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RESEARCH ARTICLE

Bird activity patterns in the understorey of an evergreen forest in Oaxaca, Mexico

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Abstract

Activity patterns of species are related to their physiology, their behaviour and the environment and can change in response to different factors, such as interactions between species. Bird species, typical of the understorey, show morphological and ecological similarities and must thus have some mechanism of ecological separation, such as temporal niche partitioning. The objective of this study was to provide information about activity patterns and activity overlap of bird species typical of the understorey. We expected temporal niche partitioning between ecologically-similar species. We placed camera traps in 29 sampling points in a high evergreen forest in the southeast of Mexico between 2011 and 2013. All species were mainly diurnal and, contrary to what we expected, there was temporal partitioning between tinamids, but not in galliforms and columbiforms. The degree of activity overlap might reflect a solitary or group lifestyle of the three sets of species, as well as shared behavioural preferences and similar adaptations. These results contribute to our knowledge of the basic biology and behavioural ecology of birds of the understorey.

Keywords

Activity overlap, camera traps, Columbidae, Cracidae, Tinamidae

Introduction

The activity patterns of species, that is, the time invested in rest and movement, are related to their circadian rhythm, physiology and behaviour, as well as to the environment where they develop (Ashby 1972; Kronfeld-Schor and Dayan 2003). Each species depends on these factors to adapt to the amount of light and darkness, to generate adaptive responses to environmental and their own changes and to inter- and intra-specific interactions (Bennie et al. 2014). Two species that use similar resources may avoid times when their competitors are active and minimise direct confrontation when resources are limited (Schoener 1974). The effects may be more intense when the species have taxonomic or morphological proximity (Schoener 1974; Kronfeld-Schor and Dayan 2003).

Various groups of bird species perform most of their activities at the ground level of tropical forests of the Neotropics and some of these species are morphologically, taxonomically and ecologically similar. For example, species from the orders Galliformes, Tinamiformes and Columbiformes forage at ground level, feed on fruits, seeds, leaves, shoots and arthropods, whose proportions vary with species and item availability and show a high diet overlap (Muñoz and Kattan 2007; Baur 2008; López et al. 2014). They nest and rest both on the ground and in the tree stratum and show a high overlap in the use of both strata (Baur 2008; López et al. 2014). Therefore, possible competitive interactions may be stronger between these similar species (Brooks et al. 2004; Roncal et al. 2019).

One of the regions with the most biodiverse avifauna in Mexico is Los Chimalapas, in the northeast of the State of Oaxaca. Bird diversity studies have been carried out in this region, but there are only a few ecological studies on ground-dwelling birds (Pérez-Irineo and Santos-Moreno 2017). This is a zone of difficult access with dense vegetation cover, which complicates the study of these species in such conditions. Furthermore, bird species typical of the understorey tend to be cryptic, shy and elusive (López et al. 2014; Negret et al. 2015). Camera trapping is a regular and widely-used method in bird studies and it is a useful alternative in topographically heterogeneous areas, such as Los Chimalapas.

The objective of this study was to provide information about the activity patterns and activity overlap between bird species present in the understorey of an evergreen forest. We expected temporal niche partitioning between morphologically, taxonomically and ecologically similar species as a mechanism to minimise the risk of competition. This information contributes to our understanding of how bird species respond to the presence of competitors in a dense tropical environment.

Materials and methods

Study area

The study area is in the north region of Los Chimalapas, in the Municipality of Santa María Chimalapa (17°9'N, 94°21'W), Oaxaca, Mexico. This region covers almost 6000 km^2, 64% is covered by high and medium evergreen forest and the vegetation layer comprises species of the genera *Bursera*, *Cordia*, *Dialium*, *Elaeagia*, *Guatteria* and *Ficus*, amongst others. Other important elements are palm trees of the genera

Astrocarpyum, *Desmoncus* and *Chamaedorea* and bejucos of the genera *Discorea*, as well as a wide diversity of epiphytes and ferns (Salas Morales et al. 2001). The climate is hot-humid, with a mean annual temperature fluctuating between 22 and 26 °C. The precipitation ranges from 2000 to 2500 mm (Trejo 2004) and the rainy season is from mid-May to December. The topography ranged from 100 to 2550 metres above sea level (Salas Morales et al. 2001). In the area, there were no roads in the study areas, except trails on livestock areas. The human presence was scarce (140 inhabitants) and poaching was only for local consumption. For this study, we considered twilight as the period from the beginning of dawn to the output of the sun and since the sunset until nightfall, characterised by diffuse light.

