American Journal of Primatology

WILEY

AMERICAN JOURNAL OF PRIMATOLOGY

RESEARCH ARTICLE OPEN ACCESS

Motherhood and Sex Predict Emotional Reactivity During a Predator Confrontation in Two Macaque Species

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Received: 7 October 2025 | **Revised:** 9 February 2026 | **Accepted:** 16 March 2026

Funding: European Union's Horizon 2020 Marie Skłodowska-Curie Action research and innovation program, Grant/Award Number: H2020-MSCA-IF-2019-893016

Keywords: affective states | dimensional approach | macaque species | motherhood | non-invasive techniques | stress

ABSTRACT

Understanding how animal emotions influence behavior and physiology is essential to comprehend animals' emotional responses and how these may differ between individuals. However, accurately assessing animal emotions is challenging due to their multifaceted nature and the need for multimodal approaches. This study investigates the effect of maternal status (mothers vs. females without dependent offspring), sex, and species on the emotional reactivity of two macaque species (long-tailed and rhesus macaques) confronted with a threatening situation. Using a non-invasive and multidimensional approach, we collected data on their behavior, facial temperature changes, and vocal reactivity during a predator exposure. We show that mothers produced a stronger initial physiological response, that is, a decrease in the nose tip temperature, whereas males and non-mothers showed a stronger behavioral response, with an increase in stress-related behaviors 10 min after exposure. Vocal behavior, however, did not differ across groups or species. Long-tailed macaques had a stronger initial physiological response and showed more stress-related behaviors at the beginning of the experiment than rhesus, while rhesus macaques showed more stress-related behaviors at the end. While mothers showed a stronger internal physiological response, non-mothers and males may be in a position to afford stronger behavioral reactions. Long-tailed macaques seem to respond faster to threats than rhesus macaques, which is in line with them being more vulnerable to predators. In conclusion, our study shows that emotional responses to a potential danger differ across maternal status, sex, and species, and concurrently highlights the importance of a multidimensional approach when studying such differences.

1 | Introduction

The question of whether animals experience emotions has been a longstanding topic of both scientific exploration and philosophical debate. Over the past three decades, many empirical studies have rendered the statement “Animals do have emotions” as undeniable. This has accelerated investigation toward the understanding of the potentially rich and deep emotional life of animals (Mendl et al. 2022; de Waal and Andrews 2022; Kret et al. 2022), and emphasized the need for empirical evidence (Dawkins 2006; LeDoux 2021; Carranza-Pinedo et al. 2025), improving our understanding of the evolution of emotions and allowing us to better assess the animals' affective states (i.e., animal welfare).

https://doi.org/10.1002/ajp.70143

Summary

- To better understand animals' emotional reactivity, a multidimensional approach is essential.
- Behavioral, vocal, and physiological parameters reveal different patterns regarding long-tailed and rhesus macaques' emotional reactions to a predator model.
- In particular, maternal status, sex, and species influence these differences in macaques' emotional responses.

Although there was an initial lack of consensus about how researchers can describe and study animal emotions, more recent work shows a general agreement across different research fields (Mendl et al. 2010; Bliss-Moreau 2017; de Waal and Andrews 2022; Zipple et al. 2024). Similar to human emotions, animal emotions can be defined as a multidimensional response composed of physiological, behavioral, and cognitive reactions (Paul and Mendl 2018; Bliss-Moreau 2017; Massen et al. 2019; Kremer et al. 2020) that are triggered by social and environmental events (Panksepp 2005). These multidimensional responses have been recently studied using the "dimensional approach" (cf., Mendl et al. 2010). This theoretical framework views emotions as the set of responses falling along a continuum of two dimensions; that is, "valence and arousal" (Mendl et al. 2010; Mendl and Paul 2020; Mendl et al. 2022; Briefer 2012). Valence is based on the positive and negative reaction to a specific situation, and arousal is based on the intensity of this reaction (Mendl et al. 2010; Mendl et al. 2022). This framework provides researchers with an alternative and less anthropomorphic perspective to the traditional view of emotions that classifies them into discrete categories (e.g., fear, sadness, or happiness) (Mendl et al. 2010).

Contemporary studies use the dimensional approach and emphasize the need for a multimodal approach toward animal emotions, that is, by incorporating different parameters (i.e., physiological, behavioral, and cognitive) to avoid confusion about animals' assumed emotional states (Paul and Mendl 2018; Bliss-Moreau 2017; Massen et al. 2019; Kremer et al. 2020). For example, a single parameter, such as a physiological elevation in cortisol levels, can elicit a distinct behavioral response (e.g., approach or flee), depending on the valence (positive or negative) of a perceived stimulus (Paul et al. 2005). Furthermore, these studies also emphasize the importance of adopting non-invasive methods where animals can behave freely in specific and naturalistic situations, allowing for a more realistic and ecologically valid understanding of their emotional responses (Massen et al. 2019), particularly since invasive or interacting methods may in fact influence the emotion one tries to measure.

Spontaneously occurring behavior in social contexts is considered a non-invasive and well-studied indicator of emotions, for example, stress-related behaviors such as scratching and body shake (Maestripieri 1993; Bekoff 2000; Troisi 2002; Paul et al. 2005; Bhattacharjee et al. 2026a). More specifically, scratching and body shakes are spontaneous behaviors that have been related to stressful events such as maternal anxiety, being paired with an unknown conspecific, or being in proximity to the dominant male (Maestripieri 1993; Schino et al. 1990; Troisi and Schino1987). Similarly, the production and modulation of vocalizations can be regarded as spontaneous expressions of an animals' emotional states (Briefer 2012). Vocal behavior reflects human and non-human animals' emotional responses, particularly when focusing on changes in specific vocal parameters, and is related to both of the recognized dimensions of emotions, that is, arousal and valence (Fichtel et al. 2001; Briefer 2012; Mendl et al. 2010). Briefer (2020) reviewed the effects of emotional arousal on animal vocalizations, showing that in multiple studies higher arousal states led to a faster calling rate, higher fundamental (F0) and formant (F1 and F2) frequencies, a higher peak frequency, and a less stable F0 (Gouzoules and Gouzoules 1989; Bachorowski and Owren 1995; Maestripieri et al. 2000; Fichtel et al. 2001; Gruber and Grandjean 2017; Schwartz et al. 2020; Schwartz et al. 2022). Duration, on the other hand, seems to be an indicator of emotional valence, with negative emotions having been related to vocalizations with longer durations. Moreover, negative emotions were found to be related to higher-pitched and more variable (less stable F0) vocalizations than positive emotions (Briefer 2012; Friel et al. 2019; Schwartz et al. 2022). Due to the multidimensionality of emotions, a combination of these behavioral measures with physiological measures has the potential to generate even more precise information about the emotional arousal and valence in a response, as there still exists a considerable knowledge gap, especially in the effects of emotions on vocalizations and their interpretation.

Although behavior and vocalizations can be easily studied non-invasively and without direct interaction with animals, the study of physiological changes often needs invasive methods in controlled or non-naturalistic settings. In recent years, a novel and non-invasive technique to measure one of the physiological components of animal emotions has gained popularity, that is, infrared thermography (IRT). IRT is a non-contact technique that measures body temperature. Although there still is only a relatively small number of studies that have used this technique, it was found to be a reliable tool to measure changes in affective states in some wild and captive animal species (Nakayama et al. 2005; Kuraoka and Nakamura 2011; Dezecache et al. 2017; Travain and Valsecchi 2021; Bhattacharjee et al. 2024), and its use in scientific studies is increasing exponentially (Travain and Valsecchi 2021). This technique makes use of the fact that emotional reactions are related to changes in the blood flow underneath the skin that are caused by stimulations of the sympathetic and parasympathetic nervous systems (Travain and Valsecchi 2021). These changes increase and decrease the blood flow toward and from specific regions of the body, such as the face (Chotard et al. 2018), providing immediate information about the individual's physiological reaction toward a specific situation (Bhattacharjee et al. 2024). For example, three previous studies showed a significant decrease in nasal temperature when macaque monkeys were exposed to a highly arousing negative situation, such as the presence of a specific threat (Nakayama et al. 2005; Kuraoka and Nakamura 2011; Kano et al. 2016; Bhattacharjee et al. 2024). However, these physiological reactions might be species-specific and individual-based (cf. Bhattacharjee et al. 2024). Hence, the addition of facial temperature as a dimension (Bhattacharjee et al. 2026b) in a multi-facetted approach combining both physiology and behavior provides more accurate information (i.e., valence and arousal) on the animals' emotional state.

