



INTERSPECIFIC AGGRESSION FOR NEST SITES: MODEL EXPERIMENTS WITH LONG-TAILED FINCHES (*POEPHILA ACUTICAUDA*) AND ENDANGERED GOULDIAN FINCHES (*ERYTHRURA GOULDIAE*)

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ABSTRACT.—For cavity-nesting birds, tree cavities often represent a critical, defendable, and limiting resource that is frequently under intense interspecific competition. However, the dynamics of interspecific conflict resolution, especially between species of similar size, are often unclear. We experimentally tested aggression and nest-defense behaviors in Gouldian Finches (*Erythrura gouldiae*) and Long-tailed Finches (*Poephila acuticauda*), two sympatric, cavity-nesting estrildid finches that are very similar in size, ecology, and nest-site requirements. Mounted taxidermic models of conspecific and heterospecific nest-site competitors (black and red Gouldian Finch morph and Long-tailed Finch models), as well as a control noncompetitor (Black-chinned Honeyeater [*Melithreptus gularis*]), were presented to Gouldian and Long-tailed finches. These two competing species differed in their overall responses to simulated intruders and in their relative aggression toward conspecific and heterospecific intruders. Long-tailed Finches reacted more quickly to models, approached closer, and were more likely to attack models (i.e., make physical contact) than Gouldian Finches, which suggests that Long-tailed Finches are intrinsically more aggressive. In addition, Long-tailed Finches were more aggressive toward Gouldian Finches than toward conspecific models. By contrast, Gouldian Finches were more aggressive to conspecific models and avoided approaching Long-tailed Finch models. Male Gouldian Finches were particularly aggressive toward conspecifics, and red head-color morphs were more aggressive than black morphs. These results suggest that the outcomes of competitive asymmetries within and between these species are driven by differences in aggression. Together with the substantial overlap in nest-site use, the Long-tailed Finch's aggressive domination of limited nest sites may lead to competitive exclusion of the endangered Gouldian Finch. Received 14 April 2011, accepted 25 May 2011.

Key words: cavity nesting, *Erythrura gouldiae*, Gouldian Finch, heterospecific aggression, interspecific competition, Long-tailed Finch, *Poephila acuticauda*.

Agression interspécifique pour les sites de nidification : expériences sur modèles avec *Poephila acuticauda* et *Erythrura gouldiae*

RÉSUMÉ.—Pour les oiseaux nichant dans des cavités, les cavités d'arbres représentent souvent une ressource critique, devant être défendue et limitante, qui fait fréquemment l'objet d'une compétition interspécifique intense. Cependant, la dynamique de résolution des conflits interspécifiques, en particulier entre les espèces de taille semblable, est souvent obscure. Nous avons testé expérimentalement les comportements d'agression et de défense du nid chez *Erythrura gouldiae* et *Poephila acuticauda*, deux espèces d'estrildidés sympatriques nichant dans des cavités et qui sont très similaires en taille, en écologie et en besoins en sites de nidification. Des modèles naturalisés de compétiteurs conspécifiques et hétérospécifiques pour les sites de nidification (modèles de *P. acuticauda* et des formes noire et rouge d'*E. gouldiae*), ainsi que de non-compétiteurs témoins (*Melithreptus gularis*), ont été présentés à des individus d'*E. gouldiae* et *P. acuticauda*. Ces deux espèces compétitrices ont différé dans leurs réponses globales aux intrus simulés et dans leur agression relative envers les intrus conspécifiques et hétérospécifiques. Les individus de *P. acuticauda* ont réagi plus rapidement aux modèles, se sont approchés plus près et tendaient davantage d'attaquer les modèles (contact physique) que ceux d'*E. gouldiae*, ce qui suggère que *P. acuticauda* est intrinsèquement plus agressif. De plus, les individus de cette espèce étaient plus agressifs envers ceux d'*E. gouldiae* qu'envers les modèles de leurs congénères. En revanche, les individus d'*E. gouldiae* étaient plus agressifs envers les modèles de leurs congénères et évitaient de s'approcher des modèles de *P. acuticauda*. Les mâles d'*E. gouldiae* étaient particulièrement agressifs envers leurs congénères et la forme à tête rouge était plus agressive que la forme noire. Ces résultats suggèrent que les asymétries compétitives au sein et entre ces espèces sont guidées par les différences dans l'agression. Avec le chevauchement substantiel dans l'utilisation des sites de nidification, la domination agressive de *P. acuticauda* pour les sites de nidification limités peut mener à une exclusion compétitive d'*E. gouldiae*, une espèce en voie de disparition.

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CAVITY-NESTING BIRDS provide a model system for exploring the behavioral dynamics of interspecific competition because tree cavities are often discrete and defensible resources. In addition, tree cavities provide a crucial breeding resource for secondary cavity-nesting birds, and the supply and availability of tree cavities in many environments is limited by low production and high demand (Newton 1994, 1998). Therefore, the likelihood of an individual (or breeding pair) acquiring and defending a nest site will often depend on its success in direct competition. However, there is surprisingly little experimental support to show interference competition between competing species. Most studies have explored changes in the local densities of secondary cavity-nesting birds after manipulation of nest-site availability (i.e., usually after artificial nest boxes are provided; Newton 1998). Typically, local densities of secondary cavity-nesting birds respond to nest-site supplementation, demonstrating that cavities are the limiting resource (reviewed in Newton 1998). Interspecific competition is then implied if there are complementary changes in breeding densities of two or more competing species (Minot and Perrins 1986, Gustafsson 1988).

