

1 **Effects of domestication on neophobia: A comparison between the domesticated Bengalese**
2 **finch (*Lonchura striata* var. *domestica*) and its wild ancestor, the white-rumped munia**
3 **(*Lonchura striata*)**

4

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20 **ABSTRACT**

21 Bengalese finches (*Lonchura striata* var. *domestica*) have more complex song traits than their wild
22 ancestors, white-rumped munias (*Lonchura striata*). Domesticated finches are likely able to allocate
23 more resources to song development rather than allocating resources to mechanisms aimed at coping
24 with predation, which are no longer needed under domesticated conditions. Here, we aimed to
25 examine the effects of changes in selection pressure due to domestication on the behaviour of
26 Bengalese finches and to contemplate the possible evolutionary mechanisms underlying these
27 changes. To do so, we compared neophobic responses to novel-object conditions as an assessment of
28 reactions to potential predators. We studied groups of Bengalese finches and white-rumped munias
29 and found that Bengalese finches were more likely to eat the food provided to them under
30 novel-object conditions. Bengalese finches had a shorter latency time to eat, and this latency time
31 was less affected by the novel object in the case of Bengalese finches compared to white-rumped
32 munias. Therefore, Bengalese finches have reduced neophobic responses due to domestication. The
33 behavioural strategies of white-rumped munias appear to be more suitable for natural environments,
34 which include unpredictable risks, whereas Bengalese finches have likely adapted their behaviour to
35 the conditions of artificial selection.

36

37 **Keywords:** Bengalese finch (*Lonchura striata* var. *domestica*); Domestication; Neophobia;

38 Neophobic response; White-rumped munia (*Lonchura striata*)

39 **Abbreviations**

40 BF, Bengalese finch; WRM, white-rumped munia.

41

42 **1. Introduction**

43 The Bengalese finch (BF, *Lonchura striata* var. *domestica*) is a domesticated variety of the
44 wild white-rumped munia (WRM, *Lonchura striata*), which was imported from China to Japan
45 approximately 250 years ago (Washio, 1996; Okanoya, 2004a; Svanberg, 2008). BFs sing
46 phonologically and syntactically complex songs, as opposed to the stereotypical simple songs sung
47 by WRMs (Honda and Okanoya, 1999; Okanoya, 2004a, b). The complex songs of BF have not
48 been selected artificially (Washio, 1996). Complex song as a high-quality sexual trait is
49 believed to have evolved through the domestication process in BFs (Okanoya, 2004a, b). WRMs are
50 thought to experience strong natural selection pressures in wild environments. Conversely,
51 domesticated BFs experience safe and resource-rich conditions under human-controlled rearing
52 conditions (i.e., no environmental perturbations, no predation, abundant food, and low risk of
53 parasitism and injury). Thus, we hypothesised that the relaxation of natural selection pressures and
54 the presence of artificial selection may have led BFs to allocate fewer resources to behaviours
55 associated with efforts for survival and more to efforts associated with reproduction.

56 Domestication results in species being removed from many natural selection pressures;

57 however, domesticated species are exposed to artificial selection pressures exerted by their captive
58 environments and by humans (Fox, 1968; Boice, 1973; Ratner and Boice, 1975; Price, 1984). This
59 change in selection pressure results in changes in physiological and behavioural traits (Hale, 1969;
60 Price, 1984, Künzl and Sachser, 1999; Lepage et al., 2000). Domesticated species have reduced
61 behavioural expressions related to ontogenetic survival, such as fear responses (Desforges and
62 Wood-Gush, 1975; Schütz et al., 2001; Campler et al., 2009), and have enhanced behavioural traits
63 that are not directly related to survival, such as sexual and reproductive behaviours (Künzl and
64 Sachser, 1999). Therefore, these behavioural changes have been a major target of domestication
65 effects.

