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Improving primate detection using thermal infrared imaging: availability and observer errors in drone surveys of mixed tropical forests

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ABSTRACT

Drones with thermal infrared (TIR) cameras are increasingly used to survey terrestrial endotherms, including primates, but the relative lack of standardized protocols hampers their effectiveness. Detection errors, both observer (animal is available for detection but missed/misidentified by the observer) and availability errors (animal is present but unavailable for detection), vary across species, habitats and flight parameters, and may be exacerbated by anti-predator responses. We evaluated the suitability of drone-mounted TIR cameras in surveys of long-tailed macaques (*Macaca fascicularis*) by measuring detection errors for different flight altitudes (70, 60, 50 and 40 m above ground level [AGL]) and camera angles (45° and 90°) in two secondary forest habitats in Mauritius, characterized by open canopy with low thermal contrast and closed canopy with high thermal contrast. First, we determined the true size of three habituated macaque groups with full-day follows, and assessed their response to the drone. Next, we measured availability error (detection rate) in TIR videos after correcting for observer error (misidentification rate) using corresponding red-green-blue (RGB) videos. Finally, we assessed whether adjusting counts with mean detection rates improved group size estimates for different flight parameter combinations. Both error types were lowest for morning flights at 50 and 60 m AGL (40 and 50 m above canopy respectively) and with 45° camera angle in high thermal contrast conditions. The higher detection rates at 50 and 60 m compared to 40 m resulted from milder anti-predator behaviours (increased vigilance instead of dispersal). In secondary forest habitats with few dominant canopy species (e.g. *Eucalyptus*, *Litsea* and *Pinus* spp.), and for primate species with behavioural ecology comparable to long-

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tailed macaques, we recommend surveying at 40–50 m above closed-canopy vegetation with a 45° camera angle. With other flight parameters, we recommend incorporating detection rates from this study, along with their errors, into final counts.

1. Introduction

As human activities continue to degrade natural habitats, and conservation resources remain either limited or poorly allocated (Wiedenfeld et al. 2021), there is a pressing need to effectively monitor animal populations to evaluate the success of conservation activities, such as habitat restoration, threatened species protection, and invasive species control. Drones have become an invaluable tool for this purpose due to their increased accessibility and affordability (Buchelt et al. 2024; Wich and Koh 2018). They offer various advantages over ground-based survey methods, such as enabling researchers to survey habitats that would otherwise be difficult to access (e.g. thorny shrubland, swamps, montane areas and dense forests) (Burke et al. 2019; Trinh-Dinh et al. 2024) and require some disturbance to access (e.g. cutting trails) (Buckland et al. 2010). When mounted with thermal infrared (TIR) cameras, drones can even survey at night and in low-light conditions (Burke et al. 2019). Indeed, they have been successfully used for detecting and counting arboreal animals that sleep or rest in the forest canopy, such as primates (Gazagne et al. 2023; Kays et al. 2019; Spaan et al. 2019), or mammals that forage at night (McCarthy et al. 2021). However, developing standardized protocols for drone surveys of primates with TIR cameras remains challenging as detection error (also known as detection probability) varies between species, habitats, weather conditions, and flight parameters (Brack, Kindel, and Oliveira 2018; Burke et al. 2019; Pinel-Ramos et al. 2024).

Detection errors in drone surveys with TIR cameras (and other image-based surveys) can be broadly categorized as follows: (1) observer errors and (2) availability errors (Brack, Kindel, and Oliveira 2018; Delisle et al. 2023). Observer errors are a result of the observer missing, misidentifying or double counting animals that are available for detection. Availability errors, on the other hand are caused by the environment and/or study species' behaviour, leading to false conclusions about the absence of an animal (the animal was present is the study area but not visible to the observer). These two types of error are not mutually exclusive (Fuentes et al. 2015) and can be exacerbated by stress or anti-predator responses of the study animal to the drone (e.g. moving between adjacent sampling strips or fleeing the sampled area) (Brack, Kindel, and Oliveira 2018).

Addressing observer errors is usually less challenging than accounting for availability error (Brack, Kindel, and Oliveira 2018; Delisle et al. 2023). One way to measure the latter is to determine the true size of the population in the surveyed area and the proportion of individuals detected by the drone. This is particularly difficult for highly mobile animals (Delisle et al. 2023) and those not easily visible from the ground (Spaan et al. 2019). Fortunately, during the optimal usage time for TIR cameras (e.g. dusk, night or dawn), diurnal primates tend to remain stationary in their sleeping sites, making them easier to detect than during the day (Gazagne et al. 2023; Spaan et al. 2019). Consequently, it is often possible to measure availability error for well-studied primate groups or in reserves where the exact number of individuals is known (Gazagne et al. 2023; He et al. 2020) after correcting for observer error (Brack et al. 2023).

Availability error in drone survey of primates is influenced by a combination of climate (Burke et al. 2019; Gazagne, Gray, Wich, et al. 2024), forest and landscape features, and primate behaviour. Examples of forest and landscape features include canopy openness and high vs. low thermal contrast zones (e.g. due to presence of rocks and anthropogenic structures that absorb a lot of radiation during the day under open canopy) (Pinel-Ramos et al. 2024; Rahman and Setiawan 2020). Some behavioural factors include primates' sleeping habits (e.g. sleeping in tree cavities, on bare branches, or cliffs) (Fruth, Tagg, and Stewart 2018), group size (larger groups may be more easily detected) (Cook and Jacobson 1979), and spatial organization at sleeping sites (e.g. proximity to the canopy and group dispersion across trees) (Gazagne, Gray, Nguyễn, et al. 2024). Availability error also varies for different drone flight parameters, such as camera angle and flight altitude. When primates perch on branches beneath the top canopy (as opposed to resting in the top canopy), they may be more easily detected with an angled camera rather than by one directed vertically at the ground, as gaps between branches and leaves become more visible when viewed from the side (Gazagne et al. 2023). Lower flight altitudes improve the clarity of animal thermal signatures by improving image resolution (providing clearer animal contours) and reducing surface temperature blending with surrounding objects (Burke et al. 2019), aiding in the ability to distinguish closely huddled individuals. In contrast, flying at lower altitudes may decrease detectability if drones induce stress or trigger anti-predator behaviours in primates (Gazagne et al. 2023; Spaan et al. 2019). These responses can be mitigated in large groups due to the 'many eyes effect' and reduced predation risk (Roberts 1996). Additionally, repeated drone exposure may increase the species' tolerance over time, further minimizing anti-predator responses (Spaan et al. 2019). Nevertheless, flying too low reduces the horizontal field of view (FoV), meaning that increased detectability comes at the expense of total survey coverage. Therefore, to develop standardized drone survey protocols for specific species or habitats, it is essential to quantify the variation in availability error while accounting for observer error and anti-predator responses. To determine the optimal flight parameters, researchers should then also make a trade-off between detectability and survey area, balancing the need for accurate detection with sufficient spatial coverage.

Mauritius provides an excellent environment to investigate this variation in the population of non-native long-tailed macaques (*Macaca fascicularis*, Cercopithecidae), a diurnal and arboreal primate native to Southeast Asia (IUCN status: Endangered) (Fooden 1995; Hansen et al. 2022). Introduced around 1602 (Sussman and Tattersall 1986), these macaques are invasive and cause multiple detrimental impacts on native biota (Baider and Florens 2006, 2013, 2022; Baider et al. 2012; Bissessur et al. 2019; Jones et al. 1992; Reinegger et al. 2021). They occupy all forested regions in Mauritius, which are heavily fragmented (Florens 2013) and often border anthropogenic environments. Here, macaques are often habituated to humans and frequently travel by ground, facilitating group size estimation. Additionally, the macaques tend to re-use only a few sleeping sites (Reinegger et al. 2023; Sussman, Shaffer, and Guidi 2011), making it easier to locate groups (Reinegger et al. 2023). Moreover, following severe, human-driven defaunation (Heinen et al. 2018), the island's next largest endotherm is the volant and medium-sized

Mauritius flying fox (*Pteropus niger*, Pteropodidae) (body length without tail 23 cm compared to the macaque's 40–47 cm), reducing misidentification risks with TIR cameras. The last survey of long-tailed macaques in Mauritius dates back to 1977–1984 (Sussman and Tattersall 1986). New survey methods are needed as ground-based survey methods are challenging due to the very dense stands of invasive alien plants (mostly strawberry guava [*Psidium cattleyanum*]) in most forests and rugged hilly to mountainous terrain (Florens et al. 2016).

