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Beyond mood: judgement bias is not associated with maternal aggression in canaries

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Abstract

Maternal aggression (MA) — offspring-directed aggression expressed by breeding females — occurs across diverse taxa, yet its proximate drivers remain poorly understood. One candidate mechanism is individual variation in affective state. Females in a more negative emotional disposition may show reduced tolerance to offspring demands, lowering the threshold for aggressive responses. We tested this hypothesis in breeding female canaries (*Serinus canaria*) using a cognitive judgement bias test (JBT), in which approach latency to an ambiguous stimulus served as a proxy for judgement bias. Females reliably discriminated between rewarded and unrewarded stimuli, validating the JBT. However, when accounting for individual differences in approach speed, the JBT score did not differ between MA and non-aggressive females. These results indicate that judgement bias, did not predict the subsequent expression of MA in this system, suggesting that offspring-directed aggression is not a direct consequence of a pessimistic affective disposition.

INTRODUCTION

Maternal care, encompassing behaviours such as nest guarding, brooding, and food provisioning, is widespread in the animal kingdom and contributes positively to offspring development and survival (Clutton-Brock, 1991; Royle et al., 2012). Yet, mothers occasionally direct aggression towards their own offspring (Garcia-Co et al., 2025; Maestripieri & Carroll, 2000; Shizuka & Lyon, 2013). This behavior appears paradoxical and maladaptive, yet it occurs across diverse taxa (Maestripieri & Carroll, 2000; Mock & Parker, 1997; Shizuka & Lyon, 2013). In some species, such offspring-directed aggression is part of an adaptive parental strategy, contributing to brood reduction, or in the context of a weaning conflict, or encouraging fledging and independence (Kilner & Drummond, 2007; Mock & Parker, 1997; Trivers, 1974). However, maternal aggression (MA) also occurs under conditions in which these classic evolutionary explanations appear insufficient (Maestripieri, 2005). Characterising the proximate mechanisms that predispose some females, but not others, to express offspring-directed aggression may yield critical insights into the etiology of this behaviour.

Affective states — that is, valenced emotional conditions characterized by a positive or negative quality and emerging from the interplay between physiology and environmental context — could represent a key integrative component in the regulation of maternal care (Mendl et al., 2010; Paul et al., 2005). Affective states influence how individuals perceive and interpret environmental cues, while they are simultaneously modulated by those same cues. It is through this bidirectional dynamic that they come to influence decision-making (Jirkof et al., 2019; Mendl et al., 2010). In the context of parental care, a more negative affective state may reduce responsiveness to offspring demands or lower the threshold for triggering aggressive responses, which may affect the interpretation of ambiguous offspring signals. For instance, mothers may perceive appropriate begging as excessive or aversive (Bosch et al., 2005; McEwen, 2006; Neville et al., 2020). This in turn may affect parental care behaviors (Jirkof et al., 2019; Laubu et al., 2019; Neville et al., 2020; Zidar et al., 2018). Yet, no study has tested whether a mother's

affective state predicts the likelihood of MA which may be partly due to the difficulty of measuring affective states in animals.

Judgement Bias Tests (JBTs) provide a robust approach to inferring affective states in non-human animals (e.g., Jirkof et al., 2019). Based on the principle that affective state biases the interpretation of ambiguous information, JBTs assess whether individuals respond to ambiguous cues with an optimistic bias (anticipating reward) or a pessimistic bias (anticipating punishment; Jirkof et al., 2019). This approach has been validated across diverse taxa, including birds (Laubu et al., 2019; Neville et al., 2020; Zidar et al., 2018). Although JBTs are often described as measures of current affective state, the individual differences they capture tend to be stable across repeated testing and can correlate with other trait-like measures such as personality and coping style (Lagisz et al., 2020; Réale et al., 2007).

