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SPACE USE, DIURNAL MOVEMENT, AND ROOSTING OF A VARIEGATED ANT-PITTA (*GRALLARIA VARIA*) IN CENTRAL AMAZONIA

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Abstract · The Variegated Antpitta (*Grallaria varia*) is the largest member of the terrestrial insectivores guild within its Amazonian range. Despite the bird's large size and loud vocalizations, however, basic aspects of *G. varia*'s natural history remain poorly understood. In this study, we conducted intensive tracking of one individual in a nature reserve in the state of Amazonas, Brazil, describing - for the first time with radio telemetry - space use, movement patterns, and roosting sites of *G. varia*. Over the course of 50 days in July and August 2017, the tracked individual moved slowly through a home range covering ~ 17.6 ha and was generally quiet, singing at only two of 68 locations that together comprised its home range. Of five roosting sites, four included visual observations where the bird slept 3–7 (mean 4.5) m aboveground in relatively open mid-story trees. We found no evidence of commutes to regular roost sites as all nocturnal locations were located close (mean 59.6 m, range 24–101 m) to the most recent diurnal locations. Slow movements on the ground without commutes to foraging or roosting sites help explain low capture rates in mist nets for this species. Our telemetry data suggest that *G. varia* home range may be larger than previously estimated in studies that relied heavily on bird vocalizations to determine area needs, though such methods may yield adequate results at times when birds vocalize frequently. Regardless, large area requirements help to explain the disappearance of *G. varia* documented in tropical forest fragments.

Resumo · Uso do espaço, movimento diurno e áreas de dormitório do tovacuçu (*Grallaria varia*) na Amazônia Central

O tovacuçu (*Grallaria varia*) é o maior dos insetívoros terrestres dentro da sua distribuição na Amazônia. Apesar do seu tamanho e vocalizações altas, alguns aspectos básicos da história natural de *G. varia* ainda são pouco compreendidos. Neste estudo, nós realizamos o rastreamento intensivo de um indivíduo em uma reserva natural no estado do Amazonas, Brasil, descrevendo - pela primeira vez com rádio-telemetria - o uso do espaço, padrões de movimento, e poleiros noturnos de *G. varia*. Durante 50 dias em julho e agosto de 2017, este indivíduo de *G. varia* moveu-se lentamente na sua área de vida (cobrindo aproximadamente 17,9 ha) geralmente em silêncio, cantando somente em duas das 68 localizações que, juntas, formam sua área de vida. Dos cinco poleiros noturnos encontrados, quatro incluíram observações visuais onde a ave dormiu de 3 a 7 (média 4,5) m acima do solo, em um ambiente relativamente aberto no sub-bosque. Não encontramos evidência de viagens regulares para poleiros usados a noite, uma vez que todos os poleiros noturnos estavam perto (média 59,6; amplitude 24–101 m) das localizações diurnas mais recentes do indivíduo. Mo-vimentos lentos no solo, sem deslocamentos para sítios de forrageamento ou poleiros noturnos, ajudam a explicar a baixa taxa de captura em redes-de-neblina para esta espécie. Os dados de telemetria sugerem que a área de vida de *G. varia* é maior do que se estimava previamente em estudos que se baseavam principalmente em vocalizações para determinar o seu tamanho, embora tais métodos possam produzir resultados adequados quando as aves vocalizam com frequência. O requerimento de grandes áreas de vida ajuda a explicar o desaparecimento de registros de *G. varia* em fragmentos de floresta tropical.

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INTRODUCTION

Terrestrial insectivorous birds have consistently been identified as one of the most vulnerable guilds to anthropogenic habitat alteration, a trend that has been confirmed throughout the tropics world-wide (Renjifo 1999, Stratford & Stouffer 1999, Canaday & Rivadeneyra 2001, Shankar Raman & Sukumar 2002, Newmark 2006, Cleary et al. 2007). Species in the Grallariidae, a predominantly South American family, typically form a core component of any Neotropical terrestrial insectivore community. Although *Grallaria*, the most speciose genus in the family Grallariidae, reaches peak diversity in the Andes, only a single member of this genus - the Variegated Antpitta (*G. varia*) - occupies a wide swath of lowland forests in Amazonia, as well as a disjunct range in the Atlantic Forest (Ridgely & Tudor 1994, Krabbe & Schulenberg 2003).

