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VARIATION IN FORAGING STRATEGY WITH FOREST AGE FOR THE BLACK-CROWNED ANTSHRIKE (*THAMNOPHILUS ATRINUCHA*)

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Resumen. – Variación en la estrategia de forrajeo en relación a la edad del bosque por el Batará Pizarroso Occidental (*Thamnophilus atrinucha*). – La deforestación rápida causa la pérdida y degradación de hábitat para las aves de bosque. La reforestación y regeneración natural crean bosques secundarios que pueden jugar un papel importante en la mantención de la biodiversidad de aves. En los trópicos muchas aves insectívoras de sotobosque se encuentran ausentes de bosques secundarios, pero no se conoce razón. La variación en el comportamiento alimentario puede revelar cambios en la comunidad de insectos presa que podrían estar causando este efecto. Nosotros investigamos el comportamiento de alimentación de una especie común de insectívoro de sotobosque, el Batará Pizarroso Occidental (*Thamnophilus atrinucha*), en tres bosques de distinta edad para evaluar la hipótesis que la comunidad de insectos presa varía con la edad del bosque. No encontramos diferencias entre bosques en la tasa de ataque a presas o en la tasa de éxito de captura, lo que sugiere similar esfuerzo de alimentación. Sin embargo, los individuos consumieron menor cantidad de presas grandes en el bosque secundario joven. Además, la altura de alimentación disminuyó en bosques secundarios jóvenes de 8,5 ± 1,3 m a 4,5 ± 0,6 m. El rango de movimiento horizontal se redujo en bosques secundarios jóvenes, limitando el movimiento en la vegetación durante la alimentación. Estos resultados indicarían, de manera indirecta, un cambio en la comunidad de insectos presa con la edad de bosque. Los batarás parecen tener cierto grado de flexibilidad en su comportamiento de alimentación, característica que puede no ser compartida por otras especies similares. Sin embargo, el menor consumo de biomasa, asociado con tasas de ataque y éxito de captura de presas similares en bosques de distintas edades, sugieren que los individuos en bosques jóvenes pueden estar en desventaja. Estudios futuros deberían evaluar la generalidad de estos resultados y la capacidad para alimentarse de manera flexible en otras especies de sotobosque.

Abstract. – Variation in foraging strategy with forest age for the Black-crowned Antshrike (*Thamnophilus atrinucha*). – Rapid deforestation leads to loss and degradation of avian habitat. Reforestation and natural regeneration create secondary forests that may play an important role in maintaining avian biodiversity. In the tropics, many understory insectivores are absent from secondary forests; however the mechanisms responsible for this pattern are unknown. Differences in foraging behavior can be used to identify changes to the insect community, which may contribute to this pattern. We investigated foraging behavior in a common understory insectivore, the Black-crowned Antshrike (*Thamnophilus atrinucha*), across three forest-age groups to test the hypothesis that insect (prey) communities differ with forest age. We observed no difference in attack or foraging success rates by Black-crowned Antshrikes, suggesting equal foraging effort during focal observations. However, individuals consumed less high-quality (large) prey in secondary forest. Additionally, foraging range shifted downwards from 8.5 ± 1.3 m to 4.5 ±

0.6 m and was compressed horizontally in secondary forests, reducing inter-vegetation movement during foraging bouts. We suggest that this provides indirect support for a change in the insect community across forest ages. Black-crowned Antshrikes appear flexible in their foraging strategies; an ability that may not be shared by other species. However, reduced biomass consumption coupled with constant attack/success rates suggest individuals are performing poorly in young forest. Further research should investigate the generality of this pattern and the capacity for flexible foraging strategies in other avian species.

Key words: Avian behavior, Black-crowned Antshrike, foraging, Panama, *Thamnophilus atrinucha*, tropical moist forest, understory insectivores.

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INTRODUCTION

Tropical forests are centers of avian biodiversity. However, this diversity is threatened by rapid deforestation, such that tropical forests are susceptible to a disproportionate loss of avian species (Dent & Wright 2009). The degradation of tropical forests produces a compositional shift in the avian community. Overall avian diversity is considerably lower in more recently disturbed compared to mature forests (Dent & Wright 2009, Catterall *et al.* 2011). Additionally, certain guilds are able to persist in secondary forests (e.g., canopy-dwelling frugivores, pollinators), whereas others, such as understory insectivores, do not (Johns 1991, Stratford & Stouffer 1999, Şekercioğlu *et al.* 2002, Sigel *et al.* 2010). Currently, only 36% of the globe's remaining forest cover is considered 'primary' forest (FAO 2010). Yet since 2000, the net rate of deforestation has started to slow by up to 3 million ha/year (FAO 2010), a changing rate that is partly due to active reforestation and natural regeneration equivalent to 7% and 57% of all forests, respectively (FAO 2010). The increase in forest restoration (active or passive) combined with the poor persistence of certain guilds like understory insectivores in secondary forests, raises questions concerning the effectiveness of secondary forests for conserving biodiversity. Whether secondary forests have the capacity to maintain avian communities until habitat regeneration has approached a mature state is a concept that is heavily debated (Wright & Muller-Landau 2006, Gardner *et al.* 2007, Dent & Wright 2009).

Several hypotheses attempt to explain the inability of understory insectivores to re-establish and maintain populations in secondary forests. These include: 1) naturally low densities preventing viable populations in small or degraded patches (Sigel *et al.* 2010); 2) poor dispersal ability between forest patches (Şekercioğlu *et al.* 2002, Moore *et al.* 2008); 3) greater nest predation due to meso-predator release (Sieving 1992); and 4) changes in insect (prey) communities (Ford *et al.* 2001). The first two hypotheses address habitat fragmentation, which is often associated with secondary forests, while the latter two directly address fundamental issues within secondary forests. Few studies have tested these hypotheses at the species level to explore the mechanisms driving low diversity of insectivorous birds in secondary forests (Sigel *et al.* 2010), while controlling for the confounding effects of fragmentation.