We evaluated the suitability of drone-mounted TIR cameras for surveying long-tailed macaques by investigating variation in availability errors across different forest habitats in Mauritius (open vs. closed canopy and low vs. high thermal contrast) and various flight parameters (flight altitudes of 70, 60, 50 and 40 m above ground level [AGL] and camera angles of 45° and 90°). We also accounted for observer-related errors and anti-predator responses. First, we determined the true size of three habituated macaque groups by doing several full-day follows and visual counts. Second, we assessed their stress and anti-predator behaviours in response to the drone at different flight altitudes. Third, we compared TIR video counts from four observers for different flight parameters, calculated inter-observer reliability and estimated observer errors (misidentification) by cross-checking with red-green-blue (RGB) videos recorded simultaneously with the TIR videos. Finally, we measured availability error (proportion of group members detected) after correcting for misidentification. We discuss the optimal flight parameters and provide availability errors for correcting counts of long-tailed macaques in areas with unknown population size.

2. Methods

2.1. Drone model

For this study, we used the DJI Mavic 3T, a lightweight drone (~1 kg) equipped with both high-resolution TIR and RGB sensors. The TIR sensor features a resolution of 640 × 512 pixels, a 45 × 37 angular FoV, a 12-μm pixel pitch, a 9.1 mm true focal length, 16 × zoom, a 30 hz frame rate and approximate temperature measurement accuracy of 2°C. The RGB sensor includes both a wide (8000 × 6000 pixels, 4.4 mm true focal length, 72 × 57 angular FoV) and a zoom lens (4000 × 3000 pixels, 12 × 9 angular FoV, 29.9 mm true focal length, 56 × digital zoom). The zoom lens was not used during the study. The noise level measured next to the propeller was ~70 dB (using the Sound Meter app, Pony Inc.) but dropped to ~45 dB at 50 m flight altitude, similar to other DJI Mavic drones (Duporge et al. 2021).

2.2. Study site and survey protocol

Mauritius (centred on 20°15′S and 57°35′E, 828 m a.s.l, 1,865 km^2) is a tropical oceanic island situated in the Indian Ocean about 875 km east of Madagascar. We selected habituated groups of macaques in three different study sites (one group per study site): Balfour Garden, Gorges Viewpoint and Grand Bassin (Figure 1).

In all three sites, the study groups occupy anthropogenic environments and are provisioned in part by residents and tourists. Their sleeping sites are in patches of secondary forest bordering these environments, representing major secondary forest areas in Mauritius, including both humid and wet habitats (Table 1). These are often

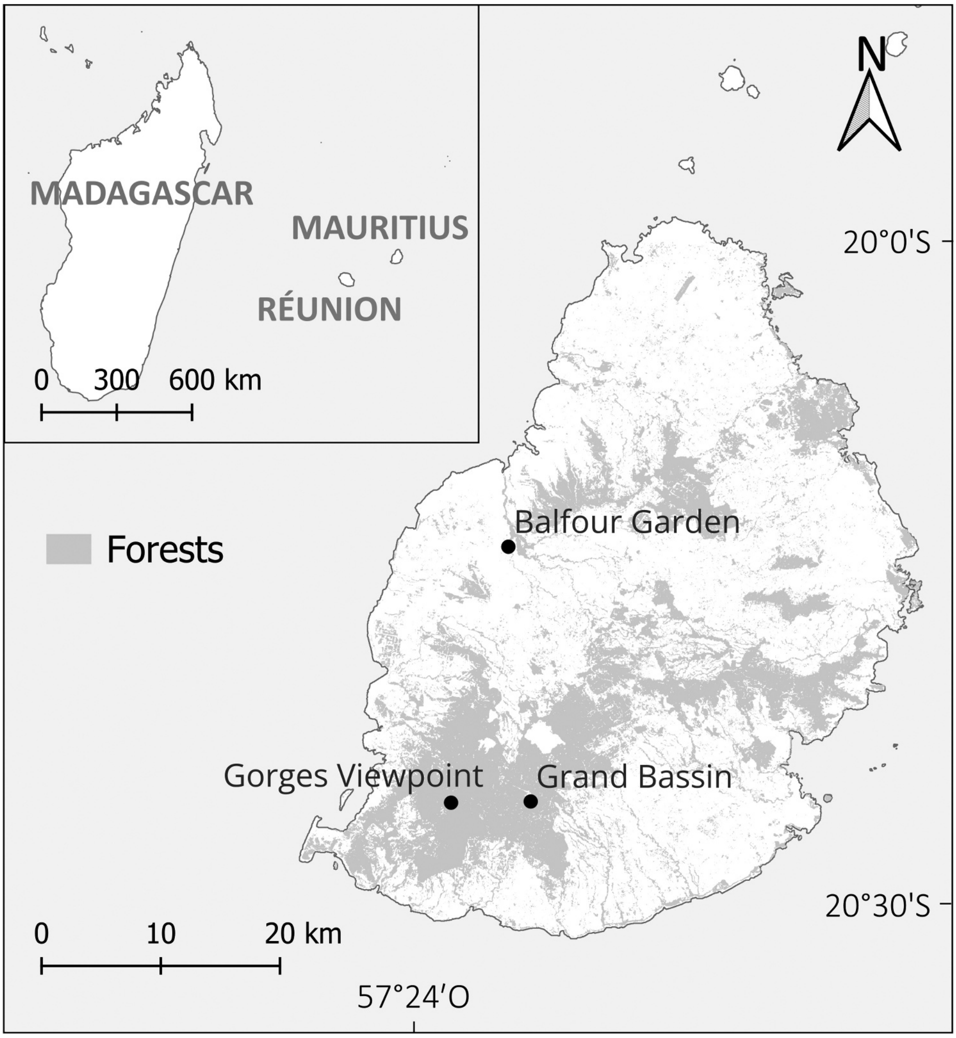

Figure 1. Location of Mauritius relative to Madagascar (insert) and the specific study sites within Mauritius. Here we evaluated the suitability of thermal infrared (TIR) cameras for detection of long-tailed macaques (*Macaca fascicularis*) from January to June 2024.

former plantation forests (e.g. *Eucalyptus* and *Pinus* spp.) and forests dominated by invasive plants (e.g. *Ligustrum robustum*, *Litsea glutinosa*, *L. monopetala*, *P. cattleyanum* and *Ravenala madagascariensis*) (Forestry 2018; NPCS 2018), characterized by relatively simple canopies (single tree layer with height <15 m) with few dominant species (Vaughan and Wiehe 1937).

We followed each group for 3 to 4 full days to familiarize ourselves with their sleeping sites (each group reused 1–3 sleeping sites spaced by 100–300 m in the same forest patch) (Table 1) and conducted visual counts of macaques within a 10 m range. To ensure accurate counts, we categorized members into five age/sex classes, based on body size, facial hair, level of development of sexual organs and size of the nipples in females

Table 1. Study site characteristics including different landscape, environmental, vegetation and long-tailed macaque (*Macaca fascicularis*) study group parameters.

	Site		
Characteristics	Balfour Garden	Gorges Viewpoint	Grand Bassin
Group size (n)	16	28	9
Individuals per age/sex class (n)			
– Adult male	2	2	2
– Adult female	6	9	2
– Subadult male	1	2	0
– Juvenile/old infant	7	15	5
Rainfall (mm/year)[a]	1,200–1,400	2,200–2,400	3,400–3,600
Altitude above mean sea level	250	660	650
Climate[b]	Humid	Wet	Wet
Canopy type	Open canopy	Closed canopy	Closed canopy
Canopy height (m)	10–14	8–10	11–15
Commonly used sleeping trees	*Eucalyptus tereticornis, Mangifera indica, Terminalia catappa*	*Calophyllum tacamahaca Sideroxylon puberulum Syzygium glomeratum*	*Eucalyptus robusta* *Litsea monopetala* *Pinus elliottii*
Thermal contrast zone[c]	Low	High	High
Sleeping sites (n)	2	1	3

[a] According to Willaime (1984). The average is based on annual rainfall data from 1931–1960.
[b] According to Halais and Davy (1969).
[c] Illustrated by Figure 2.
The study was conducted in Mauritius from January to June 2024.

(Supplementary Information 1). We also identified members by distinctive features like injuries (e.g. broken fingers, missing tail) (Supplementary Information 1). Young infants were excluded from counts as they are carried by their mothers and not visible from the air as a result. Even though our fieldwork period overlapped with the primary birth peak in Mauritian long-tailed macaques (March) (Jamieson 1998), young infants constituted only a small portion of the study groups (one young infant for the Balfour Garden and Grand Bassin groups, and three for the Gorges Viewpoint group). Accurate counts were eased by the groups' frequent travel via roads, walls, overhead power lines and open areas, particularly when returning to their sleeping sites (Supplementary Information 1). We estimated canopy height at each sleeping site by flying the drone at the edge (maintaining a 50 m distance from the macaques) with the camera positioned horizontally (0°) and gradually raising it until the canopy was no longer visible.

High thermal contrast zones were defined as study sites that contained only forest elements with continuous canopies, where macaques could easily be distinguished from their surroundings. Low thermal contrast zones were defined as study sites with open canopies, characterized by gaps between trees with little to no vegetation or only grasses and forbs, as well as the presence of walls, roads and buildings beneath sleeping trees (Figure 2) (Pinel-Ramos et al. 2024).

