

Predictors of aggressive response towards simulated intruders depend on context and sex in Crimson Finches (*Neochmia phaeton*)



Catherine Mary Young^{a,*}, Kristal Elaine Cain^{a,b}, Nina Svedin^a,
Patricia Ruth Yvonne Backwell^a, Sarah Rosalind Pryke^a

^a The Australian National University, Division of Ecology, Evolution and Genetic, Research School of Biology, Building 44 Daley Road, Acton, Canberra, ACT 2601, Australia

^b University of Auckland, School of Biological Sciences, Auckland 1010, New Zealand

ARTICLE INFO

Article history:

Received 26 August 2016
Received in revised form 27 January 2017
Accepted 27 January 2017
Available online 1 February 2017

Keywords:

Aggression
Plasticity
Crimson Finch
Sex roles
Nest defence

ABSTRACT

Quantifying differences in aggressive behaviour across contexts can be useful in developing an understanding of life histories and breeding systems, as well as the relative costs and benefits of such behaviour. We investigated whether age, relative body size and colouration, sex, and breeding stage influenced levels of aggressive behaviour in two contexts, towards conspecific and heterospecific intruders (mounts) around active nests of group living Crimson Finches (*Neochmia phaeton*). We found that when responding to a conspecific mount, relative body size, and age were important in predicting the aggressive response of males toward a conspecific, with older males and those close in size to their opponent showing a higher aggressive response. On the other hand, factors relating to female aggression were not as clear. In contrast, response to a heterospecific mount was unrelated to age, colour or size in either sex. Additionally, although birds were equally aggressive to conspecific and heterospecific mount types, we found no evidence that individuals are consistent in their level of aggression across these contexts. This suggests that aggressive behaviour in Crimson Finches is at least partially plastic and that individuals may be capable of assessing and responding to situations independently.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Aggressive behaviour has been well studied in many species across a variety of social contexts due to its conspicuous nature and potentially high costs (e.g. dominance; Rohwer, 1975, resource defence; Garcia and Arroyo, 2002, competition for mates; Hagelin, 2002, territoriality; and behavioural syndromes; Sih et al., 2004a). The costs and benefits of aggression, and thus the optimal level of aggression can be influenced by internal and external factors such as age, sex, class of competitors (conspecific or heterospecific), and previous experience as winners or losers, of aggressive encounters (e.g. Fedy and Stutchbury, 2005; Edler and Friedl, 2010). By examining differences in aggressive behaviour, we can develop a better understanding of the relative costs/benefits and gain insight into

the evolution and maintenance of species life histories and breeding systems.

For example, in conspecific territory or nest-site interactions, if males are more abundant than females they are often also found to be more aggressive in defence of their mating position (Fedy and Stutchbury, 2005; Senar and Domènech, 2011). However, females may also show high aggression towards male intruders if females are the primary territory defenders (Illes and Yunes-Jimenez, 2009), or the presence of another male decreases paternity certainty, leading to reduced paternal investment by the resident male (Westneat and Stewart, 2003). Sex specific aggression towards intruders is also common; males often defending more vigorously against male intruders and females against female intruders (Freed, 1987; Cain et al., 2011; Cain and Langmore, 2015). Additionally, reproductive context such as nesting stage (nest building, incubation or nestling feeding), brood value (nesting stage or clutch size), and date may influence aggression around the nest (e.g. Margalida and Bertran, 2005; Jukkala and Piper, 2015; Cain and Langmore, 2015).

Many types of behaviours show limited plasticity, meaning an individual's responses across contexts are not always independent;

* Corresponding author. Tel.: +61 2 6125 1019.