Although such correlations suggest that competition is occurring, these types of data are unable to uncover the nature or proximate mechanism driving the resolution of interspecific conflicts. To date, the evidence for differences in aggressive behavior in nest-site competition between species has mainly been observational (e.g., Slagsvold 1975, Gustafsson 1988, Winge and Järvi 1988, Meek and Robertson 1994, Merilä and Wiggins 1995). The few experimental tests of interspecific aggressive responses have typically used song playback or models (artificial or mounted specimens) to assess the responses of competing species (Järvi et al. 1968, Král and Bieć 1992, Martin and Martin 2001, Krist 2004). However, most of these studies have not included suitable control treatments (e.g., a noncompetitor), and therefore it is unclear whether the observed mutual aggressive behaviors are attributable to a species' general aggressiveness (e.g., nest defense) or specifically targeted at individuals considered to be direct nest-site competitors. Furthermore, the numerous correlative studies implicating interspecific interference competition in cavity-nesting systems have shown that the outcomes of species pairwise interactions are consistently determined by differences in body size (i.e., larger species typically dominate smaller species; Minot and Perrins 1986, Robinson and Terborgh 1995, Rychlik and Zwolak 2006, Aitken and Martin 2008). However, it is often unclear how interspecific conflicts are resolved when similar-sized species compete (but see Cordero and Senar 1990, McDonald et al. 2001).

Here, we experimentally test for differences in aggressive behavior between two cavity-nesting species that are similar in size. Gouldian Finches (*Erythrura gouldiae*) and Long-tailed Finches (*Poephila acuticauda*) are sympatric grassfinches (estrildids), endemic to the tropical savannas of northern Australia. They are similar in body size (~14.5 g; 15–16 mm body length), breeding phenology, and other aspects of ecology (Higgins et al. 2006). Both species are granivorous, nest in tree cavities with similar characteristics (Brazill-Boast et al. 2010), and have overlapping breeding seasons (Gouldian: February–June; Long-tailed: February–September; Higgins et al. 2006). Until recently, Gouldian and Long-tailed finches had identical geographic ranges covering most of northern tropical Australia

(Immelmann 1965). Over the past 50 years, however, the Gouldian Finch's range and population size have severely declined, and the species is now listed as endangered (Garnett and Crowley 2000). By contrast, Long-tailed Finch populations have remained relatively stable (Higgins et al. 2006). These species' habitat has been subject to various and severe anthropogenic disturbances, such as changes in the frequency and intensity of seasonal fires and habitat clearing (Williams et al. 1999, Kutt and Woinarski 2007). Most attempts to explain the Gouldian Finch's decline have focused on changes in the availability of seeding grasses (Franklin 1999, Dostine et al. 2001, Franklin et al. 2005), but recent studies suggest that these anthropogenic disturbances have severely affected the distribution and availability of cavity-bearing trees (Williams et al. 1999, Lehmann et al. 2008) and that the limited tree cavities are under direct competition because of these species' significant ecological niche overlap (Brazill-Boast et al. 2010, 2011). Therefore, as in many cavity-nesting systems, the opportunity to breed and relative nest-site quality will be closely related to the outcome of direct competition (e.g., Minot and Perrins 1986, Wiebe 2003, Aitken and Martin 2008). Recent work has shown that the more numerous Long-tailed Finch acquires disproportionately more nest cavities than Gouldian Finches (Brazill-Boast et al. 2010), and high interference rates from Long-tailed Finches reduce Gouldian Finches' reproductive success (Brazill-Boast et al. 2011). However, experimental tests of relative aggression are required to assess whether the outcome of interspecific interactions is due to intrinsic differences between the species or a result of the much higher densities of Long-tailed Finches.

In addition to potential interspecific differences in aggression, studies with captive Gouldian Finches have demonstrated intraspecific behavioral differences related to the expression of genetically determined red and black head-color morphs. In both sexes, red birds are socially dominant, outcompeting black birds for access to food (Pryke and Griffith 2006, Pryke 2007) and higher-quality nest sites (Pryke and Griffith 2009). Red functions as a status signal of dominance and intimidation (Pryke 2009), and red males are also intrinsically more aggressive (Pryke and Griffith 2006, Pryke 2009). However, morph-related differences in behavior and aggression have not been examined in wild populations, despite their potential influence on individual fitness, especially in nest-site-limited populations.

To experimentally test the aggressive responses within and between Gouldian and Long-tailed finches, we presented taxidermic models of (1) conspecific competitors (red and black Gouldian Finch morphs), (2) heterospecific competitors (Long-tailed Finch), and (3) a noncompetitor (Black-chinned Honeyeater [*Melithrepus gularis*]; hereafter "honeyeater") to active Gouldian and Long-tailed finch nests. We predicted that Long-tailed and Gouldian finches would show aggressive responses and nest-defense behaviors toward both Long-tailed and Gouldian finch models, but not toward the noncompetitive honeyeater. In particular, because the ubiquitous Long-tailed Finch acquires disproportionately more nest sites than the endangered Gouldian Finch (Brazill-Boast et al. 2010), we predicted that the Long-tailed Finch would be the superior competitor, exhibiting higher aggressive responses to intruders than Gouldian Finches. By examining the dominance relationship between Gouldian and Long-tailed finches in the

wild, we gain valuable insight into the outcome of behavioral interactions for limited nest sites, as well as the potential negative effects of competition on an endangered species.