If a more negative affective state lowers the threshold for offspring-directed aggression, females with a more pessimistic judgement bias should be more likely to exhibit MA. We tested this prediction in domestic canaries (*Serinus canaria*), in which a substantial proportion of breeding females exhibit offspring-directed aggression during the nestling period (Garcia-Co et al., 2025, 2026).

MATERIALS AND METHODS

STUDY SPECIES AND ANIMAL HOUSING

All birds used in this study belonged to a captive population of Five Fancy canaries (*Serinus canaria*) maintained at the University of Antwerp. In February, individuals selected for breeding were housed in single-sex indoor aviaries (2 x 2 x 2 m^3) at 19–24°C under long-day photoperiod (14h light: 10h dark; Estramil et al., 2014). Breeding pairs were then formed (N = 103 pairs) by introducing the male first into a standard breeding cage (50×64×40 cm; GEHU cages, The Netherlands), followed by the female a few days later. Breeding cages were equipped with two perches, a nest-cup, nesting material, cuttlefish bones, shell sand, egg food (twice weekly; Van Camp, Belgium), canary seed mixture (Van Camp, Belgium), and water *ad libitum*.

Once pairs completed nest-building, egg-laying was monitored daily, and eggs were weighed at laying. To disentangle genetic from early environmental effects on offspring traits, all clutches were reciprocally cross-fostered two to three days after clutch completion (see Garcia-Co et al., 2026 for the full procedure). Foster nests were matched on mean egg weight (< 0.2 g difference), clutch size (± 1 egg), and day when the last egg was laid (± 1 day). Although the cross-fostering is not directly relevant to the present study, it determined the rearing environment experienced by all nestlings (and breeding females). Hatching was monitored daily from day 14 after laying of the first egg (i.e., minimum incubation duration). From hatching onwards, parents were provided daily with egg food and regularly supplemented with freshly germinated seeds.

JUDGMENT BIAS TEST

To infer the females' affective state, we used a JBT consisting of dishes containing or not containing egg food, which were initially covered with a coloured lid (black or white). When exposed to an ambiguous stimulus (grey lid), females showing shorter approach latencies (controlled for individual differences in overall speed) were assumed to be in a more positive affective state because they anticipated a reward; those showing longer latencies were assumed to be in a more negative affective state (Laubu et al., 2019; Mendl et al., 2009; Neville et al., 2020; Paul et al., 2005; Zidar et al., 2018).

The JBT was conducted when nestlings were 17–18 days old, the period preceding the peak of MA (Garcia-Co et al., 2025; see Categorisation of Maternal Aggression, below). Prior to testing, males and food were temporarily removed from the breeding cage, and fresh sand was provided to prevent the consumption of leftover food. All trials were video recorded (Vizu Extreme X6S) in the absence of human observers to minimize disturbance. Before the experiment, all females were individually habituated to the food dishes, food type, and coloured lids (see Supplementary Information S1 for full habituation procedure). The rewarded stimulus consisted of a dish containing egg food, covered with a coloured lid (black or white); the unrewarded stimulus consisted of an identical but empty dish covered with a lid of the opposite colour. The colour and spatial position (left or right) associated with rewarded versus unrewarded were randomized during habituation and held constant throughout the experiment.

The experiment consisted of two phases conducted on the same day: a training phase in the morning and a test phase four hours later in the afternoon. During the intervening period, food was provided *ad libitum* to ensure nestling nutritional needs were met. The training phase consisted of five trials in a fixed alternating sequence (rewarded, unrewarded, rewarded, unrewarded, rewarded). The first two trials served as reminders of the reward contingencies; the final trial was administered to maintain motivation and was excluded from analysis.

