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Factors affecting spatial occupancy and local abundance of the Forest Thrush, *Turdus lherminieri*, in Guadeloupe forests

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Abstract

The Forest Thrush (FT), *Turdus lherminieri*, is a secretive, ground-dwelling forest bird species of conservation concern, endemic to only four Caribbean islands. Factors influencing habitat selection and abundance by FT have been seldom documented so far. We assessed variation in the presence and abundance of FT in various forested habitats in Guadeloupe. To that end, we deployed 5-camera-trap arrays over 14 days on 24 different survey stations resulting in 1680 trap days. We observed FT more frequently at camera trap stations where rainforest dominated, with local abundance declining with increasing canopy openness. Furthermore, temperature was the most important factor affecting the presence of FT at our study sites. FT was essentially diurnal, with some activity at dawn and dusk. We document for the first-time spatial co-occurrence between FT and potential mammal predators. FT co-occurred positively with rats and negatively with cats. Although FT is globally listed as near threatened by IUCN, the species the species appeared to be relatively abundant in Guadeloupe, possibly as a consequence of the suspension of hunting since 2014 and/or the almost total protection of the Guadeloupe tropical rainforest. We recommend the use of camera traps to improve knowledge for the conservation status of the species in other part of its area of distribution and to provide additional information on the potential impact of exotic predatory mammals.

Keywords Bird · Camera-trap · Canopy openness · Exotic mammal predators · Tropical rainforest · Temperature

Introduction

Extensive habitat destruction is a major source of biodiversity loss worldwide (Pimm et al. 2006; Brook et al. 2008). This phenomenon mainly results from human activities such as logging, agricultural expansion, or human settlement (Wilcove et al. 2013; Dávalos et al. 2016). In this respect, the conservation of tropical forests is of prime importance, as they support more than two-thirds of the World's biodiversity despite covering less than 10% of the Earth's land surface. However, they are particularly exposed to unabated deforestation and forest fragmentation (Bradshaw et al. 2009; Hansen et al. 2013; Giam 2017). Consequently, many tropical forest species are declining, particularly in restricted areas, such as oceanic islands (Alroy 2017). This is particularly true of birds, with more than 600 globally threatened species (Stattersfield et al. 1998; Ricketts et al. 2005) and more than 90% of species extinctions having occurred on islands (Johnson and Stattersfield 1990; Banko et al. 2013).

The Caribbean islands constitute one of the 25 hotspots of biodiversity on Earth (Myers et al. 2000; Pimm et al. 2014), with a high diversity of bird species and high levels of avian endemism (Vázquez-Miranda et al. 2007; Catanach et al. 2021). However, the small extension of this hotspot makes it one of the most vulnerable areas of conservation importance (Brooks et al. 2002). Deforestation is in particular widespread in the insular Caribbean due to human exploitation (Tole 2001; Dolisca et al. 2007; Hedges et al. 2018) and natural disasters (Wiley and Wunderle 1993; Eppinga and Pucko 2018). This phenomenon is particularly affecting the avifauna, with several Caribbean endemic bird species being declining (Wunderle 2008; Arendt et al. 2013; Lloyd et al. 2016; Devenish-Nelson et al. 2019; Akresh et al. 2021). In addition, scientific attention given to Caribbean forest-dependent varies markedly among Caribbean islands and family groups (Devenish-Nelson et al. 2019).

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In this context, we studied the Caribbean-endemic Forest Thrush (hereafter FT), *Turdus lherminieri,* typically found in various forest habitat types (Benito-Espinal and Hautcastel 2003; Arnoux 2012; Parashuram et al. 2015). The species' distribution area is restricted to four islands in the Lesser Antilles, Montserrat, Guadeloupe, Dominica, and St Lucia (Benito-Espinal and Hautcastel 2003; Eraud et al. 2012). Currently, FT is globally listed as near threatened by IUCN, considering the impact of anthropogenic deforestation and introduced predators. The Montserrat population declined abruptly following the 1995–1997 volcanic eruptions but appears to have recovered since then (Dalsgaard et al. 2007). A small, possibly declining, population exists in Dominica (Durand and Baptiste 2008), whereas the St Lucia population might be limited to a few individuals, if not extinct (Toussaint et al. 2009; Arnoux et al. 2014). The larger Guadeloupe FT population appears to be stable, according to data from audio-count surveys and mist netting (Eraud et al. 2013; Guillemot et al. 2020). The four populations have been considered as distinct subspecies according to plumage patterns (Clement and Hathway 2000; Zuccon 2011). Accordingly, Arnoux et al. (2013, 2014) provided some evidence for morphological and genetic differentiation between Montserrat, Guadeloupe, and Dominica, as well as within Guadeloupe, possibly as a result of habitat fragmentation.

At a more local scale, Parashuram et al. (2015) studied the influence of local habitat structure on FT abundance in Montserrat, relying on visual and acoustic detection during point count surveys. They concluded that FT prefers mature mesic and wet forests at mid elevations. However, the performance of methods relying on visual and auditory cues to survey tropical forest birds may vary according to habitat type, in direct relation to habitat characteristics and sound attenuation (Waide and Narins 1988; Anderson et al. 2015), possibly affecting conclusions about habitat selection. In addition, auditory point count method has maximal efficiency only when conducted during the peak of calling activity (Levesque and Lartiges 2000; Rivera-Milán et al. 2022) and/or when broadcasting the call of the target species (Cambrone et al. 2021). A potential alternative survey method consists in relying on camera traps. In comparison with point count surveys, the use of camera traps allows the collection of various and valuable ecological information such as the presence of other species and diel activity. The method is particularly suitable for studying discrete and recluse bird species such as FT (O'Connell et al. 2011; Suwanrat et al. 2015; Smith et al. 2017; Cook et al. 2020; Jean-Pierre et al. 2022). Finally, species distribution coupled with environmental variables can easily be modelled from camera-trap data (Maseko et al. 2017; Smith et al. 2017).

We therefore relied on camera traps to [1] estimate FT local abundance, detection and occupancy in Guadeloupe forests, [2] understand the influence of environmental variables on occupancy, detection and abundance, and [3] assess spatiotemporal co-occurrence between FT and potential mammal predators, including humans.

