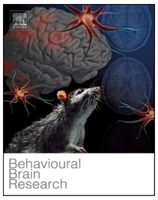
Behavioural Brain Research 503 (2026) 116075

Contents lists available at ScienceDirect

Behavioural Brain Research

journal homepage: www.elsevier.com/locate/bbr



Research article

Beak wiping stereotypies are correlated with neophobia and lack of enrichment in captive house sparrows (*Passer domesticus*)

Danna F. Masri [a], William J. Frazier [a], Melanie G. Kimball [a,b], Christine R. Lattin [a,*]

[a] *Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, USA*
[b] *Department of Neurobiology, Physiology and Behaviour, University of California Davis, Davis, CA, USA*

ARTICLE INFO

Keywords:
Behaviour
Stress
Anxiety
Songbird
Animal welfare

ABSTRACT

Behavioural syndromes are suites of correlated behaviours at the population or species level that can affect how wild animals respond to their environments, including potentially stressful situations such as captivity. In this study, we assessed whether beak wiping, a stereotyped anxiety-linked behaviour where birds wipe their beaks on a perch in a “windshield wiper” motion, was correlated with another anxiety-linked behaviour, neophobia towards novel objects presented with food, in captive house sparrows (*Passer domesticus*). We predicted that more neophobic sparrows would also exhibit more beak-wiping stereotypies. We analyzed 1 h long control videos (when sparrows were presented with a normal food dish only; $n = 54$) from three previous neophobia studies to assess beak wiping frequency, mean beak wiping bout duration, and total bout duration. Sparrows' reluctance to feed in the presence of novel objects was significantly correlated with the mean duration of beak wiping bouts during control trials. We also found that simple enrichment (rubber perches, manzanita branch perches, and/or artificial pine branches) decreased both the frequency and duration of beak wiping. These findings suggest that high neophobia and high levels of stereotypy may arise due to similar neuroendocrine mechanisms and reflect a “high anxiety” behavioural syndrome. This work also highlights the importance of providing species-appropriate environmental enrichment to decrease the prevalence of stereotypic behaviours in captive songbirds.

1. Introduction

Consistent individual differences in behaviour – known as personalities, temperaments, behavioural syndromes, or coping styles [1,2] – have been described in dozens of different animal species [3–7]. An animal's personality affects many behaviours that impact its fitness, from finding food [8,9] to coping with competition [10,11]. The existence of behavioural syndromes means that individuals may not be able to act optimally in every situation, as they can act as a potential constraint upon behavioural plasticity [12]. Therefore, understanding links between different behaviours is critical for understanding why animals sometimes fail to respond appropriately to environmental challenges.

One potential challenge wild animals can face is being transferred from the wild to a captive environment for research, conservation, or education purposes. The transition to captivity is often highly stressful for wildlife, partly due to differences between natural environments and controlled lab or zoo conditions, including forced proximity to humans, novel foods, artificial lighting, and restricted movement [13]. Captivity stress in turn can cause physiological and behavioural changes, including the development of abnormal repetitive behaviours such as stereotypies [14,15]. Stereotypies are short, repetitive sets of behaviours that appear functionless and replace the comparatively longer and more diverse range of behaviours observed in wild animals [16]. For example, because flight is inhibited by small cages, somersaulting stereotypies (where birds perform an aerial backflip off their perches, land on the cage floor, and fly back up to repeat the loop) may develop in captive birds as a response to thwarted escape behaviours [17]. Alternatively, some stereotypies involve natural behaviours that become disassociated from their natural context, such as beak wiping stereotypies that can develop in captive house sparrows (*Passer domesticus*) [18]. Beak (or bill) wiping is a natural avian behaviour used to clean the beak after feeding [19], but in captivity it can become disassociated from feeding and much more frequent.

Stereotypic behaviour of captive animals is of scientific interest for several reasons. First, the performance of stereotypy can be used as a proxy for animal welfare, where less stereotypic behaviour is often (but not always) associated with better welfare [20,21]. Providing

---

* Correspondence to: Department of Biological Sciences, Louisiana State University, 131 Life Sciences Building, Baton Rouge, LA 70803, USA.
E-mail address: christinelattin@lsu.edu (C.R. Lattin).

https://doi.org/10.1016/j.bbr.2026.116075
Received 10 October 2025; Received in revised form 28 January 2026; Accepted 30 January 2026

environmental enrichment that allows for greater expression of natural behaviours such as movement, hiding, and grooming can substantially reduce stereotypies [22]. For example, European starlings (*Sturnus vulgaris*) housed in larger and longer cages that allowed for more flight exhibited fewer stereotypies compared to starlings in smaller cages [23]. Stereotypies can also impose a threat to the external validity and replicability of research on captive animals; if stereotypy induces behavioural inhibition, then behaviour-based assessments such as open field tests, reactions to novelty, or extinction and reversal learning may be affected [24]. However, not all wild species housed in captivity develop stereotypies [25], and there is wide individual variation within species in the amount of stereotypic behaviours performed in captive environments [26–28]. For example, licking stereotypies varied from 19 % to 35 % of observations among four captive northern giraffes (*Giraffa camelopardalis*) housed in an Indian zoo [29]. This across- and within-species variation suggests stereotypies may be related to variation in animals' underlying neurobiology or physiology.

In this project, we investigated the connection between neophobia (novelty avoidance) and beak wiping stereotypies in captive house sparrows. We predicted that neophobia and beak wiping stereotypies might reflect a high-anxiety behavioural syndrome resulting from shared neuroendocrine mechanisms [30]. For example, there is wide individual variation in glucocorticoid production in house sparrows in the wild and in captivity, and experimental evidence has linked glucocorticoids both to neophobia and to the development of beak wiping stereotypies in this species [31,32]. We watched control videos from three previous studies of captive wild house sparrows, quantified the frequency, total duration, and mean duration of beak wiping bouts, and assessed whether any of these measures were correlated with a previously assessed measure of neophobia in the same birds, average latency to feed in the presence of novel objects [33–35]. Analyzing control videos (where the familiar food dish was replaced without novel objects) allowed us to assess beak wiping in a context separate from neophobia. Meta-analysis approaches find that most correlated behaviours show small effect sizes [36,37], which suggests that many studies do not have sufficient sample size to reveal behavioural syndromes. Combining data from multiple studies provided us with a relatively robust sample size (n = 54 birds) to look for evidence of a behavioural syndrome.