METHODS

Study site.—The study was conducted from April to July 2009 (i.e., the overlapping breeding season of Gouldian and Long-tailed finches) in the eastern Kimberley region of Western Australia (S15°33', E128°08'). Breeding areas are characterized by west-facing, gently sloping sandstone ridges dominated by Variegated Bloodwood (*Corymbia dichromophloia*) (dominant nest trees) and an understorey dominated by Speargrass (*Sorghum stipoidum*) and Curly Spinifex (*Triodia bitextura*).

The study site was provisioned with custom-designed nest boxes. Nest boxes were constructed using naturally hollowed *Corymbia* branches (i.e., they closely resembled natural cavities) to specifically target Gouldian Finches; however, they were also suitable for Long-tailed Finches because the two species' preferences for nest sites overlap considerably (Brazill-Boast et al. 2010). Artificial nest boxes were used for two reasons. First, they allow access to nest contents for monitoring offspring and, thus, standardized model presentations to nests with broods of similar age. Second, they provide a standardized resource for all individuals to defend (i.e., limited variation in nest-site quality), as well as a standard method for presenting and positioning models during the experiment (Fig. 1).

Monitoring breeding.—All nest boxes in the study area were checked at least once every 7–10 days for signs of nest initiation (nest building or eggs). Once a nest had been initiated, it was checked every 2–3 days to record hatching date and to identify the occupying species. Following hatching, nest boxes were checked every 2–4 days.

Parents were captured at the nest using a hand net and given a numbered aluminum leg band, as well as a unique combination of three colored plastic leg bands. Gouldian Finches are sexually dichromatic; males display a bright purple breast, yellow belly, green back and wings, and an ultraviolet-blue head collar, whereas females have similar but much less intensely colored patches (Pryke and Griffith 2006). By contrast, Long-tailed Finches are sexually

monomorphic (Van Rooij and Griffith 2010). Therefore, the sex of adult Long-tailed Finches was determined from a small blood sample (2–3 drops from the brachial vein) using polymerase chain reaction to amplify sex-linked markers P2 and P8 following standard protocols (Griffiths et al. 1998).

Model presentations.—Taxidermic models were made from skins of adult male birds. Gouldian and Long-tailed finch models were constructed from males that died naturally in our captive populations. To test for differences in aggression toward conspecific and heterospecific models, both Gouldian and Long-tailed finch models were presented to Gouldian and Long-tailed finches. Because of behavioral differences between aggressive red and nonaggressive black Gouldian Finch morphs (Pryke and Griffith 2006, Pryke 2007), models of both morph-types were included in the experiment (but only one was presented to each nest). To control for the novelty of model presentations, we also included a model of a noncompetitive but sympatric species, the sexually monomorphic honeyeater (weight: 20 g; length: 14 cm), which was borrowed from the Australian Natural History Museum (Sydney). Honeyeaters are common within the study site, but they are nectivorous, construct a free-standing bark nest, and therefore do not compete with Gouldian or Long-tailed finches for food or nest sites. Because some individuals attacked and damaged the models (see below), a total of four Gouldian Finch models (2 red- and 2 black-headed), three Long-tailed Finch models, and one honeyeater model were used.

All models were constructed in a vigilant posture typically displayed by conspicuously perched birds near their nests, with the beak directed upward and wings closed. We fastened these models onto a 10-cm length of wooden dowel that could be attached to the nest box in the field (Fig. 1). Models were placed within 5 cm of the entrance to the nest and, thus, situated conspicuously so that they were visible from all directions.

We presented the three models (Gouldian Finch, Long-tailed Finch, and honeyeater) to parents of 19 Gouldian Finch (7 red and 12 black) and 23 Long-tailed Finch nests (total 84 individuals; 252 presentations). All model presentations were made during the period of intense chick provisioning (8–17 days of age; most presentations [79%] occurred on days 14–16). Although competition is likely to be more intense during nest acquisition than during breeding, in preliminary trials at the nest acquisition stage none of the tested Gouldian Finches ($n = 12$) bred in the nest boxes after being presented with Long-tailed Finch models. Therefore, to permit effective comparisons of aggressive behavior between the species, and to minimize disruption of breeding, all model presentations were made during the chick-provisioning stage. No nests were abandoned during this stage, and all nests successfully fledged offspring.

The presentation of the three different model species was randomized, and only one model was presented each day to a nest, to reduce the risk of habituation. To minimize any potential disturbance effects, all models were positioned when both parents were absent from the nest. Most Long-tailed Finch parents returned to the nest together (97% of 73 trials). By contrast, male and female Gouldian Finches typically returned individually and sequentially to the nest (65% of 107 trials). Thus, there was a significant difference in parental visitation behaviors (i.e., alone or in pairs) between the species ($\chi^2 = 24.08$, $P < 0.001$). For all nests where only one parent returned during the model-presentation