Material and methods

Study area

Field work took place on Basse-Terre and Grande-Terre, the two main islands of the Guadeloupe archipelago, French West Indies, which are separated by a narrow sea channel. The western island of Basse-Terre is mainly mountainous, with a maximum height of 1467 m (Gadalia et al. 1988), whereas the eastern island of Grande-Terre is lower and flatter, with a maximum height of 177 m, and is of coral-limestone formation (Lasserre 1961). The elevation gradient translates into a high diversity of habitats, with tropical forest dominating over tropical dry forest and tropical wet coastal forest (Rousseau 1996a).

Data collection

Data on the presence of FT and that of potential mammalian predators were collected during a study initially aimed at documenting the presence and abundance of two quail-dove species (Jean-Pierre et al. 2022). We relied on passive infrared camera traps (Moultrie© M-40i, with a 125° angle of view) to document the presence and assess the abundance of FT and other species. To that end, we surveyed 24 stations (each station consisting of an array of 5 camera traps) over 2 separate 7-day periods between February and May 2019, including 6 tropical dry forest stations, 6 tropical wet coastal forest stations and 12 tropical rainforest stations (Fig. 1, see Jean-Pierre et al. 2022 for additional information).

Although Guadeloupe has a high diversity of forest habitats, steep landscape and extensive urban areas are particularly present. Consequently, stations were set to be representative of the islands' high diversity of forest habitats, along the altitudinal gradient (Smith 2004; Talvitie et al. 2006; Louppe et al. 2021; Jean-Pierre et al. 2022). Stations were set at elevations ranging from 0.76 m to 768.65 m.

At each station, we set up five camera traps along a straight line, with a 200-m distance between adjacent cameras. Each camera-trap location was surveyed twice for a period of seven consecutive days, between February and March 2019 and again between April and May 2019, resulting in 1680 days of trapping. At each camera-trap location, we attached a single camera to a robust tree at a height of between 20 and 30 cm, according to the small body size of the targeted bird species (O'Connell et al. 2011). We selected trees at locations where the vegetation was not
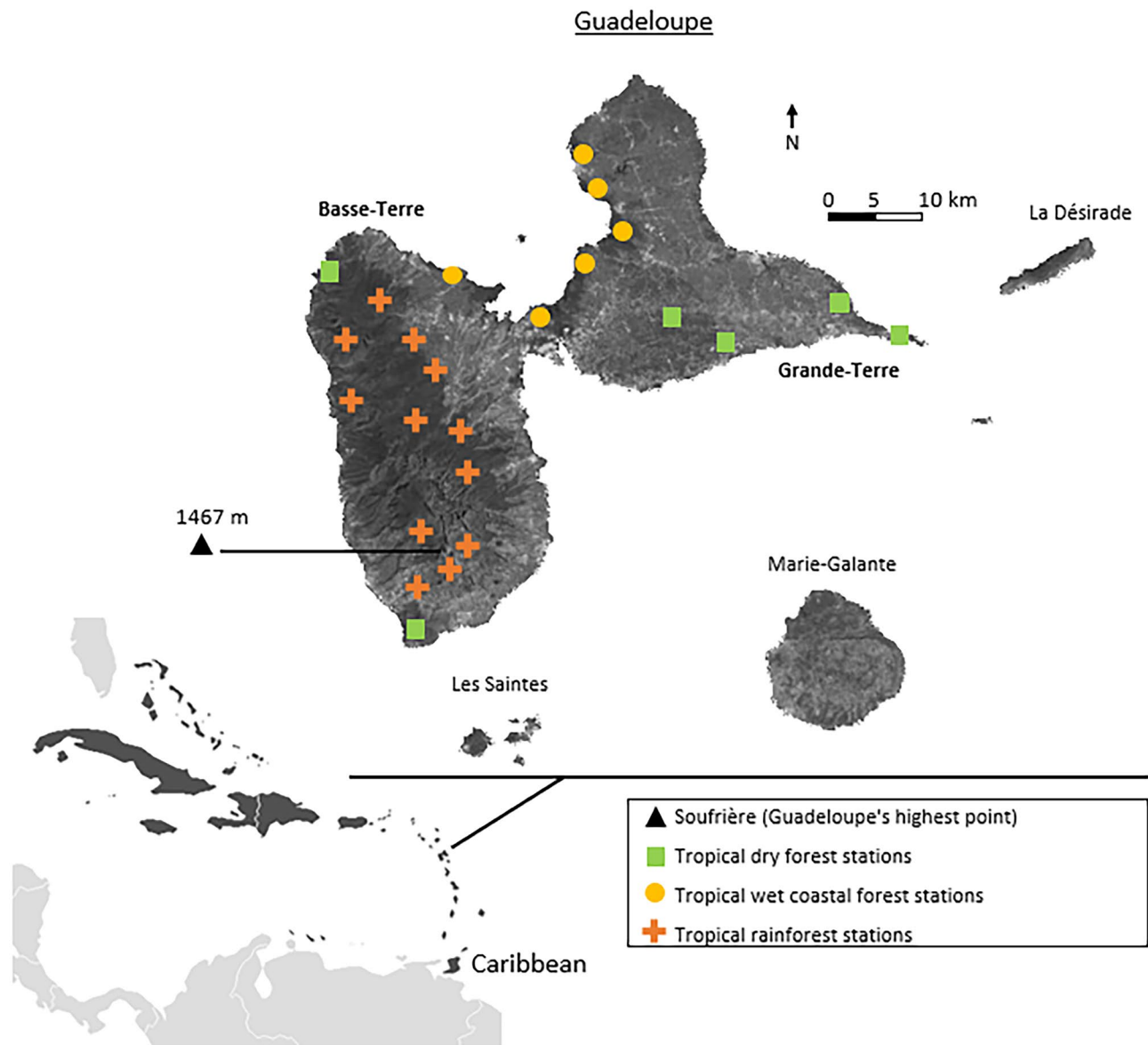
Fig. 1 Locations of the 24 camera trap stations investigated in Guadeloupe between February and May 2019. This includes 6 tropical dry forest stations, 6 tropical wet coastal forest stations and 12 tropical rainforest stations. Each station had five cameras that were monitored for two 7-day periods. The distance between these stations ranged from 2.82 km to 9.81 km

