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Heterogeneous movement of insectivorous Amazonian birds through primary and secondary forest: A case study using multistate models with radiotelemetry data



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ABSTRACT

Given rates of deforestation, disturbance, and secondary forest accumulation in tropical rainforests, there is a great need to quantify habitat use and movement among different habitats. This need is particularly pronounced for animals most sensitive to disturbance, such as insectivorous understory birds. Here we use multistate capture–recapture models with radiotelemetry data to determine the successional stage at which within-day movement probabilities of Amazonian birds in secondary forest are similar to those in primary forest. We radio-tracked three common understory insectivore species in primary and secondary forest at the Biological Dynamics of Forest Fragments project near Manaus, Brazil: two woodcreepers, *Glyphorhynchus spirurus* ($n = 19$) and *Xiphorhynchus pardalotus* ($n = 18$), and the terrestrial antthrush *Formicarius colma* ($n = 19$). Forest age was a strong predictor of fidelity to a given habitat. All three species showed greater fidelity to primary forest than to 8–14-year-old secondary forest, indicating the latter's relatively poor quality. The two woodcreeper species used 12–18-year-old secondary forest in a manner comparable to continuous forest, but *F. colma* avoided moving even to 27–31-year-old secondary forest—the oldest at our site. Our results suggest that managers concerned with less sensitive species can assume that forest reserves connected by 12–18-year-old secondary forest corridors are effectively connected. On the other hand, >30 years are required after land abandonment before secondary forest serves as a primary forest-like conduit for movement by *F. colma*; more sensitive terrestrial insectivores may take longer still.

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1. Introduction

Quantifying habitat quality for wildlife is an exceedingly challenging task. We can view habitat quality as the expected fitness of an individual in that habitat (Fretwell, 1972), but this is far easier to conceptualize than to estimate. Given current rates of anthropogenic habitat alterations throughout tropical rainforests, it is critical that we identify techniques that can reveal the quality of human modified habitats for disturbance-sensitive species such

as insectivorous understory birds (Powell et al., 2015). In particular, regenerating secondary forests are now widespread and expanding in the tropics, yet the quality of this habitat to rainforest animals remains poorly understood and much debated (Brook et al., 2006; Wright and Muller-Landau, 2006a,b; Chazdon et al., 2009). For example, by 2002, the area of secondary forest in the Brazilian Amazon had increased to 161,000 km², about the size of Uruguay (Neeff et al., 2006). As secondary forest matures, it becomes increasingly similar to primary forest (Norden et al., 2011), but it is not clear at what point in the successional process it regains habitat quality comparable to that of primary forest. This basic question of the quality of secondary forest is a critical conservation issue because secondary forest and other human-altered habitats are being created quickly, producing landscapes that are a heterogeneous mix of habitats. Secondary forests are thought to be useful as corridors between patches of primary forest (Lees

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and Peres, 2008), but the age at which secondary forest has matured enough to facilitate movement of rainforest animals remains unquantified for most rainforest taxa. By evaluating habitat quality for rainforest animals as secondary forest matures, land managers can establish the value of secondary forest and strategically design heterogeneous landscapes to maximize connectivity through the use of corridors, buffers, etc.

Understory birds are considered excellent study organisms in tropical rainforests because they are diverse, relatively easy to capture, and vary enormously in sensitivity to disturbance (Stouffer and Bierregaard, 1995; Şekerciöğlu et al., 2002). Despite these advantages, it remains challenging to quantify habitat quality. For example, estimates of species abundance are often used to infer habitat quality, but abundance alone can be a misleading indicator of habitat quality if dominant individuals push subordinates into suboptimal habitat (Fretwell, 1972; Van Horne, 1983; Skagen and Yackel Adams, 2011). Further, nest success studies are difficult to undertake in the tropics (but see Visco and Sherry, 2015) because predation is high, nest success is low (Brawn et al., 2011), and breeding seasons are often not confined to a short time window (Stouffer et al., 2013). Long-term survival estimates, which can provide perhaps the most direct indices of habitat quality for individuals that remain in one habitat type, are challenging to estimate in the tropics because precisely quantifying variation in survival across habitats can require an extraordinary amount of data collected at sampling intervals conducive to existing survival models (Ruiz-Gutiérrez et al., 2012). Finally, there are difficulties in linking annual survival to specific habitats for birds that spend their time in multiple habitats (Conroy et al., 1996).

The ideal free distribution predicts that animals will distribute themselves in the highest quality habitat available, where quality is defined in terms of the fitness of individuals in that habitat (Fretwell and Lucas, 1969). It follows that given availability, individuals will move to and remain in high rather than low quality habitat. Thus at any temporal scale, the probability of movement between habitats should be a function of the quality of those habitats, with a relatively high probability of moving from low to high quality habitat; and conversely, a relatively high probability of fidelity to high quality habitat (Fretwell and Lucas, 1969; Fretwell, 1972; Nichols and Kendall, 1995). For example, Senar et al. (2002) found that between-year movement of Citril Finches (*Serinus citronella*) from pinecone-poor low quality habitat to pinecone-rich high quality habitat was much more common than the reverse movement.