Our overall hypothesis was that neophobia and stereotypy are behaviours with similar underlying neuroendocrine mechanisms such as specific glucocorticoid or dopamine profiles; therefore, we predicted that object neophobia and beak wiping would be positively correlated. Because housing conditions in these three studies varied slightly, this also gave us the opportunity to determine the effects of captive enrichment on stereotypies in wild-caught songbirds. We predicted that species-appropriate environmental enrichment (specifically, rubber perches, manzanita branch perches, and/or artificial pine branches) would result in fewer sparrow beak wiping bouts by allowing for more naturalistic behaviours, thereby attenuating the need for stereotypy [23]. Although rubber, manzanita wood, and plastic pine are unlikely to have been previously encountered by sparrows, these items were present in cages during the entire period of captivity, are more natural colors (tan, brown, and green) than the novel objects used in neophobia assays, are similar to objects in the natural environment (e.g., bare tree branches, grasses, and pine branches), and allow for a wider range of natural behaviours (e.g., hiding behind artificial pine branches, bouncing on rubber perches) than the novel objects used in neophobia assays.

2. Methodology

2.1. Sparrow capture and enrichment

Adult house sparrows (n = 54, 39 males and 15 females) used in this study were caught in three cohorts in East Baton Rouge Parish using mist nets; cohort capture dates were: A) June-July 2019 (n = 22) [33], B) April-July 2022 (n = 12) [35], and C) February 2022-April 2023 (n = 20) [34]. Note that although birds were captured at different times of year, previous research did not find any seasonal effects on neophobia [38], nor any difference in beak wiping behaviour between breeding and winter [39] in captive house sparrows. Sparrows in Cohort A were part of a study examining the effects of exposure to novel objects or control conditions on neuronal activity; control videos used in the present study were from novel object, novel food, or novel object habituation trials [33]. Sparrows in Cohort B were part of a study aiming to understand the function of the avian hippocampus in neophobia. Control videos used for the present study were from novel object testing prior to the administration of any experimental treatments [35]. Finally, sparrows in Cohort C were part of a study investigating the effect of conspecific alarm calls on neophobia; we used control videos from the initial week of novel object trials before sparrows were exposed to calls [34].

Birds in all cohorts were allowed to habituate to captivity for at least three weeks before behaviour trials began. All sparrows were collected under Louisiana Scientific Research and Collecting Permits, and the Louisiana State University Institutional Animal Care and Use Committee approved all protocols (96–2018, 10–2021, 56–2022, 92–2023). To minimize social learning and group size effects on neophobia [40,41], sparrows were singly housed in cages measuring 56 cm× 45 cm x 33 cm in the Louisiana State University vivarium. Note that previous avian studies suggest that group housing often increases neophobia in birds [40,41]. This could reflect a "socially induced" neophobia where birds are either picking up on anxiety cues from more neophobic conspecifics and behaving more fearfully, or seeking to minimize risk to themselves at others' expense.

All sparrows had unlimited access to grit, mixed seeds, a vitamin-rich food supplement (Mazuri small songbird diet), and water; however, cohorts differed in the amount of environmental enrichment provided. For Cohort A, cages contained a plastic perch extending from the front to the back of the cage. For Cohort B, cages had the same plastic perch, a perch made of rubber tubing positioned diagonally, and a manzanita branch perch. Finally, the cages of Cohort C included the plastic and rubber tubing perches, plus an artificial pine branch hanging in the back of the cage (added as a possible hiding spot for sparrows) (Fig. 1**.**) Note that prior to neophobia trials all sparrows also had a dish of sand for dustbathing, but these were removed during neophobia trials because they often contained food.

2.2. Behaviour analysis and quantification

In all three cohorts, sparrows were randomly assigned to different novel objects presented with food (n = 3) or food alone as a control (n = 2) during a week of novel object trials. For the three studies from which videos were pulled, a random number generator was used to select one of the control videos per sparrow to analyze for beak-wiping behaviours (n = 54, 1 control video per sparrow). Each sparrow's neophobia was quantified as previously published [33]; briefly, this was defined as an individual's average latency to feed from the food dish when a novel object was present during three 1 h trials. To ensure that birds were motivated to feed during trials, food was removed overnight, and trials were conducted the following morning 30 min after lights on. To quantify neophobia, observers watched videos and recorded the bird's first time eating from the food dish. If the bird did not feed, it was assigned a maximum time of 1 h. After the 1 h trials were complete, video recordings were stopped, all objects removed, and the normal food dish was present for the rest of the day.

Beak wiping, which we defined as a bird repeatedly wiping its beak back and forth in a "windshield wiper" motion, was used as a measure of stereotypy; each single event (dubbed a "bout") was separated by 2 s [18]. Beak wiping stereotypy was recorded using BORIS software [42]. Two observers watched 1 h control videos and pressed a key to signify the beginning of a bout. When the bout ended, a key was pressed to indicate the end of the bout. This gave us three measures of stereotypy related to beak wiping: mean bout duration, total bout duration, and

Fig. 1. Environmental enrichment provided to house sparrows in: a) Cohort A (n = 22); b) Cohort B (n = 12); and c) Cohort C (n = 20). All cohorts had a central longitudinal plastic perch. Cohort A received no additional enrichment during behaviour trials. Cohort B also received a manzanita branch perch and a diagonally-spanning rubber tubing perch; Cohort C received an artificial pine branch and a diagonally-spanning rubber tubing perch.

beak wiping frequency. Mean bout duration represents the average amount of time a bird spent in a single beak-wiping bout. Total bout duration is the cumulative time of all beak-wiping bouts recorded over a 1 h period. Finally, beak wiping frequency refers to the total number of beak-wiping bouts (each separated by at least 2 s) observed within an hour. Past research on beak wiping in house sparrows [18,32] only counted numbers of bouts; however, because bouts can differ widely in length (e.g., if a sparrow performs two sets of wipes vs. twenty sets of wipes) and a key part of stereotypy is its repetitive nature, we decided to quantify beak wiping using multiple measures to determine if any aspect of this stereotypical behaviour was more clearly linked to neophobia or enrichment availability.