too dense to allow an optimal range of camera sensor in closed habitats. Cameras were active 24 h d^{-1}. In order to avoid multiple photographs of the same individual over short periods of time, camera-traps were set to take three pictures each time a movement was detected, with a 30-s delay between pictures (Smith et al. 2017). We assessed habitat type, forest structuration, canopy openness and temperature at each camera-trap location. Following (Rousteau 1996b), we considered four forest habitat types (tropical dry forest, tropical rainforest, tropical wet coastal forest) based on direct observations in the field. We visually estimated the forest structuration as dense ($\geq$ 66% tree cover) or sparse ($\leq$ 66% tree cover), with a corresponding score of 1 or -1, respectively. At each station, we calculated an average value for the five camera-traps, thus resulting in a continuous forest structuration index ranging from -1 to 1. We visually estimated canopy openness at each camera-trap location as open ($\geq$ 66% open), partially open (33–66 open), or closed (0–33% open), with a corresponding score of 1, 0.5 or 0, respectively, (see Jean-Pierre et al. 2022). We then calculated an average for the five camera-traps to obtain a continuous canopy openness index ranging from 0 to 1, for each station (Cook et al. 2020). We collected elevation data and ambient temperature at each camera-trap location

using a Garmin Dakota 20 GPS and camera-trap records, respectively. On each FT detection, ambient temperature was automatically recoded by the camera. Otherwise, we estimated average daily temperature using other diurnal species captured by the camera traps. According to the pattern of diel activity of FT (see results), we only took into account captures at morning, noon and afternoon.

Statistical analysis

We used the total number of individuals (captures) of each species at each camera trap location to assess local abundance (Preston 1948). Then, we calculated the total abundance per station by combining the local abundances of the five camera traps at each location. We used a Wilcoxon signed-rank test for paired data (Rosner et al. 2006) to compare estimates of local abundance obtained at each station between the two sampling periods, as the data did not follow a normal distribution (Shapiro–Wilk normality test p < 0.01; Mohd Razali and Bee Wah 2011).

To compare the median number of more than two groups, we used a Kruskal–Wallis analysis of variance by ranks, followed by Dunn's tests to perform subsequent pairwise comparisons between groups. We calculated naïve occupancy for each species by dividing the number of camera-trap locations where at least one individual was photographed, by the total number of camera-trap locations. For each species, we also calculated capture per unit effort (camera-trapping sampling occasion) by dividing the number of photographed individuals by 100 trap-days.

The influence of environmental variables on detection and abundance was then assessed using Royle and Nichols' heterogeneity model (Royle and Nichols 2003), which links abundance and heterogeneous detection probabilities. This method is especially recommended for assessing site occupancy at different spatial scales in the case of almost undetectable populations of unmarked individuals (Royle and Nichols 2003; Besnard and Salles 2010). Using data from 7-day trapping sessions, detection was considered as a binary variable (1 = detection, 0 = non-detection, correcting for occasional camera malfunction) at each station considering all identifiable species. Species detection (1) and non-detection (0) were extracted for each camera-trap day (i.e., 24 h period) at each station, with a 10 min buffer time between detections of the same species. Thus, abundance modelling was only concerned with species binary detection history under specific habitat conditions, not with species abundance history. According to Royle and Nichols (2003), the most important source of heterogeneity in site-specific detection probabilities is variation in animal abundance, N_i. The model assumes that all individuals of site i during sample j, have the same detection probabilities, r_{ij}, and that

detections are independent. If at least one individual is found within the site, the species is recorded. Thus, the probability of detecting a species is linked to the probability of detecting an individual by:

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

To maximize observation independence, we analysed data at the station level. In addition, we relied on occupancy-detection models to evaluate the influence of environmental variables on FT distribution. We used the R package « unmarked» v0.13–0 (Fiske and Chandler 2011) to build abundance-detection models and occupancy-detection models.

We modelled abundance (λ) and occupancy (ψ) based on temperature, elevation, canopy openness, and forest type, and probability of detection (p) based on forest structure and temperature. We first ran a model in which both detection probability and abundance (or occupancy) were independent of covariate influence, e.g. p(.),λ(.) or p(.),ψ(.). We did not include all environmental variables influencing abundance (or occupancy) and detection in a global model because several of them were highly correlated (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). However, we chose to keep all the environmental variables for modelling occupancy and abundance, as model selection allowed us to separately consider highly correlated variables. Accordingly, we modelled the influence of each environmental variable on p while holding λ (or ψ) constant, and vice versa, e.g., [p(covariate1), λ(.)] and [p(covariate1), ψ(.)] or [p(.), λ(covariate1)] and [p(.),ψ(covariate1)]. Finally, each environmental variable was tested on p, without or with additive effects, e.g., [p(covariate1 + covariate2), ψ(covariate1)] or [p(covariate1 + covariate2), λ(covariate1)] or [p(covariate1), ψ(covariate1 + covariate2)] and [p(covariate1), λ(covariate1 + covariate2)]. Only covariates that were not correlated between themselves were included in additive effects.

We used Akaike's information criterion to rank models, and models with AICc < 2 were considered to assess the significance of covariates (Burnham et al. 2011). The ratio of AIC weights was used to calculate evidence for the best model in comparison to other models. Using 10,000 parametric bootstraps, we checked for goodness-of-fit and mean dispersion parameter ĉ for all valid models (Burnham and Anderson 1998; MacKenzie and Bailey 2004).

Following Jean-Pierre et al. (2022), we examined spatial and temporal overlap between FT and potential predators, including: domestic cats (*Felis catus* Linnaeus, 1758), domestic dogs (*Canis familiaris* Linnaeus, 1758), rodents (pooling all species), northern raccoons (*Procyon lotor*, 1758), small Indian mongooses (*Urva auropunctata*, 1836),

and humans. We then considered four different time periods of unequal length to assess diel activity (Lucherini et al. 2009; Gerber et al. 2012; Monterroso et al. 2014): 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 considered variation in daylength between the two trapping periods by defining average sunrise and sunset dates for each of them. We first used Fisher's exact test (Fisher 1922, 1992; Agresti 1992) to compare the proportion of birds caught during different periods of the diel cycle (night, dawn, day and dusk) between the two trapping periods. We then used Jacobs Selectivity Index (JSI, Jacobs 1974) to assess selectivity in diel rhythm activity, as described by Monterroso et al. (2014). The JSI scale runs from -1 to 1, with -1 representing total avoidance, 0 representing no preference, and 1 representing total preference. We employed bootstrap resampling (500 replicates) and recalculated the JSI for each bootstrap sample to determine the average JSI index and 95 percent confidence intervals for each period and species. When the 95 percent CI of the JSI was positive (or negative) and did not overlap zero, the four periods were considered positively (or negatively) selected (i.e., used as expected by chance). A paired-sample Wilcoxon test was used to compare the JSI index between the two sampling periods for each species.

