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POPULATION ECOLOGY – ORIGINAL RESEARCH

Phenotypic variation in a neotropical understory bird driven by environmental change in an urbanizing Amazonian landscape

Stefano Spiteri Avilla[1] · **Kathryn E. Sieving**[2] · **Marina Anciães**[1] · **Cintia Cornelius**[3]

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Abstract

Environmental change through habitat fragmentation and urbanization drives biodiversity loss in the Neotropics at an alarming rate. Some individuals and species confined to habitat fragments may develop phenotypic adjustments that allow populations to persist, even in landscapes made harsh by human activities. Behavioral and morphological adjustments may enhance a population's ability to cope with anthropogenic hazards. We examined potential differences in the behavioral and morphological phenotype of populations of the neotropical Wedge-billed Woodcreeper (*Glyphorynchus spirurus*)—an understory forest specialist insectivorous bird—between populations from urban fragmented forests and continuous preserved forests. We evaluated exploratory behavior and morphological traits using generalized linear models and linear discriminant analysis to quantify phenotypical differences among populations. We used failure time analysis to compare latency to explore and move during exploration in a Novel Environment Test (NET). Our analyses detected differences in certain movement behaviors (latencies to move during NET), indicating that individuals from fragmented forests are slow explorers in relation to individuals from the continuous forest. We also found shorter tarsi and tails in the fragmented forest population which were attributed to an overall reduction in body size in these populations. Our results suggest that environmental change driven by fragmentation in an urban landscape is causing population differentiation, but we cannot ascribe observed variations to evolutionary processes only, as the differences observed may be explained by other processes too. However, we suggest that phenotypic differences may be aiding this small understory forest specialist to persist in an urban fragmented landscape.

Keywords Phenotypic variation · Fragmentation · Forest bird · Amazon

Introduction

Habitat loss and fragmentation driven by human activities threatens biodiversity, in part, by isolating individuals in remnant habitat patches surrounded by inhospitable human-altered areas (referred to as matrix; Fahrig 2003; Haddad et al. 2015). For animal species affected by fragmentation, individuals must either survive in fragments or attempt dispersal through a hostile matrix to reach new habitat patches. Either way, animals exposed to fragmentation of once continuous habitat experience a high probability of mortality. Animals forced to disperse are likely to make non-optimal (dangerous) movements in unfamiliar landscapes (Fahrig 2007), and animals that stay in remnant patches may be extirpated by stochastic and deterministic forces degrading the viability of restricted-size populations (e.g., extinction vortices; Fagan and Holmes 2006). Extensive work on forest fragmentation in neotropical systems has revealed dramatic changes in environmental conditions within fragments (Laurance et al. 2018), including habitat structure and microclimate alterations that restrict animal food supply in habitat patches (e.g., Cahill et al. 2021). Moreover, modified animal movement patterns (Develey and Stouffer 2001; Powell et al. 2015; Awade et al. 2017) and other factors consistently lead to reduced species richness and abundance in neotropical

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✉ Stefano Spiteri Avilla
stspiteri@hotmail.com

[1] Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, AM 69067-375, Brazil

[2] Department of Wildlife Ecology and Conservation, University of Florida (UFL), Gainesville, FL, USA

[3] Departamento de Biologia, Instituto de Ciências Biológicas, Universidade Federal do Amazonas (UFAM), Manaus, AM 69080-900, Brazil

forests experiencing fragmentation (Laurance et al. 2011; Püttker et al. 2020).

When associated with urbanization, fragmentation can be even more devastating for biodiversity (Parris 2016). Constant human activity within an urban matrix drastically decreases matrix permeability and habitat quality of remaining forest fragments (Piano et al. 2020). Yet even in neotropical areas, a number of native species can occur in urban landscapes (Aronson et al. 2017; Barbosa et al. 2020) while coping with hostile environmental conditions and novel landscape elements and species (Parris 2016). Urban environments may promote differences in behavior or morphology of individuals potentially distinct from traits promoted by environmental conditions in non-urban (or rural) fragmented landscapes (Cheptou et al. 2017; Corsini et al. 2021). The potential role(s) of phenotypic plasticity in organisms experiencing rapid environmental change under human influences is complex; plasticity may help or hinder adaptation to novel environments (Fox et al. 2019). Given the constant expansion of human urban settlements into all ecosystem types, it is important to study animal populations persisting in urban landscapes to establish detailed patterns of phenotypic (morphological, behavioral, physiological, etc.) variation in response to anthropogenic conditions.

Adjustments in behavioral phenotype

A variety of behavioral adjustments to urbanization and fragmentation are known in birds. Birds adjust when and how they use acoustic signals when dealing with urban noise (Fuller et al. 2007) or with impoverished communities due to habitat fragmentation (Bicudo et al. 2016). Behavioral types of birds, such as shy and bold types, are also nonrandomly distributed in urban environments, suggesting a major role for certain behavioral traits in the evolutionary ecology of urban environments (Sprau and Dingemanse 2017). Exploratory behavior, or how individuals respond to novel environments and objects, is a complex and variable set of behaviors important in environmental information gathering concerning potential resources and hazards (Dingemanse et al. 2002; Mettke-Hofmann et al. 2006). Verbeeck et al. (1994) first described exploratory behavior variation in natural bird populations, based on individual exploration scores in unfamiliar (caged) environments and latencies to approach novel objects. Individuals with high exploration scores moved quickly through the environment and rapidly approached new objects, while those with low scores moved slowly during exploration of the environment and approach to objects (Verbeek et al. 1994). Thus, individuals could be classified as "fast" or "slow" explorers after exposure to Novel Environment Tests (NET). Continued work on avian exploratory behavior reveals links to perception and acquisition of information and to decision making while exploring novelty (Dingemanse et al. 2002). Fast exploring individuals take less time to explore a novel environment, poorly assimilate new environmental information, are less likely to notice hazards, and are more prone to high-risk decisions (Van Oers et al. 2004). In contrast, slow exploring individuals are highly reactive to novelty (e.g., usually avoid it), and are more efficient at identifying inconspicuous environmental cues or hazards (Verbeek et al. 1996).

Variation in population-level exploratory behavior has been linked to different environmental conditions (Poblete et al. 2018) and environmental stochasticity (Dingemanse et al. 2004), but also to deterministic human-driven landscape change and habitat fragmentation. For example, in a neotropical forest specialist bird, individuals from fragmented populations were slow explorers when compared to individuals from undisturbed continuous forests. Moreover, slow exploration of individuals from the fragmented forest was related to their ability to successfully traverse areas of inhospitable matrix surrounding fragments they attempted to emigrate from (Cornelius et al. 2017). Woodland butterflies from different origins exhibited similar patterns; butterflies originating from continuous woodlands were less reactive to possible hazards (e.g., predation) and readily traversed open areas whereas butterfly individuals from fragmented forests tended to avoid crossing woodland boundaries (Merckx et al. 2003). Thus, individuals from populations inhabiting forest fragments surrounded by an anthropogenic matrix may adjust to slower exploratory behavior. By taking more time to explore, the efficiency of assimilating environmental information may increase, thereby allowing them to better perceive hazards before undertaking behaviors (such as patch emigration) carrying a high mortality risk. Patterns such as these suggest that land cover change in the form of fragmentation and urbanization may rapidly select for beneficial shifts in behavioral traits, fostering persistence in species that can respond (e.g., Cote et al. 2017; Patankar et al. 2021). However, which behavioral types will succeed after fragmentation relies on habitat affinities. A forest specialist persisting in habitat remnants may avoid urban areas as it offers many hazards, thus slow exploration benefits individual survival, but in a generalist species for example, that inhabits and uses resources available in the urbanized matrix, individuals may benefit from bold and aggressive behaviors during exploration, allowing fast exploration to thrive on certain human-disturbed environments (Charmantier et al. 2017; Senar et al. 2017; Sprau and Dingemanse 2017).