The test phase comprised five trials (rewarded, unrewarded, ambiguous, rewarded, unrewarded), each trial lasting a maximum of 10 minutes with a single stimulus being presented per trial. The ambiguous stimulus consisted of an unrewarded dish covered with a grey lid (intermediate colour between black and white) placed centrally between the rewarded and unrewarded stimulus positions (i.e., intermediate position). The use of a grey lid intermediate between black and white as the ambiguous stimulus follows established JBT protocols in birds, in which subtle colour differences between the ambiguous and reference stimuli are sufficient to produce discriminable responses (Matheson et al., 2008; Zidar et al., 2018). A schematic overview of the full experimental timeline is provided in Supplementary Table S1.

From an initial breeding cohort of 103 pairs, 67 were randomly selected for participation in the JBT. Of these, 10 were excluded for failing to discriminate between stimuli, yielding a final sample of 57 females. Behaviours were annotated using BORIS v8.27.7 (Friard & Gamba, 2016) according to a predefined ethogram (Supplementary Table S2). Latency to open the dish (i.e., the time between first approaching and successfully removing the lid) was additionally recorded as a secondary measure. This measure was analysed using raw latency rather than the normalised score, as the normalisation formula requires

a rewarded and unrewarded reference latency for each individual that was not available for the open latency measure. Results are reported in Supplementary Tables S6a–S7 and Supplementary Figure S3.

CATEGORIZATION OF MATERNAL AGGRESSION

Maternal aggression (MA) was defined as evidence of feather plucking directed towards nestlings consistent with the criterion used in Garcia-Co et al. (2025, 2026). Although both parents contribute to parental care post-hatching, male aggression toward offspring is negligible in frequency and intensity (Garcia-Co et al., 2025). Maternal behaviour, therefore, represents the main source of early adverse social experience. Females were classified as MA (aggression present) or noMA (aggression absent) based on daily visual inspection of all nestlings in a brood: a female was assigned to the MA category if at least one nestling exhibited visible feather plucking at any point during the nestling period, which most typically began around day 19 post-hatching. MA occurrence was therefore determined after the JBT had already taken place, ensuring that the affective state measure was not confounded by prior MA expression. Of the 67 females, 36 were classified as MA and 31 as noMA.

ETHICS STATEMENT

All procedures complied with the Flemish and Belgian institutional regulations and were approved by the Ethical Committee on Animal Experimentation (ECD) at the University of Antwerp (license ECD-2022-87). No abnormalities in appearance, health, or behaviour attributable to the experimental procedures were observed.

STATISTICAL ANALYSES

All analyses were performed using the software package R v4.5.1 (R Core Team, 2025). Latency data were log-transformed prior to analysis to satisfy model assumptions. Model fit was evaluated using diagnostic plots generated with the packages *performance* (v0.10.3; Lüdecke et al., 2021) and *DHARMa* (v0.4.6; Hartig, 2016). Pairwise comparisons were conducted using emmeans (v1.10.3; Lenth et al., 2026). Statistical significance was set at $\alpha = 0.05$. Trials were excluded if a nestling contacted or removed the lid before the focal female (N = 9). Only the final three test phases (ambiguous, rewarded, unrewarded) were included in analyses, as the initial two trials served as within-session anchors.

To validate the JBT paradigm, we first tested whether approach latency differed across stimulus types using a linear mixed model (LMM) with stimulus type (rewarded, unrewarded, ambiguous) as a fixed effect and female identity as a random intercept. To test our primary hypothesis, that MA females exhibit a more pessimistic judgement bias, we calculated a normalized JBT score for each female following Harding et al. (2004): Score = [Latency(ambiguous) − Latency(rewarded)] / [Latency(unrewarded) − Latency(rewarded)]. This score removes the confound of individual differences in overall approach speed. A value of 0.5 indicates an intermediate state in which the latency to the ambiguous stimulus fell exactly between that of the rewarded and unrewarded stimuli. Values below 0.5 indicate that the

ambiguous stimulus is approached more similarly to the rewarded stimulus (optimistic); values above 0.5 indicate that the ambiguous stimulus is treated more similarly to the unrewarded stimulus (pessimistic). Although scores between 0 and 1 represent the theoretically expected range, occurring when the ambiguous latency falls between the rewarded and unrewarded latencies, values outside this range are possible when the ambiguous latency is faster than the rewarded or slower than the unrewarded stimulus, and become extreme when the difference between rewarded and unrewarded latencies is close to zero. Such cases reflect females who did not discriminate strongly between the two reference stimuli; the observed range in the present sample was approximately − 15 to + 15, and these females were retained in all analyses since the non-parametric tests used are robust to such extreme values and excluding them did not change the direction or significance of any reported result.