We examined spatial co-occurrence of FT with predators using the probabilistic model proposed by Veech (2013), included in the R package "cooccur" v1.0 (Griffith et al. 2016). This model determines to what extent the frequency of co-occurrence of two species differs from what would be expected under the null hypothesis of independent distributions.

In addition, to explore temporal activity and overlap, we calculated kernel density estimates of diel activity (Meredith and Ridout 2016), using the R "Overlap" v1.1 package (Niedballa et al. 2016). We favoured $\Delta 4$ over $\Delta 1$ as a non-parametric estimator of the coefficient of overlapping as our sample size was larger than 75 (Schmid and Schmidt 2006), as recommended by Ridout and Linkie (2009). We calculated an average value from 10,000 bootstrap samples for each pair of species to estimate the precision of overlap coefficients.

Results

Out of a total of 9450 detection-events, 330 corresponded to FT, 1056 to rodents, 483 to small Indian mongooses, 107 to dogs, 72 to domestic cats, and 101 to racoons, (see Jean-Pierre et al. 2022).

Forest Thrush naïve occupancy and local abundance

As FT local abundance at each trapping station did not differ between the two sessions (Wilcoxon's test, $P = 0.26$), we pooled the two data sets for further analysis. Overall, FT was detected on 16 of the 24 camera trapping stations, corresponding to a naïve occupancy rate of 0.67, and a camera trapping rate (number of individual detections/100 trap-days) of 18. Moreover, FT was found in all forest types, although more frequently in survey stations located in the tropical rainforest [$N_{tropical\ forest} = 11/12$, $N_{tropical\ wet\ coastal\ forest} = 3/6$, $N_{tropical\ dry\ forest} = 2/6$; Fisher's exact test, $p = 0.02$; Fig. 2].
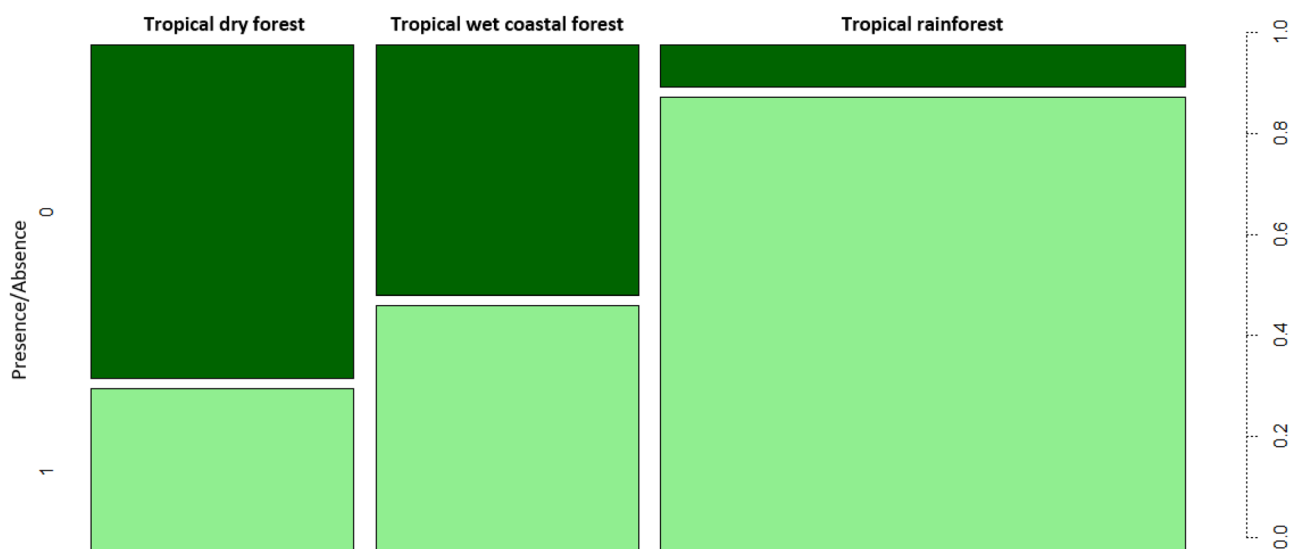
Fig. 2 Presence/absence of the Forest Thrush in all forest types studied, including 12 tropical rainforest stations, 6 tropical wet coastal forest stations, and 6 tropical dry forest stations
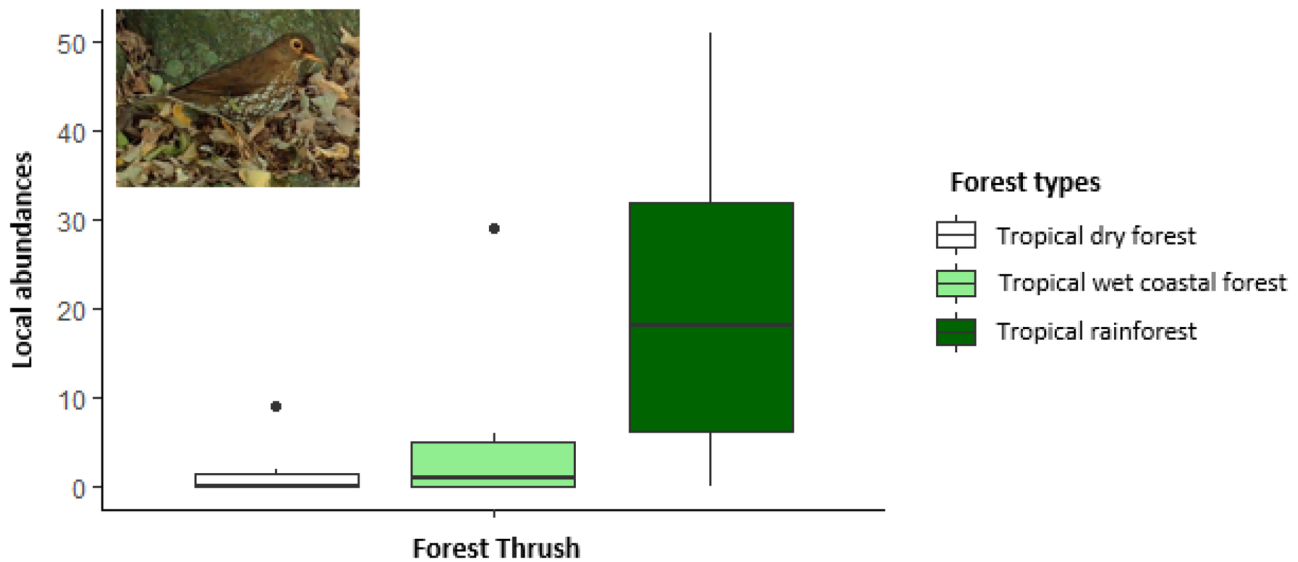
Fig. 3 Local abundance at camera-trap survey locations (including 6 tropical dry forest stations: white; 6 tropical wet coastal forest stations: light-green; 12 tropical rainforest stations: green) where the Forest Thrush was observed in Guadeloupe

