

## RESEARCH ARTICLE

## Are recaptures of banded birds efficient at detecting altitudinal migrations in the Atlantic Forest?

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**ABSTRACT.** Altitudinal migration in birds comprises seasonal movements between breeding and non-breeding areas in mountainous regions, attributed to biotic and abiotic factors. Different authors have suggested the existence of altitudinal migration between high and low areas of the mountains of the Atlantic Forest, with movement from high to low during the winter when birds would be fleeing the cold and in search of food, but there is no documented evidence. Through recaptures of understory birds, we investigated possible altitudinal migration in a region of the Atlantic Forest in Southeast Brazil. Twenty mist-nets were set at four locations between 15 and 729 m a.s.l. during 143 days of field work, distributed over 54 months and covering all seasons of the year. A total of 1946 birds (98 species) were captured/banded with 558 being recaptured (28.6%; 45 species). However, only 42 of the recaptures were at a different elevation. Most of the movements were of short distances and performed only once by birds, showing no seasonal pattern. These movements may be better interpreted as daily movements undertaken by birds of mixed-species flocks looking for food or moving around their respective home-ranges. Our results show that mist-nets may not be an effective tool in detecting altitudinal movements of birds and that other methods should be evaluated for this purpose.

**KEY WORDS.** Bird banding, banded bird recovery, Serra do Mar, Southeast Brazil.

### INTRODUCTION

The altitudinal migration of birds — the regular, seasonal movements of birds up and down mountain slopes — is a widely known phenomenon, although it is poorly understood. Such movements have been commonly attributed to seasonal variation in environmental factors, such as temperature, precipitation, availability of resources, and predation risk (Hsiung et al. 2018). In contrast to traditional migrations (i.e., latitudinal and/or longitudinal migrations), altitudinal migrations cover shorter distances, with a significant occurrence of partial seasonal altitudinal movements; that is, migrations carried out only by individuals of a population of a given species (Johnson and Maclean 1994, Boyle 2011, Hsiung et al. 2018).

Birds stand out as the most studied vertebrate group with regards to altitudinal migration. Global knowledge of altitudinal migrations of birds have been obtained via five main methodical approaches: 1) presence/absence sampling (observations) at different altitudes (e.g., Dixon and Gilbert 1964, Dixit et al. 2016); 2) sampling with mist-nets (e.g., Loiselle and Blake 1991) or by point-counts (e.g., Betts et al. 2005) to determine seasonal fluctuations in abundance; 3) altitudinal recapture of banded birds (e.g., Rabenold and Rabenold 1985); 4) radiotelemetry and GPS (e.g., Laymon 1989, Norbu et al. 2013); and 5) analysis of stable hydrogen isotopes using biological samples from birds (e.g., Hardesty and Fraser 2010). The use of mist-nets to recapture marked individuals has generated some data, but with extremely low recapture rates among different altitudes (Rabenold and

Rabenold 1985 in the United States; Loiselle and Blake 1991 in Costa Rica; Burgess and Mlingwa 2000 and Fraser et al. 2008 in Africa; and Merkord 2010 in Peru).

Altitudinal movements of birds have been anecdotally mentioned since the beginning of the 19<sup>th</sup> Century for a mountainous region of the Atlantic Forest called the Serra do Mar, located in the Southeast and South regions of Brazil (Descourtilz 1983, Goeldi 1894). The Serra do Mar is a geological formation that extends latitudinally for about 1000 km between the states of Rio de Janeiro (RJ) and Santa Catarina (SC), in Southeast and South regions, respectively; and is recognized as a steep plateau edge facing the Atlantic Ocean with an average of 800 m a.s.l. difference in level with a maximum peak of 2,275 m a.s.l. in the Serra dos Órgãos, RJ (Almeida and Carneiro 1998). This geological formation presents different environmental characteristics along its altitudinal range involving temperature (a decrease of 0.6 °C for every 100 m of elevation), humidity (higher at higher altitudes), soil (poorer nutrients at the highest altitudes), fauna and flora (with partially distinct altitudinal compositions), and many plants (e.g., Juçara palm) with seasonal fruit ripening throughout the year in relation to altitude (Sick 1997, Galetti et al. 1999, Nettesheim et al. 2010, Joly et al. 2012, Cagliioni et al. 2018). Based on this environmental and climatic variation, along with variation in bird behavior, some authors (e.g., Santos 1940, Berla 1944, Davis 1945, Mitchell 1957, Sick 1968, 1979, 1983, Sick and Pabst 1968, Snow 1973, 1982, Willis 1979, Gonzaga 1983), have independently described a possible pattern of altitudinal migration of birds. Accordingly, birds, mainly frugivores, which occupy the canopy and forest understory (e.g., Bare-throated Bellbird *Procnias nudicollis* (Vieillot, 1817) and White-necked Thrush *Turdus albicollis* (Vieillot, 1818)), move from the high part to the low part of the Serra do Mar during the coldest period of the year (May-August), presumably to escape the more intense low temperatures of the high part during the winter and to seek food in the coastal plains, following the fruiting of some plant species. *Turdus albicollis* is the only bird species from the Atlantic Forest/Serra do Mar that has had an altitudinal movement of 800 m detected by individual marking. One individual was banded in May 2006 at 800 m a.s.l and recaptured in August of the same year at sea level (Schunck et al. 2022). This proposed altitudinal migration continued to be widely mentioned by different authors (e.g., Barçante et al. 2017, Somenzari et al. 2018 – that cite 16 species), including the review by Schunck (2019) that mentions 80 species, but the few studies that have focused on this subject (e.g., Galetti et al. 1997, Galetti 2001, Castro et al. 2012) failed to detect such migrations and so there remains a significant knowledge gap about the movements and ecology of Atlantic Forest birds.

