

## Research

### Examining the microclimate hypothesis in Amazonian birds: indirect tests of the ‘visual constraints’ mechanism

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#### Oikos

128: 798–810, 2019

doi: 10.1111/oik.05781

Subject Editor: Paul Caplat  
Editor-in-Chief: Dries Bonte  
Accepted 19 December 2018

Proposed mechanisms for the decline of terrestrial and understory insectivorous birds in the tropics include a related subset that together has been termed the ‘microclimate hypothesis’. One prediction from this hypothesis is that sensitivity to bright light environments discourages birds of the dimly lit rainforest interior from using edges, gaps, or disturbed forest. Using a hierarchical Bayesian framework and capture data across time and space, we tested this by first determining vulnerability based on differences in within-species capture rates between disturbed and undisturbed forest for 64 bird species at the Biological Dynamics of Forest Fragments Project in central Amazonian Brazil. We found that 35 species (55%) were vulnerable to anthropogenic habitat degradation, whereas only four (6%) were more commonly captured in degraded forest. To infer visual sensitivity, we then examined two different characters: eye size (maximum pupil diameter) relative to body mass and the initiation time of dawn song, which presumably reflects a species’ visual capacity under low light intensities. We predicted that species with large relative eye sizes and birds with earlier dawn songs would exhibit increased vulnerability in degraded habitats with bright light. Contrary to our predictions, however, vulnerability was positively correlated with the mean start time of dawn song. This indicates that species that wait to initiate dawn song are also more vulnerable to habitat degradation. After correcting for body size, there was no effect of eye size on vulnerability. Together, our results do not provide quantitative support for the light sensitivity mechanism of the microclimate hypothesis. More sensitive experimental tests, such as behavioral assays with controlled light environments, especially in a comparative framework, are needed to rigorously evaluate the role of light sensitivity as an aspect of the microclimate hypothesis among Neotropical birds.

Keywords: dawn song, eye size, habitat degradation, light environments, Neotropics, vulnerability



## Introduction

Insectivores that forage on or near the ground have consistently been identified among the most sensitive of tropical birds to anthropogenic habitat alteration (Stouffer and Bierregaard 1995, Canaday 1996, Stratford and Stouffer 1999, Sekercioglu et al. 2002, Stouffer et al. 2009, 2011). A variety of mechanisms has been proposed for the decline of these terrestrial and understory insectivores in the tropics, including limited dispersal ability, ecological specialization, food scarcity, physiological constraints, visual constraints and increased nest predation (Johns 1986, Canaday 1996, Sekercioglu et al. 2002, Stratford and Robinson 2005, Moore et al. 2008, Robinson and Sherry 2012). Yet mechanistic evidence for these hypotheses remains scarce or equivocal. Therefore, it is critical to assess proposed hypotheses that aim to identify the processes responsible for the decline of particularly sensitive species and guilds (Canaday 1996, Stratford and Robinson 2005, Robinson and Sherry 2012).

Humid tropical forest understories are characterized by low and predictable environmental variability; such conditions produce a selective environment that narrows the microclimatic niche of resident birds (Janzen 1967). Aside from light gaps and associated gap-specialist birds, one feature that unites terrestrial and understory insectivores is that they share a stable, low-light environment. In a terra firme forest outside of Manaus, Brazil, only ~1% of light that reaches the canopy penetrates to the lower understory (Shuttleworth et al. 1984). Moreover, light intensity exhibits relatively low diurnal and seasonal variability within tropical forest understories, much like other microclimatic variables (Chazdon and Fetcher 1984, Pollock et al. 2014). By contrast, disturbed microhabitats such as rainforest clearings show more extreme daily and seasonal fluctuations than heavily shaded forest understory (Chazdon and Fetcher 1984). At the Biological Dynamics of Forest Fragments Project (BDFFP) in Brazil, elevated light levels at the edge of a forest fragment extend markedly to 20 m and more subtly as far as 40 m into the understory (Kapos 1989), similar to the ~50 m distance of increased light penetration in other tropical studies (Patten and Smith-Patten 2012).

Most forest-dependent insectivorous guilds show strong aversions to these brightly lit microhabitats, avoiding crossing even narrow gaps (i.e. gap avoidance; Develey and Stouffer 2001, Lees and Peres 2009) and, for especially sensitive birds, avoiding edge habitat as well (Laurance 2004, Laurance et al. 2004). Edge and gap avoidance are correlated and likely act in concert to reduce gap-crossing events (Laurance et al. 2004). Even some experimentally translocated species – *Formicarius colma* and *Willisornis poecilinotus*, a terrestrial and understory insectivore, respectively – did not immediately traverse a 50–75 m gap to return to their territories during the first day after being released, instead moving back-and-forth along the forest edge until dusk (Laurance and Gomez 2005). However, all marked birds were found on territory within about 90 min after dawn the next day, suggesting these birds returned while

it was still relatively dark (Susan G. Laurance, pers. comm., Laurance and Gomez 2005).

Although other mechanisms besides light sensitivity may constrain understory insectivores, bright light environments in more open habitats could discourage use of forest edges or gaps (Stratford and Robinson 2005). The visual constraints mechanism (or sensitivity to light) falls under what has together been termed the ‘microclimate hypothesis’ (the physiological sensitivity of an organism to light, temperature, relative humidity, etc.) – a focus of recent research in Central America (Patten and Smith-Patten 2012, Pollock et al. 2014). For a suite of species at one of two sites, Patten and Smith-Patten (2012) found that a species’ light environment predicted its regional population trend, particularly for those birds occupying low-light habitats, which tended to be more vulnerable to extirpation. By contrast, Pollock et al. (2014) found no evidence of microclimate selectivity for nine understory insectivores, although these species did avoid microhabitats with high light intensity. Additionally, Walther (2002) showed that within a foraging stratum, birds moved downward and into denser cover during periods of bright sunlight. Empirical studies have also shown that high light intensity can affect vigilance and predator detection, which may lead to the avoidance of sunlit patches (Fernandez-Juricic and Tran 2007, Fernandez-Juricic et al. 2012). Light sensitivity may be an unlikely trait for declining temperate birds, but specialized terrestrial or lower understory species in the tropics may have unique adaptations that allow them to forage in low-light levels (Stratford and Robinson 2005).

Broadly, vertebrate visual systems represent a tradeoff between sensitivity (detecting low light intensity) and resolution (distinguishing detail; Land and Nilsson 2002). All else remaining equal, this depends upon the pupil aperture and focal length of the eye, where the wider the aperture, the more photons can be captured and the longer the focal length, the larger the image that is projected across the retina’s photoreceptors (Martin 1993, Land and Nilsson 2002). In birds, a number of indirect metrics have been used to infer minimum visual sensitivity and resolution, including eye size and behaviors that are assumed to be light-limited, such as the onset of foraging or singing at dawn (Thomas et al. 2002, 2004, Berg et al. 2006, Ockendon et al. 2009). Thomas et al. (2002) found that temperate songbirds with relatively large eyes (controlled for body mass) begin singing earlier at dawn than those with comparatively small eyes. Similarly, Berg et al. (2006) found that tropical species with larger eyes also initiate dawn song earlier, but this result hinged on controlling for foraging strata; understory species began singing later than canopy species due to light attenuation by vegetation. Visual capabilities have also been linked to the initiation of foraging at backyard feeding stations, where species with larger absolute and relative eye sizes arrive at feeders earlier than those with smaller eyes (Ockendon et al. 2009). Further, Thomas et al. (2004) found that experimentally shifting artificial light intensity earlier in the morning causes European robins *Erithacus rubecula* to both forage and sing earlier.

On the other hand, there is also empirical evidence that long-range calling increases predation risk (reviewed in Zuk and Kolluru 1998, Hale 2004) and Krams (2001) found that life-like models of a songbird were attacked more frequently by a sparrowhawk *Accipiter nisus* when presented with playback than without. Together, these studies suggest that an onset of activity at dawn (such as the time of first song) indicates that ambient light has reached a level at which a bird is visually capable of social communication and predator avoidance. Assuming a tradeoff between visual capacity at low and high light levels, we predict that species capable of activity at low light levels will be sensitive to bright light in degraded habitats (i.e. edges, gaps and young secondary forest). A recent study also demonstrated that species with increasing relative eye size exhibited increased edge avoidance, although their metric for edge avoidance (location of singing birds) was coarse and the pattern was not related to vulnerability more broadly across the landscape (Martínez-Ortega et al. 2014).