Similarly, FT local abundance differed significantly between the three forest habitats, (Kruskal Wallis analysis of variance, $X^2 = 9.50$, $p = 0.009$). However, this was mainly due to FT abundance being significantly higher at tropical rainforest stations than at tropical wet coastal or tropical dry forest stations (post-hoc Dunn's test, $p = 0.031$ and $p = 0.005$, respectively; Fig. 3), whereas FT abundance does not differ between stations located in tropical dry forests and tropical wet coastal forests ($p = 0.574$).

Modelling occupancy and detection

We used a subset of our camera-trap records for modelling purposes (see methods). After considering a buffer time of
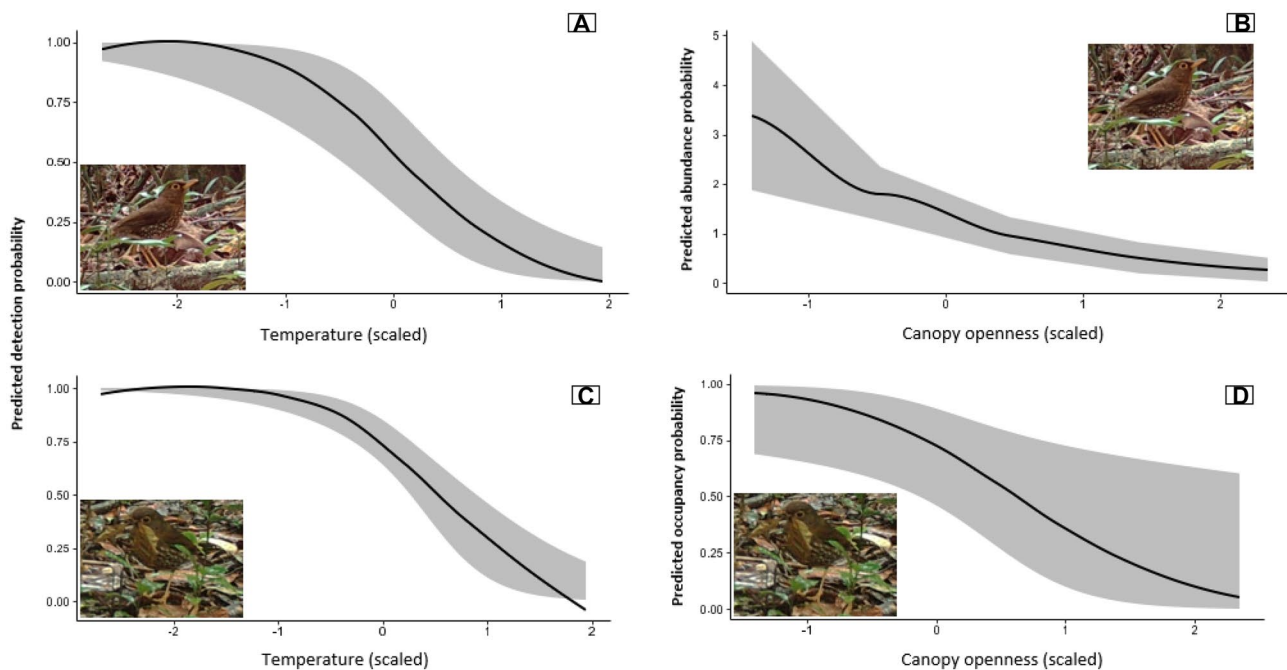
Fig. 4 Predicted detection – abundance probability (**A**, **B**) and predicted detection – occupancy probability (**C, D**) for the Forest Thrush (predicted covariate effects with 95% CI, when all other covariates are held constant at their mean)

10 min between detections of the same species, we retained 297 captures of FT, resulting in 83 detections in model matrices. According to the best model (M1), temperature was the only environmental variable affecting detection ($\beta = -2.27$, SE $= 0.49$, p < 0.01), with decreasing detection with increasing temperature (Fig. 4).

In addition, the best model suggested that canopy openness influenced FT occupancy, with decreasing FT occupancy with increasing canopy openness ($\beta = -1.58$, SE $= 0.69$, p < 0.03; Table 1).

Mean dispersion parameters $\hat{c}$ obtained using MacKenzie and Bailey's goodness-of-fit test for the four abundance-detection best models were: $\hat{c}_{M1} = 0.70$, $\hat{c}_{M2} = 0.69$, $\hat{c}_{M3} = 0.60$, $\hat{c}_{M4} = 0.66$ and for the occupancy-detection best model was: $\hat{c}_{M1} = 0.78$.

The four best models (ΔAICc < 2) retained temperature as the only informative environmental variable affecting detection ($\beta = -2.17$, SE $= 0.59$, CI: $-3.33, -1$, Table 1), with decreasing level of detection with increasing temperature (Fig. 4). Indeed, although forest structure was retained in model M4, it did not significantly affect FT detection ($\psi = 0.60$, SE $= 0.46$, p > 0.05). We therefore retained canopy openness as the only informative environmental variable affecting abundance ($\beta = -0.58$, SE $= 0.31$; Fig. 4). Indeed, although temperature was retained in the M2 model, it did not significantly affect FT abundance ($\lambda = -0.53$, SE $= 0.31$, p > 0.05).