A method for studying arousal in a negatively valenced situation is to perform an experiment in which animals are exposed to a novel and/or threatening stimulus, such as a predator. This method has been used to study fear and anxiety in animals (Barros et al. 2000; Barros and Tomaz 2002; Machado et al. 2009; Dinh et al. 2022; van Dijk et al. 2023; Bhattacharjee et al. 2024). Based on the dimensional emotional perspective (Mendl et al. 2010), these experiments are assumed to cause a negative, highly arousing emotional state in animals that are exposed to the predator. Across individuals, however, the arousal response to a dangerous situation (e.g., in terms of the speed to reach peak arousal or to get back to baseline (Rothbart and Derryberry 1981; Shapero et al. 2016), may vary as a result of individual differences, such as sex and social status, social context, and even genetic predispositions (Bhattacharjee et al. 2024). For example, male rodents behave more risk-prone than females during a novel context situation (Hegab et al. 2018), and in three species of macaques, it was found that males acted less cautious and more aggressive than females in the presence of a unknown human intruder (Sussman et al. 2013), which may in part be due to the sexual size dimorphism with males being bigger than females (Fooden 2006). In addition, even within the sexes, large differences in emotional reactivity may exist that depend on maternal status. For instance, females with dependent offspring (hereafter referred to as “mothers”) may act more reactively and anxiously than females without dependent offspring (hereafter referred to as “non-mothers”) to threats that specifically jeopardize their infants' survival. This may specifically be the case in the first part of their infant's life when the offspring's survival depends entirely on the mother (Coria-Avila et al. 2022), and they face the highest risks of mortality (Gage and Dyke 1988; Mandalaywala et al. 2014). In fact, primate mothers have been found to experience physiological and behavioral changes (measured as self-directed behaviors) caused by the perception of a threat to the offspring (Maestripieri 2011). Furthermore, lactating rhesus macaque females show higher levels of plasma cortisol than non-mothers during stressful situations, indicating higher responsiveness to stress associated with the perception of risks to infants (Maestripieri et al. 2008), leading to higher arousal.

Here, we therefore used an experimental predator confrontation paradigm to study the fear responses of mothers, non-mothers, and males of two non-human group-living primate species, that is, long-tailed (*Macaca fascicularis*) and rhesus macaques (*Macaca mulatta*). We used a multidimensional approach including both behavioral and physiological parameters.

During the experimental exposure, we used IRT to observe facial temperature changes of the focal individuals as a physiological dimension. Moreover, we recorded both vocal and non-vocal behavior in response to the predator model exposure. We expected mothers to show a stronger emotional reaction (Maestripieri et al. 2008; Maestripieri 2011) characterized by lower nasal temperature, highly emotional vocalizations, more stress-related behaviors, and less time in proximity to the predator model compared to non-mothers and males Furthermore, based on the sexual dimorphism in these species (Fooden 2006), we expected adult females to show a stronger emotional reaction, characterized by lower nasal temperature, highly emotional vocalizations, and more fearful behavior, compared to males (Sussman et al. 2013). Finally, given the smaller relative body size of long-tailed macaques compared to rhesus macaques (Fooden 2006), as well as evidence of long-tailed macaques' more fearful reactions to unknown observers in comparison to rhesus macaques (Clarke and Mason 1988), we expected the long-tailed macaques to act more fearfully in comparison to rhesus macaques in response to predator exposure.

2 | Methods

2.1 | Subjects

The study was performed at the Biomedical Primate Research Center in Rijswijk, The Netherlands, between December 2021 and October 2022. We collected experimental data on three long-tailed macaque groups and two rhesus macaque groups during two rounds: the first between December 2021 and July 2022, and the second between May and October 2022. Two rhesus- and one long-tailed macaque groups comprised a naturalistic multigenerational breeding group (cf. Rox et al. 2022) composed of one adult male, multiple adult females, and their offspring. One long-tailed macaque group consisted of a multigenerational group of only adult females and their offspring, and one was a peer group consisting of four adult males.

In total, for the long-tailed macaques, we collected data on seven males, ranging from 3 to 20 years, and 18 adult females, ranging from 3 to 15 years. Seven of these females had offspring ≤ 1 year old at the start of the study and were therefore categorized as “mothers” (with dependent offspring) in our analyses. By contrast, a total of 11 females did not have dependent offspring at the time of the testing and were therefore categorized as “non-mothers” (Table S1). For the rhesus macaques, we collected data from two adult males, 10 and 20 years of age, and 26 adult females, ranging from 3 to 24 years. Seventeen of these females had offspring ≤ 1 year old at the start of the study and were thus again categorized as mothers, and nine females did not have dependent offspring at the time of the testing and were thus categorized as non-mothers (Table S1). After starting the experiment, however, three long-tailed macaque non-mothers and four rhesus macaque non-mothers gave birth, and were thus also considered mothers in analyses on the data collected after they gave birth.

The four multigenerational groups have an inside enclosure (72 m^2, 2.85 m high) consisting of three to four interconnected compartments separated by walls and wired mesh, and an outside enclosure (208 m^2, 3.1 m high) that also contained three to four interconnected compartments, each separated by wired mesh. The enclosure of the all-male peer group of long-tailed macaque was smaller, with only one inside (35 m^2) and one outside compartment (32 m^2). All animals had the freedom to move around the inside and outside enclosures. Food was provided twice a day (in the morning: monkey chow, and in the afternoon: vegetables/fruit). This feeding regime was not altered for our experiments. Water was available *ad libitum*.

2.2 | Experimental Design

2.2.1 | *Procedures*

Predator exposure experiments followed the protocol described by Massen et al. (2013) (also see Kluiver et al. 2022). The predator experiment consisted of exposing the macaques on different days to a total of two types of models: a rubber snake model ~150 cm long in coiled posture with African rock python patterns (Kluiver et al. 2022), and a bird of prey (eagle) model in attack position (78.5 × 21.5 × 30.5 cm; 3.25 kg) (Figure 1) as these are natural predators for these species (Van Schaik et al. 1983; Van Noordwijk and van Schaik 1999; Fooden 2000). A stuffed tiger model in a sitting position was initially also included (approximately 75 × 42 × 35 cm); however, its use was discontinued due to a considerable reduction in the monkeys' visibility during these trials as they retreated from it out of sight.

As this study was part of a larger comparative personality research project, the experiments were repeated 2–3 months after the initial two exposures. Therefore, we ran these experiments from December 2021 to July 2022 (first session) and from May 2022 to October 2022 (second session). Within each session, the order of the two different predators exposed was randomized. In four groups, the tests were performed in the inside enclosure, in which the temperature was controlled. In the remaining group (i.e., the four-male group), the tests were performed in their outside compartment. The predators were located outside of their enclosure ±50 cm from the enclosure's fences. In all groups, animals had full visual access to the models from all their inside compartments. For the four-male group, animals were only able to see the models from their outside compartment.

One week before the experiments, the animals were familiarized with and habituated to all the observers by having them sit in front of their enclosure for at least 1 h to a maximum of 2 h a day between 2 and 3 days. One day prior to the experiment, animals were additionally habituated for 30–60 min to the IRT camera device and audio recording equipment. During these habituation phases, the experimenters would sit in front of the group's enclosure with the IRT camera and the auditory recording device in hand, in the same position as during the experiment. All animals had been previously accustomed to the use of video cameras by experimenters during general focal protocols. After all habituation sessions, animals were habituated, that is, engaging in their regular behavioral interactions (foraging, eating, sitting, playing, etc.) and were not interacting or actively observing the experimenters and the material.

On testing days, the experimenters entered the animals' enclosure 30 min before the start of the experiment. The audio and video recording material, as well as the two experimenters, were positioned within 1 meter of the wire mesh. In four of the groups, the observers were holding the IRT thermal camera in their hands. In the all-male peer group, however, the two thermal cameras were positioned on tripods in front of the enclosure. This ensured that the neighboring groups were not disturbed. We collected baseline measures for facial temperatures during this period.

In the four larger groups, after 30 min, the caretakers locked the animals outside for < 4 min. The animals are familiar with this procedure as they are locked outside on a regular basis for enclosure cleaning purposes. During this time, the predator model was positioned in front of their mesh gate (outside of their view), and the cameras, audio recording, and IRT camera were started. The experiment was then started and lasted 30 min from the moment the gates to the outside compartment were opened, and the monkeys were able to move back in.

For the all-male peer group, however, the animals were not locked inside their enclosure during predator positioning. Their enclosure was considerably smaller, and the animals were less accustomed to being locked in the inside part of the enclosure. In this situation, researchers transported the predator model in a plastic bag or physically hid it to prevent the animals from seeing the model before and during its placement. The experiment started once the predator was placed in front of the enclosure, and it lasted for 30 min.

During the experiment, all the monkeys of all groups could move between the inside and outside enclosures. After the 30-min experimental time, one experimenter removed the predator model.

