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Intra- and inter-specific territorial response of diurnal raptors in the tropical dry forest of western Mexico

Respuesta territorial intra- e interespecífica de rapaces diurnas en el bosque tropical seco

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Abstract

Little is known of intra- and inter-specific territoriality in Neotropical raptors that may defend territories throughout the year, and face greater inter-specific competition for resources. We evaluated intra- and inter-specific territorial responses of four species of Neotropical raptors in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve, Mexico. We conducted broadcast calls in territories of the Collared Forest-Falcon (*Micrastur semitorquatus*), Crane Hawk (*Geranospiza caerulescens*), Gray Hawk (*Buteo plagiatus*), and Roadside Hawk (*Rupornis magnirostris*), and measured the latency, duration, and type of territorial response to broadcast calls of conspecifics and sympatric raptor species. We applied repeated measures analysis to determine differences in intra- and inter-specific territorial responses of raptors, and GLMMs to evaluate whether traits of body size, nest type, and hunting technique were associated with territorial response by focal raptors. Large-bodied focal raptor species showed high intra-specific territoriality, giving faster, prolonged responses of various types, including duets and combined responses, to broadcast calls of conspecifics compared to sympatric species. All focal raptors showed some inter-specific territorial response, but this was mainly as vocalizations or displacements towards sympatric species broadcast calls. Species traits of body size, nest type, and hunting technique were associated with latency and duration of territorial response by the larger raptor species that nest in the forest canopy. These traits may be more strongly associated with territorial response of forest raptors that defend limited resources in a structurally complex environment.

Keywords: Chamela-Cuixmala; Neotropical raptors; territorial behavior; tropical dry forest; sympatric raptors.

Resumen

Se conoce poco acerca de la territorialidad intra- e interespecífica de rapaces Neotropicales que pueden defender territorios durante todo el año y enfrentar una mayor competencia interespecífica por los recursos. Evaluamos la respuesta territorial intra- e inter-

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específica de cuatro especies de rapaces Neotropicales en el bosque tropical seco de la Reserva de la Biosfera Chamela-Cuixmala, Jalisco, México. Usamos provocaciones auditivas en territorios del halcón selvático de collar (*Micrastur semitortuatus*), el gavilán zancón (*Geranospiza caerulescens*), el aguililla gris (*Buteo plagiatus*) y el aguililla caminera (*Rupornis magnirostris*), y medimos la latencia, duración y tipo de la respuesta territorial hacia provocaciones auditivas de conespecíficos y rapaces simpátricas. Aplicamos análisis de medidas repetidas para determinar diferencias en la respuesta territorial intra- e interespecífica de las rapaces, y GLMMs para evaluar si los rasgos de tamaño corporal, tipo de nido y técnica de caza estuvieron asociados con la respuesta territorial de las rapaces focales. Las rapaces de mayor tamaño mostraron alta territorialidad intra-específica, con respuestas más rápidas y prolongadas de varios tipos, incluyendo duetos y respuestas combinadas, hacia provocaciones de conespecíficos comparado con rapaces simpátricas. Todas las rapaces focales mostraron alguna respuesta territorial interespecífica, dada principalmente por vocalizaciones o desplazamientos hacia provocaciones auditivas de rapaces simpátricas. Los rasgos de tamaño corporal, tipo de nido, y técnica de caza estuvieron asociados con la latencia y duración de la respuesta territorial de las rapaces de mayor tamaño que anidan en el dosel del bosque. Estos rasgos podrían estar más fuertemente asociados con la respuesta territorial de rapaces del bosque que defienden recursos limitados en un ambiente estructuralmente complejo.

Palabras clave: Chamela-Cuixmala; comportamiento territorial, rapaces neotropicales; bosque tropical seco; rapaces simpátricas.

Introduction

Competition is considered to play an important role in regulating populations of top predators (Lack 1946, Hairston et al. 1960, Schoener 1982), as given their position at the top of terrestrial food webs, large, vertebrate carnivores have no or few species that prey on them (Lourenço et al. 2013). A mathematical model developed by Berestycki and Zilio (2019) shows that strong interference competition between predators gives rise to territoriality, with increased competition for resources yielding stronger territorial behavior. Intraspecific territoriality prioritizes access to resources by establishing an hierarchy among conspecifics (Wittenberger 1981), and influences the distribution of individuals within a population (Katzner et al. 2003). On the other hand, interspecific territoriality may arise among sympatric species with similar biological traits or ecological requirements (Garcia and Arroyo 2002).

