

Short communication

Competition for resources mediated by intrinsic social dominance in sympatric finches

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Gouldian *Erythrura gouldiae* and Long-tailed Finches *Poephila acuticauda* are morphologically and ecologically similar sympatric species, for which social dominance relationships are likely to determine access to critical limiting resources. Building on previous research showing that Long-tailed Finches dominate competition for nest-sites, I staged dyadic contests for food between the two species in captivity in order to test social dominance dynamics under controlled conditions. Long-tailed Finches were likely to dominate interactions with Gouldian Finches and expressed higher levels of aggression while competing for access to food. These results suggest a stable dominance relationship between the two species which could be affecting Gouldian Finches' access to food resources in the wild, potentially constraining their ability to recover from recent population declines.

Keywords: aggression, *Erythrura gouldiae*, Gouldian Finch, interspecific competition, Long-tailed Finch, *Poephila acuticauda*.

Social dominance relationships among individuals are crucial to the outcome of direct competition for resources, which will in turn strongly influence variation in reproduction and survival. Empirical studies have demonstrated the effects of social dominance on interspecific interference competition in a variety of taxa, including reptiles (e.g. Langkilde & Shine 2007), mammals (e.g. Tannerfeldt *et al.* 2002), fish (e.g. Berec *et al.* 2006) and birds (e.g. Cresswell 1997, Wiebe 2003). When resources are under direct competition, social

dominance relationships (generally predicted by body size; Caldwell & Dingle 1979, Persson 1985) are more likely to affect the relative fitness of competitors. Consequently, it is rare to observe two species simultaneously exhibiting complete (or near complete) niche overlap for such a resource, as well as behavioural dominance asymmetry, because the subordinate species should be competitively excluded (Armstrong & McGehee 1980).

The Gouldian Finch *Erythrura gouldiae* and the Long-tailed Finch *Poephila acuticauda* are sympatric estrildids endemic to the tropical savannas of northern Australia. The two species have similar ecology, specifically exhibiting a significant overlap in diet (Dostine & Franklin 2002) and nest-site requirements (Brazill-Boast *et al.* 2010). There is strong interspecific competition for nest-sites, in which Long-tailed Finches dominate, resulting in relatively greater fitness costs to Gouldian Finches (Brazill-Boast *et al.* 2011). Little is known, however, about competition over access to food, despite the fact that both species rely on the same grasses (*Sarga* species; Dostine & Franklin 2002), feed in mixed flocks (Woinarski & Tidemann 1992) and that food availability has been cited as the most likely cause of the decline of Gouldian Finch (Crowley & Garnett 1999, Franklin *et al.* 2005).

To test the effects of interspecific competition for access to critical food resources on Gouldian Finches, I performed controlled experiments using captive birds using a standard method of staged dyadic contests that has previously been used to demonstrate dominance relationships between several species, including Gouldian Finches (Pryke & Griffith 2006). Similar studies have also shown that social dominance behaviour in captivity reflects behaviour in the wild (Herborn *et al.* 2010).

METHODS

Subjects and housing

Gouldian Finches were black and red morph individuals from a large captive-bred colony (effective population size > 1000). Long-tailed Finches were all wild-type, captive-bred and sourced from multiple different breeders with similar effective population sizes. All individuals of both species were under 2 years old and were raised in single-species groups, and so were naïve to heterospecifics.

Birds were housed indoors for 4 months before experiments began, in single species/sex cages (1.2 m³) which were visually but not acoustically isolated from each other. All birds were provided with daily fresh-sprouted seed mix, as well as *ad libitum* dry seed mix, cuttlebone and water. Long-tailed Finches were supplemented daily with fly larvae, a preferred protein source, to mirror their diet in the wild (Dostine & Franklin 2002).

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Morphological measurements

Mass (0.1 g) and tarsus length (0.01 mm) were measured for all experimental birds following testing, as well as for a sample of wild birds for comparison. These data were collected from sympatric populations of Gouldian Finches and Long-tailed Finches caught in the East Kimberley region of Western Australia (15°34'S, 128°09'E) in March–June 2008 (see Table 1 for sample sizes). Both metrics were used to compare body weight as well as skeletal size.

Dyadic contests

Contests were staged in an isolated, wire mesh cage (850 × 750 × 450 mm) containing two perches positioned on opposite sides at a height of 200 mm, together with a small dish (35 mm) for holding fresh sprouted seed that was secured to the base of the cage in the centre, such that only one bird could feed at a time. The wire cage base was suspended above a tray to prevent access to spilled seed. For each contest, one individual of each species, matched for sex and unfed for 12 h, was randomly selected (from among those not tested) and both birds were released simultaneously into the test cage. Birds remained in the test cage for 32 min (2 min acclimatization, 30 min observation) and were recorded via a video camera placed 1 m from the cage front. All testing took place from September to November 2008, following breeding and moult for both species. In total, 73 different individual Gouldian Finches (43 male, 30 female; 37 black, 36 red) and 73 Long-tailed Finches (43 male, 30 female) participated in dyadic contests over 11 days.