Here we infer habitat quality by determining the stage of forest succession at which within-day movement and fidelity between primary and secondary forest are equal. Specifically, our approach was to ask at what stand age do within-day bird movement probabilities to and from secondary forest become similar. We acknowledge that other approaches exist to ascertain habitat quality (e.g., survival, nest success, behavior), but given the challenges of other techniques, here we sought an alternative metric of habitat quality using typical within-home-range movement of individuals among habitats. Notably, most insectivorous Amazonian forest birds are territorial (Stouffer, 2007), and after pasture abandonment there are no forest birds in regenerating patches (P. Stouffer, pers. obs.), so those patches are truly available to adjacent territorial birds. Thus during the process of succession, decisions made by birds to move into and show fidelity to regenerating secondary forest should represent the recovery process: as habitat quality improves, birds increasingly move into second growth and show increasing fidelity to second growth.

Here we use multistate capture–recapture models to quantify within-day movement probabilities of three radio-tagged insectivorous understory bird species among habitats of differing quality. Our primary objective was to use a gradient of secondary

growth age classes to determine the age at which within-day avian movement probabilities to and from secondary forest were approximately equal to those within primary forest (hereafter “recovery”). In other words, we sought to quantify the age of recovery of secondary forest, which we defined here as similar avian movement probabilities in either direction between primary and secondary forest. Our primary hypothesis was that stand age would affect movement and fidelity of resident birds; further, as secondary forest becomes structurally similar to primary forest with time (Norden et al., 2011), we predicted that movement probabilities would converge to those of primary forest. Given the general vulnerability of insectivorous tropical rainforest birds to anthropogenic disturbance (Şekerciöğlu et al., 2002; Bregman et al., 2014; Arcilla et al., 2015; Cordeiro et al., 2015; Pavlacky et al., 2015; Powell et al., 2015), we were interested in comparing understory insectivores with a broad range of sensitivity to disturbance. Among the understory insectivores, terrestrial species (those that forage by walking on the ground) are believed to be particularly vulnerable to disturbance (Canaday and Rivasdenezra, 2001; Peh et al., 2005; Stouffer and Bierregaard, 1995; Powell et al., 2013). Accordingly, we predicted that the terrestrial ant-thrush *Formicarius colma* would require older secondary forest than our two other focal species before exhibiting movement patterns similar to those in primary forest. Conversely, the small, ubiquitous woodcreeper *Glyphorhynchus spirurus* is often found along edges and in small fragments, so we predicted it would show primary forest-like movement patterns in younger secondary forest than our other focal species. We predicted that the mixed-species flocking woodcreeper *Xiphorhynchus pardalotus* would show an intermediate response. Finally, because heat and light levels are thought to affect movement of tropical understory birds throughout the day (Patten and Smith-Patten, 2012), we predicted a quadratic effect of time of day on bird movement, with the highest habitat fidelity during midday when light and heat levels are at their highest.

2. Methods

2.1. Study site

We conducted fieldwork during the dry seasons (June through October) of 2009–2011 at the Biological Dynamics of Forest Fragments Project (BDFFP), near Manaus, Amazonas, Brazil. Although originally designed to evaluate the effects of area and isolation on wildlife (Bierregaard et al., 2001; Laurance et al., 2011), abandonment of clearcut areas at the BDFFP beginning in the early 1980s has created the opportunity to study the dynamics of secondary forest recovery (Stouffer and Bierregaard, 2007; Sberze et al., 2009; Powell et al., 2013). The experimental forest at the BDFFP consists of 11 forest fragments (5 of 1-ha, 4 of 10-ha, and 2 of 100-ha) embedded in a variable inter-habitat matrix. We tracked radio-tagged birds in 9 of these forest fragments and in secondary and primary forest (see supplementary Fig. S1 for map). Primary forest at the BDFFP in areas used by our focal birds averaged about 23 m-tall with occasional emergent trees up to 55 m (Gascon and Bierregaard, 2001). Due to the temporal pattern of clear-cutting, secondary forest available to our radio-tagged birds was generally distributed into four age classes—the youngest secondary forest (hereafter “SF₁”) was 8–14 years old with a mean canopy height of about 6 m. We defined SF₂ as 15–18 years old with a canopy of ~14-m, and SF₃ was 21–24 years old with a ~16-m canopy. The oldest secondary forest at the BDFFP (SF₄) was 27–31-years-old, with a ~19-m canopy. All of the SF₄ was located near the fragments at “Cidade Powell” and was never burned; practically all other secondary forest classes were burned

periodically since initial isolation (Bierregaard and Gascon 2001). Mean canopy heights listed here are from areas used by radio-tagged birds and were estimated from a LiDAR canopy height model from 2007 (Michael Lefsky and Scott Saleska, unpublished data).

2.2. Study species

We selected three study species that were common and catchable enough for us to obtain a reasonable sample size, and varied in their vulnerabilities to disturbance and abundance in secondary forest.

At 14 g, *G. spirurus* (Wedge-billed woodcreeper) is the smallest of 13 woodcreeper species at the BDFFP and perhaps the most versatile in habitat use and association with mixed-species flocks. The species is abundant at the BDFFP, with primary forest densities of 33 per 100-ha (Johnson et al., 2011), and considerable overlap among home ranges (Gradwohl and Greenberg, 1980; Darrah, 2013). The species is abundant in the interiors of primary forest, but also common along edges, in 1-ha forest fragments, and in secondary forest (Levey, 1988; Cohn-Haft et al., 1997; Stratford and Stouffer, 2001; Marantz et al., 2003). *G. spirurus* forages by shimmying up tree trunks, rapidly chiseling at the bark with its short, pointed bill, in search of invertebrate prey (Skutch, 1969). Numerous analyses of diet suggest that the species is exclusively insectivorous (Marantz et al., 2003). Individuals can forage in pairs, alone, or with understory mixed-species flocks led by *Thamnomanes* antshrikes passing through their territories (LLP pers. obs.).

