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ORIGINAL ARTICLE

Food supplementation by an invasive fleshy-fruited shrub sustains body condition of a native frugivorous bird during winter

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Abstract

Birds tend to adjust their behavior and physiology to changes in food availability in their environment. Seasonal fluctuation of food resources may act as an energetic challenge, augmenting hypothalamus–pituitary–adrenal axis (HPA axis) activity, leading to an increase in corticosterone concentrations and promoting the metabolism of energy stores. Plant invasions may alter seasonal food fluctuations by providing a food supply during scarce seasons. This could attenuate the energetic challenge, reducing HPA axis activity and the metabolism of reserves. Using a system with seasonal fluctuation in food availability, we tested if fruit supplementation by the invasive fleshy-fruited *Pyracantha angustifolia* during the season of native fruit scarcity decreases the consumption of energy stores through activity attenuation of the HPA axis. We measured changes in body condition and circulating corticosterone (CORT) concentration in *Turdus chiguanco* occurring at sites both invaded and not invaded by *P. angustifolia* over 3 time periods that correspond to the periods prior to, during and after highest fruit production of the plant. Fruit scarcity in the ecosystem appears as an energetic challenge for *T. chiguanco*, given that body mass, fat score and residuals of body mass/tarsus length decreased during winter in a site not invaded by the exotic shrub. Conversely, the presence of the invasive plant seemed to attenuate the metabolism of energetic reserves, as we did not record changes in body condition in birds inhabiting the invaded site. Unexpectedly, plasma CORT concentration did not vary between sites or periods. Further evaluation is required to elucidate how enhanced body condition, resulting from the consumption of a fleshy-fruited invasive plant, affects survivorship and reproductive performance in *T. chiguanco*.

Key words: biological invasion, energetic reserves, food fluctuation, frugivory, plasma corticosterone

INTRODUCTION

Animals tend to adjust their behavior and physiology to changes in food availability in their environment (Gleditsch & Carlo 2011; Sofaer *et al.* 2013; Paredes *et al.* 2014). In seasonal environments, fluctuation of food resources is the norm (i.e. winters in temperate latitudes and dry seasons in tropical and subtropical latitudes are

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commonly associated with reductions in food availability; Varela 2003; Chapman *et al.* 2006; Kitaysky *et al.* 2007,2010; Jordano 2014). Consequently, animals either migrate or adjust both their physiology by depleting energy stores and their behavior by incorporating other elements in their diet (Wingfield *et al.* 1998; Harding *et al.* 2011; Crespi *et al.* 2013). However, in the current scenario of global changes induced by human activities, natural cycles of resource fluctuations may be severely affected. Biological invasions are one of the most significant changes that may affect these natural processes, either by altering the quantity or the quality of resources (Gledistch & Carlo 2011; Vergara-Tabares & Rojas 2016). Accordingly, biological invasions may induce behavioral or physiological readjustments in native animals that consume these new invasive resources. Biological invasions that provide new food resources (Mokotjomela *et al.* 2013) may modify natural fluctuation in food availability in seasonal environments. These changes in food availability may either accentuate or ameliorate this fluctuation, depending on when the new food resource is available (Gleditsch & Carlo 2011; Mokotjomela *et al.* 2013; Vergara-Tabares *et al.* 2016). Should its resources be available at an opportune time, the alien species could mitigate energetic challenges to animals during food scarcity periods.