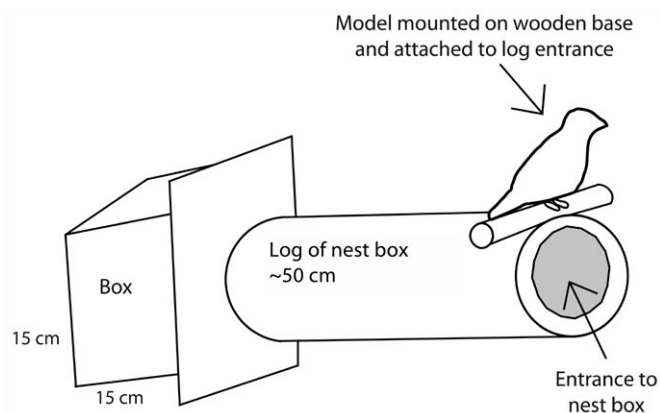


FIG. 1. Placement of taxidermic models at the entrance of active Gouldian and Long-tailed finch nests for all model presentations.

period, the model was retested on another day by positioning it after the tested bird had left the nest (i.e., before the untested bird returned).

All trials were recorded between 0600 and 1100 hours by both an observer (D.P. or S.R.P.) and a video camera (Sony DCR-DVD101E; video analyzed by D.P.). Trials started when a resident bird returned to the tree. For each individual, we recorded the response time (time from when the bird returned to the tree until it approached the model) and the distance of the closest approach (using a 0.1-m-interval meter-scale set up underneath the nest). We also recorded all behaviors during this time, including the number of times an individual attacked the model, flew by it, or hovered near it. On the basis of these behaviors, individuals were assigned an aggression score that corresponded to their most extreme aggressive response (Table 1), similar to those used in other studies (e.g., Hakkarainen et al. 1998, Duckworth 2006). Trials were completed when (1) the resident bird attacked the model physically or showed a threatening display; (2) the resident bird showed distressed or repetitive behaviors (e.g., calling to chicks or hopping repetitively from one branch to another); or (3) after a maximum period of 30 min, irrespective of the behavioral response of the test bird.

To further test for species-specific behavioral differences in nest-approach behaviors (in the absence of models), the average time taken by individual birds to enter their nests (after arriving in the tree) was recorded prior to the model presentations (chicks 6–15 days old) for all parents, using the same methodology described above.

Statistical analyses.—Outcomes from the model presentations were analyzed using the repeated-measures general-linear-model procedure in GENSTAT, version 9 (Rothamsted Experimental Station, Harpendon, United Kingdom). Individual identities were entered as the repeated measure (i.e., for within-individual comparisons) for each of the different response variables, including reaction time, closest distance to the model, and aggression score. The significance of the predictor variables was tested by the change in deviance of the different models using a chi-square approximation. All possible effects, combinations, and interactions (two- and three-way interactions) were initially modeled, including model species, morph (of model), parent species, parent sex, parent morph (Gouldian Finches), order of model presentation, trial date, age of chicks, and whether parents were

alone or together. Second-order Akaike's information criterion (AIC_c) weights were calculated for each model. The AIC_c (used for smaller sample sizes) balances the fit of the model against the number of parameters and was used to effectively compare different models (i.e., it indicates the probability that a model is the best among the tested models). For simplicity, only final models (and significant interactions) are reported, given that all models had an AIC_c weight of $\geq 81.3\%$ compared with other potential models. Significant probability values were derived from having all relevant terms fitted in the final model together, whereas those of nonsignificant terms were obtained from having all significant terms in the final model and each nonsignificant term fitted individually. Results are presented as means \pm SE.

RESULTS

Pre-experimental behavior.—Prior to the experiments (i.e., in the absence of models), there were no differences in the time taken by Long-tailed Finches (282 ± 47.05 s) and Gouldian Finches (196 ± 30.19 s) to enter their nests after arriving in the tree ($F = 1.52$, $df = 1$ and 251 , $P = 0.11$). There were also no sex-related differences in nest-approach behavior for either Long-tailed Finches ($F = 1.79$, $df = 1$ and 137 , $P = 0.21$) or Gouldian Finches ($F = 1.67$, $df = 1$ and 113 , $P = 0.17$), or morph-specific differences between red and black Gouldian Finch head-color morphs ($F = 0.87$, $df = 1$ and 113 , $P = 0.32$).

Reaction time to models.—Long-tailed and Gouldian finches responded differently to the models ($F = 2.86$, $df = 1$ and 251 , $P = 0.01$; Fig. 2A). Overall, Long-tailed Finches reacted more quickly than Gouldian Finches ($F = 4.28$, $df = 1$ and 251 , $P = 0.001$), but there were no species differences in reaction time to each of the three different models ($F = 4.85$, $df = 1$ and 183 , $P = 0.12$; model \times species: $F = 1.25$, $df = 4$ and 181 , $P = 0.29$). There were also no sex-related differences in reaction time for either Long-tailed Finches ($F = 1.72$, $df = 1$ and 137 , $P = 0.19$) or Gouldian Finches ($F = 0.27$, $df = 1$ and 113 , $P = 0.76$). However, red Gouldian Finches reacted more quickly (141 ± 38.7 s) than black morphs (207 ± 58.4 s) to the Gouldian Finch models ($F = 4.82$, $df = 1$ and 113 , $P = 0.03$); however, this effect was independent of the model bird's head color ($F = 1.34$, $df = 1$ and 113 , $P = 0.29$). There was no difference in reaction time of Long-tailed Finches to black or red morphs of the Gouldian Finch model ($F = 2.41$, $df = 1$ and 137 , $P = 0.14$).