Adjustments in morphological phenotype

Additionally, changes in morphology may also play an important role in coping with the challenges imposed by human-modified landscapes; both fragmented and urbanizing areas. Dispersal-related traits are of paramount importance in adaptation to fragmented landscapes (Cheptou et al. 2017). Dispersal is a key evolutionary process facilitating gene flow between populations as it defines the ability of individuals to reach and colonize new habitats (Clobert et al. 2012). Human-induced fragmentation often inhibits dispersive events with the insertion of new and hostile matrix environments between occupied habitat patches. Forest specialists with a large home range are typical of those species most affected (Slade et al. 2013). In urban environments, morphological shifts reflect allometry that facilitates avoidance of collisions with human-made structures (Brown and Brown 2013), or body-size changes related to climatic variation and habitat fragmentation (Merckx et al. 2018a,b). Another consequence of fragmentation and urbanization is biotic homogenization observed at both the community (Olden and Rooney 2006) and population-level with reported dispersal traits homogenization as a consequence of human-driven landscape changes (Martin et al. 2017). Thus, urbanized landscapes with fragmented habitats offer unique opportunities to study population differentiation patterns related to dispersal in addition to other factors that arise because of the extreme conditions that the urban matrix imposes on wildlife.

Phenotypic differences expected in urban populations may also include those not related to dispersal. For example, nestlings in urban populations have reduced developmental pace and reduced body mass (Corsini et al. 2021) and differences in bill shape have been correlated to the use of feeders and novel food types in urban environments (Bosse et al. 2017). Additionally, leg morphology can determine the range of possible movements while foraging which may vary in human-altered environments. Blue Tits (*Cyanistes caeruleus*) with shorter tarsi are more adept at clinging and hanging, enabling them to access a wider array of foraging niches (Carrascal et al. 1995). For birds that forage vertically on tree trunks such as treecreepers, woodcreepers, and woodpeckers, tarsus and tail length are directly related to trunk climbing performance (Norberg, 1979; Tubaro et al. 2002; Zefffer and Norberg 2003, Milá et al. 2009). In woodcreepers, the tip of the tail rachis is adapted to support body mass and prevent lateral deflection while climbing (Tubaro et al. 2002). Woodcreepers in forest fragments may be exposed to different challenges while foraging because of microhabitat changes associated with edge effects, such as changes in epiphyte cover on trunks due to reduced humidity (e.g., Laurance et al. 2018; Parra-Sanchez and Banks-Leite 2020), and these changes may alter their foraging substrate (i.e. trunks) and food supply. Therefore, tarsus, tail length, and other body structures that define foraging maneuvers may be influenced by the myriad of factors altered by fragmentation within urbanizing landscapes.

Objectives

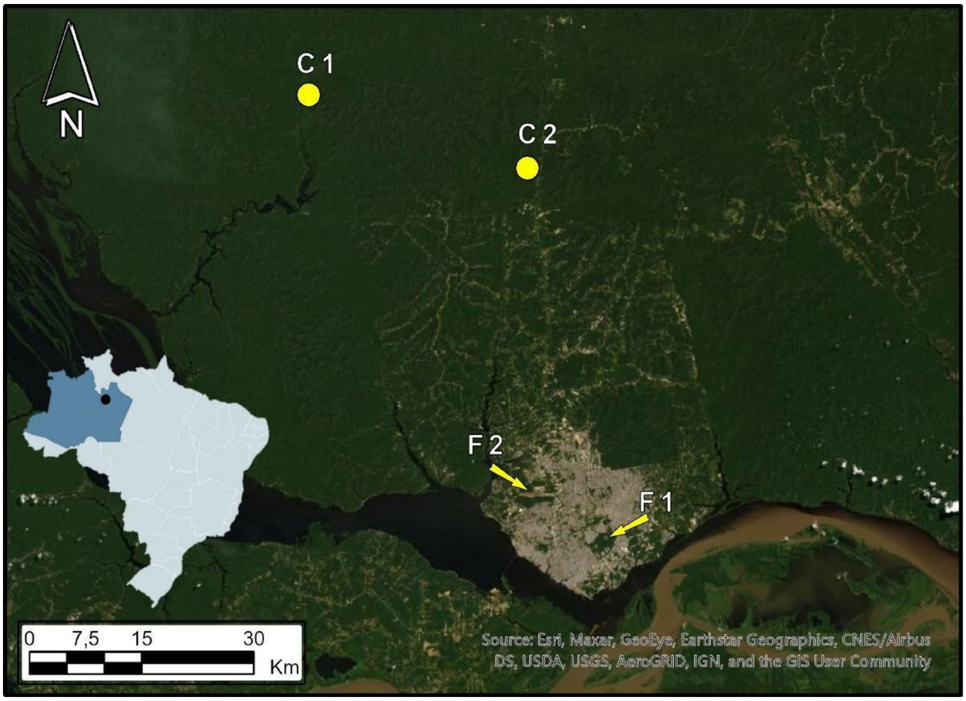
We investigated behavioral and morphological phenotypes of an understory forest specialist woodcreeper that persists in forest fragments in the most populated city in Central Amazonia. Understory birds are especially sensitive to forest fragmentation (Lees and Peres 2008; Sekercioğlu et al. 2002) and are usually the first group of birds to be extirpated in a forest fragmentation scenario with only a reduced number of species persisting in forest fragments (Van Houtan et al. 2007). Our goal was to describe phenotypic patterns on both behavior and morphology between urban and continuous forest populations of the Wedge-billed Woodcreeper (*Glyphorynchus spirurus,* Furnariidae) by using a quasi-experimental design of "fragmented *versus* continuous" landscapes.

We hypothesize that populations from forest fragments differ in behavior and morphology phenotypes when compared to populations from continuous forests. Individuals from forest fragments may differ in exploration pace and in the morphology of wing traits related to dispersal (long-distance movements) and in morphology traits related to environmental exploration during foraging (short distance routine movements). Specifically, we predicted that individuals from the fragmented landscape (1) score lower for exploratory behavior traits, taking longer to explore a novel environment and objects, (2) have a higher index of dispersal ability related to wing morphology as a consequence of possible selective pressures imposed by isolation due to the inhospitable matrix favoring individuals with greater dispersal ability and (3) have different tarsus and tail lengths allowing them to cope better with foraging while tree-climbing in the modified environment of forest fragments.

Methods

Study site and experimental design

Most of central and western Brazilian Amazonia is still preserved with large continuous areas that retain natural vegetation cover. On most of Amazonas State's (Brazil) natural systems with little or no human disturbance can be still sampled and studied. We sampled within "terra firme" forests (Lowland humid, non-flooded forests) in sites located in two landscape types: (1) sites in fragmented forests surrounded by an urban matrix in the capital city (Manaus) and (2) continuous and preserved forest sites (Fig. 1). To guarantee discrepant environmental conditions between preserved and disturbed environments, continuous forest sites were set at more than 30 km north of Manaus's urban periphery. At shorter distances forests are fragmented by secondary roads, small agricultural settlements, and country houses.



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Fig. 1 Sites in the urban area of Manaus, arrows indicate (f1) the UFAM campus site and (f2) the international airport fragment site. Sites in the continuous forests area, (c1) the Cuieiras site and (c2) the FAEXP site

In continuous forests, we sampled in two different sites: the Experimental Farm of the Amazonas Federal University (FAEXP) and the "Cuieiras" research base of the National Institute of Amazonian Research (INPA). Both continuous sites are represented by the primary "terra firme" forest. FAEXP has a RAPELD plot system (Magnusson et al. 2005) that we used for sampling and on INPA's base we sampled along trails opened for research purposes in the interior of continuous forest.