Despite the fact that *G. varia* has been labeled as a "conspicuous" and "common" terrestrial insectivore in the *terra firme* forests of Central Amazonia, its shy and retiring habits seldom allow it to be seen, and it is almost never captured in mist nets (Ridgely & Tudor 1994, Stouffer 2007). As such, very little is known about the basic natural history of this species. For example, there are few published estimates of density and territory size, and those that exist vary substantially across the Guiana Shield (Thiollay 1994, Stouffer 2007, Johnson et al. 2011). In French Guiana, Thiollay (1994) noted that *G. varia* is present at very low densities (1.5 pairs 100 ha^{-1}), due to the species' large, isolated territories. Farther southwest at the Biological Dynamics of Forest Fragments Project (BDFFP), ~ 80 km north of Manaus, Brazil, two estimates from the same primary forest reserve suggest that density is much higher there: 7.5 pairs 100 ha^{-1} and 6.5 pairs 100 ha^{-1}, with territories averaging 8–9 ha (Stouffer 2007, Johnson et al. 2011). A potential limitation of these estimates, however, is that they were not derived from tracking tagged birds but from spot-mapping vocalizing individuals, which has been shown to drastically underestimate territory size and may not accurately reflect the bird's space use (Anich et al. 2009, Streby et al. 2012).

Species-specific patterns of space use (e.g., area requirements) and mobility have important consequences for persistence in fragmented rainforests, and these data are particularly critical for members of vulnerable guilds like terrestrial insectivores (Lens et al. 2002, Ferraz et al. 2007). Here, we describe the space use, movement, and roosting ecology of a single radio-tracked *G. varia*. Our objectives were to a) quantify movement and space use of *G. varia*, and b) describe this species' roosting ecology.

METHODS

Study area. This study was conducted at reserve 1501 (also called "Km41") at the Biological Dynamics of Forest Fragments Project in the state of Amazonas,

Brazil. The BDFFP spreads over 1000 km^2 of *terra firme* forest along the southern edge of the Guiana Shield, typified by low relief with scattered, narrow stream valleys (see Laurance et al. 2018 for a more detailed description of the study area). Reserve 1501 is situated within continuous primary forest, with a narrow dirt access road (ZF-3) to the south the only visible signs of local disturbance. Several abandoned farms abut ZF-3 to the east and west, whereas to the north, the forest stretches undisturbed for 45 km until bisected by a paved road (AM-240). Within the reserve, a 100-m grid of trails has been in place since the 1980s, although most of the network is currently overgrown.

Capture and tracking. We trapped one *G. varia* using playback of conspecific vocalizations on 5 July 2017. Once we detected the target bird, capture effort was substantial, comprising 8.5 hours of playback over two days near open mist nets. Each time we initiated playback, the target bird appeared instantly, but stayed within the mid-story (~ 10 m high), where it remained and sang for the duration of trapping effort. Following capture, we banded and outfitted the bird with a VHF radio transmitter (1.5 g, Pip Ag392, Lotek Wireless, Newmarket, Ontario, Canada) fastened to the bird's back with the leg-loop harness method (Rappole & Tipton 1991). We used 2 mm-wide tubular Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania, USA) for the harness, ensuring proper fit by adjusting the harness on the bird and then crimping the ribbon ends together with a metal leader sleeve (#3, American Fishing Wire, Coatesville, Pennsylvania, USA). Though this approach does not allow early tag self-detachment following culmination of fieldwork, it provides lightweight, nonabrasive harness, that is custom-fitted to the bird while preventing premature tag loss. The entire tag was ~ 1% of body weight (lighter than is generally recommended), which - especially for a resident, terrestrial species - likely caused little inconvenience to the bird. *Grallaria varia* is sexually monochromatic, but the strong, vocal response to playback may indicate that it was a male; however, the lack of external breeding characters makes sex determination based solely on song dubious, as the literature suggests that female *Grallaria* also sing (Krabbe & Schulenberg 2003, Kikuchi 2009). Feather attributes suggested that the bird was in definitive basic plumage (i.e., an "adult"; Johnson & Wolfe 2017).