Closest approach distance to models.—Gouldian and Long-tailed finches differed in their approach distance to the models ($F = 7.14$, $df = 1$ and 251 , $P < 0.001$), with Long-tailed Finches approaching the models more closely than Gouldian Finches (Fig. 2B). Furthermore, the two species responded differently to the type of model presented ($F = 0.86$, $df = 1$ and 251 , $P = 0.42$; species \times model: $F = 6.47$, $df = 4$ and 247 , $P = 0.003$). In particular, compared to Gouldian Finches, Long-tailed Finches more closely approached both the Gouldian Finch model ($t = 4.73$, $P < 0.001$) and the Long-tailed Finch model ($t = 2.69$, $P = 0.008$), although there were no species-dependent differences in approach distance to the honeyeater model ($t = 0.63$, $P = 0.53$).

There were no differences in approach distance between male and female Long-tailed Finches ($F = 1.26$, $df = 1$ and 137 , $P = 0.15$), but male Gouldian Finches approached the models more closely than females ($F = 3.62$, $df = 1$ and 113 , $P = 0.02$; Fig. 3A). In particular, male Gouldian Finches more closely approached Gouldian

TABLE 1. Aggression index used to score aggressive behaviors of Gouldian and Long-tailed finches. Individuals were assigned a score that corresponded to the most extreme behavior observed during the model presentations.

Aggression score	Description
0	No aggression (displays or physical contact)
1	Threatening display (hover, open beak display)
2	Aerial dive without contact
3	Aerial dive with contact
4	Aerial attack (repeatedly attack model in flight)
5	Stationary attack (repeated pecking 3–10 times)
6	Stationary attack (repeated pecking >10 times)
7	Landing on model (e.g., back) and pecking

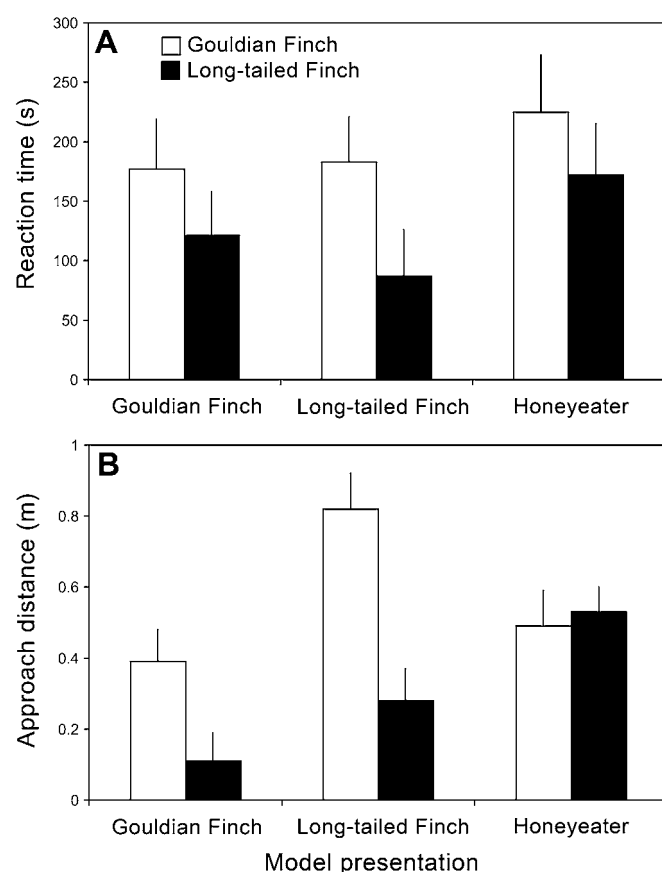


FIG. 2. Average (\pm SE) (A) reaction time and (B) closest distance approached of Gouldian and Long-tailed finches presented with conspecific and heterospecific competitors (Gouldian Finch and Long-tailed Finch models) and a heterospecific noncompetitor (Black-chinned Honeyeater model).

Finch models than females ($t = 4.22$, $P < 0.001$), but there were no sex-related differences in approach distance to the Long-tailed Finch ($t = 0.80$, $P = 0.43$) or honeyeater models ($t = 1.20$, $P = 0.23$).

In response to red and black Gouldian Finch models, there were no differences in the approach distance of either Long-tailed ($F = 0.81$, $df = 1$ and 137 , $P = 0.37$) or Gouldian Finches ($F = 1.58$, $df = 1$ and 113 , $P = 0.25$). However, in Gouldian Finches, red birds more closely approached the models than black birds (resident morph: $F = 2.61$, $df = 1$ and 113 , $P = 0.06$; model: $F = 0.39$, $df = 2$ and 111 , $P = 0.54$; model \times resident morph: $F = 7.28$, $df = 4$ and 109 , $P = 0.008$). In particular, red birds approached both the Gouldian Finch ($t = 2.88$, $P = 0.004$) and Long-tailed Finch models ($t = 2.65$, $P = 0.009$) more closely than black birds, whereas there was no difference in approach distance between the morphs to the honeyeater model ($t = 1.15$, $P = 0.26$; Fig. 4A).