Forest fragments were inside the urban perimeter of Manaus, a ca. 2 million people city (available at: https://www.ibge.gov.br/, accessed in September 2020). Manaus experienced a large and abrupt expansion since the 1970´s leaving a large number of native forest remnants embedded in a highly transformed urban matrix. Currently, most native forest fragments (80%) are smaller than 1 ha with a few very large remnants (> 100 ha) mostly belonging to governmental entities and public universities (Conceição 2013). We selected two of these large fragments because of the known occurrence of the Wedge-billed Woodcreepers: a ca. 600 ha forest fragment in which the Amazonas Federal University campus (UFAM) is located (F1) and a 180 ha forest fragment in which the "Eduardo Gomes" International Airport is located (F2) (Fig. 1). The UFAM fragment is located in the central-eastern region of Manaus and the Airport fragment is located near the urban periphery to the west (Fig. 1). Both fragments are mostly covered by old secondary forest with small patches of primary "terra firme" forest, with buildings, roads, and other human-made structures. The UFAM fragment has 10 pairs of permanent monitoring plots (separated by 400 m–3 km) in riparian and non-riparian habitats, at various distances from forest edges (100 m–1 km), which we used for sampling. In the Airport fragment, we gave preference to core areas, sampling no less than 100 m from forest edges.

We captured subjects with mist nets (Ecotone© 12 m, 36 mm mesh) and defined sampling effort in 'net-hours' (1 net open for one hour = 1 net-hour). Depending on field conditions, we used six to 10 nets in continuous forests and eight to 20 nets in forest fragments. Between June of 2019 and January of 2020 we sampled 19 subjects from forest fragments (10 from the UFAM fragment and 9 from the Airport fragment), and 19 subjects from continuous forest sites (five from the INPA's Cuieras base and 14 from the FAEXP). Accumulated sampling effort in the continuous forest sites was 575 'net-hours' and 2611 'net-hours' in forest fragments. Young birds exhibiting fledgling stage traits (e.g., yellow-colored gape or immature feathers) were not tested or measured.

We selected the Wedge-billed Woodcreeper (*Glyphorynchus spirurus*) as it is a "terra firme" forest specialist. *Glyphorynchus spirurus* is a small (ca. 15 g) insectivorous understory forest bird that forages by vertically searching for food in crevices and bark of trees. It nests in existing tree-cavities and breeding in the study region occurs year-round with a peak extending from December to February in central Amazon (Stouffer et al. 2013). It is a non-migratory species, locally resident, abundant, and disturbance tolerant bird in the understory of primary and old secondary "terra-firme" forest (Marantz et al. 2020; Powell et al. 2015). It is one of the few understory forest specialists that still persists in forest fragments in the city of Manaus (Conceição 2013) and its conservation status is considered as "least-concern" (available at: http://www.birdlife.org/, accessed at February 2021). It is widely distributed in the Amazon Basin, with some taxonomic divergence among populations from different sides of large Amazon rivers (Fernandes et al. 2013). Therefore, sampling sites were established on the same margin of the "Rio Negro" to avoid the bias of sampling different subspecies.

Novel environment test and behavioral traits

We tested exploratory behavior with a Novel Environment Test (NET) based on the method proposed by Verbeek et al. (1994). Each bird was individually presented to an unfamiliar environment: a cage (3.0 m × 2.0 m × 3.0 m) of aluminum structure, covered with a 2 mm mesh and a plastic sheet, to prevent escaping behavior (Huang et al. 2015; Fig. 2). The cage was set up in the field next to each sampling site. The ceiling had a pyramid shape covered with a plastic sheet. Given that *G. spirurus* is a bark forager, five tree trunks were used as perches (1.5 m tall and 0.3 m wide) and placed inside the cage to induce exploration (Fig. 2). Beside the perches, individuals could also explore walls and the ceiling, so we considered those as objects for exploration as well, yielding a total of 13 objects (five perches, four walls, and four sides of the ceiling).

After capture, we measured, banded, and transported subjects in cloth bags to a testing site where the NET was set up. Tests were always conducted near the capture site, inside forested areas, and only one bird was used for each test. Before tests, we placed individuals in a small box inside the testing cage for acclimation. The box had a string tied to its cover, which allowed us to release the bird from a distance outside the testing cage. After 5 min of acclimation, the box was opened and access to the cage was allowed for 20 min (1200 s). At the end of the test, we used a small net to recapture and immediately release individuals. From the moment that subjects were placed in the acclimation box until the end of the test, no more than 30 min passed and all disturbances from human presence were avoided.

Activity inside the cage was recorded with three cameras and analyzed by the same observer (SSA). We defined exploratory behavior by four traits: (1) time spent in the NET cage but outside the acclimation box (Exploration time), (2) number of visiting events (each time a subject changed

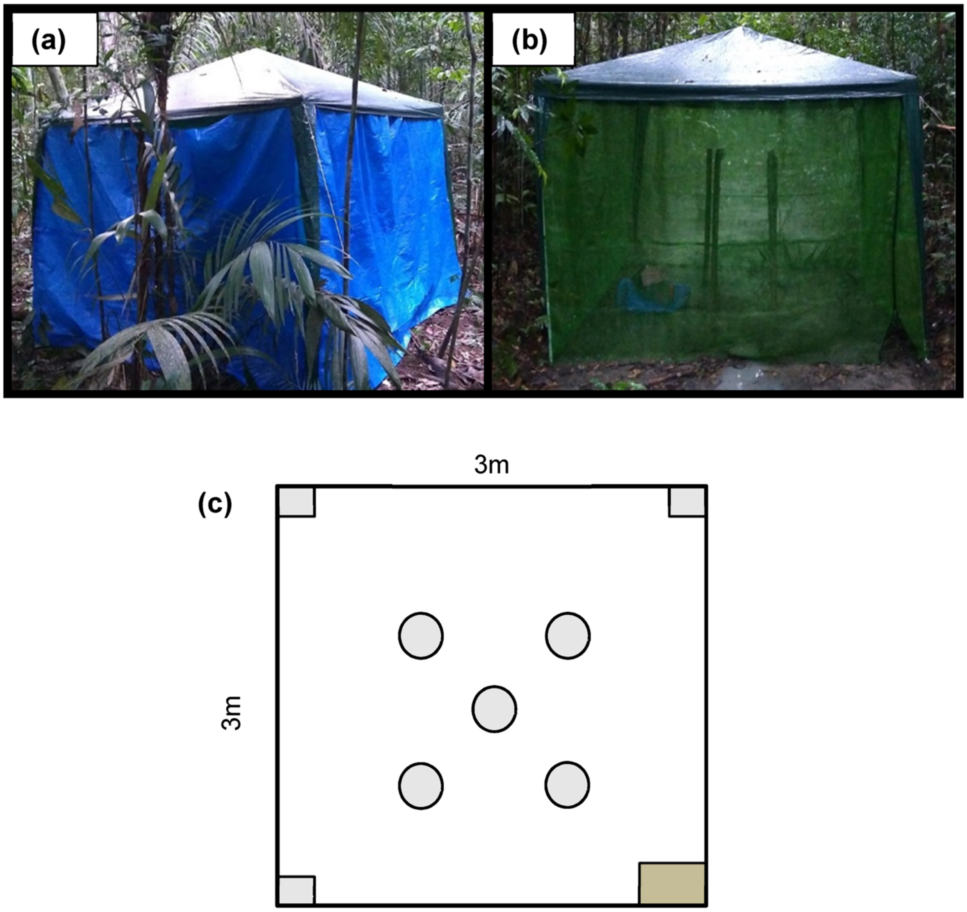


Fig. 2 **a** Novel Environment Test cage (3.0 m × 3.0 m × 2.0 m) with a plastic sheet cover and **b** without it, showing the mesh underneath and **c** cage interior overview with five vertical perches (circles) to stimulate exploration, cameras positioned in corners (small boxes) and the acclimation box next to the entry (large box)

from one object to another), (3) number of objects visited (total number objects visited during the test – perches, walls and ceiling), and (4) the number of hops and flights during the entire test duration (adapted from Verbeek et al. 1994; Dingemanse et al. 2003, 2004). We also registered latency times from the start of the test ($t = 0$ s) until (1) subjects left the acclimation box and (2) subjects visited each of the five perches. Latency times were used as a measure for aversion to novelty. Perches were numbered according to the order in which each subject visited them. The longer a bird took to leave the acclimation box and/or to explore a perch, the higher was its risk aversion. We quantified behavioral metrics using BORIS (Behavioral Observation Research Interactive Software; Friard and Gamba 2016).