We tracked the bird using radio telemetry over a 50-day interval starting 6 July 2017 and ending 24 August 2017. We began telemetry 31 hours after capture in order to ensure that the bird had sufficient time to resume normal activities. We assumed that there were no adverse effects of the capture and harness, as the bird appeared to move without trouble and, when prompted with conspecific song playback on 18 July, flew up into the forest mid-story and sang incessantly, just as prior to trapping. During diurnal tracking, we homed in on the bird's signal using a

combination of a three-element Yagi antenna and a receiver (R410, Advanced Telemetry Systems, Isanti, Minnesota, USA). Because the bird appeared to be wary of our presence, we employed short-distance triangulation (≤ 50 m) as outlined in Jirinec et al. (2015). In an attempt to allow for the biological independence of location data (Barg et al. 2005), we elected to leave a minimum of 20 min between subsequent relocations. This interval ranges widely in movement studies and has been set, for example, at 60 s to 20 min in studies of other passerines (Barg et al. 2005, Anich et al. 2009, Jirinec et al. 2015), with highly mobile species tracked over shorter intervals. Our tracking data eventually revealed that 20 min is much too short to meet the biological independence assumption for *G. varia* (see Results). To account for any daytime variation in space use (Anich et al. 2012), we recorded at least one location during each hour between 06:00 h and 18:00 h AMT. We recorded whether the bird was silent or vocalizing for each diurnal location.

Additionally, we located the bird at night on five occasions. Nocturnal tracking was conducted on nights 15, 17, 19, 20, and 43 of the diurnal tracking interval. We initiated tracking at least one hour after sunset and completed it by midnight. In order to describe the roosting habitat, height, and whether the bird was solitary, we approached the roost site in an attempt to directly observe the sleeping bird. This was impossible during only one of these nights, as the bird slept in a densely vegetated area and we were therefore forced to triangulate the bird's position from adjacent trails. To better examine if *G. varia* commutes to roosts away from diurnal use areas (e.g., Jirinec et al. 2015), we recorded at least one diurnal location on the day prior to nocturnal tracking.

Analysis. We used tracking data to estimate *G. varia* home range with the minimum convex polygon (MCP) as well as the 95% isopleth of the fixed kernel density estimation (KDE). Every location was used to construct home ranges with both methods. All movement analyses were done in R version 3.4.1 (R Core Team 2017), with packages adehabitatHR version 0.4.14 and adehabitatLT version 0.3.21 (Calenge 2006), and visualized in a Geographic Information System (ArcMap 10.5; ESRI, Redlands, California, USA). For the KDE home range, we used least squares cross-validation as the bandwidth selection method (Gitzen & Millspaugh 2003). Home range area, distance to roost, and elevation descriptions were calculated in ArcMap.

RESULTS

We obtained 68 diurnal locations for home range estimation. Tracking was spread over 23 discrete days during July and August 2017, with a mean of 3.0 locations per tracking day (range 1–9). Considering the entire tracking interval (6 July to 24 August), the

elapsed time between successive observations was (mean ± SE) 17.5 ± 8.1 hours (range 0.3–512.4 hours). Daytime tracking revealed little distance between consecutive relocations (63.0 ± 8.4 m, range 3.5–322.1 m), with slow travel times (49.4 ± 6.1 m h^{-1}, range 0.2–219.5 m h^{-1}), as the bird generally remained within a small area during any given tracking day. Only once we observed a relatively "rapid" movement between locations (106 m in 29 min). We never obtained a visual observation during daytime tracking as the study individual proved to be remarkably reclusive and aware of observer presence at a distance of ~ 30 m, at which point the bird started moving away, unseen.

Home range size differed between the MCP and KDE methods (Figure 1). The MCP (17.6 ha) was over twice the area of the KDE home range (8.3 ha). However, the movement pattern depicted in Figure 1 along with autocorrelation in bird positions suggest the MCP is a better model of the true home range size: the MCP includes areas the bird certainly traversed, yet they are excluded by the 95% KDE isopleth.

Home range topography generally contained little relief. Using a digital elevation model with 30-m resolution, the lowest and highest points of the MCP and KDE ranged from 110–134 m and 106–134 m, respectively. The bird did not use deeper streamcuts along the northern and western edges of the home range.

The bird was almost always silent during daytime tracking, vocalizing only twice (3%) out of the 68 times that we located it. Both of those instances occurred during late August (20th and 23rd), ~ 20 min before sunset (we have 12 additional non-vocal locations within one hour of sunset). The bird sang repeatedly at these two points, 369 m apart, which both represent vertices of the MCP (Figure 1), suggesting vocal defense of a territory boundary (though we did not detect any conspecifics vocalizing nearby during tracking).