The use of mist-nets to investigate possible altitudinal movements of birds in Brazil has long been recommended (e.g., Gonzaga 1983, Alves 2007) but still little applied in the field, raising doubts about its effectiveness. Among the studies that have used mist-nets, only three, which remain unpublished abstracts

from ornithological meetings or theses, mention the recapture of individually marked birds at different altitudes (Gouvêa et al. 1996, Gouvêa 2006, Barçante 2013). Based on this scenario, and to determine whether mist-nets are effective for studies on altitudinal migration, we present the results of a long-term investigation based on the extensive capture/recapture of understory birds in a region of the Serra do Mar in Southeast Brazil.

## MATERIAL AND METHODS

### Study area

Núcleo Curucutu (23°56'S; 46°39'W) is one of ten administrative centres of the Parque Estadual da Serra do Mar, the largest conservation unit in the state of São Paulo and one of the largest in the Atlantic Forest of Southeast Brazil, with around 332,000 ha (Fig. 1). Núcleo Curucutu encompasses 36,134 ha with an altitudinal gradient ranging from 5 m to 1,050 m above sea level, with different vegetation typologies (Garcia and Pirani 2003, Pessenda et al. 2009). According to Tarifa and Armani (2000), the climate of the region is Tropical Super Humid through the interior of the Atlantic Plateau, and Tropical Oceanic Super Humid on the seaward face. Temperature varies between 0 °C (winter) and 34 °C (summer), with annual rainfall ranging from 3,497 to 4,435 mm between 2008 and 2011 (data from the local meteorological station; Malagoli 2013).

### Data collection

The following four locations were sampled, with average altitude following the name: Location A – Cota 30 (31 a.s.l.); Location B – Cota 200 (247 a.s.l.); Location C – Cota 400 (533 a.s.l.); and Location D – Cota 700 (717 a.s.l.). The locations are situated along a slope facing the Atlantic Ocean with continuous forest cover. The vegetation at locations A, B and C is predominantly Dense Ombrophilous Forest while that at locality D is Dense High Montane Ombrophilous Forest (Fig. 1; Supplementary Material – Table S1). Data were collected during 18 field campaigns between May 2007 and June 2011. Each campaign spent three days at each location such that data were collected at all locations four times/year (one location at a time), for a total of 143 days of fieldwork (Supplementary Material – Table S2).

Twenty mist-nets (30 mm, 12 x 2 m, four bags) were used per location with two lines of 10 nets each with at least 100 m distance between net lines and the bird banding base. The nets were opened at dawn and closed at dusk for the first two days and closed at 12:00 pm on the third day. The straight-line distance and altitudinal difference between net lines of adjacent locations, in sequence from low to high altitude, are as follows: A to B = 900 m distance and 130 m altitudinal difference; B to C = 770 m distance and 285 m altitudinal difference; and C to D = 1,700 m distance and 255 m altitudinal difference (Figs 1, 2). This method produced a total sampling effort of 21,237.8 net-hr, allocated among locations as follows: A = 18 campaigns, 51 days, 8,058.2 net-hr; B = 14 campaigns, 39 days, 5,288.1 net-hr; C = 14

