & Shanker 2013). Therefore, whether birds spend more time feeding and less time looking out for predators, or they increase their foraging efficiency, both hypotheses maintain that birds in mixed flocks obtain benefits (Hino 2000, Beauchamp 2005). For this reason, mixed flock formation could serve as a strategy to cope with difficult conditions imposed upon them such as climatic conditions that ultimately affect the predation pressure and/or food resources (Morse 1970). That being said, birds most likely employ foraging and predation avoidance behaviors depending on pressures that vary temporally. Thus, the benefits of flocking may vary seasonally and in the short term, depending on the occurrence of conditions that would act as behavioral triggers for bird species to form and join mixed flocks.

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In forests with contrasting seasonal conditions, both hypotheses predict that bird species will have a higher flocking propensity and that mixed flocks will occur more frequently during the dry and cold seasons, which generally match with the fall and winter. During the fall and winter, the forests lose their foliage and birds are more exposed to predators (Berner & Grubb 1985, Dolby & Grubb 1998) while food resources become scarcer (Develey & Peres 2000, Blendinger *et al.* 2012). On the other hand, within seasons the predictions of both hypotheses differ. While predation risk can be considered as fairly constant within a season (there are no obvious factors that would lead to short-term changes in the predation pressure for birds), food availability can change markedly within a season. Arthropod communities can evoke quick responses to short-term changes in climatic conditions. Small amounts of rainfall within the period of a week can have strong positive effects on the number of arthropods detected (Wolda 1978, Tanaka & Tanaka 1982), and rises in temperature immediately increase arthropod mobility, ultimately enhancing the detectability of arthropods as prey for birds (Avery & Krebs 1984). Thus, changes in flocking behavior within a season in conjunction with climatic conditions that influence food availability would support the foraging efficiency hypothesis and would weaken the predation avoidance hypothesis.

In the subtropical forests of northwest Argentina (Hunzinger 1997), conditions can generally be described as being between those in tropical rain forest and temperate forests. During spring and summer, the weather is mild, forests have a considerable amount of foliage (Beek & Bramao 1969, Brown *et al.* 2002), and most bird species take advantage of these conditions to breed (Dinelli 1918, Auer *et al.* 2007). On the contrary, during fall and winter the weather becomes drier to the point that forests lose their foliage cover and temperatures decrease considerably (Brown *et al.* 2002). These phenological changes could result in a higher exposure to predators due to foliage loss (Berner & Grubb 1985, Dolby & Grubb 1998), diminished fruit production (Blendinger *et al.* 2012) and reduced arthropod abundance during the dry season (Develey & Peres 2000). The combination of these changes during the dry season appears to represent a period of resource scarcity and energy deficit for birds (Seoane *et al.* 2013). Many bird species avoid this rough season by migrating away toward better areas (Chesser & Levey 1998), but those that stay must have adequate mechanisms to cope with these difficult conditions (Dolby & Grubb 1999). One such mechanism would be the formation of mixed flocks, which would allow birds to diminish predation risk or increase foraging efficiency (Morse 1970, Klein 1988). Previous studies in subtropical forests of South America reported that mixed flocks are seasonal, following the same pattern of temperate forests (Contreras 1981, Vides-Almonacid 1992, Herzorg *et al.* 2002, Fanjul & Echevarria 2015, Fanjul 2016). However, these studies have not pursued year-round studies to test this idea. For that reason, the Subtropical Yungas forest presents an opportunity to examine and compare the seasonality of mixed-species flocks in subtropical climatic conditions and to understand how birds respond to seasonal and short-term changes in climatic conditions between and within seasons. This study aimed to describe the seasonal pattern of mixed flock formation and clarify the role of climatic conditions in promoting flocking behavior, through strict surveys within and across seasons during three years. The final goal was to discuss and evaluate whether birds form mixed flocks to cope with the difficult conditions imposed upon them by climatic conditions, between and within seasons, which ultimately influence food resources for birds that make up mixed flocks.

In this study, we compared how the presence or absence of mixed flocks, the frequency of mixed flock encounters per hour, the flocking propensity of bird species, the number of species and the number of individuals in mixed flocks respond to seasonal changes and to short-term changes in two climatic variables (temperature and humidity percentage). Specifically, we evaluated three sets of predictions. First, if birds form mixed-species flocks to cope with cold and dry conditions imposed by the climate in northwest Argentina, we predict that mixed flocks will form more often and bird species will have a higher flocking propensity and a higher proportion of individuals during the dry fall–winter seasons than during the wet spring–summer seasons and that in general, the probability of recording a mixed flock will increase when climatic conditions are colder and drier in comparison with more hotter and humid conditions. Second, as the breeding season represents a subset of the wet spring-summer season, we expect lower flocking propensity and fewer mixed flocks during this season compared to the non-breeding season. Third, if some climatic variables act as behavioral triggers of flocking behavior in the short term, we expect that the probability of mixed flocks presence and the flocking propensity of bird species increase on colder days within all seasons (wet and dry, and breeding and non-breeding).