Field sampling

Sampling was carried out from March 2011 to June 2013 in 29 camera trapping stations with Wildgame (Digital Game Scouting Camera IR4 with 4MP), HCO Outdoor Products ScoutGuard SG550/SG550V Infrared Digital Scouting Camera and Bushnell Trophy Cam. We placed the camera traps on trails created by animals, edges of hills, rivers and next to grazing areas. All trapping stations were within the evergreen forest, without attractants and at a height of 30 cm above the ground. The distance between traps varied between 0.5 and 1.5 km, covering an area of 22 km^2. Each trap was programmed to remain active during 24 h and the time delay between photographs was set to a minimum of 0.3 and 1min.

Although the effect of camera trap location on the activity patterns of birds has not been evaluated, previous studies have shown that the record rate does not differ between camera traps on and off trails (Blake and Mosquera 2014). In addition, our sampling effort was adequate in order to minimise a possible bias in the number of records according to a previous study (Cusack et al. 2015). Therefore, we considered that the placement strategy in our study did not affect our results and our results reflect the activity patterns of bird species at the ground level.

Photographed species were identified using bird identification guides (Peterson and Chalif 1973; Howell and Webb 1995; Edwards 1998), the Checklist of North and Middle American Birds of the American Ornithological Society and the risk categories of the Official Mexican Norm NOM-2010-SEMARNAT (SEMARNAT 2010) and the International Union for Conservation of Nature (IUCN 2020). Photographic records were deposited in the Mammal Reference Collection of the Laboratory of Animal Ecology of the Interdisciplinary Center of Research for Integral Regional Development, Oaxaca Unit, Instituto Politécnico Nacional de México (ECOAN-MAM).

Activity pattern

In order to describe the patterns of activity, we divided the periods of 24 h into 1 h segments and classified each independent record within these intervals. An independent record was defined as all photographs belonging to the same species taken in each sampling station in a period of 1 h (Santos-Moreno et al. 2019). In the case of photos with more than one individual, we did not consider everyone as an independent record, rather, the group was considered as an independent record. We only evaluated those with 11 records or more in all analyses.

We defined three categories of activity: diurnal (07:00–19:00 h), twilight (i.e. approximately one hour before and one after sunset: 05:00–07:00 h and 19:00–21:00 h) and nocturnal (21:00–05:00 h). Each species was classified in one of these categories if at least 50% of the records corresponded to that time. If the percentage were less than 50%, then we considered it as cathemeral. Given that rainy and dry seasons can affect the activity pattern of the species, we tested significant differences between dry and rainy seasons in the species analysed through the non-parametric Mardia-Watson-Wheeler (W) test in the package Circular (Agostinelli and Lund 2017).

We compared activity overlap between pairs of species with ecological, morphological and taxonomic similarity (i.e. taxonomic group, body size, main diet; see Table 1). The independent detection records for each target species were used to estimate the proportion of activity located within that period using kernel density and to estimate the overlap coefficient (Ridout and Linkie 2009). The overlap coefficient, Δ1, ranges from 0 (no overlap) to 1 (complete overlap) and we considered the degree of overlap as three categories: low ($\Delta_1 \leq 50\%$), moderate ($50 < \Delta_1 > 75\%$) and high ($\Delta_1 \geq 75\%$), following Monterroso et al. (2014). We used 10 000 replicates

Table 1. Some characteristics of the ten recorded bird species with more than 11 records, as well as their conservation category according to the Official Mexican Norm (NOM-059) and the International Union for Conservation of Nature (IUCN), in the understorey of a high evergreen forest in Los Chimalapas, Oaxaca, Mexico. LC = Least Concern; NT = Near Threatened; SP = Special Protection; T = Threatened; V = Vulnerable.