Because subjects left the acclimation box at different times after the lid was opened, and therefore spent different time exploring the cage, we standardized values for hops and flights, objects visited, and visiting events to the number per minute to facilitate unbiased comparisons among subjects. We first standardized the units of exploration time to 5 min (300 s; $t_{\text{standardized}} = t_{\text{test}}/300$) periods, because the shortest exploration time for a subject was five minutes. We then divided the value of each exploratory trait by the standardized exploration time (its 5 min rate) and multiplied by 100, rendering to the trait score ($\text{score}_{\text{trait}} = \text{trait value}/\text{t}_{\text{standardized}} * 100$). After examining the normality of exploratory variables, only the variable “visiting events” was log transformed due to high dispersion of values from a normal distribution.

Morphological traits

We chose two categories of morphological traits related to movement: long-distance movement traits (related to dispersal) and short-distance movement traits (related to foraging and routine movements). As a long-distance movement trait, we used the Hand-Wing Index (HWI; Dawideit et al. 2009). Dispersal ability is usually measured with the Hand-Wind Index, as a proxy for avian morphological ability to traverse open areas (Claramunt et al. 2012), and is calculated using the distance from the carpal joint to the tip of the longest primary (PD) and secondary (SD) feather: 100*(PD/PD-SD; adapted from Claramunt et al. 2012). In addition to the HWI we also investigated patterns between populations of raw values for the distance from the carpal joint to the tip of the longest primary and secondary feathers (hereafter feather length). As short-distance movement traits, we used tarsus and tail length. Avian treecreepers use tarsus and tail for climbing and their length is related to clinging performance (Norberg 1979; Zeffer et al. 2003; Tubaro et al. 2002). In addition to the length of tarsus and tail, we also investigated if the proportion of these traits changed between the two populations, and to control for overall changes in body size in opposition to changes of these traits independent of body-size we used the distance from the carpal joint to the tip of the longest primary feather as a measure of body size, and compared the ratio between these traits (tarsus/primary feather and tail/primary feather). We also recorded body mass (weight) as it is a trait relevant for both, long and short-distance movements. All measurements were made by the same person (SSA).

Statistical analyses

Variation of behavioral and morphological traits

We analyzed the variation of behavioral and morphological traits among sampled individuals with generalized linear models (GLM). Models were run with a landscape of origin as a predictor variable (continuous vs. fragmented landscape) or with a sampling site as predictor variable (the two sites in the fragmented and the two sites in the continuous landscape). To determine if the landscape of origin or the site of origin better represents observed variation for each variable, we used a model selection approach based on Akaike Information Criterion (AIC) (Burnham et al. 2002). Models with $\Delta\text{AIC}_c < 2$ were considered as equally plausible and weight values (w_i) were compared among contrasted models. A constant model was also included in the model set. Models were adjusted based on the median of residual deviance and were accepted if medians lay between + 1 and − 1. We used a Gamma distribution for behavioral traits and Gaussian distribution for morphological traits. We also relied on GLMs with multiple response variables to investigate a multivariate shift in behavioral and/or morphological traits among landscapes and sites. Models with multiple response variables were also run with a landscape of origin or site as predictors, also contrasted based on ΔAIC_c. Generalized linear models analysis was conducted with *stats* package and AIC analysis with *bbmle* package, both in R version 3.6.2 software (R-Core-Team 2018).

We used a linear discriminant analysis (LDA) with pooled morphological and behavioral metrics to determine if variation in morphological and behavioral traits was enough to clearly separate individuals into two groups, fragmented and continuous forest. LDA describes the distinctiveness of groupings using misclassification matrices. We chose this method over other ordination methods, e.g. Principal Component Analysis (PCA), as LDA uses less scores to classify samples and it is more efficient with low sample sizes. This analysis was conducted with the *stats* package using R.

Variation in latency times

We chose a failure analysis approach (Fox 2001) for analyzing the latency times for subjects to leave the acclimation box and to reach each perch, registering observations at every second for 20 min (1200 s). This approach considers time until a certain event occurs in an observation period, thus scoring as survival the time before the event and as failure once the event has occurred (Fox 2001). As such, every one-second observation in which individuals were in the acclimation box was still occupied or when a perch was not yet visited was considered a survival event. A failure event was considered when the individual left the box or reached a perch. Failure could happen once for the acclimation box and multiple times for perches, but only the first failure (visit) for each perch was considered. Because subjects could not visit more than one perch at the same time, only one perch could fail at each observation. A hazard rate was given by the chance that a failure event would occur in a given time. To evaluate how time may affect the hazard rate, we tested a survival model with a distribution defined by a shape (ρ) parameter. When $\rho < 1$, hazard chance decreases over time, e.g., the longer a subject remains in the box, lower is the chance to leave it, but if $\rho > 1$, the opposite is true. When $\rho \neq 1$, the distribution is called Weibull. If $\rho = 1$ the hazard rate is constant, that is, the chance for a certain event to happen is the same at any given observation time (exponential distribution). If a certain event was never observed during our observation time (e.g., a subject that never left the box or a certain number of perches that were never visited), it was considered as censored data.

We modeled latency times for each response variable (time to leave the box and time to reach each perch) using the *survreg* function in R version 3.6.2 software (R-Core-Team 2018) and with the landscape of origin (continuous or fragmented) or sampling sites as predictor variables. We modeled the hazard rate with *Weibull* and *Exponential* distributions, which lead to six models for each response variable: (1) latency time ~ *landscape origin (Weibull*), (2) latency time ~ *landscape origin (Exponential*), (3) latency time ~ *sample site (Weibull*), (4) latency time ~ *sample site (Exponential*), (5) latency time ~ 1 *(Weibull*) and (6) latency time ~ 1 (*Exponential*); for each latency time: (1) time to leave acclimation box, (2) time to reach the first (3) second, (4) third, (5) fourth and (6) fifth perch. We used the same approach of model selection with AIC_c values used for GLM variables (Burnham et al. 2002) and models with $\Delta\text{AIC}_\text{c} < 2$ were considered equally plausible and model weight values (w_i) were compared among contrasted models. Latency time was graphically represented as Kaplan–Meier survival curves (Kaplan et al. 1958). Curves were plotted according to the best-fitted models, e.g., if a latency time was best fitted for a model with the landscape of origin or sites as a predictor variable, two or four curves, respectively, were used to represent failure time. Survival analyses were conducted with the package *survival* in R version 3.6.2 software (R-Core-Team 2018).

Results

Exploratory behavior and morphology

Analyses for behavioral traits were conducted with 17 subjects from forest fragments and 18 from continuous forests, as two and one subject, respectively, never left the acclimation box. Models contrasted with AIC_c for each behavioral variable are presented in Table 1. For all behavioral variables, and for the global multivariate model, the constant model was always selected as the most plausible model with $\Delta\text{AIC}_\text{c} < 2$ (Table 1), indicating no evidence for differences in these traits among sites nor landscapes (Fig. 3, for summary statistics of behavioral traits, see Tables S1-S4 in supplementary material).