Here we examine whether the effects of deforestation and forest fragmentation on avian abundance in the central Amazon might be explained by indirect metrics of light sensitivity. Specifically, we examine if eye size and the onset of dawn song are related to a species' vulnerability to habitat degradation. We quantify vulnerability using long-term mist-net capture data from sites in primary and degraded forests at the same project. We predict that understory and midstory species with large relative eye sizes and those birds with earlier dawn songs will show increased vulnerability.

## Material and methods

### Study area

We tested our predictions by quantifying vulnerability and two metrics of light sensitivity at the Biological Dynamics of Forest Fragments Project (2°20'S, 60°W, Fig. 1). The BDFFP is located ~80 km north of Manaus, Amazonas, Brazil, and is the largest experiment on tropical forest fragmentation in the world (Bierregaard et al. 2001, Laurance et al. 2011). In collaboration with cattle ranchers in the 1980s, researchers experimentally isolated 11 forest fragments of 1, 10 and 100-ha on three ~15 000 ha fazendas (Fig. 1). However, these cattle ranches have since been largely abandoned and replaced by regenerating second growth, resulting in a mosaic of open pastures, second growth and forest fragments embedded within a region that continues to be dominated by continuous primary terra firme forest (Fig. 1). Regional terra firme forests lie atop nutrient-poor soils that support a typical canopy height of 25–30 m at the BDFFP (CLR, unpubl.). Average annual rainfall – as measured at Reserva Ducke, approximately 40 km to the south – is >2500 mm, which predominately accumulates during a six-month rainy season (December–May; Luiz Antonio Candido, pers. comm.).

### Bird capture data

To derive species-specific vulnerability estimates, we compared mist-net capture data collected from 2007 to 2016 in

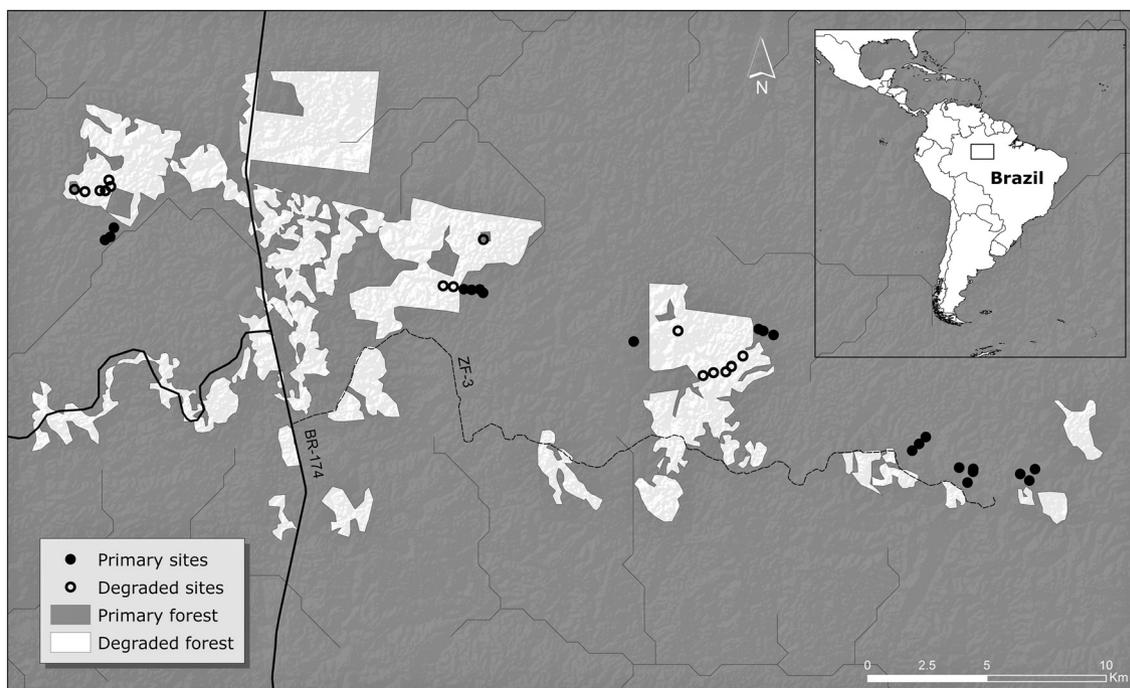


Figure 1. Study sites at the Biological Dynamics of Forest Fragments Project, showing the location of the three historic cattle ranches that were cleared within a landscape that is otherwise surrounded by continuous primary forest. We here plot the 21 primary forest (solid circles) and 15 degraded forest sites (empty circles) from which bird vulnerability estimates were derived using long-term mist-net capture data.

two forest types at the BDFFP – primary and degraded forest (Fig. 1). Our vulnerability metric quantifies within-species relative abundance in two habitat classes. It is not meant to reflect absolute abundance or interspecific differences in abundance. Twenty-one primary forest mist-netting sites were within forest tracts that were never cut or burned and stretched with minimal disturbance for 100s of km, especially to the north and east. Degraded sites ( $n = 15$ ) were comprised of four sites in 1-ha fragments, three in 10-ha fragments and eight in secondary forest. In both primary and degraded forest, birds were captured with linear transects of 12-m mist nets. Sites consist of a single, fixed net line arranged as 16 consecutive mist nets, open from sunrise (~6:00) until 14:00 on every sampling day; the lone exception is 1-ha fragments, which can only fit a linear transect of eight nets. Every site (net line) was sampled at least four days during this 10-year window (i.e.  $\geq$ four 8-h periods) during the dry season (June–November). Taxonomy follows the South American Classification Committee (Remsen et al. 2018).

### Eye size and dawn song field data

During routine passive banding operations at the BDFFP, we obtained reproducible, non-invasive maximum pupil diameter measurements of live birds using portrait photographs and a scale overlay, thus minimizing the inherent risk of directly measuring the eye with calipers (Thomas et al. 2002, Ockendon et al. 2009, Martínez-Ortega et al. 2014, Schutz and Schulze 2014). Subsequently, we measured these photographs in ImageJ (ver. 1.50i) using a scaled pixel length (Fig. 2). To obtain accurate absolute diameter estimates, we measured each photographed eye along three different axes and averaged the result for a single measurement per individual. We then corrected these mean absolute lengths for body size (resulting in a relative eye size variable), using that individual's body mass at the time of capture, except for six individuals without mass data. For these six exceptions, we corrected for body size using the average species-specific mass (or the sex-specific mass in sexually-dimorphic species; Johnson and Wolfe 2017). Because there was a wider variation in body mass than eye size, we present relative eye sizes as the residuals from a linear regression of  $\log(\text{eye length})$  on  $\log(\text{body mass})$ , following previous studies (Thomas et al. 2002, Ockendon et al. 2009, Martínez-Ortega et al. 2014). Here, relative (or residual) eye size is an indication of physiological cost: the relative investment in eye size above or below what would be expected given a bird's body size (Hall and Heesy 2011). As we have only a single response variable per species (vulnerability), we averaged relative eye size by species. Furthermore, in order to ensure our measures of maximum pupil diameters are biologically relevant, we also obtained direct transverse eye diameters from Ritland (1982) for a subset of species ( $n = 39$ ). These transverse eye diameters, averaged between the minimum and maximum transverse eye diameters, were measured on eyes removed by dissection from wet-preserved specimens. However, we continued to use average species-specific mass data from our site (Johnson

and Wolfe 2017), as 'weight' in Ritland (1982) was estimated using wing length (Supplementary material Appendix 1 Fig. A1, A2).