E-mail addresses: catherinemaryyoung@gmail.com (C.M. Young), kristalcain@gmail.com (K.E. Cain), nina.svedin@anu.edu.au (N. Svedin), pat.backwell@anu.edu.au (P.R.Y. Backwell), sarah.pryke@anu.edu.au (S.R. Pryke).

i.e. a behavioural syndrome (Sih et al., 2004a,b; Bell et al., 2009). This can mean for example, that individual display similar levels of aggression regardless if it is in the context of a conspecific competitor or heterospecific intruder. However, while more aggressive individuals may do well in competitive situations, aggression may be costly in other contexts such as in the presence of a predator (Sih et al., 2004b; Bell, 2007). Consequently, costs in terms of time and energy invested (Logue et al., 2011) as well as the added costs associated with regulators of aggressive behaviour (e.g. testosterone, Soma, 2006) and behavioural trade-offs (Duckworth, 2006), might exceed the benefits gained from the interaction (Sih et al., 2004a,b). Alternatively, different forms of aggression may be decoupled, in which case individual levels of aggression across contexts would be uncorrelated and vary according to context, e.g. conspecific or heterospecific intruder (Sih et al., 2004a). Aggression in reproductive contexts is often mediated by testosterone for both sexes (McGlothlin et al., 2007; Cain and Ketterson, 2012). However, in many tropical birds the testosterone-aggression link appears to be weaker (Hau, 2000; Apfelbeck and Goymann, 2011) which may allow different forms of aggression to be mediated by separate mechanisms.

Because aggressive behaviour is costly in terms of time, energy and risk of injury, individuals may mediate the potential risks by adjusting levels of aggression according to context (Brunton et al., 2008). Logue et al. (2011) suggested that the benefits of aggressive behaviour depend on the extent to which those behaviours influence the outcome of a contest. For example, if relative body size is important in winning aggressive interactions, individuals who are unlikely to win due to their smaller size, would benefit from curtailing displays early (Sih et al., 2004b). Consequently, when assessing variation in aggression we need to take into account the characteristics of both contestants and the way in which they interact with each other (i.e. mutual assessment model, Arnott and Elwood, 2009). Body size is often considered to be an honest indicator of quality because it is difficult to fake (Maynard-Smith and Harper, 1988; Taylor et al., 2000). Honest signals allow competitors to assess each other from afar and determine dominance without incurring the costs of direct confrontation (e.g. physical injury; status signaling hypothesis – Rohwer, 1975; reviewed in Santos et al., 2011). For example, Hagelin (2002) found that body size in two species of quail (*Callipepla gambelii* and *C. squamata*) was related to dominance in paired contests. The same study found that in contests, larger males did not need to engage in aggressive behaviour as often as small birds, in order to win contests.

Certain plumage colours have also been suggested to be honest signals of dominance or fighting ability, and may influence the behaviour observed between competitors (Dawkins and Krebs, 1978; Senar, 2006). In particular, red colouration, created from carotenoid pigments, has been found to be a signal of aggression and dominance in many species (Brush, 1981; Pryke, 2009). The link between plumage carotenoids and diet (reviewed in Olson and Owens, 2005) suggests that carotenoid-based plumage colouration may also be an honest indicator of individual quality (Hill, 2006). Consequently, differences in individual colouration (relative to an opponent) may even be more important than absolute colour to contest outcome and should be taken into consideration in the context of each encounter (Pryke et al., 2001; Young et al., 2016).

In a previous study, we investigated the role of both plumage colouration and body condition as predictors of male-male interactions and contest outcome in a group living passerine, the Crimson Finch (*Neochmia phaeton*, Young et al., 2016). We found that during the non-breeding season red plumage colouration was an important signal of dominance in staged dyadic contests in captive males. However, it is unclear whether the relationship between plumage traits and agonistic behaviour in the non-breeding season is retained in the breeding season or under natural conditions.

Crimson finches are well known for aggressive behaviour both in the wild and in captivity (Forshaw et al., 2012; Young et al., 2016). The function and mediation of this aggressive behaviour is still poorly understood. In the current study we investigated factors that may affect aggression towards both conspecific and heterospecific intruders around active nests in free-living Crimson Finches. Further, we investigated whether conspecific and heterospecific aggression are related, and whether there are differences in aggression levels between age and sex classes.