Analyses for morphological traits were conducted with 17 subjects from forest fragments and 18 from continuous forests (See Tables S5-S8 in supplementary materials for summary statistics). Models contrasted with AIC_c for each morphological trait are presented in Table 2. For the three morphological variables related to long-distance movements and for bodyweight the constant model was selected as the most plausible model or it was within the most plausible models with $\Delta\text{AIC}_\text{c} < 2$ (Table 2), indicating no evidence for differences in these traits among sites nor landscapes (Tables S5 and S7). For tail length, a single model was selected

Table 1 Model selection results based on ΔAIC for four behavioral traits recorded for *G. spirurus* in novel environment tests and for the global multivariate model, as a function of (~) the landscape of origin (Landscape), site of origin (Site) or constant model (1)

Response variable	Model	AIC_c	$\Delta\text{AIC}_\text{c}$	*df*	w_i
Exploration time	~ 1	94.8	0.0	2	0.52
	~ Landscape	95.5	0.7	3	0.36
	~ Site	97.7	2.9	5	0.12
Hops and flight	~ 1	337.7	0.0	3	0.697
	~ Landscape	340.1	2.4	5	0.214
	~ Site	341.8	4.1	2	0.089
Objects visited	~ 1	425.8	0.0	3	0.734
	~ Landscape	428	2.2	2	0.239
	~ Site	432.4	6.6	5	0.027
Visiting events	~ 1	52.8	0.0	2	0.729
	~ Landscape	55.2	2.4	3	0.22
	~ Site	58.1	5.3	5	0.052
Global	~ 1	440.9	0.0	2	0.735
	~ Landscape	443.2	2.3	3	0.230
	~ Site	447.0	6.1	5	0.035

A constant model was also included in each model set. AIC_c is the information score of the model, $\Delta\text{AIC}_\text{c}$ is the difference between the best model and the model being compared with, *df* is degrees of freedom/number of parameters in the model and w_i is model weight

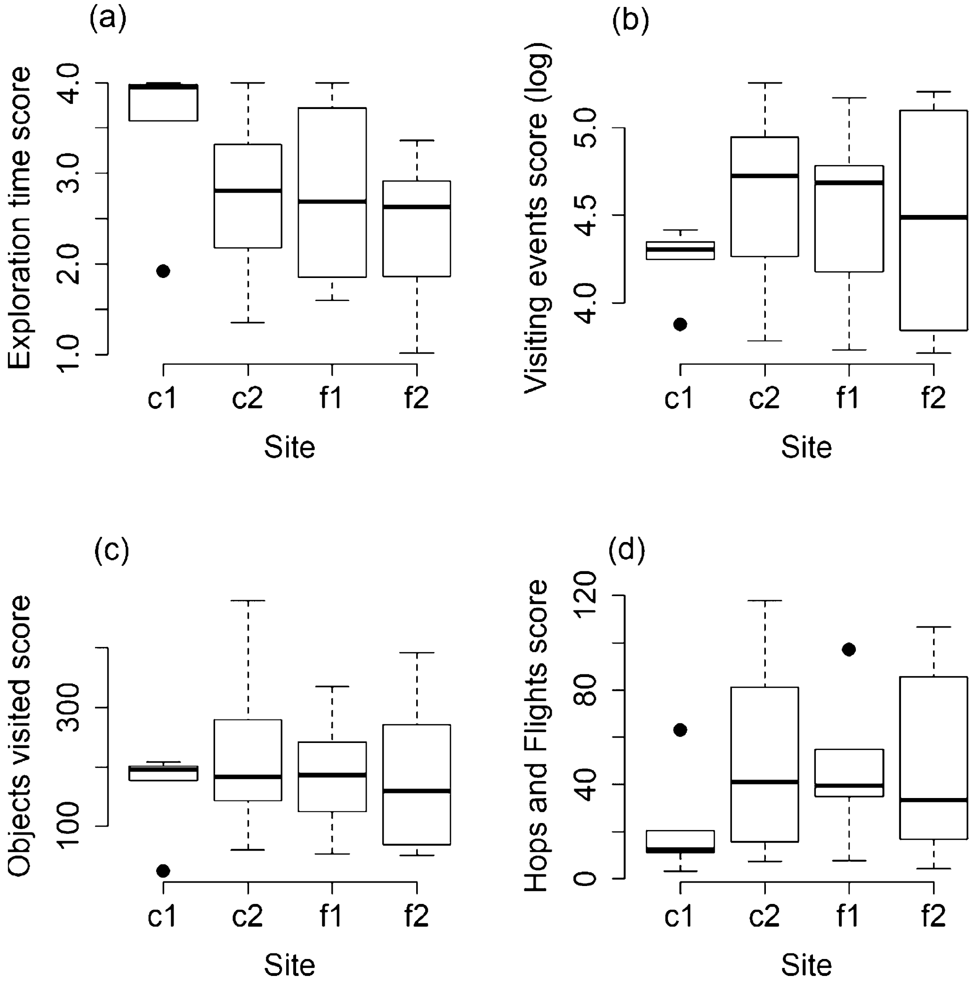


Fig. 3 Box-plots for exploratory traits obtained during the novel environment test for *G. Spirurus* subjects: **a** time spent exploring the testing cage – normalized to 5 min intervals -, **b** score of visiting events, **c** score of objects visited – including perches, walls and ceiling -, **d** score of hops and lights during the whole test time (see methods). Sampling sites: Cuieiras (c1), FAEXP (c2), UFAM (f1) and Airport (f2)

with high model weight ($AIC_c = 198.4$, $w = 0.83$) supporting evidence for shorter tails in individuals from the fragmented landscape than from the continuous forest (Table 3 and Fig. 4). For tarsus two plausible models were selected, the best model ($AIC_c = 139.1$, $w = 0.52$) supports evidence for shorter tarci in the fragmented landscape than in the continuous forest (Table 3, Fig. 4), but the second model with lower weight ($AIC_c = 139.8$, $w = 0.36$) supports at least with some evidence for longer tarsi in the continuous forest Cueiras site than in any other site (Table 3), suggesting that differences among landscapes might be driven by individuals from the Cueiras site (for summary statistics of morphological traits see Tables S8 and S10 in the Supplementary Material). However, for the tail and tarsus ratio in relation to the primary feather length, the constant model was among the selected models indicating that these ratios do not differ among populations, and hence shorter tarsi and tails in the fragmented population derive from overall reduced body-size. Moreover, for the tail/tarsus ratio the constant model was also selected as the best model indicating that the ratio of these traits remains constant among the continuous and the fragmented populations (Table 2). The best model selected for the morphological multivariate models was the model considering the landscape of origin as the predictor ($AIC_c = 243$, $w = 0.85$) (Table 2), supporting evidence for a combined response of morphological variables among the continuous and fragmented landscape.

Linear discriminant analysis (LDA) was conducted with 18 and 17 subjects for the continuous and fragmented forest, respectively. Because three subjects did not have values for behavioral traits, their morphological measurements were excluded from this analysis. LDA presented 94.5% sensitivity (17 out of 18) in classifying subjects from continuous forests and 82.3% (14 out of 17) from forest fragments, giving a total of 88.5% of sensitivity (31 out of 35). Considering morphological and behavioral traits together yielded the highest sensitivity (Table 4). Probabilities for discriminant scores using behavioral and morphological traits had the best separation between groups, although with some overlapping (Fig. 5). Subjects with similar scores were grouped within the same origin class (fragmented or continuous), e.g., subjects with approximately -1 score have about 50% chance of belonging to the continuous group and about 30% chance of belonging to the fragmented group (Fig. 5).

Table 2 Model selection results based on ΔAIC for six morphological traits for *G. spirurus* and for the global multivariate model, as a function of (~) the landscape of origin (Landscape), site of origin (Site) and constant model (1)

Response variable	Model	AIC_c	ΔAIC_c	*df*	w_i
HWI	~Site	179.4	0.0	5	0.56
	~1	180.4	1.0	2	0.34
	~Landscape	182.7	3.3	3	0.11
Primary feather	~1	167.7	0.0	2	0.56
	~Landscape	168.5	0.8	3	0.38
	~Site	172.5	4.8	5	0.05
Secondary feather	~1	177.6	0.0	2	0.69
	~Landscape	179.5	1.9	3	0.26
	~Site	183.2	5.7	5	0.04
Weight	~1	121.9	0.0	2	0.58
	~Landscape	122.8	0.9	3	0.36
	~Site	126.4	4.5	5	0.06
Tail	~Landscape	189.4	0.0	3	0.83
	~Site	194.0	4.6	5	0.08
	~1	194.2	4.7	2	0.07
Tarsus	~Landscape	139.1	0.0	3	0.52
	~Site	139.8	0.7	5	0.36
	~1	142.0	2.9	2	0.12
Tail/ Tarsus	~1	63.0	0.0	2	0.62
	~Landscape	64.4	1.3	3	0.33
	~Site	67.7	4.7	5	0.06
Tail/ primary	~Landscape	−108.8	0.0	3	0.58
	~1	−107.6	1.2	2	0.31
	~Site	−105.3	3.5	5	0.10
Tarsus/ primary	~Site	−150.2	0.0	5	0.42
	~Landscape	−149.8	0.4	3	0.35
	~1	−149.1	1.1	2	0.24
Global	~Landscape	243	0	3	0.85
	~site	247.8	4.8	5	0.07
	~1	248.1	5.1	2	0.06