3 | Data Collection and Preparation

During the 30 min of predator exposure, facial temperature, vocalizations, and behavioral data of the monkeys were opportunistically collected using two IRT cameras (FLIR E96 with 640 × 480 resolution), auditory recording equipment (Marantz PMD561 paired with a Sennheiser MKE600 directional microphone), and two to three video-cameras (JVC Everio R, Canon Legria HF G25, and Sony FDR AX100E 4K). The data were collected only from those animals that were observable, which influenced the final sample sizes per maternal status and sex and per measure. Only one long-tailed macaque female was not present during all four experimental

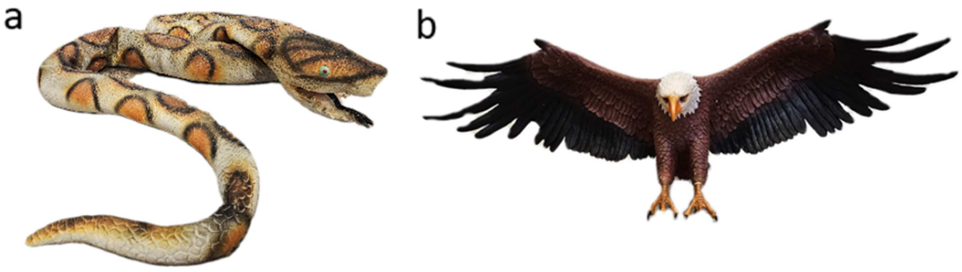

FIGURE 1 | Images of the predator models. (a) Rubber snake model~ 150 cm long in coiled posture with African rock python patterns. (b) A bird of prey: resembling an eagle in attack position (78.5 × 21.5 × 30.5 cm; 3.25 kg).

TABLE 1 | Ethogram of stress-related behaviors and position in long-tailed and rhesus macaques.

Behavior	Type	Description
Stress-related behavior		
Self-groom	Event	Individual inspects their own skin, nails, hands, toes, or other body parts.
Scratch	Event	Individual uses finger, hand, or foot to rake across own skin.
Body shake	Event	Rapid body movement involving turning in at least two directions.
Yawn	Event	Wide mouth gape, deep inhalation, and often brief eye closure.
Location		
Ground proximity	Duration	Individual is located on the ground, within 1 m from the wire mesh behind which the predator stimulus was located within aprox. 50 centimeters.

trials. We excluded this animal from the analyses. This individual was a non-mother female in the first phase and a mother in the second phase.

3.1 | Stress-Related Behavior and Location

We used focal sampling (Altmann 1974) to code point and durational behavioral parameters (Table 1). Specifically, we were interested in stress-related behavior (Table 1), which has been shown to increase significantly after predator exposure (Barros et al. 2000; Barros and Tomaz 2002; van Dijk et al. 2023; Bhattacharjee et al. 2024; this study: for details see Supporting Information S2; Figure S1). Note, however, that we here are not necessarily interested in the differences between baseline and predator exposure, but instead, in the different responses depending on maternal status, sex, and species. Therefore, we calculated rates (behavioral rate $= \frac{\text{number of occurences}}{\text{observation time}}$, i.e., while in sight) from these behavioral parameters combined during all the experiments. In addition to stress-related behaviors, we determined the animals' location (Table 1) during the predator experiment to assess their spatial responses. Specifically, we calculated ground proximity, that is, the total time each individual spent on the ground within 1 meter distance to the wire mesh.

Behaviors were scored manually by three experimenters, and inter-rater reliability was calculated (for previous data on long-tailed macaques, see Bhattacharjee et al. 2024; for rhesus macaques, inter-rater agreement was checked between one of the previous coders and an additional coder. It showed full agreement (based on ~10% data, Cohen's Kappa = 0.918, $z = 6.57$, $p < 0.001$; ICC(3,K) $= 1$, $p < 0.001$).

During the 30-min experimental period, we collected data from every visible animal opportunistically. To be able to compare thermal and behavioral results in response to the predator exposure (e.g., potential peak stress response and recovery), we additionally divided the experimental period into three time windows since predator exposure: 0–10 min, 10–20 min, and 20–30 min. Note that as the animals could move freely between the inside and outside enclosure, we were unable to collect behavioral data on eight individuals during certain experiments (Session 1/Snake: one rhesus macaque mother and one rhesus macaque female; Session 1/Bird: one rhesus macaque mother and one rhesus macaque female; Session 2/Snake: one long-tailed macaque mother and, six rhesus macaque mothers; Session 2/Bird: two rhesus macaque mothers). Consequently, the sample sizes for analyses on the behavioral parameters differ from the total sample size, and may differ per comparison, related to narrower time windows (see below; Figure 3).

3.2 | Vocalizations

Vocalizations were recorded during the full experimental session period by one of the experimenters. To ensure reliability, we only analyzed vocalizations produced by animals visible in the camera and where the vocalization could be reliably identified as emitted by a particular individual.

We were interested in the spectral information and the vocal rates related to emotional arousal for calls produced in response to the predator's presence (i.e., threatening calls: barks, kra's, grunts, pant-threats; and alarm calls: screams, squeaks, screeches: Thierry 1985; Palombit 1992; Partan 2002; NC3Rs n.d.). Note that we observed that while long-tailed macaques predominantly use bark and kra calls, rhesus macaques mainly combined pant-threats with grunts during the experimental sessions, while producing nearly no barks. We counted the calls and calculated each animal's total vocal rate (vocal rate $= \frac{\text{number of vocalizations}}{\text{observation time}}$), for a total of 9 non-mothers, 18 mothers, and 7 males that vocalized. We isolated the calls with Audacity software (version 3.0.2). Two observers independently categorized the vocalizations into vocal types. Inter-rater reliability indicated a high level of consistency with 90% agreement between observers. We only used calls with sufficient acoustic quality (clear and unambiguous) for further acoustic analyses. Hence, we excluded vocalizations that were intertwined with other individuals' calls and background noises. In total, this led to 92 recordings of predator-related vocalizations for which the caller ID was accurate and that were free from any noises produced by other individuals or by the animals' movements. Twenty-one of these vocalizations were produced by males (16 by 3 long-tails and 5 by 1 rhesus), 18 by females (11 by 2 long-tails; 7 by 4 rhesus), and fifty-three by mothers (17 by 2 long-tails; 36 by 11 rhesus). Due to the variable production of different call types across individuals and the relatively low number of clear recordings, we finally had to combine all predator-related calls per individual. To balance the number of calls per individual, we only analyzed up to the first four good-quality (see above) calls per individual.

Vocalizations were analyzed using PRAAT Software (Boersma and Weenink 2023: version 6.2.12). In PRAAT, spectrograms were generated using default settings (44.1 kHz sampling rate, 0.005 s window length, dynamic range of 70 dB), except for the maximum frequency, which was set to 10,000 Hz for better visualization. We extracted the following temporal and spectral parameters: call duration (ms), Formant 1 frequency (F1), and Formant 2 frequency (F2). Formant frequencies were determined with the Burg LPC algorithm (pre-emphasis 50 Hz; formant ceiling: max. 5500.0 Hz; number of formants: 5; dynamic range: 30 dB; window length: 0.025). Formant trajectories were manually reviewed to ensure consistency with visible spectral energy bands. Acoustic parameters such as fundamental frequency, jitter, and shimmer were excluded from the analyses because many calls did not have a clear pulse structure, rendering the measurement of these variables impossible or unreliable. Due to the limited sample size per time window, we could not include the time window factor in further statistical analyses on vocal rate or vocal parameters. We grouped them over the whole experiment to assess the effect of predator presence on vocal behavior across maternal status, sex and, species.

3.3 | IRT

Before collecting the facial temperature data, the IRT camera atmospheric settings (room temperature, humidity, and reflected temperature) were adjusted using two ThermoPro TP50 thermo-hygrometer devices. The emissivity was set at 0.97 (Travain and Valsecchi 2021). Throughout the experiment, atmospheric settings were checked to ensure there were no changes in their atmosphere (cf., Lake et al. 2025).

Since body temperature can differ between individuals, responses to, for example, a predator need to be relative to the baseline, therefore, as described previously, we collected both baseline IRT data 30 min prior to the experiment and IRT data during the 30 min experimental period. Data were collected only from those animals located within 2 meters distance from the experimenters (Figure 2), as measurements from further away could potentially become unreliable due to reduced image resolution (Bhattacharjee et al. 2024). Baseline measurements were taken when the individual was located in front of the fence (Figure 2b), standing or sitting. Baseline measures during or after stressful or agonistic interactions were omitted/avoided as they may influence animals' thermal measurements (Travain and Valsecchi 2021). Experimental measurements were taken throughout the experimental period. However, we excluded the data recorded for the first 2 min (i.e., between 0 and 2 min) since nose temperature can be affected by variable weather conditions outside before the experiments and the movement procedures between the in- and outside.

Facial temperature was extracted from IRT video recordings using the FLIR Tools Software (version 6.4.18039.1003). Data were extracted from all video frames where the individuals were facing the IRT camera at an angle of 45°. We used a 2 × 2 square pixel box to extract the nose tip temperature (Figure 2a). To ensure consistency and accuracy, we zoomed the image frame to ±606% every time and located the square pixel-box in the region of interest (Figure 2a). For adult individuals, the square shape size was 2/2. For young individuals, the square-shaped box was 1/1. All thermal readings were extracted by one experimenter. To ensure that the outcomes were reliable, another researcher coded 64 thermal picture frames. Full agreement was met when comparing both data measurements [ICC (3, k) = 0.93, $p < 0.001$] (cf. Bhattacharjee et al. 2024).