Pattern of diel activity and spatial and temporal co-occurrence with potential predators

As the proportions of FT captured during night, dawn, day, and dusk did not differ between the two sampling periods analysis (Fisher exact test, $p = 1$), data were pooled for subsequent analyses. FT was essentially diurnal, with however some activity at dawn and dusk (Table 2).

Domestic dogs, mongooses, humans, were essentially diurnal, whereas rodents, raccoons and domestic cats were essentially nocturnal (see Jean-Pierre et al. 2022). FT positively co-occurred spatially with rodents and negatively with domestic cats (Table 3).

However, rodents were essentially nocturnal (see Jean-Pierre et al. 2022), such that FT activity (Table 2) and rodent activity showed little overlap (Table 4).

Discussion

Forest Thrush local abundance, detection and occupancy in Guadeloupe forests

From previous studies conducted in Guadeloupe (Eraud et al. 2012; Arnoux et al. 2013; Levesque et al. 2020), FT was known to occur mainly in areas of continuous tropical rainforest, from 100 to 1,400 m above sea level and tropical wet coastal forests. On Monserrat, Parashuram et al. (2015) concluded from auditory and visual point counts that FT prefers mature mesic forest, with birds being more abundant at mid-elevations under closed canopies. We therefore expected to obtained similar results, since tropical rainforests and tropical wet coastal forests have not been much altered by fragmentation, thanks to effective protection by local authorities. Our results confirm the global pattern. We detected FT predominantly in the tropical rainforest habitat and, to a lesser extent, in the tropical wet coastal forest habitat. In addition, their abundance decreased with canopy openness. Comparing to previous studies, however, we also detected the FT in the tropical dry forest habitat, albeit at lower apparent abundance. This is particularly noticeable, as in Guadeloupe this forest ecosystem has been severely degraded by human pressure (Magnin 2018). For example, we detected the presence of FT at Deshaies, a touristic town in Northwestern Basse-Terre. This area, bordering the beaches of Guadeloupe, is particularly subject to human pressure, with high forest fragmentation and intense human frequentation. We therefore suggest monitoring this FT population over the long term in order to estimate demographic trends and connectivity with populations in other habitats, possibly through a capture-mark-recapture study and molecular tools.

In addition, our results provide new information about FT ecology and conservation status in Guadeloupe. First, our data indicate that forest thrushes are relatively abundant in Guadeloupe. Indeed, detection rates and estimates of naïve occupancy obtained in the present study are among the highest values reported so far for ground-dwelling bird species using the same methodology (Supplementary materials Table S1). This might be explained by a combination of factors. First, hunting has been suspended since 2014 in Guadeloupe. More precisely, before the hunting ban, the Guadeloupe FT population was estimated at 46,900—49,500 pairs (93,800—99,000 mature individuals; Eraud et al. 2012). However, the estimation has not been updated since then. On the other hand, from 2015 to 2017, the FT population trend was estimated from 10 sites in Guadeloupe (Guillemot et al. 2020). Although the number of recaptured birds was relatively stable, FT frequency of occurrence increased from 2015 to 2017, possibly as a consequence of the hunting ban. Second, a large proportion of the tropical rainforest habitat is under protection in Guadeloupe (Magnin 2018). Unfortunately, there are no studies comparing FT population trends before and after the protection of its main natural habitat. We then suggest comparing FT population trends between protected and unprotected tropical rainforests to better assess the importance of habitat protection for conservation.

However, a multiyear survey of the Guadeloupe FT population is necessary to ascertain population trends. In particular, comparison of adult survival and breeding success between habitat types would be quite valuable for future management plans. This could be achieved through combining the use of camera-traps with capture that of

Table 1 Occupancy, abundance and detection models for the Forest Thrush in Guadeloupe forests. Occupancy (ψ) and abundance (λ) were 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

	Models	AICc	ΔAICc	Weight	loglLik	d.f
Occupancy-detection models for the Forest Thrush						
M1	**p(temp),ψ(co)**	**116.70**	**0.00**	**0.48**	**-53.30**	**4**
M2	p(fs + temp),ψ(co)	118.98	2.28	0.15	-52.82	5
M3	p(temp),ψ(temp)	120.51	3.81	0.07	-55.20	4
M4	p(temp),ψ(elevation)	120.93	4.23	0.06	-55.41	4
M5	p(temp),ψ(1)	121.08	4.38	0.05	-56.94	3
M6	p(temp),ψ(forest)	121.22	4.52	0.05	-53.94	5
M7	p(temp),ψ(forest + co)	122.54	5.84	0.03	-52.80	6
M8	p(fs + temp),ψ(temp)	122.91	6.21	0.02	-54.79	5
M9	p(fs + temp),ψ(1)	123.18	6.48	0.02	-56.54	4
M10	p(fs + temp),ψ(elevation)	123.45	6.75	0.02	-55.06	5
M11	p(fs + temp),ψ(forest)	123.92	7.22	0.01	-53.49	6
M12	p(temp),ψ(forest + elevation)	124.56	7.86	0.01	-53.81	6
M13	p(temp),ψ(forest + temp)	124.78	8.08	0.01	-53.92	6
M14	p(fs + temp),ψ(forest + co)	125.83	9.13	0.01	-52.41	7
M15	p(temp),ψ(forest + elevation + co)	126.23	9.53	0.00	-52.62	7
M16	p(fs + temp),ψ(forest + elevation)	127.73	11.03	0.00	-53.37	7
M17	p(fs + temp),ψ(forest + temp)	127.96	11.26	0.00	-53.48	7
M18	p(fs + temp),ψ(forest + elevation + co)	130.08	13.38	0.00	-52.24	8
M19	p(fs),ψ(co)	148.63	31.93	0.00	-69.26	4
M20	p(fs),ψ(temp)	152.25	35.55	0.00	-71.07	4
M21	p(fs),ψ(elevation)	153.00	36.30	0.00	-71.45	4
M22	p(fs),ψ(forest)	153.39	36.69	0.00	-70.03	5
M23	p(fs),ψ(1)	153.89	37.19	0.00	-73.34	3
M24	p(fs),ψ(forest + co)	154.35	37.65	0.00	-68.71	6
M25	p(1),ψ(co)	156.60	39.90	0.00	-74.70	3
M26	p(fs),ψ(forest + elevation)	156.79	40.09	0.00	-69.93	6
M27	p(fs),ψ(forest + temp)	156.84	40.14	0.00	-69.95	6
M28	p(fs),ψ(forest + elevation + co)	158.11	41.41	0.00	-68.56	7
M29	p(1),ψ(temp)	160.51	43.81	0.00	-76.66	3
M30	p(1),ψ(forest)	161.06	44.35	0.00	-75.48	4
M31	p(1),ψ(elevation)	161.45	44.75	0.00	-77.12	3
M32	p(1),ψ(forest + co)	161.64	44.94	0.00	-74.15	5
M33	p(.),ψ(.)	163.23	46.53	0.00	-79.33	2
M34	p(1),ψ(forest + elevation)	164.07	47.36	0.00	-75.37	5
M35	p(1),ψ(forest + temp)	164.14	47.43	0.00	-75.40	5
M36	p(1),ψ(forest + elevation + co)	164.91	48.21	0.00	-73.99	6
Abundance-detection models for the Forest Thrush						
M1	**p(temp),λ(co)**	**115.21**	**0.00**	**0.23**	**-52.55**	**4**
M2	**p(temp),λ(temp)**	**115.91**	**0.70**	**0.17**	**-52.90**	**4**
M3	**p(temp),λ(.)**	**116.08**	**0.87**	**0.15**	**-54.44**	**3**
M4	**p(fs + temp),λ(co)**	**116.80**	**1.59**	**0.11**	**-51.73**	**5**
M5	p(temp),λ(forest)	117.62	2.40	0.07	-52.14	5
M6	p(temp),λ(elevation)	117.63	2.42	0.07	-53.76	4
M7	p(fs + temp),λ(temp)	118.40	3.18	0.05	-52.53	5
M8	p(fs + temp),λ(.)	118.70	3.49	0.04	-54.30	4
M9	p(fs + temp),λ(forest)	119.53	4.31	0.03	-51.29	6
M10	p(temp),λ(forest + co)	120.21	5.00	0.02	-51.63	6
M11	p(fs + temp),λ(elevation)	120.43	5.22	0.02	-53.55	5
M12	p(temp),λ(forest + elevation)	120.56	5.35	0.02	-51.81	6
M13	p(temp),λ(forest + temp)	120.91	5.69	0.01	-51.98	6