Raptors are top predator, vertebrate carnivores, the majority of which are territorial (Newton 1979, Martínez-Hesterkamp et al. 2018), and defending territories that appear to be regularly spaced (Rothfels and Lein 1983, Pandolfi and Pino 1992). In a phylogenetic analysis of 74 Paleartic and New World diurnal raptor species, Martínez-Hesterkamp et al. (2018) determined that territoriality may be the product of recent evolution in raptors, and that territorial behavior was associated with ecological predictors of prey agility, and structural complexity of nest-site protection, while territory size was significantly associated with body mass.

Intra- or inter-specific competition or territoriality is frequently cited to explain variations in nest spacing, habitat use, and diet of raptors and other species (Stamps 1994). Temperate zone raptors have been found to show greater intra-specific than inter-specific territoriality (Rothfels and Lein 1983, Bergo 1987, Garcia and Arroyo 2002), and intra-specific territoriality tends to be higher early in the breeding season during the pre-laying period (Bergo 1987, Garcia and Arroyo 2002, Margalida and Bertran 2005). Studies of temperate zone raptors have also determined inter-specific territoriality towards sympatric raptor species with similarity in diet or nest-site requirements, body size, or in behavioral characteristics (Nilsson 1984, Bertran and Margalida 2002, Garcia and Arroyo 2002).

Compared with temperate-zone raptors, little is known of the territorial behavior of Neotropical raptors, which may differ from that of temperate raptor species, given the greater diversity by unit area of tropical raptors (Bildstein et al. 1998). Resident tropical birds may also show ecological and behavioral differences to temperate species as they may defend territories throughout the year (Morton and Stutchbury 2000), and could face greater inter-specific competition for food. However, empirical evidence is required on territorial behavior, particularly in the tropics, to elucidate the factors influencing territoriality in this avian group.

We evaluated intra and inter-specific territorial responses of four Neotropical raptor species towards conspecifics and towards sympatric raptor species. Given that conspecifics represent direct competition for resources, we expected greater territorial responses towards conspecifics by our focal raptor species: the Collared Forest-Falcon (*Micrastur semitorquatus*), Crane Hawk (*Geranospiza caerulescens*), Gray Hawk (*Buteo plagiatus*), and the Roadside Hawk (*Rupornis magnirostris*). We also expected territorial responses of raptors to be associated with traits of body size, nest type, and hunting technique, since more similar sympatric species may have similar ecological requirements

Methods

Study area

We conducted the study in the Chamela Biological Station (19°29'56" N, 105°02'40" W), of the Instituto de Biología, Universidad Nacional Autónoma de México, which is located within the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico. The region comprises low-lying hills with alluvial plains along streams and rivers (Lott and Atkinson 2002), within the tropical dry forest biome (Olson et al. 2001). The dominant vegetation is tropical deciduous forest on the hills, with small patches of semi-deciduous forest in valleys and along streams (Lott et al. 1987, Lott 1993). Average annual temperature is 24.4°C, and average annual rainfall 748 mm, with a marked rainy season from July to November followed by a prolonged period of drought (Bullock 1986).

Focal raptor species

Collared Forest-Falcons, Crane Hawks, Gray Hawks, and Roadside Hawks are four of the most abundant resident raptor species in the tropical dry forest along the coast of Jalisco (Martínez-Ruiz et al. 2020). These four focal species include a range of body size and varying ecological requirements (Brown and Amadon 1968, Johnsgard 1990, Panasci 2012, Sutter 2012, Thorstrom 2012, Bibles et al. 2020). Collared Forest-Falcons (560-940 g) and Crane Hawks (495 g) are medium-sized raptors (Brown and Amadon 1968) of the forest interior (Thorstrom 2000, Sutter et al. 2001, Thorstrom 2012). Collared Forest Falcons nest in tree cavities and hunt from a perch in dense vegetation (Thorstrom 2012), while Crane Hawks build nests in the forest canopy and employ a distinctive search-and-probe hunting technique seeking prey in tree hollows, epiphytes, and behind bark (Sutton 1954, Jehl 1968, Sutter et al. 2001). Gray Hawks (364 g) and Roadside Hawks (259-284 g) were the smallest focal raptor species (Brown and Amadon 1968) that hunt from perches and construct nests in open canopy forest (Panasci and Whitacre 2000, Bibles et al. 2020, La Porte et al. 2020).