METHODS

STUDY SITES.—We conducted the study at two sites in the province of Salta, Argentina: *Estancia Miraflores* (25°16′12″ S, 64°44′13″ W, 600–1500 m asl) near El Galpón city in the southern foothill of the Lumbreras mountain range, and *Estancia Ovando* (25°46′02″ S, 65°02′16″ W, 800–1500 m asl) near Rosario de la Frontera in the eastern foothill of the Metan mountain range (Fig. 1). Both study sites are located in the wide transitional foothill forest that links the Yungas to the dry Chaco (Cabrera 1976). This subtropical transitional foothill forest is a deciduous forest where canopy height can reach 20–30 m from the ground and two or three vegetation strata are present besides epiphytes (orchids, bromeliads and ferns). Trees are represented primarily by *Anadenanthera colubrina*, *Parapiptadenia excelsa, Phyllostylon rhamnoides*, *Schinopsis lorentzi*, *Fagara coco*, *Fagara rhoifolia* and *Handroanthus impetiginosus* (Brown *et al.* 2002). Climate is seasonal with wet and dry seasons; 90 percent of rainfall occurs during austral summer (December through March), averaging 100–300 mm per month, while during austral winter (May through September) less than 10 percent occurs, with 0–10 mm per month (Bianchi *et al.* 1992, Hunzinger 1997).

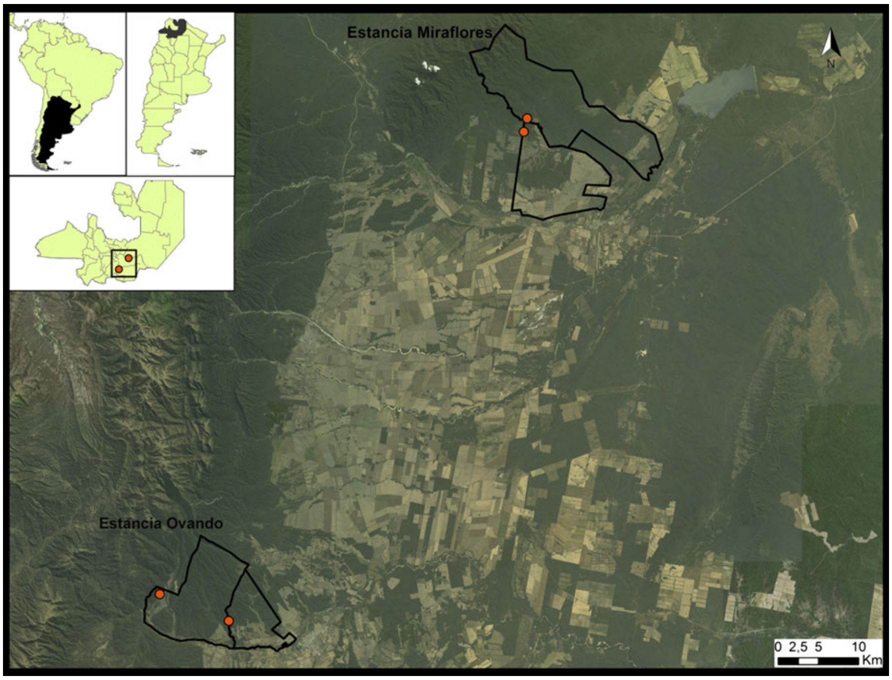

FIGURE 1. Geographic distribution of surveyed sites, with limits shown. In the north Ea. Miraflores, in the south Ea. Ovando. Orange dots show the main sites where transects were cleared; six were cleared in Ea. Miraflores and four in Ea. Ovando.

SAMPLING AND SAMPLING DESIGN.—To obtain data on mixed-species flocks, we established 10 transects, each 100 m long and with a distance of at least 150 m between each one in well-preserved forest (six in *Estancia Miraflores*, four in *Estancia Ovando*; these study sites are 90 km away from each other Fig. 1). Each transect was visited twice per research field trip for one hour in the morning and one hour in the evening in an effort to standardize the possible flocking behavior variability between these two periods of the day (see Herzog *et al.* 2002). However, no differences in the activity of mixed flocks were found between the morning and the afternoon (Wilcoxon test $P = 0.5$; 57 mixed flocks found during the morning and 59 mixed flocks during the afternoon).