2. Methods

2.1. Study species and field site

Crimson Finches are a sexually dimorphic grass finch native to northern Australia (Higgins et al., 2006). They breed in colonies of four to forty individuals and are socially monogamous with a divorce rate of 2.9% within a breeding season and nil between seasons (Milenkaya et al., 2011). Pairs are not regarded as territorial but will defend the small area around their nest, this appears to be variable between individuals and populations but generally encompasses the 1–2 m directly around the nest (C. Young, pers. obs.). Fieldwork was conducted in the East Kimberley region of Western Australia (15°34'S, 128°09'E) between January and March 2014. All birds used in this study ($n=40$) were caught in mist nets and banded with a numbered metal band from the Australian Bird and Bat Banding Scheme as well as a unique combination of three colour bands for individual identification in the field. Birds were aged as 'young' if they were in their first breeding season or 'old' if they were at least in their second breeding season. Young birds were either known from the previous breeding season or distinguished by the presence of juvenile primary covert feathers (described in Milenkaya et al., 2011). Plumage colour measurements and morphometrics (tarsus, wing length, bill length, depth and mass) were taken at the time of capture. Tarsus length (to 0.1 mm) was subsequently used as an indicator of skeletal size, hereafter referred to as body size (Freeman and Jackson, 1990). At all nests, the sex and age of the focal bird, brood size and nesting stage (eggs, young nestlings [<9 days] or old nestlings [>10 days]) were also recorded.

Plumage colouration of both mounts and wild birds was quantified using a Jaz spectral sensing suite (Ocean Optics, Dunedin USA) with illumination from a xenon Ocean Optics PX-2 light source (Ocean Optics, Dunedin USA) and a fibreoptic probe with a 4 mm measuring diameter. The probe was fitted with a 1 cm long tip to standardise the distance between the plumage and the probe. Measurements were taken for 18 males, 13 females and all Crimson Finch mounts (see below). The integration time was set to 40 milliseconds and boxcar to 10. All measurements were taken relative to dark and white standards (WS-2), which were scanned immediately before each individual was measured. To get a good representation of overall red colour, measurements were taken from the face, back, rump and chest. Chest measurements were only taken from males as Crimson Finches are sexually dimorphic in colour and only males have a red chest (see Young et al., 2016). Three measurements were taken from the centre of each of the four areas and averaged for each individual between wavelengths of 320 and 700 nm (the visual range of most birds, Bennett and Théry, 2007).

2.2. Mount presentations

At active nests, free-living Crimson Finches were presented with two taxodermic mounts in random order on different days: one conspecific competitor (male Crimson Finch), and one heterospecific non-competitor, a Gouldian Finch (*Erythrura gouldiae*);

as Gouldian finches are colour polymorphic and dichromatic, we used black-head female mounts. Mounts were captive bred birds that had died of natural causes, and were subsequently freeze-dried sitting in a natural position on a dowel perch (three Crimson Finches and four Gouldian Finches). Due to high quality diet of captive birds, our Crimson Finch mounts were on average bigger than the wild birds tested. However, the largest mount was still within the natural size range of the wild population (tarsus length range; wild population; males 16.51–19.05 mm, females 16.10–18.83 (C. Young, unpublished data), focal birds; males 16.51–18.30 mm, females 16.34–18.45 mm, mounts 17.8–19.04 mm). Although Crimson Finches are sexually size dimorphic, with males being on average larger, there is almost complete overlap in tarsus length ranges (Milenkaya et al., 2011). Each mount was assigned a number and randomly selected for each experiment. The Gouldian Finch was chosen as the non-competitor because of their overlap in distribution and ecology and because they are similar size and shape as Crimson Finches, but are not known to be competitors for either food or nesting sites (although both are seed eaters, they specialise on separate species in different microhabitats). All mounts were positioned while the nest owners were away, level with the nest height and within one metre of the nest. The order of conspecific versus heterospecific mount was randomised with 1–4 days between presentations, but within the same breeding stage. Breeding stage was classified as eggs, young nestlings (<9 days,) or old nestlings (>10 days); Crimson Finches fledge at ~21 days old. Mounts were presented to twenty-four males and thirteen females at a total of twenty-four nests in six colonies. However, some individuals were removed from some analyses as a number of colour measurements were not available due to equipment malfunction (three females and six males). This resulted in complete data for thirteen females and eighteen males in response to the conspecific mount, and ten females and eighteen males in response to the heterospecific mount. Presentations were all made before 9:30 a.m. to minimise the effects of time-of-day and high daytime temperatures. The observer was blind to body size and redness scores during the observation.

