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The impact of domestication on fearfulness: A comparison of tonic immobility reactions in wild and domesticated finches

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ABSTRACT

We examined differences in the fear response between Bengalese finches and their wild ancestor, the white-backed munia, to explore the evolutionary mechanisms of behavioural changes due to domestication. The Bengalese finch (*Lonchura striata* var. *domestica*) was domesticated from the wild-living white-backed munia (*L. striata*) approximately 250 years ago. A previous study indicated that Bengalese finches sing much more complex songs than white-backed munias. We hypothesised that Bengalese finches are likely able to allocate more resources to reproduction in exchange for reduced survival effort. We measured tonic immobility (TI) reactions as a response to physical restraint to evaluate fearfulness related to coping with predation. The results showed that Bengalese finches exhibited decreased TI responses compared with white-backed munias. TI responses were unaffected by sex, body weight or growth conditions. These differences suggest that the fearfulness in Bengalese finches has been reduced by selective pressure during domestication. Bengalese finches may have been able to increase the investment of energy in reproduction in exchange for reduced costs of predation and coping necessary to survive in the wild; these behavioural changes may have been a major target of domestication effects in this species.

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1. Introduction

The Bengalese finch (*Lonchura striata* var. *domestica*, Fig. 1A) is a domesticated strain of the wild-living white-backed munia (*L. striata*; also known as white-rumped munia, white-rumped manikin, Fig. 1B), which was imported from China to Japan approximately 250 years ago (Washio, 1996; Okanoya, 2004a,b). The domestication process alters selective pressure by relaxing natural selection pressures and exposing animals to artificial selection pressures that affect their physiology and behaviour (Fox, 1968; Hale, 1969; Boice, 1973; Desforges and Wood-Gush, 1975; Ratner and Boice, 1975; Price, 1984; Künzl and Sachser, 1999; Lepage et al., 2000; Campler et al., 2009). The Bengalese finch and its wild ancestor, the white-backed munia, have different song characteristics during male courtship behaviour. Bengalese finches sing phonologically and syntactically complex songs with louder and pure tone-like sounds, whereas white-backed munias sing stereotypical simple songs that are quieter and contain more noise-like sounds (Honda and Okanoya, 1999; Okanoya, 2004a,b). Females of both varieties tend to prefer more complex songs (Okanoya, 2004a,b). However, male white-backed munias cannot sing the complex songs that the Bengalese finch can sing. Thus, the complex song is a high-quality sexual trait for mate choice that is believed to have evolved by domestication of the Bengalese finch (Okanoya, 2004a,b).

One possibility is that the complex song has been selected by humans, similar to the song of the domestic canary. However, the complex songs of the Bengalese finch have not been subjected to direct artificial selection by humans (Washio, 1996). White-backed munias are undergoing natural selection pressure in wild environments. In contrast, Bengalese finches have been exposed to safe and resource-rich human-controlled rearing conditions (i.e., no predation, abundant food and no environmental perturbations) as well as artificial selection by humans. Thus, we hypothesised that, as a predation coping process, Bengalese finches are likely able to allocate more resources than they would in the wild for reproduction in exchange for survival cost due to alterations in selective pressures under domestic conditions. Trade-off relationships may exist between the investment for reproductive success and investment in the ability to survive in the wild. Due to their natural history, these varieties are useful for analysing the mechanisms of the effects of domestication on behavioural traits. Understanding the changes in coping style in response to predation as the ability

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Fig. 1. (A) Bengalese finches (*L. striata* var. *domestica*). (B) White-backed munia (*L. striata*, also known as white-rumped munia, white-rumped manikin). The Bengalese finch is a domestic strain of the wild white-backed munia.

to survive by domestication is a key point in clarifying the evolutionary mechanisms underlying behavioural traits in the Bengalese finch.