2.3. Statistical analyses

Analyses were run in in JMP Student Edition 18.2.2 (SAS Institute). We used three different sets of linear mixed models (one for each measure of beak wiping) to analyze the relationship between beak wiping and average latency to feed from a food bowl when novel objects were present. Initially, we tested whether the different types of enrichment found in Cohorts B and C (rubber tubing and a manzanita branch, and rubber tubing and an artificial pine branch, respectively) mattered for beak wiping behaviour, but because these two groups did not differ from each other (data not shown) they were combined as a "high enrichment" group (relative to the "low enrichment" Cohort A). For each model, we included fixed model effects of sparrow sex (male vs. female; determined by clear plumage features [43]), high enrichment (Cohort A = no, Cohorts B and C = yes), video quality (some videos were very dark or blurry and the two watchers made note of this in their data sheets; poor quality vs. not poor quality), and average latency to feed in the presence of three novel objects (in s) and added video watcher as a random effect. We ran linear mixed models using Restricted Maximum Likelihood (REML) with unbounded variance components to prevent bias in estimation of fixed effects; we also calculated r^2 values for each model. We inspected residual plots and verified that the homoscedasticity and linearity assumptions of linear models were met for each model.

3. Results

Mean beak wiping bout duration ($F_{1,49}$=4.48, p = 0.040, r^2 = 0.60) was correlated with neophobia, while total beak wiping duration ($F_{1,49}$=0.86, p = 0.36, r^2 = 0.32) and beak wiping frequency ($F_{1,1.6}$=1.09, p = 0.43, r^2 = 0.048) were not (Fig. 2). Thus, sparrows that took longer to feed in the presence of novel objects also tended to have longer beak wiping bouts. Of the other fixed effects we examined in relation to beak wiping stereotypies (i.e., sparrow sex, presence of enrichment, and video quality), only environmental enrichment was significantly associated with all three measures of beak wiping (Fig. 3, Table 1), where birds with high enrichment (i.e., Cohorts B and C) had shorter beak wiping bouts, spent less total time beak wiping, and beak wiped less frequently compared to birds in Cohort A. Video quality and sex were also correlated with mean wipe duration, where observers watching darker or lower-quality videos recorded lower mean bout times (Fig. 4, Table 1) and males had longer beak wiping bouts than females (Fig. 5, Table 1).

4. Discussion

In this project, we re-analyzed 1 h control videos from three past studies of object neophobia in captive house sparrows to test two sets of predictions. First, we predicted that a sparrow's average neophobia towards three different novel objects would be correlated with the amount of beak-wiping behaviour it performed during a control feeding trial; and second, that the amount of beak-wiping behaviour performed would be related to the amount of enrichment in its cage. As predicted, neophobia and beak wiping stereotypy were correlated within individual sparrows, though only for one of the three measures of beak wiping we tested, mean bout duration. All three measures of beak wiping were increased in sparrows that were housed in cages with low enrichment, and we also found effects of sparrow sex on the mean duration of beak wiping bouts. Poor video quality affected viewers' measure of mean beak wiping bout duration, but not the other two measures.

Although little previous research has investigated within-individual associations between stereotypies and neophobia, studies examining links between stereotypy and a preference for or attraction to novel stimuli (neophilia) have found mixed results [26,27,44]. (Note that the opposite of neophobia is probably not neophilia, but indifference towards novelty; previous work suggests that neophobia and neophilia are distinct axes of behaviour [45,46].) Glucocorticoid production has been linked to both neophobia and stereotypy development in captive house sparrows [31,32]; therefore, these two behaviours may be linked via this shared hormonal mechanism, where, perhaps, sparrows with increased circulating levels of glucocorticoids or increased glucocorticoid receptor density in captivity might be more likely to be neophobic and have longer beak wiping bouts. Centrally-acting corticosterone releasing hormone, known to be involved in avian behavioural responses to stress, may also play a role in both beak wiping and neophobia [47]. Another shared neurobiological mechanism between neophobia and stereotypies could involve the brain's dopamine system [32,48]. A study in captive house sparrows found that peripheral injections of the mixed dopamine D2/3 receptor agonist quinpirole resulted in a large and rapid reduction in beak wiping, showing a clear causal role for dopamine in this behaviour [32]. Further research is needed to test the role of individual variation in neuroendocrine physiology in mediating anxiety behaviours in house sparrows and other birds.

As mentioned above, only mean bout duration, and not beak wiping frequency or total bout duration, was significantly correlated with neophobia. This suggests that different measures of stereotypy may be