The majority of *X. pardalotus* (Chestnut-rumped woodcreeper; approx. 38 g) at the BDFFP are core members of understory mixed-species flocks led by *Thamnomanes* antshrikes. Although most often found in mixed-species flocks (Develey and Stouffer, 2001), *X. pardalotus* is not considered an obligate mixed-species participant; rather, it is known as a “flock dropout” as it also forages individually, in pairs, or occasionally at swarms of army ants (Marantz et al., 2003; Stouffer et al., 2006). Both *X. pardalotus* and *G. spirurus* are capable of leaving primary forest, as both regularly crossed edges created by 20-year-old forested roads at the BDFFP (Laurance et al., 2004). Densities of *X. pardalotus* in primary forest are 14 per 100-ha at the BDFFP (Johnson et al., 2011), with territorial pairs maintaining home ranges with little overlap; generally there is only one pair per flock. The species uses its stiff tail to shimmy up trunks where it forages for invertebrates, using a wide variety of foraging maneuvers including pecking, sallying, probing, gleaning and flaking (LLP, unpublished data). At a time when secondary growth at the BDFFP was considerably younger (i.e., <17 years old), Cohn-Haft et al. (1997) listed the species as an exclusively primary forest resident, although Willis (1977) and others (Marantz et al., 2003) have reported the species' use of older secondary growth.

F. colma (Rufous-capped Antthrush; approx. 46 g) is a common understory terrestrial insectivore found mainly in primary forest. The species is not generally known to occupy secondary forest (Cohn-Haft et al., 1997; Krabbe and Schulenberg, 2003), and movement by the species was strongly impeded by 20-year-old edges created by forest road clearings at the BDFFP (Laurance et al., 2004). The species does not forage with mixed-species flocks or at army ant swarms; rather, it walks along the forest floor alone or in pairs, where it forages by picking invertebrates from leaf litter, flipping leaves as it goes (Krabbe and Schulenberg, 2003). Density of the species in primary forest at the BDFFP is 11 per 100-ha (Johnson et al., 2011) and territorial pairs maintain home ranges with little overlap (Stouffer, 2007).

2.3. Captures

We captured target species with both passive and target netting techniques and marked captured birds with uniquely numbered

aluminum bands distributed by CEMAVE (for more detail, see Powell, 2013). We fitted each bird with a radio transmitter (<5% of body weight) from Holohil Systems Ltd. (Carp, Ontario; model BD-2) using a 0.8-mm-diameter elastic thread harness (Rappole and Tipton, 1991). Here we analyzed data from 19 *G. spirurus*, 18 *X. pardalotus* and 19 *F. colma*. The 19 *F. colma* included 7 young, 11 adults, and 1 bird of unknown age. The woodcreepers could not be reliably aged after their skulls ossified, so we tracked only “adult” woodcreepers with completely ossified skulls. To limit the sample to birds that had regular access to the interface between habitats, we excluded birds captured greater than 200 m from the interface of primary and secondary forest.

2.4. Radio-tracking

We tracked each individual as frequently as possible over a period lasting an average of 23.6 (± 3.0 SE) days beginning 24 h after release with a transmitter. We tracked each individual during the dry season of only one year. We stratified daylight hours (0600–1800 h) into four equal time blocks, collecting at least five locations within each time block to control for diurnal patterns in bird activity (Otis and White, 1999). Consecutive locations were separated by a minimum of 15 min. Given that all three species can fly, none has a territory >17 ha (Powell, 2013), and the fact that many individual birds had multiple transitions among habitats per day, the 15 min intervals were certainly long enough to achieve biological independence: “a sampling interval long enough to allow the animal to move from any point in its home range to any other point” (Lair, 1987:1099). For logistical reasons, we generally collected data in one or two sessions of five consecutive locations per bird per day (i.e., 5 or 10 locations per day). We did not radio-track *G. spirurus* in SF₄; rather, we chose to use our transmitters and time to explore the effect of older secondary forest on the other two species, which are less tolerant of secondary forest. We recorded 700 locations of *G. spirurus* (mean = 37 ± 2.4 SE per individual), 717 of *X. pardalotus* (40 ± 3.0 SE) and 814 of *F. colma* (43 ± 3.2 SE). For more detail on capture and radio tracking, refer to Powell (2013).

2.5. Data analysis

To estimate movement probabilities and survival for animals occupying habitats of varying quality, wildlife ecologists often employ multistate capture–recapture models—generally with data from capture-mark-recapture (or resight) efforts in the field (Hestbeck et al., 1991; Brownie et al., 1993; Lebreton et al., 2009). Transition probabilities estimate the probability that an animal, assuming that it survives, will move from one state to another. States can refer to different age classes, habitats, etc. Although such models can be adapted to accommodate data from animals with radio transmitters (Nichols, 1996), to date there have been few studies exploiting the existing statistical framework for radio-tagged animals (but see Martin et al., 2006).