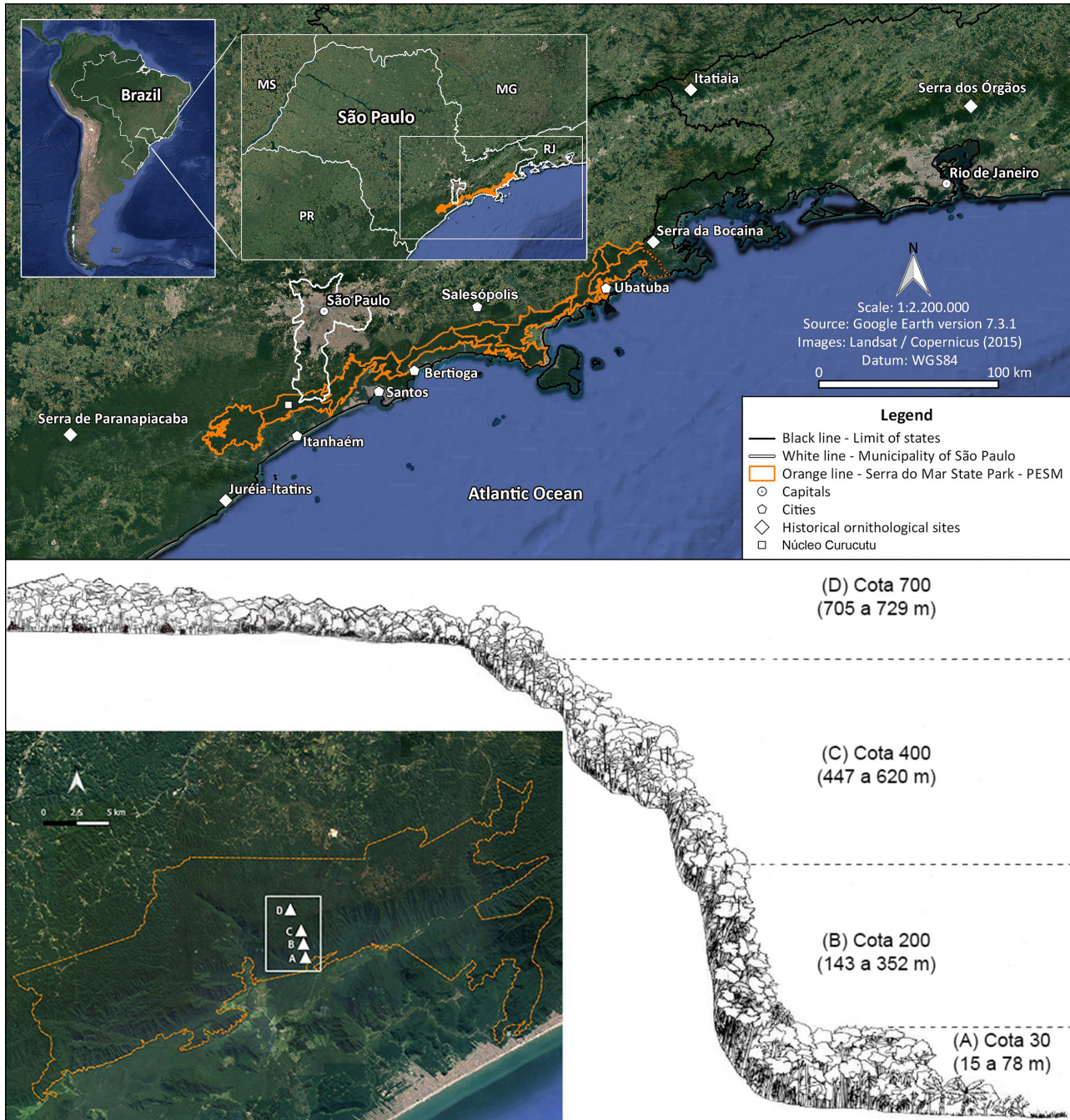


Figure 1. Geographic location of the Curucutu region. Altitudinal schematic of Núcleo Curucutu, showing the study locations A. Cota 30; B. Cota 200; C. Cota 400 and D. Cota 700, highlighted by the white rectangle. Model adapted from Malagoli (2013).

campaigns, 41 days and 6,086.5 net-hr; and D = 04 campaigns, 12 days, 1,805 net-hr. Due to unfavourable weather events and logistical problems (common occurrences for studies carried out in mountains, according to Blake and Loiselle 2000), we had less sampling effort at location D, which made it impossible to

fully standardize field effort (Supplementary Material – Table S2). Captured birds were photographed and marked with a metal band from Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE/ICMBio), and basic biometric and biological data were taken.

Biological and climatic data were not collected from the study locations because the main objective of the study was to detect whether there is seasonal altitudinal migration in the Serra do Mar, and then investigate possible causes.

### Characteristics of the movements

Recaptures at different altitudes were classified according to their: (i) direction of travel (higher to lower elevation, lower to higher elevation); (ii) seasonality (dry season = autumn and winter; rainy season = spring and summer); (iii) number of recaptures of each individual at a given altitude (how many times the same individual was recaptured at a different location (altitude) from where it was marked or last captured); (iv) altitudinal range of movements based on the distance between locations (short distance = adjacent locations; medium distance = non-adjacent locations; long distance = between the extremes of the altitudinal gradient); and (v) age and sex of birds, when possible.

