Special issue Title: Tropical Insectivores

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

Luke L. Powell [a,b,*], Jared D. Wolfe [a,b,1], Erik I. Johnson [a,b,2], James E. Hines [c], James D. Nichols [c], Philip C Stouffer [a,b]

[a] Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia, CP 478, Manaus, AM 69011-0970, Brazil
[b] School of Renewable Natural Resources, RNR 227, Louisiana State University and Louisiana State University Agriculture Center, Baton Rouge, LA 70803-6202, USA
[c] USGS Biological Resources Division, Patuxent Wildlife Research Center, Laurel, MD 20708, USA

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, *Glyphorynchus 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.

Published by Elsevier Ltd.

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

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; Şekercioğlu 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 (Şekercioğlu 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 Rivadeneyra, 2001; Peh et al., 2005; Stouffer and Bierregaard, 1995; Powell et al., 2013). Accordingly, we predicted that the terrestrial antthrush *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 *Glyphorynchus spirurus* is often found along edges and in small fragments, so we predicted it would show primary forest-like movement patters 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 "SF_1") was 8–14 years old with a mean canopy height of about 6 m. We defined SF_2 as 15–18 years old with a canopy of ~14-m, and SF_3 was 21–24 years old with a ~16-m canopy. The oldest secondary forest at the BDFFP (SF_4) was 27–31-years-old, with a ~19-m canopy. All of the SF_4 was located near the fragments at "*Cidade* Powell" and was never burned; practically all other secondary forest classes were burned