We obtained five nocturnal locations on five separate nights for roost site description. Of these, four were visual observations where we recorded roost characteristics. In each instance, the bird was confirmed sleeping alone in a mid-story tree perched on one leg (Figure 2), 3–7 (mean 4.5) m aboveground, at least 1 m away from the trunk. The roost perch was generally situated away from vegetation cover (Figure 2).

We observed the bird to be sleeping close to the last diurnal location we recorded on the day prior to nocturnal tracking (Figure 1; mean 59.6 m, range 24–101 m). These last points were recorded 0.9–8.0 (mean 3.3) hours before sunset. Though we approached the roost site slowly and quietly, the bird twice flushed from its perch, landing in the mid-story nearby and continuing to sleep there. This happened when the observer was ~ 10 m away, prompting us to spotlight the roost from 30–40 m away on subsequent nights.
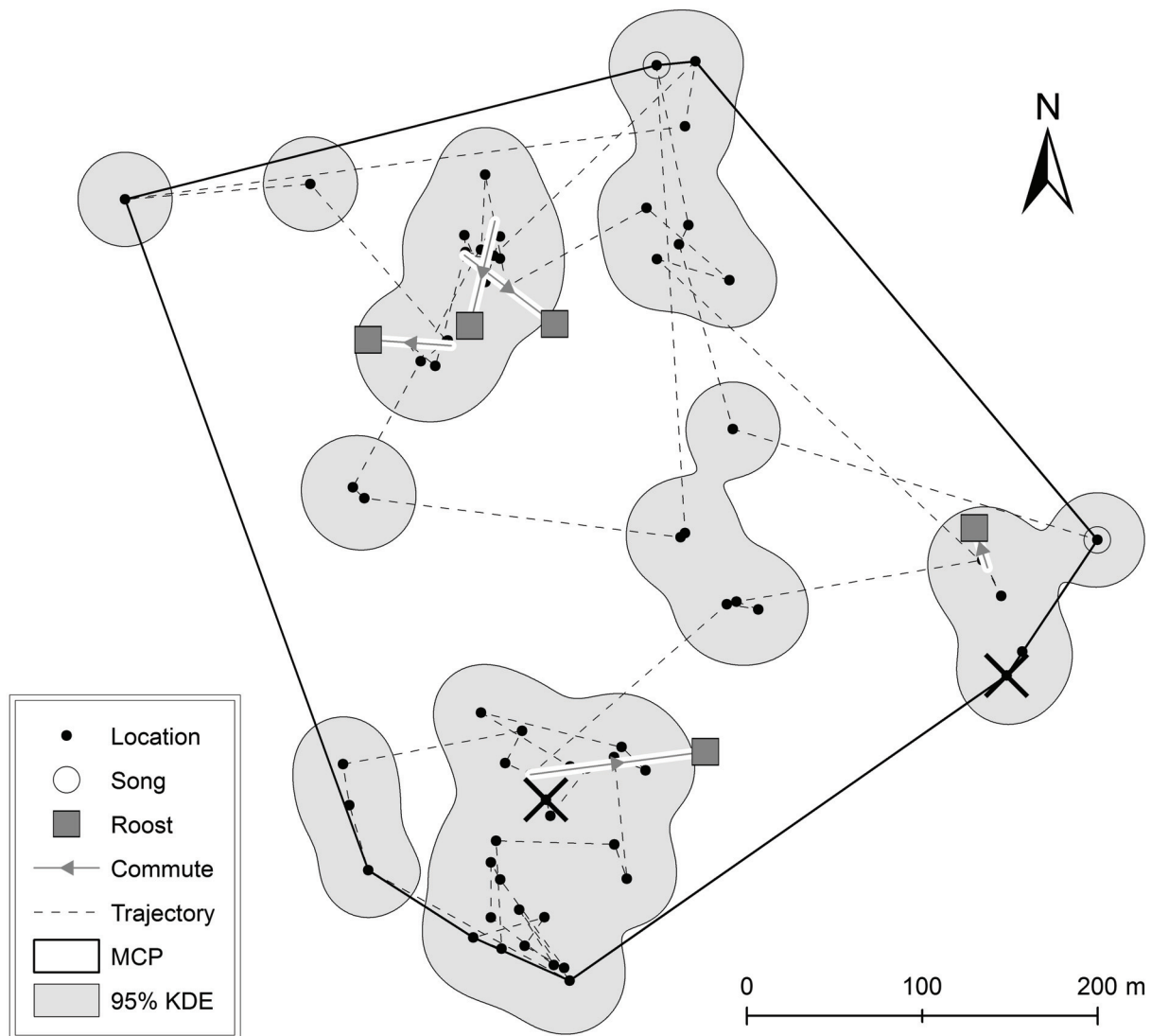
Figure 1. Space use of a Variegated Antpitta (*Grallaria varia*) at the Biological Dynamics of Forest Fragments Project, in the state of Amazonas, Brazil, between 6 July and 24 August 2017. We estimated the home range with the bird's locations (black points) using the minimum convex polygon (MCP; 17.6 ha) and 95% fixed kernel density estimation (KDE; 8.3 ha). Circles denote locations at which the bird was singing at the time of detection; sequential locations are connected with a dashed line (trajectory) starting in the southwest (left cross) and ending in the southeast (right cross). We also found roost sites (squares), and connected each roost with the last diurnal location recorded on the day prior to its respective roost (gray arrows).