### Analyses

Given that count data are usually not normally distributed (Bolker 2008), we assessed the occurrence of seasonal altitudinal movements using General Linear Models with Poisson-type distribution of errors. We grouped all species for this analysis because the main hypothesis deals with the altitudinal migration of “birds” from Serra do Mar, and consequently the low number of observations prevented analysing species separately (see Introduction). Despite this grouping and the lower sampling effort in one location (D), we believe that this analysis can detect seasonal altitudinal movements if they are held by the most abundant captured species. Therefore, this analysis is based on the detection of seasonal altitudinal movements by the most abundant species, since detection of movements is a much more informative result than lack of detection.

We built three candidate models (scenarios) in which the number of altitudinal movements varied depending on different variables or combinations of variables: (1) ‘Season Model’, in which the number of movements varied only according to season (dry/rainy), a scenario that represents an increase in movements according to season, regardless of direction; (2) ‘Season x Displacement Direction Model’, in which the number of movements varied according to an interaction between season and direction of displacement, a scenario that represents seasonal altitudinal movements (i.e., the direction of movements would change depending on the season) and (3) ‘Null Model’, in which movements would vary at random, a scenario that represents an absence of a pattern for the movements with regard to season or direction. Candidate models were selected using the Akaike information criterion (AIC) and related metrics (Burnham and Anderson 2002). The analyses were performed using R software (R Core Team 2020).

Maps were prepared using QGIS 2.14 software. The layout of the latitudinal profile of the slope of Núcleo Curucutu (including vegetation) from Malagoli (2013) was adapted. Satellite imagery of the locations of net lines and the movements of marked birds was obtained from Google Earth Pro version 7.3.1.

The species list used adopted the taxonomy and nomenclature of the Brazilian Committee for Ornithological Records (Pacheco et al. 2021). Endemic species of the Atlantic Forest follows Vale et al. (2018). Threatened species follows IUCN (2022), MMA (2022), and São Paulo (2018), brought together in a single category when coincident. All birds were captured and banded under appropriate permits for Brazil and authorization by the respective ethics committees.

## RESULTS

A total of 1946 individuals of 98 species were captured and marked with metal bands, of which 558 were recaptured (28.6%, 45 species). The captures included no threatened species but seven Atlantic Forest endemic species. However, only 42 individuals of 14 species were recaptured at different altitudes (locations) from where they had been originally banded. Of the total of 98 species captured, 21 are considered altitudinal migrants in the Brazilian literature (Schunck 2019), but only four were recaptured at different altitudes. The species of birds recaptured at different altitudes represent three orders and ten families and are mostly understory birds that are usually detected with mist-nets (Table 1; Supplementary Material – Tables S3, S4).

There were 28 higher to lower altitudinal movements (done by 14 species) and 17 lower to higher (done by seven species). There were 28 movements during the dry season, with 15 in winter and 13 in autumn, and 17 during the rainy season, with 10 in spring and seven in summer. Of the 28 movements made from higher to lower elevations, 17 were during the dry season (nine in winter and eight in autumn) and 11 in rainy season (eight in spring and three in summer). For the 17 movements from lower to higher elevations, 11 were during the dry season (six in winter and five in fall) and six were during rainy season (four in summer and two in spring) (Fig. 2; Supplementary Material – Table S3).

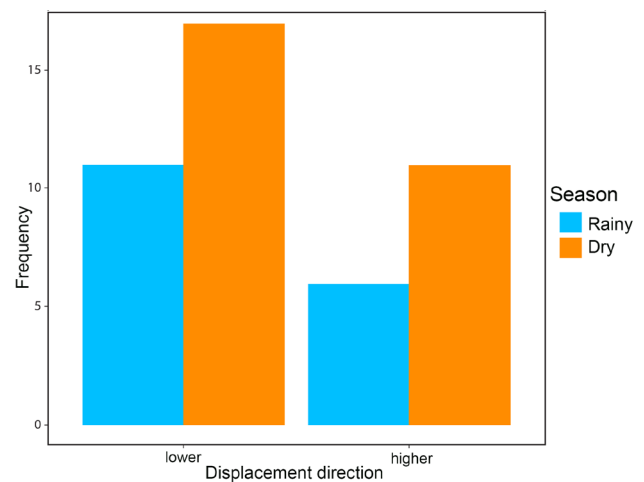


Figure 2. Frequency of altitudinal movements by season (Rainy and Dry) and displacement direction (lower and higher).

Table 1. Species recaptured at different altitudes.