Behavioural observations (e.g. vocalisations, physical aggression) towards the mount were recorded for 10 min, starting when the bird was within the observers' visual range of the nest (approximately 15 m). Each bird was given an aggression score between 1 and 6 (following e.g. Duckworth, 2006): (1) no aggressive response, ignores the mount and does not vocalise, (2) marginal aggressive response, high latency to approach (>5 min), few quiet vocalisations, no physical contact with mount, (3) modest aggressive response, slight delay in approach (>2 min), moderate vocalisations and close approach distance (1–2 m), (4) moderate aggressive response, minimal delay in approach (~1 min), high levels of vocalisations and close approach, some physical contact (pecking), (5) high aggressive response, approached quickly (<30 s) with nearly constant, loud vocalisations, lots of physical contact (removing feathers from mount), (6) extreme aggressive response, approached quickly (<30 s) with constant, loud vocalisations, extreme physical contact (mount damaged).

2.3. Analysis and statistics

We briefly describe colour analysis methods here, but see Young et al. (2016) for further details of parameters used. We applied the Vorobyev-Osorio model (Vorobyev and Osorio, 1998; Siddiqi et al., 2004) to the spectrometer measurements, which estimates the difference between two areas (red plumage against a neutral background – 30% grey) in units of discrimination threshold or “Just Noticeable Differences” (JND's, Vorobyev et al., 1998). This model was used to analyse both chromatic (hue) and achromatic (brightness) differences with an ultra-violet sensitive (UVS) model (Hart

et al., 2000; Endler and Mielke, 2005) taking into account photoreceptor noise (Vorobyev and Osorio, 1998; Osorio and Vorobyev, 2008, noise = neutral). To reduce the number of terms in the final model, we used a principal component analysis (PCA), to condense the spectral scores of the red plumage areas measured (face, back, rump and chest – chest for males only) for chromatic and achromatic measures. Separate models and principal component (PC) scores of colour, were created for males and females, as well as PCs of colour difference between focal birds and mounts (colour difference). Principal components analysis was conducted in JMP 11.0 while all other analyses were conducted in R (Maia et al., 2013, R Development Core Team, 2014). Colour models were run in the 'Pavo' package (Maia et al., 2013).

To determine which factors might influence aggressive behaviour in Crimson Finches in different social contexts, we used general linear models (GLM) with Poisson error and model averaging techniques (Burnham and Anderson, 2002). Prior to analysis we standardised variables using the package 'arm' (Gelman and Su, 2014) and checked for over dispersion prior to averaging (residual deviance was not greater than the degrees of freedom). All models are ranked according to goodness-of-fit to the data, based on Akaike information criterion corrected for small sample size (AICc; Grueber et al., 2011; Symonds and Moussalli, 2011). We calculated the differences in AICc (Δ AICc) between the best model (i.e. with the lowest AICc) and every other model, including the null model and averaged only the top models (Δ AICc < 2) using the package MuMIn (Bartońf, 2014). The relative importance of each variable in the top models was calculated by summing the weights of all models containing that variable. This is a representation of how each variable improves the model fit and estimates the probability that it is part of the best model (Symonds and Moussalli, 2011).

First, we analysed the influence of observer, brood size, nesting stage, presence of a partner and individual characteristics of the focal bird (age, colouration and relative size) on aggressive behaviour towards a conspecific mount. To test whether the reaction of the focal bird was dependent on the relative body size or relative ornamentation/colouration of the intruder to themselves, we used the differences in body size and colour measurements between the conspecific mount and the focal bird in analysis. Body size difference (from now on referred to as relative size) refers to how much bigger the mount was compared to the focal bird, while relative colour refers to if the focal bird was redder (chromatic) or brighter (achromatic) than the intruder. As red colouration has been shown to be a signal of aggression in Crimson Finches (Young et al., 2016) we also included the focal birds colour measurements (absolute colour). We followed the same analysis methodology with the heterospecific mount, using only absolute colour rather than relative colour, as the heterospecific mount lacked red plumage.