Females were excluded only if latency data were missing for any trial type (N = 5), or if rewarded and unrewarded latencies were mathematically identical, producing an undefined denominator (N = 2); this yielded a final N = 40. Given the heavy-tailed distribution of scores driven by a small number of females with near-zero denominators, we used a Wilcoxon rank-sum test as the primary test of the MA effect, and a one-sample Wilcoxon signed-rank test to assess whether the population median score differed from 0.5. Brood size was included as a covariate; full models including brood size are reported in Supplementary Material.

RESULTS

Validation of the judgement bias paradigm: effect of stimulus type on approach latency

Approach latency differed significantly across stimulus types (Fig. 1; Supplementary Table S4a–S4b). Females approached both the rewarded (estimate = -1.15 ± 0.27 SE, t= -4.18, p = < 0.001) and ambiguous stimuli (estimate = -1.15 ± 0.27 SE, t= -4.18, p = < 0.001) significantly faster than the unrewarded stimulus. Approach latencies did not differ significantly between the rewarded and ambiguous stimuli (p = 1.000), indicating that females responded to the ambiguous stimulus more similarly to the rewarded than to the unrewarded stimuli. The result remained robust after excluding three individuals with notably long approach latencies.

Figure 1. Latency to approach the stimuli as a function of stimulus type. Points represent individual observations (jittered for clarity), and black dots with error bars indicate mean ± SE.

Maternal aggression and normalized bias score

The normalised JBT score did not differ significantly between MA and noMA females (Wilcoxon W = 226, p = 0.459; Fig. 2). Both groups had median scores close to zero (MA: 0.11, noMA: 0.02), indicating a slight tendency to treat the ambiguous stimulus more similarly to the rewarded than the unrewarded condition. At the population level, the median bias score (0.03) did not differ significantly from 0.5

(Wilcoxon signed-rank V = 311, p = 0.188), indicating that neither group showed a detectable optimistic or pessimistic bias once individual differences in overall approach speed were accounted for.

DISCUSSION

We investigated whether judgement bias, as measured by a single JBT session, is associated with the occurrence of maternal aggression (MA) in breeding female canaries (*Serinus canaria*). The JBT was successfully validated under breeding conditions. Females reliably discriminated between rewarded and unrewarded stimuli, confirming that the paradigm successfully captured differential responding to both types of stimuli. Interestingly, females approached the ambiguous stimulus at a latency similar to the rewarded condition rather than at a latency intermediate between the rewarded and unrewarded stimuli, a pattern that we discuss further below. However, contrary to our prediction, the normalized JBT score — which accounts for individual differences in overall speed — did not differ between MA and noMA females, indicating no significant affective bias in either direction. Together, these results provide no evidence that stable judgement bias predicts the later expression of offspring-directed MA.

One possible explanation for the null result is that MA is triggered by short-lived emotional responses to specific offspring cues, such as heightened begging intensity or nestling competition (Godfray, 1995; Neuenschwander et al., 2003), rather than reflecting a chronic underlying affective disposition. Internal physiological signals may compound this effect: fluctuations in glucocorticoids during the energetically demanding phase of chick-rearing can alter behavioural reactivity on very short timescales (McEwen, 2006; Wingfield & Sapolsky, 2003), potentially predisposing females towards aggression independently of their general affective state. If so, a single JBT session would be unlikely to detect the relevant affective variation. This possibility relates to a broader question about what JBTs actually measure. Individual differences in JBT performance are typically stable when animals are retested, and often correlate with independent measures of personality, boldness, exploratory tendency, and coping style rather than with concurrent mood alone (Koolhaas et al., 1999; Lagisz et al., 2020; Réale et al., 2007).