Surveys were divided into four seasons according to rainfall (Bianchi *et al.* 1992, Hunzinger 1997): early wet (EWS, October to December, austral spring), late wet (LWS, January to March, austral summer), early dry (EDS, April to June, austral autumn) and late dry season (LDS, July to September, austral winter). Data were allocated *a posteriori* to breeding (October to February) and non-breeding (April to August) seasons, excluding two months (September and March) that represent the lower and upper boundaries (Dinelli 1918, Auer *et al.* 2007). Transects were surveyed during 17 research field trips from 28 June 2014 to 10 February 2017. Prior to data collection, G. Mangini was trained for 18 months to detect all bird species in the area and to record flocking species through visual observations, contact calls and aural records totaling more than 500 h of training and 340 h of data collection (97 d). When collecting the data, we surveyed transects by walking slowly, recording all bird species found and recording the social condition of each spotted individual in two exclusive categories: inside a mixed flock or outside a mixed flock. We defined a mixed flock as an interspecific aggregation of at least three individuals belonging to two different species connected by social actions and moving in the same direction for five or more minutes while looking for food (Morse 1970, Powell 1985, Terborgh *et al.* 1990, Stotz 1993). Each time a mixed flock was detected, we recorded the number of species and the number of individuals per species in the flock. Bird species and individuals were considered members of a mixed flock when recorded following other species or being followed for at least 5 min.

As mixed flocks are readily detected because of the simultaneous calling of several different species, the presence of lone individuals could have been underestimated. However, we recorded more lone individuals when we recorded fewer mixed flocks during the wet seasons, at a time when the foliage cover is denser and supposedly hinders bird observation. In other words, the observed pattern goes against the expected outcome regarding detection of lone individuals and thus supports our dataset. Additionally, the number of recorded bird species did not show significant differences between seasons (see '*Results*').

We measured two climatic variables: temperature (degrees Celsius) and humidity (percentage). Each climatic variable was recorded three times in each one-hour transect (at the beginning, after thirty minutes and at the end) using a portable meteorological station (Mini environmental Quality Meter, Sper scientific 850070). These three values were averaged to obtain one value for each climatic variable per transect sample.

DATA ANALYSIS.—To evaluate our predictions, we analyzed the presence (or absence) of mixed flocks during one-hour transects, the flock encounter rate (number of mixed flocks/hour), the flocking propensity of bird species (number of species within mixed flocks/number of recorded bird species that could form mixed flocks), and the number of species and individuals participating in mixed flocks in relation to our predictive variables: season (early and late wet seasons, early and late dry seasons, and breeding and non-breeding seasons), and climatic variables (temperature and humidity). To evaluate the effects of explanatory variables on response variables, we employed generalized linear models (GLM; Crawley 2007).

To evaluate whether the formation of mixed flocks was seasonal, we conducted χ^2-tests of the number of mixed flocks per season. To evaluate differences in the size of mixed flocks between seasons (number of species and individuals within mixed flocks), we performed generalized linear models with negative binomial distribution. To evaluate the predictions that presence or absence of mixed flocks, flocking propensity, and the number of species and individuals are related to climatic variables, we performed generalized linear models (GLM) and linear regression models (LM).

To evaluate the relationship between mixed flocks and climatic variables, three sets of GLMs were performed. The first set of models lumped all seasons together to analyze the presence or absence of mixed flocks, number of bird species and individuals within flocks and flocking propensity. The second set used data from the four seasons as defined by rainfall, and the third one used data from the breeding and non-breeding seasons; both sets evaluated the presence or absence of mixed flocks and flocking propensity of bird species within each season. The type of data we worked with determined the type of family distributions. Binomial family was used for presence or absence of mixed flocks and flocking propensity of bird species with logit-link function, and Poisson family for number of species and individuals with log-link function. After checking for overdispersion, and when necessary, we worked with quasipoisson, quasibinomial or negative binomial families. The effects of temperature and humidity were evaluated as continuous variables. Temperature effect was evaluated as a lineal and quadratic term, as this term allows a change in the flocking behavior trend for large values of the predictor variable (*i.e.*, high values of temperature).

To evaluate short-term responses on a daily basis across all seasons and within the wet and dry seasons, we compared the change in flocking encounter rate between two consecutive days to the change in temperature in the same consecutive days with a linear regression model (after checking for normality with Shapiro–Wilk test $P > 0.05$). We calculated the difference between the daily temperature average (per morning and afternoon sets) and the previous day average temperature (per morning and afternoon sets) and contrasted it with the difference between the flock encounter rate per day (per morning and afternoon) and the flock encounter rate (per morning and afternoon sets) on the previous day.

In all analyses, we employed a stepwise regression, removing non-significant terms from the model, one by one, in decreasing order of *P* values (Crawley 2007). For statistical analyses, we used the R software, v. 3.4.1 and Infostat (v. 2016e) software. All mean values are expressed as mean ± SD, except where noted.

RESULTS

Flocking behavior and seasonality.—We recorded a total of 116 mixed-species flocks, and the number of mixed flocks was higher during the early dry ($N = 35$) and late dry ($N = 48$) seasons than during the early ($N = 16$) and late wet seasons ($N = 17$; Table 1; χ^2-test, $P < 0.001$). During the non-breeding seasons, there were more mixed flocks than during the breeding seasons (Table 1; χ^2-test, $P < 0.001$). The flock encounter rate (number of mixed flocks per hour/number of hours surveyed within each season) followed a seasonal pattern, increasing during the dry seasons and decreasing during the wet ones in the three consecutive years of sampling (Fig. 2).