Understory insectivore loss is not obligatory and some species inhabit a range of forest ages. The wide-spread occurrence of certain species may allow one to test fundamental hypotheses, such as variable abundances of arthropod-based food resources. However, quantifying these resources is difficult. While techniques exist, each is biased due to differences in measuring mechanics and bird perception of prey (Robinson & Holmes 1982). Additionally, the presence of prey does not necessarily indicate use (Hutto 1990, Poulin & Lefebvre 1997). Species-specific resource availability may be a function of several variables, including: 1) prey abundance, 2) habitat characteristics affecting prey detectability, and 3) the ability to perceive and capture prey (Holmes & Schultz 1988). Focusing on resource use by observing foraging behavior and prey choice provides a better indication of species-specific resource availability and allows comparison across habitats which may differ in vegetation structure and prey composition (Lovette & Holmes 1995, Lyons 2005). We used foraging behavior (attack rate, foraging location, and prey choice) of the Black-crowned Antshrike (*Thamnophilus atrinucha*) to study foraging strategies and test differences in the insect community across forest age from the perspective of an insectivore. Black-crowned Antshrikes (hereafter antshrike) are general insectivores inhabiting forests from western Ecuador to the Caribbean slope of Belize (Tarwater & Kelley 2010). It is an excellent species for investigating resource availability across habitats because it is common and has diverse foraging techniques that suggest the capacity to successfully overcome changes in resources by adjusting foraging strategies.

Secondary forests often have greater aboveground net primary productivity (Murty *et al.* 1995), due to greater stand-leaf area than mature forests (Ryan *et al.* 1997). Greater density and diversity of insects, and subsequently birds, are observed in forest strata with the greatest concentration of young foliage (Schulze *et al.* 2001, Philpott *et al.* 2009). In secondary forests, this stratum tends to be the understory (DeWalt *et al.* 2003). However, the proportion of young foliage is a relative, within-forest, comparison, and other studies indicate that overall insect availability can remain at lower levels in secondary forests than established forests (Watt *et al.* 1997, Basset *et al.* 2008). We therefore expect reduced resource quality and quantity in younger forests. Classical foraging models describe how birds should forage in habitats of differing qualities (reviewed in Pulliam 1974, Charnov 1976). For example, if secondary forests have lower insect availability, birds may be forced to spend more time foraging while selecting lower quality prey (e.g., smaller). Thus, as proxies of insect availability, we quantified foraging attempts, success rate, and prey choice. If resource quality does vary across forest age, either observed foraging success will also vary, or individuals will adjust foraging tactics to maintain similar biomass intake levels. Since antshrikes are generalists, we predict individuals will modify their foraging strategy to adjust for differences in prey size and availability. We hypothesize that prey choice will shift to smaller sizes in younger forest, depicting reduced prey quality compared to mature forests. This will coincide with increased attack and success rates in younger forest to maintain biomass consumption. Spatial changes in prey availability can be detected by altered foraging locations at the landscape level, or vertically within the vegetation column. Philpott *et al.* (2009) suggested that insectivores are drawn to the greater relative prey concentrations in the dense understory of secondary forests. Thus, we additionally hypothesize antshrikes will be less abundant and forage lower in the vegetation column in younger forest. Alternatively, a shift in foraging location could be explained by competitive release, allowing antshrikes to exploit resources in new micro-habitats with the loss of direct competitors that may be less robust to habitat change. We address this possibility with greater detail in the Discussion.

METHODS

Study site. We conducted observations in Soberanía National Park, near Gamboa, Panama (9°07'42"N, 79°42'55"W). The park comprises 19,545 ha of lowland tropical moist forest (< 100 m a.s.l.) along the eastern bank of the Panama Canal. Annual precipitation is 2500 mm and average temperatures reach about 28°C during the rainy season (Robinson *et al.* 2004). Vegetation diversity is high, with an estimated 420–470 woody plant species (Ibáñez *et al.* 2002).

Due to clear-cutting during the construction of the canal, the landscape is dominated by secondary forest with only a handful of established forest patches remaining (Ibáñez *et al.* 2002). Deforestation ceased intermittently along Pipeline Road forming a continuous gradient of forest age which increases with distance from the road (G. Angehr, W. D. Robinson pers. com.). This gradient provides an ideal site for comparing biological phenomenon across forest age, and its contiguous nature removes potential confounds introduced by fragmentation. We performed our study within forests of three age classes varying by time since last disturbance: 1) 25–50 years, 2) 80–100 years, and 3) 200–300 years (Fig. 1, W. D. Robinson pers. com.). All observations were conducted > 100 m from forest edges, both abrupt (road) or representing transitions from one age to another, to reduce potential edge effects. Study sites were within 2 km of each other and thus were assumed to experience similar environmental conditions.

Focal species. Antbirds are New World suboscine passerines that include 61 genera and 230 species (Gill & Donsker 2014). They are predominately insectivorous and occupy the forest understory to mid-canopy (Zimmer & Isler 2003). The family includes many of the understory insectivore species absent from secondary forests. The Black-crowned Antshrike is a highly generalist insectivore within the genus *Thamnophilus* (family *Thamnophilidae*). It is an ideal species to study behavioral differences in secondary forests because it occurs across a wide range of forest ages, exhibits diverse foraging techniques, and is a slow, methodical forager that can be easily observed (Tarwater & Kelley 2010). Antshrikes are affected by habitat degradation with reduced abundance in highly modified (Van Bael *et al.* 2007) or recently disturbed forests (Cody 2000, Libsch 2005). However, it appears more robust than many understory insectivorous species as it is capable of maintaining populations in habitats where other understory insectivores have failed to reestablish populations (Tarwater & Kelley 2010). The antshrike is predominately a foliage-gleaning insectivore (Tarwater & Kelley 2010). It forages in various microhabitats, opportunistically follows army ant swarms, and consumes a wide range of insects and small lizards (Oniki 1975). It also forages both in the understory and mid-canopy (Cody 2000). This variation in foraging traits and location suggests the potential to alter foraging strategies in response to different resource distributions, such as may be found across different forest ages.