Before we began data collection with our drone, we carried out preliminary drone flights above the sleeping sites of our study groups at different flight altitudes to determine the maximum altitude AGL at which macaques could still be clearly distinguished from the background. We found that at 80 m AGL macaques could no longer clearly be detected (65–72 m distance between drone and canopy). Thereafter, we carried

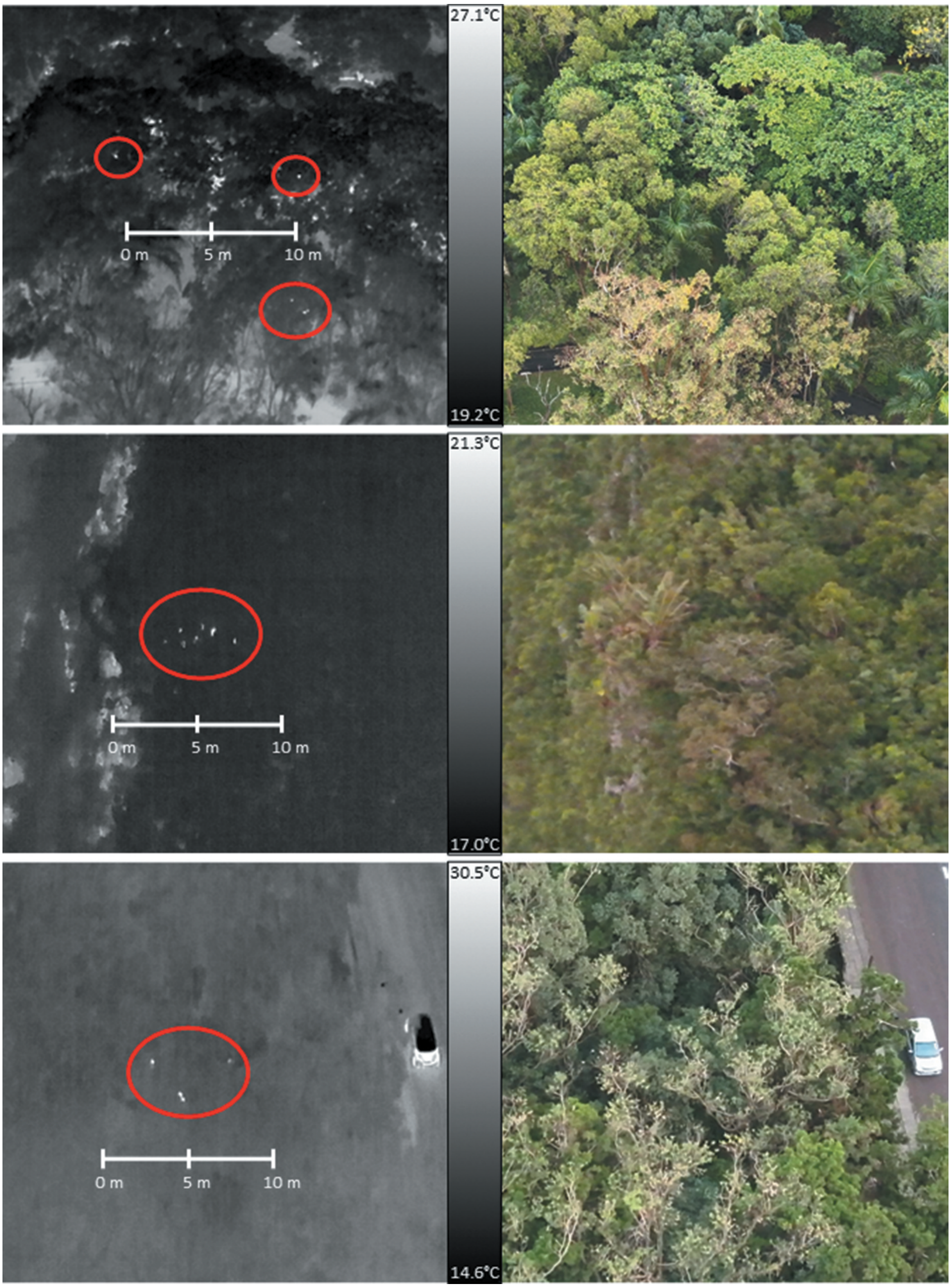

Figure 2. Screenshots of thermal infrared camera (left) and matching red-green-blue camera videos (right) showing long-tailed macaques (*Macaca fascicularis*) at a sleeping site in Balfour Garden (top), Gorges Viewpoint (middle) and Grand Bassin (bottom). Features with similar surface temperature as macaques (e.g., concrete and dirt roads, walls and roofs) are visible in between the open canopy at Balfour Garden, representing a low thermal contrast zone. These features are absent under the continuous canopy at Gorges Viewpoint and Grand Bassin (macaques are clearly distinguishable from the foliage), representing high thermal contrast zones. In each thermal image, macaques are highlighted with a red circle. An approximate scale bar based on the horizontal field of view in the middle of the camera screen has been added to illustrate the spread of macaques at each sleeping site. Videos were taken in the morning with similar weather conditions at 50 m flight altitude above ground level with 45° camera angle. The study was conducted in Mauritius from January to June 2024.

out flights along line transects at four different altitudes (70, 60, 50 and 40 m AGL) with two different TIR camera angles (90° and 45°) in the evening (from 15 minutes before until 15 minutes after sunset) and the following mornings (from 15 minutes before until 15 minutes after sunrise) over 47 days from January to June 2024. The flight routes for each sleeping site were first created in Google Earth Pro (version 7.3.6.9796) and the resulting kml files transferred to the DJI Smart Controller and converted to way-point flights in the DJI Pilot 2 app. On days that the group's location had shifted slightly within a sleeping site (10–20 m), we created an additional line transect on site to realign the flight path with the group. All study sites were relatively flat, with maximum mean sea level (msl) changes of four m along line transects. On the day of each evening flight, we arrived 3 hours early to locate and follow the study group back to their sleeping trees, confirming all group members were present. None of the study groups changed in size during our study period. Sometimes the group split into two subgroups that slept in separate locations (~100 m distance between subgroup sleeping trees). In such cases, we followed a single subgroup and counted the individuals present.

Once the group (or subgroup) entered their sleeping trees, we flew the drone at 2 m/s over the sleeping site along a 50–100 m line transect. We repeated this transect four times (one for each flight altitude), starting at 70 m and decreasing the altitude with every successive flight. For each flight, we recorded a video with a camera angle of 45° and switched to 90° when the first macaque left the horizontal FoV at the bottom of the screen. The RGB and TIR cameras recorded simultaneously (using the White-Hot colour palette for TIR videos). Still images were taken to measure the macaques' surface temperature for comparison to the background temperature using the DJI Thermal Analysis Tool 3 (Figure 3). We stopped recording 90° videos at Balfour Garden after 3 days of unsuccessful attempts, as the low thermal contrast made it impossible to distinguish the macaques from the background at this angle. Additionally, flights conducted with a 90° angle in Balfour Garden often required extending slightly beyond the park's perimeter into residential areas to ensure coverage of sleeping trees located near the park's edge, which would have been in violation

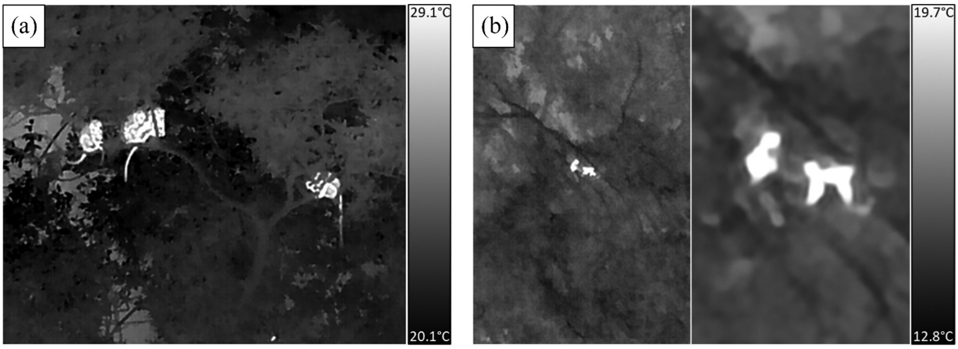

Figure 3. Thermal signatures of long-tailed macaques (*Macaca fascicularis*) sitting in a tree at Gorges Viewpoint recorded with the thermal infrared camera from the ground at ~10 m distance in the evening (A) and two macaques at Grand Bassin recorded at 40 m flight altitude (~30 m distance between drone and canopy) with a camera angle of 45° in the morning with (B right) and without x4 zoom (B left). The study was conducted in Mauritius from January to June 2024.

of the permit conditions established by the Department of Civil Aviation in Mauritius for this study.