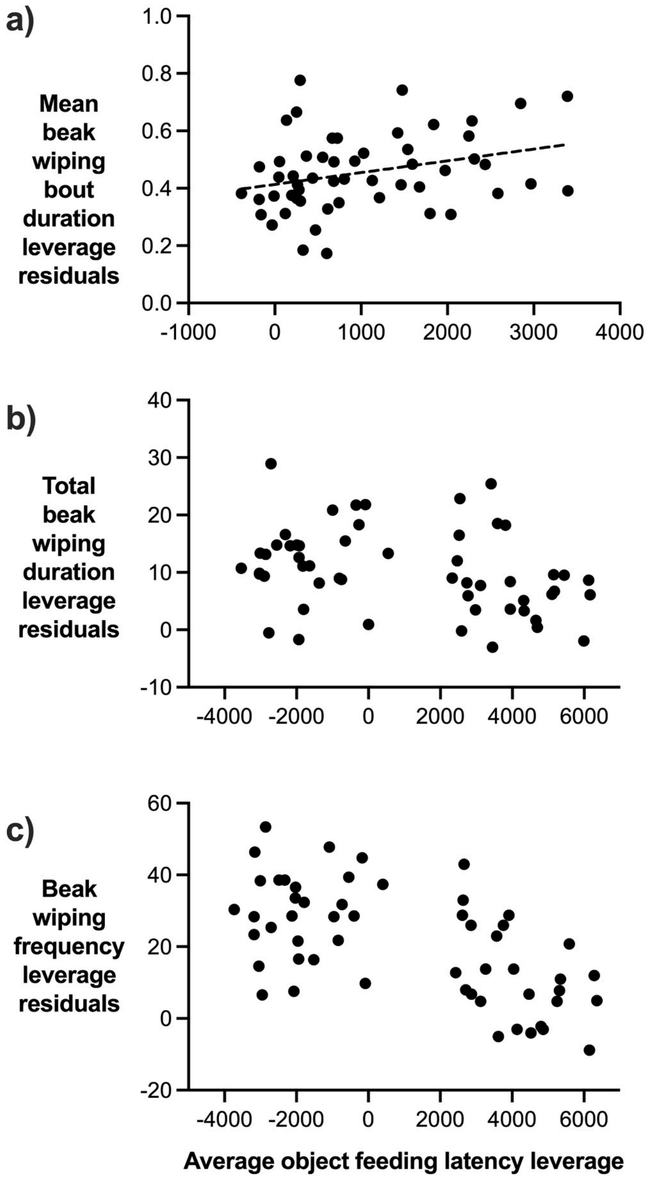


Fig. 2. Leverage plots of mean beak wiping bout duration (a), total beak wiping duration (b), and beak wiping frequency (c) in a 1 h control video (when the normal food dish was replaced) relative to house sparrows' average latency to feed in the presence of novel objects (n = 3 trials/bird, n = 54 sparrows total). Mean beak wiping bout duration (a) was positively correlated with average object feeding latency, while beak wiping frequency and total bout duration (b, c) were not related to neophobia. These effect leverage plots show the impact of adding sparrows' average object feeding latency (our measure of neophobia) to the three models examining different measures of beak wiping behaviour, given all the other effects that are already in the models (for these models: fixed effects of sparrow sex, high vs. low enrichment, and video quality, as well as a random effect of video watcher). The y-axis is plotted as standardized leverage residuals of each data point, with each dot representing one sparrow.

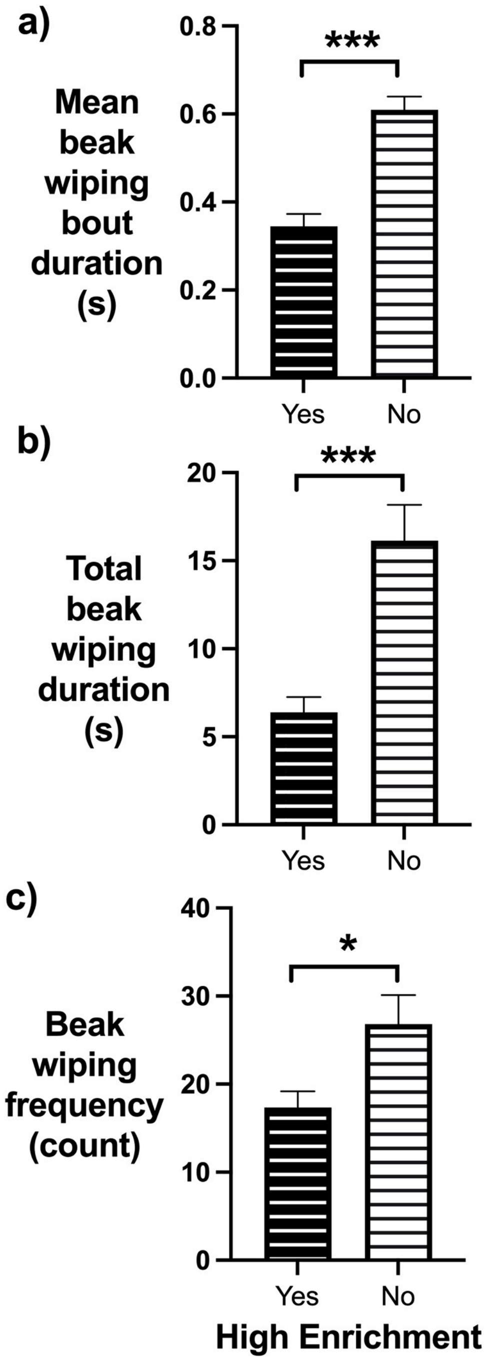


Fig. 3. Increased enrichment significantly affected mean beak wiping bout duration (a); total beak wiping duration (b); and beak wiping frequency (c) in captive house sparrows during 1 h control videos (n = 54). The presence of more enrichment (rubber perches and either manzanita branches or artificial pine branches) in Cohorts B and C significantly reduced all measures of beak wiping stereotypies compared to birds in Cohort A. * denotes p ≤ 0.05 and *** denotes p ≤ 0.0001; error bars depict SEM.

more or less representative of an individual's "average" stereotypy and likely to be correlated with other behaviours. Behavioural syndrome research often emphasizes the importance of observing the same behaviour across different contexts to test whether a syndrome exists [49]. Because beak wiping observations took place exclusively during neutral (control) feeding contexts, follow-up studies could examine whether beak-wiping behaviours in more anxiety-inducing contexts—such as during novel food or object trials—are also correlated with neophobia. One limitation of this study was that birds were housed individually during both neophobia and beak wiping measures, whereas house sparrows are a gregarious species in the wild [50]. Therefore, an additional context to examine in future studies is the effect of solo vs. group housing on beak wiping and other stereotypies in house sparrows.

Videos rated "poor quality" by watchers (these were usually a bit dark) consistently yielded shorter mean beak wiping bouts, suggesting that future studies may wish to use additional lighting in the bird room to minimize confounding effects of video quality on viewers' measures of beak wiping behavior. Note that alternative explanations for these data could be that birds in darker cages felt calmer, and performed less

Table 1
Fixed effect results from linear mixed models assessing the effects of captive house sparrow sex, increased enrichment, and video quality on three different measures of beak wiping stereotypies assessed during a 1 h control video ($n = 54$). Video watcher was included as a random effect in the model and average time to feed in the presence of novel objects was an additional fixed effect in the model (see Results). Allowing for unbounded variance components affected degrees of freedom in some models. Significant effects are noted with a *.

		DF	DFDen	F Ratio	Prob > F
Mean beak wiping bout duration	Sex	1	49	4.72	0.035*
	Increased enrichment	1	48	62.08	< 0.0001*
	Video quality	1	49	7.35	0.0092*
Total beak wiping duration	Sex	1	49	0.55	0.46
	Increased enrichment	1	49	20.55	< 0.0001*
	Video quality	1	49	2.17	0.15
Beak wiping frequency	Sex	1	22	0.021	0.89
	Increased enrichment	1	49	4.33	0.043*
	Video quality	1	33	0.85	0.36

beak wiping as a result [51], or that diurnal house sparrows were less active in dimmer cages [50]. Male sparrows also performed slightly longer beak wiping bouts than females. Although we do not typically see sex differences in neophobia in house sparrows [52], many anxiety-linked behaviours can differ by sex, and may be higher or lower in females depending on the species and behavioural paradigm used [53, 54].