Order Family Species	Common name	Size (cm)	Main diet	NOM-059	IUCN
Tinamiformes					
Tinamidae					
Crypturellus boucardi	Slaty-breasted Tinamou	25–28	Fruits, leaves, berries, seeds, insects	T	LC
Crypturellus cinnamomeus	Eastern Thicket Tinamou	25–30	Fruits, leaves, berries, seeds, insects	SP	LC
Tinamus major	Great Tinamou	40–46	Fruits, leaves, berries, seeds, insects	T	NT
Galliformes					
Cracidae					
Crax rubra	Great Curassow	76–96	Seeds, fruits, flowers, leaves, barriers, insects	T	V
Penelope purpurascens	Crested Guan	76–96	Seeds, fruits, flowers, leaves, barriers, insects	T	LC
Odontophoridae					
Odontophorus guttatus	Spotted Wood-quail	23–26	Seeds, fruits, flowers, leaves, barriers, insects	SP	LC
Columbiformes					
Columbidae					
Geotrygon montana	Ruddy Quail-dove	21–25	Seeds, fruits, insects		LC
Leptotila plumbeiceps	Grey-headed Dove	25–28	Seeds, fruits, insects		LC
Zentrygon albifacies	White-faced Quail-dove	26–31	Seeds, fruits, insects	T	LC
Passeriformes					
Formicariidae					
Formicarius moniliger	Mayan Antthrush	16–18	Insects and other small invertebrates.		LC

in the method of bootstrap to calculate the 95% confidence interval for Δ_1. We performed the analyses with the package Overlap (Meredith and Ridout 2018) in R version 3.5.0 (R Core Team 2017).

Results

A total sampling effort of 8,529 days·trap resulted in 5,269 photographs, 862 of which were classified as independent records of birds from 10 orders, 15 families, 22 genera and 27 species. Of the total number of records, 93.55% were obtained during the day, 6.3% during twilight (including sunrise and sunset) and 0.15% during the night (Fig. 1).

Of the total number of species, we recorded 10 species with 11 or more records. All these species were diurnal, with two activity peaks, one in the morning (06:00 – 10:00 h) and one in the afternoon (15:00 – 18:00 h; Fig. 1). *Crypturellus boucardi* (Slaty-breasted Tinamou), *Tinamus major* (Great Tinamou; Fig. 2a), *Crax rubra* (Great Curassow; Fig. 2b), *Geotrygon montana* (Ruddy Quail-dove; Fig. 2c) and *Formicarius moniliger* (Mayan Antthrush) were also active at dawn and dusk (Fig. 1).

Only two species had enough records in both seasons which allowed a comparison, *C. rubra* and *T. major*. The differences in activity between seasons were not significant (W dry-rainy 2012 = 3.64, P = 0.16 for *C. rubra*; W dry-rainy 2011 = 5.40, P = 0.06 and W dry-rainy 2012 = 0.81, P = 0.66 for *T. major*), except in 2011 for *C. rubra* (W dry-rainy 2011 = 9.81, P = 0.007). Considering this, we carried out the following analyses without considering seasonality.