For analysis of the thermal data, we divided the experimental time into three time windows: 2–10, 10–20, and 20–30 min, to measure potential differences in both the initial emotional reaction as well as differences in recovery time (cf. Bhattacharjee et al. 2024). We furthermore added the baseline values collected prior to the start of the experiment. Like the behavioral parameters, these measurements were collected opportunistically, which means we did not have measurements of all individuals (during each time window), and thus the sample size of the analyses differs from the total sample, and similarly, sample sizes from the different comparisons may differ (Figure 5; Table S3).

4 | Statistical Analyses

All the analyses were performed in R (RStudio Software, 2023.03.1 + 446). Thermal and behavioral (i.e., stress-related behaviors, location data, as well as vocalizations) data contained three categories of maternal status and sex (mothers, non-mothers, and males) and two species (long-tailed and rhesus macaques). We used Generalized Linear Mixed Model (GLMM) analyses, using the *glmmTMB* package (Brooks et al. 2017; McGillycuddy et al. 2025) to investigate the different outcomes depending on the maternal status, sex, and species. Marginal

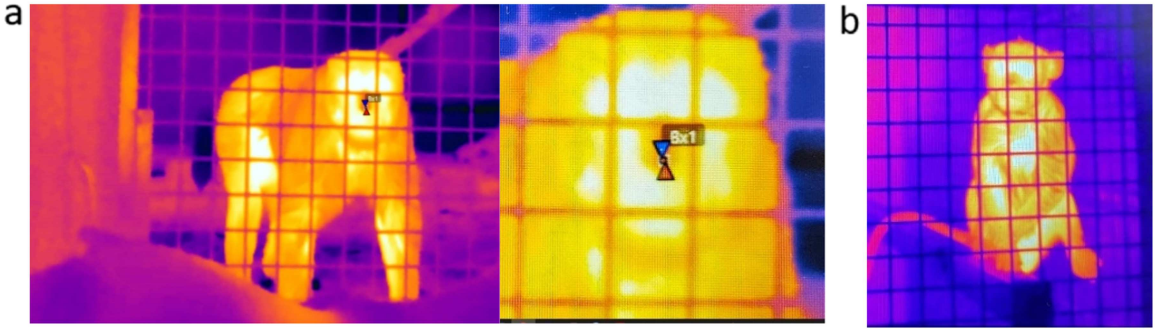

FIGURE 2 | Examples of IRT images. (a) To the left, a thermal image of a female during the real-time bird of prey experimental exposure. (b) This thermal image zoomed in. The tip-nose temperature was extracted using a 2 × 2 pixel box. (c) Monkey's position during baseline measurements.

means were estimated using the *emmeans* package (Lenth 2025), and α was set at 0.05.

4.1 | Stress-Related Behaviors and Location

Data were grouped in three time windows (0–10 min, 10–20 min, and 20–30 min). Dependent variables included the rate of stress-related behaviors and time spent in ground proximity (Table 1). The main predictors of the models were time window, maternal status, sex and, species. In addition, predator type and session were included in the model as control variables to control for any effect caused by these two factors. Random effects were included to control for repeated measures (i.e., individual ID over the different sessions) and the nested structure (i.e., multiple social groups) of our data. Specifically, we added an individual ID nested in a group (group/individual) as a random intercept to our models.

To reduce noise in our stress-related behavior data, we excluded from our model data from the time windows in which an animal was present for less than 30 s (< 5% visible). In addition, we found a considerable proportion of animals that did not show any stress-related behaviors in at least one time window within an experiment. We, therefore, applied a two-step analytic strategy. First, we used a binomial hurdle to model the probability of observing stress-related behaviors in an animal, depending on time window, maternal status, sex, and species. Second, we analyzed the variation in the frequency of stress-related behaviors of those animals that showed at least one such behavior in a time window, and again analyzed whether this frequency was dependent on the time window, maternal status, sex, and species.

For modeling the time spent in ground proximity, we included all the data from all the animals, since we considered the absence of time spent in close proximity to the predator relevant information as well, as it indicates a meaningful behavioral response such as avoidance behavior. To model the rate of stress-related behaviors (number of occurrences/time observed), we used the *glmmTMB* with a Beta distribution and a logit link function. The beta distribution is an appropriate family to model proportions (Ferrari and Cribari-Neto 2004). To model time spent in ground proximity, we used the *glmmTMB* with a Tweedie distribution and a log link function. These data were continuous, positive, right-skewed, and included zeros (ground proximity) and zero values. The Tweedie family with a log link function was appropriate for addressing this kind of data (So and Deng 2025). The model assumptions were met. The residuals showed normality, no overdispersion, and no outlier effects.

4.2 | Vocalizations

As mentioned previously, the vocal data were limited, and we could not separate the data into the three time windows. For vocal rates, call duration, F1 and F2 frequency, the model's main predictors were, therefore, maternal status, sex, and species.

Predator type and session were included in the models as control variables. In addition, random effects were included to control for repeated measures (i.e., individual ID over the different sessions) and the nested structure of our data (i.e., multiple social groups). Specifically, we added individual id nested in group (group/individual) as a random intercept to our models. Furthermore, we included vocal type as a random effect because of the clear distinction in the vocal strategies of long-tailed macaques and rhesus macaques. Vocal rate and vocal parameters (F1 and F2, and call duration) were used as the dependent variables for further analyses.

To model vocal rate, we used the *glmmTMB* package with a Tweedie distribution and a log link function. For this analysis, we excluded the animals that were present for less than 90 s (< 5% visible) of the total experimental time. For call duration, we used the *glmmTMB* package with a Gaussian distribution. To model F1, we used the *glmmTMB* package with a Gaussian distribution with a log link function, and to model F2, we used the *glmmTMB* package with a gamma distribution with a log link function. All these models fitted best to our data, and model assumptions were met. The model diagnostics indicated normality, no overdispersion, and no outlier effects.

4.3 | IRT

For thermal data, an additional time window was added (leading to four time windows; i.e., baseline, 2–10 min, 10–20 min, and 20–30 min). The dependent variable in all analyses was nose tip temperature, and, as in our behavioral data, our main predictors were the four time windows, maternal status, sex, and species. In addition, predator type and session were included in the model as control variables. Random effects were included to account for repeated measures (i.e., individual ID over the different sessions) and the nested structure (i.e., multiple social groups) of our data. Specifically, we added an individual ID nested in a group (group/individual) as a random intercept to our models.

IRT data were log-transformed. We then analyzed the data using the *glmmTMB* with Gaussian distribution and an identity link function. Although the Kolmogorov–Smirnov test indicated a significant deviation from normality, other diagnostics showed no signs of overdispersion or outlier effects. Given the potential for biological data to exhibit non-constant variance, particularly in behavioral research, we incorporated a structured dispersion model using the disp formula option in the GLMM to strengthen our models. The dispersion component was statistically significant, indicating heteroskedasticity in the residuals (see Table S7b). This supports the inclusion of the dispersion term to improve the accuracy of standard error estimates and account for variance that may systematically change across maternal status, sex, and species.

5 | Results

5.1 | Stress-Related Behaviors

First, we investigated whether maternal status, sex, species, and experimental time window had an effect on the likelihood of animals showing stress-related behaviors; that is, the first hurdle of a hurdle approach. Here, we first compared a model with interactions to one without interactions and found that the latter had a better fit. We found that the likelihood of showing stress-related behaviors was affected by the time window after exposure to the predator. However, post hoc comparisons showed no significant differences when comparing the first 0–10 min compared to the 10–20 min time window (odds ratio = 0.571, $p = 0.0546$). We also did not find significant differences between the other time windows (0–10 vs. 20–30: OR = 0.742, $p = 0.4877$; 10–20 vs. 20–30: OR = 1.300, $p = 0.6101$).

The likelihood of showing stress-related behaviors did not differ significantly between maternal status and sex. Pairwise comparisons showed no differences when comparing mothers with non-mothers (OR = 1.393, $p = 0.4585$) and with males (OR = 0.827, $p = 0.9368$), or between females and males (OR = 0.594, $p = 0.6375$). Finally, we found no effects of species on the likelihood of showing stress-related behaviors (OR = 1.8, $p = 0.3914$). Overall, these results indicate that maternal status, sex, and species did not affect the behavioral response, while the time window within the experimental session had an effect.

Subsequently, we fitted only the data of individuals that showed at least one stress-related behavior into a GLMM, testing the effect of maternal status, sex, species, and experimental time window on rates of stress-related behaviors; that is, the second hurdle in a hurdle approach. Again, we first compared a model with interactions with a model without interactions, and here we found that the former had a better fit. In that model, we found no effects when comparing maternal status, sex, and time windows (see Table S4). However, we did find an effect when comparing species and a significant interaction effect on the rate of stress-related behaviors between maternal status and sex, and time window, and between species and time window (see Table S4). With regard to the interaction between maternal status and sex, and time window, post hoc contrast revealed that mothers showed less stress related behaviors than females in the 10–20 min time period ($ß = -0.5855$, SE = 0.157, $t = -3.723$, $p = 0.0006$). Mothers tended to show less stress-related behaviors than males during the end of the experiment (20–30: $ß = -0.5419$, SE = 0.232, $t = -2.335$, $p = 0.0511$). Females and males did not significantly differ within any time windows (Figure 3a).