Aggressive response to models.—Using aggression scores as an index of aggressiveness, Long-tailed Finches were more aggressive than Gouldian Finches ($F = 5.94$, $df = 1$ and 251 , $P < 0.001$; Fig. 5A). In particular, aggression differed in response to the different models ($F = 7.74$, $df = 1$ and 251 , $P < 0.001$; species \times model: $F = 2.79$, $df = 4$ and 247 , $P = 0.03$); Long-tailed Finches were more aggressive

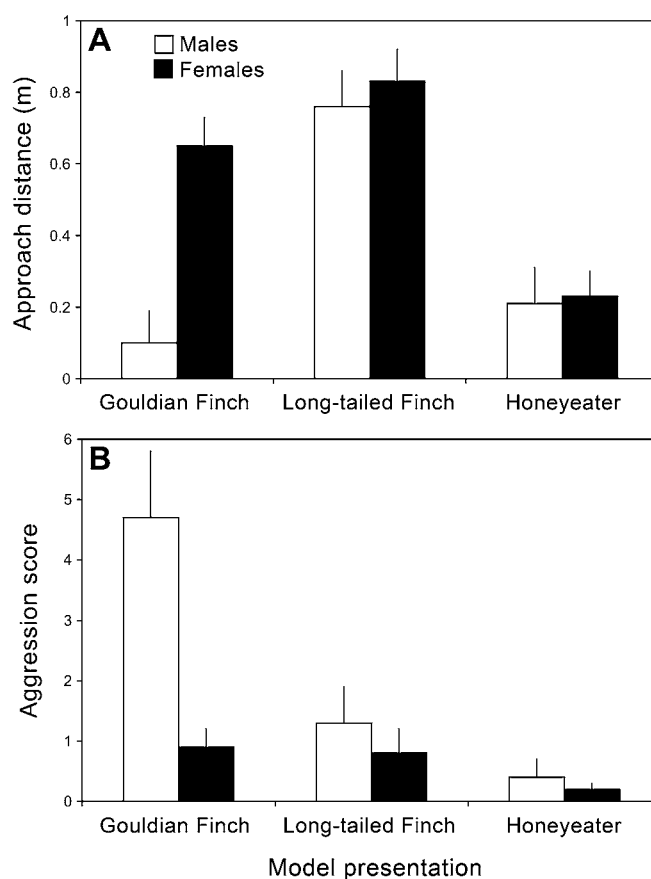


FIG. 3. Mean (\pm SE) (A) closest approach distance and (B) aggression score for male and female Gouldian Finches in response to the Gouldian Finch, Long-tailed Finch, and Black-chinned Honeyeater models.

than Gouldian Finches toward both the Gouldian Finch ($t = 7.66$, $P < 0.001$) and Long-tailed Finch models ($t = 4.74$, $P < 0.001$). However, there was no difference between the species in aggression response to the honeyeater model ($t = 0.94$, $P = 0.35$).

Although there were no sex-related differences in aggression for Long-tailed Finches ($F = 1.08$, $df = 1$ and 137 , $P = 0.31$), male Gouldian Finches were more aggressive than females ($F = 11.98$, $df = 1$ and 113 , $P = 0.002$). Male Gouldian Finches also responded differently to the different models (sex \times model: $F = 10.34$, $df = 4$ and 109 , $P = 0.003$), with males exhibiting more aggression toward the Gouldian Finch models ($t = 3.92$, $P < 0.001$) than toward either the Long-tailed Finch ($t = 0.98$, $P = 0.38$) or honeyeater models ($t = 0.09$, $P = 0.91$; Fig. 3B). Furthermore, red Gouldian Finches were more aggressive than black morphs (resident morph: $F = 6.34$, $df = 1$ and 113 , $P < 0.01$; model: $F = 0.41$, $df = 2$ and 111 , $P = 0.59$; model \times resident morph: $F = 6.87$, $df = 4$ and 109 , $P = 0.009$), showing significantly higher aggressive responses to Gouldian Finch models ($t = 3.14$, $P = 0.02$) and Long-tailed Finch models ($t = 2.83$, $P = 0.007$) (Fig. 4B). There was no difference in aggression directed to black and red models by either Gouldian Finches ($F = 0.03$, $df = 1$ and 113 , $P = 0.96$) or Long-tailed Finches ($F = 1.01$, $df = 1$ and 137 , $P = 0.42$).