At five evenly spaced (300 m) sites in each of two primary forest plots, we recorded the time of first song (i.e. onset of dawn song) for all species. We visited each of these ten sites three times across seven months (November 2015–February 2016; June–August 2016) in order to register as many species as possible, while concurrently ensuring multiple observations per species. Each dawn song census began at nautical twilight (time 0), when the sun is  $12^\circ$  below the horizon (~45 min prior to local sunrise), and continued for 75 min; the time of first song was recorded as the deviation from nautical twilight. Here, time is used as a proxy for ambient light levels due to the strong correlation between time and light at twilight (Berg et al. 2006). Daily nautical twilight times were obtained from the Astronomical Applications Department of the US Naval Observatory (<<http://aa.usno.navy.mil>>) for coordinates in close proximity to one of the primary forest plots ( $2^\circ 24' \text{ S}$ ,  $59^\circ 53' \text{ W}$ ). In all, 116 of 136 detected species were recorded on more than one morning. We pooled data across days and sites following Berg et al. (2006) using the mean time of first song for all species. Because foraging strata has been shown to predict when a species begins to sing at dawn (Berg et al. 2006), we excluded canopy species, using the categorical foraging height classifications in Cohn-Haft et al. (1997).

### Statistical analysis

We developed models in a hierarchical Bayesian framework to first test for the effect of degraded versus primary forest on counts of 64 species that each had  $>5$  total captures in our combined forest capture datasets. The coefficient for forest represents a species' vulnerability – high coefficients represent species that are more often found in primary forest (vulnerable) and low coefficients refer to species that are more often found in degraded forest (less vulnerable). Given the relatively large number of species-specific vulnerability estimates, our second question was what biological or ecological characteristics may have an effect on vulnerability. In other words, do species that have negative or positive vulnerabilities share common characteristics?

We developed a hierarchical model with two levels. Level 1 estimates the vulnerability for each species, where species are random effects, and level 2 models those random effect estimates against hypothesized predictors that test for effects of dawn song and relative eye size. Level 2 thus provides a test of whether species-level predictors are significant factors in describing vulnerability, and our hierarchical formulation means that uncertainty is accounted for in a way that reflects the system we are modeling (compared to including a species-level predictor like eye size into level 1 of the model, which would model the individuals within a species). For level 1 of the model, we used a zero-inflated Poisson, which permits the estimation of true zeros (i.e. a species does not occur) separate from count zeros (i.e. a species does occur, but abundance

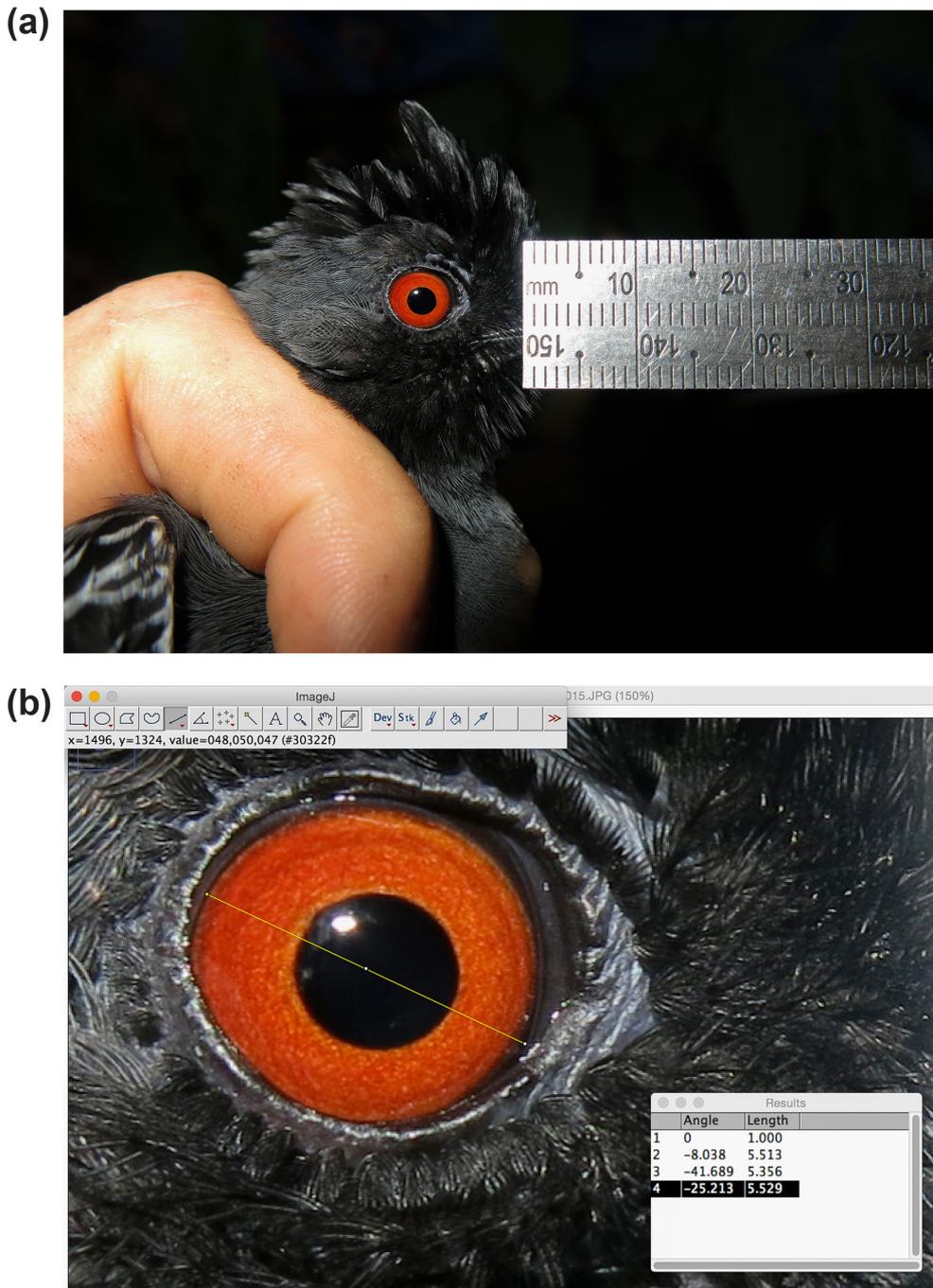


Figure 2. (a) Portrait photo of a male black-headed antbird *Percnostola rufifrons* with a wing chord ruler used as a scale overlay. (b) In ImageJ, 1 mm was translated to a scaled pixel length, which was then used to obtain an accurate measurement of maximum pupil diameter. We measured three different axes and averaged the results for a single diameter measurement per individual.

is zero). Level 1 of the model also includes an effort offset variable, which is essentially a covariate to account for different net hours at different sites. Our primary interest in level 1 of the model is the random slope estimates, which can be considered species-specific estimates of vulnerability (or the within-species change in counts between forest habitats). These 64 slope estimates are then modeled in level 2, where they are separately regressed against dawn song and relative eye size. Significant effects of the level 2 predictors would

suggest that dawn song or relative eye size are related to species' vulnerability. Finally, we included family (where  $k=19$  families) as a level 2 random effect to account for phylogenetic non-independence among species. While this approach is not as direct as eigenvector-based methods on phylogenetic distance matrices, it is satisfactory at this phylogenetic scale because the vast majority of our species are from a single order (89%; Passeriformes) and are the sole representative of their genus in our sample (80%; Marc Kéry, pers. comm.).

The full statistical description of these models and the evaluation criteria we used are available in Appendix 1.

### Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.8301107>> (Rutt et al. 2018).

### Results

Across the two forest types, we compiled 4182 captures for our 64 species (Appendix 2). This includes 2537 captures of all species at 21 primary forest sites (13 507 net-hours in effort) and 1645 captures of 57 species at 15 degraded forest sites (16 756 net-hours). Effort per site in primary forest was  $643.2 \pm 138.7$  net-hours (mean  $\pm$  SD) and  $1117.1 \pm 658.0$  net-hours in degraded forest. For our predictor variables, we measured maximum pupil diameter on 263 individuals of 63 species ( $n = 4.17 \pm 1.28$  measurements/species, range 1–6 individuals). Absolute eye size ranged from 3.2 mm (*Myrmotherula menetriesii*) to 9.3 mm (*Momotus momota*), whereas relative eye size was smallest for *Campylorhynchus*, *Xenops* and *Philydor* and largest for *Bucco*, *Malacoptila* and *Platyrinchus coronatus*. Out of the 30 dawn song censuses, mean number of detections per species was  $9.4 \pm 7.74$  SD (range: 2–27) for 45 species that were registered on at least two different mornings. Mean onset of dawn song ranged from 22 to 68 min after nautical twilight, with *Campylorhynchus*, *Bucco*, *Momotus*, *Micrastur* and

*Dendrocolaptes* among the earliest singers and *Myrmotherula axillaris*, *Dixiphia*, *Gymnophytus*, *Cyphorhinus* and *Schiffornis* among the latest.