When analyzing each maternal status and sex separately across time windows, we found that only non-mothers showed less stress-related behaviors in the first 0–10 min of the experiment compared with 10–20 min ($ß = -0.4036$, SE = 0.165, $t = -2.440$, $p = 0.0390$) and a tendency when compared with the 20–30 min ($ß = -0.4381$, SE = 0.192, $t = -2.284$, $p = 0.0581$). This pattern was not present in mothers or males, where the rate of stress-related behaviors remained consistent across time windows (Figure 3b).

With regard to the interaction between species and the different time windows, post hoc contrasts (*emmeans*) revealed that in the first 10 min of the experiment, long-tailed macaques showed more stress related behavior than rhesus macaques ($ß = 0.5572$, SE = 0.277, $t = 2.010$, $p = 0.0444$), whereas we did not find any differences between the species in the other time windows.

When analyzing each species separately across time windows, we found that while long-tailed macaques remained stable in showing stress-related behaviors throughout the experiments,

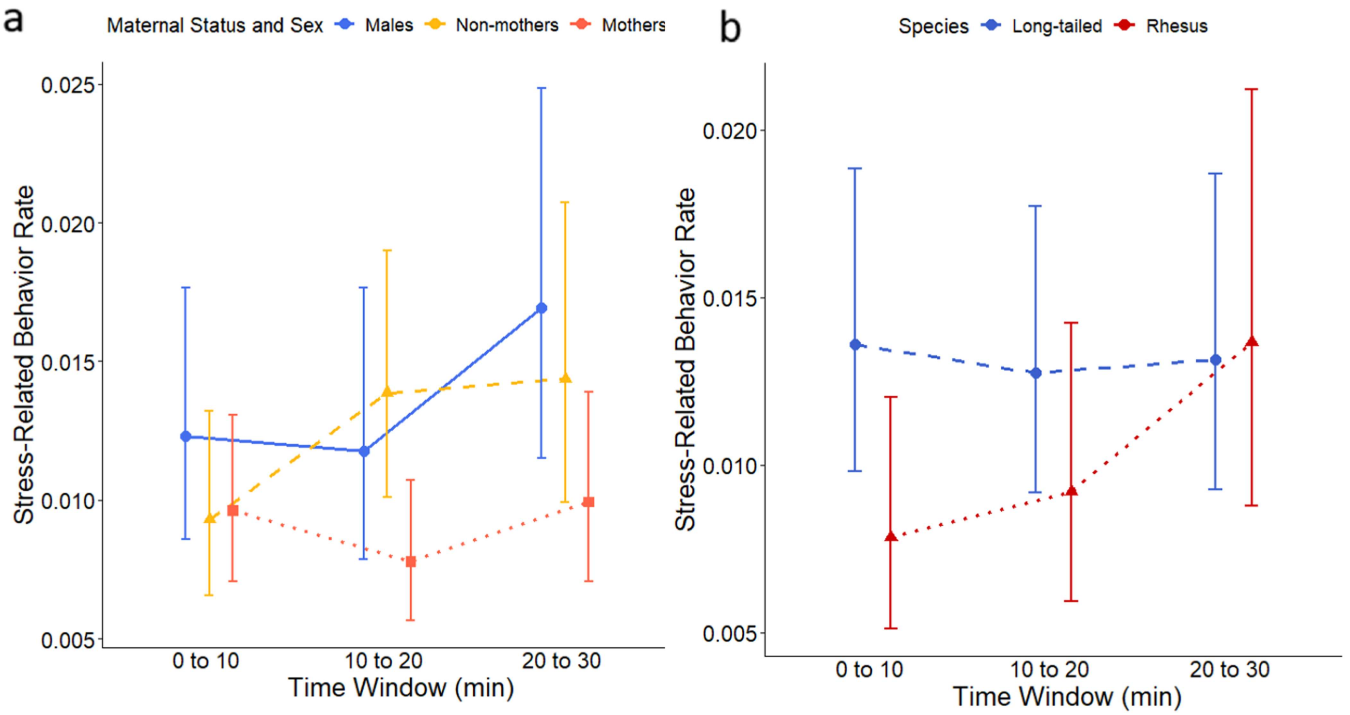

FIGURE 3 | Rate of stress-related behaviors during a 30 min predator exposure depending on (a) maternal status and sex [mothers: 0–10 min (n= 23), 10–20 min ($n = 22$), 20–30 min ($n = 19$); non-mothers: 0–10 min ($n = 15$), 10–20 min ($n = 15$), 20–30 min ($n = 10$); and males: 0–10 min ($n = 7$), 10–20 min ($n = 7$), 20–30 min ($n = 7$)] and (b) macaque species [long-tailed macaques: 0–10 min ($n = 20$), 10–20 min ($n = 21$), 20–30 min ($n = 16$); rhesus macaques: 0–10 min ($n = 22$), 10–20 min ($n = 22$) 20–30 min ($n = 19$)]. Colors represent (a) maternal status and sex (red: mothers; yellow: non-mothers; blue: males) and (b) the two species (red: rhesus macaques; blue: long-tailed macaques). Shapes indicate the model-predicted means, while lines represent the 95% confidence intervals.

rhesus macaques showed less stress related behaviors at the start of the experiment when comparing the first 10 min of the experiment with the end of the experiment (0–10 min vs. 20–30 min: $ß = -0.5617$, SE $= 0.174$, $t = -3.237$, $p = 0.0035$).

5.2 | Ground Proximity

We explored whether ground proximity to the predator model (or the avoidance thereof) was dependent on maternal status, sex, and species. We ran GLMMs with and without interaction effects and found that the former had a better fit. In that model, maternal status and sex were significant predictors of the time spent in ground proximity to the predator. Post hoc contrast revealed only a significant difference between mothers and non-mothers. Non-mothers spent more time in ground proximity to the predator compared to mothers ($ß = -0.858$, SE $= 0.315$, $z = -2.728$, $p = 0.0175$). We did not find significant differences when comparing mothers and males and non-mothers and males. We also found significant interactions between maternal status and sex, and time window and species (Table S5). Specifically, post hoc analyses revealed that during the first 10 min of the experiment, mothers spent less time in ground proximity to the predator than non-mothers ($ß = -1.141$, SE $= 0.376$, $t = -3.035$, $p = 0.0068$) and males ($ß = -1.390$, SE $= 0.555$, $t = -2.506$, $p = 0.0327$). Non-mothers, however, did not spend less time in ground proximity than males. After 10 min of the start of the experiment, maternal status and sex did not seem to have an effect on the time spent in ground proximity anymore (see Figure 4a).

When analyzing each maternal status and sex seperataly across time windows, we found that males and non-mothers spent more time in ground proximity in the first 10 min compared to the 10–20 min time window (females: $ß = 0.791$, SE $= 0.319$, $t = 2.478$, $p = 0.0353$; males: $ß = 2.154$, SE $= 0.528$, $t = 4.083$, $p = 0.0001$) and compared to the last 10 min (20–30 min time window) of the experiment (females: $ß = 1.058$, SE $= 0.335$, $t = 3.161$, $p = 0.0045$; males: $ß = 1.677$, SE $= 0.476$, $t = 3.520$, $p = 0.0013$) (Figure 2a). We did not find significant differences when comparing the 10–20 and the 20–30 time windows. On the contrary, mothers remained consistently low in their time spent in ground proximity to the predator across the experiment (Figure 4a).

With regard to the interaction between species and the different time windows, we found that in the first 10 min long-tailed macaques tend to spend less time in ground proximity than rhesus macaques ($ß = -0.763$, SE $= 0.406$, $t = -1.877$, $p = 0.0605$), whereas after 20 min the long-tailed macaques spend significantly more time in ground proximity than the rhesus macaques ($ß = 0.983$, SE $= 0.460$, $t = 2.139$, $p = 0.0324$; Figure 4b).

When analyzing each species separately, we found that long-tailed macaques remained stable in their time spent in ground proximity to the predator across the experiment, whereas rhesus macaques spent more time in ground proximity in the first 10 min compared to the 10–20 min time window ($ß = 1.543$, SE $= 0.299$, $t = 5.160$ $p \leq 0.0001$) and compared to the last 10 min of the experiment ($ß = 2.014$, SE $= 0.326$, $t = 6.184$, $p \leq 0.0001$), and no significant differences were found when comparing 10–20 and 20–30 (Figure 4b).