In addition, performance may also be influenced by motivational state, reward sensitivity, exploratory tendency, or impulsivity, all of which can affect approach behaviour independently of affective state (Lagisz et al., 2020; Mendl et al., 2009). This has led some authors to argue that JBT scores index a relatively enduring, trait-like disposition, closer to what personality research would call emotional reactivity, rather than a fluctuating affective state (Briefer et al., 2015; Zidar et al., 2018). Moreover, JBTs primarily capture optimism-pessimism in the evaluation of ambiguous information and may be less sensitive to more reactive emotional states, such as frustration or irritability, that could more directly precipitate aggression (Carver & Scheier, 2013; Frijda et al., 2014). Our results therefore suggest that stable judgement bias does not predict MA, but do not exclude a role for more transient emotional processes. Future studies should therefore assess affective state and MA simultaneously, ideally through repeated within-individual measures that can distinguish trait-like from state-like variation.

Direct tests of the relationship between judgement bias and aggression are scarce, and the few studies that exist point in different directions. In domestic dogs, individuals rated by their owners as more fearful or aggressive showed a more pessimistic judgement bias (Barnard et al., 2018). In gestating sows, the opposite pattern was found and sows independently classified as more aggressive or dominant approached the ambiguous stimulus faster, which would be interpreted as a more optimistic bias (Horback & Parsons, 2022). A systematic review across taxa confirms that JBT scores reliably track manipulations of housing and welfare conditions, but notes that comparatively few studies have examined links to naturally occurring individual differences in social behaviour such as aggression (Lagisz et al., 2020). Taken together, the limited literature provides no consistent evidence that judgement bias predicts aggressive behaviour across taxa.

Moreover, not all negative emotional states necessarily increase the likelihood of aggression. Whereas frustration or irritability are associated with reactive action, other negatively valenced states such as despondency or withdrawal may not (Carver & Scheier, 2013; Frijda et al., 2014). Consequently, the absence of differences in judgement bias does not exclude an emotional contribution to MA but instead suggests that the relevant emotional processes may lie outside the optimism-pessimism axis captured by the JBT.

Females approached the ambiguous stimulus at a latency statistically indistinguishable from the rewarded stimulus, rather than at a latency intermediate between the rewarded and unrewarded conditions. While this pattern is consistent with a population-level optimistic bias and has been reported in other JBT studies (e.g., Matheson et al., 2008), it also raises the possibility that our grey stimulus was perceived as closer to the rewarded end of the colour continuum than intended, reducing its ambiguity. If the grey stimulus was perceived as relatively rewarding, between-individual variation in judgement bias would necessarily have been reduced, making biologically meaningful differences more difficult to detect. Future work could mitigate this by using multiple, graded ambiguous stimuli spanning the colour continuum, which would also allow bias to be estimated as a continuous function of stimulus ambiguity rather than from a single intermediate probe. In the same line of thinking, another limitation could be that we treated MA as a binary trait based on the occurrence of feather plucking. Capturing the severity or frequency of aggression with a graded measure along with an individual based estimate (i.e., towards which nestling MA is directed) might provide the resolution needed to detect links with affective state or brood size.