Data collection. All observations were conducted in 2013 during the rainy season (mid-June to late August). In our study locations of differing forest age, we quantified: 1) vegetation structure, 2) antshrike abundance, 3) foraging behavior, 4) prey choice, and 5) prey availability. Birds were not banded, so to address potential pseudo-replication we separated point counts by at least 100 m, and same-day focal observations by at least 50 m. On average, five focal observations were conducted consecutively per day and thus 50 m was deemed sufficient to ensure independence because we left one pair to immediately

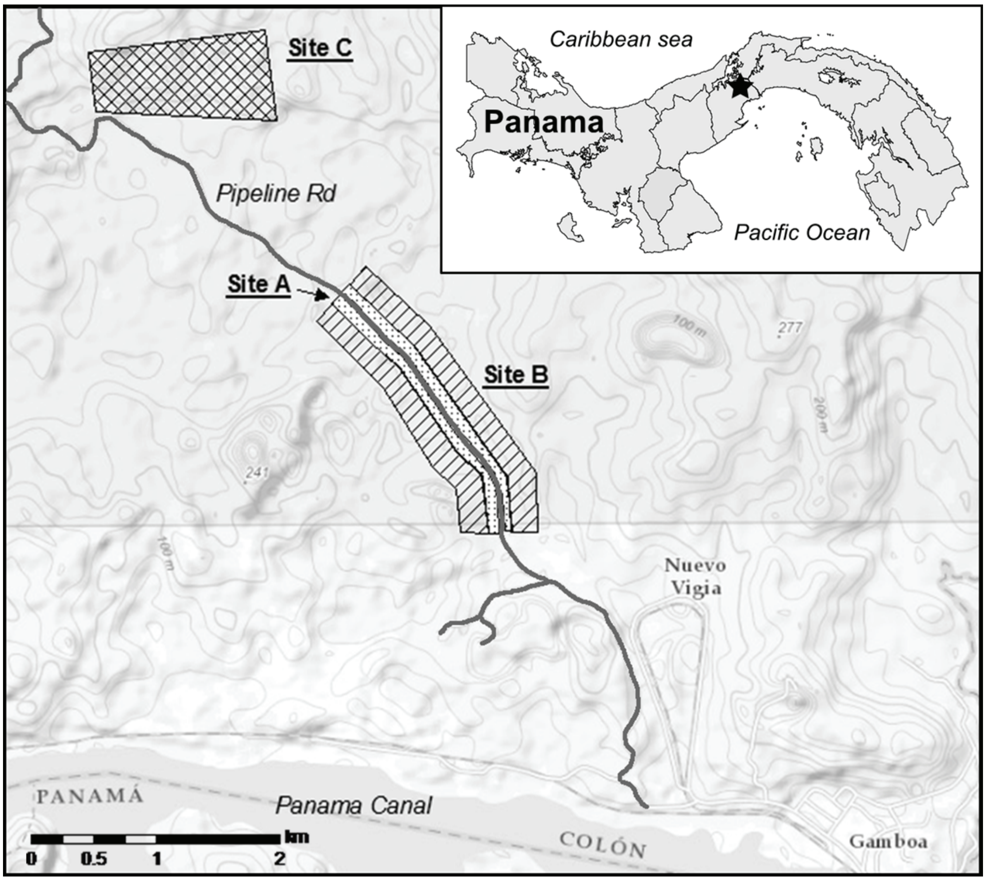

FIG. 1. All three study sites were located along Pipeline road in Soberanía National Park, Colón, Panama. Sites were chosen based on their distance from the path and age of last disturbance. Site A refers to young forest (25–50 years), Site B is mid-range forest (80–100 years), and Site C is old forest (200–300 years). The young forest site was approximately 45 ha in area, mid-range was 60 ha, and old forest was 105 ha. All study areas were similar elevation (< 100 m a.s.l.). Study site outlines are approximations and not to scale.

observe an adjacent pair. Focal observations conducted on different days were separated by > 500 m (GPS verified). We acknowledge that with an average territory size of 0.8 ha (Roper 1996, Robinson *et al.* 2000) some, very few, focal observations may be of a pair already observed that day, but this possibility is minimal and should not interfere with any analyses or interpretations and was the most efficient alternative in the absence of uniquely color-banded birds.

To establish a relationship between forest age of last known disturbance and vegetation structure, we measured: diameter at breast height (DBH), distance to the three closest neighbours, tree height, and percentage of canopy cover. In each forest-age group, we used 50 trees as the focal point for vegetation measurements for a total of 150 trees across all sites. Trees were selected by random compass direction from a transect line at 50 m intervals. We used 10 randomly assigned transect lines with 5 trees per transect in each site. Following DeWalt *et al.* 2003, we classified a tree as > 2 m tall and > 5 cm DBH, while understory growth was considered > 1 m tall and < 5 cm DBH. Distance to the three closest neighbours is the sum of the three shortest distances to vegetation structures (tree or understory growth) from the same focal tree. Tree height was estimated prior to measuring true height with a clinometer, permitting post-hoc calculations of a conversion metric for foraging height estimates during focal observations. Photographs were taken of the canopy 2 m from the base of the tree with a Pentax WG-3 GPS digital camera (Ricoh Imaging, Tokyo, Japan) and GIMP 2.8 software (GIMP Documentation Team 2013) was used to calculate canopy coverage.

We conducted point counts of antshrikes to estimate potential differences in density between young, mid, and older forests. We completed 20 fixed radius (40 m) audio point counts per site. Each count consisted of three consecutive 2 min intervals. The first interval was passive while the last two each started with a 5 s play-back of an antshrike territorial song to stimulate response from otherwise silent individuals allowing calculation of detection probability. Antshrikes are strongly territorial (Tarwater & Kelley 2010), i.e., both sexes sing frequently and are responsive to playbacks. All point counts were conducted between 08:00 h and 11:00 h EST during fair weather (no precipitation) in early July to avoid bias introduced by variable weather and differences in territoriality (peak breeding season is April–July; Tarwater & Kelley 2010).

Two to 20 min focal observations of all individuals were conducted from > 5 m distance. Overall, we conducted 108 focal observations of which 43 were in young forest (25–50 years), 37 in mid-ranged forest (80–100 years), and 28 in established forest (200–300 years). All observations occurred between 06:30 h and 13:00 h and were spoken into a voice recorder. Foraging variables were attack rate, foraging success (efficiency), foraging location, and mixed-species flock association. An attack was any manoeuvre that culminated in a strike and attack rate was the number of strikes (successful or failed) observed during active foraging bouts. We defined an active foraging bout as a combination of obvious, constant movements of the head, infrequent territorial songs, and near-constant changes in body position. A successful attack was denoted as visualization of prey caught or bill-wiping (Keeler-Wolf 1986). The success variable we used is a ratio of successful to total attacks to indicate efficiency.