The average number of bird species that could potentially form mixed flocks per transect did not show significant differences between seasons (Kruskal–Wallis $P > 0.05$; late wet season $\bar{X}$ 19.39 ± 5.78, early dry season $\bar{X}$ 16.81 ± 5.70, late dry season $\bar{X}$ 18.40 ± 6.50 and early wet season $\bar{X}$ 18.20 ± 5.43).

We recorded a total of 79 bird species that joined mixed flocks in our study area (Table S1—Online Supplementary Material). Mixed flocks had on average 7.51 ± 6.24 species and 13.36 ± 13.15 individuals (Table 1). The number of bird species and individuals recorded within mixed flocks did not show significant differences between rainfall seasons (GLM negative binomial $\chi^2_3 = 4.2$, $P = 0.23$ for species and $\chi^2_3 = 2.52$, $P = 0.47$ for individuals). The flocking propensity of bird species was significantly different between rainfall seasons (GLM quasibinomial $\chi^2_3 = 155.3$, $P < 0.001$); the highest propensity was found in the dry seasons with 32.14 percent of bird species occurring in mixed flocks in the early dry season, 24.34 percent in the late dry

TABLE 1. *Number of bird mixed-species flocks, number of transects surveyed and number of species and individuals in mixed flocks in regard to rainfall and breeding and non-breeding seasons in northwest Argentina (2014–2017). Number of mixed flocks [Number of surveyed transects]. Average number of bird species and individuals per mixed flock ± SD (range).*

	Mixed flocks [surveyed transects]	Bird species	Bird individuals
DRY (April–September)			
Early	35 [44]	8.09 ± 7.04 (2–29)	13.51 ± 13.52 (3–49)
Late	48 [52]	6.15 ± 4.90 (2–22)	12.23 ± 14.10 (3–79)
Non-breeding (April–August)	71 [95]	6.92 ± 6.04 (2–29)	13.04 ± 14.10 (3–79)
WET (October–March)			
Early	16 [52]	6.88 ± 3.54 (2–15)	10.13 ± 7.22 (3–28)
Late	17 [40]	9.65 ± 7.97 (2–29)	15.59 ± 14.76 (3–58)
Breeding (October–February)	19 [74]	6.84 ± 4.21 (2–16)	12.26 ± 8.13 (3–28)

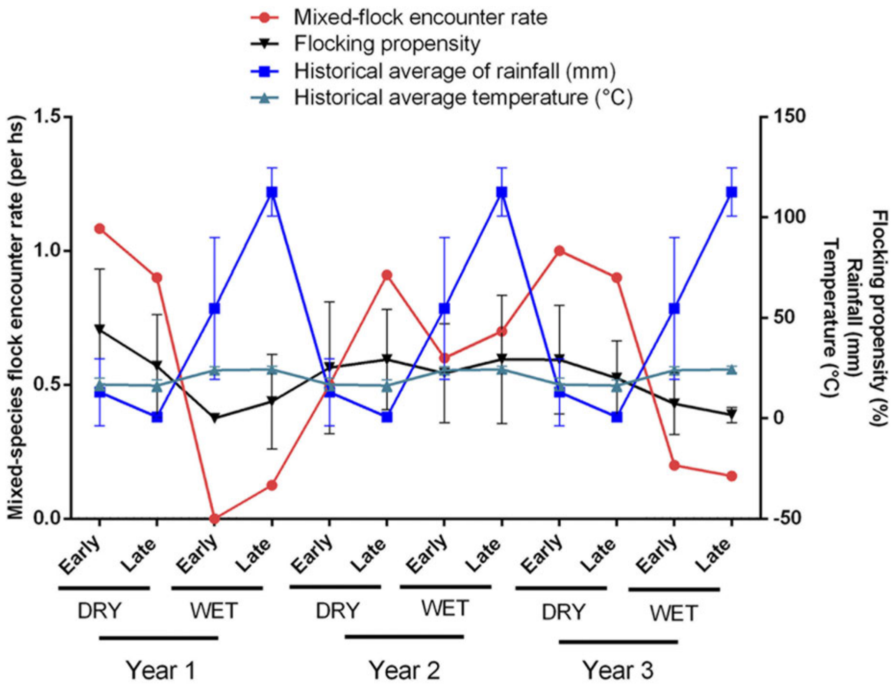

FIGURE 2. Bird mixed-species flock encounter rate per season in Yungas foothill forest in Northwest Argentina during three consecutive years (in red, 2014 to 2017). Flocking propensity of bird species across seasons (in black, 2014–2017). Historical average monthly rainfall in Northwest Argentina per season (in blue, from Bianchi et al. 1992) and historical average temperature per season (in light blue).