Response variables are weight, three long-distance movement traits: HWI, primary feather length, secondary feather length; and two short-distance movement traits: tail and tarsus length. AIC_c is the information score of the model, ΔAIC_c is the difference between the best model and the model being compared with, *df* is degrees of freedom/number of parameters in the model and w_i is model weight

Table 3 Parameter estimates (β) for selected models of morphological traits tarsus and tail length as a function of the landscape of origin or site of origin

Effect	Estimate (ß)	Std. error
Tail ~ landscape		
(Intercept) continuous	69.067	0.799
Fragmented	−3.131	1.146
Tarsus ~ landscape		
(Intercept) continuous	16.556	0.390
Fragmented	−1.297	0.558
Tarsus ~ site		
(Intercept) Cuieras	17.800	0.713
FAEXP	−1.723	0.839
Airport	−2.400	0.909
UFAM	−2.667	0.890

Latency times

Failure analyses for the latency times were run with 19 subjects from forest fragments and 19 from continuous forests. Two subjects from forest fragments and one from continuous forest never left the acclimation box and were included as censored data in the model. Fifteen subjects from the continuous forest explored at least one perch, with four subjects never reaching the first perch and preferred to use the cage walls and ceiling. Only five subjects from forest fragments explored at least one perch. Ten subjects from the continuous forest and four from forest fragments explored at least two perches. Three subjects from continuous forests and one from forest fragments explored all five perches.

For box latency time (time until subjects left the acclimation box), the constant model was selected as one of the plausible models with $\Delta AIC_c < 2$ (Table 5), indicating no evidence for differences in box latency time between landscapes nor among sites (Fig. 6a). The constant Weibull distribution model was selected as the second-best model ($AIC_c = 501.5$, $w = 0.257$) supporting some evidence for a positive influence of time on box latency time, (Table 5). For time to reach the first perch two models were selected supporting an effect of the landscape of origin on this response variable. The best model ($AIC_c = 325.7$, $w = 0.543$) supports evidence for a longer time to reach the first perch for individuals from the fragmented landscape than for individuals from the continuous landscape (Fig. 6b). However, it is unclear how time influences this decision, as both Weibull and Exponential distributions were selected within the plausible models (Table 5). For the time to reach the second, third, fourth, and fifth perches, there was a lot of uncertainty associated with models, and the constant model was always selected as plausible for all events, indicating no evidence for an effect of the landscape of origin nor site of origin as a factor that influenced time until reaching these perches (Table 5, Fig. 6c–f). Time for these models also returned uncertainty about how it influenced subjects' decisions, but for the second perch, all plausible models selected had Exponential distribution for time, suggesting that the time had no influence for visiting the second perch.

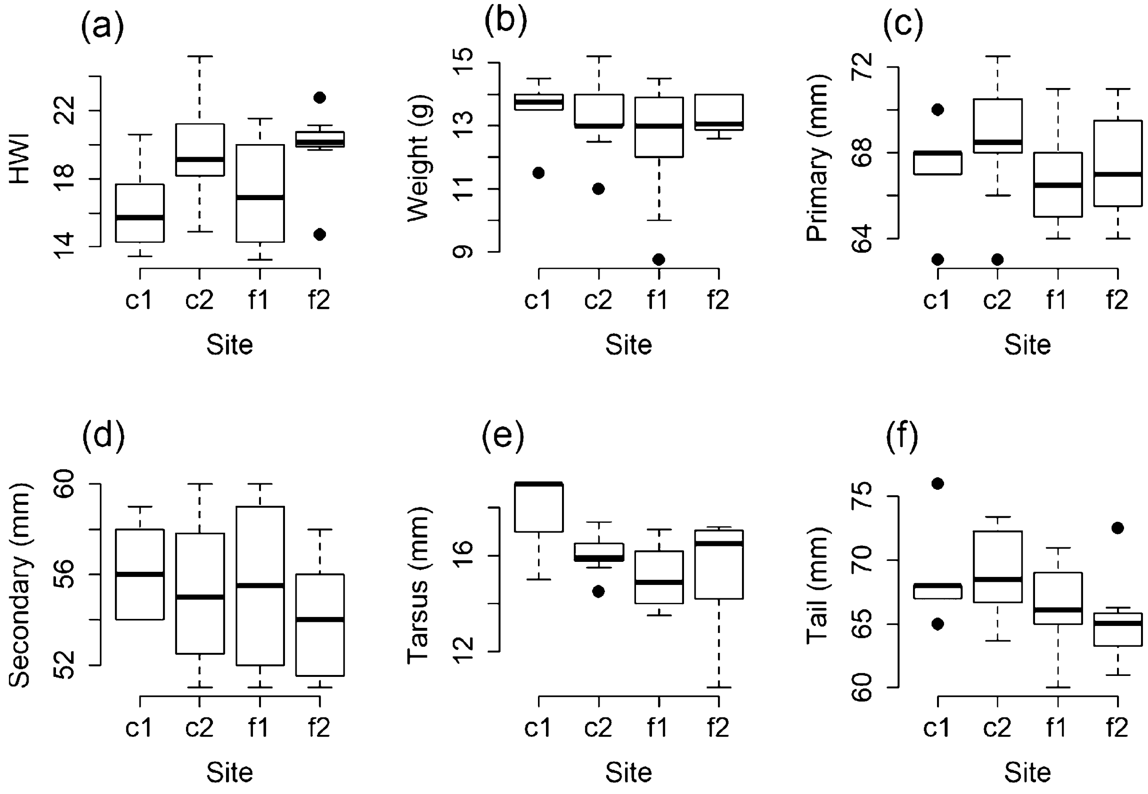


Fig. 4 Box-plots for morphological traits recorded for *G. spirurus* subjects: **a** Hand-Wing Index (HWI; Dawideit et al. 2009), **b** weight, **c** longest primary and **d** secondary feathers, **e** tarsus and **f** tail length, according to Baldwin et al. (1931). Sampling sites: Cuieiras (c1), FAEXP (c2), UFAM (f1) and Airport (f2)

Table 4 Misclassification matrix using LDA's sensitivity for assigning *G. spirurus* individuals to the continuous or fragmented landscape group

Observed	Estimative		
	Continuous	Fragmented	Sensitivity (%)
Behavior			
Continuous	13	5	72.2
Fragmented	8	9	52.9
Morphology			
Continuous	14	4	77.8
Fragmented	6	11	64.7
Behavior + Morphology			
Continuous	17	1	94.5
Fragmented	3	14	82.3

Estimates are presented for each run of the analysis with just behavioral or just morphological variables included or with behavioral and morphological variables combined. Given that the observed samples for continuous and fragmented sites were 18 and 17 subjects, respectively, estimative values represent the number of true positive (correct) and false negative (incorrect) classifications by LDA attempts for each line (category). Sensitivity (%) is equal to the number of true positives/total samples taken (observed) in each category

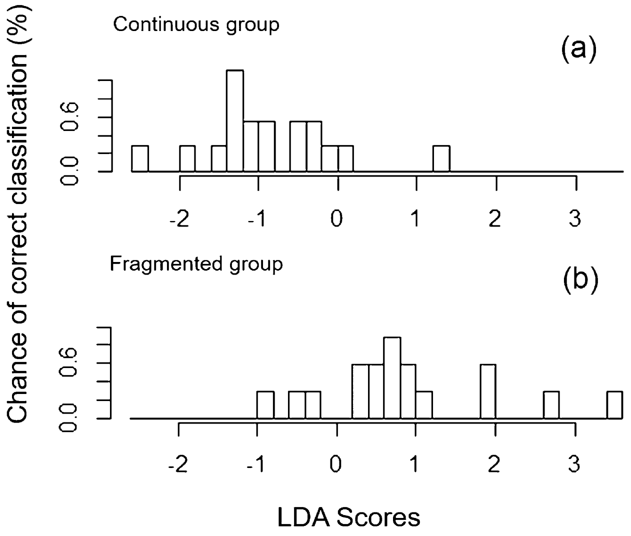


Fig. 5 LDA score for **a** subjects from continuous landscapes and **b** from fragmented landscapes with morphological and behavioral traits. The *x* axis represents the interval of scores for LDA, while the *y* axis represents the probability of an individual to be correctly classified within the group of its origin based on individual LDA score