Of the 64 species we examined for level 1 of the model, 35 (54.7%) are classified as vulnerable (positive estimates that do not overlap with zero), whereas only four (6.3%) are invulnerable (i.e. the number of slope estimates ( $\beta_s$ ) with 95% credible intervals (CRI) that are entirely negative and do not overlap zero; Fig. 3). The remaining 25 species (39.1%) have 95% CRIs that overlap zero and therefore have vulnerability estimates that are not statistically different from zero, despite most having point estimates greater than zero (i.e. more vulnerable than not). Together, these vulnerability estimates indicate that the majority of species for which we have sufficient capture data are more commonly captured in primary forest than in degraded forest such as small forest fragments and secondary forest.

We ran two separate models for the two separate level 2 covariates (i.e. dawn song and relative eye size) in order to maximize the number of species included. (If we had reduced the dataset to include only those species with data for both covariates, we would have lost nearly a third ( $n=20$ ) of the present species suite.) In contrast to expectations (Thomas et al. 2002, Berg et al. 2006), dawn song and relative eye size were not highly correlated (Supplementary material Appendix 1 Fig. A3). Thus, it made sense to retain both level 2 covariates separately as each covariate provided unique information.

After accounting for family, vulnerability was positively correlated with the mean start time of dawn song (posterior

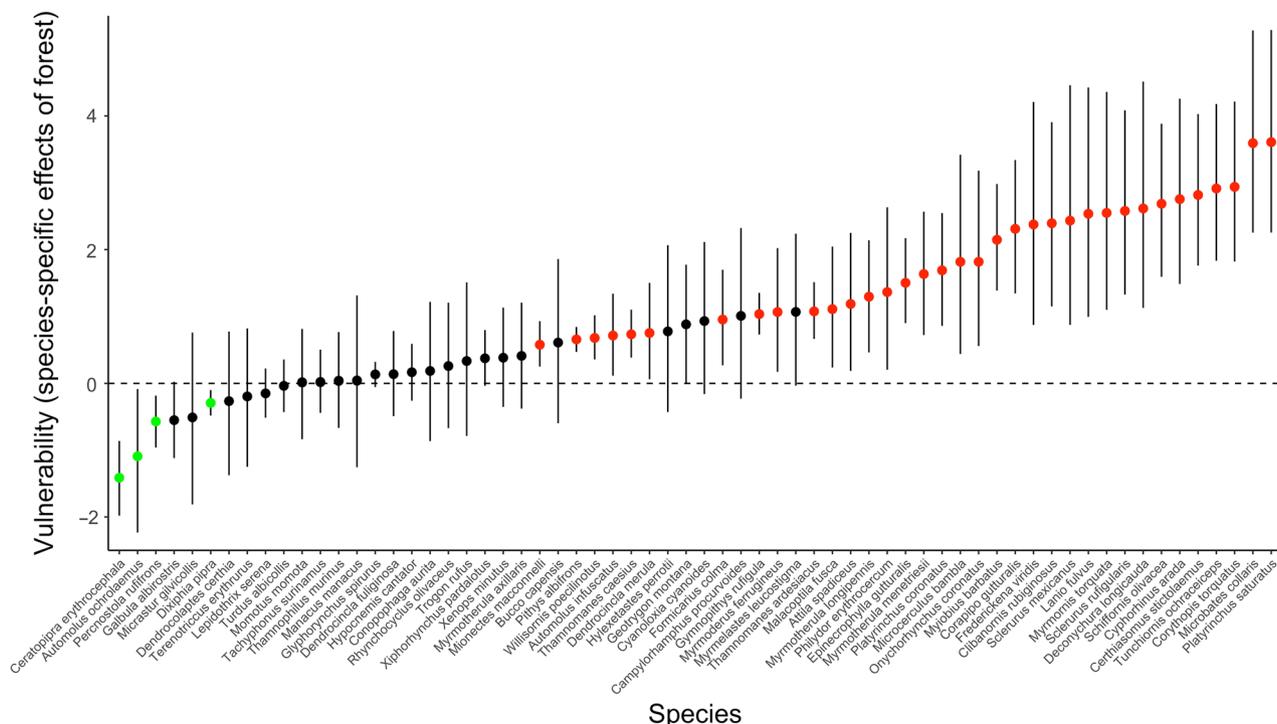


Figure 3. Means (dots) and 95% credible interval (lines) estimates of vulnerability for  $n=64$  species included in this study. Species are ordered by their means, from least vulnerable to most vulnerable, with green or red dots highlighting species that are invulnerable ( $\beta_j < 0$ ) or vulnerable ( $\beta_j > 0$ ), respectively, based on 95% credible intervals that do not overlap zero. The dashed line at zero separates species more often captured in degraded forest (below) from those more often captured in primary forest (above).

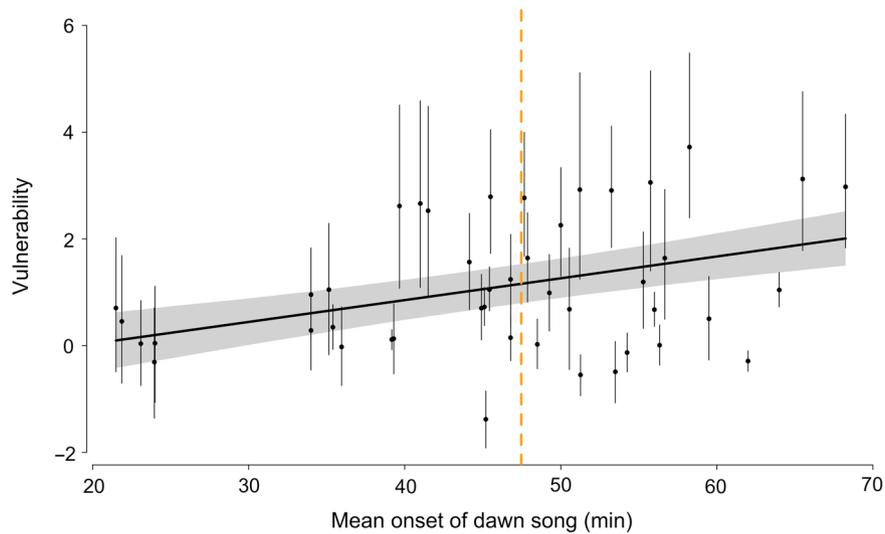


Figure 4. Relationship between the mean onset of dawn song and vulnerability for 45 species of birds. Vulnerability estimates are species-specific posterior mean slopes for the effect of forest (solid circles) and 95% CRI (vertical lines), where high coefficients represent species more often found in primary forest (vulnerable) and low coefficients refer to species more often captured in degraded forest (less vulnerable). The solid regression line is bounded by a 90% CRI shaded region. Minutes on the x-axis are deviation from nautical twilight, or when the sun is  $12^\circ$  below the horizon. The position of mean local sunrise (47.5 min) is illustrated with a vertical, dashed line.

mean and 95% CRI = 0.04 [0.02, 0.06]; Fig. 4). After accounting for body size, however, relative eye size was not associated with vulnerability (posterior mean and 95% CRI = 0.188 [-2.223, 2.637]; Fig. 5). As specified in Methods, we ran full models with a random intercept for family included in level 2, for which there was no effect. However, since this prevented us from modeling a global slope on level 2 covariates, we re-fit the models without family in order to plot a global slope effect.

## Discussion

It has long been recognized that many understory tropical birds, dwelling in dim light environments, have large eyes (Orians 1969). We considered whether this morphological relationship has implications for vulnerability to rainforest disturbance. We used two broad, albeit indirect, tests of light sensitivity under the microclimate hypothesis, relating these to robust species-specific estimates of vulnerability (Fig. 3).

