


Turdus flavipes altitudinal migration in the Atlantic Forest The Yellow-legged Thrush is a partial altitudinal migrant in the Atlantic Forest

Avian Biology Research
2022, Vol. 0(0) 1–8
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DOI: 10.1177/117581559221097269
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Abstract

Few studies on bird migration address altitudinal migration in South America, a regional-scale movement currently known for only nine species within the threatened Atlantic Forest biome. The Yellow-legged Thrush *Turdus flavipes* (YLTH) is one of such migrants thus far studied within a narrow altitudinal gradient and for which only fruits are pointed as the likely triggers of its seasonal movements. Here, we expand this knowledge by testing the hypotheses that arthropod and fleshy fruit availabilities, and climatic variables may all play roles in the seasonal abundance of this species along a broader altitudinal gradient (10–1,100 m asl) in the Atlantic Forest. We estimated YLTH density and its food resource availability in sites at three different altitudes. Besides supporting previous findings on the YLTH migratory behaviour, our findings reveal a novel and complex seasonal density variation of the species across altitudes, consistent with a partial altitudinal migration from higher altitudes. Aside from fruit availability, rainfall also partially influenced such behaviour, a new perspective for this species. Besides providing a broader picture for the altitudinal migration of YLTHs, we conclude by stressing the need for further studies on the understudied altitudinal migration system of birds within South America, including the assessment of the general validity of current hypotheses on the mechanisms underlying this interesting behaviour and its evolution.

Keywords

altitudinal migration, climatic variables, intratropical migration, line transect census, partial migration, resource availability, Turdidae

Birds have a wide variety of migratory strategies and patterns in the Neotropics (1) and the studies within the South American intratropical migration system are steadily increasing in number (e.g. 2–12). Nevertheless, knowledge is still incipient, especially when considering the complexity of migratory movements in this region in which partial and facultative migrant species abound (13). Within such short-distance migratory movements, altitudinal migration stands out as the least studied migratory behaviour of birds and in which individuals usually move between breeding at highland sites and overwintering at lowland sites (14).

Brazil is the largest country within South America (15, 16) and hosts the third richest avifauna of the world (17). A recent review reports that ~10% ($N = 198$) of the Brazilian bird species have some migratory behaviour, but only 11 show evidence of altitudinal migration (13). Among them, nine inhabit the Brazilian Atlantic Forest (13), a fragmented biodiversity hotspot (18). The numerous mountain ranges within this domain potentially contain still unknown altitudinal migrants (e.g. 6, 19), supporting the recurrent appeals urging for more bird migration studies in the region (1, 13, 14, 19, 20).

The Yellow-legged Thrush *Turdus flavipes* (Turdidae; hereafter ‘YLTH’) is often described as an altitudinal migrant species in the Atlantic Forest (20–25), but there is a lack of

consensus (9, 13, 26). According to censuses in Atlantic Forest lowlands at altitudes ranging from the sea level up to 350 m (23) and 250 m asl (24), the species migrates altitudinally during the winter (i.e., May–August). During these movements, birds seem to track the availability of fleshy fruits of only one species, the Juçara Palm (*Euterpe edulis*) (24). This palm tree producing energy-rich fruits during the dry season is key for frugivores (27) and has been found to be an important predictor of the YLTH seasonal altitudinal movements (22, 24, 28). Nevertheless, all previous studies have failed to consider a number of other cues known to be tracked by altitudinal migrants, including but not

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restricted to the availability of other food items (e.g. arthropods) and weather, specifically rainfall (reviewed in 14).