Macaques in the same sleeping site never slept further apart than the smallest horizontal FoV (32 m at 40 m flight altitude). We calculated horizontal FoV using the equations and images provided by Burke et al. (2019) (Table 1 in Supplementary Information 2). Each flight lasted ~1–3 minutes, enabling us to complete all four successive flights within 15 minutes. The flight plan was repeated the following morning. After each morning flight, we waited for the macaques to emerge from their trees to confirm that all members counted on the previous evening were still present. The drone's take-off location was always 50–100 m away from the sleeping site. Flights were only carried out on clear days and cancelled when it started raining. We recorded air temperature (°C) 5 minutes before every flight using the UAV Forecast app (UAV Forecast 2025).

2.3. Macaque response to the drone

Long-tailed macaques express different verbal and non-verbal behaviours in agonistic interactions or in response to predators (Aureli and Van Schaik 1991; Palombit 1992; Thierry 1985; Van Schaik and Mitrasetia 1990). Even though in Mauritius macaques have no natural predators, these anti-predator responses can often be observed when macaques encounter humans (if unhabituated) or stray dogs (*Canis lupus familiaris*, Canidae) (Reinegger pers. obs. 2019; 2020; 2023). To assess the response of macaques to the drone, we defined a four-point stress response scale, ranging from no response to severe stress/anti-predator responses (Table 2).

Table 2. The four-point scale used to describe stress/anti-predator responses of long-tailed macaques (*Macaca fascicularis*) in our study groups to the drone.

Severity	Description	Expected impact on detection
No response	Individuals show no visible reaction to the drone, continuing their regular activities without interruption or signs of stress.	Detection rates are optimal, facilitating accurate counts.
Mild	One or few individuals display vigilance behaviours, such as moving up to the canopy to monitor the drone, accompanied by brief and infrequent vocalizations (screech or 'kra'-call), yawning, and minor self-directed behaviours like grooming or scratching.	Detection remains largely effective, as individuals stay in the same relative location, primarily expressing curiosity and vigilance. Detection rate improves if more individuals move up to the canopy.
Moderate	Several individuals become alert, with some changing position in the canopy to monitor or avoid the drone. Infrequent vocalizations (screech, 'kra' or alarm call) or non-verbal anti-predator behaviours, such as yawning or branch-shaking, may occur. Some movement between sleeping trees can occur, but individuals remain within their sleeping site and the drone's Field of View (FoV).	Detection is still feasible and may improve if individuals move up to the canopy, but may begin to decline if individuals start to avoid the drone.
Severe	The group displays clear signs of distress, with increased vocalizations and alarm calls. Many individuals may shift locations or disperse from the immediate area and outside the drone's FoV.	Severe stress responses lead to panic and fleeing, significantly impairing detection and requiring drone flight termination.

The study was conducted in Mauritius from January to June 2024.

Mild-to-moderate stress responses in macaques are acceptable, as they remain in the same location and mainly express curiosity or increased vigilance (e.g. monitoring the drone). However, severe stress responses, which result in panic and fleeing from the sleeping site, should be avoided. To monitor the macaques' responses during drone flights at different altitudes, one observer remained 15–20 m from the sleeping site. Over the course of the full-day observations macaques ignored the observer at this distance when resting at their sleeping sites. If macaques fled their sleeping trees at a particular flight altitude, we aborted the drone flight.

2.4. *Observer-related error*

We investigated the consistency of different observers in identifying and counting macaques using TIR imaging with drones. Two experienced observers trained two volunteers from two local research and conservation organizations (National Parks and Conservation Service [NPCS] and University of Mauritius), who had no prior experience viewing thermal videos but had experience observing wild macaques. During the training, they viewed TIR videos containing thermal signatures of arboreal (macaques and bats) and ground-dwelling mammals (stray dogs can sometimes be visible under open canopy but have very different locomotion patterns from macaques) at different flight altitudes to familiarize themselves with distinguishing features of macaques versus other animals. Before the observers viewed the TIR videos collected in our three study sites, we established a set of criteria to handle different thermal signatures and macaque clumps to minimize misidentification and double counting. These criteria were summarized in an instruction manual for the observers (Supplementary Information 3). The videos were first independently viewed by all four observers. Each video, lasting 20–40 seconds, was rewound and paused three to four times, resulting in a total viewing time of ~4 hours for all videos ($n = 239$) per observer (~1 minute per video). Unfortunately, detections from different observers could not be matched, because thermal signatures could not be labelled time-effectively. Therefore, all observers conferred after completing their respective counts and agreed that unclear thermal signatures (bright dots with no clear contours or movement) were the primary source of mismatches between independent counts. Subsequently, the two experienced observers cross-checked all videos simultaneously, using the RGB camera combined with the Windows magnifier when possible (Figure 4). They conferred about unclear thermal signatures while viewing videos and disregarded them when the RGB footage did not improve detection certainty, accommodating misidentification in availability error (Brack, Kindel, and Oliveira 2018).

For each flight parameter combination, we then calculated percent error (δ) per observer (percentage of misidentified macaques) as follows:

$$\delta_i = \frac{V_i - V_{Cross}}{V_{Cross}} * 100\% \qquad (1)$$

where δ_i is the percentage error for observer i (1, 2, 3 or 4), V_{Cross} is the value of the cross-checked count and V_i is the independent count of observer i.

Figure 4. Screenshots of thermal infrared camera (left) and matching red-green-blue camera videos with x4 zoom using the Windows Magnifier (right) of a long-tailed macaque (*Macaca fascicularis*) moving along a branch at Grand Bassin (top), a stray dog (*Canis lupus familiaris*) walking on the ground at Balfour Garden (middle) and a Mauritian flying fox (*Pteropus niger*) roosting close to Gorges Viewpoint (bottom). All videos were recorded at 50 m flight altitude (~40 m distance between drone and canopy) with a camera angle of 45°. The study was conducted in Mauritius from January to June 2024.

2.5. Availability error

After correcting for observer error, we calculated detection rates per video (DR) as follows:

$$DR = \frac{V_{Cross}}{V_{True}} \tag{2}$$

where V_{Cross} is the cross-checked count per video and V_{True} the total number of animals that were followed back to the sleeping site (for evening flights) or emerged from the sleeping site (for morning flights) when the video was recorded. We also determined whether averaged detection rates for different flight parameter combinations could improve group size estimates by dividing cross-checked counts for specific flight parameter combinations by their respective averaged detection rates. We then calculated the percentage error of unadjusted and adjusted cross-checked counts compared to the true group sizes using Equation 1, with δ_i now representing the percentage error for cross-checked count i (unadjusted or adjusted) and replacing V_i with the (unadjusted or adjusted) cross-checked count and V_{cross} with the true group size. We also calculated the percentage of total flights for which the group size estimate improved with adjustment.

2.6. Statistical analyses

2.6.1. Macaque response to the drone

To test the effect of flight altitude on the severity of macaque stress/anti-predator responses, we used a Bayesian mixed effects ordinal regression model (using package *brms*) (Bürkner 2024) with stress response as dependent variable. The model included a two-way interaction between site and flight altitude as a predictor. We incorporated days of exposure to the drone ($N = 16$, 17 and 14 days for Balfour Garden, Gorges Viewpoint and Grand Bassin respectively) and group size as covariates (both treated as continuous variables), given that larger groups can exhibit reduced anti-predator behaviour (Roberts 1996), and individuals may show increased tolerance to the drone with repeated exposure (Spaan et al. 2019). Flight day was included as a random effect to account for potential temporal autocorrelation between successive flights, as vigilance may increase across repeated flights within a single day (Spaan et al. 2019).

We used the cumulative model since stress responses observed at higher flight altitudes could also occur at lower ones. Model fit was assessed by comparing predicted probabilities for each stress response (i.e. the predicted proportions of flights in which each stress response occurred at different flight altitudes) to the observed proportions of flights with each stress response at different altitudes. Additionally, we compared the distributions of the observed and simulated datasets. We evaluated the model's performance against a null model using Leave-One-Out (LOO) cross-validation, with smaller LOO information criterion (LOOIC) values indicating a better fit (Bürkner and Vuorre 2019). Pairwise comparisons were tested using 95% credible intervals (CIs) (Nakagawa and Cuthill 2007) with the package *emmeans* (Lenth et al. 2024), with 90%, 95% and 99% CIs used to classify the strength of evidence as weak, moderate, or strong, respectively (Muff et al. 2022).

2.6.2. Observer-related error

We measured inter-observer reliability for different time slots (morning and evening), flight altitudes (70, 60, 50 and 40 m) and camera angles (45° and 90°) in every site by calculating Krippendorff's alpha for the independent observer counts. Values ≥0.80 indicate good inter-observer reliability (Krippendorff 2019). We bootstrapped Krippendorff's alpha values by resampling counts ($n = 1000$ resamples) for all available observer pairs for each flight parameter combination, to compute 95% confidence intervals (Krippendorff 2019).