Physiological responses to seasonal changes in food availability are generally linked to elevations in circulating energy mobilization hormones (Sapolsky *et al.* 2000; Johnstone *et al.* 2012; Duarte *et al.* 2015). One energy mobilization hormone found in birds is corticosterone (CORT), a stress-related hormone (Wingfield *et al.* 1998; Cohen *et al.* 2012). Concentration of circulating CORT is controlled by the hypothalamus–pituitary–adrenal (HPA) axis (Sapolsky *et al.* 2000). The activity of this axis is stimulated by energy-demanding situations (e.g. reduced food availability, presence of predators and extreme climatic situations) that require an increase in energy availability (Cohen *et al.* 2012; Crespi *et al.* 2013). The main action of CORT is to catabolize reserves stored in tissues (e.g. fat or muscle tissue), thereby liberating energy for use in the system during energetically-challenging situations (Sapolsky *et al.* 2000; Crespi *et al.* 2013; Hennin *et al.* 2016). As a consequence, circulating CORT levels could quantitatively affect energy balance in birds (Wingfield *et al.* 1998; Kitaysky *et al.* 2001; Davies *et al.* 2013; Crino *et al.* 2014). If changes in food resources caused by biological invasions can ameliorate food fluctuations and energetic challenges to animals, one would expect a consequent attenuation in the activity of the HPA axis. In other words, greater food availability provided by an alien species in a system could result in animals with lower plasma CORT levels and reduced usage of reserve stores (Sapolsky *et al.* 2000; Johnstone *et al.* 2012; Crespi *et al.* 2013) when compared to animals without access to food provided by the invasive species.

In the mountain Chaco woodland of Argentina, extensive areas have been invaded by alien fleshy-fruited plants (Giorgis *et al.* 2011; Giorgis & Tecco 2014). Of these invasive species, *Pyracantha angustifolia* is one of the most widespread in the region and may form isolated patches of varying extensions among native vegetation stands, depending on the topography of the invaded area (Giorgis *et al.* 2011). In contrast to native fruiting shrubs which fruit between November and April (e.g. *Celtis ehrenbergiana*, *Lithraea molleoides*, *Condalia* sp.; Giorgis & Tecco 2014), *P. angustifolia* and other invasive fruiting shrubs fruit from late May to late September (Vergara-Tabares *et al.* 2016). In areas not yet invaded by alien plants, frugivorous birds are exposed to a reduction in native fruit resources during winter (late May to early October), whereas, in areas invaded by *P. angustifolia*, frugivorous birds have access to a supplementary source of fruit during the fall–winter (Vergara-Tabares *et al.* 2016). Fruits of *P. angustifolia* represent an important item in the diet of a variety of fruit-consuming species (Vergara-Tabares *et al.* 2016). The most abundant and main consumer of *P. angustifolia* fruits is the Chiguanco thrush (*Turdus chiguanco,* Vergara-Tabares *et al.* 2016; Vergara-Tabares 2017). This system provides an interesting natural experiment to test the effects of seasonal food fluctuations and invasion of alien food resources on the dynamics of a fruit consumer's energy storage. In natural areas not yet invaded by *P. angustifolia*, reduction in native fruit availability during fall–winter may act as an environmental energetic challenge (i.e. food shortage per se or the need to spend energy searching for food). Such an energetic challenge is expected to activate the HPA axis and cause an increase in circulating CORT and catabolism of stored reserves. In contrast, in areas invaded by fleshy-fruited exotic plants that fruit in fall–winter, the activation of the HPA axis could be attenuated and result in lower circulating CORT, and, thus, a lower rate of catabolism of stored tissue reserves in individuals that have access to a supplementary source of food. The aim of this work was to test the effect of fruit supplementation by the alien fleshy-fruited plant *P. angustifolia* during fall–winter on circulating plasma CORT and energy storage in the Chiguanco thrush in the mountain Chaco woodland of Sierras Grandes, Córdoba, Argentina.

MATERIALS AND METHODS

Study system

We carried out the study in the occidental slopes of Sierras Grandes de Córdoba, Argentina, a locale which is characterized by stands of vegetation both invaded by and free of *P. angustifolia*. *P. angustifolia*, a species native to China, was introduced as an ornamental to central Argentina approximately 100 years ago (Deluchi 1991), and has since invaded vast areas in this region. This plant is a thorny shrub that belongs to the Rosaceae family and produces fruit as a very dense and colorful (red–orange) infructescense (Weber 2017). Although *P. angustifolia* may facilitate the invasion of other exotic species (e.g. *Ligustrum lucidum*; Tecco *et al.* 2006), *P. angustifolia* is largely the only and by far the most abundant alien species at our study sites. This alien plant integrates into the native woodland matrix in disturbed areas (e.g. post-fire land and floodplains) and rarely forms monotypic stands (Giorgis *et al.* 2011).