Table 1 (continued)

	Models	AICc	ΔAICc	Weight	loglLik	d.f
M14	p(fs + temp),λ(forest + elevation)	122.47	7.26	0.01	-50.74	7
M15	p(fs + temp),λ(forest + co)	122.51	7.30	0.01	-50.76	7
M16	p(fs + temp),λ(forest + temp)	123.42	8.20	0.00	-51.21	7
M17	P(temp),λ(forest + elevation + co)	123.75	8.54	0.00	-51.37	7
M18	p(fs + temp),λ(forest + elevation + co)	126.21	10.99	0.00	-50.30	8
M19	p(fs),λ(temp)	132.89	17.68	0.00	-61.39	4
M20	p(.),λ(temp)	133.08	17.87	0.00	-62.94	3
M21	p(.),λ(forest + temp)	136.42	21.21	0.00	-61.54	5
M22	p(.),λ(forest)	137.89	22.68	0.00	-63.89	4
M23	p(fs),λ(elevation)	137.98	22.76	0.00	-63.94	4
M24	p(fs),λ(forest + temp)	138.18	22.97	0.00	-60.62	6
M25	p(fs),λ(co)	138.36	23.15	0.00	-64.13	4
M26	p(.),λ(co)	138.63	23.42	0.00	-65.72	3
M27	p(fs),λ(forest)	138.66	23.45	0.00	-62.66	5
M28	p(.),λ(forest + co)	139.25	24.03	0.00	-62.96	5
M29	p(fs),λ(.)	140.53	25.32	0.00	-66.67	3
M30	p(.),λ(elevation)	140.58	25.37	0.00	-66.69	3
M31	p(fs),λ(forest + co)	140.86	25.65	0.00	-61.96	6
M32	p(.),λ(forest + elevation)	140.95	25.74	0.00	-63.81	5
M33	p(fs),λ(forest + elevation)	142.07	26.86	0.00	-62.57	6
M34	p(.),λ(forest + elevation + co)	142.54	27.33	0.00	-62.80	6
M35	p(fs),λ(forest + elevation + co)	144.61	29.39	0.00	-61.80	7
M36	p(.),λ(.)	148.28	33.06	0.00	-71.85	2

combinations of colour rings allowing subsequent individual identification of marked individuals in the field from photographic records (Toy et al. 2017; Brides et al. 2018; Santangeli et al. 2020).

Second, an important outcome from model selection is that temperature, rather than elevation per se, was the most important factor influencing the presence of forest thrushes at our study sites. Obviously, the two variables are highly correlated between themselves as the species is predominantly found in the tropical rainforest, characterized by its rainy and cold climate due to the higher elevation in the southern half of Basse-Terre (Grubb 1971; Laere et al. 2016). Interestingly, forest type was not retained in the best model, indicating that difference in suitability between habitats might be related to a large extent to difference in ambient temperature. Indeed, due to marked difference in elevations, Basse-Terre, which is home to the tropical rainforest, has generally higher temperatures than Grande-Terre, which is home to a large part of the tropical dry forest and the tropical wet coastal forest (Rousteau 1996a, b; MDDEE 2012; Laere et al. 2016).

The importance of temperature is particularly relevant in the context of current global warming (Crick 2004; Descamps et al. 2017). Our findings are consistent with other studies, showing that rising temperatures may directly affect bird species, positively or negatively, via their limited thermal niche (Şekercioğlu et al. 2012), particularly in rainforest montane birds (de la Fuente et al. 2023). However, the effect of increased mean temperature and variability

Table 2 Jacobs Selectivity Index [JSI] for each of the defined periods of the Forest Thrush diel cycle: night, dawn, day, and dusk

	Night	Dawn	Day	Dusk
JSI	**-1.00**	**-0.45**	0.72	**-0.46**
	[-1.00;-1.00]*	[-0.74;-0.15]*	[0.56;0.88]*	[-0.68;-0.23]*

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

Table 3 Co-occurrence probabilities of Forest Thrush with potential predators, including humans, in Guadeloupe

	Co-occurrences				
Co-occurring species	Observed	Probability	Expected	P_{less}	$P_{greater}$
Domestic cats	8	0.12	13.8	0.0135	0.9960
Rodents	45	0.30	35.8	1.0000	0.0001
Domestic dogs	14	0.11	13.30	0.6887	0.4700
Mongooses	40	0.30	35.80	0.9738	0.0648
Raccoons	10	0.10	12.10	0.2480	0.8685
Humans	22	0.18	21.70	0.6226	0.5243