Species	Family	Number of recaptures
Saw-billed Hermit <i>Ramphodon naevius</i> #	Trochilidae	6
Blond-crested Woodpecker <i>Ceelus flavescens</i>	Picidae	1
Star-throated Antwren <i>Rhopias gularis</i> #	Thamnophilidae	1
White-shouldered Fire-eye <i>Pyriglena leucoptera</i> #	Thamnophilidae	3
Plain-winged Woodcreeper <i>Dendrocincla turdina</i> *#	Dendrocolaptidae	7
Olivaceous Woodcreeper <i>Sittasomus griseicapillus</i>	Dendrocolaptidae	1
Lesser Woodcreeper <i>Xiphorhynchus fuscus</i> #	Dendrocolaptidae	1
Planalto Woodcreeper <i>Dendrocolaptes platyrostris</i>	Dendrocolaptidae	1
Greenish Schiffornis <i>Schiffornis virescens</i> #	Tityridae	3
White-throated Spadebill <i>Platyrinchus mystaceus</i>	Platyrinchidae	1
Gray-hooded Flycatcher <i>Mionectes rufiventris</i> *#	Rhynchocyclidae	5
White-necked Thrush <i>Turdus albicollis</i> *	Turdidae	4
Black-goggled Tanager <i>Trichothraupis melanops</i> *	Thraupidae	7
Red-crowned Ant-Tanager <i>Habia rubica</i>	Cardinalidae	1

\* Indicates that the species is mentioned in the Brazilian literature as an altitudinal migrant (Schunck 2019).

# Indicates endemic species of the Atlantic Forest (Vale et al. 2018).

Among the three GLM models evaluated, only two were considered plausible (i.e., with AIC > 3, Table 2). The model that best fit the data was the 'Null Model' ( $\Delta AIC = 0$ ,  $wAIC = 0.7$ ) followed by the 'Season Model' ( $\Delta AIC = 2.19$ ,  $wAIC = 0.2$ ), suggesting that altitudinal movements varied by chance, with a tendency that their frequency (regardless of direction) differed between seasons (more movements in the dry season). Nevertheless, the effect of season in the latter model did not differ significantly from zero (Table 3), suggesting that the hypothesis of random altitudinal movements is the most plausible according to the data.

Table 2. AIC values and related metrics for the three models built to explain the number of altitudinal movements. Modnames: Model name; K: Number of parameters of each model; AICc: Akaike Information Criterion (corrected for small sample sizes) of each model; Delta\_AICc: Difference between AICc of each model and model with lowest AICc value; Modellik: Likelihood of each model; AICcWt: Akaike Information Criterion weight for each model; Cum. Wt: Cumulative Akaike Information Criterion weight.

Modnames	K	AICc	Delta_AICc	Modellik	AICcWt	Cum.Wt
Null	1	92.09302	0.00000	1.00000	0.679566	0.679566
Season	2	94.28571	2.192691	0.33409	0.227036	0.906601
Season*Type	3	99.00000	6.906977	0.031635	0.021498	1.000000

Table 3. Values of parameters estimated by the 'Season' model. Parameter: model parameter; Estimate: parameter value estimated according to data; std.error: standard error of each parameter estimate; statistic: value of t statistic for each parameter estimation; p.value: p-value for each parameter estimation.

Parameter	Estimate	std.error	statistic	p.value
(Intercept)	1.02835E-17	0.242536	4.23998E-17	1
Dry Season	-1.73134E-18	0.307470	-5.63091E-18	1

As for the number of recaptures at different altitudes, 39 individuals had only one recapture and three had two. The altitudinal range of movements included 38 short-distance movements, that is between adjacent altitudinal levels, and seven medium-distance movements, between non-adjacent altitudinal levels. There were no long-distance movements, that is, movements between locations A and D at opposite extremes of the altitudinal gradient (Fig. 3; Supplementary Material – Table S3). Nine of the short-distance movements were from location A to location B, and 14 in the opposite direction, about 900 m straight-line distance and an altitudinal difference of 130 m. Four short-distance movements were from B to C, and 11 in the opposite direction, about 770 m straight-line distance and an altitudinal difference of 285 m. Two medium-distance movements were from A to C, and three in the opposite direction, about 1,650 m straight-line distance and an altitudinal difference of 415 m. Two other individuals were included in this category but performed movements over a higher altitudinal range than the others as they moved from the slope (locations B and C) to the plateau (location D), passing precisely through the region of location C where mist-nets could not be employed due to the steep slope and irregularities of the terrain (Figs 1, 2). The first individual was Black-goggled Tanager *Trichothraupis melanops* (Vieillot, 1818), which moved from locality C to locality D, a straight-line distance of about 1,700 m and an altitudinal difference of 255 m. The second was White-shouldered Fire-eye *Pyriglena leucoptera* (Vieillot, 1818), which moved from B to D, a straight-line distance of about 2,450 m and an altitudinal difference of 540 m, the greatest distance and greatest altitudinal range obtained by a recapture on the Curucutu slope (Fig 3; Supplementary Material – Table S3).