2.6.3. Availability error

To identify optimal flight parameters, we tested the effects of flight altitude and camera angle on detection rates using a Generalized Linear Mixed Model (GLMM) with two-way interactions among site, time slot, camera angle and flight altitude (*glmmTMB* package; Magnusson et al. 2024). We excluded complex four-way interactions due to small sample size ($n = 3$ for two combinations), with exclusion validated by plotting detection rate against site, time slot, camera angle and flight altitude, which revealed site-driven variations (Figure 1 in Supplementary Information 2). Although the effect of climatic variables on detectability is probably small when flying at altitude <100 m (Burke et al. 2019), we included air temperature as covariate. We also included macaque group size as a continuous variable and flight day as a random effect to address temporal autocorrelation. A likelihood ratio test confirmed that including this random effect improved model performance (Verbeke and Molenberghs 2000). We did not include sleeping site ID as covariate as the small number of sleeping sites (1–3) reused by each study group were all located in the same small (homogeneous) forest patch. The model maintained an adequate parameter-to-sample ratio (n/k ratio ≥10), reducing risks of overparameterization (Harrison et al. 2018).

We evaluated the global model's fit using residual diagnostic plots from package *DHARMa* (Hartig 2022), an established method for assessment of goodness of fit (Burnham and Anderson 2002). We examined the variance explained by the fixed and random effects using marginal and conditional R^2 values respectively (Nakagawa, Johnson, and Schielzeth 2017). To assess model performance, we compared observed vs. predicted values by plotting them and fitting a best-fit line to see how closely it aligned with an ideal correlation ($r = 1$). Additionally, we computed marginal means for detection rates across all combinations of site, time slot, camera angle and flight altitude, and evaluated agreement between observed and predicted means. For inference, we relied on the global model, which offers a balanced view of both statistically significant and non-significant results (Forstmeier and Schielzeth 2011). We compared the global model to a null model using a likelihood ratio test to assess the probability of significant effects due to sampling variation alone, applying the same statistical significance criteria as in the Bayesian mixed-effects model (Forstmeier and Schielzeth 2011). All analyses were conducted in R (version 4.3.1) (R Core Team 2023).

We also tested whether cross-checked counts became closer to actual group sizes (indicated by a decrease in percentage error) after adjusting them with mean detection rates for the different combinations of flight parameters using a Linear Mixed Model (LMM). We used percentage error as response variable and included the same two-way interactions and random effect as in the GLMM testing the effects of different flight parameters on detection rate. However, the two-way interactions were expanded to three-way interactions by adding cross-checked count type (adjusted or unadjusted) to each interaction. For model fit evaluation and inference, we used the same methods as for the GLMM.

3. Results

3.1. Macaque response to drone

In Balfour Garden, flights at 40 m (~30 m above the canopy) caused macaques to panic and move outside of the drone's FoV ($n = 5$ flights). In the other two sites, macaque moved outside FoV in 46% of flights at 40 m ($n = 12$). At 50 m, severe anti-predator responses were observed only in Balfour Garden (38% of the flights, $n = 5$), though less extreme than at 40 m. No severe anti-predator responses were observed at 60 ($n = 70$ flights) or 70 m ($n = 70$) in any sites.

Our model indicated that mild or no response were more likely at higher flight altitudes, while more severe stress responses (moderate and severe) were more likely at lower altitudes (Table 1 in Supplementary Information 4; Figure 5). Although not all differences in stress response probabilities were statistically significant, coefficients for pairwise comparisons had consistent direction across sites (except for mild responses) (Table 1 in Supplementary Information 4).

We found no effect of exposure frequency on stress response severity, with changes in probabilities with one additional day of exposure smaller than 0.1%, and 10% credible intervals containing zero. However, group size moderately affected the likelihood of

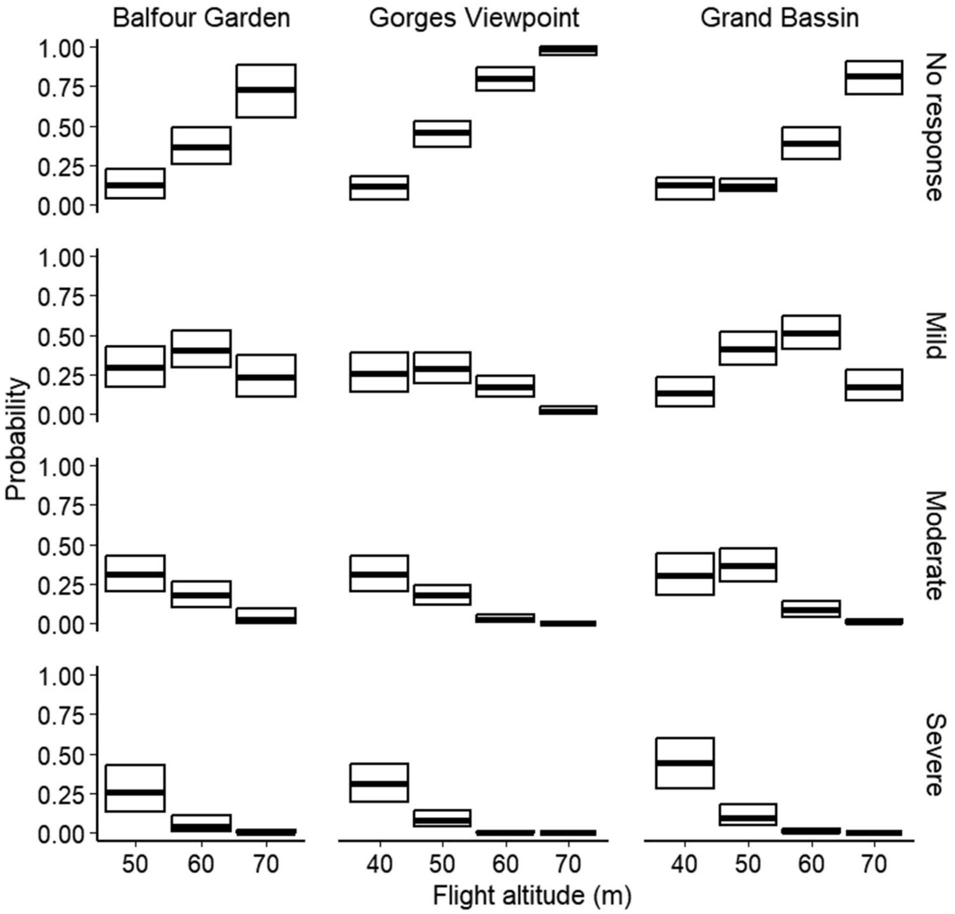

Figure 5. Predicted probabilities with 95% credible intervals for different categories of stress/anti-predator response (no response, mild, moderate and severe) of long-tailed macaques (*Macaca fascicularis*) at different flight altitudes in the three study sites as estimated by the Bayesian mixed effects ordinal regression model. The study was conducted in Mauritius from January to June 2024.

response, with larger groups more likely to react to the drone (coefficient ± *SE* = −0.03 ± 0.01, $\mathrm{CI}_{\mathrm{low}} = -2.31$, $\mathrm{CI}_{\mathrm{up}} = 0.02$). Model performance was good, with predicted probabilities aligning with observed values (Table 2 in Supplementary Information 2). The LOOIC indicated a better fit for our model (LOOIC = 333.5) compared to the null model (LOOIC = 532.9).

3.2. Observer error

Observer agreement was generally high in two out of three study sites (Gorges Viewpoint and Grand Bassin) for all combinations of time slots, camera angles and flight altitudes, with Krippendorff's alpha values >0.8 and narrow confidence intervals (Table 3). Lower values (<0.8) with wide confidence intervals were found only for flights in Balfour Garden, flights at 70 or 40 m altitude and flights with a camera angle of 90° (especially in the evening), indicating that morning flights at 60 and 50 m with a camera angle of 45° over sites with continuous canopy cover provide the highest and most consistent inter-observer reliability (Table 3). These values were reflected by high and variable percent error (δ) for both experienced and inexperienced observers in the evening in Balfour Garden and in the evening at Grand Bassin with a 90°Camera angle (Table 2 in Supplementary Information 4). The surface temperature of detected macaques across all sites varied little between mornings (mean ± *SD* = 19.3 ± 1.4°C, *N* = 25 images) and evenings (19.1 ± 1.8°C, *N* = 27 images), providing a thermal contrast with the canopy of 1.5 ± 0.9°C and 1.95 ± 1.0°C respectively. Surface temperatures of concrete structures, roads, rocks and cliffs were similar to those of macaques (19.4 ± 2.8°C, *N* = 32 images). Air temperature ranged from 18°C to 28°C (22.5 ± 2.6°C, *N* = 25 days) and 16°C to 27°C (21.6 ± 2.8°C, *N* = 22 days) in the evenings and mornings, respectively.