We selected the Chiguanco thrush, the most abundant resident species, as a focal species in the study. It is a frugivorous species with high territoriality and short distance movements (Collar 2017, TNR & DLV-T, personal observation), consuming fleshy fruits from native (*L. molleoides*, *C. ehrenbergiana*, *Condalia* sp.) and exotic (*P. angustifolia*, *Ligustrumlucidum*, *Morus* sp.) plants (TNR & DLV-T, personal observation). The Chiguanco thrush feeds mainly on fruit when available but may be able to incorporate arthropods, earthworms and small reptiles into its diet (Collar 2017). Thrushes have been reported to be important seed dispersers worldwide, for not only native species but also introduced ones, including several species belonging to the Rosaceae family (e.g. Sallabanks 1992; Jordano 1995).

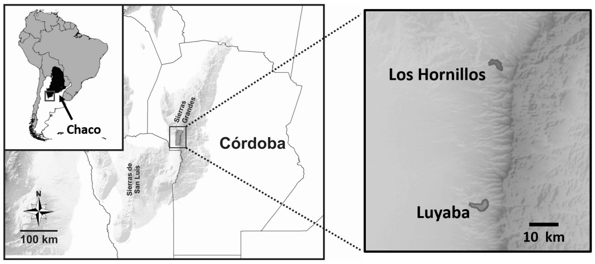

Figure 1 Map of the location of study sites. The left inset shows the location of the Chaco region in South America and Argentina. In the right inset, we highlight both study sites, the site invaded by *Pyracantha angustifolia* in Los Hornillos and the non-invaded site in Luyaba.

We selected 2 areas of sufficient distance from each other to guarantee independence of observations (see Fig. 1). The area invaded by *P. angustifolia* is located at Los Hornillos (hereinafter, "invaded site," 31°54′13″S, 64°59′22″W). The area found to be free of *P. angustifolia* is located at the Wildlife Refuge Los Barrancos, Luyaba (hereinafter, "non-invaded site," 31°48'S, 65°02'W). The sites are at an aerial distance of 26.7 km from each other, being separated by several hills. Study areas show a physiognomy that belongs to the mountain Chaco woodland, an open to semi-closed forest (Cabrera 1976; Giorgis *et al.* 2011). Both sites have the same altitude (900–1000 m above sea level) and similar native floristic composition, with assemblages dominated by *L. molleoides*, *C. ehrenbergiana*, *Acacia caven*, *Bougainvillea stipitata*, *Heterotalamus alienus*, *Flourensia* sp. and *Baccharis* sp. (Giorgis *et al.* 2011). Regarding plant composition, the only difference between the invaded and non-invaded study areas is the presence of *P. angustifolia*. Mean annual precipitation at both sites is approximately 700–800 mm (concentrated in summer) and mean annual temperature is 17.5 °C (data taken at the station La Ventana, Acosta *et al.* 1992).

Bird capture and blood sampling

We mounted mist nets once during summer of 2014 (March, when both invaded and non-invaded areas have similar fruit availability), twice in winter of 2014 (period when native fruits are scarce at both non-invaded and invaded areas), in July (peak of *P. angustifolia* fruit production at invaded site) and in September (nadir of *Pyracantha* fruit production at invaded site). Each capture period lasted approximately 20 days, with alternating captures between invaded and non-invaded sites. We opened mist nets from sunrise until 1100 hours and then in the evening from 1400 hours to sunset. To infer energetic reserves, we used 3 body condition indices that relate to energetic reserves in birds (Peig & Green 2009; Labocha & Hayes 2012): (1) body mass; (2) residuals of an OLS of linear regression between body mass and tarsus length (hereinafter, "Rs. BM/TL"; Schulte-Hostedde *et al.* 2005; Salewski *et al.* 2009; Labocha & Hayes 2012); and (3) categorical estimation of subcutaneous fat (hereinafter, "fat score"; Kaiser 1993). The fat score consists of assigning a numerical score to the fat deposits in the furcular cavity, ranging from 0 (lack of visible fat) to 6 (furcular cavity overflowing with fat) (Kaiser 1993; Dunn 2003). The same observer (TNR) assessed fat scoring in all birds. Finally, we banded all captured birds with unique color combinations of rings to avoid individual resampling.