To look for relationships between age (categorical) and relative size or colouration (continuous) we used separate unpaired *t*-tests for males and females towards each mount. Pearson's correlations were used to examine the relationship between relative size and colouration in the same way. Fractional degrees of freedom are displayed in these results as obtained by default from Welch's *t*-test conducted in R (R Development Core Team, 2014). Welch's test does not assume that the two samples have equal variance, instead estimating the variance and adjusting the degrees of freedom accordingly. A GLM with Poisson error was used to investigate the relationship between aggression, sex and mount type, with aggression score as the response variable. A Spearman's rank-order correlation was used for males and females to investigate consistency in aggression scores within individuals towards the conspecific and heterospecific mounts.

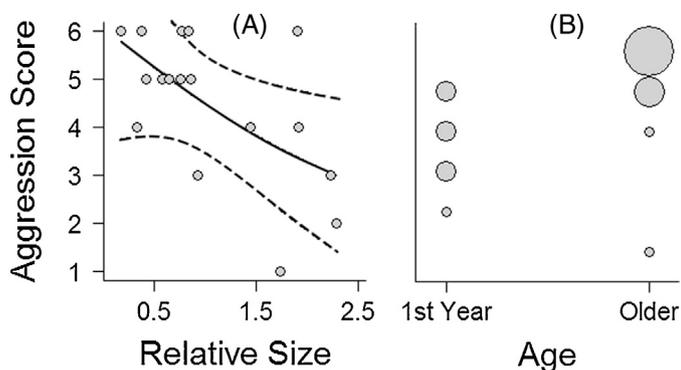


Fig. 1. The relationship between male aggression towards a conspecific mount and (a) relative size (mm) of the mount to focal bird (the line indicates values predicted from GLM model and 95% confidence intervals); (b) focal male age, presented as scatter plots of raw data. The size of the data point is relative to how many individuals it represents ($n = 18$).

3. Results

3.1. Principal component analysis of plumage coloration

The principal components analysis (PCA) of red plumage areas (face, back, rump and, for males only, chest) produced PCs for both chromatic (hue) and achromatic (brightness) measures in males and females (Table 1). Only PCs with an eigenvalue >1 were retained for analysis. The male PCA (differences in colour between the focal bird and the conspecific mount) resulted in three PCs, two for chromatic and one for achromatic colour, explaining 76.4% and 56% of the variance respectively. The female PCA for relative colour, resulted in two PCs, one chromatic (52.7%) and one achromatic (56.6%). The analysis of these absolute colour scores resulted in four PC scores with an eigenvalue of >1 for both males and females, two chromatic and two achromatic for each sex (male chromatic; 67.6%, achromatic; 77.2%, female chromatic; 91.5%, achromatic 79.5%).

With the adult birds there were no detectable age differences in body size (unpaired t -test, males; $t(9.1) = 0.2$, $p = 0.81$, females; $t(2.8) = -0.3$, $p = 0.77$), or colour (chromatic colour; unpaired t -test, males PC1; $t(14.2) = 0.5$, $p = 0.60$, PC2; $t(13.6) = -0.9$, $p = 0.36$, females PC1; $t(3.1) = 0.2$, $p = 0.88$, PC2; $t(5.8) = 0.8$, $p = 0.47$, achromatic colour; t -test, males; $t(6.8) = 0.5$, $p = 0.60$, females; $t(2.5) = -0.1$, $p = 0.89$). And there was no correlation between body size and colour in either sex (Pearson's Correlation; chromatic colour; males PC1; $r = 0.23$, $p = 0.36$, PC2; $r = -0.43$, $p = 0.08$, females PC1; $r = 0.35$, $p = 0.32$, PC2; $r = 0.56$, $p = 0.09$, achromatic colour males; $r = -0.43$, $p = 0.09$, females; $r = -0.31$, $p = 0.38$).