DISCUSSION

Movement patterns are important ecological aspects of any organism, because they reveal space use, area requirements, and territoriality, among others. For the elusive *G. varia*, the largest regional member of sensitive terrestrial insectivores, this information has previously been derived through coarser techniques such as spot-mapping. Despite our very small sample size (N = 1), this is the first time that space use and movement patterns have been obtained for this species using high-resolution radio telemetry. Additionally, we provide the first description of *G. varia* roosting ecology, which remains unstudied for most diurnal birds (Jirinec et al. 2015).

The home range size for this individual was larger than previously published estimates for *G. varia*. The

MCP home range area of 17.6 ha is about twice the size of other *G. varia* home range estimates from the BDFFP (Stouffer 2007, Johnson et al. 2011). These studies, however, employed spot-mapping, a technique that relies heavily on vocalizations of target birds. Despite being within ∼ 50 m of the study bird while tracking, we never saw our study bird and only encountered it vocalizing twice (3% of locations; Figure 1). Spot-mapping would severely underestimate home range size under these circumstances, but might fare better during the species' periods of high vocal activity. It is possible that our *G. varia* vocalized more outside telemetry sessions, such as before dawn or after sunset. Overall, *G. varia* appeared to vocalize more frequently in May at our site, before we began radio tracking, when we often detected several singing individuals at dawn and dusk. This coincides

Figure 2. Roosting Variegated Antpitta (*Grallaria varia*) at the Biological Dynamics of Forest Fragments Project, state of Amazonas, Brazil, on 25 July 2017. This image depicts a typical roosting position, sleeping perched on one leg on a relatively exposed horizontal branch. Photo by Vitek Jirinec.

with the end of the wet season here (Stouffer et al. 2013), a likely period of peak breeding activity for *G. varia* at the BDFFP, when birds may be defending territories more actively. Supporting evidence from the BDFFP comes from two nests with nestlings in June (Quintela 1987, PCS pers. observ.), along with juveniles and adults with brood patches captured in June and July (Johnson & Wolfe 2017). We found no evidence of breeding activity for our bird, though it is likely that external breeding characters may have disappeared by the date of capture. The bird did concentrate space use in the southwestern part of its home range 6–20 July (locations 1–28) before moving north (Figure 1), but we never detected a nest, fledglings, or a second adult. Regardless of the pattern driving singing activity, spot-mapping singing adults likely only reveals the bird's territory - the actively defended area (Noble 1939) - which could be smaller than all used areas, the definition of home range we employ

here (Burt 1943). However, when compared to spot-mapping, radio telemetry is clearly the more expensive option. If the goal of the researcher is to describe space use without radio-tagging birds, fieldwork should probably coincide with the breeding season.

We selected the MCP as the best home range model for our bird for two reasons. First, the MCP included areas that our bird must have traversed, but our tracking schedule missed (Figure 1). Second, the bird's slow travel resulted in highly auto-correlated locations much beyond our 20-min tracking interval, violating the location independence assumption for conventional KDE estimates (Worton 1989). *Grallaria varia* movement pattern would lend itself well to analysis using Brownian bridge kernels, which account for time and distance between consecutive locations (Horne et al. 2007). However, for optimal home range estimation, such analysis requires relatively constant time lag between relocations (Horne

et al. 2007). Due to logistics of remote fieldwork, large gaps in radio tracking were, unfortunately, unavoidable.