Analysis of telemetry data using multistate capture–recapture models frequently admits simplifying assumptions such that survival and detectability need not be estimated (Nichols, 1996). For example, define S_t^r as the probability that a marked animal alive in state r at sampling occasion t survives until sampling occasion $t + 1$, p_t^r as the probability that a marked animal alive in location r at sampling occasion t is detected at that time, and ψ_t^{rs} as the probability that an animal that survived in location r at sampling occasion t and is alive in the study system at sampling occasion $t + 1$, is located in location s at $t + 1$. Consider a marked animal detected in habitat A at sampling occasion 1 and habitat B at sampling occasions 2 and 3; detection history is (A B B). Under a

general multistate capture–recapture model, the probability associated with this history, conditional on release of a marked animal in habitat A at occasion 1 can be written as:

$$\Pr(A \ B \ B | \text{release in A at 1}) = \psi_1^A \psi_1^{AB} p_2^B \psi_2^{BB} p_3^B \quad (1)$$

Many capture–recapture studies using multistate modeling are characterized by $p_i^r < 1$ and are focused on longer time horizons (e.g., multiple years) such that $S_i^r < 1$, requiring that both sets of parameters be estimated in addition to the transition parameters, ψ_i^{rs} . However, in our study, detection probability for radio-tagged birds approached 1, so detectability can be fixed, $p_i^r = 1$. The relatively short temporal window constrained by transmitter life in our study insured that individual survival approached 1 as well, so we fixed $S_i^r = 1$. These constraints allow us to rewrite Eq. (1) as:

$$\Pr(A \ B \ B | \text{release in A at 1}) = \psi_1^{AB} \psi_2^{BB} \quad (2)$$

If we had followed each bird for entire days of sampling, our encounter histories would be populated with habitat states at every sampling occasion, i.e., at the end of each 15-min interval separating successive radio locations. But the need to collect data from multiple telemetered birds and to travel between areas frequented by different birds produced detection histories with many sampling occasions at which no sampling occurred. If we use MARK (White and Burnham, 1999) notation and denote an occasion with no sampling using a “.”, then the first 3 entries of a detection history might be as follows: A · B, indicating no sampling at occasion 2. Habitat state associated with the radioed bird at occasion 2 is thus unknown, so the model for the encounter history must incorporate this uncertainty. For example, if there are only 2 possible habitat states, A and B, then we can write the probability associated with this encounter history as:

$$\Pr(A \cdot B | \text{release in A at 1}) = \psi_1^{AB} [1 - \psi_2^{BA}] + [1 - \psi_1^{AB}] \psi_2^{AB} \quad (3)$$

Expression 3 differs from 2 in admitting the possibility that the bird could have been in either state A or B at sampling occasion 2. In standard multistate capture–recapture models, state uncertainty is associated with nondetection, whereas in our analysis, uncertainty is associated with unsampled occasions. In both cases, multistate models provide a natural way to model this uncertainty.

Our analysis focused on modeling the fidelity probability, ψ_i^{rr} (hereafter “fidelity”), associated with an individual remaining in a given habitat between consecutive occasions. Restated, this is the probability that given a bird was found in a given forest age state (i.e., habitat) at time t , it would be found in that same state at time $t + 1$. Conversely, $1 - \psi_i^{rr}$, reflects movement away from state r to habitat of some other state, $r \neq s$. We initially developed models with 5 states, primary forest and 4 age classes of secondary forest. However, for a given bird, most movement was between primary forest and the most abundant secondary forest age class within the bird’s range. Thus, our data were too sparse to support a general multistate model for 5 habitat states. Instead, we simplified and defined two states for each bird: primary forest (HABITAT = 1) and secondary forest (HABITAT = 2). We used multistate models in program MARK (White and Burnham, 1999) with detectability fixed to 1.0 and survival fixed to 1.0. Only one bird died during the study: a *G. spirurus* that was depredated by a raptor; we only included the data on that individual from the days prior to the depredation. Given the generally high survival and the fact that all birds were easily detected using radiotelemetry, mortality did not confound detection or habitat, so our model simplifications seemed appropriate.

Individual encounter histories were created for each combination of bird and day. Each 15-min period from 0600 h to 1759 h was used as an encounter occasion for a total of 48 15-min occasions. Occasions with ≤ 5 total encounters were removed and

replaced with “.”. Observations were recorded as state “1” (primary forest) or “2” (secondary forest). We added a covariate for each individual based on the age class of secondary forest (SF₁–SF₄ as defined above) most available to that individual. We defined available habitat as that contained in a circle originating at the individual’s capture location with an area equal to the average home range size for that species (Powell, 2013). For SF₁–SF₄, the 95% confidence interval of the proportion of available primary forest on the landscape relative to the secondary forest age class corresponding to that group overlapped 0.50. In other words, in each group, the availability of primary and secondary forest age class was similar (approximately equal); the exception was *F. colma* in the SF₃ group ($n = 3$), for which our estimate of fidelity should be interpreted cautiously due to the greater availability of primary forest habitat (0.65) and the poor precision of the estimate (see Section 4). We performed statistical analyses using these secondary forest age groups as categorical variables.