Finally, increased enrichment successfully reduced all three measures of stereotypy. Whether birds received rubber tubing and a manzanita branch (Cohort B) or rubber tubing and an artificial pine branch (Cohort C) did not matter: the presence of any additional level of environmental enrichment over that found in Cohort A significantly reduced beak wiping frequency, mean bout duration, and total bout duration. This is consistent with studies in other wild species finding that a more enriched environment can reduce stereotypical and anxiety behaviours in captivity [55–57], although this is not always the case [58].

In conclusion, this study found that beak wiping bout length and neophobia were correlated behaviours in captive house sparrows. This suggests that a “high anxiety” behavioural syndrome may exist in sparrows, possibly due to shared neuroendocrine mechanisms that affect both behaviours. Future work should examine more anxiety and stress-linked behaviours in house sparrows, such as preening, freezing, and feather ruffling [59–61], as well as test these associations in a wider variety of birds, to assess the generalizability of these results. We also found that male sparrows performed longer beak wiping bouts than females, that poor video quality was a confounding variable that affected viewers’ measures of beak wiping bout duration, and that all beak wiping measures were reduced in sparrows exposed to higher levels of enrichment. This work highlights the need for researchers to provide access to species-appropriate enrichment to maximize the wellbeing of songbirds and other research animals [23], while still being careful not to expose animals to novel objects, foods, or other stimuli that might induce neophobia and a stress response [62–64]. Appropriate environmental conditions are essential not only to ensure animal welfare in captivity, but also to elicit meaningful and generalizable responses to captive behaviour assays [24].

Author contributions (CRediT guidelines)

DFM and CRL conceptualized the project. CRL secured funding for the project. DFM, WJF, and MGK collected data. CRL led the data analysis, with support from DFM. DFM and CRL prepared the original draft of the manuscript. All authors contributed to the review and editing of the finalized manuscript, approved for publication, and agreed to be accountable for the accuracy and integrity of their work performed on this project.

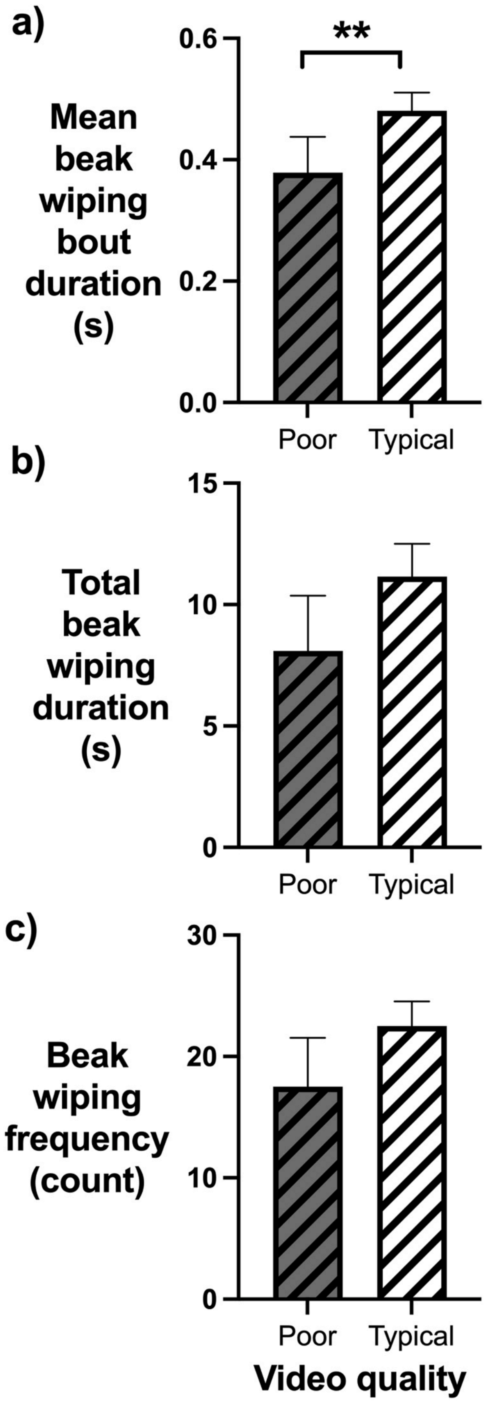


Fig. 4. Poor video quality significantly affected viewers’ measures of mean beak wiping bout duration (a) but not total beak wiping duration (b) or beak wiping frequency (c) in captive house sparrows during 1 h control videos ($n = 54$). Dark or blurry videos led to shorter mean beak wiping bouts being recorded compared to typical video quality. ** denotes $p \leq 0.01$; error bars depict SEM.

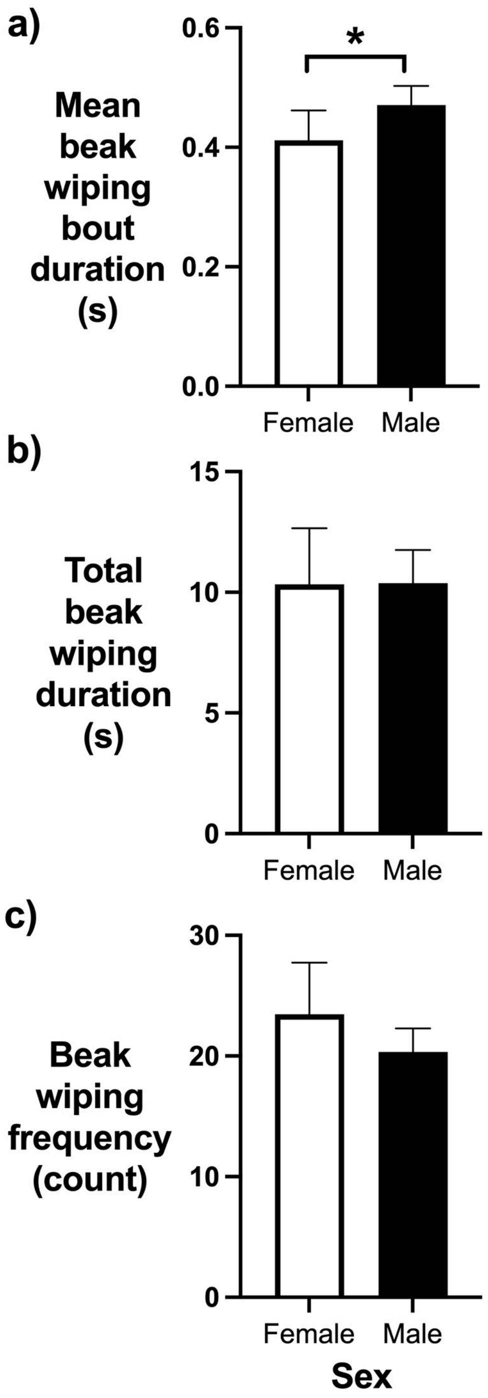


Fig. 5. Sparrow sex significantly affected mean beak wiping bout duration (a) but not total beak wiping duration (b) or beak wiping frequency (c) in captive house sparrows during 1 h control videos (n = 54). Male sparrows had longer mean beak wiping bouts than female sparrows. * denotes $p \leq 0.05$; error bars depict SEM.