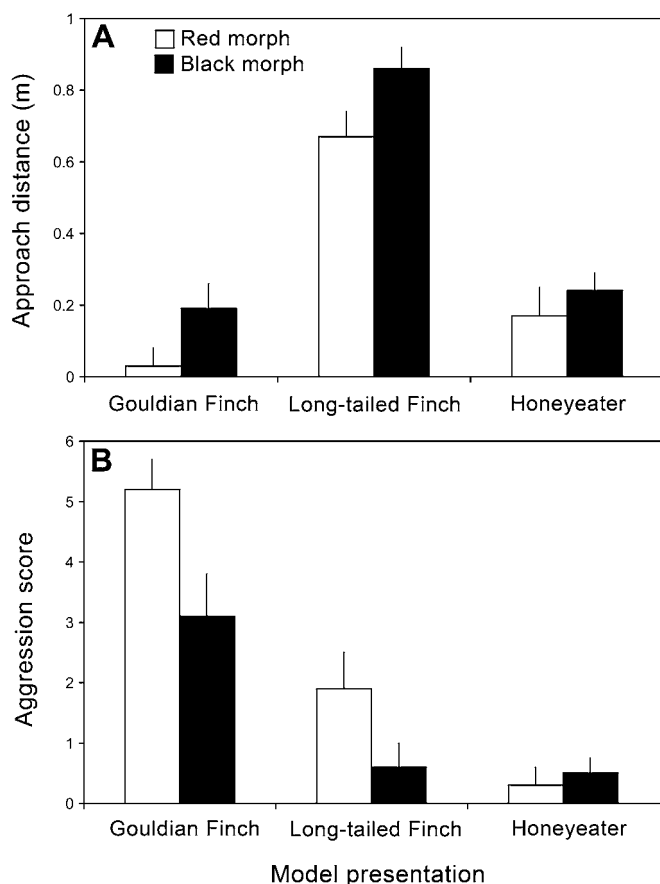


FIG. 4. Mean (\pm SE) (A) closest approach distance and (B) aggression score for red and black male Gouldian Finch head-color morphs in response to the Gouldian Finch, Long-tailed Finch, and Black-chinned Honeyeater models.

Overall, Long-tailed Finches were more aggressive than Gouldian Finches (Fig. 5B). Long-tailed Finches aggressively attacked the models in 46% of all trials, and in two trials completely removed the wing or tail of the model. Most aggressive attacks (i.e., direct hits) by Long-tailed Finches were directed at the Gouldian Finch model (82%) and fewer at the conspecific Long-tailed Finch model (52%). By contrast, Gouldian Finches physically attacked the models in only 16% of all trials, and aggressively attacked the conspecific Gouldian Finch model (38%) more than the Long-tailed Finch model (4%). There were few aggressive responses to the honeyeater model, with only two Long-tailed Finches (5%) and no Gouldian Finches physically attacking the model.

DISCUSSION

Long-tailed Finches were more aggressive than Gouldian Finches at their nest sites. Long-tailed Finches reacted more quickly to models, approached more closely, and were more likely to physically attack models than Gouldian Finches. Furthermore, Long-tailed Finches were significantly more aggressive toward Gouldian Finch models than toward Long-tailed Finch models, whereas Gouldian Finches were more aggressive toward Gouldian Finch

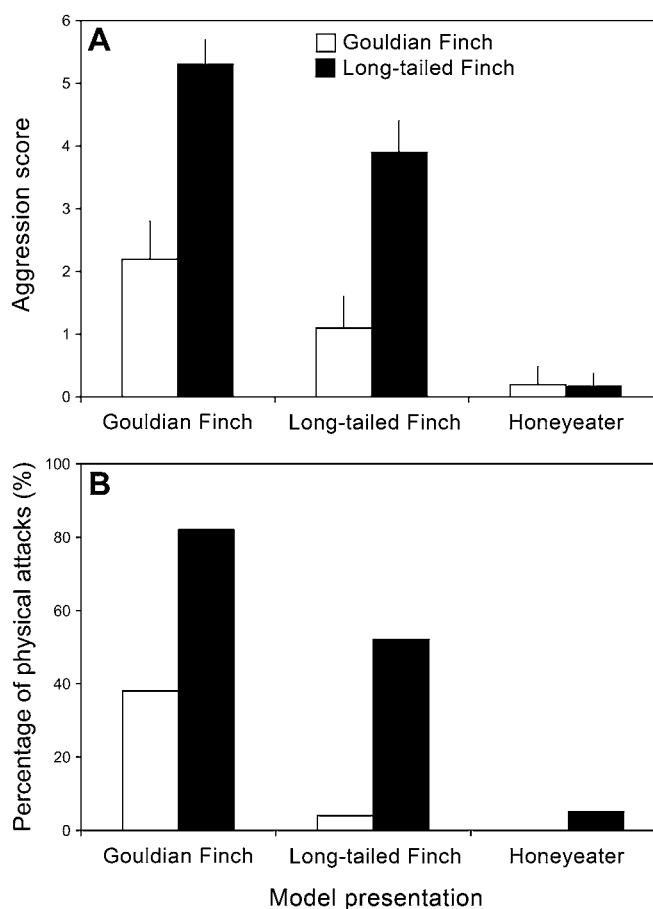


FIG. 5. (A) Average (\pm SE) aggression score and (B) percentage of physical attacks by Gouldian and Long-tailed finches directed at conspecific and heterospecific competitors (Gouldian Finch and Long-tailed Finch models) and a heterospecific noncompetitor (Black-chinned Honeyeater model).

than toward Long-tailed Finch models. Thus, the two species differed in their overall responses to simulated intruders, as well as in their aggressive responses to conspecific and heterospecific competitors.

In these simulated encounters, theoretically, individuals defending their nest site are predicted to display higher aggression to potential competitors (Trivers 1972, Redondo and Carranza 1989, Becerril-Morales and Macias-Ordóñez 2009). The asymmetry in nest-defense behaviors between Gouldian and Long-tailed finches is likely related to the divergent competitive ability and perceived dominance threat of the intruding species. In particular, the low aggressive response of Gouldian Finches to heterospecific Long-tailed Finches may be because they view them as superior competitors and avoid initiating potentially costly conflicts with an aggressive and dominant intruder. Similar avoidance behaviors have been found in competing Gouldian Finches: individuals avoided initiating conflicts with naturally and experimentally painted birds of the aggressive red morph (Pryke and Griffith 2006, Pryke 2009). Previous work has shown that Long-tail Finches dominate access to limited nest sites (Brazill-Boast et al. 2011), and the present study suggests that this is because Long-tailed Finches are intrinsically more aggressive than Gouldian Finches.