Broadcast call surveys

We located territories of focal raptor species and conducted broadcast call surveys during February to March 2020, the field season being curtailed by the COVID-19 pandemic. We conducted initial surveys in the late afternoon (1800 – 1930 H) from high vantage points to detect raptors, and determined their approximate location with a 20-60 x 78 zoom telescope (Orion, Monterey Bay, USA, Arcadia model spotting scope). At 0700 – 1200 H, we walked transects of 1 km in length at a slow speed in each of the areas where a focal raptor species had been detected from vantage point observations, and conducted broadcast calls every 500 m within the territory. The approximate center of each territory was determined as the area within the territory where most sightings or responses to broadcasts were obtained for each focal raptor species.

We then established survey stations within each territory to broadcast calls and measure intra- and inter-specific territorial responses. We broadcast calls at 300-m intervals moving from the approximate center of each territory outwards in the four cardinal directions (N, W, S, E), with each direction conducted on a different day on non-consecutive days to prevent raptors from habituating to broadcast calls. We used a maximum of 6 survey stations per route within a territory to reduce the possibility of extending too far from the approximate center of the territory. We thereby conducted broadcast calls in a total of 75 stations in 3 territories of the Collared Forest-Falcon, 28 stations in 2 territories of the Crane Hawk, 49 stations in 4 territories of the Roadside Hawk, and 46 stations in 4 territories of the Gray Hawk.

At each broadcast station, we first waited for 3 mins to locate raptors, then we broadcast vocalizations of each of four raptor species (conspecific, and three sympatric species), played in order from smallest to largest body size. A broadcast cycle for each species consisted of 30 sec of vocalizations, followed by 30 sec of silence to await a response. Finally, we waited for 3 mins at the end of the last broadcast to determine late responses (Whitacre et al. 1992). We used a game-caller speaker (FOXPRO Inc, Lewistown, PA, USA; Crossfire digital wildlife caller) set at the highest volume level to broadcast calls. The same pre-recorded vocalizations were used for all broadcast experiments, and these were call vocalizations downloaded from Xeno-Canto (https://xeno-canto.org/). We included vocalizations of the Laughing Falcon (*Herpetotheres cachinnans*) as a sympatric species for Collared Forest-Falcons, as this species also nests in tree-cavities (Parker et al. 2012). In addition, we included the Great Black Hawk (*Buteogallus urubitinga*) in broadcast calls as a sympatric large-bodied forest raptor (Gerhardt et al. 2012).

Territorial response

At each broadcast station, we recorded the time in seconds that focal raptors took to respond to broadcast calls (latency), the duration of the territorial response, and the type of response. The type of territorial response was categorized as: 1 = vocalization only, 2 = displacement towards the speaker, 3 = vocal + displacement toward speaker, and 4 = duet vocalization (Martínez-Ruiz et al. 2016). We registered an additional category of 5 when any other combination of responses was recorded. We obtained a response to at least one of the 4 broadcast calls at 36 stations for the Collared Forest-Falcon, 7 stations for the Crane Hawk, 18 stations for the Gray Hawk, and 16 stations for the Roadside Hawk. A lack of response to a broadcast call within a focal raptor's territory was recorded as 0 for type of response, and duration of response, whereas for latency we recorded 240 sec when no response was obtained, considering either the entire period of 4 broadcast cycles, or the final broadcast cycle (60 secs) plus 3 mins waiting time for a response.

Variables associated with territorial response

We determined whether territorial response was associated with traits of body size, nest-type and hunting technique, considering latency and duration of response by each focal bird within its territory towards broadcast calls of conspecifics and sympatric species. For body size, we used maximum body mass registered in Birds of the World-Cornell Lab of Ornithology (Billerman et al. 2022). Nest-type was set as a categorical variable (1 = open nests, 2 = cavity nests). Finally, we defined a categorical variable of hunting technique as: 1 = hunts from a perch, 2 = hunts from a perch and in flight with equal frequency, and 3 = search-and-probe hunting technique.