Scoring behaviour

For each interaction during a contest, the 'dominant' individual was identified as either the individual expressing 'aggressive' behaviour or the opponent of the

individual expressing 'submissive' behaviour. Aggressive behaviours included displacements (one individual forces the other to move position), bill fencing/pecking and direct contact, and submissive behaviour was fleeing in response to the opponent's approach. When an interaction involved mutually aggressive behaviours (< 2%) neither individual was identified as dominant. The total time spent by each individual dominating access to the food dish in a trial was recorded.

Categorical win/loss/tie scores were assigned for a contest as follows: an individual won (and the opponent lost) if they were dominant in $\geq 80\%$ of interactions in a contest, or (if this condition was not met) if they dominated the food for $\geq 80\%$ of the total time. If neither of these conditions was met, the contest was defined as a tie. Contests involving no feeding or interactions were removed from subsequent analyses. No individual was used more than once in contests included for analysis.

Statistical analysis

Contest win/loss outcomes (tied contests excluded) were modelled using a binary regression with a logit link function. Each trial constituted a replicate, and Gouldian Finch/Long-tailed Finch win was the binary response (1 and 0, respectively).

Displacement frequency was analysed using a negative binomial regression, and distribution of time spent feeding was categorized into three levels (0, 0–9, 9–29 min; categories represent approximately equal frequencies), then analysed with a multinomial logistic regression. Both of these models treated individuals as independent replicates with body size indices, sex and Gouldian Finch morph as explanatory variables, and contest as a random factor.

The logistic regression model was analysed using LOGXACT 8 (Cytel Inc. 2007, Cambridge, MA, USA); all other models used SPSS 16.0 (SPSS Inc. 2007, Chicago, USA).

RESULTS

Morphology

In the experimental populations, Gouldian Finches were 4.4% heavier than Long-tailed Finches, and Long-tailed Finches had 7.4% longer tarsi (Table 1). These differences were qualitatively similar to those found in wild sympatric populations (Table 1).

Dyadic contests

Of the 73 staged dyadic contests, 19 involved no interactions or feeding, and were excluded from subsequent analyses. No morphological variables significantly

Table 1. Standard morphometrics (mean \pm sd) for captive and wild Gouldian and Long-tailed Finch populations. Sample sizes for captive: $n_{GF} = 73$, $n_{LTF} = 64$, for wild: $n_{GF} = 178$, $n_{LTF} = 158$. Means were compared using independent sample *t*-tests.

	Gouldian	Long-tailed	<i>P</i> -value
Captive			
mass (g)	16.2 \pm 1.0	15.5 \pm 1.3	0.01
tarsus (mm)	13.8 \pm 1.3	14.9 \pm 1.1	<0.01
Wild			
mass (g)	16.0 \pm 1.2	14.3 \pm 1.0	<0.01
tarsus (mm)	14.4 \pm 0.6	15.1 \pm 0.5	<0.01

predicted an individual's likelihood of interaction. A further six contests were defined as a tie, and removed from the win/loss contest model. Interactions occurred at an overall frequency of 1.43 ± 0.29 (mean \pm se) per contest and birds spent 10.53 ± 1.30 min feeding. Of the 48 contests with a clear result, 41 were won by Long-tailed Finches and seven by Gouldian Finches (odds ratio = 0.17, $\chi^2_1 = 24.08$, $P < 0.001$). Species was the only significant single predictor of contest outcome (odds ratio = 0.15, $\chi^2_6 = 26.40$, $P < 0.001$; model likelihood = 27.68, $P < 0.001$). When tarsus length was included in a model with species, then both variables (longer tarsus = more successful) were significant predictors, and the species odds ratio increased to 0.22 (Table 2), meaning that tarsus length explained just 3.2% (1.3 contests) of the variation in contest outcome.

Species was the only variable to predict dominance significantly in individual interactions (Table 3), with Long-tailed Finches expressing more aggressive behaviours than Gouldian Finches (Fig. 1). Similarly, species was the only significant predictor of time spent feeding, with Long-tailed Finches spending more time feeding than Gouldian Finches ($\chi^2_6 = 5.38$, $P = 0.020$). This effect discriminated only the 0 and 0–9 min categories, and not the 0–9 or 9–29 min categories ($\chi^2_6 = 2.40$, $P = 0.121$). In effect, this meant that the species differed in their likelihood to feed, with 40% (19) of Gouldian Finches feeding, compared with 69% (33) of Long-tailed Finches.

DISCUSSION

In staged dyadic contests over limited food in a controlled environment, Long-tailed Finches were six times more likely to win than were Gouldian Finches, exhibited more aggressive behaviour, dominated significantly

Table 2. Binary regression (response = Gouldian/Long-tailed Finch win) for the model predicting contest outcome. Model likelihood ratio = 28.46, $P < 0.001$, $n = 48$.

	Odds ratio*	95% confidence		P -value†
		lower	upper	
Constant (species)	0.222	0.000	0.603	0.002
Sex	0.385	0.000	1.030	0.057
Morph	0.558	0.000	2.392	0.429
Tarsus (mm)	0.065	0.002	0.562	0.004

*For the constant term, this is the predicted likelihood of a Gouldian Finch winning a contest. For the remaining terms, it predicts by what factor this win likelihood will change with one unit change in the term.