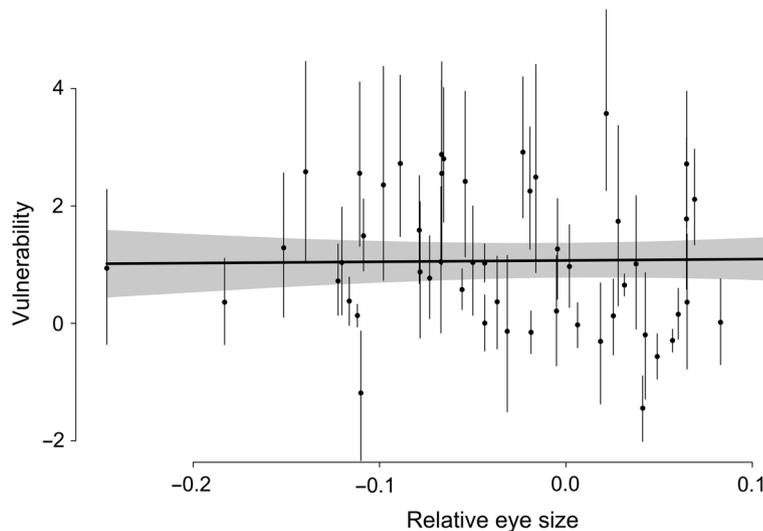


Figure 5. Relationship between relative eye size and vulnerability for 63 species of birds. Relative eye size is the average species-specific residual from a linear regression of  $\log(\text{maximum pupil diameter})$  on  $\log(\text{body mass})$ . Vulnerability estimates are species-specific posterior mean slopes for the effect of forest (solid circles) and 95% CRI (vertical lines), where high coefficients represent species more often found in primary forest (vulnerable) and low coefficients refer to species more often captured in degraded forest (less vulnerable). The solid regression line is bounded by a 90% CRI shaded region.

Previous studies have focused on light/microclimate associations (Patten and Smith-Patten 2012), light/microclimate selection as compared to random sites (Pollock et al. 2014), and edge avoidance based on the decline of song detections along a transect 100 m from an edge (Martínez-Ortega et al. 2014). Here, we analyzed vulnerability for a total of 64 species between dawn song (45 species) and eye size (63 species).

Although our results did not support our predictions, we found a significant relationship between species' vulnerability to habitat degradation and dawn song. Assuming that visual sensitivity (detecting low light intensity) influences the order of dawn song initiation and is enhanced for those species with large eyes, we predicted that the most intuitive support of the visual constraints mechanism would demonstrate that large-eyed, early-singing species would be most vulnerable to habitat degradation. Indeed, that is what Martínez-Ortega (2014) found at nearby Reserva Ducke if we equate their edge avoidance index with our vulnerability metric: species with larger relative eye sizes increasingly avoided edges (a positive relationship). However, despite close proximity (~40 km apart) between the two study sites, we found no relationship between relative eye size and vulnerability, even when we similarly subsetted species by strata to separately examine understory and midstory species. This discrepancy could be due to the fact that the two datasets shared relatively few species, and the Reserva Ducke study included species that are common in major disturbed areas along the outskirts of Manaus, but unlikely to be found in interior primary forest. Uniquely, and contrary to our expectations, the mean start time of dawn song was positively correlated with vulnerability, indicating that species that wait to initiate dawn song were more vulnerable to habitat degradation. However, we found no evidence that early-singing species that vocalize in relative darkness were captured less often in degraded forest – habitat characterized by high-intensity light conditions.

Staicer et al. (1996) reviewed at least a dozen non-mutually exclusive ultimate hypotheses to explain why many birds produce peak bouts of singing at dawn, broadly classified by intrinsic (hormonal levels), social (mate and territorial communication), and environmental (e.g. abiotic conditions) factors. For timing of first song, light intensity is clearly an important proximal cue (Staicer et al. 1996). Initiation times for dawn song are repeatable within a species, given in a predictable order within a community, and track sunrise/civil twilight curves throughout the boreal summer, beginning rather precisely at a narrow range of light intensities, suggesting that the structuring of dawn song across species is strongly related to light availability (Wright 1913, Allard 1930, Leopold and Eynon 1961, Staicer et al. 1996, Berg et al. 2006). Characteristics that are associated with species' vulnerability should be informative to define what makes a species sensitive to forest degradation, particularly in stable environments with highly specialized birds. Because we did not find a correlation between relative eye size and vulnerability nor dawn song and relative eye size, our results for dawn song suggest that there may be an unrelated third

factor that links vulnerability and late onset of dawn song. One such possibility is low density, which has been shown to depress dawn singing in *Tyrannus tyrannus*, delaying onset and even suppressing dawn song entirely (Sexton et al. 2007). Furthermore, Hodgson et al. (2018) found that two species of Turdidae could be induced to advance singing at dawn (by 8 and 17 min, though not earlier) by conspecific playback, suggesting a putative mechanism for density mediating the onset of dawn song. Consistent with reduced densities, we detected the 12 most vulnerable species only half as frequently as the average species during the dawn song censuses. However, to fully explore this hypothesis, we would need to know the territory configuration around the individuals that were censused.

A closer inspection of the organization of species-specific vulnerability values by dawn song reveals some interesting patterns. No vulnerable species initiated dawn song until ~40 min after nautical twilight (39.7 min; *Deconychura longicauda*), which is ~7.5 min prior to mean local sunrise (47.5 min; Fig. 4). Twelve species, however, started singing between 20 and 40 min after nautical twilight. Half of these invulnerable species were woodcreepers (Dendrocolaptinae), but this list also included a puffbird (Bucconidae), motmot (Momotidae), falcon (Falconidae), ovenbird (Furnariidae), dove (Columbidae) and antbird (Thamnophilidae). On the other end, the average start time for the 12 most vulnerable species was 51.5 min after nautical twilight. Many of these are terrestrial insectivores or species associated with mixed-species flocks, two ecological guilds that have long been identified as vulnerable (Stratford and Stouffer 1999, Canaday and Rivadeneyra 2001, Laurance 2004, Stouffer et al. 2006). For mixed-species flock members, most obligate species initiated dawn song shortly before sunrise (44.1–47.7 min after nautical twilight), but the earliest (34 min; *Xenops minutus*) is the least vulnerable of the group, whereas the two latest (*Lanio fulvus* [51.2 min] and *Tunchiornis ochraceiceps* [53.3 min]) are the most vulnerable. Surprisingly, no terrestrial or near-ground insectivores included in our analysis began singing prior to 40 min after nautical twilight, despite these species occupying the lowest and darkest stratum of the forest. That said, rarely captured terrestrial insectivores (antpittas; Grallariidae), with insufficient captures to estimate vulnerability, are among the earliest singing songbirds at our site (*Grallaria varia* [20 min], *Hyllopezus macularius* [28.5 min] and *Myrmothera campanisona* [28.5 min]).

In light of these results, additional metrics of visual sensitivity may better demonstrate sensitivity to high light intensities. Staying within the realm of presumably light-limited behaviors, for example, the morning cessation of dawn song or attenuation of foraging rates are likely more informative than initiation, though this would be more difficult to quantify unambiguously. Conversely, the re-initiation of these activities towards the end of the day would be easier to quantify, although probably less striking and with fewer species involved. Further, measuring axial (or focal) length in addition to maximum pupil aperture would help characterize eye

structure more holistically, without examining the eye internally (Martin 1993, Land and Nilsson 2002, Martin et al. 2004, Thomas et al. 2004). For live birds, however, manipulations with artificial light or controlled light environments would likely yield the most robust results. In order to more accurately measure maximum pupil aperture, Thomas et al. (2004) suggest photographing a dark-adapted eye (e.g. a bird in a dark room) with an infrared camera and scale overlay. Alternatively, this could be done in a bright room (i.e. a fixed high light intensity) to measure the minimum pupil diameter or the time it takes for an eye to adapt to bright sunlight or complete darkness. Stratford and Robinson (2005) propose examining internal eye structure (density/size of photoreceptors) and cell sensitivities in a comparative framework, such as between closely related gap specialists and forest-interior denizens (e.g. *Percnostola rufifrons* and *Myrmelastes leucostigma*, respectively, in our study system). This could be done directly in the lab using electroretinography or with behavioral assays as an indirect proxy. The best approach, however, would be to collect specimens, immediately extract the eyes, and examine them physiologically (Esteban Fernández-Juricic, pers. comm.). Finally, quantifying the full range of natural light environments (including use of bright microenvironments such as sunflecks) for phylogenetically-controlled species pairs that differ in vulnerability would also provide valuable insight.