66 In natural environments, birds must be vigilant of unpredictable risks such as predation
67 when foraging or eating; this is particularly important while approaching novel conditions such as
68 novel places, objects, and food items. Neophobia is the aversion that an animal displays while
69 approaching novel conditions (Greenberg, 2003). In birds, the most well-established behavioural
70 responses to novel conditions (neophobic responses) are the reactions to potential predators
71 (Greenberg, 1990). In the wild, the presence of unpredictable risks is considered to enhance induced
72 neophobia (Brown et al., 2020). Domesticated BFs are likely able to allocate more resources to
73 reproduction (e.g., song development) as a trade-off for a reduction in the behaviours and strategies
74 aimed at coping with predation (e.g., neophobic responses). In the present study, to examine the

75 effects of changes in selection pressure due to domestication on the behaviour of BFs, and to
76 contemplate the evolutionary mechanisms underlying these effects, we compared neophobic
77 responses to novel conditions in BFs and their wild ancestors, WRMs. To the best of our knowledge,
78 this is the first study that evaluates neophobia in Bengalese finches and white-rumped munias, which
79 also explores the evolutionary mechanisms of behavioural changes in domesticated animals,
80 including the evolution of complex songs through human self-domestication.

81

82 **2. Materials and methods**

83 *2.1 Birds used in this study*

84 Seventy BFs and 60 WRMs were used in the experiment. All the birds were sexually
85 mature. BFs (n = 10) were bought from local suppliers and others (n = 60) were bred in our
86 laboratory. WRMs were captured in the wild in Taiwan. These captured birds were reared for
87 more than a year in our laboratory before being used in this study. Birds were housed in a
88 group of 8 (one group of WRM) or 10 per cage resulting in us using seven groups of BFs and six
89 groups of WRMs for our experiments. Sex ratios of the birds that made up the groups were different
90 for each cage (BF-1 and WRM-1: all females, BF-2, 3 and WRM-2: all males, BF-4, 5 and WRM-3,
91 4: 50% of each sex, BF-6, 7 and WRM-5, 6: 6 males and 4 females). Birds were housed in stainless
92 steel cages (370 × 415 × 440 mm) within an animal-rearing room at RIKEN Brain Science Institute

93 (BSI) and given finch seed mixture, shell grit, and vitamin-enhanced water *ad libitum*. The light
94 cycle was kept constant at 14 h light and 10 h dark. The room was maintained at an ambient
95 temperature of approximately 25 °C, with a humidity of 50 %. The birds were acclimatized for at
96 least four months to the animal-rearing room before performing the experiments. All experimental
97 procedures and the housing conditions of the birds were approved by the Animal Experiments
98 Committee at RIKEN (#H20-2-231, #H22-2-217), and all the birds were cared for in accordance
99 with the Institutional Guidelines of RIKEN for experiments using animals.

100

101 *2.2 Novel-object experiment*

102 Before the experiment, each group of birds was transferred from their home cage in the
103 animal-rearing room to a testing cage (with the same dimensions and characteristics as the home
104 cage) in a sound-proof box. To avoid the effects of isolation stress, experiments were conducted
105 using the same groups of birds that were housed together during keeping. The test cage was
106 equipped with two wooden perches and with food and water. Experiments were conducted under two
107 conditions: the control (non-object) condition and the novel-object condition. Experiments were
108 carried out under the different conditions on different days. New food and water were provided at the
109 beginning of the experiments. Under the novel-object condition, a novel object (a small toy dog,
110 approximately 15 mm × 15 mm × 20 mm) was placed on the food. The behaviour of birds was

111 recorded for 60 min using a video camera. We quantified the number of groups of birds that ate food
112 during the observation period (at least one bird in the group) and the latency time (the time that
113 passed before first birds started eating the food) under both conditions. If the birds did not approach
114 or eat the food during the test period, the latency time of the birds was set at the maximum time
115 (3600 s). All groups were used only once under both conditions. All tests were conducted between
116 13:00 and 15:00 to avoid other factors that could affect our results, such as diurnal changes in
117 activity, hunger, and hormone levels.