Data analysis

We performed Chi-square tests to evaluate whether frequency of type of response by each focal raptor species was significantly associated with the raptor species broadcast (conspecific and three sympatric species). We conducted two forms of repeated-measures ANOVA with post-hoc pairwise comparisons to determine differences in the latency and duration of territorial response by focal raptors to broadcast calls of conspecifics and sympatric species. We conducted repeated measure analysis by broadcast station using non-parametric Friedman ANOVA (Zar 1999). Finally, we used generalized linear mixed models to determine how traits of body size, nest-type, and hunting technique influenced territorial response of the four focal raptor species. We constructed one model for each response variable (latency and duration) of each focal raptor species, with the variables body mass, nest type, and hunting technique as predictors, and territory identity as a random variable. For these models, body mass was incorporated as a continuous variable, whereas nest type and hunting technique were categorical factors of 2 and 3 levels respectively. All analyses were conducted in R (R Core Team 2020) considering a $P < 0.05$ significance level, and we present descriptive statistics of mean with standard deviation.

Results

Intra and interspecific territorial response

Focal raptor species showed both intra- and inter-specific response to broadcast calls of conspecifics and sympatric species. However, in general focal raptors gave various types of territorial responses to broadcast calls of conspecifics, and gave mainly vocal and/or displacement responses to broadcast calls of sympatric species (Fig 1). In particular, type of territorial response by the Collared Forest-Falcon was marginally associated with broadcast species ($\chi^2_{15} = 23.95$, $P = 0.06$), with mainly vocal responses towards sympatric species, and all response types, including combined responses, to conspecifics (Fig 1). The Crane Hawk and Gray Hawk also showed a variety of responses to conspecific broadcasts, and mainly vocalizations or displacement to sympatric species broadcasts (Fig 1). Only the Roadside Hawk showed little differentiation in types of response to conspecifics and sympatric species (Fig 1).

The Collared Forest-Falcon also differed significantly in latency ($\chi^2_3 = 28$, $P < 0.001$) and duration (χ^2_3 = 16.8, P = 0.001) of response to calls at each broadcast station, responding significantly faster and for a longer period to conspecific broadcasts compared to sympatric species broadcasts (Fig 2). The Crane Hawk showed significantly longer duration (χ^2_3 = 10.6, P = 0.014) of response to broadcast calls of conspecifics compared to sympatric species (Fig 2). Only the Roadside Hawk differed significantly in latency (χ^2_3 = 8.6, P = 0.034) and duration (χ^2_3 = 11.0, P = 0.012) of response to broadcast calls among sympatric species at each broadcast station, showing a faster, longer response to broadcast calls of the Gray Hawk compared to the Great Black Hawk (Fig 2). By comparison, the Gray Hawk showed no significant difference in latency or duration of response to broadcast calls at each station.

Association of territorial response with species' traits

Body mass was a significant predictor of territorial response for the Collared Forest-Falcon, Crane Hawk, and Roadside Hawk (Table 1). Faster and more prolonged territorial responses by Collared Forest-Falcons and Crane Hawks were positively associated with greater body mass, whereas the Roadside Hawk showed delayed and shorter duration of responses towards species with larger body mass. Nest type and hunting technique were also significant predictors in territorial responses of Collared Forest-Falcons and Crane Hawks, with a delayed, shorter territorial response to cavity nesting and a perch and flight hunting technique (Table 1). However, models for the Roadside Hawk had very low explicative power (PseudoR2 <4%), while territorial response by the Gray Hawk showed no significant association with species traits.

Discussion

Our results indicate that the large-bodied focal raptor species of the Collared Forest-Falcon and the