For blood sampling, we bled birds from the right jugular vein using heparinized syringes (1 mL; less than 1% of mean Chiguanco thrush body weight; Collar 2016) within 2 min of capture to avoid an increase in glucocorticoid concentrations caused by manipulation stress (Romero & Reed 2005; Owen 2011). Then, we kept blood samples on ice (4–5 °C) for less than 6 h until they were centrifuged at 708.48 *g* for 10 min. We then recovered plasma and stored at –20 °C until we conducted the hormone assay (Owen 2011; see below).

Hormone assay

We determined CORT concentrations in plasma samples using EIA. The polyclonal anti-CORT antibody (CJM006, kindly provided by C. Munro, Department of Population Health and Reproduction, UC Davis, CA, USA) was found to cross-react as follows: corticosterone 100%, desoxycorticosterone 12.45%, progesterone 2.65%, tetrahydrocorticosterone 0.90%, testosterone 0.64%, cortisol 0.23%, prednisolone 0.07%, 11-desoxycortisol 0.03%, prednisone <0.01%, cortisone <0.01% and estradiol <0.01%. We performed assays according to the general technique described by Munro & Lasley (1988). Briefly, we assayed plasma samples in duplicate using flat-bottom microtiter plates (Nunc Maxisorp, VWR, Mississauga, ON, Canada). First, we coated the plates with 50 μL of anti-CORT antibody stock diluted in coating buffer (50 mM bicarbonate buffer, pH 9.6, 1:15 000), covered with acetate sealers to prevent evaporation and incubated overnight at 4°C. After 16–24 h, we washed the plates to remove any unbound antibody with 0.02% Tween 20 solution using a Bio-Tek ELx 405VR microplate washer (Bio-Tek Instruments, Winooski, VT). Immediately after washing, we added 50 μL of samples, standards and controls in duplicate, followed by 50 μL of horseradish peroxidase conjugate diluted in EIA buffer (1:70 000). Then, we covered the plates and incubated at room temperature (21 °C) for 2 h in an orbital shaker. Following incubation, we washed the plates, blotted them dry, and added 100 μL of substrate solution (50-mM citrate, 1.6-mM hydrogen peroxide and 0.4-mM 2, 20-azino-di-[3-ethylbenzthiazoline sulfonic acid] diammonium salt, pH 4.0) to each well (Munro *et al.* 1991). We measure absorbance at 405 nm using a microplate reader (Thermo Electron Corporation, USA). For all hormonal determinations, the measured intra-assay and inter-assay coefficients of variation for the high and low control samples were <12% and <3.4%, respectively. Assay sensitivity was 0.078 ng/mL.

Statistical analysis

First, we explored the data with boxplots. We performed general linear mixed models (GLMMs) with site, period and their interaction as fixed effects, and bird age (adult or juvenile) and capture time (morning or evening) as random effects. For all analyses of body mass, Rs. BM/TL, and the log-transformed CORT values, we used Guassian error distributions. For the analysis of fat scores, we used a logistic error distribution because the fat score is an ordinal variable. Finally, we tested the relationship between energetic reserves (i.e. body condition indices) and CORT with GLMMs. We included energetic reserves as response variables, CORT as a fixed effect, and bird age and capture time as random effects. We corrected *P*-values for multiple comparisons using the Benjamini and Hochberg method (1995), as it controls for a false discovery rate and is a less conservative method than a strict Bonferroni correction, avoiding augmentation of type II error (Shaffer 1995; Abdi 2007). We conducted all statistical analyses in R environment (R Development Core Team 2016). We used ggplot2 (Wickham 2009) to build boxplots, fitdistrplus (Delignette-Muller & Dutang 2015) to fit error distributions, and lme4 (Bates *et al.* 2015) and MASS (Venables & Ripley 2002) to perform the GLMMs. We established the significance level in all analyses at *P*-value < 0.05. All models satisfied homoscedasticity and independence assumptions.

