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Spatial Occupancy, Local Abundance and Activity Rhythm of Three Ground Dwelling Columbid Species in the Forests of Guadeloupe in Relation to Environmental Factors

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Abstract: Although forest-dependent, tropical island endemic birds are particularly at risk of extinction, they remain largely understudied. In this context, we assessed the spatial occupancy, local abundance, and diel activity in three forest columbid species of hunting interest, the Ruddy Quail-Dove (RQD), *Geotrygon montana*; the Bridled Quail-Dove (BQD), *Geotrygon mystacea*; and the Zenaida Dove (ZD), *Zenaida aurita*, in Guadeloupe (French West Indies), using 5 camera-traps over 14 days on 24 survey stations, resulting in 1680 trap days. The number of observed RQD was too small to allow for a statistical comparison between habitats. BQD were more frequently observed at camera-trap stations that were dominated by tropical rainforest than those that were dominated by flooded forest. Conversely, ZD were more frequently observed at stations that were dominated by flooded forest and dry forest than at those that were dominated by tropical rainforest. High temperatures negatively affected the abundance of BQD, while the abundance of ZD was significantly lower in tropical rainforests compared to dry and flooded forests and tended to increase with canopy openness. The three species were diurnal. BQD significantly positively co-occurred spatially and temporally with small Indian mongooses, *Urva auropunctata*, whereas the temporal and spatial distribution of ZD overlapped significantly with that of domestic dogs, *Canis familiaris*, and domestic cats, *Felis catus*. Our results provide firm evidence that RQD remains scarce and is largely outnumbered by BQD in Guadeloupe which is in contrast with has been reported for other Caribbean islands.

Keywords: Bridled Quail-Dove; camera-trap; Caribbean; *Geotrygon montana*; *Geotrygon mystacea*; Ruddy Quail-Dove; *Zenaida aurita*; Zenaida Dove

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1. Introduction

The Caribbean islands constitute one of the major hotspots of biodiversity on Earth [1–3] and are particularly characterized by high diversity and high levels of avian endemism [4]. However, several Caribbean endemic bird species [5–9], including species of least concern [10,11], are currently declining as the result of environmental degradation.

In particular, Caribbean forest-dependent columbid species appear to be threatened by habitat fragmentation or destruction, extreme climatic events, introduction of exotic species, and poorly regulated hunting pressure [12–19]. The decline of columbid species is particularly worrying as pigeons and doves often play a crucial role in the dynamics and diversity of tropical or semi-arid forest through seed dispersal [20–24]. However, little information is available on the conservation status, population levels, and habitat use of Caribbean columbid species [25].

In this context, we assessed the spatial occupancy, local abundance, and diel activity patterns of three columbid species of hunting interest in Guadeloupe, French West Indies. The Bridled Quail-Dove (BQD hereafter), *Geotrygon mystacea*, is endemic to the Caribbean region, ranging from Puerto Rico to Saint Lucia [26,27]. The congeneric Ruddy Quail-Dove (RQD hereafter), *G. montana*, has a much wider range, stretching from the Caribbean Basin to the northern half of South America [28]. The Zenaida Dove (ZD hereafter), *Zenaida aurita*, is widely distributed through the Caribbean region, from the tip of the Yucatán Peninsula to the south of the Lesser Antilles, with weak morphological and genetic differentiation between populations [29]. All three species forage on the ground, eating mainly seeds and fallen fruits, but can also feed upon insects, earthworms, and gastropods [30–32].

Although the three species are listed as Least Concern on the IUCN red list, they differ markedly in relation to their conservation status in the Caribbean region and their degree of scientific attention. BQD is uncommon to rare in the Lesser Antilles and is a very rare resident in Puerto Rico [33]. Populations are considered to be declining on most Caribbean islands [14,19,34,35], with the possible exception of Guadeloupe [36,37]. RQD is a common to rare resident in the insular Caribbean [33]. By contrast, ZD is a common and cosmopolite species in the insular Caribbean, being present in large numbers in open woodlands, edges, mangroves, but also in cultivated fields, gardens, and the urban environment [33,38,39]. The behavior and population biology of the species has been well documented (see [40,41] and references therein). In comparison, very little attention has been given to the two quail-dove species in the scientific literature, reflecting a general focus on non-threatened species compared to threatened ones [42].

In Guadeloupe, the ZD and, to a lesser extent, the two Quail-Dove species are highly sought after by local hunters for personal food use [43], although the precise impact of hunting pressure on population dynamics remains undocumented. The three species are likely be vulnerable to predation by several invasive mammal species [44,45]. However, little is known about the overlap in the distribution and activity rhythms between the three columbid species and their potential predators. Currently, RQD is considered uncommon in Guadeloupe, with a frequency of occurrence being about three to four times lower than that of BQD, based on auditory point counts [37]. However, RQD is especially shy and hard to approach [46]. In addition, the performance of the auditory point count method for the survey of columbid species in tropical forests has been recently shown to be limited [47]. ZD, on the other hand, is very common in Guadeloupe with a marked increase in population size between 2014 and 2019 [37].

We, therefore, relied on camera-traps to document the presence, local abundance, and diel patterns of activity of the three species in various forest habitats in Guadeloupe. The use of camera-traps is a particularly suitable method for the study of both discrete and recluse bird species such as quail-doves [48–53]. In addition, it is an important tool in modelling species distribution coupled with environmental characteristics [53–57]. Here, we specifically aimed at (1) estimating the local abundance and detection of the three columbid species in Guadeloupe forests, (2) testing for the influence of environmental variables on detection and abundance, and (3) assessing the spatio-temporal co-occurrence between ZD, RQD, and BQD as well as with potential mammal predators, including humans.

2. Materials and Methods

2.1. Study Area and Data Collection

This study took place in Guadeloupe, French West Indies. Covering a surface area of 1628 km^2, Guadeloupe consists of two main contiguous islands: Basse-Terre and Grande-Terre. The first one is mountainous with the tallest volcano in the Lesser Antilles, culminating at 1467 m [58]. The second is limestone, lower, and flatter [59]. From the coast to the mountains, different forest types can be observed, according to elevation and rainfall. Tropical rainforest is the dominant type, amounting for about 40% of forest cover [60]. Dry forest is characterized by low rainfall, moderate elevation, and limestone or ancient volcanic soils. Flooded forest includes mangroves and swamp forests.