To determine the environmental variables affecting fidelity, we compiled *a priori* candidate models in a model selection framework separately for each species (Burnham and Anderson, 2002), including models with combinations of five variables that we believed to be biologically meaningful relative to movement probabilities, as based on the literature and our field observations of the species. Candidate sets included 11 models for each species. Support for models including the variable HABITAT would indicate that the probability that a bird remained in secondary forest differed from the probability that the bird remained in primary forest (i.e., $\psi_1^{11} \neq \psi_2^{22}$ regardless of $\psi_1^{AB} \psi_2^{BB}$ secondary forest age). We included HABITAT in all models except the null, as this is a central focus of our analysis. Further, to determine how fidelity varied as secondary forest matured, we included models with variable 2°AGE in which fidelity differed for the four secondary forest age class groups SF₁–SF₄. We were also interested in whether fidelity increased or decreased in ordinal fashion with age of secondary growth (Powell et al., 2013); thus, we included a variable in the candidate set (TREND) that treated secondary forest classes as ordinal categories. From our field observations, we knew that bird movement varies widely by time of day, thus we included a variable for time of day (TIME) and a quadratic version of the variable (TIME²) that allowed movement to vary with time in quadratic fashion; for example, we predicted that most movement ($1 - \psi_i^{rr}$) takes place at the beginning and the end of the day, for birds that are most active near dawn and dusk. TIME refers to 48 15-min sampling occasions throughout the day where a given bird could have ≤ 1 observation per occasion. Preliminary analyses produced no support for the effect of bird age on fidelity of *F. colma*, the only species that could be reliably aged in the hand; thus we did not include bird age in this analysis.

There is no available goodness-of-fit test that is ideal for our models; thus to determine if models fit the data, we used an *ad-hoc* procedure. For the most complex model (greatest number of parameters) in each model set (species), we plotted residuals (differences between the observed and expected numbers of each detection history). We then computed a Pearson chi-square test, pooling adjacent histories with expected value < 2 until the expected value of the sum was > 2 . We then re-ordered the histories randomly and computed another chi-square using the same pooling algorithm. The chi-square statistic was recomputed 4000 times to evaluate lack of fit.

To quantify the relative support of competing models, we compared AIC_c values (Akaike’s Information Criterion for small sample sizes; Burnham and Anderson 2002) among models and computed AIC_c and model weights, w_i . We based conclusions on parameter estimates that were model-averaged from the entire candidate set; figures also depict model-averaged parameter estimates.

3. Results

Our limited evaluation of model fit provided no indication of lack of fit for the most highly parameterized models for each species. Specifically, the iterated Pearson chi-square test gave no indication of lack-of-model-fit, regardless of the order of the capture-histories. The generality of the some of our models led us to predict reasonable fit as well. Null models for all three species received essentially no support (Table 1; $\sum w_i = <0.01$).

Model selection results for *G. spirurus* indicated state-specificity (HABITAT) and strong effects of 2°AGE and TIME² on fidelity, as all three variables were included in the three top models ($\sum w_i = 0.93$; Table 1). The top model included variation associated with HABITAT as well as an interaction between 2°AGE and the quadratic effect of time (TIME²), which allowed the shape of the fidelity curve to vary by habitat and 2°AGE. Throughout the day, fidelity was higher in primary vs. secondary forest for birds in the SF₁ group (Fig. 1a); this pattern reversed for SF₂ birds (Fig. 1b). The pattern reversed again for SF₃ birds (Fig. 1c). *G. spirurus* models including TREND in fidelity among SF classes received effectively no support, which was not surprising, as secondary forest fidelity did not increase steadily with increasingly mature SF (Fig. 1).

Table 1

Well-supported models^a describing movement probabilities of three radio-tagged avian understory insectivores occupying primary and secondary forest at the Biological Dynamics of Forest Fragments Project.

Model ^a	Deviance	K ^b	ΔAIC _c ^b	w _i
<i>Glyphorhynchus spirurus</i>				
2°AGE ^c * HABITAT * TIME ²	348	10	0	0.57
2°AGE * HABITAT * TIME	354	8	1.4	0.28
<i>Xiphorhynchus pardalotus</i>				
2°AGE * HABITAT	326	8	0	0.42
2°AGE * HABITAT * TIME	324	10	1.9	0.16
2°AGE * HABITAT * TIME ²	324	10	2.0	0.16
2°AGE * HABITAT * TIME	326	9	2.0	0.15
<i>Formicarius colma</i>				
HABITAT * TIME ²	182	4	0	0.29
2°AGE * HABITAT * TIME ²	170	10	0.9	0.18
HABITAT	187	2	1.1	0.17
2°AGE * HABITAT * TIME ²	167	12	1.8	0.12

^a 11 candidate models total per species. Models with ΔAIC_c < 2.8 are shown. $\sum w_i$ of null models for each species = 0.0. Models containing TREND (a linear trend among secondary forest age classes) received little support (ΔAIC_c > 4; $w_i < 0.05$).

^b K: Number of parameters; AIC_c: AIC adjusted for small sample size; ΔAIC_c: difference in AIC_c relative to the most parsimonious value; w_i: Akaike weight.

^c Variables: 2°AGE: secondary forest age class; HABITAT: primary vs. secondary forest; TIME: time of day; TIME²: quadratic effect of time with structure TIME + TIME².

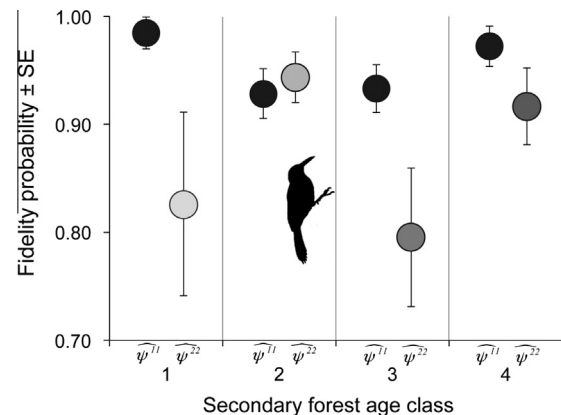


Fig. 2. Model-averaged estimates of within-day fidelity probability (ψ^T) for radio-tagged *Xiphorhynchus pardalotus* in primary forest (dark circles) and secondary forest (light circles) of four different age classes. Fidelity did not vary by time of day for this species, so single estimates are shown for each secondary forest age class. Fig. 1 caption defines ψ^{11} and ψ^{22} .