CRediT authorship contribution statement

William J. Frazier: Writing – review & editing, Investigation. **Melanie G. Kimball:** Writing – review & editing, Methodology, Investigation, Data curation. **Christine R. Lattin:** Writing – review & editing, Visualization, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Danna F. Masri:** Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

Acknowledgements

The authors thank animal caretakers and veterinary staff in the LSU Division of Laboratory Animal Research for sparrow husbandry and care, landowners who provided property access for capturing sparrows, and Juhee Haam and David Young for providing feedback on an earlier version of this manuscript.

Data availability

Raw data are available as a supplementary.csv file.

References

[1] J.R. MacKay, M.J. Haskell, Consistent individual behavioral variation: the difference between temperament, personality and behavioral syndromes, Anim. (Basel) 5 (3) (2015) 455–478.
[2] J.M. Koolhaas, S.M. Korte, S.F. De Boer, B.J. Van Der Vegt, C.G. Van Reenen, H. Hopster, I.C. De Jong, M.A.W. Ruis, H.J. Blokhuis, Coping styles in animals: current status in behavior and stress-physiology, Neurosci. Biobehav. Rev. 23 (7) (1999) 925–935.
[3] B.E. Carlson, S.J. Tetzlaff, C. Rutz, Long-term behavioral repeatability in wild adult and captive juvenile turtles (Terrapene carolina): Implications for personality development, Ethology 126 (6) (2020) 668–678.
[4] T.O. Cornwell, I.D. McCarthy, P.A. Biro, Integration of physiology, behaviour and life history traits: personality and pace of life in a marine gastropod, Anim. Behav. 163 (2020) 155–162.
[5] T.S.O. Costa, S.L.G. Nogueira-Filho, K.M. De Vleeschouwer, L.C. Oliveira, M.B.C. de Sousa, M. Mendl, L.S. Catenacci, S.S.C. Nogueira, Individual behavioral differences and health of golden-headed lion tamarins (Leontopithecus chrysomelas), Am. J. Primatol. 82 (5) (2020) e23118.
[6] A.M. Fisher, G.I. Holwell, T.A.R. Price, Behavioural correlations and aggression in praying mantids, Behav. Ecol. Sociobiol. 74 (5) (2020).
[7] H.R. Thomson, S.D. Lamb, A.A. Besson, S.L. Johnson, Long-term repeatability of behaviours in zebrafish (Danio rerio), Ethol. N./a(N./a (2020).
[8] L.M. Aplin, D.R. Farine, R.P. Mann, B.C. Sheldon, Individual-level personality influences social foraging and collective behaviour in wild birds, P R. Soc. B 281 (1789) (2014) 20141016.
[9] U.A. Bergvall, A. Schäpers, P. Kjellander, A. Weiss, Personality and foraging decisions in fallow deer, Dama dama, Anim. Behav. 81 (1) (2011) 101–112.
[10] D. Bierbach, C. Sommer-Trembo, J. Hanisch, M. Wolf, M. Plath, Personality affects mate choice: bolder males show stronger audience effects under high competition, Behav. Ecol. 26 (5) (2015) 1314–1325.
[11] L.C. Garnham, S.A. Porthén, S. Child, S. Forslind, H. Løvlie, The role of personality, cognition, and affective state in same-sex contests in the red junglefowl, Behav. Ecol. Sociobiol. 73 (11) (2019).
[12] A. Sih, A. Bell, J.C. Johnson, Behavioral syndromes: an ecological and evolutionary overview, Trends Ecol. Evol. 19 (7) (2004) 372–378.
[13] K. Morgan, C. Tromborg, Sources of Stress in Captivity, Appl. Anim. Behav. Sci. 102 (2007) 262–302.
[14] G.J. Mason, Stereotypies: a critival review, Anim. Behav. 41 (6) (1991) 1015–1037.
[15] R.M. Calisi, G.E. Bentley, Lab and field experiments: are they the same animal? Horm. Behav. 56 (1) (2009) 1–10.
[16] D. Eilam, R. Zor, H. Szechtman, H. Hermesh, Rituals, stereotypy and compulsive behavior in animals and humans, Neurosci. Biobehav. Rev. 30 (4) (2006) 456–471.
[17] G. Feenders, M. Bateson, The development of stereotypic behavior in caged European starlings, Sturnus vulgaris, Dev. Psychobiol. 54 (8) (2012) 773–784.
[18] C.R. Lattin, A.V. Pechenenko, R.E. Carson, Experimentally reducing corticosterone mitigates rapid captivity effects on behavior, but not body composition, in a wild bird, Horm. Behav. 89 (2017) 121–129.
[19] I. Cuthill, M. Witter, L. Clarke, The function of bill-wiping, Anim. Behav. 43 (1) (1992) 103–115.
[20] D.L. Wells, Sensory stimulation as environmental enrichment for captive animals: A review, Appl. Anim. Behav. Sci. 118 (1-2) (2009) 1–11.
[21] G.J. Mason, N.R. Latham, Can't stop, won't stop: is stereotypy a reliable animal welfare indicator? Anim. Welf. 13 (S1) (2004) S57–S69.
[22] R. Swaisgood, D. Shepherdson, Environmental enrichment as a strategy for mitigating stereotypies in zoo animals: a literature review and meta-analysis, Stereo Anim. Behav. Fundam. Appl. Welf. (2006) 256–285.
[23] M. Bateson, G. Feenders, The use of passerine bird species in laboratory research: implications of basic biology for husbandry and welfare, ILAR J. 51 (4) (2010) 394–408.
[24] J.P. Garner, G.J. Mason, Evidence for a relationship between cage stereotypies and behavioural disinhibition in laboratory rodents, Behav. Brain Res. 136 (1) (2002) 83–92.
[25] G.J. Mason, Species differences in responses to captivity: stress, welfare and the comparative method, Trends Ecol. Evol. 25 (12) (2010) 713–721.