We assessed the presence of the three ground-dwelling columbid species and that of potential mammalian predators using camera-traps. To this aim, 24 stations (each station involving 5 camera-traps operating over two separate 7-day periods) were surveyed between February and May 2019, including 6 dry forest stations, 6 flooded forest stations, and 12 tropical rainforest stations (Figure 1, Supplementary Table S2).

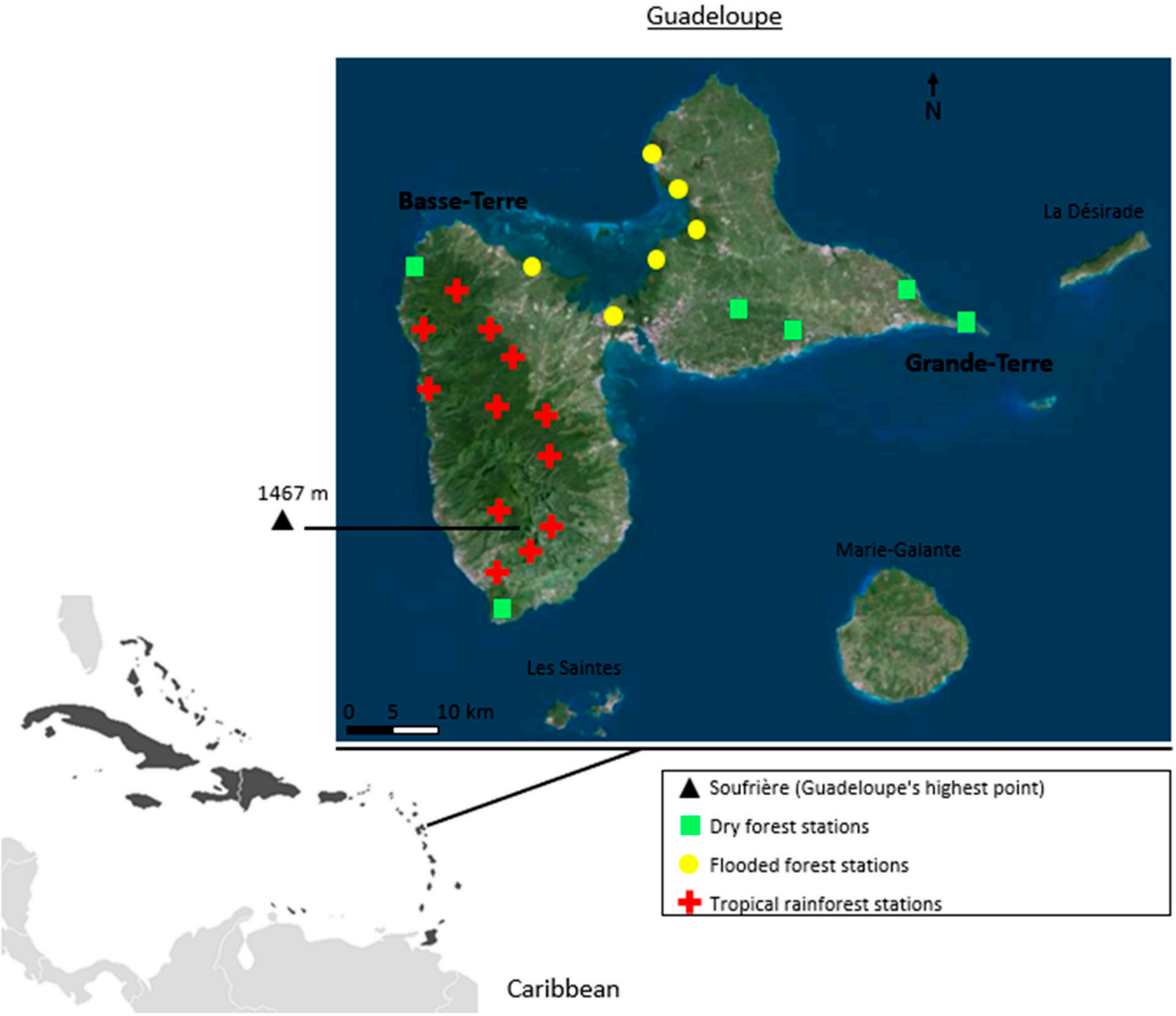

Figure 1. The 24 camera-trap locations that were surveyed between February and May 2019 in Guadeloupe, including 6 dry forest stations, 6 flooded forest stations, and 12 tropical rainforest stations. Each station had 5 cameras that surveyed for two 7-day periods. The distance between these camera-trap locations ranged from 2.82 km to 62 km.

Following Louppe et al. [45], stations were not chosen using an aerial grid due to the very steep landscape and extensive urban areas characterizing Guadeloupe, but rather to best cover the islands high diversity of forest habitats and to obtain a representative sample of elevations [61,62]. At each station (with a distance between stations that ranged from 2.82 km to 62 km), we arranged five passive infrared camera-traps (Moultrie© M-40i, with a detection range of about 24 m over a 125° angle of view) in a straight line, with a 200-m distance between adjacent cameras. The camera-traps were active for seven consecutive days during two separate trapping sessions, one in February-March and the other in April-May, resulting in 1680 days of trapping.

Each single camera was attached to a robust tree at a height of between 20 and 30 cm, in accordance with the small body size of the targeted bird species [48]. However, our traps were also effective in capturing mammal species. The cameras were operational 24 h day^{-1}.

The trigger was set to take three pictures each time a movement was detected, and we set a 30-s delay between the pictures to avoid multiple photographs of the same individual over short time periods [53]. In order to ensure uniformity in the radius of action of each camera, we selected trees at locations where the vegetation was not too dense, thus allowing an optimal range of the camera sensor in closed habitats. The selected parameters (high sensitivity of the shutter trigger, height positioning of the camera-trap, and distance of detection range) maximized the probability that all the columbid species that were present the survey areas would be detected.