Numerous empirical studies of interspecific dominance relationships have shown that differences in competitive abilities are largely related to asymmetries in body size (Persson 1985, Robinson and Terborgh 1995, Rychlik and Zwolak 2006). Gouldian and Long-tailed finches are very similar in size (~14.5 g) and also have strikingly similar nesting and feeding behaviors. However, differences in their life-history behavior, especially parental care (Brazill-Boast et al. 2011), may contribute to the observed divergent aggressive responses. Gouldian Finches typically visit the nest alone, with males and females sequentially provisioning the nest throughout the day (and the nest left unattended between feeding visits), and, thus, are rarely seen together at the nest. By contrast, Long-tailed Finch parents typically visit their nests as a pair. Potentially, the dual response of Long-tailed Finches (vs. the singular Gouldian Finch response) may contribute to their increased aggression, perhaps because the presence of two birds (vs. one) increases their risk-taking behavior, their perception of winning, or both. However, individual Long-tailed Finches also dominate individual Gouldian Finches in staged dyadic contests (Brazill-Boast et al. 2011), which suggests that Long-tailed Finches are also innately more aggressive. Nevertheless, irrespective of the exact mechanism, our results suggest that Long-tailed Finches will be more effective at defending their nest sites than Gouldian Finches.

Although Gouldian Finches rarely showed aggression toward Long-tailed Finches, males in particular were aggressive toward conspecific male models. In Gouldian Finches, males typically perform most of the nest-prospecting and nest-building behaviors (Pryke and Griffith 2009) and, therefore, may also be primarily responsible for nest defense. However, previous studies have shown that female Gouldian Finches often interfere with active nests (Brazill-Boast et al. 2011) and will also aggressively defend their nests from intruders in captivity (Pryke and Griffith 2009). Another possibility is that the male intruder is perceived not just as a nest-site competitor, but also as a potential extrapair partner searching for paternity opportunities and, thus, a direct threat to the male's fitness (Pryke et al. 2010). Therefore, although breeding pairs rarely visit the nest together, the aggressive behavior displayed by males toward conspecific male models may represent mate-guarding behavior.

Similar to findings in other color polymorphic birds—for example, White-crowned Sparrows (*Zonotrichia leucophrys*; Tuttle 2003) and Northern Flickers (*Colaptes auratus*; Flockhart and Wiebe 2009)—there were also morph-specific differences in aggression by Gouldian Finches. Red morphs reacted more quickly to the models, approached them more closely, and showed more overt aggression than black morphs. These results fit with findings from previous captive studies (Pryke and Griffith 2006, 2009; Pryke 2007). In particular, red males are intrinsically more aggressive than black males (Pryke and Griffith 2006, Pryke et al. 2007), which may explain their higher aggressive response than black males to the stimulated intruders. Thus, in defending their nest sites, red males are expected to be relatively more successful in competing against both conspecifics and the aggressive heterospecific Long-tailed Finches. However, despite Gouldian Finches demonstrating an innate avoidance and intimidation response to red coloration in dyadic contests (Pryke 2009), there were no differences in aggressive responses directed to either red or black models. Although aggressive red birds are avoided during staged dyadic contests over

food in which both birds have equal motivation for winning (Pryke and Griffith 2006, Pryke 2009), in this case, the nest-site owner may be willing to invest more in potential contests because the fitness costs of losing the active nest site (or female) is likely to be much higher (i.e., value asymmetry hypothesis: Trivers 1972, Beletsky and Orians 1989, Tobias 1997, Becerril-Morales and Macias-Ordóñez 2009). Therefore, owners defending their nest sites may compete more vigorously, irrespective of the perceived competitive abilities of the challenger, because their perception of their own dominance or their willingness to invest more into potential conflicts is likely to be greater than the intruder's.

Our results show that Gouldian and Long-tailed finches differ in their aggressive response to conspecific and heterospecific intruders. In particular, Long-tailed Finches are more intrinsically aggressive than Gouldian Finches and more aggressive toward heterospecific Gouldian Finches. The extent to which Long-tailed Finch aggressiveness will affect the fitness of Gouldian Finches is contingent on the frequency and strength of interference competition between these species (Goss-Custard and Dit Durell 1988, Rands et al. 2006). Nest sites used by these two competing species overlap significantly, with the specialized nest-site requirements of Gouldian Finches included within the Long-tailed Finch's much broader nest-site characteristics (Brazill-Boast et al. 2010). Consequently, in addition to general declines in cavity-bearing trees throughout Australia's northern savannas (Williams et al. 1999, Lehmann et al. 2008), suitable nest cavities for Gouldian Finches are highly limited in the environment (Brazill-Boast et al. 2010), leading to severe intra- and interspecific competition for access to nest sites (Brazill-Boast et al. 2011). As seen in other studies that implicated interspecific aggression over nest sites as the cause of population declines (e.g., Bennett 1990, Kerpez and Smith 1990, Ellis and Good 2006), interspecific competition from the aggressive and ubiquitous Long-tailed Finch may be contributing to the recent population declines, or at least the lack of recovery, of the endangered Gouldian Finch. Further studies are needed to uncover the effects of behavioral asymmetries in aggression on the fitness and population dynamics of these competing species.

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