118

119 *2.3 Statistical analyses*

120 The numbers of groups of BFs and WRMs that ate the food during the observation period
121 were compared with Fisher's exact test. The latency times to start eating the food are represented as
122 the mean \pm standard error of the mean (SEM). The latency times in BFs and WRMs were analysed
123 using a repeated measures two-way analysis of variance (ANOVA) (birds \times conditions) with
124 post-hoc Bonferroni/Dunn tests. The difference in the effect of the novel object on the latency times
125 (calculated as the latency times under the novel-object conditions - the latency times under control
126 conditions) between BFs and WRMs were analysed by an unpaired *t*-test with a Welch's correction.
127 Values of $p < 0.05$ were considered significant. We used three different statistical software packages
128 for analyses. Statistical analyses were performed using R statistical software (version 4.03, R

129 Foundation for Statistical Computing, Vienna, Austria) for Fisher's exact test, Stat View software
130 (version 5, SAS Institute Inc., Cary, NC, USA) for repeated measures 2-way ANOVA with post-hoc
131 Bonferroni/Dunn tests, and GraphPad Prism software (version 4, GraphPad Software Inc., San
132 Diego, CA, USA) for *t*-tests with a Welch's correction.

133

134 **3. Results**

135 *3.1 Responses of BFs and WRMs to novel objects*

136 We examined the effects of domestication on behavioural responses to novel objects in
137 BFs and WRMs. Under control conditions, all groups of birds (both BFs and WRMs) ate the food at
138 some point during the observation time (BFs: 7/7, 100 %; WRMs: 6/6, 100 %). Thus, there were no
139 differences between BFs and WRMs ($p = 1.00$). However, under the novel-object conditions, six of
140 the seven groups of BFs (6/7, 85.7 %) ate the food at some point during the observation time,
141 whereas none of the WRMs groups ate the food (0/6, 0 %). Therefore, there were significant
142 differences between BFs and WRMs ($p < 0.01$). In BFs, there were no significant differences in the
143 number of groups that ate the food between the control and novel-object conditions ($p > 0.90$).
144 However, WRMs were significantly less likely to eat the food under the novel-object conditions ($p <$
145 0.01).

146

147 *3.2 Latency times in BFs and WRMs to start eating food under control and novel-object conditions*

148 The latency times to start eating the food were compared between BFs and WRMs (Fig.
149 1). Under the control conditions, the latency times were 25.6 ± 9.0 s for BFs and 159.0 ± 46.7 s for
150 WRMs. Under the novel-object conditions, the latency times were 1204.9 ± 524.9 s for BFs, but
151 none of the WRMs approached the food within the observation time (3600.0 ± 0.0 s). The latency
152 times was significantly affected by the birds (BF or WRM, $F(1, 11) = 16.9, p < 0.01$), conditions
153 (novel object or control, $F(1, 11) = 69.4, p < 0.0001$), and interactions (birds \times conditions, $F(1, 11)$
154 $= 12.7, p < 0.01$). Latency times to eat were significantly shorter in BFs than in WRMs regardless of
155 the presence or absence of novel objects (control conditions: $p < 0.05$, novel-object conditions: $p <$
156 0.01). In both species, the latency times were extended by the presence of the novel object (BFs: $p <$
157 0.05 , WRMs: $p < 0.0001$), and the extended times were significantly longer in WRMs than those in
158 BFs (BFs: 1379.3 ± 530.7 s, WRM: 3441.0 ± 46.7 s; $t = 3.87, p < 0.01$).