As noted in the Introduction, offspring-directed aggression can, in some species, form part of an adaptive strategy tied to brood reduction or weaning conflict (Kilner & Drummond, 2007; Mock & Parker, 1997). Life-history theory predicts that parental care should balance current offspring value against the mother's residual reproductive potential (Clutton-Brock, 1991; Trivers, 1974), and decisions structured around such long-term strategies may be less susceptible to transient affective fluctuations than responses to immediate stressors (Mendl et al., 2010). Thus, an alternative, non-mutually exclusive explanation is that MA represents a parental care strategy, shaped by evolutionary trade-offs rather than an emotion-driven response. Consistent with this, the absence of a brood size effect on the normalised

JBT score suggests that the females' affective bias was not modulated by offspring demand. A larger brood could be expected to increase motivation or optimism if affective state tracks current energetic need. Yet, no such pattern was observed. Crucially, however, affective states and parental care strategies are not mutually exclusive, and affect may act as a modulatory filter, shifting the threshold for the expression of parental care behaviours without being the primary driver (Mendl et al., 2010; Paul et al., 2005).

MA and noMA females may experience similar affective baselines but differ in their behavioural sensitivity to internal signals. This is consistent with frameworks of animal personality and coping styles, in which individuals differ in behavioural reactivity despite facing comparable environmental or physiological stressors (Dingemanse & Réale, 2005; Koolhaas et al., 1999). Indeed, complementary work in this population shows that females that later express MA already differ, before aggression begins, in how they allocate food according to offspring body mass and begging persistence (Garcia-Co et al., *under revision*). This suggests that MA may be embedded within broader maternal decision-making rather than arising abruptly from a stable affective disposition. However, this interpretation remains speculative and aggression expressed during weaning or after fledging may serve different functions, such as promoting offspring independence, and could relate differently to judgement bias or affective state.

In conclusion, we found no evidence that stable judgement bias predicts the later expression of MA in breeding canaries. This should not be interpreted as evidence that affective processes do not play a role in MA, but rather that this particular task did not detect an association. Short-lived emotional states, behavioural reactivity, and state-dependent parental strategies remain plausible mechanisms that warrant further investigation. Distinguishing among these alternatives will likely require repeated assessments of judgement bias across the reproductive cycle combined with physiological measures of stress and more detailed quantification of MA.

Declarations

DATA AVAILABILITY

The dataset supporting this article is archived in Mendeley Data: Putteneers S, Garcia-Co C, Verbruggen F, Morales J, Müller W. 2026. Dataset for: Beyond mood: maternal aggression in canaries is unrelated to affective state. Mendeley Data. (https://data.mendeley.com/datasets/gz6gvr7p6c/1).

The video recordings of all JBT trials used in the analyses are archived in Zenodo: Garcia-Co C, & Putteneers S. (2026). Video recordings of judgement bias test trials in breeding domestic canaries (*Serinus canaria*): dataset for "Beyond mood: maternal aggression in canaries is unrelated to affective state". Zenodo. (https://zenodo.org/records/20134414).

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During the preparation of this work, the authors used Claude (Anthropic; claude.ai, approximately February 2026 – May 2026) to assist with language editing and improvement of fluency and readability. Specifically, AI assistance was used in the following sections: Abstract, Introduction, Materials and Methods, Results, Discussion, and Supplementary Material. The AI was not used to generate scientific content, design analyses, interpret results, or formulate conclusions. All AI-assisted text was reviewed, verified, and edited by the authors, who take full responsibility for the accuracy and integrity of the published work.

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AUTHOR CONTRIBUTIONS

Simon Putteneers: Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Writing – original draft & editing. **Clara Garcia-Co:** Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Writing – original draft & editing. **Judith Morales:** Funding acquisition; Supervision; Validation; Writing – review & editing. **Frederick Verbruggen:** Funding acquisition; Supervision; Validation; Writing – review & editing. **Wendt Müller:** Conceptualization; Funding acquisition; Investigation (supporting); Methodology (supporting); Resources; Supervision; Validation; Writing – review & editing.

COMPETING INTERESTS

The authors declare no competing or financial interests.