Both vertical and horizontal metrics of foraging location within the vegetation column were recorded. Individual height estimates may lack independence; for example, a bird foraging at 10 m is more likely to continue foraging at this height. To control for this, foraging height was only estimated when individuals moved to a different position along the vertical plane and the average was used for foraging height. Foraging range was calculated as the difference between the highest and lowest height, at which an individual was observed foraging during a focal observation ($\text{Height}_{\text{Max}} - \text{Height}_{\text{Min}}$). Horizontal location was determined by the hop-to-flight ratio as a greater use of hops indicates a tendency to forage within one vegetation column.

Foraging associations can explain variation in foraging success or indicate differences in antshrike age distributions. During focal observations, we noted the presence of mixed-species flocks, mating partners, and fledglings. Mixed-species flock participation can significantly increase foraging success (Sridhar *et al.* 2009). Therefore, an indication of the frequency that antshrikes participate in mixed-species flocks allowed us to control for variation in attack and success rates within forest age categories. Additionally, fledgling and mating partner presence were recorded as a rough indication of antshrike mating success across sites in an attempt to identify despotic distribution which could confound results if low quality individuals were more likely to inhabit a specific forest age. We believe that these proxies are sufficient for our purposes because: 1) individuals almost always forage in pairs unless they are unsuccessful in finding a mate (termed "floater"), and 2) adults care for fledglings for approximately 55 days post-fledge (Tarwater & Brawn 2010). Therefore, the likelihood of identifying either the presence of a mate or a successful pair with a fledgling are relatively high because focal observations occurred over a short span of two months during peak breeding season. We acknowledge that these variables are rough indications of mating success. A female may not be present because she is incubating, and it is likely that some fledglings had already gained independence before observation. Yet, 76% of focal observations included a mate (de Zwaan, unpubl.) and peak breeding season is April–July (Tarwater & Kelley 2010), suggesting some capacity to identify meaningful variation in mating success using these metrics. These proxies exist within the limitations of an observational study and we encourage that these results be treated with caution.

We collected two metrics of prey availability: prey choice and prey abundance. Prey choice was quantified during focal observations to indicate prey availability from the perspective of an individual antshrike. Each captured prey was assigned to one of three size categories (smaller than, equal to, or larger than bill size) as a crude metric of energy content. Classic foraging theory (e.g., Schoener 1979) suggests within the range of acceptable sizes, larger prey should be preferred. Larger prey, such as caterpillars and katydids, are indeed most commonly chosen by antshrikes (Tarwater *et al.* 2009). Thus, we consider large arthropods as high quality prey for antshrikes. We also estimated the rate of biomass consumption for each individual. The average bill length of a Black-crowned Antshrike is 19.7 ± 1.2 mm (mean ± SD), with no difference between sexes (Tarwater unpub. data). Therefore, since we estimated prey size relative to bill length, we can roughly calculate prey length using the conversion ratios of 0.25, 1, and 3 times bill length for smallest to largest prey, respectively. We estimated prey mass from size using the power model $y = a(x)^b$ (Rogers *et al.* 1977), where y = mass, x = length, and a and b are model parameters. We followed (Sabo *et al.* 2002) and used model parameters derived for terrestrial insects in California. We used the parameter estimates from the general Insecta model because the model fit was quite high ($R^2 = 0.81$) despite variation in body size (Sabo *et al.* 2002), and we assume these estimates are robust across ecosystems because the parameters closely matched those in a separate study on Hawaiian insects (Gruner 2003). We acknowledge the limitations in accuracy that may stem from this approach; however, we believe this provides a coarse estimate of biomass consumed across forest ages.

Prey abundance was quantified to serve as a baseline metric for prey availability, independent of predator preference. We conducted 20 transects per study site. Each transect was 100 m in a random compass direction and was standardized to 15 min duration. The foliage, stem, and ground surfaces were inspected within 3 m vertically and 1 m horizontally on either side of the transect line. All arthropods were identified to order and were assigned to the same size categories as the prey choice metric to allow comparison. We acknowledge that this methodology is not exhaustive and is limited to the 0–3 m forest strata. However, it does allow relative comparison across forest age for the understory and provides some indication of the similarity between prey availability and prey choice for each site. For all point counts, focal observations, and arthropod surveys we recorded weather as either "cloudy" (no visible blue sky) or "partially cloudy" (visible blue sky). We found this difference in overall ambient light was more relevant to arthropod activity than temperature as mean daily temperature varied little throughout the study period. No observations were conducted during rain.

Statistical analysis. All data analysis was conducted using R version 3.1.1 (R Core Team 2013). Differences in vegetation structure between forest ages were analyzed using a MANOVA with four vegetation response variables and the explanatory variable, forest age, as a factor with three levels (25–50 years, 80–100 years, and 200–300 years). To determine significance, regression estimates were used as effect sizes and 95% confidence intervals were calculated for each estimate.

Antshrike abundance across sites was compared with a linear mixed effects model (LMM) using the R package "lme4" (Bates *et al.* 2014). Forest age was modelled as a fixed effect while weather and time of day were included as covariates. Date was considered a random effect to control for unexplained variation between days. We found no difference in the three consecutive 2-min intervals differing by playback stimulus within each point count, indicating a consistently high detection probability. Therefore, the response variable was the sum of all unique detections across the 6-min time period for each point count.

To analyze prey availability, we used LMM with the response variable prey size, and forest age as the fixed effect. Weather and time were included as covariates to control for variation in arthropod activity due to differences in ambient light and time of day. Date was modelled as the random effect to address unknown variation; all arthropod transects were carried out within a 2-week interval to avoid seasonal effects on counts.