3.3. Availability error

Mean detection rates were highest in sites with high thermal contrast (Gorges Viewpoint and Grand Bassin) and generally decreased with increasing flight altitude (Table 3 in Supplementary Information 2). Detection rates were higher at 60 and 50 m compared to 70 m across all sites, time slots and camera angles. At 40 m, detection rates were slightly lower than at 50 m in Grand Bassin, probably due to macaques dispersing into neighbouring trees outside of the drone's FoV in response to the drone. Failing to detect macaques when they were present only occurred at Balfour Garden and Grand Bassin in the evening and at 70 m (Figure 6). Averaged across both sites with high thermal contrast (Gorges Viewpoint and Grand Bassin), the detection rate for morning flights with 45° camera angle was 0.67 ± 0.08 (mean ± SE) for 50 m and 0.62 ± 0.08 for 60 m. With a 90° camera angle the averaged detection rates were 0.60 ± 0.09 and 0.56 ± 0.09 for morning flights at 50 and 60 m, respectively.

The global GLMM explaining the effects of time slot, camera angle and flight altitude on detection rate in the three study sites confirmed that these differences were not caused by random variation alone. We found moderate-to-strong evidence that detection rate decreases with drone flight altitude at the Gorges Viewpoint and Grand Bassin (Table 4, Figure 6). There was weak-to-moderate evidence that detection rate is higher in the morning compared to the evening in Balfour Garden and Grand Bassin and strong

Table 3. Krippendorff's alpha (α) together with bootstrapped 95% confidence intervals for long-tailed macaques (*Macaca fascicularis*) counted by four observers in thermal videos taken with a drone with different camera angles and flight altitudes in two timeslots (morning and evening) and three sites: Balfour Garden (low thermal contrast zone), Gorges Viewpoint (high thermal contrast zone) and Grand Bassin (high thermal contrast zone).

	α (CI_{low}, CI_{up})					
	Balfour Garden		Gorges Viewpoint		Grand Bassin	
Angle and flight altitude	Morning	Evening	Morning	Evening	Morning	Evening
45° – 70 m	0.29 (0.21, 0.92)	0.46 (0.39, 0.96)	**0.87 (0.86, 1.00)**	**0.87 (0.83, 1.00)**	0.50 (0.50, 0.99)	**0.96 (0.95, 1.00)**
45° – 60 m	0.51 (0.51, 0.97)	0.70 (0.55, 0.99)	**0.89 (0.86, 0.98)**	**0.91 (0.88, 0.98)**	**0.90 (0.90, 1.00)**	**0.81 (0.78, 1.00)**
45° – 50 m	0.62 (0.59, 1.00)	0.62 (0.43, 0.97)	**0.93 (0.92, 0.99)**	**0.81 (0.76, 0.99)**	**0.81 (0.81, 0.96)**	**0.86 (0.85, 0.98)**
45° – 40 m	–	–	**0.81 (0.76, 0.99)**	**0.83 (0.83, 1.00)**	0.73 (0.56, 1.00)	0.77 (0.76, 0.99)
90° – 70 m	–	–	**0.91 (0.88, 0.98)**	**0.84 (0.78, 0.99)**	0.75 (0.73, 0.99)	0.42 (0.39, 0.99)
90° – 60 m	–	–	**0.85 (0.83, 0.97)**	**0.92 (0.91, 0.99)**	**0.84 (0.81, 0.97)**	**0.99 (0.98, 1.00)**
90° – 50 m	–	–	**0.89 (0.86, 0.99)**	**0.95 (0.95, 0.99)**	0.75 (0.66, 1.00)	0.69 (0.50, 0.99)
90° – 40 m	–	–	0.77 (0.74, 0.97)	**0.84 (0.78, 1.00)**	**0.84 (0.73, 0.99)**	0.36 (0.26, 0.92)

Krippendorff's alpha values ≥ 0.8 have been highlighted in bold, indicating good inter-observer reliability. The study was conducted in Mauritius from January to June 2024.

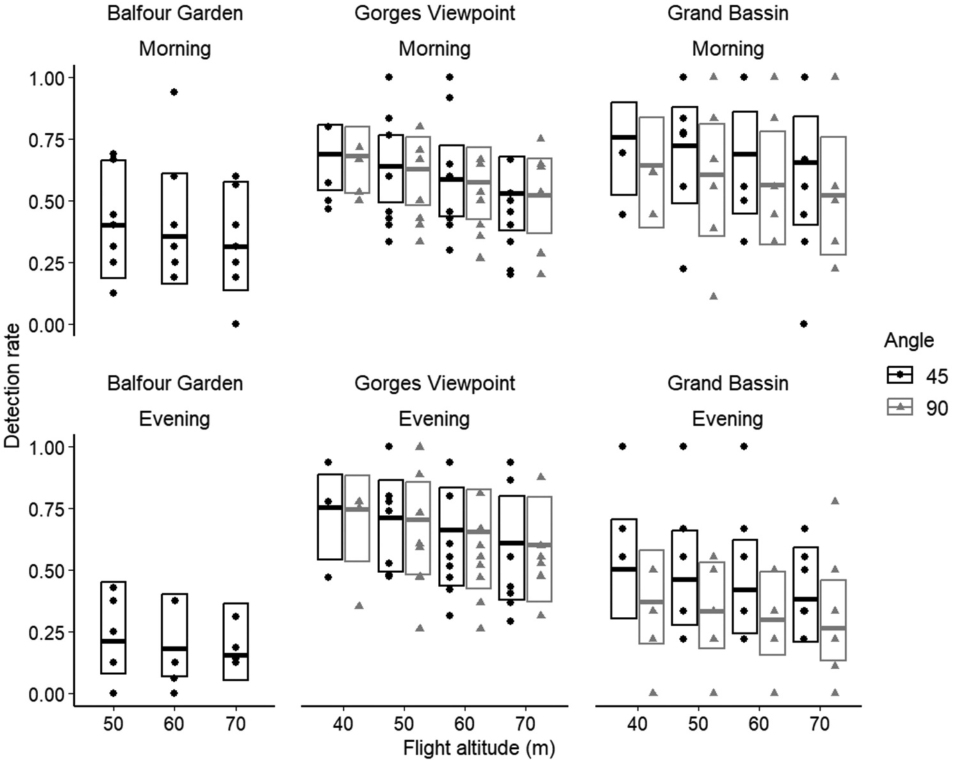

Figure 6. Predicted means with 95% confidence intervals for long-tailed macaque (*Macaca fascicularis*) detection rate at different flight altitudes and camera angles in the three study sites as estimated by the Generalised Linear Mixed Model (GLMM) with binomial error distribution. The data points used for prediction by the GLMM are also plotted. Balfour Garden represents a low thermal contrast zone, whereas the other two sites represent high thermal contrast zones. The study was conducted in Mauritius from January to June 2024.

evidence that detection rate improves with a camera angle of 45° compared to 90° in Grand Bassin (Table 4).

Even though we did not find evidence for a relationship between detection rate, flight altitude, time slot, and camera angle across all sites, the coefficients for the pairwise comparisons had the same direction in most sites. The only exception was the pairwise comparison between the two camera angles in Gorges Viewpoint (Table 4). We found strong evidence for differences in detection rate between Balfour Garden and Gorges Viewpoint at all flight altitudes, and no evidence for differences between Gorges Viewpoint and Grand Bassin or between Grand Bassin and Balfour Garden (Table 5). We also found weak evidence that detection rate decreased with increasing macaque group size (coefficient ± $SE = -0.01 \pm 0.01$, $\mathrm{CI}_{\mathrm{low}} = -0.03$, $\mathrm{CI}_{\mathrm{up}} = 7e^{-5}$) and no evidence for an effect of air temperature on detection rate (0.01 ± 0.03, $\mathrm{CI}_{\mathrm{low}} = -0.04$, $\mathrm{CI}_{\mathrm{up}} = 0.07$).

The predictors in our model explained only 11% of the variation in detection rate ($R^2_{\mathrm{marginal}} = 0.11$, $R^2_{\mathrm{conditional}} = 0.21$), indicating a large proportion of variation is explained by unmodelled heterogeneity. Nevertheless, the best fit line for the observed vs. predicted points closely matched the line of perfect correlation ($r = 1$) between observed and

Table 4. Pairwise comparisons in between predicted detection rates (detected proportion of total long-tailed macaques, *Macaca fascicularis*, present during a flight) between different flight altitudes, camera angles and time slots in the three study sites as estimated by the Generalized Linear Mixed Model (GLMM) with binomial error distribution.