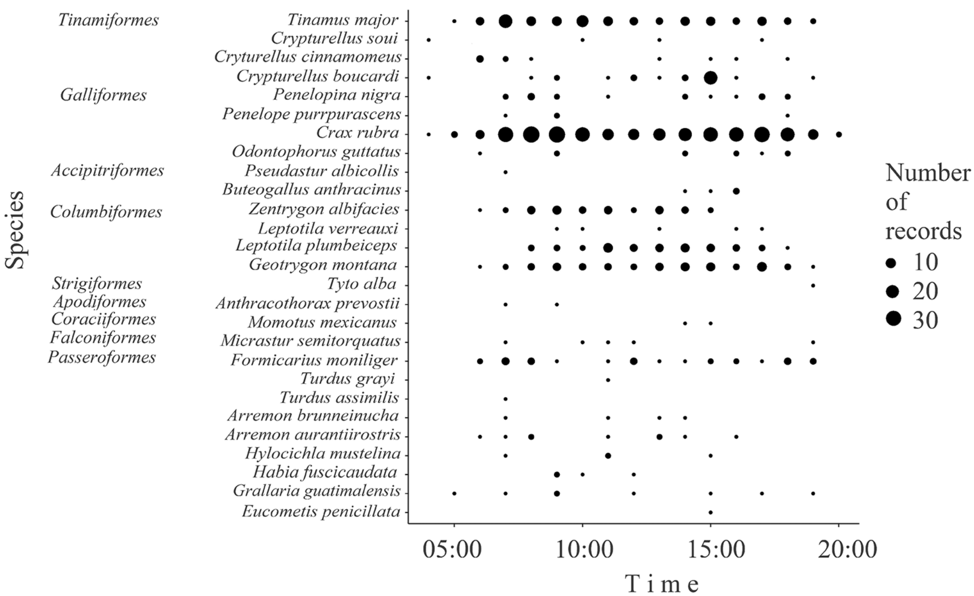

Figure 1. Distribution of the number of records of birds obtained by camera trapping in a 24 h cycle in the understorey of an evergreen forest in Los Chimalapas, Oaxaca, Mexico.

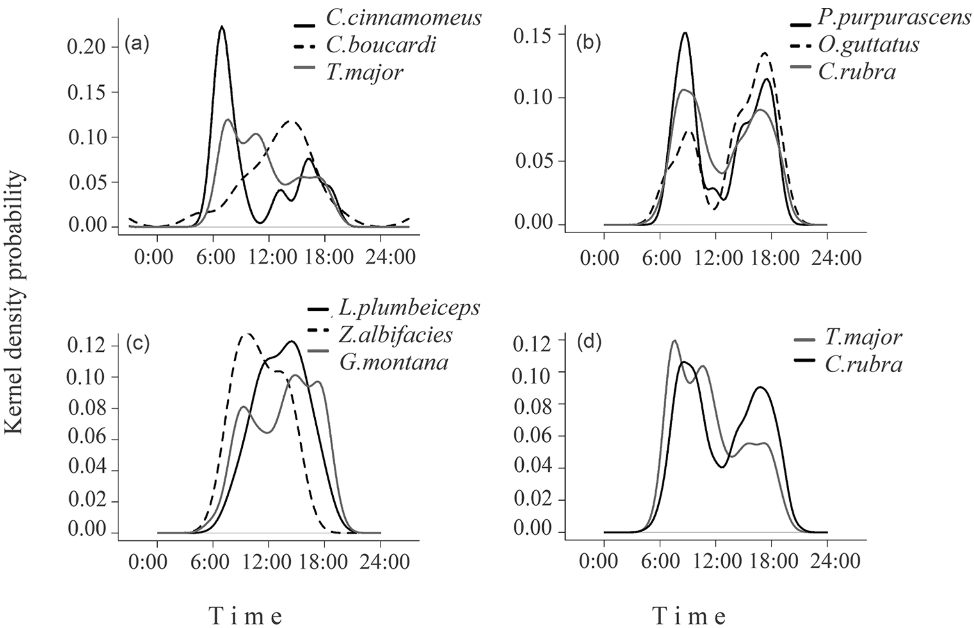

Figure 2. Activity patterns of some Tinamiformes (**a**), Galliformes (**b**) and Columbiformes (**c**) with similar size and ecological characteristics, as well as between pair species of larger body size (**d**) in the understorey of an evergreen forest in Los Chimalapas, Oaxaca, Mexico.

Table 2. Overlap coefficient (Δ_1) of activity patterns between pairs of bird species with similar ecological characteristics recorded in the understorey of a high evergreen forest in Los Chimalapas, Oaxaca, Mexico.

Order	Species pair	Δ_1 (95% confidence interval)
Tinamiformes	*T. major-C. boucardi*	0.69 (0.50–0.84)
	T. major-C. cinnamomeus	0.63 (0.46–0.88)
	C. boucardi-C. cinnamomeus	0.48 (0.23–0.74)
Galliformes	*C. rubra-P. purpurascens*	0.79 (0.68–0.96)
	C. rubra-O. guttatus	0.71 (0.58–0.94)
	C. rubra-T. major	0.82 (0.73–0.88)
	P. purpurascens -O. guttatus	0.66 (0.55–0.97)
Columbiformes	*G. montana-L. plumbeiceps*	0.81 (0.67–0.91)
	G. montana-Z. albifacies	0.69 (0.54–0.81)
	L. plumbeiceps-Z. albifacies	0.71 (0.56–0.86)

Of the ten species with 11 or more records, we made comparisons for nine of them. We excluded *F. moniliger* because this species shows taxonomic and ecological differences with respect to the other species: it was the only representative of the order Passeriformes and is primarily insectivorous (Table 1).