There was a prevalence of adult individuals among the birds that showed altitudinal movements, with only three *T. melanops* being captured and recaptured as younglings, while the rest of the younglings were recaptured as adults, even over short time intervals, in which case they were probably subadult individuals when recaptured. A low number of individuals had their sex determined, with 10 males and eight females (Supplementary Material – Table S3).

## DISCUSSION

This study contributes to filling a knowledge gap in Brazilian ornithology, and thus addresses the recommendations made by different researchers (e.g., Gonzaga 1983, Alves 2007) regarding the need to use mist nets to obtain data on altitudinal recaptures of individually banded birds in mountainous regions of Brazil.

Our data of altitudinal recaptures suggest an absence of seasonal patterns of altitudinal movements for the understory birds sampled in the region of Núcleo Curucutu, contrary to descriptions of annual migrations for Atlantic Forest birds by several authors (e.g., Sick 1997, Somenzari et al. 2018). Nonetheless, our data did show the presence of altitudinal movement

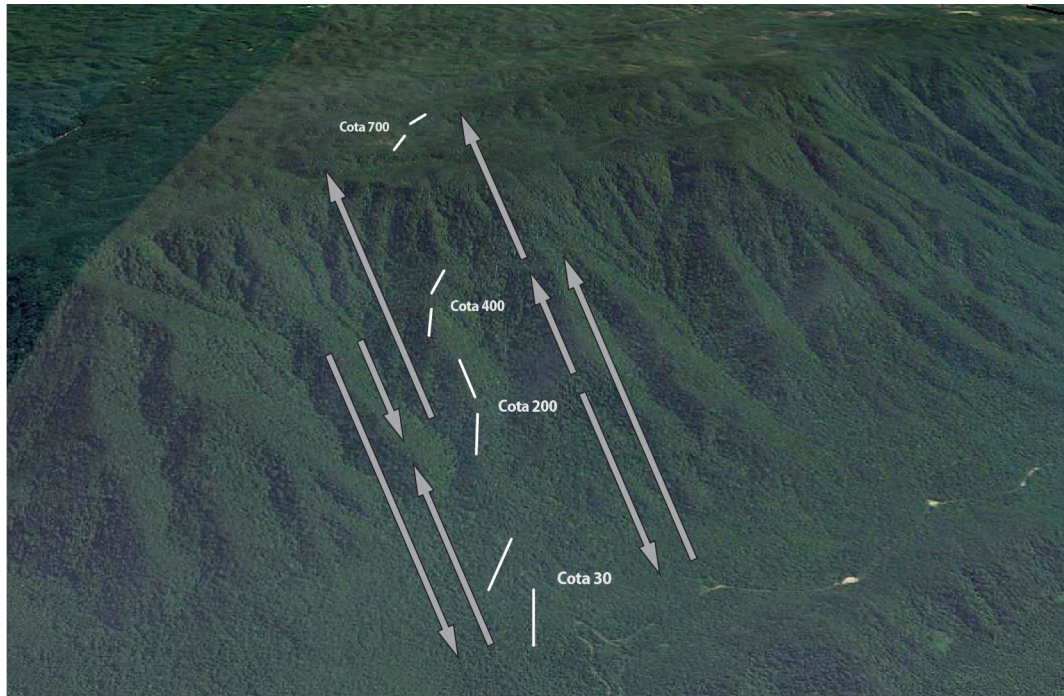


Figure 3. Schematic illustration of the altitudinal movements recorded on the slope of Núcleo Curucutu by the recapture of individually marked birds. White lines indicate the two lines of mist-nets at each locality. Source: Google Earth Pro (Image Landsat/Copernicus 2015).

by understory birds along the slope of Curucutu, allowing some inferences to be made.

Núcleo Curucutu stands out as one of the best-known regions, with regard to bird biology and distribution, along the entire Atlantic Forest domain, with a confirmed total of 382 bird species (Schunck et al. 2019). The high diversity of bird species, coupled with our significant field effort, are the main factors responsible for the 1,946 banded individuals of 98 species, with a total of 558 recaptures (28.6%, 45 species). A sampling effort of more than four continuous years is uncommon in standardized ornithological studies carried out in the Atlantic Forest. Studies in this domain are usually done over shorter periods of time (one year or less), with most having up to three years of field sampling (e.g., Develey 2004, Castro et al. 2012, Hasui et al. 2012). Gouvêa et al. (1996) stands out as the only partially published study (conference abstract) that included data about altitudinal movements. During the 10 years of sampling in Itatiaia, RJ, Gouveia et al. (1996) recaptured 10% of their 3,090 banded birds, with only three altitudinal recaptures: Gray-hooded Flycatcher *Mionectes rufiventris* Cabanis, 1846, Ruby-crowned Tanager *Tachyphonus coronatus* (Vieillot, 1822), and Swallow-tailed Manakin *Chiroxiphia caudata* (Shaw & Nodder, 1793). Movements of all three of these species were short-range, between 400 and 500 m in altitude, in a region with altitudinal variation (in relation to sea level) between 400 and 1,200 m a.s.l., but the straight-line distances between locations were not provided by the authors.