For *X. pardalotus*, fidelity was state-specific (HABITAT) and affected by 2°AGE. Although three models including TIME received some support, the reduced model without TIME received more support (Table 1), and no model-averaged fidelity estimates varied more than 0.04 over the course of the day, indicating that TIME had a negligible effect for this species. For *X. pardalotus* in SF₁, primary forest fidelity was clearly greater than secondary forest fidelity (Fig. 2), but this effect was no longer evident for SF₂. Birds in SF₃ were surprisingly unlikely to remain there, as primary forest fidelity was more than twice as high as secondary forest fidelity. In SF₄, fidelity was marginally higher for primary forest. TREND received little support for *X. pardalotus*.

Fidelity of *F. colma* was habitat-specific and affected by TIME² and 2°AGE. TIME showed a quadratic effect and little evidence for an interaction with HABITAT. The species showed high fidelity at midday relative to dawn and dusk (Fig. 3). 2°AGE was not included in the top model (it was included in the second best model, ΔAIC_c = 0.9; Table 1), but model-averaged parameter estimates indicated a considerable difference in fidelity estimates among secondary forest age classes (Fig. 3). Secondary forest fidelity was relatively low in SF₁, and highest in SF₂ and SF₄ (Fig. 3). Critically, for most of the day, error bars for SF₄ primary forest fidelity and secondary forest fidelity did not overlap (Fig. 3c) suggesting that even in primary forest abutting 27–31 year-old secondary forest that was never burned, *F. colma* was more likely to remain in primary forest than to remain in secondary forest.

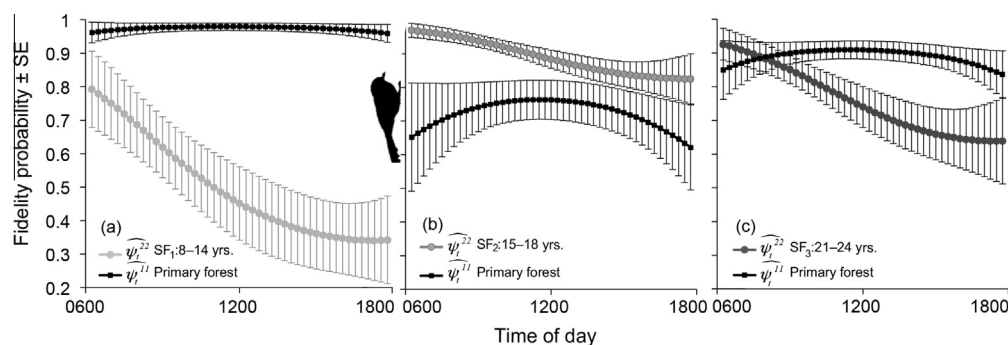


Fig. 1. Model-averaged within-day estimates of fidelity probabilities ($\psi^T \pm SE$) for radio-tagged *Glyphorhynchus spirurus* occupying primary forest and secondary forest of three different age classes (SF₁:SF₃). ψ^{11} : probability that a bird occupying primary forest at a given time step will also occupy primary forest in the following time step; ψ^{22} : probability of remaining in secondary forest from one time step to the next.

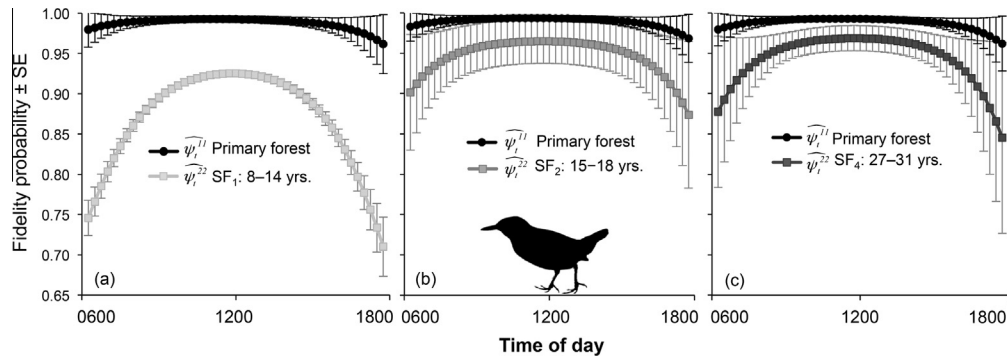


Fig. 3. Model-averaged estimates of fidelity probability ($\hat{\psi}_t^T \pm \text{SE}$) over the course of the day for radio-tagged *Formicarius colma* occupying primary forest and secondary forest of three different age classes (SF₁, SF₂, SF₄). SF₃ (21–24 years-old) estimates not shown due to imprecision ($\hat{\psi}_t^{11} = 0.99 \pm 0.01$, $\hat{\psi}_t^{22} = 0.62 \pm 0.43$). Fig. 1 caption defines $\hat{\psi}_t^{11}$ and $\hat{\psi}_t^{22}$.

The mean estimate of secondary forest fidelity for group SF₃ was lower than other groups at 0.62 (range throughout the day: 0.58–0.63), but large standard errors (range: 0.41–0.44) reflected a lack of precision about this estimate. We found no support for models containing TREND (Table 1).