We built Generalized LMMs for each of the following behavioral response variables: mixed-species flock occurrence, attack rate, success rate, foraging height, vertical foraging range, hop-to-flight ratio, large prey choice, and prey choice biomass. Mixed-species flock was modelled as a binomial variable with either absence or presence (0 or 1) during foraging bouts. Large prey was defined as the combined value of greater-than and equal-to bill size prey, and biomass as the sum of all insect masses consumed by each individual over the observation period. Forest age and sex were included in all models as fixed effects. Weather and time were included as covariates, while date and individual were random effects for all models. Mixed-species flock presence was included in attack and success rate models to control for differences introduced by a social foraging behavior (Sridhar *et al.* 2009). Time actively foraging was included as a covariate for all models to standardize between focal observation lengths, except for success rate which, as a ratio, is already standardized. Finally, tree density and foraging height were included in the attack-rate model to account for varying rates introduced by differences in vegetation structure. In all cases, the full model tests the hypothesis that forest age has a strong effect on the response variable. Table 1 outlines the global model for each behavioral response variable.

We used Akaike Information Criterion corrected for small sample sizes (AICc) for model simplification (Anderson *et al.* 2001). The R package "MuMIn" (Barton 2014) was used to rank all possible reduced models by their AICc scores and AICc differences (ΔAICc). Models with strong support (ΔAICc ≤ 2) were selected to estimate effect sizes using model averaging (Anderson & Burnham 2002). Explanatory variables were considered biologically significant if the confidence interval of the model estimate did

TABLE 1. Description of the global model for each of the eight foraging response variables before AICc calculation and model averaging. Abbreviations are as follows: AF = time actively foraging, FH = foraging height, DT = distance between trees, MF = mixed flock presence, TM = total movements (the sum of all hops and flights), and PT = prey total (the total number of prey caught for each individual, regardless of size). Time indicates time of day and large prey is the combination of bill-sized and greater than bill-sized prey.

Response	Global model
Mixed flock	~ Forest age + Weather + Time + Date
Attack rate	~ Forest age + Sex + Weather + Time + AF + FH + DT + MF + Date
Success rate	~ Forest age + Sex + Weather + Time + Attacks + MF + Date
Foraging height	~ Forest age + Sex + Weather + Time + AF + Date
Foraging range	~ Forest age + Sex + Weather + Time + AF + Date
Hop:Flight	~ Forest age + AF + Sex + Weather + Time + TM + MF + Date
Large prey	~ Forest age + Weather + Sex + PT + AF + Time + Date
Prey biomass	~ Forest age + Weather + AF + Date

not contain zero (Anderson *et al.* 2001). Model fit was evaluated using the coefficient of determination (R^2) or Nagelkerke R^2 for models with non-Gaussian residual distributions (Nagelkerke 1991).

RESULTS

Vegetation structure. Vegetation structure varied across sites, confirming a difference in forest age (Table 2). Forest age was positively associated with both DBH ($F_{2, 147} = 12.9$, $P < 0.001$) and distance between trees ($F_{2, 147} = 11.7$, $P = < 0.001$). Average DBH was (SEM) 9.4 ± 1.5 cm, 13.1 ± 1.6 cm, and 30.3 ± 6.0 cm, while the average distance between trees was 2.36 ± 0.13 m, 2.84 ± 0.15 m, and 3.37 ± 0.17 m from young to established forest, respectively. Therefore, lower strata had a greater density of vegetation in regenerating forest. Tree height ($F_{2, 136} = 8.6$, $P < 0.001$) and percent canopy cover ($F_{2, 144} = 6.6$, $P < 0.01$) did not follow the same pattern, only increasing in established forest (Height: young = 8.7 ± 0.8 m; mid = 9.1 ± 0.7 m; old = 13.8 ± 1.2 m: Canopy cover: young = 94.7 ± 0.1%; mid = 94.3 ± 0.1%; old = 95.5 ± 0.1%). This suggests that canopy structure remains relatively constant until a more mature state and the increase in tree height for oldest forest is likely due to a more pronounced emergent layer (see Table 2 for age-specific model estimates and 95% confidence intervals).

Abundance and associations. Average antshrike abundance based on 20 point counts per site was 2.6 ± 0.2, 2.2 ± 0.3, and 2.0 ±0.2 (SEM) individuals for youngest to oldest sites, respectively. Abundance did not differ across forest age ($B = -0.3$, 95% CI = –0.7 to 0.1). Foraging associations also did not vary across sites. The top models ($\Delta AICc \leq 2$) for the presence of mixed-species flocks included forest age, but the confidence interval for the model averaged estimate included zero ($B = 0.4$, 95% CI: –0.2 to 0.9; Table 3). Finally, there was no support for an effect of forest age on partner and fledgling presence, as forest age did not appear in any of the top models. Thus, we assume that antshrike population density and age structure are similar among forest ages in this system.

Foraging behavior. We observed 26 males and 17 females in young forest, 20 males and 17 females in mid-ranged forest, and 18 males

TABLE 2. Regression coefficients and 95% confidence intervals for each of the four linear regressions on the response variables: DBH, distance, height, and canopy cover. Canopy cover is measured as the number of pixels representing open sky. Effect sizes are with respect to youngest forest (25–50 years) for each model. The sample size was 50 measurements per site or 150 overall. Values with strong support are labelled in bold and have confidence intervals that do not include zero.

Response	Age (yrs)	Estimate	CI
DBH (cm)	80–100	**0.49**	(0.092, 0.90)
	200–300	**1.04**	(0.64, 1.44)
Distance (cm)	80–100	**48.42**	(7.30, 89.53)
	200–300	**101.43**	(60.32, 142.55)
Height (m)	80–100	0.094	(-0.12, 0.32)
	200–300	**0.46**	(0.22, 0.69)
Canopy cover	80–100	4.63	(-3.53, 12.78)
(x1000 pixels)	200–300	**-10.14**	(-18.25, -2.03)

with 10 females in established forest. Average length of a focal observation was 6.0 min, 6.8 min, and 5.3 min for young to mature forest, respectively. Attack rate was explained by eight models ($\Delta AICc \leq 2$), the best of which described 28% of the variance (Nagelkerke $R^2 = 0.28$). Forest age appeared in the top models but was non-significant ($B = –0.09$, 95% CI: –0.2 to 0.06; Table 3). In contrast, active foraging time and weather had higher explanatory power. Success rate was positively correlated with attack rate, but was independent of all other variables, including forest age (Table 3).