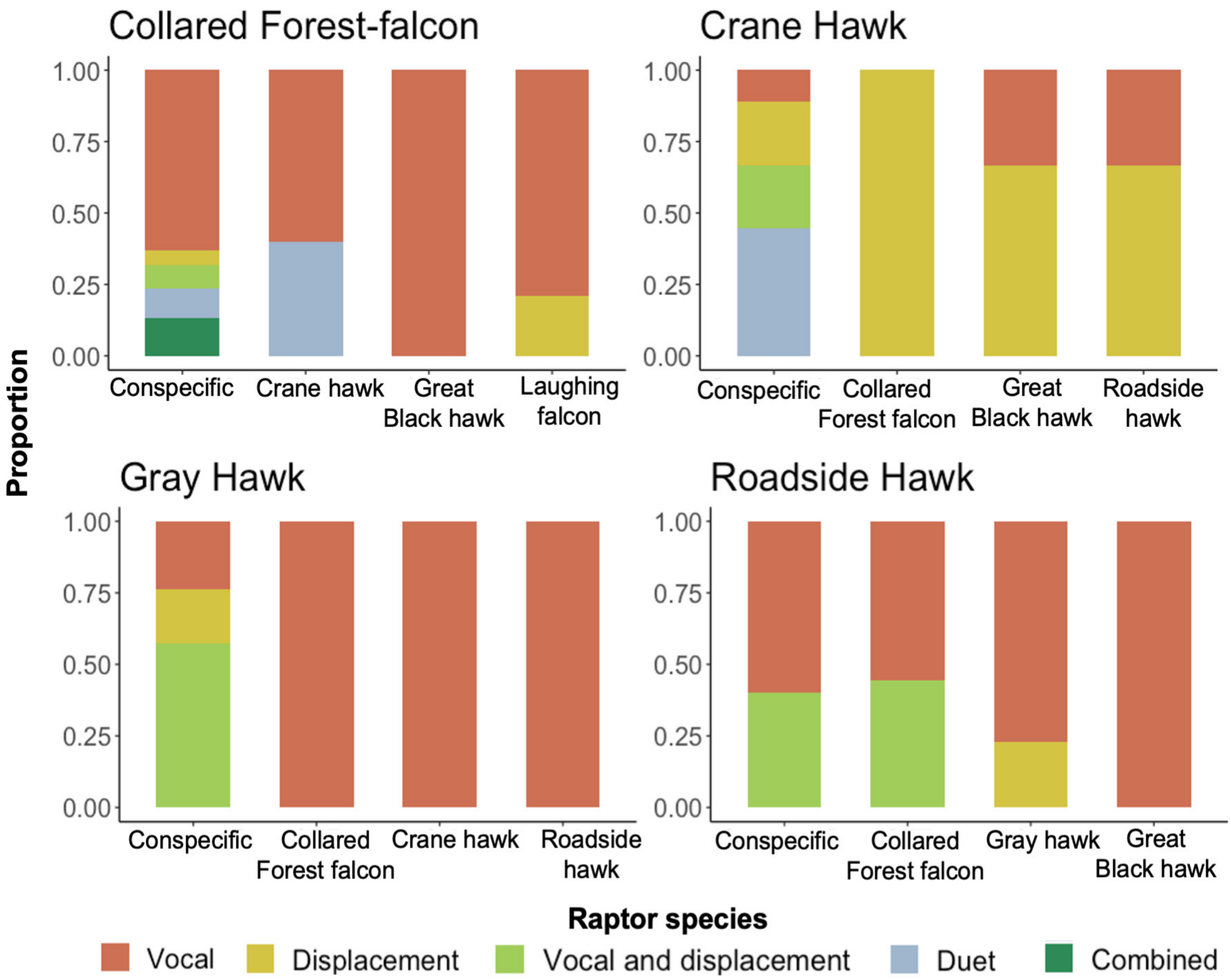

Figure 1. Proportion of types of territorial response by focal raptor species towards broadcast calls of conspecifics and sympatric raptors.