To broaden the existing knowledge on the altitudinal migration of the YLTH, we herein evaluated population-level annual seasonality of the species at three sites along the broadest altitudinal range ever considered in studies of this species (1,000-10 m *versus* <250 m asl). We also assessed the relationships between the species' local densities and abiotic (i.e., rainfall and temperature) and biotic variables (i.e., fruit and arthropod availability). We specifically aimed to check the general validity of previous findings (24) by answering the following questions: (i) does the YLTH density vary along this broad altitudinal range according to seasons? If so, (ii) what are the roles played by the biotic and abiotic factors? We expected to confirm the altitudinal migratory behaviour of YLTHs over this broadest altitudinal range, but predicted that the migratory behaviour would be explained by predictors in addition to the availability of Juçara Palm fruits, such as by arthropod availability (29) and heavy rains (30).

Methods

Study sites and climatic variables. To encompass the broadest possible altitudinal span within the Atlantic Forest, we collected data at three sites in SE Brazil: two lowland sites within the Reserva Natural Guaricica (25°18'S, 48°40'W; Fig. 1), namely L1 (99-10 m asl) and L2 (199-100 m asl) and one in the Mananciais da Serra (25°30'S, 48°59'W; Fig. 1), namely the highland site (1,100-900 m asl). The areas lie within Lagamar, a World Heritage region as designated by UNESCO (31) protected for being the largest continuous Atlantic Forest remnant (18) and thus containing important bird conservation areas (32). The fieldwork at the lowland occurred within the context of the long-term Brazilian Biodiversity Research Program in the Atlantic Forest (PPBio-MA; 33). All sites are dense and closed canopy tall evergreen forested areas (34, 35) with similar

average weather conditions, except for the highland site which is slightly colder and rainier than the lowlands (respectively: 15-18°C and 2,500-3,500 mm *versus* 19-20°C and 2,000-2,500 mm; 36). The coldest and rainiest period in the region is from June to August and coincides with the YLTH non-breeding period (February to October; 26, 37). We obtained all monthly climatic variables from the nearest weather stations to each area (Instituto SIMEPAR, www.simepar.br; highland: Curitiba station, ~35 km away from the study site; lowlands: Antonina station, ~18 km) and daylength for the study region from Daylight Calculator (<http://jan.moesen.nu/daylight-calculator>).

Population density estimates. We inferred YLTH densities throughout the year through line transects (38, 39). Despite hardly seen, the YLTH is easily detected by ear due to its constant and conspicuous singing during the breeding season and to the frequent and unique calls it emits year-round (22). We used as transects pre-existing trails within the study areas (N=3 at the highland site, N=2 in each of L1 and L2), totaling 6.5 to 7.0 km in length. We sight-estimated the perpendicular distance to the trail for each YLTH seen or heard (38, 39). We sampled all transects in each area within 2-3 non-raining consecutive days, starting ~10 min after dawn and lasting for ~2 h. We sampled the highlands monthly, but logistical constraints limited lowland sampling to six events throughout the year (white segments in Fig. 2).

Food availability. We monitored ornithochoric fruit production and the availability of arthropods throughout the study period. Sampling took place in the same months as we censused birds in multiple plots (N=1,500 m² in total) spread >50 m away from trails and roads at each site: ten 15×10 m plots at the highland and four pre-existing plots within the lowlands, one of 20×35 m and one of 20×40 m at each altitude. We used 10×42 binoculars (Bushnell™ H2O) to estimate the total amount of fruits produced per hectare in each plot by carefully counting all ripe fruits from every fleshy-fruited tree and treelet within the plot, from understory to