	Site		
Pairwise comparison	Balfour Garden	Gorges Viewpoint	Grand Bassin
Flight altitude 70 m − 60 m	−0.03 ± 0.02 (−0.07, 0.01)	**-0.05 ± 0.01 (−0.08, −0.03)**	**-0.04 ± 0.02 (−0.07, −0.01)**
Flight altitude 70 m − 50 m	−0.06 ± 0.05 (−0.15, 0.03)	**-0.11 ± 0.03 (−0.16, −0.05)**	**-0.08 ± 0.04 (−0.15, −0.01)**
Flight altitude 70 m − 40 m	–	**-0.16 ± 0.04 (−0.23, −0.08)**	**-0.11 ± 0.06 (−0.22, −0.01)**
Flight altitude 60–50 m	−0.03 ± 0.03 (−0.08, 0.02)	**-0.05 ± 0.01 (−0.08, −0.03)**	**-0.04 ± 0.02 (−0.07, −0.01)**
Flight altitude 60–40 m	–	**-0.10 ± 0.02 (−0.15, −0.05)**	**-0.08 ± 0.04 (−0.15, −0.01)**
Flight altitude 50–40 m	–	**-0.05 ± 0.01 (−0.07, −0.03)**	**-0.04 ± 0.02 (−0.07, −0.01)**
Angle 45° − 90°	–	0.01 ± 0.02 (−0.04, 0.06)	**0.13 ± 0.04 (0.05, 0.20)**
Time slot evening – morning	**-0.15 ± 0.08 (−0.31, 0.02)**	0.08 ± 0.10 (−0.12, 0.28)	**-0.27 ± 0.1 (−0.46, −0.07)**

Regression coefficients, standard errors (SEs), and 95% confidence intervals (CIs) are provided for every pairwise comparison in the following format: coefficient ± SE (CI_{low}, CI_{up}). Coefficients for which the 90%, 95% and 99% confidence intervals do not overlap 0 have been highlighted in bold. All results are given as differences in predicted proportions. Balfour Garden represents a low thermal contrast zone, whereas the other two sites represent high thermal contrast zones. The study was conducted in Mauritius from January to June 2024.

Table 5. Pairwise comparisons in between predicted detection rates (detected proportion of total long-tailed macaques, *Macaca fascicularis*, present during a flight) between sites for different altitudes as estimated by the Generalized Linear Mixed Model (GLMM) with binomial error distribution.

	Flight altitude (m)			
Pairwise comparison	70	60	50	40
Balfour Garden – Gorges Viewpoint	**-0.36 ± 0.07 (−0.50, −0.23)**	**-0.39 ± 0.06 (−0.52, −0.26)**	**-0.41 ± 0.07 (−0.55, −0.27)**	–
Balfour Garden – Grand Bassin	−0.25 ± 0.16 (−0.57, 0.06)	−0.26 ± 0.16 (−0.58, 0.06)	−0.27 ± 0.17 (−0.61, 0.07)	–
Gorges Viewpoint – Grand Bassin	0.11 ± 0.16 (−0.21, 0.42)	0.13 ± 0.16 (−0.18, 0.43)	0.14 ± 0.15 (−0.16, 0.44)	0.15 ± 0.15 (−0.14, 0.44)

Regression coefficients, standard errors (SEs), and 95% confidence intervals (CIs) are provided for every pairwise comparison in the following format: coefficient ± SE (CI_{low}, CI_{up}). Coefficients for which the 90%, 95% and 99% confidence intervals do not overlap 0 have been highlighted in bold. All results are given as differences in predicted proportions. Balfour Garden represents a low thermal contrast zone, whereas the other two sites represent high thermal contrast zones. The study was conducted in Mauritius from January to June 2024.

predicted values, indicating good model performance (Figure 2 in Supplementary Information 2). Additionally, agreement between observed and predicted means for different combinations of time slots, camera angles and flight altitudes was generally high (Supplementary Information 1, Table 3). For example, agreement in the mornings at 45° camera angle ranged from 93% to 99% at 60 m and 96% to 99% at 50 m altitude (Table 3 in Supplementary Information 2).

Correcting cross-checked counts with their respective averaged detection rates resulted in counts that were, on average, 4–50% closer to the actual group size for most flight parameter combinations across all sites (Table 3 in Supplementary Information 4). Only for some flight parameter combinations at Grand Bassin (mainly in the morning), unadjusted counts were on average more accurate than the adjusted counts. Nevertheless, for the majority of flights across all flight parameter combinations, counts became closer to the actual group size after adjustment (57–100% of flights) (Table 3 in Supplementary Information 4). However, predictions of the LMM indicated that the differences in percentage error between unadjusted and adjusted counts were not always statistically significant, particularly when flying in the morning in high thermal contrast zones and at flight altitudes of 50 m (Table 3 in Supplementary Information 4).

4. Discussion

4.1. Optimisation of drone flight parameters

We investigated how different flight parameters (flight altitude and camera angle) affect detection errors in TIR drone surveys of long-tailed macaques in different time slots and habitats. Our findings are consistent with recent studies, showing that detection errors are lowest in the morning and at sites with high thermal contrast and canopy cover (Pinel-Ramos et al. 2024; Rahman and Setiawan 2020). Aligning with Gazagne, Gray, Nguyễn, et al. (2024), we found that a 45° camera angle enhanced the detectability of our study species in two out of three sites, primarily due to clearer contours and partial visibility under the tree foliage. However, our results differ from Pinel-Ramos et al. (2024), who reported that a 90° camera angle improved detectability, as the visibility of 'hot' tree trunks and branches at a 45° angle made it difficult to distinguish them from individuals. This discrepancy may be attributed to factors such as the level of habituation to drones (the spider monkeys [*Ateles geoffroyi*, Atelidae] in their study were accustomed to the drone sound), the structural complexity of the canopy (our sites were secondary forests with few dominant tree species in the canopy), and the vertical distribution of the primates around the sleeping site. While spider monkeys sleep close to the canopy, macaques can be distributed over both shrub and tree layers (Gazagne, Gray, Nguyễn, et al. 2024), which may make detection more challenging at a 90° angle. These differences in optimal flight parameters suggest that a 45° camera angle may be more effective for detecting primates that sleep across multiple forest strata.

As in previous studies, our findings demonstrate that high levels of agreement can be achieved between observers with varying experience in detecting animals in TIR videos (Pinel-Ramos et al. 2024; Spaan et al. 2019; Whitworth et al. 2022). However, we recommend training observers beforehand to familiarize them with thermal signatures of both target and non-target species in the survey area. Moreover, we did not investigate the influence of flight speed on detection error as we only flew at low speeds. Detection error increases with flight speed, particularly if it exceeds 3–4 m/s (Pinel-Ramos et al. 2024; Whitworth et al. 2022). Therefore, we recommend maintaining flight speeds below 3–4 m/s in future surveys of long-tailed macaques in Mauritius.

Our findings indicated that adjusting counts with mean detection rates results in more accurate group size estimates in most cases, particularly when flying with non-optimal flight parameters (up to 50% more accurate). Therefore, when researchers cannot use optimal flight parameters for surveying long-tailed macaques (e.g. due to limited time or the need to cover large areas), adjusting counts with mean detection rates can be valuable. In these cases, the error associated with the estimated detection rates should also be propagated to the final counts. With optimal flight parameters, adjusting counts did not always improve accuracy, due to variability in detection rates and the increasing accuracy of unadjusted counts. Nevertheless, further refinement of detection rates would be worthwhile, especially to enhance their utility when flying with optimal flight parameters. For example, estimates for mean detection rates could be optimized using a model-selection procedure with additional data and covariates, such as canopy structural complexity.

4.2. *Macaques' response to drones*

Long-tailed macaques exhibited a range of stress and anti-predator behaviours in response to the drone, which appeared more pronounced compared to some other primate species. For example, black-shanked douc langurs (*Pygathrix nigripes*, Cercopithecidae) and spider monkeys mainly change positions (e.g. moving down the canopy) when drones fly above their sleeping sites at 35–50 m and they generally stay within the detection area (Gazagne, Gray, Nguyễn, et al. 2024; Spaan et al. 2019). Additionally, individuals increasingly ignore the drone with repeated exposure (Gazagne et al. 2023; Spaan et al. 2019). In contrast, long-tailed macaques in our study sites sometimes panicked and moved away from their sleeping trees when the drone maintained a 30 m distance from the canopy, similar to northern pig-tailed macaques (*Macaca leonina*, Cercopithecidae) and yellow-cheeked gibbons (*Nomascus gabriellae*, Hylobatidae) in Vietnam (Gazagne, Gray, Nguyễn, et al. 2024). Given that there are no large predatory birds capable of hunting macaques in Mauritius, this response is probably related to higher noise levels at lower flight altitudes and a general fear of novelty. We did not observe any reduction in stress response with repeated exposure days. While more frequent exposure might eventually habituate the macaques to drone flights (Pinel-Ramos et al. 2024), this is unlikely for large-scale surveys with limited site visitation.