RESULTS

We caught 118 individuals; however, only the 90 birds that were bled within 2 min of capture were used for hormone determinations. Moreover, we were unable to capture a representative sample size of Chiguanco thrush during summer (when both invaded and non-invaded areas have similar abundance of native fruits) because during this period thrushes are highly territorial and concentrate their foraging behavior predominantly at the top of the canopy.

Body condition indices show a consistent pattern (see Fig. 2a–c and Table 1). We detected a significant interaction effect between site and period in explaining the 3 body condition indices we used (see Table 2 for test statistic results). Body mass, fat score and Rs. BM/TL decreased between periods in the non-invaded site, while only fat score was different between periods in the invaded site (see Table 1 and Fig. 2). Fat scores were higher in September relative to July (Fig. 2c).

Circulating CORT of Chiguanco thrushes was not explained by site, period or their interaction (see Table 1 and Fig. 2d for details on values and pattern, respectively; see Table 2 for test statistics). Finally, we did not detect a demonstrable effect of CORT on energetic reserves (body mass $P = 0.203$; fat score $P = 0.107$; Rs. BM/TL $P = 0.181$).

DISCUSSION

Here, we report that food supplementation by an alien fleshy-fruited invasive plant ameliorates the consumption of energetic reserves in a native frugivore during the fruit scarcity season. In a natural scenario composed of areas invaded and not invaded by *P. angustifolia*, we found that Chiguanco thrush inhabiting a non-invaded area showed a clear decrease in energetic reserves towards the end of the winter. In contrast, for birds inhabiting an invaded area, we found no differences in energetic reserves during the study period. Contrary to our hypothesis, we found that birds from both areas showed

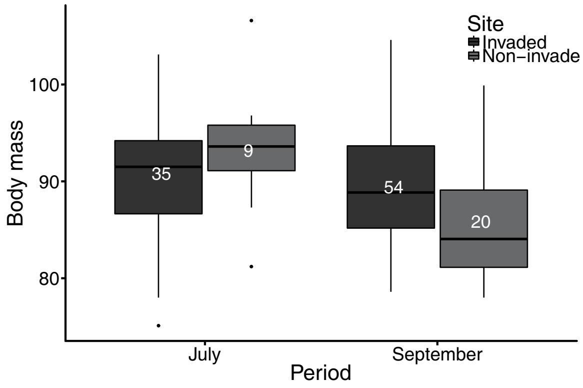

Figure 2 Measured variables of Chiguanco Thrush (*Turdus chiguanco*): (a) Body mass (grams); (b) Residuals of Body mass relative to tarsus length (Rs. BM/TL); (c) Fat score; (d) Logarithm of plasma corticosterone (log (CORT)) measured as ng/ml. Boxes in light gray represent the site invaded by *Pyracantha angustifolia* and boxes in dark gray represent the non-invaded site in 2 periods, July (early winter) and September (late winter). White numbers inside the boxes represent sample size.

Table 1 Mean and standard deviation of the 4 variables measured in Chiguanco thrushes (*Turdus chiguanco*) in 2 sites (invaded and non-invaded by *Pyracantha angustifolia*) and 2 periods (July and September)

Variable	Site	Period	*n*	Mean ± SD
Body mass (g)	Invaded	July	35	90.83 ± 6.43
		September	54	89.43 ± 6.31
	Non-invaded	July	9	93.22 ± 6.99
		September	20	85.88 ± 6.31
Rs. BM/TL	Invaded	July	35	1.57 ± 6.24
		September	54	−0.27 ± 6.29
	Non-invaded	July	9	3.83 ± 7.27
		September	20	−3.75 ± 6.04
Fat score	Invaded	July	35	3.40 ± 1.31
		September	54	3.96 ± 1.13
	Non-invaded	July	9	3.67 ± 1.22
		September	20	2.70 ± 0.98
CORT (ng/mL)	Invaded	July	25	168.63 ± 86.68
		September	42	71.17 ± 88.95
	Non-invaded	July	7	189.98 ± 129.67
		September	16	85.99 ± 106.05