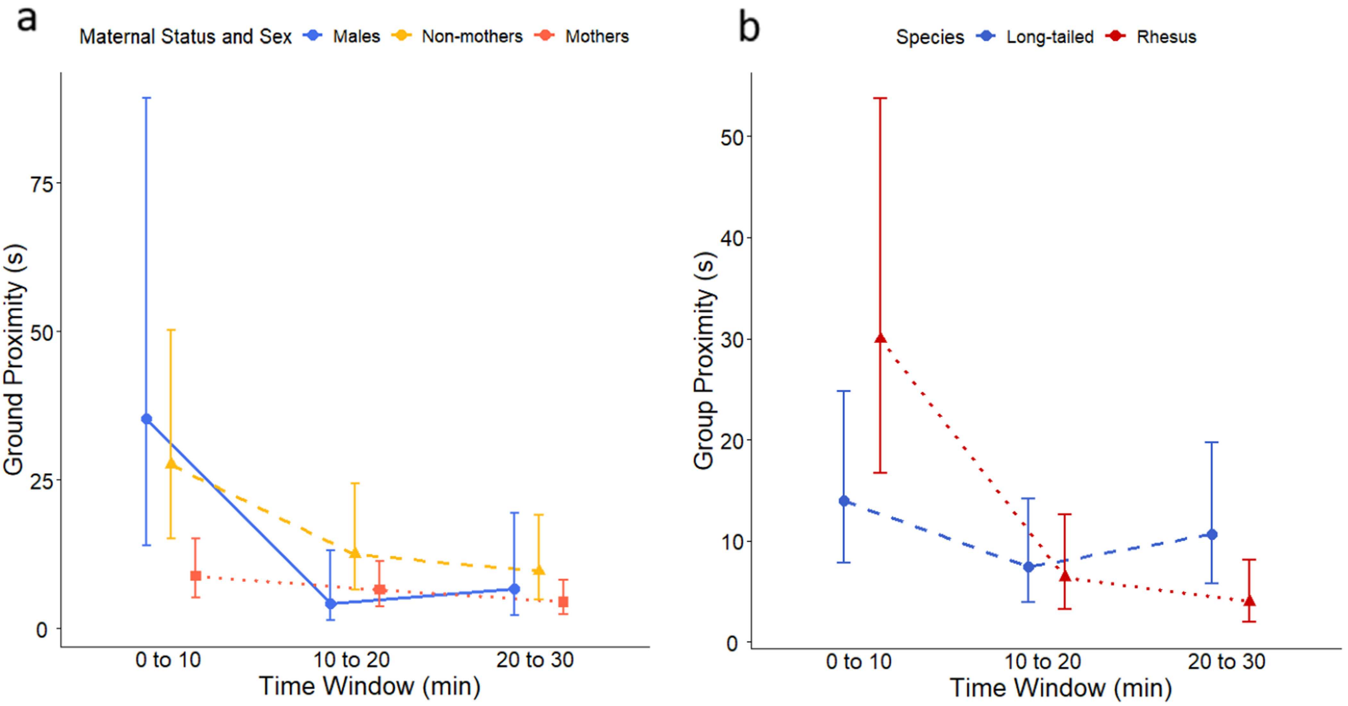

FIGURE 4 | Time spent in ground proximity during a 30 min predator exposure, depending on (a) motherhood and sex, composed of mothers, non-mothers, and males, and (b) macaque species, composed of long-tailed macaques and rhesus macaques. Colors represent (a) the maternal status and sex (red: mothers; yellow: non-mothers; blue: males) and (b) the two species (red: rhesus macaques; blue: long-tailed macaques). Shapes indicate the model-predicted means, while lines represent the 95% confidence intervals.

5.3 | Vocal Parameters

When investigating whether maternal status and sex, and species had an effect on the vocal rate and vocal spectral parameters (call duration, F1 and F2), we did not find any effect of maternal status and sex, and species on the call rate, nor on any of the vocal spectral parameters (see Table S6a,b).

5.4 | IRT

Finally, we tested the effects of maternal status, sex, species, and experimental time (Baseline, 2–10, 10–20, and 20–30) on the nose tip temperature. Again, we first compared a model with interactions to one without interactions, and we found that the former had a better fit. In this model, we found a significant effect on the nose tip temperature when comparing the baseline with every experimental time window. However, post hoc analyses revealed a significant decrease in the nose tip temperature only during the 2–10 min of the experiment compared to baseline ($\beta = 0.0533$, $SE = 0.0154$, $t = 3.458$, $p = 0.0033$). We also found an increase in the nose tip temperature when comparing the 2–10 time window to the 10–20 time window ($\beta = 0.0719$, $SE = 0.0136$, $t = 5.291$, $p = <0.0001$). However, we found no significant differences when comparing the 10–20 and 20–30 time windows to baseline. This indicates that the decrease was specific to the early phase of the predator exposure, and that after recovery, the nose temperature of the animals seemed to remain consistent throughout the rest of the experiment (i.e., no significant difference in 10–20 vs. 20–30 min). Although species was also a significant predictor of nose tip temperature changes, post hoc contrast revealed no significant differences between long-tailed and rhesus macaques.

Whereas our model did not reveal effects when comparing maternal status and sex, it did, however, show a significant interaction between time window and maternal status and sex, and between time window and species (Table S7a). With regard to the interaction between maternal status and sex, and time window, post hoc contrast (*emmeans*) revealed that only mothers had a significant decrease in their nose temperature compared to non-mothers during the 2–10 time window ($\beta = -0.8524$, $SE = 0.0225$, $t = -3.786$, $p = 0.0005$), but not across the other three time windows (baseline, 10–20, and 20–30). We also found no significant differences when comparing mothers and males and when comparing females and males (Figure 5a).

When analyzing the time windows separately, post hoc contrast revealed that the maternal status and sex had a significant effect on the nose tip temperature. We found that mothers had a decrease in the nose tip temperature during the first 2–10 min compared to baseline ($\beta = 0.11597$, $SE = 0.0234$, $t = 4.957$, $p \leq 0.0001$) and an increase in their nose tip temperature during the 10–20 min compared to 2–10 ($\beta = 0.07805$, $SE = 0.0139$, $t = 5.619$, $p \leq 0.0001$). During the 10–20 min of the predator exposure, no significant differences were found compared to baseline. The mothers thus seemed to increase their nose tip temperatures back to baseline (baseline vs. 10–20 being ns) and remained consistent until the end of the experiment (baseline vs. 20–30; 10–20 vs. 20–30 all ns) (Figure 5a). In contrast, non-mothers did not have a significant decrease on the nose tip temperature during the 2–10 min of the experiment compared to baseline, but we did find a significant increase in the nose tip