[26] S. Goswami, P.C. Tyagi, P.K. Malik, S.J. Pandit, R.F. Kadivar, M. Fitzpatrick, S. Mondol, Effects of personality and rearing-history on the welfare of captive Asiatic lions (Panthera leo persica), PeerJ 8 (2020) e8425.

[27] S. Silber, S. Joshi, N. Pillay, Behavioural syndromes in stereotypic striped mice, Appl. Anim. Behav. Sci. 212 (2019) 74–81.

[28] M.L. Fangmeier, A.L. Burns, V.A. Melfi, J. Meade, Foraging enrichment alleviates oral repetitive behaviors in captive red-tailed black cockatoos (Calyptorhynchus banksii), Zoo. Biol. 39 (1) (2020) 3–12.

[29] T.P. Kulkarni, Analysis of stereotypic behaviour and enhanced management in captive Northern Giraffe Giraffa camelopardalis housed at Zoological Garden Alipore, Kolkata, J. Threat. Taxa 12 (4) (2020) 15426–15435.

[30] J.M. Koolhaas, S.M. Korte, S.F. De Boer, B.J. Van Der Vegta, C.G. Van Reene, H. Hopster, I.C. De Jong, M.A.W. Ruis, H.J. Blokhuis, Coping styles in animals: current status in behavior and stress-physiology, Neurosci. Biobehav. Rev. (1999).

[31] T.R. Kelly, K.I. Lynch, K.E. Couvillion, J.N. Gallagher, K.R. Stansberry, M. G. Kimball, C.R. Lattin, A transient reduction in circulating corticosterone reduces object neophobia in male house sparrows, Horm. Behav. 137 (2022) 105094.

[32] C.R. Lattin, D.P. Merullo, L.V. Riters, R.E. Carson, In vivo imaging of D(2) receptors and corticosteroids predict behavioural responses to captivity stress in a wild bird, Sci. Rep. 9 (1) (2019) 10407.

[33] M.G. Kimball, K. Lynch, K.E. Couvillion, J.N. Gallagher, K.R. Stansberry, M. G. Kimball, C.R. Lattin, Novel objects alter immediate early gene expression globally for ZENK and regionally for c-Fos in neophobic and non-neophobic house sparrows, Behav. Brain Res. 428 (2022).

[34] M.G. Kimball, D.F. Masri, E.B. Gautreaux, K.R. Stansberry, T.R. Kelly, C.R. Lattin, Conspecific alarm calls prevent the attenuation of neophobia behavior in wild-caught house sparrows (Passer domesticus), Front. Bird. Sci. 3 (2024).

[35] M.G. Kimball, Invest. Eff. Environ. Perturbations House Sparrow Neurobiol. Behav. (2024).

[36] L.Z. Garamszegi, G. Markó, G. Herczeg, A meta-analysis of correlated behaviours with implications for behavioural syndromes: mean effect size, publication bias, phylogenetic effects and the role of mediator variables, Evolut. Ecol. 26 (5) (2012) 1213–1235.

[37] L.Z. Garamszegi, G. Markó, G. Herczeg, A meta-analysis of correlated behaviors with implications for behavioral syndromes: relationships between particular behavioral traits, Behav. Ecol. 24 (5) (2013) 1068–1080.

[38] C.P. Fischer, B.M.G. Gormally, L.M. Romero, Captive house sparrows (Passer domesticus) show little evidence of seasonality of neophobia responses, J. Exp. Zool. Part A Ecol. Integr. Physiol. 333 (7) (2020) 478–482.

[39] C.R. Lattin, D.P. Merullo, L.V. Riters, R.E. Carson, In vivo imaging of D2 receptors and corticosteroids predict behavioural responses to captivity stress in a wild bird, Sci. Rep. 9 (1) (2019) 10407.

[40] T.R. Kelly, M.G. Kimball, K.R. Stansberry, C.R. Lattin, No, you go first: phenotype and social context affect house sparrow neophobia, Biol. Lett. 16 (9) (2020) 20200286.

[41] M. Project, R. Miller, V. Šlipogor, K.R. Caspar, J. Lois-Milevicich, C. Soulsbury, S. A. Reber, C. Mettke-Hofmann, M. Lambert, B.J. Ashton, A.M.I. Auersperg, M. Bateson, S. Belle, B. Bilčík, L.M. Biondi, F. Bonadonna, D. Brucks, M.W. Butler, S.P. Caro, M. Charrier, T. Chatelin, J. Ching, N.S. Clayton, B.J. Cluver, E. B. Cochran, F. Cornero, E. Danby, S. Danel, M. Darwich, J.R. Davies, A. de la Colina, D. Fischer, O. Fišer, F. Foitzick, E.C. Galluccio, C. Garcia-Co, E. Garcia-Pelegrin, I. George, K.-P. Gladow, R.O. Gómez, A. Grewer, K. Grice, L.M. Guillette, D.C. Hallihan, K.J. Harrington, F. Heer, C. Henry, V. Hodova, M. Hoeschele, C. Houdelier, P.I. de Aldecoa, O.S. Iyasere, Y. Kanemitsu, M. Khodadadi, D. Khong, M.G. Kimball, A.N. Klappert, L.N. Koch, U.U. König von Borstel, L. Košt'ál, A. Krasheninnikova, L. Kubikova, C.T. Lambert, D.W. Laméris, C.G. Lampert, O. Larousse, C.R. Lattin, Z. Li, M. Lindenmeier, D.A. Lister, J.A. Mackenzie, S. Mainz, D. Masri, J.J.M. Massen, L. Mohr, W. Müller, P.M. Nealen, A. Nieder, A. Novac, N.P. Cavalcante, K. Pascual, C. Pascual-Guàrdia, A. Patel, K. Pichová, C. Pilenga, L. Prétôt, J.L. Quinn, E. Račevska, J.C. Reboreda, S. Reynolds, A. R. Ridley, T. Rössler, F. Ruiz-Raya, M. Salas, B.C. Saldanha, S.M. Santiago, N. Schlöglová, G. Seatriz, E. Serrano-Davies, E.G. Shair Ali, J. Sirovnik, Z. Skalná, K.E. Slocombe, M. Soma, T. Srdoc, S. Stanescu, M. Syrová, A.H. Taylor, C. N. Templeton, K. Thompson, S. Trigo, C.A. Troisi, U. Urhan, M. Valbert, K. van Oers, A. Velando, F. Verbruggen, J.W. Verkleij, A. Vernouillet, J. Verspeek, P. Veselý, A.M.P. von Bayern, E. Waalders, B.A. Whittaker, E.R. Williamson, V.A. D. Wilson, M.A. Winfield, N. Wittek, K.K.L. Yeung, J.A. Zanutto, A large-scale study across the avian clade identifies ecological drivers of neophobia, PLOS Biol. 23 (10) (2025).