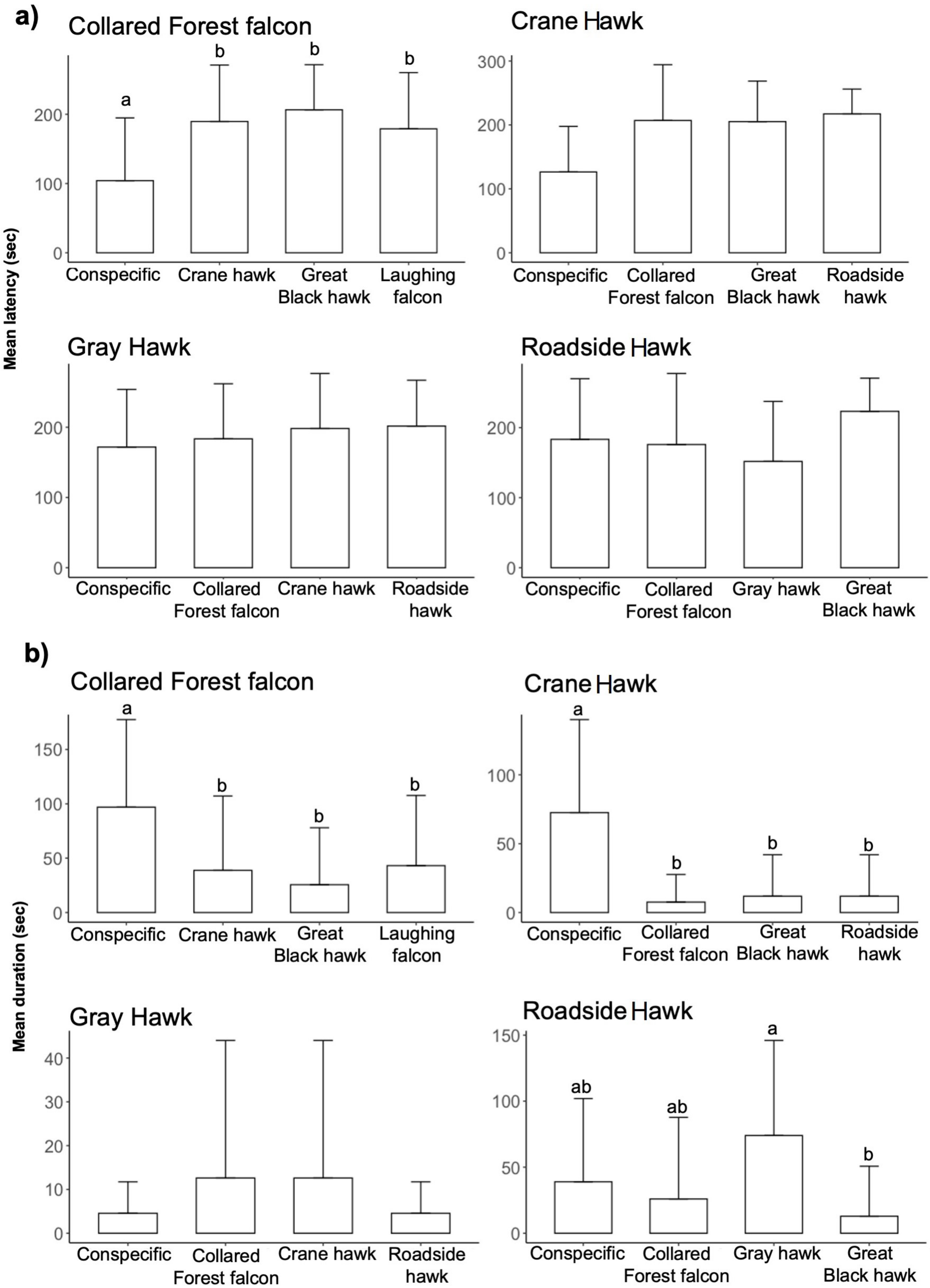

Figure 2. Mean (± SD) of latency and duration of response by focal raptors to broadcast calls of conspecifics and sympatric species. Letters above bars indicate significantly different paired comparisons.

Table 1. Results of Generalized Linear Mixed Models on the association of territorial response with species traits. Only significant predictors are shown. Std beta = Standardize beta coefficients. CI = confidence intervals. PseudoR^2 = Explanatory power of the fixed effects alone.

Response	Trait	Std beta	95% CI	*P* value	PseudoR2
Collared Forest falcon					
Latency	Body mass	-2.06	-3.29 – -0.83	< 0.001	12%
	Cavity nest	1.80	0.51 – 3.09	< 0.006	
	Hunts perch & flight	5.81	2.40 – 9.22	< 0.001	
Duration	Body mass	1.88	0.64 – 3.12	< 0.003	10%
	Cavity nest	-1.66	-2.97 – -0.35	< 0.013	
	Hunts perch & flight	-5.31	-8.77 – -1.84	< 0.003	
Crane Hawk					
Latency	Body mass	-1.67	-3.27 – -0.07	< 0.041	7%
	Cavity nest	2.03	0.23 – 3.83	< 0.028	
	Hunts perch & flight	4.21	0.34 – 8.08	< 0.033	
Duration	Body mass	1.83	0.23 – 3.42	< 0.025	7%
	Cavity nest	-2.33	-4.12 – -0.53	< 0.012	
	Hunts perch & flight	-4.68	-8.53 – -0.83	< 0.018	
Roadside Hawk					
Latency	Body mass	0.24	0.02 – 0.45	< 0.029	3%
Duration	Body mass	-0.28	-0.49 – -0.07	< 0.010	4%
	Hunts perch & flight	0.54	0.03 – 1.05	< 0.037	