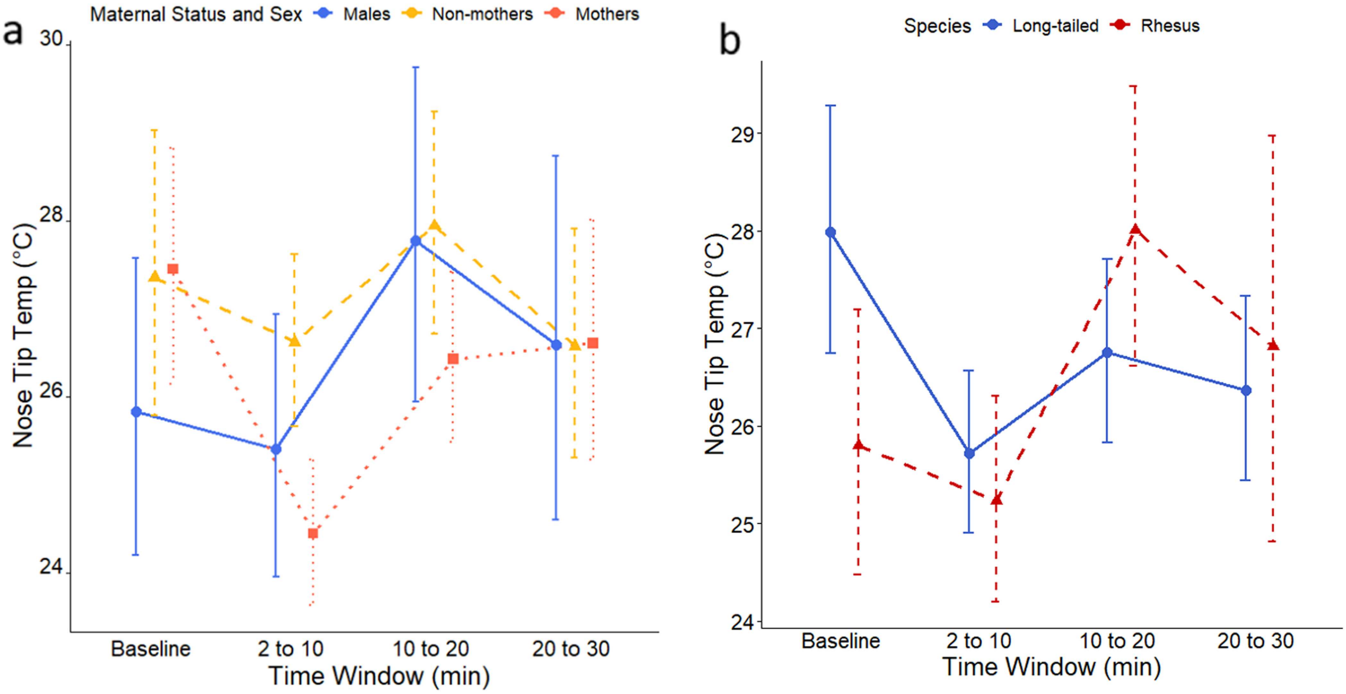

FIGURE 5 | Nose tip temperature changes during a 30-min predator exposure depending on (a) maternal status and sex. mothers: baseline (15), 2–10 min (18), 10–20 min (14), 20–30 min (8); non-mother females: baseline (9), 2–10 min (14), 10-20 min (10) 20–30 min (5); and males: baseline (9), 2–10 min (8), 10–20 min (6), 20–30 min (3), (b) macaque species [rhesus macaques: baseline (16), 2–10 min (18), 10–20 min (12), 20–30 min (3); and long-tailed macaques: baseline (16), 2–10 min (20), 10 to 20 min (17), 20–30 min (12)]. Colors represent the maternal status and sex (red: mothers; yellow: non-mothers; blue: males). Shapes indicate the model-predicted means, while lines represent the 95% confidence intervals.

temperature during the 10–20 min of the experiment compared to the 2–10 ($ß = 0.04853$, $SE = 0.0180$, $t = 2.689$, $p = 0.0369$). However, this increase was not significantly different when comparing 10–20 min to baseline, nor when comparing it to the 20–30 experimental time. Similarly, we found that males did not have a significant decrease in the nose tip temperature at the beginning of the experiment (Figure 5a); that is, we did not find significant differences in nose tip temperature during the 2–10 min compared to baseline. And similar to the findings in females, we found an increase in the nose tip temperature during the 10–20 min of the experiment compared to the 2–10 min exposure ($ß = 0.08913$, $SE = 0.0288$, $t = 3.098$, $p = 0.0110$). However, this increase was not significantly different when comparing to baseline and when comparing it to the 20–30 time window (Figure 5a).

Regarding the interaction between time windows and species, post hoc contrast revealed no significant differences when comparing long-tailed and rhesus macaques across the time windows (Figure 5b).

When analyzing the time windows separately, only long-tailed macaques showed a significant decrease in nose tip temperature during the 2–10 min of the experiment compared to baseline ($ß = 0.0844$, $SE = 0.0196$, $t = 4.316$, $p = 0.0001$), and an increase during the 10–20 min compared to 2–10 min ($ß = 0.0394$, $SE = 0.0121$, $t = 3.266$ $p = 0.0063$). Although we did not find significant differences when comparing baseline to 10–20 min, we found a significant decrease in the nose tip temperature during the 20–30 min compared to baseline ($ß = 0.0594$, $SE = 0.0206$, $t = 2.889$, $p = 0.0209$). Contrary, rhesus macaques did not have a significant decrease in nose tip temperature during 2–10 min compared baseline. However, we found a significant increase on the nose tip temperature during the 10–20 min compared to baseline ($ß = -0.0823$, $SE = 0.0290$, $t = -2.832$, $p = 0.0247$) and compared to the 2–10 min of the experiment ($ß = 0.1044$, $SE = 0.0223$, $t = 4.678$, $p = 0.0001$). Rhesus macaques, however, seemed to return to baseline during the 20–30 min of the experiment (Figure 5b).

6 | Discussion

In this study, we aimed to provide a multidimensional view of how primate emotional responses in reaction to a negative predatory stimulus are affected by their maternal status, sex, and species. For this, we combined behavioral, vocal, and physiological (nose tip temperature) responses that were collected in a non-invasive and non-interactive manner. We find differential responses of mothers in comparison to non-mothers and males, with the former showing a clear physiological response at the start of each experiment, whereas the latter show clearer behavioral responses. In addition, we find species differences; the long-tailed macaques seem to react more strongly to our stimulus with regard to their physiological and behavioral response at the beginning of the experiments, whereas the rhesus macaques tend to react later. We did not find any effects of either maternal status and sex, or species on the vocal reactions to the predators. Our findings thus reveal complex interactions between the tested domains, highlighting the complex nature of the underlying emotional reactions in animals.

6.1 | Maternal Status and Sex

In the first 10 min after predator exposure, we observed that males and non-mothers spent more time in ground proximity to the predator models than mothers. However, they did not show more stress-related behavior compared to mothers during this period. Males and non-mothers only showed more stress-related behaviors than mothers later in the experiment (i.e., in 10–20 and 20–30 time windows), albeit this was only a trend for the male-mother comparison, when non-mothers and males had reduced their time in ground proximity to the predator to similarly low levels as the mothers. Contrary to our expectations, however, we did not find these differences between maternal status and sex when looking at their vocal behavior. Interestingly, we found a different pattern in our physiological data. Mothers showed the strongest decrease in nose tip temperature (of more than one degree Celsius) compared to baseline during the first 10 min of the experiment, followed by subsequent recovery in the following 10–20 min of the experiment. Although we also found that males and non-mothers did have an increase in their nose tip temperature from 10–20 min compared to the first 10 min after exposure, neither the initial decrease in the first 10 min, nor the subsequent increase in the second 10 min differed significantly from baseline values. This means that even though non-mothers and males showed some physiological reaction toward the predator model, we cannot draw clear conclusions about the emotional effect predator exposure has on the physiological state of the non-mothers and males. This in contrast to the data of mothers that showed a clearer picture with a significant drop immediately after exposure and a subsequent recovery.

Varying behavioral strategies may potentially be attributed to the observed differences in maternal status and sex. Mothers, on one hand, may be more physiologically aroused (Maestripieri et al. 2008; Maestripieri 2011) at the beginning of the experiment, and consequently adopted a behavioral avoidance strategy which potentially could mitigate their behavioral and physiological response. Non-mothers and males, on the other hand, acted more proactively at the beginning of the experiment, and subsequently coped with the associated stress through self-directed behaviors after 10 min of the experiment. For males this is consistent with data showing that they are considered more risk-prone in novel contexts (Hegab et al. 2018; Van Schaik et al. 2022). Interestingly, non-mothers showed similar behavioral patterns to those of males. This similarity supports our idea that a greater initial risk-prone and proactive reaction may lead in a later stage to a stronger behavioral stress response.

Altogether, these results suggest that differences in coping strategies between the sexes and with female maternal status may predict the variability in behavioral and physiological patterns found across different coping styles in long-tailed macaques (Bhattacharjee et al. 2024).

Non-mothers and males gradually reduced their time in ground proximity to the predator model, and at this point, their behavioral responses were not different from mothers anymore. As close proximity has been linked to mobbing behavior (cf. Bhattacharjee et al. 2024), it does seem that the non-mothers and males reduce this over the time-course of the experiment, which may suggest that they either habituated to the presence of the predator models, or at the very least overcame their initial stress response.

The observed behavioral differences could also be explained by the effects of social buffering. Although this behavior was not included in our behavioral parameters, we frequently noticed that mothers displayed ventro-ventral (VV) behavior or proximity with their infants throughout the experiment. While research into social buffering mainly focuses on mothers acting as a social buffer to their infants (Maestripieri 1999; Hennessy et al. 2009), the role of infants as social buffers for mothers remains poorly explored. Some research suggests that infants can act as a buffer for mothers too (Hennessy et al. 2009). For instance, research on rodents showed that the presence of their offspring might decrease the cortisol levels of the mothers (Packard et al. 2021), potentially due to an oxytocin-induced downregulation of the HPA axis (cf. Uvnäs-Moberg et al. 2024; Scatliffe et al. 2019). Although there is limited evidence for this phenomenon, we could hypothesize that the social buffering caused by direct contact with their infant could explain the recovery and reduced expression of stress-related behaviors by the mothers, albeit that this is of course speculative and needs further testing.

In contrast, for the non-mothers and males stress-related behaviors may have functioned as stress coping mechanisms to regulate their internal states and reduce their negative emotional arousal (Gustison et al. 2012; Whitehouse et al. 2017).

Additionally, because maternal responses may depend on parity (Holley and Simpson 1981), we conducted exploratory analyses to observe if there were differences between primiparous and multiparous mothers. We found no significant differences between primiparous and multiparous mothers in nasal temperature changes and rates of stress-related behaviors (Table S8). However, further post hoc analyses indicated that primiparous mothers had higher odds of showing stress-related behaviors than multiparous mothers ($OR = 0.488$, $p = 0.0167$). We also found that primiparous mothers spent more time in proximity to the predator model than multiparous mothers during the 10–20 time window ($ß = -2.136$, $SE = 0.555$, $z = -3.848$, $p = 0.0001$). These results could suggest that primiparous mothers acted more vigilant during this part of the experiment, and therefore, this could also explain the higher likelihood of showing stress-related behaviors. However, our data here is limited inhibiting clear conclusions.