For Galliformes and Columbiformes, there was no temporal niche partitioning between species: the pairs *C. rubra* and *P. purpurascens*, *L. plumbeiceps* and *G. montana* and *C. rubra* and *T. major* showed a high degree of overlap (Δ_1 = 0.79, 0.81 and 0.82, respectively; Table 2). For Tinamiformes, the pair *C. boucardi* and

C. cinnamomeus showed the lowest degree of overlap (Δ_1 = 0.48) and the rest of the pairs showed a moderate degree of overlap (Table 2).

Discussion

In general, the activity patterns of birds in Los Chimalapas are consistent with behavioural studies on cracids (Fernández-Duque et al. 2013), tinamids (Brooks et al. 2004; Kuhnen et al. 2013) and doves in other areas, where there is higher activity during the morning (06:00–08:00 h) and the afternoon (17:00–18:00 h; Dias et al. 2016; Roncal et al. 2019). This bimodal activity of birds might be due to a shared behaviour to avoid high temperatures at noon, which is similar to what has been observed in previous studies (Srbek-Araujo et al. 2012; Fernández-Duque et al. 2013; Dias et al. 2016) and because they continually descend to the ground in search for food during the first hours of the day and the afternoon, even those who nest in layers above the ground level (Skutch 1963a, b; López et al. 2014).

Our results indicate possible temporal niche partitioning between species of Tinamiformes, since the level of activity overlap was intermediate (e.g. *T. major* and *C. cinnamomeus* with Δ_1 = 0.63) or low (e.g. *C. boucardi* and *C. cinnamomeus* Δ_1 = 0.48). However, our results should be taken with caution due to the small amount of data for *C. cinnamomeus* (11 records) and the scale used in the analyses.

There are variations in temporal niche partitioning in some Tinamiformes. In some cases, the activity overlap is high (> 0.80), between the tinamous *Tinamus guttatus* (White-throated Tinamou) and *Crypturellus cinereus* (Cinereous Tinamou) (Roncal et al. 2019), as well as amongst *T. major*, *Crypturellus variegates* (Variagated Tinamou) and *Tinamu tao* (Gray Tinamou; Brooks et al. 2004); in others, it is intermediate (Δ_1 = 0.69), between the tinamous *Crypturellus undulatus* (Undulated Tinamou) and *C. cinereous* (Roncal et al. 2019); and in others, it is low (Brooks et al. 2004). On the other hand, Galliformes and Columbiformes showed no temporal niche partitioning, contrary to what we expected and had a high level of overlap ($\Delta_1 \geq 75\%$). Previous studies have also shown high activity overlap between pairs of bird species that are ecologically similar, including the pair of galliforms *Psophia leucoptera* (Pale-winged Trumpeter) and *Mitu tuberosum* (Razor-billed Curassow; Roncal et al. 2019).

We consider the similarities between species as the most parsimonious factor for explaining our results. Galliformes and Tinamiformes, such as *P. purpurascens*, *T. major*, *Meleagris ocellata* (Ocellated Turkey) and *Ortalis vetula* (Plain Chachalaca), exhibit high diet overlap and shared behavioural preferences for resting and foraging times as a result of having similar adaptations (Baur 2008; López et al. 2014). These ecological similarities can generate high activity overlap between species.

Galliformes and Columbiformes are more sociable and form family groups (López et al. 2014; Pérez-Irineo and Santos-Moreno 2017), as observed in Los Chimalapas. Therefore, they may have fewer negative interactions with members of other similar species. In contrast, Tinamiformes are more solitary species, except in the reproductive season (Kuhnen et al. 2013; Brooks 2015); for example, *C. soui* has been observed to actively defend its territory (Brooks et al. 2004; Brooks 2015). Although many behavioural aspects of tinamiform species are unknown, these types of behaviour may occur in the species recorded in Los Chimalapas, favouring temporal niche partitioning (Brooks 2015).

Future studies will help to better understand if our results reflect niche separation between species of Tinamiformes or if there are factors other than competitive interactions. More studies on the activity patterns of bird species with ecological similarities will also help to determine whether what we observed in the present study is a generalised pattern.

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