Foraging height and range varied between differently aged forests. The top model for foraging height explained 44% of the variance in foraging strata ($R^2 = 0.44$) and included a strong positive association with forest age ($B = 2.2$, 95% CI: 1.6 to 2.8; Table 3). Birds foraged higher in established forests than young forests (SEM; young = 4.4 ± 0.3 m; mid = 6.1 ± 0.4 m; old = 8.4 ± 0.7 m, Fig. 2). Foraging range also included a positive association with forest age ($B = 1.0$, 95% CI: 0.3 to 1.7; Table 3). Range was least in young forests and similar in mid and old forests (SEM; young = 3.7 ± 0.3 m; mid = 5.9 ± 0.7 m; old = 5.1 ± 0.7 m; Fig. 2). Thus, birds in young forests forage lower with a compressed foraging range. This result is not simply a by-product of lower canopy height because average tree height was similar among forests (Table 2).

The hop-to-flight ratio declined with forest age ($B = –0.5$, 95% CI: –0.8 to –0.2; Table 3, Fig. 3). Young forest had a hop-to-flight ratio of 2.73 ± 0.29, compared to 2.15 ± 0.18, and 2.11 ± 0.26 (SEM) for mid and older forest, respectively. Both forest age and sex predicted hop-to-flight ratios and suggest that more hops than flights were conducted in young forests. More hops relative to flights in younger forest indicate decreased inter-vegetation movement while foraging in secondary forests.

Captured prey size was best explained by seven top models, all including forest age. Antshrikes were more likely to capture large prey in older forests ($B = 0.1$, 95% CI: 0.02 to 0.2; Table 3, Fig. 4). The mean proportion of captured large prey was 43% (n = 36), 64% (n = 38), and 67% (n = 21) from youngest to oldest forest, respectively. Large prey included larval Lepidoptera, Orthoptera such as katydids, and to a lesser extent Coleoptera and Hemiptera, suggesting a change in abundance of these orders. Antshrikes were observed preying upon an *Anolis* lizard on only three

TABLE 3: Parameter estimates (95% confidence interval) from averaged generalized linear models for each of the eight foraging behavior response variables (mixed-flock presence, attack rate, success rate, foraging height, foraging range, hop-to-flight ratio, large prey choice, and biomass consumed). *K* = parameters included in the averaged model; R^2 = Nagelkerke pseudo-R^2 for non-Gaussian residual distributions (Nagelkerke 1991) and true coefficient of determination for linear models. Control variables (e.g., time of day, active time foraging) are not included, but see Methods section for full model descriptions. Parameter estimates for sex depict the effect of males with respect to females, and weather displays the effect of partly cloudy (more sun) relative to full cloud coverage. The distribution applied to the global model is displayed below each response variable along with the degrees of freedom. Effects with strong support have 95% confidence intervals that do not include zero and are labelled in bold.

Response	Forest age	Sex	Attacks	Weather	K	R^2
Mixed flock	0.4			0.8	3	0.06
(Binomial, df = 105)	(-0.2, 0.9)			-0.2, 1.8		
Attack rate	-0.09	-0.2		**0.3**	6	0.36
(Poisson, df = 103)	(-0.2,0.06)	(-0.4, 0.05)		**0.004, 0.6**		
Success rate		-0.1	**0.2**		3	0.55
(Poisson, df = 104)		(-0.5, 0.2)	**(0.1, 0.2)**			
Foraging height	**2.2**	-0.5		0.3	4	0.44
(Gaussian, df = 102)	**(1.6, 2.8)**	(-1.4, 0.5)		-0.9, 1.5		
Foraging range	**1.0**	0.5			4	0.24
(Gaussian, df = 104)	**(0.3, 1.7)**	(-0.7, 1.7)				
Hop:Flight	**-0.5**	-0.7			5	0.22
(Gaussian, df = 103)	**(-0.8, -0.2)**	(-1.3, -0.1)				
Large prey	**0.1**			0.04	5	0.14
(Gaussian, df = 92)	**(0.02, 0.2)**			-0.2, 0.2		
Prey biomass	**124.7**			175.2	4	0.32
(Gaussian, df = 92)	**(30.1, 219.2)**			-0.3, 350.8		

occasions, and all occurred in established forest. Consumed biomass was best described by forest age, weather, and time actively foraging; explaining 32% of the variance (R^2 = 0.32). Greater biomass was consumed in more established forest (*B* = 124.7, 95% CI: 30.1 to 219.2; Table 3), and the average rates of insect biomass consumption (mg/min) were 25.83 ± 7.84, 60.33 ± 11.58, and 78.91 ± 16.26 (SEM) in youngest to oldest forest, respectively. In contrast, baseline prey availability from the arthropod transects revealed similar proportions of large prey across all forest ages (young = 48 ± 3%, mid = 44 ± 2%, old = 41 ± 2%; Fig. 4). Including weather as a covariate explained 20% of the variance (R^2 = 0.20), but forest age was unimportant (*B* = –0.02, 95% CI: –0.05 to 0.01). While prey choice and biomass consumption changed across forest age, no effect was observed for prey availability.

DISCUSSION

Studies of avian diversity indicate poor persistence of understory insectivores in secondary forests (Sigel *et al.* 2010), and one hypothesis is a reduction or change in prey availability (Ford *et al.* 2001). We show that antshrikes in more recently disturbed forest consume less overall biomass of prey, likely a result of proportionately less large prey in their diet as foraging attack and success rates were similar. However, these potential changes in prey availability did not translate into poor persis-