Table 4 Overlap in diel activity between species detected during the survey

Overlap	Cat	Dog	Mongoose	Rodents	Raccoon	Human
Cat						
Dog	0.66					
Mongoose	0.52	0.76				
Rodents	0.60	0.30	0.12			
Raccoon	0.60	0.32	0.13	0.89		
Human	0.44	0.63	0.81	0.06	0.07	
Forest Thrush	0.53	0.75	0.82	0.16	0.17	0.65

may vary between species depending on their ecology, with forest specialists and insectivores being less able to benefit from increased temperature along an elevational gradient (Dulle et al. 2016). More precisely, comparative evidence suggests that ground-dwelling tropical species with limited dispersal ability, as is the case for FT (Arnoux et al. 2014), might be more affected by climatic instability than arboreal ones (Scheffers et al. 2017). The use of data loggers placed on FT and in their different forested habitats (see Jirinec et al. 2022) in the future may provide a better understanding microhabitat selection in FT in relation to light and thermal niches.

Finally, temperature is likely to co-vary with other variables such as, for instance, soil moisture that was not measured in the present study. Spatiotemporal variation in moisture can have direct influence on arthropods diversity and abundance and, in turn, influence bird distribution in forest habitats (Petit et al. 1985; Smith et al. 2010). Parashuram et al. (2015) suggested that variations of local abundance of FT in different areas may reflect foraging habitat quality. In addition, Stanley et al. (2021) provided strong evidence for an effect of moisture on food abundance and space-use strategies of wood thrushes, *Hylocichla mustelina*, wintering in Belize. In particular, individuals in drier habitats experienced lower food abundance and were in lower body condition.

As other woodland-dwelling thrush species, FT is adapted to forage terrestrially in leaf-litter. Both moisture and a dense canopy could then provide optimal foraging conditions for FT in Guadeloupe, and, possibly, other islands. Future studies should then benefit from assessing to what extent FT spatial distribution and local abundance reflects spatial variation in food availability in leaf-litter, and how this could be affected by climate change.

The use of camera-traps allowed us to document for the first-time spatial co-occurrence between FT and potential mammal predators. FT co-occurred with rats and negatively with cats. Analysis of diel activity indicated that rodents were essentially nocturnal (see Jean-Pierre et al. 2022) whereas FT were essentially diurnal. Rodents may however, prey upon FT eggs since nests are placed at relatively low height from the ground (Benito-Espinal and Hautcastel

2003). The observed spatial segregation between FT and cats may result from active avoidance by FT of areas where cats are particularly abundant or may reflect the local impact of predation by cats on FT. Although, overall, cats were mostly active at night, some individuals were recorded during the day, and it is possible that different individuals have different diel patterns of activity (Hertel et al. 2017), particularly if they specialize on different preys (Dickman and Newsome 2015). Although predation by domestic and feral cats is a major cause of bird mortality in many areas (Loss et al. 2015; Marra and Santella 2016), including islands (Blackburn and Duncan 2007; Medina et al. 2011; Nogales et al. 2013; Doherty et al. 2016), its importance in Caribbean islands has not been documented so far. In the absence of any data on the diet of domestic and feral cats in forested habitats in Guadeloupe, their potential impact on FT populations is difficult to assess. More to the point, the interactions between cats, rats and FT might be particularly complex, particularly through what is known as the "mesopredator release effect" (Courchamp et al. 1999; Ballari et al. 2016; Takimoto and Nishijima 2022). Indeed, superpredators such as feral domestic cats may contribute to control mesopredators such as rats, such that their overall impact on FT is difficult to assess.

The use of camera traps allowed us to obtain valuable ecological information on FT spatial occupancy, abundance, diel activity, spatial co-occurrence with potential mammal predators, and their underlying factors. Similarly, several studies successfully used camera traps to study elusive ground-dwelling avian species (O'Brien and Kinnaird 2008; Ramesh and Downs 2014; Suwanrat et al. 2015; Smith et al. 2017). However, the use of camera-traps comes with some limitations (reviewed in Meek et al. 2015; Cordier et al. 2022). In particular, performance is likely to vary between camera trap models and settings (reviewed in Palencia et al. 2022), such that comparisons between studies should be done with caution. More importantly, camera traps may influence the behaviour of animals through associated mechanical noise, odor, and emitted light, although evidence is mainly limited to mammals (Caravaggi et al. 2020). We therefore used infrared-flash cameras, thus providing back and white pictures, to document the presence

of nocturnal potential predators, to avoid potential biases associated with the use of white flash cameras (Schipper 2007; but see Taggart et al. 2019 for counter evidence in domestic cats). A wise use of camera traps should therefore be based on a balance between the benefit of obtaining high quality data (i.e., color photographs for improved species and/or individual identification) and the risk of interference with the behaviour of targeted species. Faced with all these pitfalls, we suggest that researchers plan a processing time for the captures obtained. In addition, visiting camera trap locations is necessary to verify that the camera traps are working properly.

Conclusions and recommendations

Overall, our study shows that the use of unbaited camera-traps can be a reliable tool to assess spatial occupancy and local abundance of FT, as previously reported in the literature for other ground-dwelling and secretive forest bird species (Suwanrat et al. 2015; Smith et al. 2017; Murphy et al. 2018; Pérez-Irineo and Santos-Moreno 2021; Jean-Pierre et al. 2022). Contrary to auditory point count and auditory distance sampling, the method can be used with the same efficiency independently of seasonal variation in FT vocal activity or meteorological conditions. However, future survey of FT in Montserrat, Guadeloupe, Dominica, and St Lucia, as well as other forest ground-dwelling birds in the insular Caribbean (see Jean-Pierre et al. 2022), may benefit from combining the use of camera-traps with that of acoustic recorders (Buxton et al. 2018). We also suggest to further investigate the potential impact of exotic mammal predators on FT and other ground-dwelling forest birds, possibly through collecting faeces in the wild (Carrión and Valle 2018) or from direct analysis of stomach content (Balestrieri et al. 2011) following control operations.

Data availability The datasets generated during and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Declaration of Competing Interest The authors declare no competing interests.

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