[42] O. Friard, M. Gamba, BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations, Methods Ecol. Evol. 7 (11) (2016) 1325–1330.

[43] P. Lowther, C. Cink, S. Billerman, House sparrow (Passer domesticus), version 1.0, Birds World 1 (2020).

[44] S.S. Vickery, G.J. Mason, Stereotypy and perseverative responding in caged bears: Further data and analyses, Appl. Anim. Behav. Sci. 91 (3-4) (2005) 247–260.

[45] C. Mettke-Hofmann, H. Winkler, B. Leisler, The Significance of Ecological Factors for Exploration and Neophobia in Parrots, Ethology 108 (3) (2002) 249–272.

[46] M.G. Kimball, C.R. Lattin, The "Seven Deadly Sins" of Neophobia Experimental Design, Integr. Comp. Biol. (2023) 38–54.

[47] C.A. Lowry, F.L. Moore, Regulation of behavioral responses by corticotropin-releasing factor, Gen. Comp. Endocrinol. 146 (1) (2006) 19–27.

[48] F.N. Madison, V.P. Bingman, T.V. Smulders, C.R. Lattin, A bird's eye view of the hippocampus beyond space: Behavioral, neuroanatomical, and neuroendocrine perspectives, Horm. Behav. 157 (2024) 105451.

[49] A. Sih, A.M. Bell, J.C. Johnson, R.E. Ziemba, Behavioral syndromes: an integrative overview, Q. Rev. Biol. 79 (3) (2004) 241–277.

[50] P.E. Lowther, C.L. Cink, House Sparrow (*Passer domesticus*), 2020. https://doi.org/10.2173/bow.houspa.01. (Accessed January 25 2012).

[51] H. Shi, B. Li, Q. Tong, W. Zheng, D. Zeng, G. Feng, Effects of LED light color and intensity on feather pecking and fear responses of layer breeders in natural mating colony cages, Animals 9 (10) (2019).

[52] M.G. Kimball, E.B. Gautreaux, K.E. Couvillion, T.R. Kelly, K.R. Stansberry, C. R. Lattin, Novel objects alter immediate early gene expression globally for ZENK and regionally for c-Fos in neophobic and non-neophobic house sparrows, Behav. brain Res. 428 (2022) 113863.

[53] J.L. Scholl, A. Afzal, L.C. Fox, M.J. Watt, G.L. Forster, Sex differences in anxiety-like behaviors in rats, Physiol. Behav. 211 (2019) 112670.

[54] J.M. Adkins, A.M. Jasnow, J.F. Lynch, Estradiol and Sex Differences in Generalized Fear: Implications for Anxiety Disorders, Estrogens Mem. Basic Res. Clin. Implic. (2020) 433–455.

[55] V.M.A.M.A. de Sousa, B. Almeida, M.C. Castro, G. Sobral, Low-cost environmental enrichment reduces stereotypical behaviors in the blue-fronted parrot Amazona aestiva and the yellow-faced amazon Alipiopsitta xanthops, Ornithol. Res. 32 (4) (2024) 322–328.

[56] K. Donald, A. Benedetti, V.D.L.R. Goulart, A. Deming, H. Nollens, G. Stafford, S. Brando, Environmental enrichment devices are safe and effective at reducing undesirable behaviors in California sea lions and northern elephant seals during rehabilitation, Animals 13 (7) (2023).

[57] M. Vanderzwalmen, P. Carey, D. Snellgrove, K.A. Sloman, Benefits of enrichment on the behaviour of ornamental fishes during commercial transport, Aquaculture 526 (2020).

[58] S.E. Spring, J.O. Clifford, D.L. Tomko, Effect of environmental enrichment devices on behaviors of single- and group-housed squirrel monkeys (*Saimiri sciureus*), Contemp. Top. Lab. Anim. Sci. 36 (3) (1997) 72–75.

[59] M.G. Kimball, C.T. Harding, K.E. Couvillion, K.R. Stansberry, T.R. Kelly, C. R. Lattin, Effect of estradiol and predator cues on behavior and brain responses of captive female house sparrows (Passer domesticus), Front. Physiol. 14 (2023).

[60] J.E. Evans, E.L. Smith, A.T.D. Bennett, I.C. Cuthill, K.L. Buchanan, Short-term physiological and behavioural effects of high- versus low-frequency fluorescent light on captive birds, Anim. Behav. 83 (1) (2012) 25–33.

[61] S.M. Henson, L.M. Weldon, J.L. Hayward, D.J. Greene, L.C. Megna, M.C. Serem, Coping behaviour as an adaptation to stress: post-disturbance preening in colonial seabirds, J. Biol. Dyn. 6 (2012) 17–37.

[62] S. Richard, N. Wacrenier-Ceré, D. Hazard, H. Saint-Dizier, C. Arnould, J. Faure, Behavioural and endocrine fear responses in Japanese quail upon presentation of a novel object in the home cage, Behav. Process. 77 (3) (2008) 313–319.

[63] R.A. Fox, J.R. Millam, Novelty and individual differences influence neophobia in orange-winged Amazon parrots (Amazona amazonica), Appl. Anim. Behav. Sci. 104 (1-2) (2007) 107–115.

[64] T.M. Meade, E. Hutchinson, C. Krall, J. Watson, Use of an aquarium as a novel enrichment item for singly housed rhesus macaques (Macaca mulatta), J. Am. Assoc. Lab Anim. Sci. 53 (5) (2014) 472–477.