To understand patterns of habitat use by columbids and potential mammalian predators, we measured the habitat type, canopy openness, elevation, and temperature at each station. We first assessed the habitat type (dry forest, tropical rainforest, flooded forest) from Rousteau [63] and then obtained confirmation from direct observations in the field. We visually estimated the canopy openness at each camera-trap location. The canopy was considered as open (≥66% open), partially open (33–66 open), or closed (0–33% open), with a corresponding score of 1, 0.5, or 0, respectively. At each station, an average was calculated for the five camera-traps, thus resulting in a continuous canopy openness index ranging from 0 to 1 [64]. We collected the elevation data at each camera-trap location, using a Garmin Dakota 20 GPS. The ambient temperature data was systematically recorded by the camera-traps on each shooting.

2.2. Data Analysis

We estimated the local abundance (the relative representation of a species in a particular ecosystem, measured as the number of individuals found per sample; [65]) from the total number of individuals (captures) of each species at each camera-trap location. Then, we pooled the local abundances for the five camera-traps at each location to assess the total local abundance per station. As the data did not follow a normal distribution (Shapiro–Wilk normality test [66], $p < 0.01$), we relied on a Wilcoxon signed-rank test for the paired data [67] to compare the estimates of local abundance that were obtained at each station between the two sampling periods. We used a Kruskal–Wallis analysis of variance by ranks to compare the median number of more than two groups [68,69], and Dunn's test [70] to make subsequent pairwise comparisons between the groups. We estimated the naïve occupancy for each species by dividing the number of camera-trap locations where at least one individual was photographed by the overall number of camera-trap locations. We calculated the capture per unit effort (camera-trapping sampling occasion) for each species by dividing the number of photographed individuals per 100 trap-days.

We then relied on Royle and Nichols' [71] heterogeneity model, linking abundance and heterogeneous detection probabilities, to assess the influence of environmental variables on detection and abundance. This method is particularly recommended to assess site occupancy at different spatial scales in the case of populations of unmarked individuals that are difficult to detect [72,73]. Detection was considered as a binary variable (1 = detection, 0 = non-detection, correcting for occasional camera dysfunction) at each station for all identifiable species, using data from 7-day trapping sessions. Species detection (1) and non-detection (0), with a 10 min buffer time between detections of the same species, were extracted for each trap day (i.e., 24 h period) at each station. Thus, abundance modelling was not concerned with species abundance history, but only with species binary detection history under specific habitat conditions. According to Royle and Nichols [71], variation in animal abundance, N_i, is the most important source of heterogeneity in site-specific detection probabilities.

The model assumes that all individuals of site i during sample j, have identical detection probabilities, r_{ij}, and that detections are independent. The species is then recorded if at least one individual is detected within the site. Thus, species detection probability is linked to probability of detection for an individual by:

$$P_{ij} = 1 - (1 - r_{ij})^{N_i}$$

Models were built using the R package « unmarked » v0.13-0 [74]. We analyzed data at the level of stations to maximize observation independence. We modelled abundance (λ) according to temperature, elevation, canopy openness, or forest types, and modelled the probability of detection (p) according to the forest structure and temperature. We ran a first model with both detection probability and abundance being independent of covariate influence, e.g., $p(.),\lambda(.)$. We chose not to include all environmental variables influencing abundance and detection in a global model as several of them were highly correlated between themselves (Spearman rank correlation test; canopy openness and temperature: $r_s = 0.67$; elevation and temperature: $r_s = -0.82$; $p < 0.01$ in both cases). We, therefore, modelled the influence of each environmental variable individually on p while keeping λ constant, and vice versa, e.g., p(covariate1),λ(.) or p(.),λ(covariate1). Finally, each environmental variable was tested on p and λ, without additive effects, e.g., p(covariate1),λ(covariate2) and then with additive effects, e.g., p(covariate1+covariate3),λ(covariate2+covariate4), or p(covariate1+covariate3),λ(covariate2+covariate4+covariate5). The covariates that were included in the additive models were not correlated between themselves.

We ranked models using the Akaike information criterion and we considered models with ΔAICc < 2 to assess the significance of the covariates [75]. We calculated evidence for the best model in comparison to other models from the ratio of AIC weights. We checked for goodness-of-fit and mean dispersion parameter $\hat{c}$ for all valid models, using 10,000 parametric bootstraps [55,76].

In order to assess variation in the diel activity between species, we considered four different periods of unequal length [77–79]: night (from 1 h after sunset to 1 h before sunrise), dawn (from 1 h prior to 1 h after sunrise), day (from 1 h after sunrise to 1 h before sunset), and dusk (from 1 h prior to 1 h after sunset). We accounted for daylength variation between the two trapping sessions by defining the average sunrise and sunset dates for each of the two sampling periods. We first used a Fisher exact test [80–82] to compare the proportions of birds that were captured during the different periods of the diel cycle (night, dawn, day, and dusk) between the two trapping sessions. Then, following Monterroso et al. [79], we used Jacobs Selectivity Index (JSI, [83]), to assess selectivity in diel rhythm activity. JSI ranges from −1 to 1, with −1 being total avoidance, 0 no preference, and 1 total preference. To determine the average JSI index and 95% confidence intervals for each period and species, we used bootstrap resampling (500 replicates) and recalculated the JSI for each bootstrap sample. The four periods were considered positively (or negatively) selected, whenever the 95% CI of the JSI was positive (or negative) and did not overlap zero (i.e., used as expected by chance). For each species, we compared the JSI index between the two sampling periods using a paired sample Wilcoxon test.

We further assessed the spatial co-occurrence between columbid species as well as with potential competitors and potential predators. To that end, we considered seven different taxonomic groups: birds (pooling all species; Supplementary Table S1), rodents (pooling all species), domestic cats (*Felis catus* Linnaeus, 1758), domestic dogs (*Canis familiaris* Linnaeus, 1758), small Indian mongooses (*Urva auropunctata*, 1836), northern raccoons (*Procyon lotor*, 1758), and humans. Co-occurrence was assessed using the probabilistic model that was developed by Veech [84], incorporated in the R package "cooccur" v1.0 [85]. This model determines the probability that the frequency of species co-occurrence of two species differ from what would be expected if the two species were distributed independently of each other among a set of sites. This model can then be used to classify associations of species as negative, positive, or random. In addition, we relied on the kernel density estimates of diel activity [86] incorporated in the R "Overlap" v1.1 package [87] to investigate the temporal activity and overlap. Following Ridout and Linkie [88], we favoured $\Delta 4$ over $\Delta 1$ as a nonparametric estimator of the coefficient of overlapping as our sample size was above 75 [89]. We estimated the precision of overlap coefficients by calculating an average value from 10,000 bootstrap samples for each pair of species.