Prior studies have indicated that tonic immobility (TI) responses, also called death feigning, thanatosis, catalepsy, catatonia, animal hypnosis, contact defence immobility, fright paralysis, playing dead, playing possum, paroxysmal inhibition, cataplexy, sham death, and the immobility reflex, are related to levels of fearfulness (Gallup, 1977, 1979; Jones, 1986, 1987; Jones et al., 1994). The TI response (behavioural motor inhibition and reduced responsiveness to external stimulation induced by physical restraint) has been documented in such diverse species as insects, crustaceans, fish, amphibian, reptiles, birds, and mammals (Ratner, 1967; Gallup, 1974a; Miyatake et al., 2004; Marx et al., 2008). The TI reaction reduces the threat of a potential predator and increases the chances of survival (Thompson et al., 1981; Thompson and Liebreich, 1987; Miyatake et al., 2004; Marx et al., 2008). Thus, the TI response is directly implicated as an adaptive behavioural strategy to predation. Induction of TI by experimental physical restraint (TI test) has been performed as a behavioural measurement of fearfulness in domesticated chickens and quail (Gallup, 1979; Jones, 1986; Forkman et al., 2007). In the present study, this basic TI test method was applied to measure fearfulness in finches.

To explore the evolutionary mechanisms underlying behavioural changes caused by domestication, we examined the changes in predation coping style by comparing TI reactions in domesticated Bengalese finches with those in the white-backed munia.

2. Methods

2.1. Subjects and husbandry

Thirty-three Bengalese finches (23 males and 10 females) and 33 white-backed munias (23 males and 10 females) were used in this study. All birds were sexually mature. The Bengalese finches were bred in our laboratory. The white-backed munias were born in captivity ($n = 18$), purchased from local pet suppliers (imported from Taiwan; $n = 12$) or captured in the wild in Taiwan ($n = 3$). The birds were housed in uni-strain and uni-sexual groups of approximately 10–20 individuals per stainless steel cage (370 mm × 415 mm × 440 mm), together with non-experimental birds, in a 13:11-h LD photoperiod-cycled room (lights on at 07:00). Temperature and humidity were about 25 °C and 50%, respectively, and food (finch seed mixture and shell grit) and water (vitamin enhanced) were freely available. All experimental procedures and the housing conditions of the birds were approved by the Animal Experiment Committee at RIKEN (#H24-2-229), and all birds were cared for in accordance with the Institutional Guidelines for Experiments Using Animals.

2.2. TI test

We measured the TI reaction using the TI test and a general method that consistently and reliably induces TI (Jones, 1986). The most effective apparatus for inducing TI using a cradle and cloth was described in detail by Jones and Faure (1981). We made and used a U-shaped bamboo cradle (67 mm × 170 mm × 24 mm) covered with black felt cloth to perform the experiments with small birds (Fig. 2). The birds were caught from the rearing cage one by one and immediately carried to a soundproof chamber (117 cm × 152 cm × 187 cm; Music Cabin, Inc., Kawasaki, Japan) to avoid disturbance and then immediately subjected to the TI test. The cradle was placed at the centre of a desk (40 cm × 50 cm × 70 cm) on the innermost side of the chamber. For the TI test, each bird was placed on its back in the cradle with its head hanging over the edge of the cradle, restrained in that position for 15 s, and then released (Fig. 2A and B). The optimal duration of manual restraint is 15 s (Gallup et al., 1971). If a bird moved within 10 s after release, then it was considered that TI had not been induced. In that case, the restraint was repeated up to five times. After induction of TI, the experimenter silently took a few steps away from the bird and then observed the bird in the chamber (a distance of about 80 cm). The birds were recorded with a digital video camera (Handycam HDR-TG5V; Sony Ltd., Tokyo, Japan) located about 80 cm from the bird on the observer's left and at the near side in the chamber. The number of restraints required to attain TI induction (number of restraints), the latency to the first head movement (latency to head movement, Fig. 2C), and the duration of TI (TI duration, righting time, Fig. 2D) were scored by video observation. The latency to head movement was the interval from the induction of TI to the first head movement. The TI duration was the interval from the induction of TI to the righting. If the bird did not show head movement or righting during the 15 min of the test, the maximum duration of the latency to head movement or the TI duration was considered 900 s. In contrast, if TI was not induced in a maximum of five attempts, the number of restraints was considered five, and the latency time to the first head movement and the duration of TI were employed as the duration for the fifth test (<10 s). The TI test was performed in the afternoon (12:00–18:00). At the end of the test, we measured the body weights of the birds to the nearest 0.1 g.

2.3. Statistical analysis

Data are presented as means and standard error (SE). The latency to head movement and the TI duration were analysed by two-way analysis of variance (factors: strains and sex), and the data were log-transformed to fulfil the normality assumption before analysis (Zar, 1999). The normality of the distributions was evaluated with the Kolmogorov–Smirnov test (Zar, 1999). The number of

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