The low number of altitudinal recaptures in Itatiaia was probably due to the long distances between sampling localities. Low numbers of altitudinal recaptures and difficulty in obtaining this type of information with use of mist-nets have been mentioned by studies involving greater altitudinal gradients in other regions of the world (e.g., Rabenold and Rabenold 1985, Loiselle and Blake 1991 Burgess and Mlingwa 2000, Merkord 2010). The low recapture rates of these studies may be mediated, in part, by the use of coloured bands (e.g., Rabenold and Rabenold 1985, Morrissey 2004, Merkord 2010), so that re-sightings of marked birds can augment mist-net recapture data. Coloured bands have yet to be used to investigate possible seasonal altitudinal movements of birds in mountainous regions of Brazil, but they hold promise since documentation by re-sighting can be carried out by researchers, birdwatchers, and photographers, thus advancing research through complementary citizen science (Dickinson et al. 2010).

Among the species of altitudinal recaptures in Núcleo Curucutu, we highlight three families (Thamnophilidae, Platyrinchidae and Cardinalidae) and 11 species — Saw-billed Hermit *Ramphodon naevius* (Dumont, 1818), Blond-crested Woodpecker *Celeus flavescens* (Gmelin, 1788), Star-throated Antwren *Rhopias gularis* (Spix, 1825), *Pyriglena leucoptera*, Plain-winged Woodcreeper *Dendrocicla turdina* (Lichtenstein, 1820), Olivaceous Woodcreeper *Sittasomus griseicapillus* (Vieillot, 1818), Lesser Woodcreeper *Xiphorhynchus fuscus* (Vieillot, 1818),

Planalto Woodcreeper *Dendrocolaptes platyrostris* Spix, 1825, Greenish Schiffornis *Schiffornis virescens* (Lafresnaye, 1838), White-throated Spadebill *Platyrinchus mystaceus* Vieillot, 1818, and Red-crowned Ant-Tanager *Habia rubica* (Vieillot, 1817) — as never having been reported exhibiting any kind of altitudinal movement (e.g., Sick 1997, Schunck 2019).

Although there is just one record of a woodcreeper (Dendrocolaptidae) performing altitudinal movement — White-throated Woodcreeper *Xiphocolaptes albicollis* (Vieillot, 1818); Mallet-Rodrigues and Noronha (2003) —, this family represented the greatest number of movements in our study, involving four species (*D. turdina*, *S. griseicapillus*, *X. fuscus* and *D. platyrostris*), with *D. turdina* accounting for 16% of all altitudinal recaptures. The other two most frequently recorded species in our study (*R. naevius* and *T. melanops*) belong to families that are widely known for having species that perform altitudinal migrations in different regions of the Neotropics (Trochilidae and Thraupidae; Barçante et al. 2017). With the exception of *R. naevius*, all the understory species recorded by altitudinal recaptures in our study participate in some way in mixed-species flocks (Develey and Peres 2000).

The confirmation of seasonal altitudinal movements of birds through altitudinal recaptures or documented re-sighting of marked individuals is possible only if a certain pattern exists. In the case of the Serra do Mar, this general pattern would be the altitudinal movement of birds from the high plateau to low plain during the dry season (autumn-winter), possibly due to low temperatures and supposedly low food availability (several authors – see introduction). However, our data for direction of movement and season revealed no predominant pattern for the Curucutu slope. The number of recaptures of birds that moved from the higher to lower elevations in the dry season (autumn-winter; 17) was close to the number that did the reverse during the rainy season (spring-summer; 11), suggesting a balance between the two seasons, both at community and species levels. These data support the hypothesis that birds on the Curucutu slope make altitudinal movements at random, without a clear association between season and direction (Fig. 2; Supplementary Material – Table S3).

Birds that were recaptured at different altitudes only once represented 86% of all altitudinal recaptures. This high percentage of one-time recaptures was unexpected, considering the sampling effort, temporal-seasonal coverage and, mainly, the relative proximity and linearity among our sampling locations, which would be expected to provide a greater number of altitudinal recaptures if there was a pervasive seasonal altitudinal movement of birds. Additionally, 84% of the altitudinal recaptures were for short altitudinal distances and ranges, suggesting limited movements, with little environmental and climatic variation. The only two movements that reached greater distances were performed by a *P. leucoptera* and a *T. melanops* between localities B-D and C-D, respectively. These took place between autumn and winter (both in the dry season) of the same year, which is

contrary to what was expected for the Serra do Mar according to the hypothesis defended by different authors.