3. Results

3.1. Camera-Trapping Survey Results and Species Detected

There was no difference in the local abundance of each of the three columbid species at each trapping station between the two trapping sessions (Wilcoxon's test: $P_{BQD} = 0.55$, $P_{RQD} = 0.93$, $P_{ZD} = 0.50$). Therefore, the data were pooled for subsequent analysis.

From a total of 1680 trapping days, we obtained 9450 captures, including 351 captures of BQD on 16 different survey stations, 198 captures of ZD on 12 different survey stations, and 14 captures of RQD on 7 different survey stations. The naïve occupancy rate was equal to 0.67, 0.50, and 0.29, camera-trapping rates (number of individual detections/100 trap-days) were equal to 16, 10, and 1, respectively, for BQD, ZD, and RQD. Overall, columbid species were present on 22 of 24 survey stations, with a 0.92 naïve occupancy rate and an average camera-trapping rate of 9.

Although BQD were found in all forest types that were studied, they were predominant in camera-trap survey stations they were dominated by tropical rainforest ($N_{\text{tropical forest}} = 12/12$, $N_{\text{flooded forest}} = 2/6$, $N_{\text{dry forest}} = 2/6$; Fisher's exact test, $p = 0.001$). Conversely, ZD were detected more frequently in camera-trap survey stations they were dominated by flooded forest and dry forest ($N_{\text{tropical forest}} = 2/12$, $N_{\text{flooded forest}} = 5/6$, $N_{\text{dry forest}} = 5/6$; Fisher's exact test, $p = 0.004$). The proportion of stations where RQD were detected did not differ between the three forest types ($N_{\text{tropical forest}} = 5/12$, $N_{\text{flooded forest}} = 2/6$, $N_{\text{dry forest}} = 1/6$; Fisher's exact test, $p = 1$).

In terms of local abundance, there was a significant difference in the median number of columbids per station between the three habitat types (Kruskal–Wallis analysis of variance, BQD: $X^2 = 8.71$, $p = 0.013$; ZD: $X^2 = 11.32$, $p = 0.003$; Figure 2). BQD were more frequently observed at camera-trap stations they were dominated by tropical rainforest than those they were dominated by flooded forest (Dunn's test adjusted with the Bonferroni method, $p = 0.04$), whereas ZD were more frequently observed at camera-trap stations they were dominated by flooded forest and dry forest than at those they were dominated by tropical rainforest ($p = 0.02$ for each comparison). The number of observed RQD was too small to allow statistical comparison between habitats.

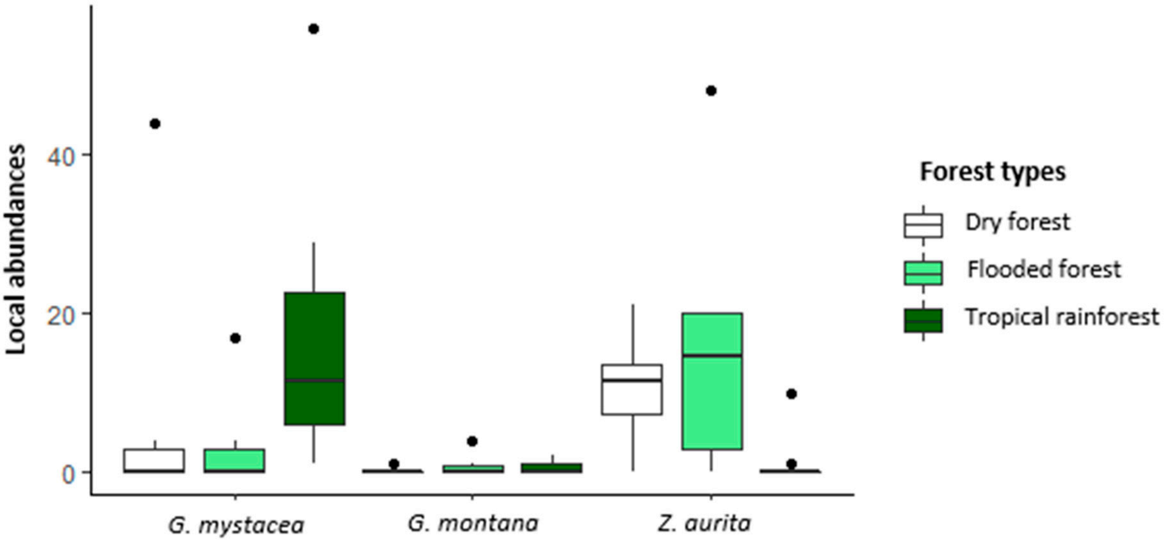

Figure 2. Local abundances of Bridled Quail-Doves, Ruddy Quail-Doves and Zenaida Doves at camera-trap survey locations in Guadeloupe, including three different forest types: dry forest (white), flooded forest (light green), and tropical rainforest (dark green).

3.2. Modelling Abundance and Detection

A subset of our trapping surveys was used for modelling purposes. After considering a 10 min buffer time between detections of the same species, we retained 262, 173, and 13 captures, respectively, for BQD, ZD, and RQD, resulting in 82, 54, and 10 detections in model matrices.

The best model for BQD retained temperature as the only environmental variable that was associated with abundance ($\beta = -0.81$, SE = 0.19, $p < 0.01$), with decreasing numbers with increasing temperature (Figure 3).

Table 1. Abundance and detection models for the Bridled Quail-Dove and the Zenaida Dove in Guadeloupe forests. Abundance (λ) was modelled according to the temperature (temp), elevation, canopy openness (co), or forest types (forest), and the probability of detection (*p*) was modelled according to the forest structure (fs) and temperature (temp). All environmental variables influencing abundance and detection were not included in a global model as they were highly correlated between themselves. We reduced the table to models within delta AIC < 6 (see Table S3 for the full table).