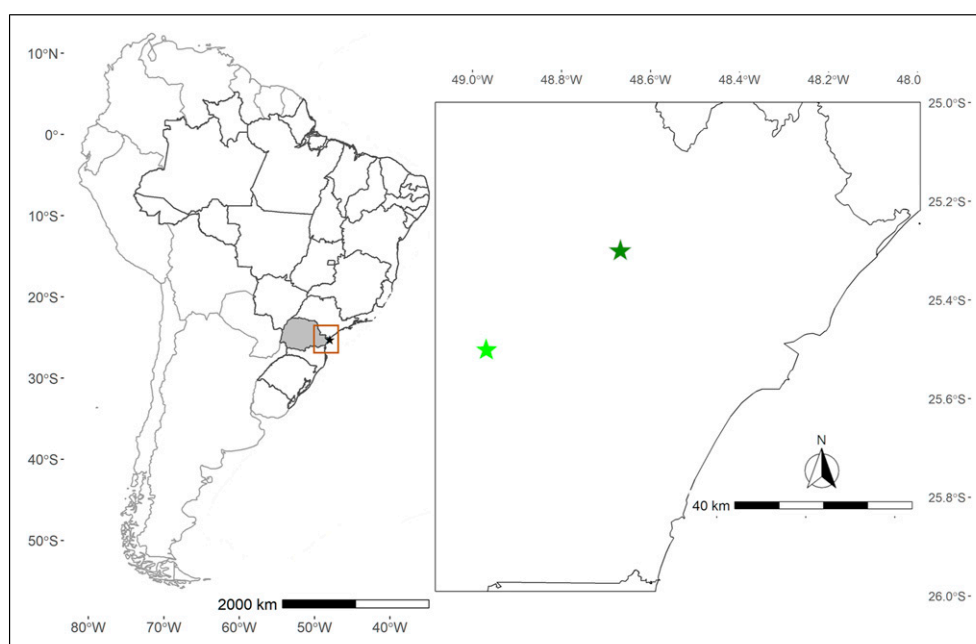


Figure 1. Location of the sampling sites in SE Brazil, at the Atlantic coast of Paraná state. The highland area lies within Mananciais da Serra (dark green star) and ranges from 1,100-900 m asl and the two lowland sites (L1 and L2) lie within the Reserva Natural Guaricica (light green star), respectively spanning from 199-100 m asl and 99-10 m asl.

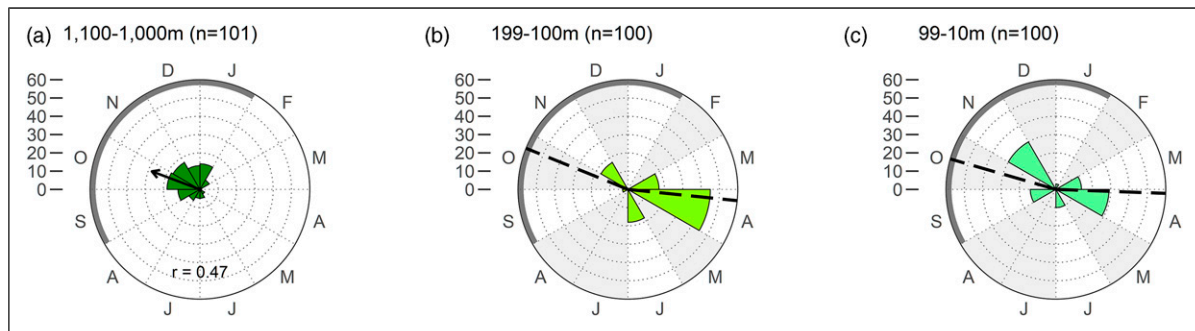


Figure 2. Annual density variation (individuals.km⁻¹) of the Yellow-legged Thrush *Turdus flavipes* at three sites along an altitudinal gradient (1,100-10 m asl) in Southern Brazil. The arrow in A points to the species' mean peak occurrence date and r is the data concentration value around it. Black dashed lines mark each of the two mean peak dates of occurrence where the species showed bimodal seasonality. Dark-shaded arcs signal the species breeding period and white segments the sampled months.