Table 5 Model selection results based on ΔAIC for latency times of *G. spirurus* individuals during the novel environment test as a function of landscape of origin or sites, tested using survival analyses

Response variable	Model	Distribution	ρ	AIC_c	ΔAIC_c	*df*	w_i
Box time							
	~ Site	Weibull	1.31	501.2	0.0	3	0.292
	~ 1	Weibull	1.34	501.5	0.3	2	0.257
	~ Site	Exponential	1	502.5	1.3	2	0.151
	~ Landscape	Weibull	1.33	502.7	1.5	3	0.14
First perch							
	~ Landscape	Exponential	1	325.7	0.0	2	0.5433
	~ Landscape	Weibull	1.16	327.5	1.8	3	0.2205
Second perch							
	~ Landscape	Exponential	1	248.1	0.0	2	0.326
	~ Site	Exponential	1	248.3	0.3	2	0.287
	~ 1	Exponential	1	249.6	1.6	1	0.148
Third perch							
	~ 1	Exponential	1	171.6	0.0	1	0.266
	~ Site	Exponential	1	172.1	0.5	2	0.204
	~ Landscape	Exponential	1	172.6	1	2	0.159
	~ 1	Weibull	0.68	172.6	1	2	0.159
	~ Site	Weibull	0.68	173.2	1.6	3	0.119
Fourth perch							
	~ 1	Exponential	1	102.8	0.0	1	0.239
	~ Landscape	Exponential	1	103	0.2	2	0.212
	~ 1	Weibull)	0.53	103.3	0.5	2	0.183
	~ Landscape	Weibull	0.52	103.6	0.8	3	0.158
	~ Site	Exponential	1	104.1	1.4	2	0.121
Fifth perch							
	~ 1	Exponential	1	84.5	0.0	1	0.31
	~ 1	Weibull	0.53	85.4	0.9	2	0.2
	~ Landscape	Exponential	1	85.7	1.2	2	0.17
	~ Site	Exponential	1	86.2	1.7	2	0.13

Distribution represents the Failure Analysis type of distribution (Exponential or Weibull) with a ρ value (hazard rate) that represents the influence of time in the observed event (Methods). AIC_c is the information score of the model, ΔAIC_c is the difference between the best model and the model being compared with, *df* is the degrees of freedom/number of parameters in the model and w_i is the model weight. Only models with $\Delta AIC < 2$ are displayed, see Supplementary Material for all models

Discussion

Our study revealed differences in morphological and behavioral traits among continuous and fragmented forest populations of the Wedge-billed Woodcreeper in a highly urbanized region in the central Amazon. We found no evidence for differentiation in long-distance movement traits, such as HWI and primary and secondary feathers length. We did detect phenotypic differences among sites in tail and tarsus length measures, however, these could not be explained independently of overall reduced body size in individuals from the fragmented landscape. Only one behavioral trait associated with exploration provided evidence for differences between populations (latency to move to perches while exploring) and this suggests that individuals persisting in forest fragments in our study are slow explorers when compared to individuals from continuous forests. This finding aligns with previous studies linking slow exploration in birds to fragmented habitats. Behavioral traits exhibited weaker differentiation among populations than morphological traits, but when all phenotypic traits were pooled to discriminate between fragmented and continuous forest sites, reliable differences in phenotypic variation were detected.

Behavioral differences

Exploration preferences have been related to trade-offs between risk exposure and resource reward (Van Oers et al. 2004). Most behavioral traits tested in our study were similar

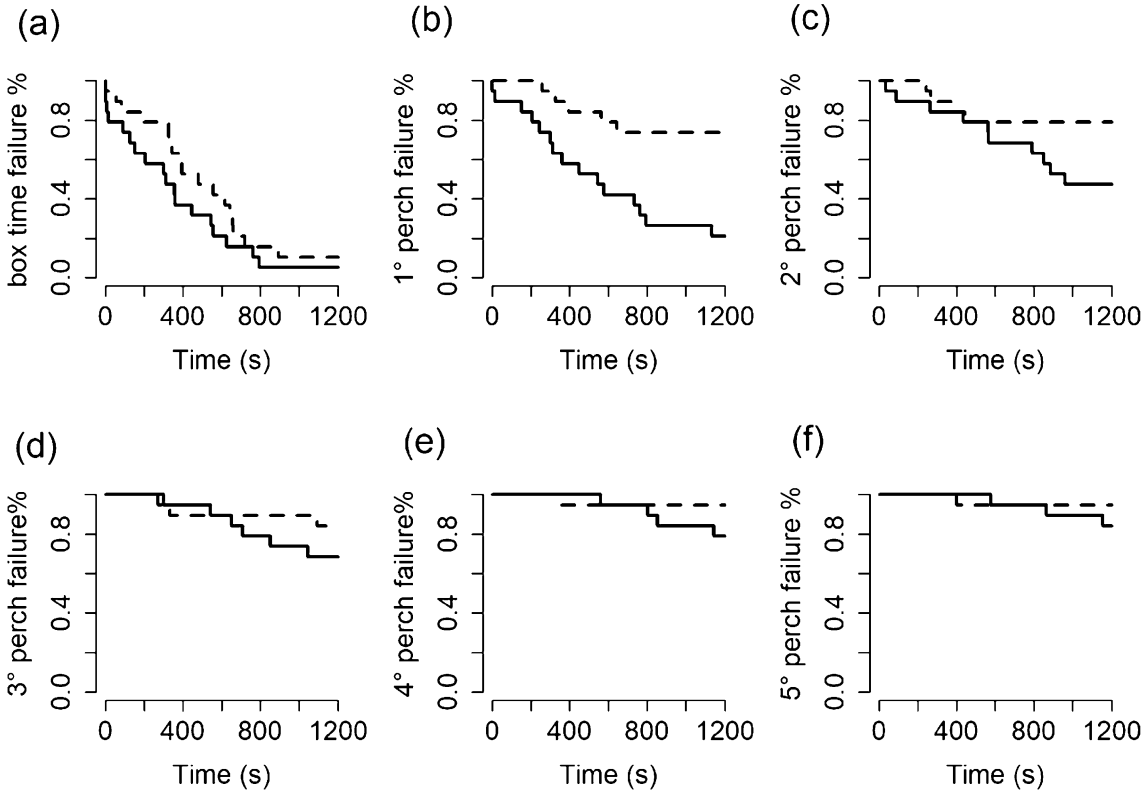


Fig. 6 Kaplan–Meier survival curves representing time to leave **a** the acclimatization box and to reach the **b** first, **c** second, **d** third, **e** fourth and **f** fifth perches, for subjects from continuous (solid lines) and fragmented (striped lines) landscapes

between populations. Exploration features for avian populations have been designed for generalist species from temperate regions, such as *Parus major* (Verbeek et al. 1996, 1994), but no exploration features have been designed specifically for trunk creeping species yet. We studied a neotropical understory avian species highly specialized in tree creeping. As far as we know, this is the first time that a species from this functional guild has been assessed regarding its exploratory behavior but we measured a small number of traits (Carter et al. 2013), and it is possible that other traits could better express exploration for *G. spirurus*. Yet, our results from linear discriminant analysis showed higher classification sensitivity of subjects to their populations when morphological and behavioral traits were combined than when traits were used separately. This suggests the existence of shifts in multiple phenotypic traits simultaneously between undisturbed and fragmented forest areas, and should encourage future work to include large numbers of traits in analyses of fragmentation and urbanization—especially when not much time has passed since initiation of landscape changes (Patankar et al. 2021).