	Models	**AICc**	**ΔAICc**	**Weight**	**loglLik**	**d.f.**
	Bridled Quail-Dove					
M1	***p*(.),λ(temp)**	**146.83**	**0.00**	**0.48**	**−69.82**	**3.00**
M2	*p*(temp),λ(temp)	149.42	2.59	0.13	−69.66	4.00
M3	*p*(fs),λ(temp)	149.44	2.61	0.13	−69.67	4.00
M4	*p*(.),λ(forest+temp)	151.03	4.20	0.06	−68.85	5.00
M5	*p*(fs+temp),λ(temp)	152.45	5.62	0.03	−69.56	5.00
M6	*p*(.),λ(forest)	152.66	5.83	0.03	−71.28	4.00
	Zenaida Dove					
M1	***p*(.),λ(forest)**	**129.96**	**0.00**	**0.21**	**−59.93**	**4**
M2	***p*(.),λ(forest+co)**	**131.06**	**1.10**	**0.12**	**−58.86**	**5**
M3	***p*(.),λ(co)**	**131.17**	**1.21**	**0.11**	**−61.98**	**3**
M4	*p*(.),λ(elevation)	132.14	2.18	0.07	−62.47	3
M5	*p*(temp),λ(forest)	132.48	2.53	0.06	−59.58	5
M6	*p*(.),λ(forest+elevation)	133.00	3.05	0.04	−59.84	5
M7	*p*(.),λ(forest+temp)	133.12	3.16	0.04	−59.89	5
M8	*p*(fs),λ(forest)	133.16	3.20	0.04	−59.91	5
M9	*p*(temp),λ(co)	133.42	3.46	0.04	−61.66	4
M10	*p*(fs),λ(co)	133.53	3.57	0.03	−61.71	4
M11	*p*(.),λ(temp)	133.94	3.98	0.03	−63.37	3
M12	*p*(temp),λ(forest+co)	134.11	4.15	0.03	−58.58	6
M13	*p*(.),λ(forest+elevation+co)	134.23	4.27	0.02	−58.64	6
M14	*p*(temp),λ(elevation)	134.56	4.60	0.02	−62.23	4
M15	*p*(fs),λ(forest+co)	134.63	4.67	0.02	−58.85	6
M16	*p*(fs),λ(elevation)	135.02	5.06	0.02	−62.46	4
M17	*p*(fs+temp),λ(co)	135.45	5.50	0.01	−61.06	5
M18	*p*(temp),λ(forest+elevation)	135.73	5.77	0.01	−59.39	6
M19	*p*(fs+temp),λ(forest)	135.82	5.86	0.01	−59.44	6

Competitive models are highlighted in bold characters. Mean dispersion parameters ($\hat{c}$) obtained using MacKenzie and Bailey's goodness-of-fit test for best models were: $\hat{c}_{\text{Bridled Quail-Dove M1}} = 0.98$; $\hat{c}_{\text{Zenaida Dove M2}} = 0.66$; $\hat{c}_{\text{Zenaida Dove M6}} = 0.68$; $\hat{c}_{\text{Zenaida Dove M3}} = 0.66$.

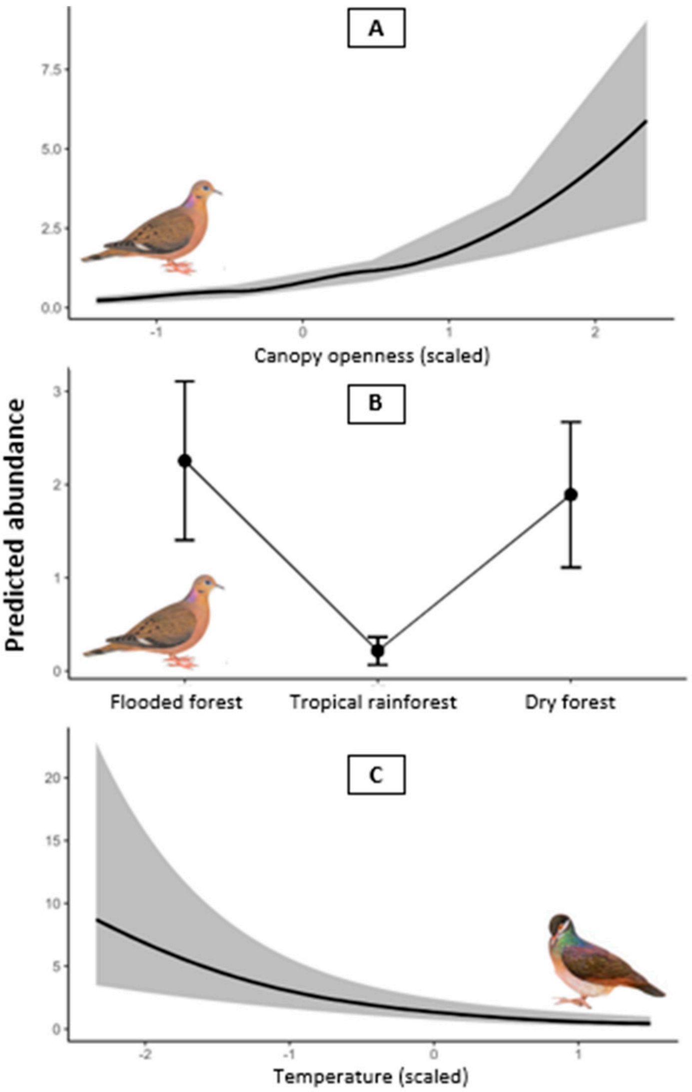

Figure 3. Selected model predictions for Zenaida Dove (**A**,**B**) and Bridled Quail-Dove (**C**), (predicted covariate effects with 95% CI, when all other covariates are held constant at their mean). These model predictions are from the best models for each of these species (see Table 1).

Moreover, this model suggested that none of the environmental variables influenced BQD detection in Guadeloupe (Table 1). Models including an influence of forest structure or temperature on detection were not retained in model selection (Table 1). Abundance-detection was not modelled for the RQD, given the small sample size (10 detections over five different stations).