The mark-and-recapture method allowed us to confirm short movements for some species, such as an individual of *X. fuscus*, which moved up and down the slope between 30 and 200 m a.s.l. in four different years. Finally, 95% of the recaptured birds were adult individuals, suggesting that they had already defined their home ranges and territories, in contrast to young birds who tend to disperse in search of new areas to settle. Some of these adult individuals were recaptured several times at the same location, showing fidelity to their respective home ranges. It was not possible to relate movements to the sex of birds since most individuals could not be sexed due to the lack of sexual dimorphism for most species (Supplementary Material – Table S3).

Our data indicate that the absence of seasonal altitudinal movements for some species may be attributed to the daily movements of birds of mixed understory flocks and movements of birds within their respective home ranges. All species recorded in the field attended mixed species flocks, five of which (*H. rubica*, *X. fuscus*, *D. turdina*, *S. griseicapillus* and *M. rufiventris*), are among the most common species in these flocks (Develey and Peres 2000). Previous studies involving mixed species flocks in the Serra do Mar did not consider altitudinal gradients with complete amplitudes (e.g., Stotz 1993, Develey and Peres 2000), which prevents a better understanding of potential seasonal altitudinal movements and behaviors of birds in mountainous regions. Such an approach with mixed flocks in mountainous areas has been carried out in other regions of the world (e.g., Merkord 2010), with interesting results for this natural system of grouping birds that move together in search of food. In Brazil, possible seasonal altitudinal movements by birds have been justified by climatic variation and the search for resources, with an emphasis on frugivorous and some insectivorous species (e.g., Sick 1997), but there is no mention of seasonal altitudinal movements by species known to participate in mixed flocks.

The home range size of understory passerine bird species vary, ranging from a few to many hectares (Sick 1997, Ribon and Marini 2016). Some species, such as *P. leucoptera*, can have home ranges of 0.3 to 2.5 ha, and even reaching up to 23.9 ha probably during the search for food when moving after army ants (Sick 1997, Hansbauer et al. 2008). This behavior of seeking food in more distant areas may explain the more significant displacement of this species on the Curucutu slope, where an individual of *P. leucoptera* moved 2,450 m straight line distance and 540 m altitudinally from location B to D. Our data indicate that, for the studied birds, daily activities within home ranges explain the movements recorded by the altitudinal recaptures on the Curucutu slope. The fact that the study area was an Atlantic slope, a geographically steep region, means that any direction of displacement carried out by birds between two different points is necessarily an altitudinal displacement, whether seasonal or not.

Based on our study, and on the results of Gouvêa et al. (1996), mist-netting may not be the ideal approach for docu-

menting altitudinal movements. Marking birds with coloured rings and tracking individuals through radio telemetry and/or GPS to obtain data with greater precision are certainly better, easier and, possibly, overall, less expensive than the continuous use of mist-nets to detect altitudinal movements, if any do exist.

It is necessary to invest in individual tracking technologies through telemetry or GPS to obtain more accurate data on possible seasonal altitudinal movements by birds in the mountains of Brazil and especially the Serra do Mar.

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#### Author Contributions

FS and CC designed the experiments and analyzed the data; FS and MA collected field data; FS wrote the main text. CC, MA and LF contributed the text.

#### Competing interests

The authors have declared that no competing interests exist.

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**Supplementary Material 1**

Table S1. Description of the study locations on the slope of the Núcleo Cuructu.

Author: Fabio Schunck

Data type: Table with descriptive text.

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**Supplementary Material 2**

Table S2. Field effort for the four study locations (A, B, C and D) on the slope of the Núcleo Curucutu.

Author: Fabio Schunck

Data type: Table with field information.

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**Supplementary Material 3**

Table S3. List of individuals recaptured at different altitudes. Sequence according to the largest number of individuals caught per species.

Campaign: number refers to one of the 18 field expeditions carried out between 2007 and 2011. Status: 'captured' is when a bird was banded; 'recapture' is when a bird was recaptured. Age: A. Adult; Y. Youngling. Sex: M. Male; F. Female; U. Undetermined.

Author: Fabio Schunck

Data type: Table with information on recaptured birds.

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**Supplementary Material 4**

Table S4. General list of species recorded at the four study locations. End. Endemic species of the Atlantic Forest (Vale et al. 2018); Thr. Threatened species (São Paulo 2018, IUCN 2022, MMA 2022).

Author: Fabio Schunck

Data type: Species table.

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