Published estimates for congeners derived through radio tracking are all much smaller than our home range estimate for *G. varia*. Kattan & Beltran (2002) described home range sizes of 4.1 ha for *Grallaria milleri* (N = 1), 1.9 ha for *G. ruficapilla* (N = 1)*,* 1.4 and 1.5 ha for *G. rufocinerea* (N = 2), 4.5 ha for *G. squamigera* (N = 1), and 9.3 ha for *G. nuchalis* (N = 1). These, notably, are all Andean species (but also are smaller than *G. varia*) and our results with *G. varia* are consistent with the trend of larger territory sizes (and subsequently lower densities) for lowland terrestrial insectivores in comparison with montane species (Kikuchi 2009).

Overall, *G. varia* movement patterns are consistent with low capture rates in mist nets, which also contributes to difficulty estimating its abundance, space use, and response to forest fragmentation. The BDFFP bird banding database contains nearly 70,000 records collected over almost four decades throughout the BDFFP landscape. Despite being labeled as common in continuous forest at the BDFFP (Stouffer 2007), the database contains only 46 (0.07% of all records) *G. varia* captures. When we examined captures from continuous forest in the 1980s, the period with most intensive sampling in continuous forest, we calculated a capture rate of 0.15 *G. varia* per 1000 mist net hours (PCS unpubl. data). Although we never directly observed our radio-tagged bird, the signal pattern suggests it moved slowly and traveled primarily along the ground. Only once did it seem possible that the bird used flight to move between successive locations. We did not quantify vegetation structure within the home range, but areas used appeared to contain enough understory vegetation to conceal the bird, despite the forest floor being relatively open. Slow terrestrial travel and (possibly) avoiding open areas likely enables the species to routinely avoid mist net capture, corroborating earlier warnings that mist net data can be inaccurate for assessing abundance of some species (Remsen & Good 1996). This study suggests *G. varia* home range can be large - a finding consistent with other studies of radio-tracked terrestrial insectivores from lowland Amazonia (Stouffer 2007). Such a pattern of large area requirements helps to explain the disappearance of terrestrial insectivores from tropical forest fragments based on mist net data and other sampling techniques (Stouffer & Bierregaard 1995, Stratford & Stouffer 1999).

Roosting observations of *G. varia* suggest the species is arboreal during the nocturnal hours. All visually confirmed roost sites revealed the bird to be sleeping in the mid-story at least 3 m aboveground. Unlike other studies of roosting passerines, where birds selected densely vegetated areas, presumably for cover from nocturnal predators (Smith et al. 2008, Townsend et al. 2009; Jirinec et al. 2011, 2015; Rimmer et al. 2017), *G. varia* appeared to roost in relatively exposed perches, often visible via spotlight from > 30 m away. Warm nocturnal temperatures in the lowland tropics suggest that roosting habitat selection should not be driven by thermoregulatory requirements, leaving predation as the likely selective pressure to determine where birds sleep. With a mean mass of 120.1 g (Johnson & Wolfe 2017), *G. varia* may be too large for predatory *Vampyrum spectrum* bats and small owls, but could be vulnerable to the four species of large owls that inhabit the primary forests of the BDFFP (Rutt et al. in press). However, virtually nothing is known about where tropical birds sleep, much less the factors shaping roosting habitat selection. It is possible that non-volant mammals or arboreal snakes are more dangerous for roosting birds in Central Amazon than more visual predators such as owls. If the landscape of fear - a concept where variation in environmental predation pressure shapes prey behavior to minimize the probability of being depredated (Laundre et al. 2010) - does not vary substantially across a bird's home range as long as it is above ground, one would not predict costly commutes to roosts. We did not find evidence of such commutes to roosts in *G. varia*, unlike in previous studies that found other species moving to consistent roosts, choosing a site that contained vegetation features different from diurnal use areas (Smith et al. 2008, Townsend et al. 2009; Jirinec et al. 2011, 2015). Although we twice alarmed the bird at its roost, we did not find evidence that such disturbance had an effect on subsequent roosting location, as the bird slept in a different place each night. Still, we cannot rule out the existence of roosting habitat selection, as we did not quantify vegetation structure at roost sites in comparison to availability. Furthermore, it is possible the bird stays near, or slowly moves to, optimal roost sites towards the end of the day. Even if that were the case, we saw no evidence of returns to regular roosting areas, as appears to be common for birds in Neotropical mixed-species flocks that gather at consistent locations to begin their daytime movements (Jullien & Thiollay 1998, Mokross et al. 2014).

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