canopy, exploiting the long-term experience of the lead author on this method and habitat (40). The estimations included all species that produce fruits narrower than the YLTH gape size (11.8 ± 0.7 mm; 41). Juçara Palms occur only in the lowland sites and thus we recorded their fruit counts separately from other fleshy-fruited species for further analytical purposes. We sampled arthropods using 12 DUET traps (42), eight at the highland site and two at each of the lowland sites, all suspended at ~ 1.5 m above ground and >10 m far from fruit counting plots and trails. Traps were active 24/7 throughout the study and monitored with the same regularity as fruit counting. Collected arthropods were preserved in 70% ethanol and later oven-dried (Marconi™ MA033/5, Piracicaba/SP – Brazil) at 60°C for 24 h in the lab for dry biomass measurement (0.1 mg precision; Toledo™ AS220, São Bernardo do Campo, SP/SP – Brazil). As is typical of many thrushes, the YLTH has a generalist diet mostly based on fruits and invertebrates (22, 28). The literature provides no further details on which arthropods the YLTH consume, but they perform low flights and ground foraging to ingest lepidopteran larvae, dipterans, and orthopterans (ACG, *personal observation*). Therefore, we used the average of arthropod biomass captured by every DUET trap as a proxy for this resource availability in each area and month, ensuring between-sites comparability through the ratio of biomass to the number of sampling days in each given area.

Data analysis. We estimated YLTH densities in each site through the uniform key function and cosine series expansion, truncated at 5% of the greatest distance (43). For that, we calculated a set of nine possible combinations of key functions (half-normal, hazard rate, and uniform) and series expansion (cosine, Hermite polynomial, and simple polynomial) implemented in the Distance package (44). We selected models based on their AIC values and assuming as a cutoff $\Delta AIC < 4$ (45). We used relative density estimates to calculate the mean occurrence peak date of YLTH at each site. Since data inspection revealed marked bimodality at the lowland sites, we calculated two mean occurrence peak dates in these areas (46), i.e., one for the breeding and another for the non-breeding seasons.

We squared-root transformed the density estimates to achieve a Gaussian distribution (Shapiro-Wilk's $W = 0.97$, $P = 0.63$) and used it as the response variable in a Linear Model (LM) to test its relation to abiotic (rainfall and temperature) and biotic (fruits and arthropod availabilities) variables. We used variance inflation factors to check for collinearity

between the predictors (i.e., $VIF > 3$; 47, 48). We ran an additional LM restricted to the lowlands data, i.e., where Juçara palm naturally occurred, for further assessing the existing hypothesis that Juçara Palm fruits seasonality influence the YLTH altitudinal migration (24). Thus, we explicitly considered Juçara Palm fruits as a variable separate from the other fleshy-fruited species for comparatively assessing the effects of their availability in YLTH temporal density variation. In this model, we also included arthropod availability and average temperature as predictors but excluded rainfall due to collinearity ($VIF = 7.54$). Paired t-tests compared the average monthly rainfall in high- and lowland areas, including cross-season comparisons (highland breeding *versus* lowland non-breeding seasons). We centered and scaled all variables in both LMs. We ran likelihood ratio tests between a full and a set of nested models, i.e., models excluding each particular predictor, for assessing model's goodness of fit (47) and hence, the explanatory power of each predictor, assuming $\alpha = 0.05$. We ran all analyses and plots in R v. 3.4.2 (49) using functions within packages *car* (50), *CircStats* (51), *circular* (52), *lme4* (53), *ggplot2* (54), *grid* (49), *cowplot* (55), and *effects* (56).

Results

Population density estimates totaled 123 km of transects (84 km at 1,100-900 m asl and 39 km at 199-10 m asl). Throughout the year, the YLTH showed different temporal patterns of density at each altitude. At the highland site, mean density peaked during the breeding period (late-October), with medium concentration of the occurrence records around this date ($r = 0.47$). This results from the spread occurrence of the YLTH throughout the breeding period in conjunction to its low numbers during all the non-breeding season but March and April (Fig. 2A). In the lowlands, population densities showed bimodal distributions, with occurrence peaks in both breeding and non-breeding seasons (dashed lines in Figs. 2B-C), therefore precluding the estimation of the concentration vectors.