At higher flight altitudes, long-tailed macaques also expressed different stress behaviours. However, we consider these responses acceptable as alternative survey methods, like line transects, would cause similar or even more extreme stress behaviours in macaques that are not accustomed to human presence (Buckland et al. 2010; Spaan et al. 2019). Moreover, anti-predator behaviours observed at 50 and 60 m altitudes helped minimize availability error during the study, because more individuals moved up to the canopy to monitor the drone. Previous studies have found similar improvements in detectability due to increased vigilance and movement in response to the drone (Rahman et al. 2020). Remarkably, smaller groups of macaques were more likely to not respond to the drone. Vigilance usually increases as group size decreases (Roberts 1996), and we may have sometimes mistaken lack of movement for 'no response' when individuals were concealed by foliage. Conversely, with larger groups, the likelihood of one macaque panicking and triggering a chain reaction of alarm in others may increase. Nevertheless, this behaviour is unlikely to affect counts, as group size did not negatively impact detection rate, possibly due to the relatively small size of our groups and the aggregation of macaques in a limited number of sleeping trees.

4.3. Challenges in drone survey accuracy

One of the main challenges we anticipate in future drone surveys of primates using TIR videos is measuring different types of observer-related error to correct survey results. Independent or dependent double-observer protocols, in which animals detected by different observers are labelled for matching, are typically used to measure perception error (probability of missing an animal) or misidentification rate (Delisle et al. 2023; Pollock et al. 2006; Vermeulen et al. 2013). Efficiently labelling thermal signatures of animals in videos requires specialized software (Delisle et al. 2023) or deep learning algorithms (Jintasuttisak et al. 2022). With our approach, we could not match detections from different observers, as the detected animals could not be labelled. Instead, we used the RGB camera to cross-check and exclude unclear thermal signatures, reducing misidentification rate and providing a less biased count (Brack, Kindel, and Oliveira 2018). However, this approach does not account for perception error. Fortunately, clear thermal signatures of macaques were generally easily spotted as our study groups were relatively small and videos short. Nevertheless, this becomes increasingly unfeasible with larger groups and longer videos. We suggest considering paid software, such as LineVision – Ultimate (GeoSystems Inc.) (Delisle et al. 2023), for tracking individuals in future surveys of larger groups. Another option would be using still images instead of videos (McCarthy et al. 2021; Vermeulen et al. 2013), but in our case movement was often essential to avoid misidentification.

Misidentification may also become more difficult to account for in surveys with multiple species of interest (Brack, Kindel, and Oliveira 2018). We confused macaques most often with immobile objects (e.g. rocks and branches), meaning that we could hide misidentification in perception and availability error by ignoring unclear thermal signatures (Brack, Kindel, and Oliveira 2018). However, this is not appropriate when the detected signature is clearly one of multiple species of interest. Our study sites had only two medium-sized arboreal animals with clear differences in body shape and size, minimizing risk of misidentification, particularly with RGB camera cross-checking.

Another concern with our method is topographic relief. The sleeping sites surveyed during our study had little variation in altitude (max 4 m msl change along line transects). Such elevational changes do not greatly influence counts (e.g. with optimal flight parameters mean detection rate only changed by 5% with a 10 m change in flight altitude). However, greater variation in topographic relief along the flight path would require adjusting flight altitude to avoid non-constant detection rates. The DJI Pilot 2 app allows for adjusting flight altitude at every waypoint in pre-programmed flights. Therefore, we recommend creating flight paths in Google Earth, to view the elevation profile along the route. This approach enables researchers to add waypoints where flight altitude adjustments are required.

Failing to detect young infants attached to their mothers can also introduce additional errors. Fortunately, during our study, young infants made up only a very small part of each study group. However, in long-tailed macaques, the infant-to-adult female ratio varies from year to year (Fooden 1995), and the proportion of infants in a group can be much higher (Sussman, Shaffer, and Guidi 2011). To avoid missing too many individuals, it would be valuable to conduct surveys before the primary birth period in March, which coincides with the start of fruiting of abundant invasive plants (e.g. *P. cattleyanum*) (Jamieson 1998). However, in areas where macaques have access to abundant orchard fruits (e.g. lychee, *Litchi chinensis*, and mango, *Mangifera indica*) that ripen in November/December, birth peaks have also been observed in October (Reinegger pers. obs. 2024). Therefore, in these areas, it may be worth avoiding October and November, as infants are completely dependent on their mothers during the first 8 weeks (Meishvili and Chalyan 2000).

4.4. Large-scale surveys and other applications

The suitability of commercially available drones for surveying larger areas requires further attention. To avoid violating assumptions of closure and independence in population surveys, surveyed plots should be sufficiently spaced to avoid detecting an animal group in multiple plots (O’Connell and Bailey 2011). Additionally, sampled areas should ideally cover the study species’ entire home range to avoid false absences (O’Connell and Bailey 2011). This may not be feasible for species with large home ranges, considering that battery life of commonly used drones ranges between 30 and 50 minutes (Gazagne et al. 2023; Pinel-Ramos et al. 2024; Rahman et al. 2020), and reception between the remote control and drone is often poor in dense forests (Gazagne, Gray, Nguyễn, et al. 2024; Reinegger pers. obs. 2024). Another option would be to use an occupancy-modelling approach with multiple surveys at each site (MacKenzie et al. 2002).

Another consideration is that flights must be completed before the study animals move away from their sleeping sites. For example, when using grid flights (flights in lawnmower pattern), animals can start moving between adjacent strips, increasing the chances of double counting. In our case, long-tailed macaques often moved away from sleeping sites ~15–20 min after sunrise. We could not start more than ~15 minutes before sunrise (to guarantee sufficient daylight for use of RGB cameras), meaning we would have a 30-minute window to complete surveys at larger spatial scales. Fortunately, home ranges of long-tailed macaques in Mauritius can be relatively small (35 ha) and the DJI Mavic 3T is capable of surveying larger areas (25 ha) within a relatively short time (~30 min) when using the recommended flight parameters (Reinegger et al. unpublished data).

The application of our survey protocol to other primates or even other *Macaca* spp. also requires further investigation. Canopies in our study sites were relatively simple, featuring a single tree layer composed of few dominant species, unlike preserved, species-rich tropical primary forests. Higher structural complexity of canopies in primary forest may reduce detection rates of macaques, as they typically sleep across multiple forest strata (Gazagne, Gray, Nguyễn, et al. 2024). Additionally, our study groups were relatively small and often slept aggregated, using a limited number of sleeping trees in close proximity. However, groups of *Macaca* spp. can be much larger ($n > 50$) and spread out over many sleeping trees (Gazagne, Gray, Nguyễn, et al. 2024). Therefore, for primates spread over large sleeping sites in structurally more complex forests than Mauritian secondary forests, further context-specific evaluation of our methods is needed.

Conservation practitioners are in constant need for more robust and accurate local and large- scale surveys to guide their management. Such novel methods, once optimized, as shown by our findings, can be promising and effective to garner new insights on population density, distribution, habitat use, behaviour and movement (Wich and Koh 2018). In Mauritius, it matters to have a reliable understanding of the population size and distribution of the invasive long-tailed macaques, to enhance management efforts. As an invasive species, these macaques disrupt local ecosystems, outcompete native species, and cause agricultural damage (Baider and Florens 2013, 2022; Reinegger et al. 2021, 2023; Sussman, Shaffer, and Guidi 2011). Using TIR cameras would allow for efficient and accurate population monitoring and by identifying high-density areas and tracking movement patterns, conservationists can prioritize intervention efforts, such as targeted removal or relocation programmes. This technology also will eventually help in assessing the effectiveness of management interventions over time through long-term monitoring, allowing for adaptive management approaches that can be fine-tuned based on real-time dat

5. Conclusion

Our study further supports the effectiveness of drone-mounted TIR cameras for detecting and counting primates. However, our findings highlight that both observer-related and availability error, as well as anti-predator responses, are context-dependent, underscoring the need for standardized protocols adapted to specific species and habitat types. In secondary forest habitats in Mauritius, we recommend conducting TIR drone surveys in high thermal contrast zones during morning hours, utilizing low-speed flights (≤4 m/s) with a 45° camera angle. Maintaining a distance of 40–50 m between the drone and canopy will optimize detection rates and enhance inter-observer reliability. The detection rates established in this study can inform adjustments in future counts of groups with unknown sizes, providing a valuable tool for wildlife monitoring and conservation planning. We particularly recommend correcting counts with averaged detection rates when flying in the evening, in low thermal contrast zones or above 50 m altitude, as they can improve group size estimates by as much as 50%. An approach similar to ours can be used to refine TIR drone survey protocols for other primates and habitats.

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Data availability statement

The videos and datasets collected and analysed for this publication are available from the corresponding author on reasonable request.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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