159

160 **4. Discussion**

161 We compared responses to novel conditions in BFs and their wild ancestor, WRMs, and
162 examined the effects of changes in selection pressure due to domestication. Our findings indicate
163 that these two birds responded differently to novel-object conditions. BFs had significantly lower
164 neophobia levels (more groups of BFs ate the food, and BFs had shorter latency times to eat under

165 novel-object conditions) than those of their wild ancestors, the WRMs. The novel objects extended
166 the latency times to eat in both birds, but latency times were significantly longer in WRMs than
167 those in BFs. Therefore, it is likely that BFs have reduced neophobic responses due to domestication.
168 Under control conditions, the proportion of the groups that ate the food was the same in BFs and
169 WRMs. However, BFs ate the food sooner than WRMs. It is probable that the WRMs were more
170 cautious about the experimental situation (the soundproof box is different from the WRMs' normal
171 environment). In a previous report, male WRMs had higher faecal corticosterone concentrations than
172 those in male BFs (Suzuki et al., 2012; 2014a, b). Therefore, WRMs are considered to have a higher
173 level of baseline vigilance than that in BFs. This strain difference with respect to vigilance seems to
174 have been further increased under novel-object conditions.

175 Our results are similar to those of a previous study that found that domesticated ducks
176 (*Anas platyrhynchos* var. *domesticus*) had lower levels of neophobia than those of wild mallards
177 (*Anas platyrhynchos*) (Desforges and Wood-Gush, 1975). In addition, laboratory mice (*Mus*
178 *musculus*) had lower levels of neophobia than those in wild mice (Meddock and Osborn, 1968). In a
179 comparison of dogs (*Canis lupus familiaris*) and wolves (*Canis lupus*), dogs had lower levels of
180 neophobia than those in wolves, but dogs had an overall lower interest in novel objects (Moretti et
181 al., 2015). In the present study, BFs showed a fear response to novel objects and were considered to
182 have no diminished interest in novel objects.

183 This study was conducted using groups of birds, and, as such, there may have been a social
184 effect. Because it was difficult to identify individuals in this study, the analysis was conducted as a
185 group-by-group comparison, and it was therefore not possible to take into account the differences in
186 the responses of each individual. Wolves and dogs spend more time approaching a novel object in
187 groups than as individuals, so risk sharing may increase vigilance (Moretti et al., 2015). Since this
188 experiment was conducted using groups, there may have been an effect of risk sharing. Responses to
189 novel objects may also be influenced by the identities of the group members. In the Gouldian finches
190 (*Chloebia gouldiae*), shy birds took more risks when they were paired with bold partners, and bold
191 birds took fewer risks when they were paired with shy partners (King et al., 2015). Therefore, in
192 experiments conducted using groups, individual differences may be reduced, and more of the
193 characteristics of the groups may be expressed. Conversely, in experiments conducted using
194 individuals, there is a high possibility that individual differences will be noticeable. Future studies on
195 BFs and WRMs should take into consideration the reactions of each individual bird to novel-object
196 conditions. In a previous study, we compared the tonic immobility response, which can be used as a
197 measure of fear responses, between individual BFs and WRMs and found that BFs had lower fear
198 responses (Suzuki et al., 2013). Therefore, we believe that the fear response is lower in BFs than that
199 in WRMs, even on an individual basis.

200 In this study, the effects of sex ratio and environmental or rearing conditions (bought from

201 local supplier, wild-caught, or bred in the laboratory) were ruled out because the groups in the cages
202 were neither separated by sex nor by environmental or rearing conditions. Moreover, previous
203 studies have shown that sex and environmental or rearing conditions of the white-rumped munia
204 (captive-born, bought from a supplier, or captured) did not affect the fear response (tonic immobility
205 reactions) (Suzuki et al., 2013). Additionally, the conditions under which Bengalese finches and
206 white-rumped munias were bred or reared did not affect the corticosterone levels, which is known to
207 affect fear responses (Suzuki et al., 2012). All the munias used in this experiment were wild-caught;
208 however, differences in rearing conditions have not been an issue in previous experiments.
209 Therefore, the magnitude of the impact of these factors is small, but it must be considered in future
210 research.

211 In summary, this is the first study that evaluates neophobia in Bengalese finches and
212 white-rumped munias. Our results suggest that the domestication process led to differences in the
213 responses of BFs and WRMs to novel conditions. The behavioural strategies of WRMs seem to be
214 suitable for the natural environment, which includes unpredictable risks, whereas BFs might have
215 adapted their behaviours to the conditions of captivity and artificial selection. BFs are likely able to
216 allocate the resources that would be needed in the wild to cope with predators to song development,
217 due to domestication. Our results can provide insights into the evolutionary mechanisms of
218 domestication phenotypes (domestication syndrome), including human self-domestication processes

219 of other domesticated species.