A total of three models were retained (ΔAICc < 2, Table 1) for ZD. The ZD abundance was significantly lower in the tropical rainforest compared to the two other habitats in both the first ($\beta = -2.34$, SE = 0.76, $p < 0.01$) and the second best ($\beta = -1.93$, SE = 0.83, $p = 0.02$) models. On the other hand, a positive effect of canopy openness on ZD abundance was retained in both the second best model $\beta = 0.5$, SE = 0.34, $p = 0.15$), and the third one ($\beta = 0.86$, SE = 0.26, $p < 0.01$; Figure 3). Forest structure and temperature had no influence on detection.

3.3. Circadian Activity, Temporal Segregation and Spatial Cooccurrence

The proportions of birds that were captured during the different periods of the diel cycle (night, dawn, day, and dusk) did not differ between the two sampling periods (Fisher exact test, PBQD =0.13, PRQD = 1, PZD =0.24). Therefore, the data were pooled for further analysis. Table 2 shows Jacobs Selectivity Index (JSI) for each of the defined periods of the diel cycle.

Table 2. Assessing the selectivity in diel rhythm activity of the studied species using the Jacobs Selectivity Index (JSI) for each of the defined periods of the diel cycle (night, dawn, day, and dusk). JSI ranges from −1 to 1, with −1 being total avoidance, 0 no preference, and 1 total preference.

Species	JSInight	JSIdawn	JSIday	JSIdusk
G. mystacea	−1.00 [−1.00; −1.00] *	−0.25 [−0.49; −0.02] *	0.72 [0.58; 0.86] *	−0.61 [−0.85; −0.37] *
G. montana	−1.00 [−1.00; −1.00] *	−0.75 [−1.41; −0.01] *	0.69 [−0.05; 1.33]	−0.81 [−1.31; −0.26] *
Z. aurita	−1.00 [−1.00; −1.00] *	−0.74 [−0.93; −0.56] *	0.93 [0.88; 0.98] *	−0.84 [−1.04; −0.64] *
F. catus	0.52 [0.21; 0.83] *	−0.83 [−1.03; −0.62] *	−0.29 [−0.69; 0.11]	−0.67 [−0.93; −0.40] *
C. familiaris	−0.39 [−0.80; 0.03] *	−0.79 [−1.03; −0.55] *	0.42 [0.01; 0.82] *	−0.73 [−1.06; −0.41] *
U. auropunctata	−0.92 [−1.00; −0.85] *	−0.68 [−0.81; −0.56] *	0.86 [0.79; 0.92] *	−0.61 [−0.77; −0.44] *
Rodents	0.90 [0.86; 0.93] *	−0.75 [−0.85; −0.66] *	−0.94 [−1.00; −0.88] *	−0.64 [−0.74; −0.53] *
P. lotor	0.84 [0.58; 1.11] *	−0.96 [−1.02; −0.91] *	−0.99 [−1.01; −0.96] *	−0.74 [−1.03; −0.44] *
Humans	−0.95 [−0.99; −0.90] *	−0.80 [−1.91; −0.69] *	0.92 [0.89; 0.96] *	−0.76 [−0.89; −0.62] *
Birds	−0.77 [−0.98; −0.56] *	−0.44 [−0.65; −0.24] *	0.70 [0.55; 0.84] *	−0.63 [−0.80; −0.46] *

* $p < 0.05$: Significant selection, whenever the 95 % confidence interval of the JSI did not overlap zero.

The essential diurnal activity of the three columbid species was largely confirmed. However, although they were most active during daytime, the three columbid species showed some activity at dawn and dusk. Domestic dogs and small Indian mongooses were mainly active during daytime, whereas rodents and raccoons were essentially nocturnal. Cats were more active during the night-time, and practically inactive at dawn. Finally, human activity essentially occurred during the daytime, with no recorded activity during the night-time.

BQD positively co-occurred spatially with mongooses, birds, rodents, and RQD (Table 3). However, BQD, mongoose, birds, and RQD presented an explicit diurnal pattern, whereas rodents presented strictly nocturnal activity (Table 2, Appendix A Figure A1).

Table 3. Spatial co-occurrence probabilities of *Geotrygon mystacea*, *Geotrygon montana, and Zenaida aurita* with birds (pooling all species; Supplementary Table S1), rodents (pooling all species), *Felis catus*, *Canis familiaris*, *Urva auropunctata*, *Procyon lotor,* as well as humans. Associations of species were classified as positive ($P_{greater}$) or negative (P_{less}). Random associations of species are not reported.

Pair of Species		Obs. Cooccur.	Prob. Cooccur.	Exp. Cooccur.	P_{less}	$P_{greater}$
G. mystacea	*U. auropunctata*	36	0.24	28.7	0.9998	0.0010
G. mystacea	Birds	33	0.22	26.3	0.9988	0.0049
G. mystacea	Rodents	36	0.24	28.7	0.9998	0.0010
Z. aurita	*C. familiaris*	14	0.08	9.3	0.9894	0.0311
Z. aurita	*F. catus*	18	0.08	9.6	1.0000	0.0003
Z. aurita	*P. lotor*	17	0.07	8.5	1.0000	0.0001
G. montana	*G. mystacea*	9	0.03	3.3	1.0000	0.0002

As a result, BQD and rodents' activity showed little if any overlap (Table 4).

ZD spatially co-occurred with domestic dogs, domestic cats, and raccoons more than expected by chance (Table 3). As ZD, domestic dogs, and mongooses presented a diurnal activity pattern (Table 2, Appendix A Figure A1), their diel activity overlapped largely, whereas raccoons and domestic cats were more active during night-time period (Table 2, Appendix A Figure A1). This resulted in a very small temporal overlap between ZD and raccoons (Table 4), since raccoons hardly showed any activity during daytime (mean JSIday values ≤ -0.94).

Table 4. Activity patterns of bird species that were detected during the survey using the kernel density estimates of diel activity. We favored Δ4 over Δ1 as a nonparametric estimator of the coefficient of overlapping as our sample size was above 75. We estimated the precision of overlap coefficients by calculating an average value from 10,000 bootstrap samples for each pair of species.