Future research should also consider parity, as well as the mother's age and dominance rank, infant's sex and age (Holley and Simpson 1981) as factors that could affect maternal responses. Some mothers were also pregnant during the experiment, therefore, gestation effect could have potentially affect the females responses. However, due to our limited sample size, these factors could not be included in our analyses.

6.2 | Species Differences

Species-level differences were not apparent in relation to their vocal behavior or the time spent in ground proximity to the predator overall. However, rhesus macaques tended to spend more time in ground proximity during the initial 0–10 time window, but significantly less time in ground proximity during the 20–30 time window than long-tailed macaques. The overall frequency of stress-related behaviors did not differ between the species, although we did find that long-tailed macaques showed more stress-related behaviors than rhesus macaques during the 0–10 min time window. While long-tailed macaques remained stable in showing stress-related behaviors and in their time in ground proximity throughout the experiment rhesus macaques reduced their time in ground proximity to the predator model after the first 10 min and significantly showed more stress-related behaviors during the last part of the experiment.

Long-tailed macaques' nose tip temperature followed the expected trajectory of a physiological stress response to a dangerous stimuli with a clear decrease in temperature in the first 10 min with a following recovery. In contrast, rhesus macaques did not show this expected physiological response. However, the nose tip temperature in rhesus macaques did show an increase in temperature after 10 min into the experiment. Although we cannot draw a definitive conclusion from these results, these tendencies could be explained by different behavioral strategies. Rhesus macaques, which are widely considered a more despotic species than long-tailed macaques (Thierry et al. 2000; Balasubramaniam et al. 2012), may act more aggressively and less fearfully toward the predator model. This is consistent with earlier research, in which long-tailed macaques were described as more reactive and rhesus as a more hostile, proactive species (Clarke and Mason 1988). In addition, the fact that long-tailed macaques are the smaller of the two species (Fooden 2006) may also predispose them to a stronger initial emotional response than rhesus macaques (Sussman et al. 2013). These findings again support our hypothesis that different copying strategies could influence both behavioral and physiological reactions to a possible danger. Specifically, initial risk-prone behaviors may lead to a stronger behavioral and even physiological stress response in a later stage.

6.3 | The Multi-Dimensional Approach to Animal Emotions

By combining behavior and physiology, our study offers detailed insights into how captive macaques respond toward a possible danger. Relying on one single method could have limited our conclusions about whether mothers in general and long-tailed macaques as a species show a stronger or weaker emotional reaction toward our predator model than males and non-mothers in general and rhesus macaques as a species. Instead, our combined results showed more complex patterns. Combining multiple methods thus gave us a deeper understanding of our results, including the potential for seeing different coping strategies, and we thus recommend that other researchers also use a multidimensional approach when studying (individual differences in) emotional reactivity.

6.4 | Limitations and Future Research

The multidimensional approach, particularly in an open, yet ecologically more relevant setting, comes with challenges. Because the experiment is conducted in a non-invasive manner, we depended on the animals' voluntary participation. The large enclosures allow the animals to freely move between the inside and outside enclosures, reducing our visibility of them. Consequently, we could only collect data from the animals that remained inside, leading to sampling bias. More stressed animals may have avoided the area, potentially skewing some of our results. Moreover, animals often vocalize while out of view, making it difficult to identify the individual caller. This limitation makes it difficult to draw conclusions about the animals' vocal rates and the potential effects of sex and maternal status on this parameter. In addition, the limited amount of vocal data did not allow us to divide our vocal data into three time windows. As a consequence, we could not adequately combine and compare the behavioral differences and vocal differences across time, maternal status, and sex. Finally, the IRT data were more restricted to camera distance; therefore, we collected the IRT data only of animals that were close enough to the cameras, resulting in gaps in the dataset. Despite this, we collected enough data to combine and compare IRT data with behavioral responses across time. Importantly, the benefits of this approach (in-group testing, non-invasive, and non-interactive) outweigh the costs. This approach allowed us to observe the animals' behavior in a less disruptive manner. Our results may show, more accurately, the animals' responses to a possible threat without significantly affecting the well-being of our subjects.

Future research could add new and innovative techniques, such as eye tracking cameras and other physiological parameters, such as endocrine measures from non-invasively extracted salivary samples, to study cortisol or even oxytocin measures to check for the HPA axis activity, as well as the potential effect of social buffering. One should potentially collect salivary samples before and after the experiment to see the HPA axis activity that happened before the experiment. Future studies could incorporate attentional systems, such as eye tracking. Eye tracking is a new non-invasive technique that could provide information about the animals' attention (Hopper et al. 2021) as well as information on pupil dilatation (Kret et al. 2013), another indicator of emotional reactivity. Moreover, the use of IRT is still a novel and understudied technique, and we need further research to completely understand its outcomes in a non-controlled setting.

7 | Conclusion

In this study, we investigate emotional responses to the threat of a predator in two macaque species. Our results showed how individual differences, in particular maternal status and sex, as well as species, impact the animals' emotional responses and coping strategies differentially. We specifically emphasize how behavioral, physiological, and vocal measures reveal different aspects of these responses, demonstrating the importance of incorporating multiple parameters to better understand these emotional reactions. Together, our study reveals the challenges of studying animal emotions and the importance of integrating a multidimensional approach that combines both behavioral and physiological measures, particularly when studying individual differences in emotional responses. Future studies should, therefore, incorporate different parameters to correctly describe the animals' emotional reactions and understand both individual and species differences.

Author Contributions

Paula Escriche Chova: conceptualization (lead), methodology (supporting), data collection (lead), formal analysis (lead), writing – original version (lead). **Debottam Bhattacharjee:** conceptualization (supporting), funding acquisition (lead), methodology (equal), data collection (supporting), formal analysis (supporting), writing – original version (supporting), funding acquisition (supporting). **Tim-Joshua Andres:** formal analyses (supporting), writing – original version (supporting). **Elisabeth H.M. Sterck:** conceptualization (supporting), funding acquisition (lead), resources (lead), supervision (supporting), writing – original version (supporting). **Anne Marijke Schel:** conceptualization (supporting), formal analyses (supporting), supervision (equal), writing – original version (supporting). **Jorg J. M. Massen:** conceptualization (lead), funding acquisition (supporting), methodology (equal), supervision (equal), writing – original version (supporting).

Acknowledgments

We thank Aníta Rut Guðjónsdóttir and Esmee Middelburg for their assistance during the experiments, and Charlotte Kluiver for her help with behavioral coding. We also want to thank Jan A.M. Langermans for his help in implementing the study at the BPRC. We sincerely thank all the caretakers who facilitated our data collection. Finally, a special mention to Paula Esteve Verdú for her assistance in preparing the graphical abstract. Part of the study received funding from the European Union's Horizon 2020 Marie Skłodowska-Curie Action research and innovation program under grant number H2020-MSCA-IF-2019-893016 (awarded to D.B.) design.

Ethics Statement

The BPRC is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AAALAC) and licensed to keep non-human primates for ethological and biomedical research. The institution follows high standards of animal welfare and refinement measures. Our study complied with all ethical regulations and guidelines for animal testing of BPRC's Animal Experiments Committee and Animal Welfare Organisation (Animal Welfare Organisation/IvD approval no. 019E). In addition, during the studies, at least one experimenter was present who was trained and certified (FELASA Accredited Laboratory Animal Science 066/19AF) to conduct animal experiments in accordance with the requirements of Article 9 of the Dutch Experiments on Animals Act. This research was consistent with the American Society of Primatologist Principles for the Ethical Treatment of Nonhuman Primates.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data of this study are available in the supplementary files.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Supplementary Table 1: Animals participants. Name, sex, kinship, and date of birth of the participating individuals from the 5 groups are summarized. **Supplementary Table 3:** Description of nasal temperature data points per time window A) per individual depending maternal status and sex and species. **Supplementary Table 4:** Effect of maternal status and sex, and species on stress-related behaviors. **Supplementary Table 5:** Effect of maternal status and sex, and species on the time spent in ground proximity to the predator model. **Supplementary Table 6a:** Effect of maternal status and sex, and species on the vocal rate. **Supplementary Table 6b:** Effect of maternal status and sex, and species on vocal parameters I) formant 1, II) formant 2 and, III) call duration. Predicted values from GLMM. **Supplementary Table 7:** Changes in nose tip temperature across experimental time windows depending of maternal status and sex, and species. **Supplementary Table 8:** Effects of parity on I) nose tip temperature (multiparous: baseline (n = 6), 2-10 (n = 8), 10-20 (n = 6), 20-30 (n = 3); primiparous: baseline (n = 9), 2-10 (n = 10), 10-20 (n = 8), 20-30 (n = 5); II) stress-related behaviors (multiparous: 0-10 (n = 12), 10-20 (n = 11), 20-30 (n = 9); primiparous: 0-10 (n = 11), 10-20 (n = 11), 20-30 (n = 10)), and III) ground proximity.