Together, our results do not provide quantitative support for the light sensitivity hypothesis; however, by focusing on metrics unique to light sensitivity, researchers can isolate physiological mechanisms associated with light sensitivity from other competing aspects of the microclimate hypothesis, which are often highly correlated in disturbed microhabitats (e.g. reduced humidity and increased temperature). Although the metrics we employed are admittedly coarse for something as complex as avian vision, our results suggest that there may still be an association between light sensitivity and species-specific vulnerability. Given various lines of evidence for light sensitivity among forest-dependent Neotropical birds, there is a critical need for more nuanced, experimental tests of this hypothesis, particularly in a comparative framework.

*Acknowledgements* – We thank the many mateiros, assistants and banders for their help collecting these data. We are particularly grateful to Erik I. Johnson and Angélica Hernández-Palma for their critical contributions of capture data. Additionally, we thank Gonçalo Ferraz for valuable logistic support and help generating funding. Additional logistical support from the staff of the Biological Dynamics of Forest Fragments Project made this research possible. The BDFFP is managed and supported by Brazil's Instituto Nacional de Pesquisas da Amazônia and the Smithsonian Institution.

*Funding* – Funding for this research was provided by the US National Science Foundation (LTREB 0545491 and 1257340), the National Geographic Society and the National Institute of Food and Agriculture, US Department of Agriculture, McIntire Stennis projects no. 94098 and no. 94327. Finally, we would like to thank Esteban Fernández-Juricic, Jeffrey D. Brawn, Cynthia A. Staicer

and Michael D. Kaller for constructive discussions and direction to pertinent resources and Kyle E. Harms for improving a previous version of this manuscript. This is publication no. 751 of the BDFFP Technical Series and no. 46 of the Amazonian Ornithology Technical Series of the INPA Collections Program. The manuscript was approved by the Director of the Louisiana State University Agricultural Center as manuscript number 2019-241-33416.

## References

- Allard, H. A. 1930. The first morning song of some birds of Washington, DC; its relation to light. – *Am. Nat.* 64: 436–469.
- Berg, K. S. et al. 2006. Phylogenetic and ecological determinants of the neotropical dawn chorus. – *Proc. R. Soc. B* 273: 999–1005.
- Bierregaard, R. O., Jr. et al. 2001. Lessons from Amazonia: the ecology and conservation of a fragmented forest. – Yale Univ. Press.
- Canaday, C. 1996. Loss of insectivorous birds along a gradient of human impact in Amazonia. – *Biol. Conserv.* 77: 63–77.
- Canaday, C. and Rivadeneira, J. 2001. Initial effects of a petroleum operation on Amazonian birds: terrestrial insectivores retreat. – *Biodivers. Conserv.* 10: 567–595.
- Chazdon, R. L. and Fetcher, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. – *J. Ecol.* 72: 553–564.
- Cohn-Haft, M. et al. 1997. A new look at the 'species-poor' central Amazon: the avifauna north of Manaus, Brazil. – *Ornithol. Monogr.* 48: 205–235.
- Develey, P. F. and Stouffer, P. C. 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. – *Conserv. Biol.* 15: 1416–1422.
- Fernandez-Juricic, E. and Tran, E. 2007. Changes in vigilance and foraging behaviour with light intensity and their effects on food intake and predator detection in house finches. – *Anim. Behav.* 74: 1381–1390.
- Fernandez-Juricic, E. et al. 2012. Predator detection is limited in microhabitats with high light intensity: an experiment with brown-headed cowbirds. – *Ethology* 118: 341–350.
- Hale, A. M. 2004. Predation risk associated with group singing in a neotropical wood-quail. – *Wilson Bull.* 116: 167–171.
- Hall, M. I. and Heesy, C. P. 2011. Eye size, flight speed and Leuckart's Law in birds. – *J. Zool.* 283: 291–297.
- Hodgson, L. et al. 2018. Early singers attend to conspecific but not heterospecific behavioural cues at dawn. – *J. Avian Biol.* 49: e01749.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – *Am. Nat.* 101: 233–249.
- Johns, A. D. 1986. Effects of selective logging on the ecological organization of a peninsular Malaysian rainforest avifauna. – *Forktail* 1: 65–79.
- Johnson, E. I. and Wolfe, J. D. 2017. Molt in neotropical birds: life history and aging criteria. – CRC Press.
- Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. – *J. Trop. Ecol.* 5: 173–185.
- Krams, I. 2001. Communication in crested tits and the risk of predation. – *Anim. Behav.* 61: 1065–1068.
- Land, M. F. and Nilsson, D. E. 2002. Animal eyes. – Oxford Univ. Press.

- Laurance, S. G. W. 2004. Responses of understory rain forest birds to road edges in central Amazonia. – *Ecol. Appl.* 14: 1344–1357.
- Laurance, S. G. W. and Gomez, M. S. 2005. Clearing width and movements of understory rainforest birds. – *Biotropica* 37: 149–152.
- Laurance, S. G. W. et al. 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. – *Conserv. Biol.* 18: 1099–1109.
- Laurance, W. F. et al. 2011. The fate of Amazonian forest fragments: a 32-year investigation. – *Biol. Conserv.* 144: 56–67.
- Lees, A. C. and Peres, C. A. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. – *Oikos* 118: 280–290.
- Leopold, A. and Eynon, A. E. 1961. Avian daybreak and evening song in relation to time and light intensity. – *Condor* 63: 269–293.
- Martin, G. R. 1993. Producing the image. – In: Zeigler, H. P. and Bischof, H. J. (eds), *Vision, brain and behavior in birds*. – MIT Press, pp. 5–24.
- Martin, G. et al. 2004. The eyes of oilbirds (*Steatornis caripensis*): pushing at the limits of sensitivity. – *Naturwissenschaften* 91: 26–29.
- Martínez-Ortega, C. et al. 2014. Species-specific differences in relative eye size are related to patterns of edge avoidance in an Amazonian rainforest bird community. – *Ecol. Evol.* 4: 3736–3745.
- Moore, R. P. et al. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. – *Ecol. Lett.* 11: 960–968.
- Ockendon, N. et al. 2009. Eye size and the time of arrival of birds at garden feeding stations in winter. – *J. Ornithol.* 150: 903–908.
- Orians, G. H. 1969. The number of bird species in some tropical forests. – *Ecology* 50: 783–801.
- Patten, M. A. and Smith-Patten, B. D. 2012. Testing the microclimate hypothesis: light environment and population trends of neotropical birds. – *Biol. Conserv.* 155: 85–93.
- Pollock, H. S. et al. 2014. Absence of microclimate selectivity in insectivorous birds of the neotropical forest understory. – *Biol. Conserv.* 188: 116–125.
- Remsen, J. V., Jr. et al. 2018. A classification of the bird species of South America. – [www.museum.lsu.edu/~Remsen/SACCBaseline.htm](http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm).
- Ritland, S. M. 1982. The allometry of the vertebrate eye. – PhD thesis, Univ. of Chicago.
- Robinson, W. D. and Sherry, T. W. 2012. Mechanisms of avian population decline and species loss in tropical forest fragments. – *J. Ornithol.* 153: S141–S152.
- Rutt, C. L. et al. 2018. Data from: examining the microclimate hypothesis in Amazonian birds: indirect tests of the ‘visual constraints’ mechanism. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.8301107>.
- Schutz, C. and Schulze, C. H. 2014. Measuring the eye size of mist-netted birds: a comparison of two non-invasive methods. – *J. Ornithol.* 155: 1077–1079.
- Sekercioglu, C. H. et al. 2002. Disappearance of insectivorous birds from tropical forest fragments. – *Proc. Natl Acad. Sci. USA* 99: 263–267.
- Sexton, K. et al. 2007. Dawn song of eastern kingbirds: intrapopulation variability and sociobiological correlates. – *Behaviour* 144: 1273–1295.
- Shuttleworth, W. J. et al. 1984. Observations of radiation exchange above and below Amazonian forest. – *Q. J. R. Meteorol. Soc.* 110: 1163–1169.
- Staicer, C. A. et al. 1996. The dawn chorus and other diel patterns in acoustic signaling. – In: Kroodsma, D. E. and Miller, E. H. (eds), *Ecology and evolution of acoustic communication in birds*. – Cornell Univ. Press, pp. 426–453.
- Stouffer, P. C. and Bierregaard, R. O. 1995. Use of Amazonian forest fragments by understory insectivorous birds. – *Ecology* 76: 2429–2445.
- Stouffer, P. C. et al. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. – *Conserv. Biol.* 20: 1212–1223.
- Stouffer, P. C. et al. 2009. Twenty years of understory bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. – *Divers. Distrib.* 15: 88–97.
- Stouffer, P. C. et al. 2011. Understory bird communities in Amazonian rainforest fragments: species turnover through 25 years post-isolation in recovering landscapes. – *PLoS One* 6: e20543.
- Stratford, J. A. and Stouffer, P. C. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. – *Conserv. Biol.* 13: 1416–1423.
- Stratford, J. A. and Robinson, W. D. 2005. Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. – *Front. Ecol. Environ.* 3: 91–98.
- Su, Y. S. and Yajima, M. 2015. R2jags: using R to run ‘JAGS’. – R package ver. 0.5–7, <https://cran.r-project.org/web/packages/R2jags/R2jags.pdf>.
- Thomas, R. J. et al. 2004. Eye design in birds and visual constraints on behavior. – *Ornithol. Neotrop.* 15: 243–250.
- Thomas, R. J. et al. 2002. Eye size in birds and the timing of song at dawn. – *Proc. R. Soc. B* 269: 831–837.
- Walther, B. A. 2002. Vertical stratification and use of vegetation and light habitats by neotropical forest birds. – *J. Ornithol.* 143: 64–81.
- Wright, H. W. 1913. Morning awakening and even-song: second paper. – *Auk* 30: 512–537.
- Zuk, M. and Kolluru, G. R. 1998. Exploitation of sexual signals by predators and parasitoids. – *Q. Rev. Biol.* 73: 415–438.