220

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225

226 **Declarations of interest**

227 None

228

229 **Author contributions**

230 **Kenta Suzuki:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology,

231 Visualization, Writing - original draft; **Maki Ikebuchi:** Conceptualization; **Hiroko Kagawa:**

232 Conceptualization, Writing - review & editing; **Taku Koike:** Data curation, Investigation; **Kazuo**

233 **Okanoya:** Conceptualization, Funding acquisition, Supervision, Writing - review & editing.

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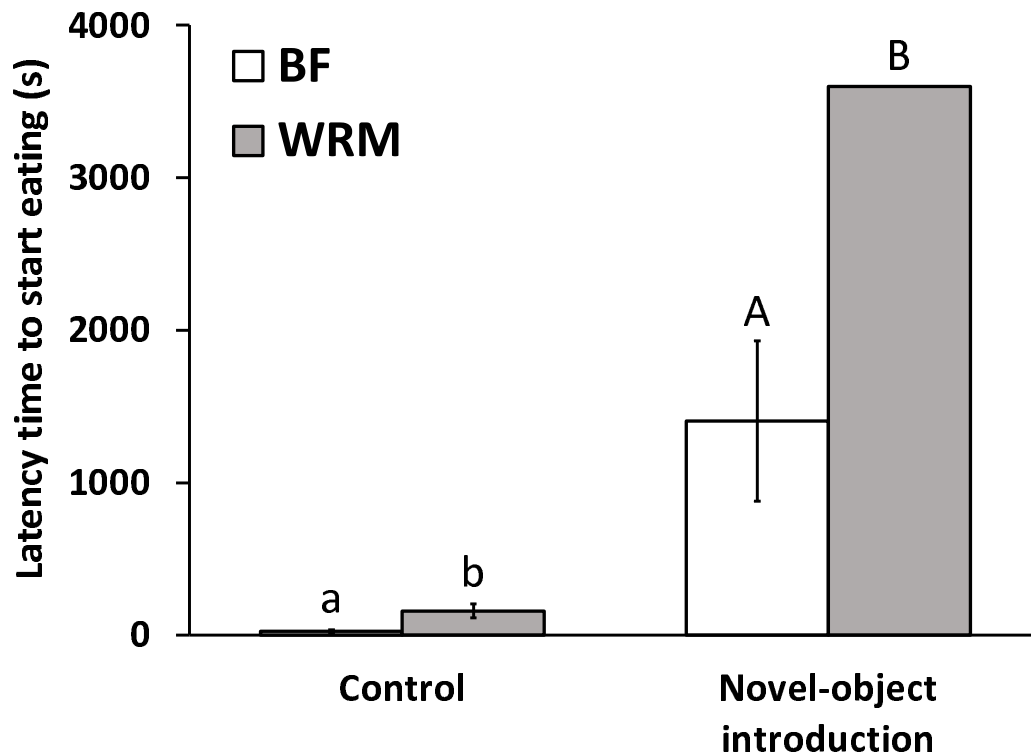
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328

329 Fig. 1. Latency times (in seconds) to start eating food in Bengalese finches (BFs, *Lonchura striata*

330 var. *domestica*) and white-rumped munias (WRMs, *Lonchura. striata*). Bars indicate means, and

331 vertical lines indicate standard errors of mean (SEM). BFs had significantly shorter latency times to

332 start eating the provided food than those WRMs under both conditions (control and exposure to a

333 novel object, i.e., a small dog toy). Latency times were extended under novel-object conditions in

334 both BFs and WRMs. Different letters indicate significant differences between groups (a vs b: $p <$

335 0.05, A vs B: $p < 0.01$, a vs A: $p < 0.05$, b vs B: $p < 0.0001$).