The YLTH density peaked at similar dates at the two lowland sites (199-10 m asl) in both breeding and non-breeding seasons (i.e., late-October and early-April, respectively). Within the censused months in these areas, the YLTH showed no clear period of continuous absence or low

Table 1. Effects of abiotic (rainfall and temperature) and biotic predictors (fleshy-fruits and arthropod availability) on the monthly variation of Yellow-legged Thrush *Turdus flavipes* population densities along altitudinal gradients in Southern Brazil. A first model considered a broader altitudinal scenario (1,100-10 m asl) in which the availability of all fleshy-fruit was considered as a predictor of the YLTH density variation. The second model was restricted to the lowland sites (199-10 m asl) and considered Juçara Palm (*Euterpe edulis*) fruits apart from other fleshy-fruits. Rainfall was excluded from the second model due to collinearity with Juçara Palm fruits availability. Significant P-values (< 0.05) are bolded.

Altitudinal range	Full model R^2_{adj}	Predictors (R^2_{adj} of the model without the predictor)	LRT (p-value)	$\beta \pm SE$	t	P-value
1,100-10 m asl	0.35	rainfall (0.16)	6.85 (0.009)	-0.09 ± 0.04	-2.49	0.02
		temperature (0.38)	0.13 (0.72)	-0.01 ± 0.04	-0.32	0.75
		fruits (0)	10.69 (0.001)	0.12 ± 0.04	3.26	0.005
		arthropods (0.38)	0.49 (0.48)	0.02 ± 0.03	0.62	0.54
199-10 m asl	0.46	temperature (0.55)	0.06 (0.81)	0.01 ± 0.06	0.17	0.87
		Juçara Palm fruits (0.49)	1.30 (0.26)	-0.04 ± 0.05	-0.83	0.45
		fruits (except Juçara Palm) (-0.15)	9.40 (0.002)	0.11 ± 0.04	2.79	0.04
		arthropods (0.41)	2.84 (0.09)	-0.04 ± 0.03	-1.28	0.26

densities (Figs. 2B-C), being absent or showing only few individuals (~ 3 individuals.km⁻¹) only in January at both lowland sites and only in September at 199-100 m asl (~ 3 individuals.km⁻¹). It is noteworthy that the density peak date during the breeding season was similar across the altitudinal gradient.

Average monthly rainfall did not correlate with food availability at each altitude (i.e., both predictors showed VIF < 3 in the models), but rainfall was similar at the high- and lowland sites (highland: 120.4 ± 35.1 mm; lowlands: 150.0 ± 90.2 mm; $t_4 = -0.86$, $P = 0.44$) even cross-seasonally ($t_4 = -0.58$, $P = 0.60$). Availability of fruits and average monthly rainfall explained monthly density variations of YLTH in all sampled sites (Table 1). When restricting our analysis to the two lowland areas (199-10 m asl), the availability of flesh-fruits other than Juçara Palm was the sole positive and significant predictor of the YLTH monthly density variation (Table 1).

Discussion

We found seasonal variation in the YLTH populations along the studied altitudinal gradient consistent with their migratory behaviour. Individual density in the highlands (1,100-900 m asl) peaked only during the breeding period, thus providing evidence for a partial migration. In the lowlands, YLTHs had a bimodal density temporal distribution, peaking during both the breeding and non-breeding periods. In the two lowland areas, the species' monthly densities varied markedly throughout the year but with no sustained absences. Despite being less straightforward than the demographic pattern at the highland site, YLTHs also showed a local occurrence pattern akin to partial migration in these lowlands. In short, the species occurred along the entire studied altitudinal range during both breeding and non-breeding periods, but our finer scale analysis supported a plausible partial migration after the breeding period from the highland to the lowland sites. The species showed more complex temporal density patterns in the lowlands, where variations were consistent with in-bound movements during both breeding and non-breeding periods. Complexity also defined the abiotic and biotic variables affecting birds' seasonality. When considering the entire altitudinal range, the YLTH

densities responded positively to fruit availability but negatively to rainfall. When narrowing our analysis for allowing comparison with previous studies, and thus with the range of occurrence of the Juçara Palm (199-10 m asl), the availability of all fleshy-fruited species, except those from this Palm, significantly and positively correlated to monthly density variations of the studied YLTH populations.