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Figures

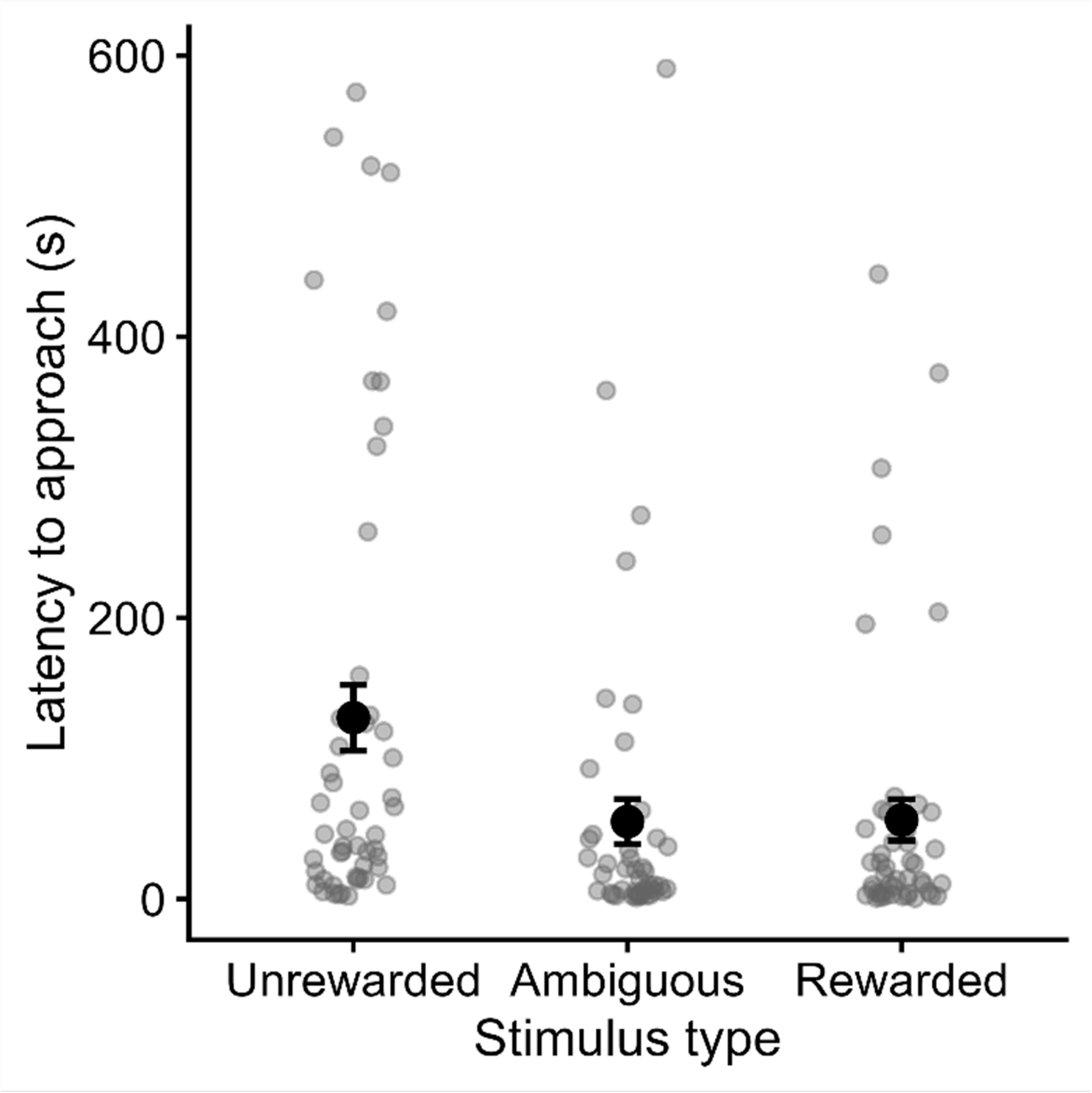


Figure 1

Latency to approach the stimuli as a function of stimulus type. Points represent individual observations (jittered for clarity), and black dots with error bars indicate mean ± SE.