4. Discussion

4.1. Within-day movement probability and forest succession

With practically every movement made by an understory tropical bird, an in-depth knowledge of perceived within home range resources is likely used to make decisions on where time will be spent. These everyday, within-home range decisions are almost certainly reflected by within-day movement probabilities representing the quality of available habitats, with birds showing the highest fidelity to high quality habitat. Understory insectivores of tropical rainforests are generally sedentary year-round residents, so use of a short time interval, rather than the more typical monthly or yearly scale, was appropriate for the questions that we sought to address. By using this within-day time scale, i.e., calculating movement probabilities across 15-min intervals, we were able to make inferences about habitat quality and the value of maturing secondary forest that may have been impossible on larger timescales. Understanding the usefulness of secondary forest as a conduit for moving animals will be critical to design of biodiversity-friendly landscapes, as previously unbroken primary forest continues to be fragmented and perforated by secondary forest.

In this study, forest type was an important predictor of within-day movement probabilities for all three species, with time of day also emerging as an important predictor for *G. spirurus* and *F. colma*. At this within-day scale, all three of our focal species were more likely to remain in primary forest than SF₁, suggesting that 8–14-year-old secondary forest is of relatively poor quality, at least in terms of bird fidelity and movement. Secondary forest recovery appears to begin after, or at least towards the end of 8–14 years, even for *G. spirurus*, one of the most disturbance-tolerant forest species at the BDFFP. This pattern of recovery beyond 8–14 years generally matches well with estimates from mist-netting studies at the BDFFP (Stouffer and Bierregaard, 2007; Powell et al., 2013).

4.2. Disturbance tolerant woodcreeper: *G. spirurus*

For *G. spirurus* there was good evidence for a quadratic effect of TIME. The shape of the quadratic curve describing fidelity over the course of the day varied between birds in primary and secondary forest (Fig. 1), suggesting crepuscular behavior, perhaps due to

avoidance of high light or temperature levels in less dense secondary forests during the middle of the day (Patten and Smith-Patten, 2012; Pollock et al., 2015). On the other hand, secondary forest fidelity was highest in the morning and tapered off later, suggesting a potential advantage to remaining in secondary forest in the morning. Due to structural differences from primary forest (Stratford and Stouffer, 2015), we speculate that sunlight penetrates secondary forest earlier in the morning, stimulating activity of invertebrates, the primary prey items of *G. spirurus*, which may explain the species' tendency to remain in secondary forest in the mornings. After accounting for the effect of TIME, it became clear that by 15–18 years after pasture abandonment, *G. spirurus* was already more likely to remain in secondary forest than remain in primary forest (i.e., $\hat{\psi}_t^{22} > \hat{\psi}_t^{11}$; Fig. 1b). By 15–18 years, secondary forest has likely passed the point of recovery for *G. spirurus*; recovery probably occurs at some point late in SF₁ or early in SF₂, i.e., approximately 12–15 years after abandonment. Powell (2013) speculated that *G. spirurus* might be released from competition in 1-ha forest fragments and young secondary growth because other woodcreepers are absent from this early successional stage, allowing them to exploit resources that are otherwise unavailable; this may help account for the high secondary forest fidelity values in SF₂.

4.3. Mixed-species flocking woodcreeper: *X. pardalotus*

As was the case with *G. spirurus*, *X. pardalotus* showed a strong effect of 2°AGE on fidelity. However, unlike the other species, fidelity was independent of TIME. Among the species we radio-tracked, *X. pardalotus* was most closely associated with mixed-species understory flocks led by *Thamnomanes* antshrikes (Jullien and Thiollay, 1998; Develey and Stouffer, 2001; Marantz et al., 2003). Most individuals we tracked participated in mixed species flocks during the majority of the time we tracked them, so their willingness to enter secondary growth is undoubtedly affected by that of other flock members, particularly *Thamnomanes* antshrikes (Mokross et al., 2013). Recovery was evident by 15–18 years after abandonment, as primary and secondary forest fidelity was no different in SF₂. Our recovery estimate of 12–18 years for the two woodcreepers matches well with estimates of Powell et al. (2013), who calculated that after cutting, burning and land abandonment, mixed-species flock dropouts at the BDFFP (defined as *G. spirurus*, *X. pardalotus* and *Myrmotherula axillaris*) took 14 years to return to pre-isolation capture rates along edges of primary and secondary forest. Our estimates also match well with recovery estimates from the edge analysis in Powell (2013; *G. spirurus*: 11–14 years; *X. pardalotus*: 15–20 years).

4.4. Terrestrial insectivore: *F. colma*

F. colma showed a strong effect of 2°AGE and TIME on movement probability. Both primary and secondary forest fidelity were highest during midday and lowest early and late in all habitats (Fig. 3), suggesting that the species' movements between habitats were crepuscular. We propose four non-mutually exclusive hypotheses for this pattern of less movement during midday: (1) high light levels agitate the birds' sensitive eyes, evolved to detect dark insects on dark leaves on the rainforest floor (Esteban Fernandez Juricic, pers. comm); (2) high light levels increase visibility by predators and thus predation risk (Patten and Smith-Patten 2012); (3) increased midday temperatures encourage thermoregulation via lethargy; (4) increased midday temperatures cause prey items (arthropods) to take shelter in leaf litter to avoid desiccation. The crepuscular movement pattern suggests that light or heat affect day-to-day movements of *F. colma*, rather than the structure of vegetation *per se* as suggested by Stratford and Robinson (2005). Conversely, Pollock et al. (2015) found no effect of light, heat, or humidity of microclimate selectivity of nine understory insectivores (two terrestrial) in Panama, so it is clear that research is needed to understand what drives understory bird movements. In future research, hypotheses involving how understory birds respond to light, heat, time of day and vegetation structure could be tested in an aviary with manipulated environmental conditions. Regardless of the mechanism, the quadratic effect of TIME on fidelity was clearly discernible in *F. colma*, suggesting that *F. colma* and possibly other terrestrial insectivores may be particularly constrained by the effects of heat, light, or vegetation structure during midday.