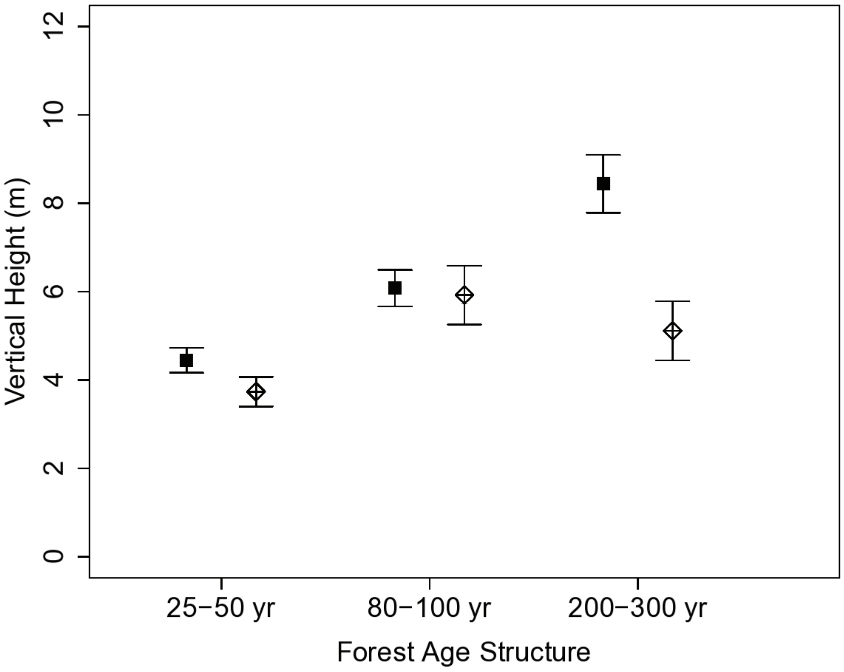

FIG. 2. Mean foraging height (filled squares) and foraging range (empty diamonds) for the Black-crowned Antshrike in 25–50 years, 80–100 years, and 200–300 years old forest age structures, along Pipeline road in Soberanía National Park, Colón, Panama. Error bars depict the standard error around the mean.

tence. Antshrikes occurred at similar densities in all forest ages, with no apparent preference for established forest. Additionally, prey composition, at least within 3 m of the forest floor, was similar across forest ages. With these results, attack and success rate are expected to be similar among forest ages. Yet, differences in foraging location, and especially prey choice and consumed biomass, suggest that resource availability for the birds varies by forest age, despite being undetectable using our transect methods. If we assume prey choice is a more accurate measure of prey availability, then these results suggest that antshrikes have flexible foraging behavior and are able to deploy different strategies in response to variation in prey availability across forest age. However, reduced biomass consumption in young forest suggests these individuals may be performing poorly despite flexible foraging behavior; the long-term effects of which are currently unknown for this species.

An overall reduction in foraging range occurred within the vegetation column of young forest. Maurer & Whitmore (1981) demonstrated a downward shift in foraging height in younger forests while studying temperate aerial insectivores. They found greater mid-canopy space and structural complexity at higher strata in older forest explained the downward shift. Changes in vegetation complexity may also drive vertical change in foraging behaviors for antshrikes. Similar to nearby Barro Colorado Island (DeWalt *et al.* 2003), we found smaller trees in greater density in younger forest. This suggests a shift in structural complexity to lower strata in more

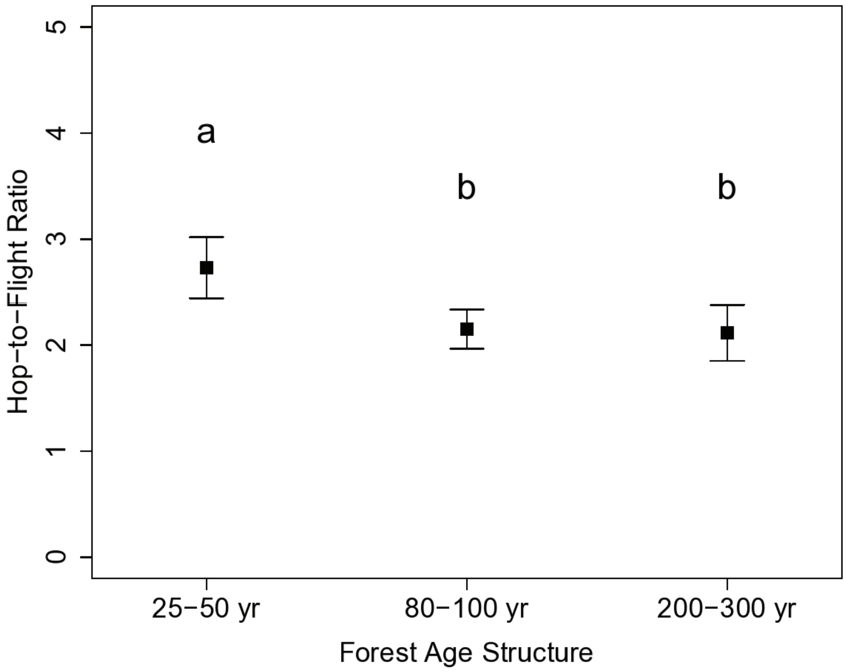

FIG. 3. Hop-to-flight ratio (total hops/total flights during a foraging bout) for Black-crowned Antshrikes in 25–50 years, 80–100 years, and 200–300 years old forest age structures in Soberanía National Park, Colón, Panama. Points with different letters are significantly different. Error bars are the standard error of the mean.

recently disturbed forest that is dominated by dense understory. Increased complexity is associated with a greater density of young foliage, providing food and refuge for arthropods (Mattson 1980). Greater vegetation density at lower strata in young forest could therefore promote a downward shift in the arthropod community, a pattern similar to that observed for butterflies in Indonesia (Fermon *et al.* 2005). Alternatively, it could simply promote an increase in understory arthropods associated with a decrease in the canopy community (Basset *et al.* 2001). Both options produce a resource disparity among forest strata, suggesting a possible mechanism for our observations of the antshrikes' decreasing foraging height in more recently disturbed forest.