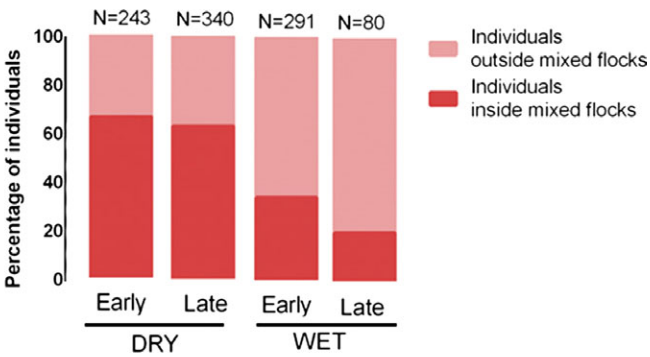

FIGURE 3. Percentage of bird individuals inside and outside of mixed-species flocks across seasons in northwest Argentina. *N*: Total number of bird individuals recorded within each season (years 2014–2016).

season, 11.54 percent in the early wet season and 17.42 percent in the late wet season (Fig. 2). Additionally, the proportion of bird individuals recorded within mixed flocks increased during the dry seasons and decreased during the wet ones (Fig. 3).

Flocking behavior and climatic variables.—The probability of finding a mixed flock showed an inverse relationship to temperature year-round (Fig. 4A), and it did not show a significant relationship to humidity (GLM binomial $\beta = -0.\ 11 \pm 0.03$ SE, $\chi^2_1 = 17.6$, $P < 0.05$ for temperature, $\chi^2_1 = 3.5$, $P = 0.06$ for humidity).

The flocking propensity of bird species was related to temperature (quadratic term). As temperature decreased, more bird species were prone to join mixed flocks (Fig. 4B), and no significant relationship was found to humidity (GLM quasibinomial $\beta = -0.0017 \pm 0.00059$ SE, $F_{1,113} = 9.9$, $P < 0.05$ for temperature and $F_{1,113} = 0.2$, $P = 0.64$ for humidity).

The number of bird species and individuals was related to temperature (quadratic term). As temperature decreased, mixed flocks had more species (Fig. 4C) and individuals (Fig. 4D) and no significant differences were found for humidity (GLM negative binomial for species $\beta = -0.00078 \pm 0.00034$ SE, $\chi^2_1 = 4.7$, $P < 0.05$ for temperature and $\chi^2_1 = 6.52$, $P = 0.010$ for humidity; for individuals $\beta = -0.00095 \pm 0.00036$ SE, $\chi^2_1 = 6.2$, $P < 0.05$ for temperature and $\chi^2_1 = 0.5$, $P = 0.44$ for humidity).

Flocking behavior within seasons.—The presence of mixed flocks was inversely related to temperature only within wet seasons (Figs. 5A and B; GLM binomial for late wet season: $\beta = -0.29 \pm 0.10$, $\chi^2_1 = 8.27$, $P < 0.05$ and for early wet season $\beta = -0.09 \pm 0.05$, $\chi^2_1 = 4.38$, $P < 0.05$). Within the dry seasons, there were no significant differences in relation to measured climatic variables (Figs. 5D and E; GLM binomial for late dry season $\chi^2_1 = 2.23$, $P = 0.13$ and for early dry season $\chi^2_1 = 1.74$, $P = 0.18$,).

During the breeding (Fig. 5C) and non-breeding (Fig. 5F) seasons, the presence of mixed flocks was inversely related to temperature (breeding GLM binomial, $\beta = -0.09 \pm 0.05$,