Any comprehensive literature survey on the migratory status of the YLTH will reveal inconsistencies. Some broad-scale studies describe it as resident (e.g. 28, 57) but others as a poorly understood austral migrant (58). Our findings add support to previous studies that describe the YLTH as migratory (9, 13, 24, 25). Specifically, our data suggest that populations of this species partially migrate altitudinally within the Brazilian Atlantic Forest, with marked between-population variation. As such, YLTHs seem to be an interesting model species for advances in knowledge about migratory connectivity level within the altitudinal migration system, an important additional element in conservation (59, 60), especially within the Atlantic Forest, one of the world's most threatened forested biomes (18).

A recent broad-scale study focused, among other subjects, on the evolution of migratory behaviour in *Turdus* spp. (61). We acknowledge that such phylogenetically controlled studies of avian life history often end up obscuring details due to logistical constraints in their analyses and data sampling protocols. Despite assigning the YLTH as a sedentary species, Nagy et al. (61) showed that *Turdus* migration evolved through a partial migratory behaviour across latitudes (i.e., longitudinal migration). Given the behaviours that the YLTH show in our study, we believe this is as an interesting model species for further studies of the evolution of migratory behaviour in *Turdus* spp. Moreover, the narrow geographic range in which these birds occur eases logistical difficulties of sampling populations with a variable degree of partial migration. Hence, this species provides an interesting opportunity to advance our knowledge of bird migration evolution as a whole (62).

Diet is an important correlate of migration evolution within *Turdus* spp. (61), with marked transitions from ancestral insectivorous migrants to frugivorous residents. However, many predictors play roles in defining the onset of bird migration on a local timescale, including food

availability, temperature and rainfall (e.g. 63, 64). Fruit availability was the only one of these variables thus far considered for understanding the migratory movements of the YLTH (24). Therefore, our study augments details of the migration ecology of YLTHs in the Atlantic Forest by including rainfall, temperature, fruits, and arthropods as predictors in the analyses. Despite the YLTH densities showing no correlation to arthropods availability, they correlated to fruit availability across our altitudinal range, thus providing additional support for the longstanding food-driven migratory movement hypothesis (63). A nearby YLTH population (~100 km north at Cardoso Island) showed seasonal density correlated only to Juçara Palm fruit availability but not to other fruiting species (24). Our studied populations showed the opposite pattern of no relationship to Juçara Palm crop size but a strong correlation to fruiting of all other zoochorous species in the area. Juçara Palm has similar density and relative abundance in both studied areas, ~87 ind/ha at Cardoso island and ~73 ind/ha at Paraná respectively, representing 6.9% and 6.5% of all zoochorous species in these areas (65, Moraes & Marques unpubl.). Therefore, a thorough in situ investigation of variations of each YLTH population in response to fruit availability seems to be a particularly interesting research topic. Moreover, previous studies state that the migratory status of a given species is under continuous microevolution (66), with current evidence of, at least, shifts from Neotropical to austral migration (e.g. Barn Swallow *Hirundo rustica* in Argentina; 67)(e.g. Barn Swallow *Hirundo rustica* in Argentina; 67), with residency and partial migration likely being an intermediate step in between these gradient extremes (e.g. 68–70). Therefore, it also seems worth assessing whether the dyads migrant-insectivory and resident-herbivory are true within the YLTH partial migration scenario, assessing whether this species may be transitioning in its migratory status.