Overlap	***G. mystacea***	***G. montana***	***Z. aurita***	***F. catus***	***C. familiaris***	***U. auropunctata***	**Rodents**	***P. lotor***	**Human**
G. montana	0.66								
Z. aurita	0.68	0.45							
F. catus	0.51	0.37	0.45						
C. familiaris	0.71	0.49	0.70	0.66					
U. auropunctata	0.84	0.57	0.84	0.52	0.76				
Rodents	0.11	0.10	0.07	0.60	0.30	0.12			
P. lotor	0.12	0.11	0.08	0.60	0.31	0.13	0.88		
Human	0.68	0.44	0.87	0.44	0.63	0.81	0.06	0.07	
Birds	0.84	0.59	0.75	0.51	0.78	0.82	0.14	0.14	0.68

4. Discussion

Overall, our results confirm the efficiency of unbaited camera-traps in documenting site occupancy, distribution, and local abundance of ground-dwelling bird species in tropical forests [90,91]. The rates of detection and estimates of naïve occupancy were similar or above what has been previously reported in the literature for two other columbids using the same method (*Aplopelia larvata*, 3 detections/100 trap-days, naïve occupancy = 0.29, Ehlers Smith et al. [53]; *Geophaps smithii*, 15 detections/100 trap days naïve occupancy = 0.30, Davies et al. [92]). Camera-traps thus appears to be a reliable tool for the monitoring of columbid species that can be difficult to observe in tropical forests due to their stealthy nature coupled with dense vegetation and limited visibility [93]. Such conditions actually limit the performance of alternative methods such as point-count sampling, distance sampling, or capture-mark-recapture (CMR) [26,50,53,94,95]. In particular, auditory point count method and auditory distance-sampling have maximal efficiency only when conducted during the peak of calling activity [96,97] and/or when broadcasting the call of the target species [47]. The CMR method allows a reliable estimation of demographic parameters of terrestrial columbid species [26,98], but requires a considerable logistical effort [41]. In addition, the sample of captured and banded birds might not be quite representative of the population studied if capture success varies according to the personality of individuals [99,100].

Our models revealed that neither forest structure nor temperature influenced detection probabilities of BQD and ZD in Guadeloupe. We detected ZD more frequently and in higher abundance at camera-trap survey locations that were dominated by flooded forest and dry forest, thus confirming previous observations [32,101,102]. In addition, Model 4 (ΔAICc = 2.18) suggested that elevation had a marginal negative influence on the abundance of ZD, confirming recent observations on Hispaniola [103]. Conversely, we observed BQD more often in the tropical rainforest habitat, as previously reported [28]. Indeed, in the Virgin Islands, Boal [19] found that BQD density was 1.13 individuals/ha in dry forests (covering 90% of the island) and 4.63 individuals/ha in rainforests (covering only 5 % of the island).

Importantly, model selection allowed us to separate the effects of temperature, elevation, and canopy openness on the abundance of BQD. Although the three factors did covary to a certain extent, the best model retained only a negative influence of temperature on abundance. The negative influence of temperature on abundance is particularly informative in the context of global warming [104–108] as increased temperatures might affect bird species [109] directly (via their thermal niche) and indirectly (through increased habitat disturbance [110]). However, very little if any information is available on the influence of elevated temperature on the ecophysiology and behavior of tropical columbids. In addition, the influence of temperature on the distribution and abundance of BQD on other Caribbean islands has not been documented so far.

Therefore, although the species is not currently considered threatened with extinction, more attention should be given to its distribution in relation to elevation and protected areas in the Caribbean islands.

The sample size for the RQD was too small to detect significant differences in the frequency of observations between habitat types. However, significant spatial and temporal co-occurrence between the two quail dove species suggest that they do not differ much in habitat selection. Indeed, a predominance of RQD in rainforest has been reported in various parts of its distribution [30,98,111].

The use of camera-traps allowed us to obtain a large amount of additional data on other species, in particular introduced alien species that potentially prey upon ground-dwelling columbid species, such as mongooses, domestic cats, domestic dogs, rats, or raccoons. Analysis of diel activity confirmed that rodents, cats, and racoons are essentially nocturnal, whereas mongooses and dogs are mainly active during the day. The small Indian mongoose was the most common invasive alien species at camera-trap survey locations, confirming its ability to thrive in various habitats on Caribbean islands [45,112,113]. Our observed naïve occupancy rate of 0.72 agrees very well with the estimate of 0.66 that was recently reported for Guadeloupe by Louppe et al. [45]. Small Indian mongooses co-occurred spatially and temporally with BQD more than would be expected by chance. On the other hand, the spatial and temporal distributions of domestic dogs and domestic cats significantly overlapped with that of ZD. However, to what extent predation by invasive exotic mammal species affects populations of ground-dwelling columbids in Guadeloupe remains unclear. Predation on terrestrial bird species by the small Indian mongoose is well established [114–117]. At the scale of the Caribbean, the extinction or decline of quail doves in various islands has been attributed to the introduction of the small Indian mongoose [114,118,119]. Although less common than mongooses (naïve occupancy rate of 0.27), feral cats were present in all habitat types, including protected areas.

The role of domestic and feral cats in the decline and extinction of vertebrate species is of major concern in conservation [120,121]. According to Medina et al. [122], domestic cats have contributed to 14% of the 238 global bird, mammal, and reptile extinctions. More specifically, predation by feral cats on several columbid species has been evidenced on Socorro Island, Mexico [123]. In addition, although racoons and rats are essentially nocturnal, they may prey upon nests and, possibly, incubating quail dove adults that place their nest at no great height [30,124]. The precise impact of exotic invasive mammals, particularly mongooses and feral cats, on columbids and other bird species of conservation interest in Guadeloupe clearly deserves further investigation. This could be achieved through studying diet composition of predators from faecal pellets and/or stomach contents, preferentially relying on modern molecular tools [125–127]. Such information could be particularly useful to contrast the impact of hunting pressure (see Carvalho et al. [128]), which is limited to a restricted hunting season in Guadeloupe, to that of exotic invasive mammals that are supposedly active all year long.