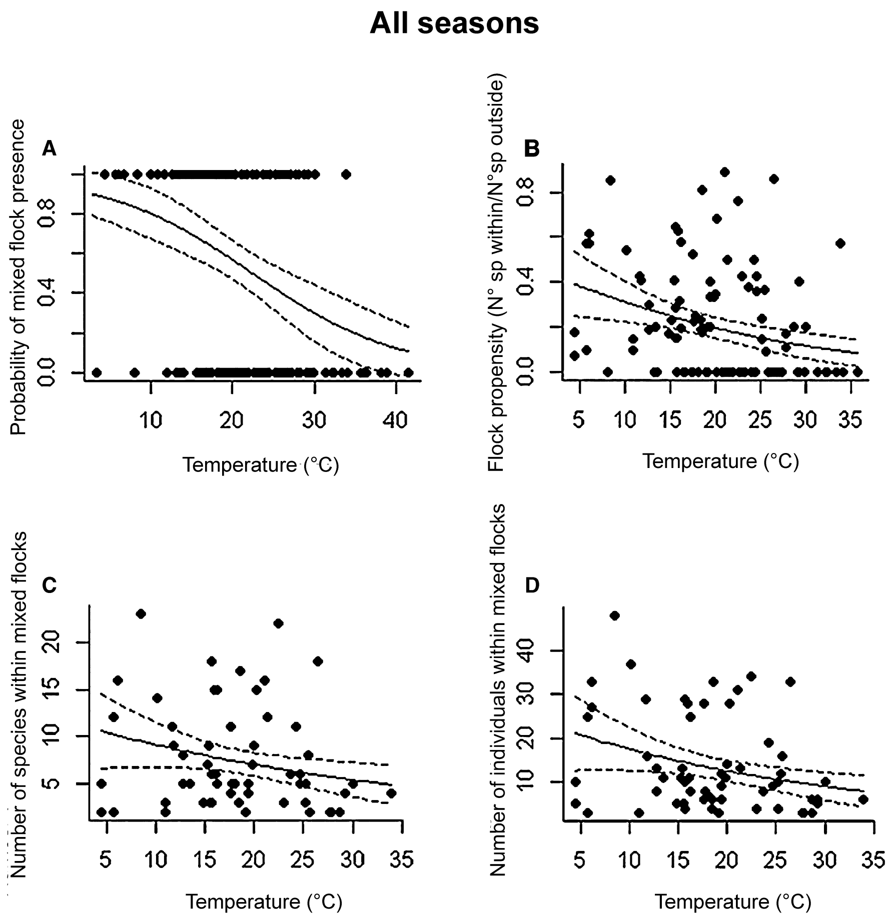

FIGURE 4. Flocking behavior showed strong response to temperature variation when analyzing data of all combined seasons from 2014 to 2017 in northwest Argentina. (A) The probability of finding one mixed flock increases as temperature decreases. (B) Flocking propensity of bird species increases as temperature decreases (more bird species are found within mixed flocks than outside). (C) Number of bird species forming mixed flocks increases at lower values of temperature. (D) Number of individuals within mixed flocks increases at lower values of temperature.

$P < 0.05$ for temperature and $\chi^2_1 = 0.27$ $P = 0.59$ for humidity; non-breeding GLM binomial, $\beta = -0.002 \pm 0.0009$, $\chi^2_1 = 2.4$, $P < 0.05$ for temperature and $\chi^2_1 = 0.7$ $P = 0.38$ for humidity). Temperature explained 3.91 percent of the variance in the presence or absence of mixed flocks during the breeding season (Fig. 5C) and 6.73 percent during the non-breeding season (Fig. 5F). The flocking propensity did not show significant relationship to any of the measured climatic variables in the breeding or non-breeding seasons (breeding: GLM quasibinomial, $F_{1,45} = 3.1$, $P = 0.08$ for temperature, $F_{1,44} = 0.6$, $P = 0.43$ for humidity; non-breeding: GLM quasibinomial $F_{1,65} = 1.57$, $P = 0.21$ for temperature and $F_{1,64} = 0.1$, $P = 0.74$ for humidity). The daily change in flock encounter rate was inversely related to the daily change in temperature both year-round (Fig. 6; LM $\beta = -0.045 \pm 0.012$ SE, $P < 0.001$) and within the wet and dry seasons (LM $\beta = -0.046 \pm 0.01$ SE, $P < 0.05$ for wet seasons and LM $\beta = -0.041 \pm 0.01$ SE, $P < 0.05$ for dry seasons).

DISCUSSION

In this study, we tested the hypothesis that mixed flock formation can be considered a mechanism to cope with difficult climatic conditions in the Subtropical Andean-foothill forests of northwest Argentina (Morse 1970, Buskirk 1972, Powell 1985, Sridhar & Shanker 2013). We predicted that the probability of recording a mixed flock would increase in colder and drier climatic conditions compared to more benign conditions. Our data support our original predictions: (1) Mixed flock formation was seasonal—mixed flocks occurred more frequently during the dry season than during the wet season, and (2) some climatic conditions led to flocking within seasons when analyzed on a daily basis—the probability of mixed flock encounters increased as temperature decreased.

Flocking, breeding and food seasonality.—At our Subtropical Yungas sites, mixed flocks were recorded throughout the year,