† P -values are calculated directly, therefore no test statistic is required.

more interactions, had greater access to food and fed more. These findings indicate a consistent asymmetry in the social dominance relationship between these two species, as also exhibited in competition for nest-sites (Brazill-Boast *et al.* 2011). Because the experimental design controlled for factors such as resource quality, resident advantage and heterospecific experience, relative dominance in these species appears to be intrinsic rather than context-dependent.

The Gouldian Finches used in the experiments were heavier than the Long-tailed Finches and had shorter tarsi, qualitatively reflecting differences found in wild populations. Relative tarsus size had a very small effect on contest outcome, and relative mass had no effect. These findings contrast with the majority of published studies on interspecific competition across diverse taxa, perhaps because the size differential between Gouldian Finches and Long-tailed Finches is not sufficiently large to mediate social dominance (e.g. Caldwell & Dingle 1979 reported a 10% threshold). The sex or head-colour morph (for Gouldian Finches) of an individual also failed to predict the outcome of interactions. Thus, the

Table 3. Results of the negative binomial regression predicting frequency of dominating interactions during a contest. Model $\chi^2 = 14.41$, $P = 0.013$, $n = 48$.

	IRR*	se	χ^2	P -value
Species	0.134	0.090	8.94	0.003
Sex	1.378	0.567	0.61	0.436
Morph	1.140	0.438	0.12	0.732
Mass	0.969	0.196	0.02	0.878
Tarsus	1.001	0.220	0.00	0.998

*Incident rate ratio: the predicted relative frequency of agonistic attacks comparing categories within the term to the reference category. Values close to 1 indicate term has negligible effect. Reference categories: species = Gouldian Finch, sex = F, morph = black-headed (i.e. Gouldian Finches are predicted to dominate at $0.134 \times$ the rate of Long-tailed Finches).

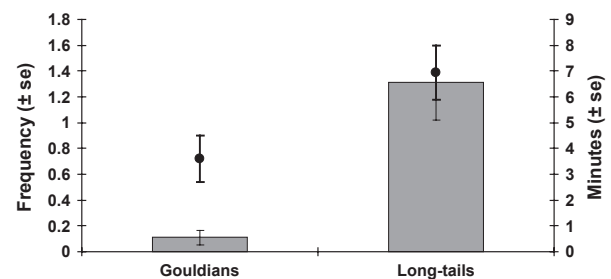


Figure 1. Mean (\pm se) frequency of aggressive behaviours (columns) and mean (\pm se) amount of time spent feeding (points) for Gouldian Finches and Long-tailed Finches in dyadic contests.

dominance relationship between these species appears to be mediated by behavioural, not morphological, differences. Either Long-tailed Finches are intrinsically more aggressive, or Gouldian Finches are responding to a dominance signal from Long-tailed Finches, or both. My findings are more consistent with the first: Long-tailed Finches tended to express aggressive behaviour more frequently. In almost every interaction, an aggressive and a submissive individual could be clearly identified, suggesting that most pair-wise dominance relationships were stable and clearly signalled to both contestants.

The efficacy of using staged contests in captivity to test relative behavioural dominance among birds has been demonstrated in many species (e.g. Pryke *et al.* 2002, Paz-y-miño *et al.* 2004), including Gouldian Finches (Pryke & Griffith 2006, Pryke 2007). Furthermore, the dynamics of dominance relationships in these captive studies reflect those observed in free-living populations of the same species, often predicting variation in individual fitness (e.g. Pryke & Andersson 2003). Although such studies have generally focused on intra-specific relationships, there is evidence that species-specific tendencies for aggressive behaviour can explain relative ecological success (Pintor *et al.* 2009). This has already been demonstrated in this system, via relative access to nest-sites and relative fitness effects of nest-site interference (Brazill-Boast *et al.* 2011).

If the social dominance dynamics exhibited by this study were to occur in the wild, then Gouldian Finch access to food and other resources may be reduced in the presence of Long-tailed Finches. This competitive asymmetry is likely to be compounded by the broader dietary niche of Long-tailed Finches (Gouldian Finches are unable to resource-shift to avoid competition; Palmer 2003), which may explain the generally higher densities of Long-tailed Finches than Gouldian Finches (e.g. Woinarski & Tidemann 1992). The extent to which social dominance of Long-tailed Finches affects the relative fitness of Gouldian Finches will depend on resource availability and frequency of direct competition. The availability of seeding grasses required by Gouldian Finches through the year is an important limiting factor for populations of several granivorous birds (Franklin 1999) and has been implicated in the decline of Gouldian Finch (Crowley & Garnett 1999). The processes driving reduction in seed availability (e.g. inappropriate fire regimes and the dominance of annual grasses) continue to act across the landscape (Franklin *et al.* 2005) and their effects on Gouldian Finches are likely to be exacerbated by the social dominance asymmetry reported here. How interspecific competition affects Gouldian Finch population dynamics remains unclear and requires large-scale, longitudinal research, but any constraint on access to resources for remaining populations can only inhibit the species' recovery.

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