Based on our results, both ZD and BQD appear to be common and relatively abundant in Guadeloupe, unlike RQD. More specifically, the difference in the local abundance between BQD and RQD at the time of the study was particularly strong, with RQD being observed in only one third of all the survey stations and with an average local abundance that was 13 times lower than that of BQD. This result is consistent with the low number of RQD observations that were reported by STOC-EPS monitoring which consisted in detecting birds by sight and/or by hearing, along line transects (RQD naïve occupancy rates of 0.05, in 2019; [37]).

Interestingly, the predominance of BQD over RQD is more an exception than a general rule in the Caribbean region. Indeed, the opposite situation has been observed in Martinique and in the Virgin Islands [94,129,130]. In that respect, further information on RQD and BQD population dynamics and ecology (particularly addressing trophic niche plasticity, individual feeding specialization, and partitioning of food resources between the two species in sympatry [131–134]) in Guadeloupe and on other Caribbean islands would be particularly valuable to understand the observed patterns of variation in the abundance of the two species. Such information would also be quite useful for the development of hunting regulations.

Based on our results, we suggest that the regular monitoring of forest columbid species of conservation interest in the Caribbean islands using camera-traps and standardized methodology should be encouraged in the future, and possibly coordinated at the regional level. One way to increase information about abundance, demographic parameters, and population trends could involve banding programs using combinations of colour rings allowing for subsequent individual identification in the field from camera-trap recordings [135,136]. Increasing information on the ecology, demographic trends, and current and future distributions of columbids in the insular Caribbean should be a high conservation priority.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/d14060480/s1, Table S1: Names and descriptions of variables used in the models; Table S2: Land cover categories used in this study. Table S3: Full table of abundance and detection models for the Bridled Quail-Dove and the Zenaida Dove in Guadeloupe forests. Abundance (λ) was modelled according to temperature (temp), elevation, canopy openness (co) or forest types (forest), and the probability of detection (p) was modelled according to forest structure (fs) and temperature (temp).

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Appendix A

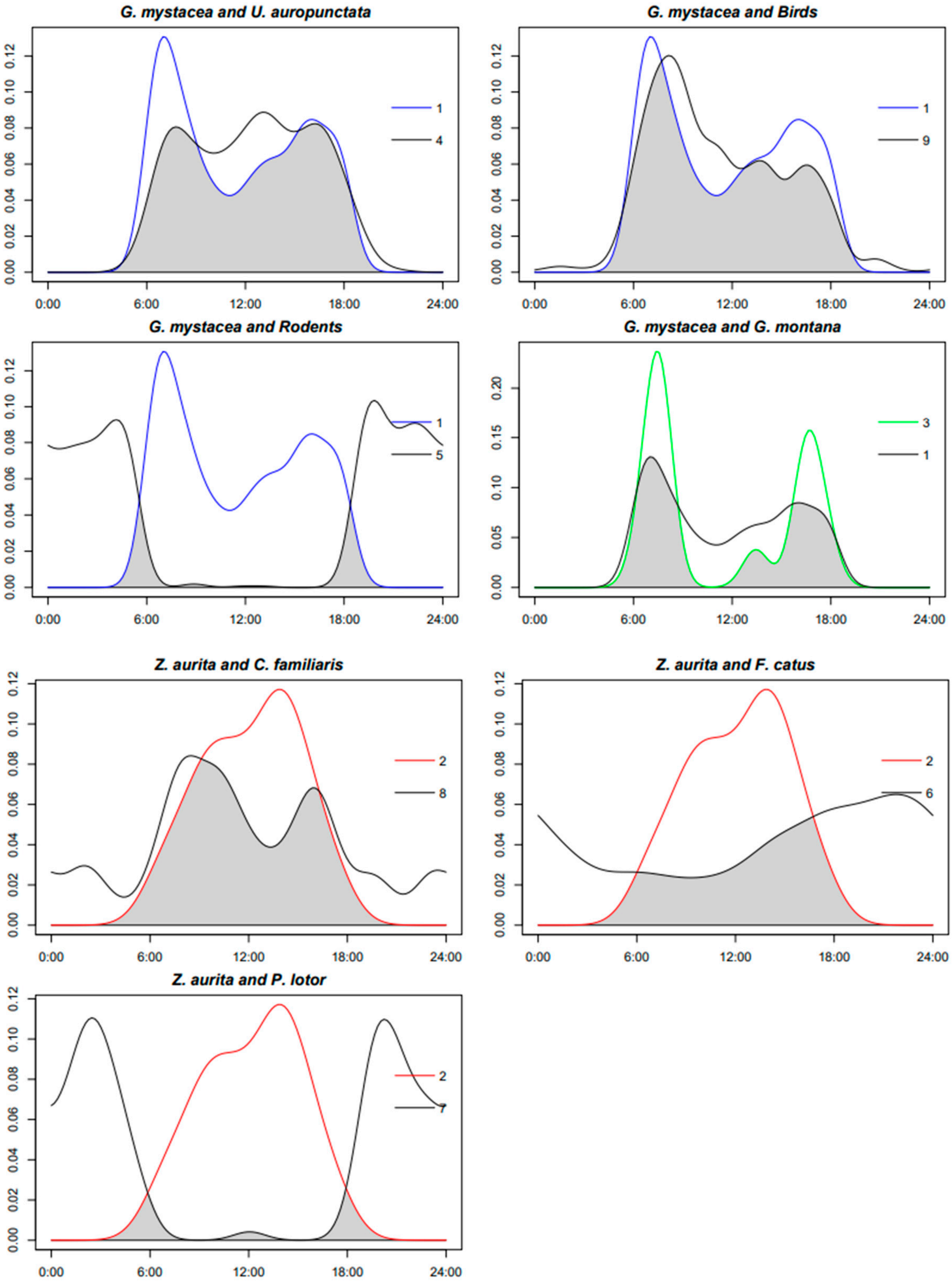

Figure A1. Activity patterns of bird and mammal species detected during this study with 1 = *Geotrygon mystacea*, 2 = *Zenaida aurita*, 3 = *Geotrygon montana*, 4 = *Urva auropunctata*, 5 = Rodents, 6 = *Felis catus*, 7 = *Procyon lotor*, 8 = *Canis familiaris* and 9 = Birds.

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