Crane Hawk showed strong intra-specific response to broadcast calls, giving faster, prolonged responses of various types to broadcast calls of conspecifics compared to sympatric species. This corresponds with studies in temperate zones that report greater territorial response of raptors towards conspecifics during the breeding season (Jamieson and Seymour 1983, García and Arroyo 2002, Krüger 2002, Katzner et al. 2003). Our study was conducted during the months of February to March at the start of the nesting season for the Collared Forest-Falcon and the Crane Hawk, which have been reported to commence egg-laying in February or March (Thorstrom et al. 2000, Sutter 2012, Thorstrom 2012). Therefore, conspecifics may represent competition for nest-sites, food resources, or mates at the start of the breeding season (Bergo 1987, Garcia and Arroyo 2002, Margalida and Bertran 2005). By comparison, the smaller-bodied species of the Roadside Hawk and the Gray Hawk showed little differentiation in response to broadcast calls. However, the Roadside Hawk and Gray Hawk are reported to lay eggs in late March (Panasci 2012), and April or May (Bibles et al. 2020) respectively, therefore it may be that these species had not yet initiated breeding activity at the time our study took place, and high intra-specific response may be expected in the pre-laying period due to competition for mates (Garcia and Arroyo 2002, Margalida and Bertran 2005).

Most of the focal raptor species also had some degree of inter-specific territorial response towards sympatric species, although the Crane Hawk showed low inter-specific response, probably because this is the most distinct species among the focal raptors in this study, being the only species with a double-jointed leg enabling a unique seek-and-probe hunting technique (Bierregaard et al. 2020). It has been suggested that this singular behavior may facilitate low dietary overlap (Sutter et al. 2001), showing low territorial response to sympatric raptors. Only Roadside Hawks demonstrated differential territorial response to sympatric species, with longer duration of territorial response towards the Gray Hawk. Inter-specific territoriality may indicate competition for resources (García and Arroyo 2002), and both species have a generalist diet, hunt from perches, and construct nests in open canopy (Panasci and Whitacre 2000, Bibles et al. 2020, La Porte et al. 2020), thereby suggesting inter-specific territoriality towards species with similar ecological requirements (Both and Visser 2003).

Latency and duration of territorial response were significantly associated with species traits of body size, nest-type, and hunting technique, particularly for the two larger raptor species that nest in the forest canopy, and hunt agile prey. These traits may be important for forest-associated raptors that require large trees for nesting or as hunting perches (Thorstrom 2012), and may need to strongly defend larger territories to compensate for lower resource availability. This accords with the finding by Martínez-Hesterkamp et al. (2018) that raptors breeding in forests are more likely to be territorial, since structural complexity of nest-sites in forests that afford greater protection, and hunting of more agile prey, are strongly associated with evolution of territorial behavior.

However, we acknowledge the small sample size and spatial limitation of our study. Furthermore, many broadcast stations obtained no response from focal raptors, although it may be that the focal bird was not near some of the stations given the total distance of 1.5 km from the first broadcast station to the last on a particular route within a territory. Nevertheless, we believe that our results provide an insight to the territorial dynamics of tropical raptors, and encourage further research on territorial responses of tropical forest raptors to elucidate how this may be affected by resource availability and forest fragmentation.

In particular, the association of territorial response with body mass confirms the existence of size hierarchy in raptors. Furthermore, large-bodied focal raptor species showed high intra-specific territoriality, which may be a key factor regulating spatial distribution of conspecifics. In accordance with Martínez-Hesterkamp et al. (2018), territorial response of these raptors in the tropical dry forest was associated with traits of body size, nest-site, and hunting technique. In particular, large forest raptors that nest in the canopy showed stronger territorial response to conspecifics, possibly as they need to defend limited resources in a structurally complex environment.

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