Supplementary material (available online as Appendix oik-05781 at [www.oikosjournal.org/appendix/oik-05781](http://www.oikosjournal.org/appendix/oik-05781)). Appendix 1.

## Appendix 1. Full statistical notation for the zero-inflated hierarchical models that we ran

We used a hierarchical zero-inflated Poisson model for counts,

$$w_i \sim \text{Bernoulli}(\psi_i)$$

where  $\psi_i$  represents the probability that a species occurs at a given site and is included to account for the abundance of zeros in the observed data (where  $i = \text{site} \times \text{species}$  observations). All  $\psi$  were between 0.166 and 0.241 (95% CRI), which is the estimate of false zeros, or the proportion of zeros in the estimated counts that are accounted for by the zero-inflated portion of the model. When  $w_i = 1$ , the species was observed at that site, and counts ( $C_i$ ) were then estimated with the parameter  $\lambda$ , which we further model with a linear predictor.

$$C_i \sim \text{Poisson}(w_i \times \lambda_i)$$

$$\lambda_i = \alpha_{j(i)} + \beta_{j(i)} x_i + A_i$$

The linear predictor includes a random intercept ( $\alpha_j$ ) and random slope ( $\beta_j$ ) for  $j$  species, such that each species has its own effect of forest (vulnerability).  $x_i$  is a dummy variable with two levels (degraded and primary) for the effect of forest.  $A_i$  represents an effort offset to account for the variable number of sampling net-hours that were amassed at each site.

In order to better understand the variation in species-level responses to forest habitat, we modeled the varying slopes (representing the effect of forest on individual species) separately in the second level of the model as a function of dawn song and eye size, both of which are indirect metrics used to infer visual sensitivity.

$$\begin{pmatrix} \alpha_{k(j)} \\ \beta_{k(j)} \end{pmatrix} \sim \text{MVN} \left( \begin{pmatrix} \mu_\alpha \\ \gamma_0^\beta + \gamma_1^\beta \times z_j \end{pmatrix}, \begin{pmatrix} \sigma_\alpha^2 & \rho \sigma_\alpha \sigma_\beta \\ \rho \sigma_\alpha \sigma_\beta & \sigma_\beta^2 \end{pmatrix} \right)$$

where  $\mu_\alpha$  is the grand-mean intercept and  $\gamma_0^\beta$  and  $\gamma_1^\beta$  are the coefficients for the regression of the predictor  $z_j$ , which represents species-specific estimates of dawn song and relative eye size in separate models.  $\sigma_\alpha^2$  and  $\sigma_\beta^2$  are conditional variances, the variance in  $\alpha_j$  and  $\beta_j$  after controlling for the effect of the covariate.  $\rho$  is the estimated correlation between the varying parameters. We included family (where  $k = 19$  families) as a level two random effect to account for phylogenetic non-independence among species. While this approach is not as direct as eigenvector-based methods on phylogenetic distance matrices, it is satisfactory at this phylogenetic scale because the vast majority of our species are from a single order (89%; Passeriformes) and are the sole representative of their genus in our sample (80%; Marc Kéry, pers. comm.).  $\mu_\alpha$ ,  $\gamma_1^\alpha$  and  $\gamma_1^\beta$  were given non-informative normal priors, while priors for  $\sigma_\alpha$  and  $\sigma_\beta$  remained non-informative uniform.

We ran three parallel Markov chains for all models, with each chain starting at its own randomly-generated value. The first 10 000 iterations of each chain were discarded, with the remaining 10 000 thinned by removing every third iteration, resulting in a total of 10 002 saved iterations per model. These remaining values allowed us to characterize the posterior distribution, which we assessed visually for convergence using trace plots and plots of posterior distributions, as well as the Brooks–Gelman–Rubin statistic,  $\hat{R}$ , where values  $< 1.1$  indicate convergence. We considered a parameter significant if the posterior distribution did not overlap zero at the 95% credible interval (CRI). All models were fit in JAGS with the package ‘R2jags’ (Su and Yajima 2015) within R (<[www.r-project.org](http://www.r-project.org)>).

Appendix 2. Suite of central Amazonian bird species with >5 total captures at 36 BDFPP sites, including all covariates used in these analyses.