A recent review of multiple taxa found that altitudinal migration is usually driven by weather and food availability (71). For instance, the altitudinal migration of a Costa Rican bird (White-ruffed Manakin *Corapipo altera*) resulted from weather-induced risk, specifically by excessive rain that may have limited birds' foraging opportunities (30). The YLTH also negatively responded to rainfall, but in a manner different from the Costa Rican scenario, where the highlands have two-fold higher rainfall than the lowlands. Our study area had a less markedly variable rainfall throughout the year and across the studied altitudinal gradient. Therefore, something different from limited time for foraging was the likely main driver of YLTH phenology. Instead, rainfall may indirectly correlate to YLTH migratory behaviour such as through between-altitudes temporal fruiting mismatch or sequential fruiting (24) or through some other biotic or abiotic variables. Understanding the mechanisms and triggers of YLTHs altitudinal migration within the Atlantic Forest may be difficult because of behavioural variations between population.

There is no clear pattern in the breeding and wintering grounds for altitudinal migrants. Some breed in the highlands and overwinter at lower altitudes (e.g. White-ruffed Manakin; 23), but others show an opposite pattern (e.g. Blue-tailed Hummingbird *Amazilia cyanura*; 72). In partial altitudinal migrants (e.g., American Dipper *Cinclus mexicanus*; 73),

describing a simple pattern of migration risks an oversimplification of their migratory strategies. The scale of our study design revealed that YLTH uses sites at every altitude considered throughout the year with variable intensities. Only finer-grained approaches such as tracking of individual birds (e.g., radio, GPS, stable isotopes) would elucidate further details of the YLTH movement patterns through the Atlantic Forest altitudinal range.

There is a growing number of bird migration studies within South America which are steadily bridging knowledge gaps (e.g. 2,3,10,11,13,64,74–76). Our study adds to them and reveals the potential for investigations along wide altitudinal gradients still connected by continuous forest remnants. After following the YLTH seasonality over a 1,000 m altitudinal range within the Atlantic Forest, our study advances knowledge in (i) elucidating the species' altitudinal migration, and (ii) revealing that these birds likely altitudinally track fleshy-fruit crops while avoiding increased rainfall at the highland site during the non-breeding period. With that, we firstly described that the complex YLTH altitudinal migration includes different patterns of partial migration at the studied altitudes and distinct responses to fruit availability and rainfall. Our results reinforce the need for more evidence for supporting or refuting the validity of mechanistic hypotheses on this subject (e.g. 29,30,77,78). Further research in the Southern Hemisphere is paramount to address the current bird migration knowledge bias in the Americas towards species occurring in the United States of America and Costa Rica (14). We must harness the power of citizen science (79) to gather Southern Hemisphere data to augment bird migration theory, including over both broad temporal and spatial scales. Nevertheless, fieldwork will always be mandatory to produce high-quality individual-based data that will allow researchers to explain the mechanisms underlying altitudinal migration in more detail.

Acknowledgements

We thank the Programa de Pesquisa de Biodiversidade da Mata Atlântica (PPBio-MA) for field support, Instituto Ambiental do Paraná (IAP), the Mananciais da Serra, and Sociedade de Pesquisa em Vida Silvestre e Educação Ambiental (SPVS) for allowing fieldwork at the study sites. Many LECO members helped during fieldwork. A.C. Guaraldo and J.C. Bczuska thank CAPES Fellowships and IdeaWild, and L.T. Manica acknowledges Conselho Nacional de Pesquisa e Desenvolvimento Científico Tecnológico (CNPq) for a grant (#455980/2014-1). Authors are in debt to the anonymous reviewers and Associated Editor J. Reynolds and Charles Deeming for invaluable comments and suggestions that largely improved this manuscript from its early versions.

Declaration of conflicting interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) - (post-doc Fellowship to A.C.G. and Master's scholarship

to J.C.B.), 1374-01-2, Idea Wild and Conselho Nacional de Pesquisa e Desenvolvimento Científico Tecnológico (CNPq) grant, 455980/2014-1.

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