Reduced horizontal movement during foraging may also be indicative of structural complexity. The hop-to-flight ratio was greatest in younger forest. Avian foraging tactics involve the minimum movement required to take an individual just beyond the limits of their visual field, reducing energy-use while maximizing searching efficiency (Robinson & Holmes 1982). Since the youngest site had greater foliage density in lower strata, the field of view was constricted, encouraging an increasing hop-to-flight ratio. This pattern may also be driven by resource availability. The dense understory of younger forests may stimulate greater populations of understory insects which are attracted to increased young leaf production (Basset *et al.* 2001). Greater insect densities reduce the need to move

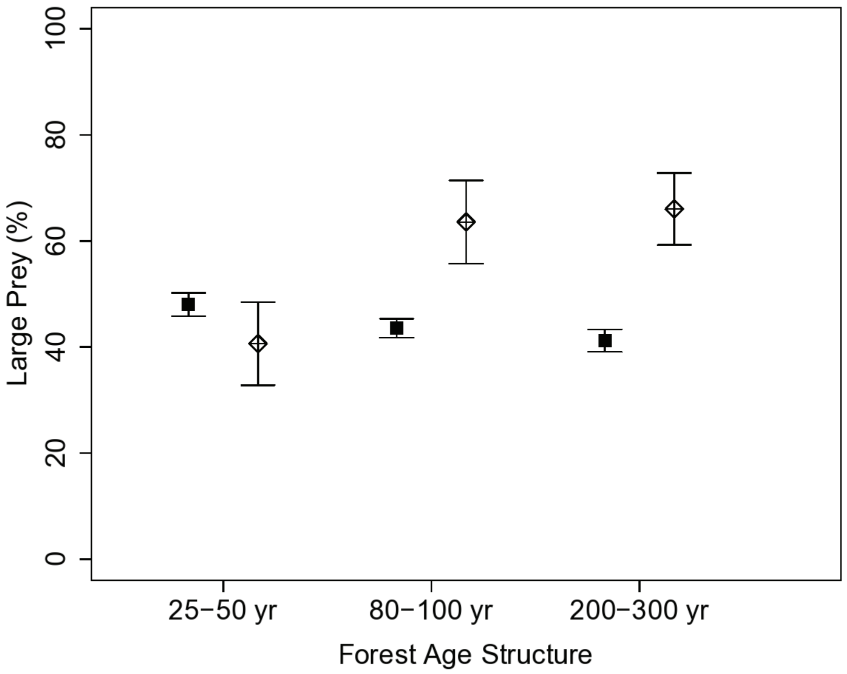

FIG. 4. The percentage of large prey (greater than and equal to bill length) observed for both arthropod transects (filled squares) and prey captured by Black-crowned Antshrikes during focal observations (empty diamonds) across the three forest age structures in Soberanía National Park: 25–50 years, 80–100 years, and 200–300 years. Error bars depict the standard error of the mean.

between vegetation structures when foraging, in comparison to older forest where insect aggregations may be more heterogeneous. Alternatively, the tendency to avoid inter-vegetation movement could be due to greater predation risk. However, there is little indication of differential adult survival across forest age (C. Tarwater pers. com.). If differences exist, one would expect higher adult mortality in older forests because known predators, such as the Collared Forest-Falcon (*Micrastur semitorquatus*), are primary forest specialists (Thorstrom *et al.* 2000). It is possible that alternative predators pose a greater threat to adults in younger forests, but to the best of our knowledge, no data exist on this subject.

Habitat quality is a complicated metric involving many factors. Our results do not support the hypothesis that younger forest is of lower quality for antshrikes. Antshrike abundance estimates did not differ across forest age, and there was no difference in the number of fledglings spotted during focal observations. However, individuals tend to choose larger prey and, as a result, consumed more insect biomass in established forest compared to younger forests. This indicates reduced resource availability for antshrikes in younger forest, assuming prey choice is an accurate indication of prey availability (Lyons 2005), and that larger prey is considered higher quality (Tarwater *et al.* 2009). Individuals in younger forest may target smaller prey due to less energy expenditure while foraging (e.g., a higher hop-to-flight ratio in dense foliage). Yet if this is the case, and if there is no difference in prey composition across sites, then one would expect prey size to remain constant and attack rate to decline in younger forest due to reduced energy requirements. This pattern was not observed, as individuals in younger forest consistently captured smaller prey despite maintaining similar attack rates to established forest, suggesting a change in prey composition.

If antshrikes are capable of flexible foraging strategies, why does the attack rate not increase in younger forests to compensate for the discrepancy in prey choice and biomass consumption? It is possible that foraging rate is constrained such that individuals are already operating at a maximum attack rate. This may be true if overall insect density was similar between forest ages, but insect composition (e.g., larger prey in older forests) differed. If so, it is possible that individuals in younger forests forage for longer periods to achieve the same level of biomass intake. Unfortunately, focal observations were too short to address this possibility. We also acknowledge the possibility that different foraging experience levels might exist across forest age. If a disparity in habitat quality exists, experienced and inexperienced individuals should occupy resource-rich and -poor territories respectfully (Tarwater 2012), which could confound our conclusions based on prey choice and behavioral metrics. Roper (2005) found equal nesting success rates for experienced and inexperienced antshrikes, suggesting similar nestling provisioning efficiency between experience levels. Therefore, foraging behavior could also be considered comparable, even in the presence of despotic distribution. Although not being conclusively shown by our study, it appears more likely that the insect community differs between forest ages, which in turn may be related to alterations in vegetation structure.

This study provides indirect support for the hypothesis that insect communities differ between forest ages, and substantiates the capacity for antshrikes to alter their foraging strategy accordingly. However, we cannot conclude from these data that altered prey communities explain a lack of persistence in secondary forests for understory insectivores, because we only studied a single species. In the light of our results, we encourage future multi-species research to address this issue. The compression and reduction in foraging range observed for antshrikes appears to correlate with a downward shift in structural complexity of vegetation, which may alter prey availability. Antshrikes may be able to persist under these conditions as indicated by abundance, but this may not be true for other birds. Although discussing other species is purely conjecture, due to the generalist diet of the antshrike, it is reasonable to assume that other understory insectivores with a narrower diet breadth may experience similar and possibly more pronounced changes in prey availability. If so, these species may be unable to persist if competition for limited resources in younger forests increased. It has been previously proposed that poor understory insectivore persistence could be driven or exacerbated by increased competition from aggressive mid-canopy species in a form of competitive release (Ford *et al.* 2001). Downward movement of birds in secondary forests has been observed (Waltert 2005) and thus may not be unique to antshrikes. Downward movement of robust species may increase interspecific competition, potentially resulting in less flexible species being unable to persist in younger forest, and promoting further expansion of mid-canopy species into lower forest strata. The absence of understory insectivores in younger forest is likely dependent on many factors, which a single-species study is unable to address. However, based on our results we suggest further investigation into the link between a changing insect community and increased interspecific competition should be pursued.

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