Species or family	Degraded forest captures	Primary forest captures	Vulnerability <sup>1</sup>	Mean dawn song <sup>2</sup>	Absolute eye size <sup>3</sup>	Mass <sup>4</sup>	Relative eye size <sup>5</sup>	Average transverse diameter <sup>6</sup>	Mass <sup>7</sup>	Relative eye size (Ritland) <sup>8</sup>
<b>Columbidae</b>										
<i>Geotrygon montana</i>	7	13	0.88	34	6.80	103.4	-0.120	12.95	113.3	-0.171
<b>Trogonidae</b>										
<i>Trogon rufus</i>	5	4	0.33	51	6.61	50.5	0.065	14.40	49.4	0.167
<b>Momotidae</b>										
<i>Momotus momota</i>	13	13	0.01	23	9.29	131.2	0.117	17.65	133.7	0.092
<b>Galbulidae</b>										
<i>Galbula albirostris</i>	35	21	-0.55	54	5.26	18.3	0.142	10.85	17.9	0.167
<b>Bucconidae</b>										
<i>Bucco capensis</i>	4	4	0.61	22	7.24	50.6	0.156	-	-	-
<i>Malacoptila fusca</i>	8	25	1.11	-	7.04	44.5	0.164	-	-	-
<b>Falconidae</b>										
<i>Micrastur gilvicollis</i>	6	4	-0.51	24	-	212.9	-	20.70	212.9	0.122
<b>Thamnophilidae</b>										
<i>Frederickena viridis</i>	0	9	2.38	56	7.57	66.3	0.117	-	-	-
<i>Thamnophilus murinus</i>	17	16	0.04	36	4.88	17.5	0.083	-	-	-
<i>Thamnomanes ardesiacus</i>	31	103	1.07	45	5.22	18.6	0.132	-	-	-
<i>Thamnomanes caestus</i>	49	75	0.73	45	5.02	16.7	0.124	9.30	17.6	0.018
<i>Epinecrophylla gutturalis</i>	14	57	1.50	-	3.25	8.5	-0.109	-	-	-
<i>Myrmotherula axillaris</i>	14	24	0.41	60	3.28	7.0	-0.037	6.90	7.7	-0.048
<i>Myrmotherula longipennis</i>	11	62	1.29	47	3.52	7.9	-0.005	-	-	-
<i>Myrmotherula menetriesii</i>	6	32	1.63	44	3.23	7.6	-0.079	-	-	-
<i>Hypocnemis cantator</i>	43	42	0.16	47	4.20	11.5	0.060	8.28	11.8	0.012
<i>Pernostola rufifrons</i>	76	41	-0.57	51	5.39	27.3	0.049	-	-	-
<i>Myrmelastes leucostigma</i>	4	8	1.07	-	5.04	22.6	0.038	-	-	-
<i>Mymoderus ferrugineus</i>	7	13	1.06	55	4.68	23.5	-0.050	9.30	24.9	-0.079
<i>Myrmornis torquata</i>	0	9	2.55	41	5.13	43.0	-0.140	-	-	-
<i>Pithys albifrons</i>	157	325	0.65	-	4.80	19.5	0.031	8.70	20.1	-0.086
<i>Gymnophythys rufigula</i>	51	133	1.03	64	4.88	26.4	-0.044	9.65	29.1	-0.085
<i>Willisornis poecilinotus</i>	49	154	0.68	56	5.08	16.3	0.142	9.88	16.8	0.090
<b>Conopophagidae</b>										
<i>Conopophaga aurita</i>	8	5	0.18	-	5.54	22.1	0.137	10.35	23.8	0.040
<b>Formicariidae</b>										
<i>Formicarius colma</i>	13	38	0.95	49	6.01	45.3	0.002	11.45	46.3	-0.045
<b>Furnariidae</b>										
<i>Sclerurus mexicanus</i>	0	6	2.43	42	4.48	24.0	-0.098	-	-	-
<i>Sclerurus rufigularis</i>	1	21	2.58	-	4.29	21.6	-0.111	-	-	-
<i>Certhiasomus stictolaemus</i>	2	45	2.82	48	4.17	17.0	-0.066	-	-	-
<i>Deconychura longicauda</i>	0	9	2.62	40	4.77	26.7	-0.067	8.90	29.1	-0.167
<i>Dendrocincla merula</i>	14	44	0.75	-	5.80	51.7	-0.073	-	-	-
<i>Dendrocincla fuliginosa</i>	20	19	0.13	39	5.96	41.1	0.025	10.63	40.2	-0.080
<i>Glyphorhynchus spirurus</i>	229	204	0.13	39	3.70	13.4	-0.112	7.63	13.7	-0.111
<i>Dendrocolaptes certhia</i>	8	3	-0.27	24	6.87	61.7	0.043	13.93	66.6	0.050
<i>Hylexastest perrotii</i>	3	6	0.77	35	7.31	109.2	-0.067	-	-	-
<i>Xiphorhynchus pardalotus</i>	40	50	0.37	35	4.95	35.2	-0.116	-	-	-
<i>Campylorhamphus procurvoides</i>	3	5	1.01	22	4.30	34.3	-0.246	-	-	-
<i>Xenops minutus</i>	16	20	0.38	34	3.28	11.4	-0.183	6.38	12.3	-0.259

(Continued)

Species or family	Degraded forest captures	Primary forest captures	Vulnerability <sup>1</sup>	Mean dawn song <sup>2</sup>	Absolute eye size <sup>3</sup>	Mass <sup>4</sup>	Relative eye size <sup>5</sup>	Average transverse diameter <sup>6</sup>	Mass <sup>7</sup>	Relative eye size (Ritland) <sup>8</sup>
<i>Philydor erythrocerum</i>	3	8	1.36	57	4.09	21.1	-0.151	8.10	23.9	-0.206
<i>Clibanomis rubiginosus</i>	1	15	2.39	-	5.32	36.5	-0.054	-	-	-
<i>Automolus ochrolaemus</i>	14	1	-1.09	-	4.86	32.7	-0.110	9.80	34.1	-0.115
<i>Automolus infuscatus</i>	18	44	0.71	45	4.74	31.3	-0.122	10.10	31.6	-0.063
<i>Corythopsis torquatus</i>	2	32	2.94	46	4.15	14.5	-0.023	8.93	14.9	0.023
Tyrannidae										
<i>Mionectes macconnelli</i>	52	88	0.57	-	3.76	11.7	-0.056	8.25	12.3	-0.002
<i>Rhynchocyclus olivaceus</i>	10	9	0.26	-	4.58	18.9	-0.005	10.30	20.0	0.084
<i>Platyrinchus saturatus</i>	0	37	3.61	-	4.19	9.5	0.115	-	-	-
<i>Platyrinchus coronatus</i>	8	42	1.69	48	4.20	8.0	0.169	8.65	8.5	0.148
<i>Onychorhynchus coronatus</i>	2	10	1.82	-	4.51	14.2	0.065	9.05	14.0	0.055
<i>Myiobius barbatus</i>	7	54	2.15	-	4.06	9.9	0.069	8.70	10.2	0.104
<i>Terenotriccus erythurus</i>	11	9	-0.20	-	3.42	6.7	0.019	7.85	6.6	0.122
<i>Attila spadiceus</i>	5	13	1.19	29	6.06	32.9	0.109	12.70	33.4	0.150
Pipridae										
<i>Corapipo gutturalis</i>	4	33	2.31	50	3.41	7.5	-0.019	7.15	8.1	-0.029
<i>Lepidobthrix serena</i>	71	51	-0.15	54	3.68	9.6	-0.019	8.00	10.5	0.012
<i>Manacus manacus</i>	5	1	0.04	-	4.18	15.3	-0.031	8.55	15.7	-0.035
<i>Dixiphia pipra</i>	274	165	-0.29	62	4.32	12.7	0.057	8.55	11.4	0.055
<i>Ceratopira erythrocephala</i>	88	14	-1.41	45	4.16	11.8	0.041	8.45	11.5	0.040
<i>Schiffornis olivacea</i>	2	40	2.69	68	5.83	33.5	0.065	12.15	33.6	0.104
Vireonidae										
<i>Tunchiornis ochraceiceps</i>	2	43	2.91	53	3.49	9.5	-0.067	7.70	10.0	-0.013
Troglodytidae										
<i>Microcerculus bamba</i>	1	5	1.82	-	4.56	16.7	0.028	-	-	-
<i>Cyphorhinus arada</i>	1	19	2.75	66	4.26	19.8	-0.089	8.70	20.2	-0.088
Poliptilidae										
<i>Microbatas collaris</i>	0	44	3.59	58	3.93	10.4	0.022	-	-	-
Turdidae										
<i>Turdus albicollis</i>	59	49	-0.04	56	6.12	47.5	0.006	12.50	49.2	0.026
Thraupidae										
<i>Tachyphonus surinamus</i>	37	35	0.02	49	4.49	20.1	-0.044	-	-	-
<i>Lanio fulvus</i>	0	7	2.54	51	4.93	25.1	-0.016	-	-	-
Cardinalidae										
<i>Cyanoloxia cyanoides</i>	4	7	0.93	-	4.61	24.7	-0.078	-	-	-

<sup>1</sup>Vulnerability estimates are derived from level one of the hierarchical Bayesian model.

<sup>2</sup>Mean time of first song measured in minutes past nautical twilight (time 0).

<sup>3</sup>Maximum pupil diameter (mm) estimates measured from portrait photographs of live birds.

<sup>4</sup>Body mass (g) at the time of capture for birds with photographed eyes.

<sup>5</sup>Residuals from a linear regression of log (maximum pupil diameter) on log (body mass).

<sup>6</sup>Average between minimum and maximum transverse eye diameters (mm) in Ritland (1982).

<sup>7</sup>Average species-specific body mass (g) from Johnson and Wolfe (2017).

<sup>8</sup>Residuals from a linear regression of log (average transverse eye diameter) and log (body mass) in the preceding column.