Although the effect of habitat on movements of *F. colma* was obvious, the effect of 2°AGE became clearer when graphing model-averaged parameter estimates (Fig. 3). SF₁ and SF₃ were obviously inferior to other habitat options, and primary forest fidelity was at least marginally higher than secondary forest fidelity in all secondary forest classes (Fig. 3).

Given the difference between primary and secondary forest fidelity for *F. colma* in SF₄ (Fig. 3c), it appears that even unburned 27–31 year old secondary forest is still subpar in terms of bird movement and fidelity. Reduced movement rates to SF₄ relative to primary forest fits with Powell et al. (2013), who estimated that at least 54 years of forest recovery would be required before terrestrial insectivores at the BDFFP, including *F. colma*, would attain pre-isolation capture rates along edges of primary forest after abandonment of unburned clearcuts. The species is also associated with thick-trunked trees, thin leaf litter, and avoids areas dense with thin trees (Stratford and Stouffer 2013; Stratford and Stouffer, 2015), which further suggests that vegetation structure takes considerable time to recover to the point when *F. colma* prefers those conditions, even if the canopy has recovered to primary-forest-like heights.

4.5. Lack of support for TREND

Although we predicted that fidelity probability would increase progressively as secondary forest matured beyond 8–14 years, TREND models received essentially no support in any species, suggesting that bird movement among habitats cannot be predicted simply as a monotonic function of secondary forest age—rather, the story is more complex. Land use history at the BDFFP and throughout Amazonia is multifaceted, with spatiotemporally variable patterns of cutting, burning, cattle grazing, and land abandonment. Our simple ordinal categorizations of ages of secondary forest as increasingly suitable for movement of birds likely could not capture the variation in land use history among secondary forests of similar age. For example, due to logistical constraints, birds

in SF₃ were tracked only at *fazenda* Dimona, which was burned multiple times before abandonment in the 1980s and used sporadically by grazing cattle; in many places grasses rather than trees have remained long after it was used as pasture. In contrast, areas in which we radio-tracked birds within SF₄ were never burned (Moreira 2003) and cattle grazing was minimal, which almost certainly contributed to substantial differences between SF₃ and SF₄. Specifically, burned and unburned plots can develop very different successional strategies that understory birds respond to heterogeneously (Borges and Stouffer 1999; Mesquita et al. 2001), and cattle compact the soil, heterogeneously consume recovering vegetation and affect soil nutrient levels (Fearnside 2005). All else being equal, fidelity probability likely increases with age of secondary forest. We suspect that the TREND model is not supported because complex variations in land use history practice at the BDFFP were not carefully accounted for in the experimental design or modeling.

4.6. Conclusions and conservation

Our models using data collected from radio-tagged birds permitted useful inferences about how the quality of secondary forest, in terms of within-day movement and fidelity, changes with forest succession. Using only time of day and age of secondary forest, we were able to account for much of the variation in movement probabilities. For the two woodcreeper species, we were able to estimate the point of recovery of secondary forest (12–18 years), and for the anthrush we determined that recovery likely takes more than 30 years.

Many rainforest birds are poor flyers and are thus unable to cross only a few hundred meters of water (Moore et al., 2008), suggesting that water, and probably pasture and asphalt, can severely limit the ability of birds to move, disperse, colonize, and persist in human modified habitat. Studies of forest fragmentation often categorize the landscape as either habitat or non-habitat (Laurance, 2008), which essentially ignores the enormous potential connectivity value of the vast tracts of secondary forest in the tropics (Chazdon et al., 2009). Based on our analyses, it is clear that that 12–18-year-old secondary forest does not impede within-day movement of our two focal woodcreepers, so land managers concerned with these two species can probably assume that primary forest reserves connected by this relatively young secondary growth matrix, for example, via corridors, are effectively connected (Lees and Peres, 2008). On the other hand, managers can expect to wait >30 years before secondary forest serves as a primary forest-like conduit for *F. colma*. More sensitive terrestrial insectivores may take longer still, such as *Myrmornis torquata*, which disappeared from all BDFFP forest fragments after initial cutting and has still not recolonized even after >30 years of secondary forest succession (P. Stouffer unpublished data). A complete look at rainforest birds' abilities to move across fragmented landscapes must include not only the within-day estimates of movement we present here, but also estimates of dispersal across different habitats. Our understanding of how tropical bird dispersal is affected by landscape features is still in its infancy (Pavlacky et al., 2012; Woltmann et al., 2012).

Once birds' abilities to move among habitats, including secondary forests, are quantified at different scales, estimates can help parameterize more representative models of metapopulation dynamics, ultimately informing conservation planning and reserve design (Stevens et al., 2006; Castellón and Sieving, 2007; Knowlton and Graham, 2010). Given rates of deforestation and secondary forest accumulation in Amazonia and other tropical rainforests, there is a great need to quantify movement among habitats and connectivity—particularly for the species and guilds thought to be most sensitive to disturbance, such as terrestrial insectivores.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.01.028>.

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