Table 2 General linear mixed model results

Variable	Factor	*t*	Degrees of freedom	*P*-value
Body mass	Site	0.979	113.02	0.560
	Period	−1.041	113.00	0.560
	Site*Period	−2.414	113.76	0.021*
Rs. BM/TL	Site	0.937	113.02	0.560
	Period	−1.373	113.00	0.560
	Site*Period	−2.330	113.76	0.021*
Fat score	Site	0.577	113.02	0.643
	Period	2.315	113.00	0.020*
	Site*Period	−2.759	113.76	0.021*
CORT	Site	0.736	86.00	0.618
	Period	−0.993	86.00	0.560
	Site*Period	−0.269	86.00	0.788

P-values are corrected by Benjamini Hochberg method. *Significant effect of factor level. We detected a consistent pattern in body mass, fat score and residuals of body mass/tarsus length (Rs. BM/TL). We found a significant effect of period (July and September)–site (invaded and non-invaded) interaction in the 3 indices used to characterize body condition of Chiguanco thrush.

similar plasma CORT levels.

Food shortage during winter appears to be a strong energetic challenge that induces changes in energy reserves through time (Fig. 2a–c). In birds inhabiting areas not invaded by *P. angustifolia*, we found a decrease in energy stores between July and September. In this area, birds are not only exposed to less food availability than at invaded sites (i.e. no native plants offer fruit during winter), but they also have to invest a considerable amount of their time and energy to capture a limited amount of insects which are not abundant during winter. The energy spent in looking for and capturing insects is expected to be much greater than that needed to retrieve fruit from highly productive shrubs with vastly aggregated distribution. Hence, it is likely that birds in the non-invaded site cope with their unmet daily energetic needs by consuming energy stores (Harding *et al.* 2011; Lerman *et al.* 2012). In contrast, for birds inhabiting invaded areas, fruits provided by *P. angustifolia* seemed to be a significant food resource to prevent metabolism of energy stores. At invaded areas, the aggregated distribution of *P. angustifolia* shrubs and its dense fruit display may not only provide a supplemental food resource but also reduce foraging costs, thereby preventing the consumption of energy stores (Pravosudov & Clayton 2001; Goymann *et al.* 2006; Harding *et al.* 2011). Another explanation for the difference in fat scores between birds from invaded and non-invaded sites may relate to changes in life history stages, such as energetic costs associated with pre-reproductive behaviors. In animals, reproduction usually diverts energy away from investment in vital somatic functions or storage for future reproduction (Stearns 1992). For example, displays and/or territorial disputes, which occur in *T. chiguanco* during September, have associated energetic costs (Williams 1966) that may reduce their ability to deposit fat in the furcular cavity when food is limited (i.e. at the non-invaded site). Yet, fat deposition is more likely to happen when *P. agustifolia* fruit is available at invaded sites. Although it may seem counterintuitive that birds from invaded areas increased their fat storage but other body indexes did not change, we understand such results as an artifact of the type of variables and the statistical analysis we conducted to interpret them. However, the 3 indexes together reflect animal body condition; hence inferences should consider integration of the 3 indexes. Even though we did not measure non-fruit avian food resources in this study, indirect evidence provided by another study conducted at the same sites suggests that the availability of other food resources such as arthropods or seeds is not affected by the presence of *P. angustifolia*. More specifically, Vergara-Tabares (2017) showed that the abundance of insectivorous and granivorous birds does not to differ between invaded and non-invaded sites. This supports the argument that food resources in the invaded and non-invaded habitats are similar except for the fruits provided by the invasive shrub, which we hypothesize are responsible for the changes in body condition observed here in Chiguanco thrushes.