Our findings highlight the utility of latency times as an efficient way to predict exploratory behaviors (Groothuis et al. 2005). The number of continuous forest subjects that explored at least one perch was three times the number of subjects from fragmented forest, and subjects from forest fragments also took longer to explore the first perch. This attribute is strongly associated with slow exploration (Verbeek et al. 1994) and provides support to our central hypothesis that slow explorers should be favored in fragmented landscapes; a finding in line with other similar studies of butterflies and birds (e.g., Merckx et al. 2003; Cornelius et al. 2017). These findings from an urbanizing Amazonian landscape thus add to the growing body of evidence that slow explorers are likely favored by, and more successful in, fragmented landscapes; whereas fast exploratory profiles make individuals more susceptible to hazards and greater risk-taking (Van Oers et al. 2004) leading to higher mortality in fragmented landscapes.

Most of NET essays usually last 10 min or less (e.g., Verbeek et al. 1994; Dingemanse et al. 2002; Huang et al. 2015; Charmantier et al. 2017) but thanks to our longer sampling period (20 min) we were able to detect for short-term adjustments in behavior that allowed us revealing emergent differences between groups of individuals. While examining recordings, we noticed that in late phases of tests most subjects reached higher areas of the cage, something that we did not aim to test statistically, but deserves to be mentioned.

Individuals from forest fragments tended to use the ceiling and walls over perches when compared to continuous forest birds, and when they did decide to visit a perch, they took longer to reach it. Individuals from forest fragments commonly flew through the cage directly to walls and ceiling, ignoring other objects, while most subjects from continuous forests used at least two perches before reaching higher areas. Considering that all tested birds were in the same stress conditions while facing unfamiliar objects and a new environment, birds with less aversion to leave the box and reach perches were taking more risks while exploring, which agrees with a more risk-taking behavior of fast explorers (Dingemanse et al. 2005). The number of birds that reached the second perch was smaller than those reaching the first perch, a pattern that applies throughout the fifth perch. Individual decisions to either keep exploring or to reach for potentially safer higher areas of the cage—ceiling and walls -, or to keep on the acclimation box until the end of the test, also suggest that subjects from the fragmented forests were also probably less prone to take risks while exploring.

Morphological differences

Wing measures, longest primary and secondary wing feathers and the Hand-Wind Index, were not different between populations. These traits represent a proxy for dispersal ability in which usually more pointed wings should favor longer dispersal distances (Claramunt et al. 2012). We expected that individuals in the fragmented landscape would be forced to disperse longer distances to access other fragments, and thus face the matrix during dispersal events. Based on the lack of discrepancy between these morphological traits, it is possible that individuals might not be dispersing at all between fragments and thus dispersal patterns within fragments are similar to those observed in the continuous forest, with short-distance dispersal events restricted to early life stages (Paradis et al. 1998). This would imply that either fragmentation is completely inhibiting dispersal movements, or that individuals are perishing in the matrix while trying to reach other fragments. A mark-recapture and telemetry study in a fragmented agricultural landscape north of Manaus showed that *G. spirurus* individuals have high fidelity for primary and for older secondary forests (> 15 yrs) but rarely or never use younger secondary forests or open areas (Powell et al 2015), suggesting that successful dispersal over the highly contrasting urban matrix is probably very unlikely. Moreover, *G. spirurus* is only found in large fragments (> 100 ha) within the urban area of Manaus (Conceição 2013). Future genetic studies should elucidate if effective dispersal movements do occur among forest fragments in this urban landscape.

Tail and tarsus were the most distinct morphological traits between populations, as individuals from forest fragments had shorter tarsi and tails than individuals from the continuous forest population. However, when correcting for body size we found that tarsus and tail were not shorter for individuals in the fragmented landscape but most likely shorter tarsi and tails reflect an overall reduction in body size. Therefore, contrary to our prediction, differences in these traits are probably not associated with their function in short-distance movements while foraging, but most likely reflect an overall reduction of body size in the fragmented landscape. Although tarsus is generally independent from body mass (Zeffer et al. 2003) tail length, on the other hand, is known to be correlated with body mass (Norberg 1979), further supporting that individuals in the fragmented landscape might be smaller overall. In a study of two passerine species in eastern Europe, nestlings in urban populations had reduced developmental pace and hence reduced body mass when adults, mostly due to overall food scarcity in urban forest remnants (Corsini et al. 2021). Given the striking difference in capture rates of *G. spirurus* in forest fragments in comparison to the continuous forests, it is possible to suggest that this species occurs at lower densities in the fragmented landscapes, which might be related to lower food availability. It has been suggested that *G. spirurus* might be released from competition in smaller fragments because of the local extinction of other woodcreepers (Powell et al. 2015), but the abundance of *G. spirurus* increases only during the initial years after fragmentation, followed by a decrease in later years (Bierregaard et al. 1989). In addition to food supply, metabolic processes are also related to body-size shifts in urban environments, with urban communities generally consisting of smaller species as a consequence of increased metabolic costs associated with the urban-heat-island effect (Merckx et al. 2018b).

Limitations and sampling bias

We also would like to discuss some limitations of our study. We cannot imply that differences observed are specifically a result of adaptation, phenotypic plasticity or genetic drift, as it would require a genetic approach with common garden experiment (e.g., Merckx et al. 2003, 2006) and direct measures of fitness (e.g., Corsini et al. 2021). Behaviors can fit different situations (Dingemanse et al. 2005), fluctuating with spatial and temporal changes (Dingemanse et al. 2010) and our work only represents a small time-frame of a slow fragmentation-response process. Additionally, captures with mist nets could bias sampling, as slow explorers tend to identify and avoid passive capture methods (Stuber et al. 2013). Given our five times higher sampling effort in forest fragments than in continuous forest to attain the same number of captured individuals, slow exploration could be underestimated. Nevertheless, if we sampled mostly faster explorers in forest fragments, those are still slower than those tested in continuous forests. Also, observed behavioral differences could potentially be related to sex-related differences, as would be expected for species in which males and females behave differently (Awade et al. 2017; Dingemanse et al. 2010). Although *G. spirurus* has no sexual dimorphism, we have no reasons to believe that males and females have significant differences in exploratory behavior, as this species is mostly observed in pairs while foraging, defending their territories and in parental care (Marantz et al. 2020; Darrah and Smith 2013). Furthermore, it is unlikely that sex-related variation in exploratory behavior would be greater than that observed between the studied populations, given the consistency of our trait values.

Conclusion

Here we highlight that populations are accumulating phenotypic differences in response to environmental change due to habitat fragmentation, specifically in very harsh conditions as in urban settings. As such, our results should not be interpreted as an overall resilience to human-induced habitat loss and fragmentation, but rather as possible adjustments that can arise during the response to environmental change in certain species while their populations thrive in habitat fragments in harsh urban environments. We do not know if these populations are viable in the long-term, or which landscape configuration features may guarantee the viability of populations in our study area. An examination of traits in demonstrably older fragments compared to newer ones, and larger versus smaller fragments of the same or different ages would help illuminate the development and function of intraspecific trait shifts we observed (Liu et al. 2019; Warzecha et al. 2016). Overall, our study highlights the importance of documenting and understanding the combined variation of behavioral and morphological traits within species that are driven by environmental change in fragmented and urbanized landscapes. Evidence for evolutionary trajectories set in motion by fragmentation and by urbanization (Johnson et al. 2017; Cheptou et al. 2017) will gain more support with future integrative studies and meta-analyses. For this, we call for an urgent effort in producing more empirical studies showing patterns of phenotypic differentiation in response to landscape change, such as our study, especially in megadiverse tropical cities where environmental change is occurring at alarming rates but a large gap of knowledge still persists.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-021-04976-x.

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Author contribution statement Conceptualization: CC, KS SSA. Methodology: CC, MA, SSA. Field testing: SSA. Formal analysis and investigation: SSA, KS, CC, MA. Writing—original draft preparation: SSA. Writing—review and editing: CC, MA, KS.

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Data availability The datasets generated and analyzed during the current study are available in a Google Drive folder that can be accessed upon request to: stspiteri@hotmail.com.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Human and animal rights All applicable institutional and/or national guidelines for the care and use of animals were followed.

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