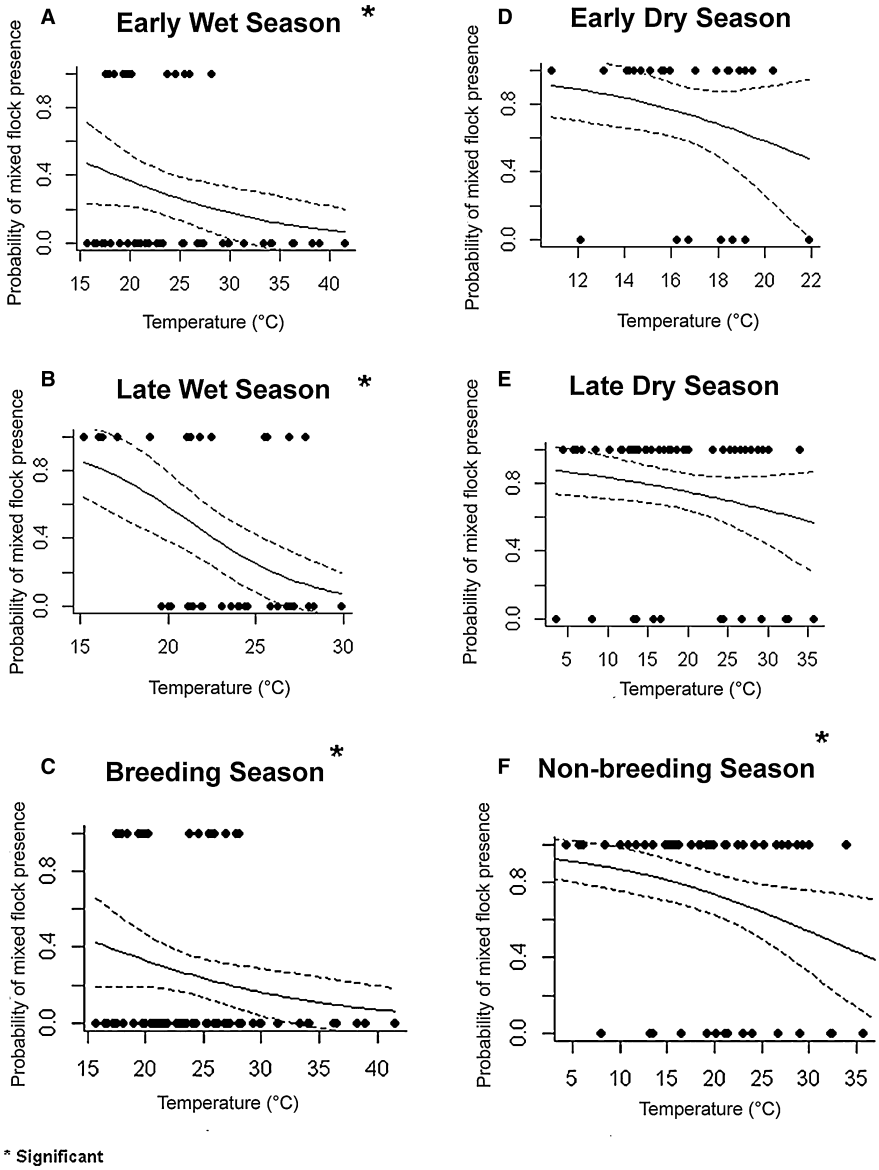

FIGURE 5. Flocking behavior within each season in northwest Argentina showed that (A) the probability of mixed flock presence within early wet season significantly increases when temperature decreases; (B) the probability of mixed flock presence within late wet season significantly increases when temperature decreases; (C) the probability of mixed flock presence within breeding season significantly increases when temperature decreases (D) the probability of mixed flock presence within early dry season increases as temperature decreases; (E) the probability of mixed flock presence within late dry season increases as temperature decreases; (F) the probability of mixed flock presence outside breeding season significantly increases when temperature decreases.

reaching the maximum encounter rate per hour during the drier and colder seasons (see '*Short-term Flocking*'). This seasonal pattern can be described as somewhere between the strictly seasonal flock formation during the fall and winter in the non-breeding season in temperate forests of North America (Morse 1970, 1977) and in Patagonian forests of Argentina (Ippi & Trejo 2003), and the annual occurrence of mixed flocks in tropical rain forests (Munn & Terborgh 1979, Powell 1979, Terborgh *et al.* 1990, Jullien & Thiollay 1998). Our results differ from previous studies reporting that mixed flocks in the Subtropical Yungas forest are seasonal and follow the same pattern as in temperate forests of North America (see Vides-Almonacid 1992, Capllonch 1997, Fanjul & Echevarria 2015, Fanjul 2016). However, these studies focused primarily on the general seasonal pattern of bird species in the region or did not perform a specific mixed flock survey to evaluate their seasonality. We did not find significant differences in the size of mixed flocks between dry and wet seasons, but differences in the encounter rates clearly show that mixed flocks are prone to occur during the fall and winter, which explains why previous studies that did not focus specifically on

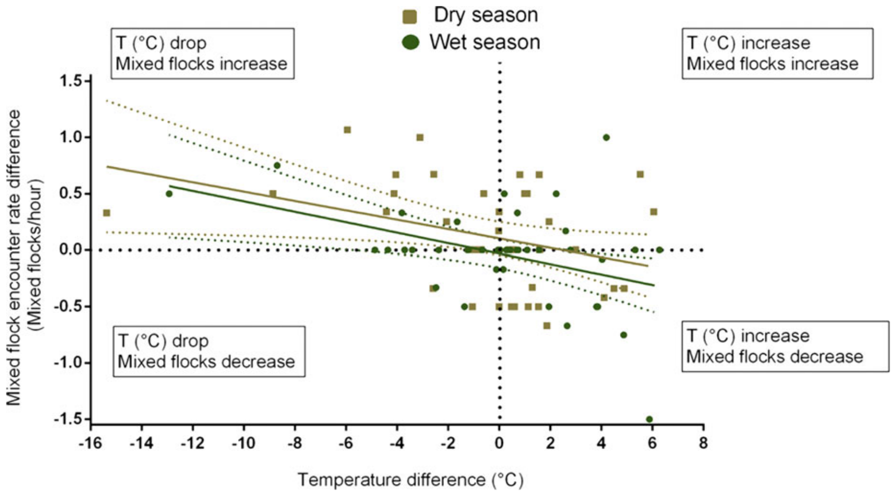

FIGURE 6. Linear regression between changes in temperature and changes in the flock encounter rate (number of mixed flocks/hour) between consecutive days in northwest Argentina (years 2014–2017). Light brown represents the linear regression within dry season. Green represents the linear regression within wet season. Each quadrant represents a different type of relation, and the main tendency shows that with every drop in temperature, between two consecutive days, more mixed flocks are recorded.