In a number of species, it has been demonstrated that changes (e.g. fluctuations or drastic reductions) in food availability are related to an activation of the HPA axis, with a consequential increase in circulating CORT (Chapman *et al.* 2006; Kitaysky *et al.* 2007; Benowitz-Fredericks *et al.* 2008; Hennin *et al.* 2016). Such changes in CORT concentration were observed under environmental conditions more extreme than the ones at Mountain Chaco Woodland, which may suggest that winter fruit scarcity in non-invaded locales may not be a stressor sufficient to affect plasma CORT levels in Chiguanco thrushes. However, we cannot disregard the influence of other stressors, as CORT is a general stress response hormone. For example, density of birds in the invaded site may increase CORT levels if the higher density exacerbates competitive interactions among individuals (Carere *et al*. 2003; Goymann & Wingfield 2004; Rivers *et al*. 2012). Although we found an important reduction in energy stores in the thrushes from non-invaded sites, it is possible that CORT is not directly responsible for the catabolism of fat tissue observed in those birds. In other words, other hormones such as ghrelin and leptin may be involved in these physiological processes (Lohmus *et al.* 2003, 2006); Kaiya *et al.* 2013; Prokop *et al.* 2014). The few studies on the effects of both ghrelin and leptin on birds are contradictory (suggesting both stimulation and inhibition of food intake), and vary depending on bird species, migratory behavior, and experimental doses and conditions tested (Lohmus *et al.* 2003, 2006; Kochan *et al.* 2006; Ohkubo & Adachi 2008; Kaiya *et al.* 2013; Prokop *et al.* 2014). Even more importantly, neither of these hormones have yet been tested on free living birds; therefore, their physiological role is still under debate.

Supplemental food resources offered by an invasive plant may affect the fitness of consumers due to its effects on individual energy stores, with further consequences at the population level. Variation in energy stores can act as both a driver and a constraint of fitness-related decisions (Stearns 1992; McNamara & Houston 1996). Individuals with greater energy stores are predicted to complete energetically demanding stages (i.e. reproduction, molt and migration) with greater success (Rowe *et al.* 1994; Kisdi *et al.* 1998; Crespi *et al.* 2013). Focusing on reproductive success, empirical evidence shows that variation in quantity and quality of supplemental food availability during the pre-breeding season may either have no effect or have negative effects on reproductive success depending on its context (Schoech *et al.* 2008; Plummer *et al.* 2013; Ruffino *et al.* 2014). Birds from invaded areas have less diverse diets than birds from non-invaded areas (Rojas *et al.* 2015). Therefore, it is likely that the Chiguanco thrushes in our study would have a less diverse diet in the invaded sites than in the non-invaded sites. Low diet diversity may result in a lack of some nutrients (e.g. proteins, essential nutrients and vitamins) that are important for egg production or molt (Raubenheimer *et al.* 2009; Johnstone *et al.* 2012; Cohen *et al.* 2013). Similarly, energy reserves can help organisms to overcome challenging situations (e.g. low temperatures, highly energy demanding activities and starvation avoidance), enhancing individual survivorship (Broggi & Brotons 2001; Turcotte & Desrochers 2008; Hennin *et al.* 2016). In line with this argument, one would predict that supplemental food provided by an invasive plant during a non-breeding season characterized by food shortage would be positive for individual survival and particularly for juveniles hatched during the previous breeding season.

Interactions between invasive fleshy-fruited plants and native birds have been widely recorded (Buckley *et al.* 2006; Traveset & Richardson 2011; Mokotjomela *et al.* 2013), although these studies have largely focused on the botanical consequences of avian interaction (i.e. enhancement of seed dispersal and facilitation of alien plant invasion by native birds; Richardson *et al.* 2000; Heleno *et al.* 2013; Mokotjomela *et al.* 2013). In contrast, previous studies investigating the effect of invasive fruit availability on birds show idiosyncratic results on refueling and health parameters (Reichard *et al.* 2001; Smith *et al.* 2015; Gleditsch 2017; Oguchi *et al.* 2017). In our study, we found that fruits offered by an alien plant prevented depletion of energy stores in a native frugivorous bird. We also know from previous studies (Vergara-Tabares *et al.* 2016; Vergara-Tabares 2017) that Chiguanco thrushes effectively disperse *P. angustifolia* seeds, thereby demonstrating their consumption of its fruit. However, further investigations are needed to determine the direct effect of such interaction on Chiguanco thrush survival and reproduction success.

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