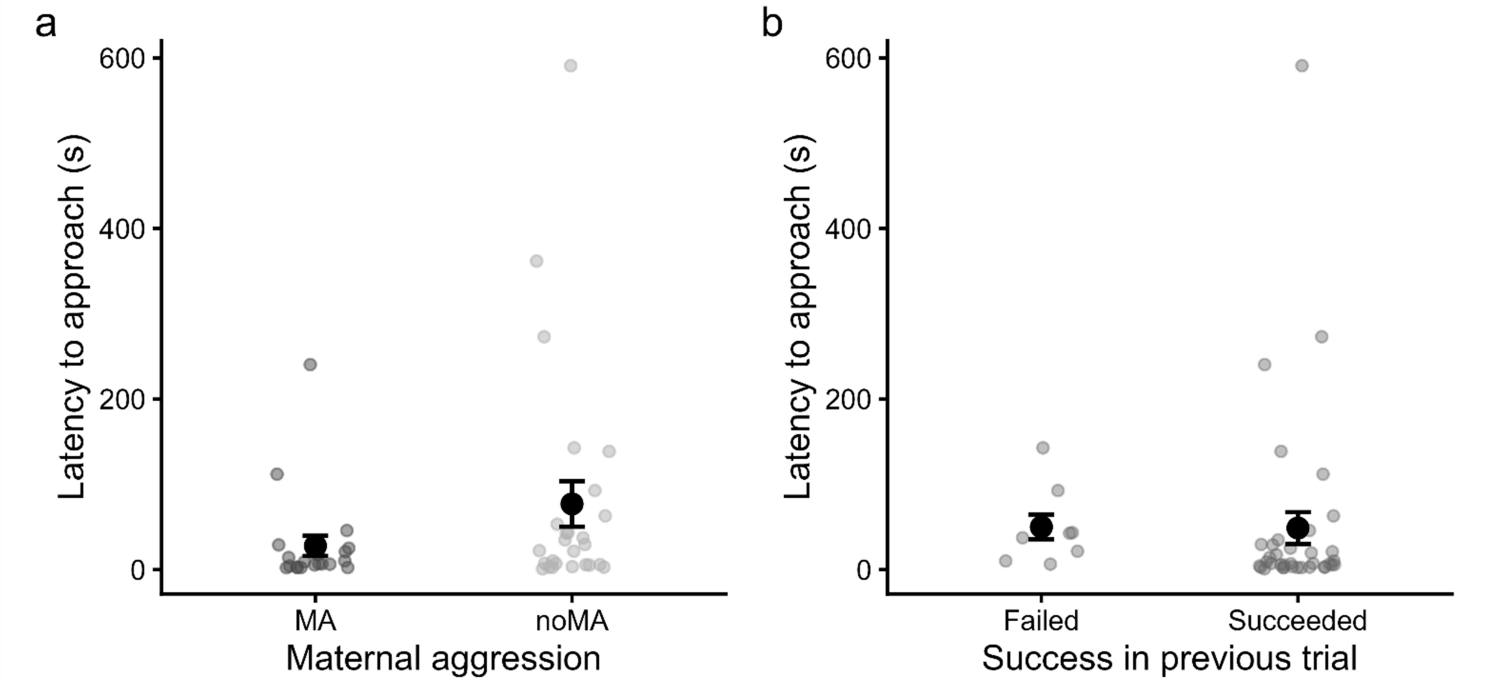


Figure 2

Normalised JBT score by maternal aggression status (MA vs. noMA). Score = [Latency(ambiguous) − Latency(rewarded)] / [Latency(unrewarded) − Latency(rewarded)]. Points represent individual females (jittered), black dots with error bars indicate mean ± SE. The dashed line marks 0.5 (exactly intermediate between rewarded and unrewarded). Scores below 0.5 indicate optimism; scores above 0.5 indicate pessimism.

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