mixed flocks only recorded them in winter. In comparison with previous studies, our results represent the first thorough description of seasonality of mixed flocks in the Subtropical Yungas forest.

At our subtropical study site and in temperate forests (Morse 1970), the majority of mixed flocks were recorded outside the breeding season (Dinelli 1918, Auer *et al.* 2007). Likewise, in the Atlantic Forest more flocks were recorded outside the breeding season, when arthropods were scarcer (Develey & Peres 2000). Conversely, in tropical rain forests, mixed flocks occur year-round, overlapping with the protracted breeding season (Munn & Terborgh 1979, Powell 1979, Jullien & Thiollay 1998, Stouffer *et al.* 2013). These contrasting seasonal patterns of mixed flock formation are related to climate seasonality, which causes seasonal changes in food availability; this, in turn, may set specific time limits to the breeding season of flocking birds (Morse 1970). Thus, both seasonality of mixed flocks and breeding seasons could ultimately be conditioned by seasonal shifts in food availability.

Buskirk and Buskirk (1976) found more arthropods during the late dry season in Costa Rica and major turnovers in arthropod species composition throughout the year, showing that the annual cycles of arthropods are composed of a series of temporally short-lived populations and that no generalization can be made about quantitative changes in the arthropod community as a whole. In subtropical forests in northwest Argentina similar to those at our study sites, more arthropods were recorded in the late dry season (Rougès 2003). If, contrary to what we expected, arthropod availability is higher during the dry season, can the formation of mixed flocks in northwest Argentina be a consequence of food shortage? Preliminary data at our study sites suggest that the most obvious changes occur in the type of arthropods available rather than in the quantity of arthropods: A higher proportion of winged adults was recorded during the wet season (Mangini *et al.* unpubl. data). Winged adults are easier to detect than non-flying stages. Thus, the chronically reduced detectability of prey may lead to regular flocking during the dry season in combination with cold and drier climatic conditions, while occasionally reduced adult mobility on colder days could trigger sporadic flocking during the wet season.

In our study area, there is also less fruit available for birds in the dry season (Rougès & Blake 2001, Blendinger *et al.* 2012, Ruggera 2013). Consequently, non-migratory and primarily frugivorous bird species in northwest Argentina must cope with this shortage in fruit production. To do so, birds may join species flocks and/or switch from a primarily frugivorous diet to an arthropod based diet (McKinnon *et al.* 2017), ultimately increasing the flocking propensity of bird species during the dry seasons.

SHORT-TERM FLOCKING.—The same factors that explained fluctuations in flocking behavior along the year may operate within each season. At our study sites, mixed flocks formed most often in the cold and dry (non-breeding) season; in addition, low temperatures explained daily flock formation within each season (Figs. 5 and 6). Even during the breeding season, bird species tended to form mixed flocks on cold days (Fig. 5C). These short-term responses strengthen the idea that mixed flocks help to cope with the consequences of dry and cold weather conditions, regardless of the life-cycle phase. On colder days within seasons arthropods that are cold-blooded lessen their activity, thus becoming less detectable for birds (Avery & Krebs 1984). This factor, combined with differences in the type OF arthropods that are available could explain why even during the more benign wet season (also breeding season) birds chose to form mixed flocks on days with lower temperatures.

CONCLUSION

This study presented strong evidence that numbers of mixed flocks, the flocking propensity of bird species and the proportion of individuals that join mixed flocks increased seasonally during periods of high-energy demand that characterize the colder and drier seasons in a subtropical forest. Short-term flocking was related to low temperature values within seasons and between consecutive days, indicating that low temperatures may act as a *behavioral trigger* that leads to flocking. Decreased food detectability due to lower temperatures rather than arthropod availability seems to be the underlying cause of short-term mixed flock formation in birds. The fact that the same factors were related to flock formation between and within seasons, strengthens the foraging efficiency hypothesis in the subtropical forest of northwest Argentina. However, it has yet to be determined whether the same or analogous mechanisms are operating in the long term. In conclusion, although the benefits derived from flocking remain to be elucidated, whatever they are should be understood in the context of seasonal variation in life-history traits.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.t5m5662 (Mangini & Areta 2018).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *List of bird species in mixed flocks in Northwest Argentina from 2014 to 2017.*

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