3.2. Aggression towards conspecifics

For Crimson Finch males ($n = 18$), the best predictor of male aggressive behaviour towards the conspecific mount was relative size (Table 2a). Males were less aggressive when the size difference was large, i.e. when the focal male was small relative to the mount (Fig. 1a). Age was also shown to be important, appearing in two of the top four models (Table 2); older birds were more aggressive than first year birds (Fig. 1b). However, all models containing age fell below the null model in $\Delta AICc$ (Table 2a) and this variable was given an importance score of just 0.32 (Table 3) and so should be interpreted with caution. We found no evidence to suggest that relative chromatic or achromatic colour scores influenced aggressive behaviour of the focal birds towards the mounts and found no effect of nestling stage, brood size, presence of a partner, or focal male's absolute body size on male aggression scores (model selection Table S1a).

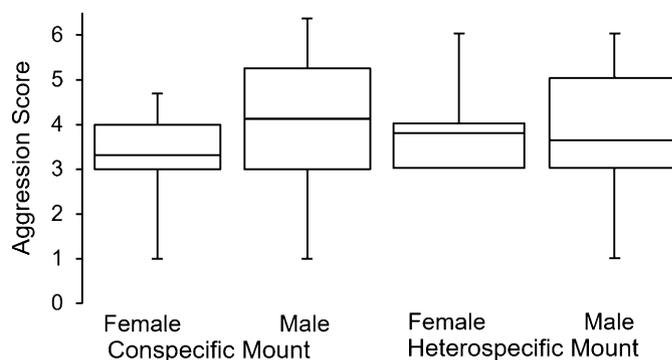


Fig. 2. Tukey's box plots displaying similarities between the aggressive behaviour of male and female Crimson Finches towards conspecific (male = 18, female = 13) and heterospecific mounts (male = 18, female = 10).

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2017.01.017>.

For female Crimson Finches ($n = 13$), there was weak evidence that both absolute achromatic and chromatic colour were related to aggression (Table 2a). The absolute achromatic colour (brightness) of the focal bird was positively related to aggression scores, while absolute chromatic (hue) scores were negatively related. However, the importance scores for these variables were low (achromatic 0.21, chromatic 0.25; Table 3) and the null model was found to be the best fitting model based on $\Delta AICc$'s. None of the remaining variables measured (age, relative achromatic and chromatic colour, observer ID, presence of a partner, body size, relative size, nesting stage or brood size) had an influence on the observed aggression scores as none appeared in the top models ($\Delta AICc < 2$, model selection Table S1b).

3.3. Aggression towards heterospecifics

We found no relationship between aggression towards a heterospecific mount and any of the variables measured (focal bird age, observer ID, chromatic/achromatic colour, presence of a partner, body size, relative size, nestling stage or brood size; model selection Table S1c and d); for both sexes (males $n = 18$; females $n = 10$) the null model was found to be the best fitting model by $>2 \Delta AICc$'s (Table 2b).

3.4. Sex differences and aggression across contexts

Aggression towards mounts was not influenced by either mount type (conspecific or heterospecific mount), sex of the focal bird or the interaction between the two ($n = 24$ males, 11 females, GLM (Wald test); mount type; estimate = 0.64, $p = 0.31$, sex; estimate = 0.85, $p = 0.12$, mount \times sex; estimate = -1.13 , $p = 0.14$). The range of aggression scores assigned to females (coefficient of variance; conspecific 0.35, heterospecific 0.2) were more limited than those assigned to males (coefficient of variance; conspecific 0.4, heterospecific 0.4, Fig. 2). We did not find any detectable consistency in aggression within individuals between intruder types (conspecific vs heterospecific mounts; Spearman's rank-order males; -0.23 , $p = 0.86$, females; -0.06 , $p = 0.57$, Fig. 3).

4. Discussion

We examined the aggressive response of male and female Crimson Finches towards conspecific and heterospecific intruders near the nest. We found male aggression towards conspecific intruders could be explained by their size relative to the intruder

Table 1

Results from principal components analysis for chromatic (hue) and achromatic (brightness) colour measures using a correlation matrix, including eigenvalue and percentage variance explained by each PC. Separate PC's are shown for males and females in relation to colour differences between focal birds and a conspecific intruder (relative colour) as well as their absolute colour. Only PCs with an eigenvalue >1 are shown as they were retained for analysis.

Relative colour	Face	Back	Rump	Chest	Eigen	Variance (%)
Males (n = 18)						
PC1 chromatic	-0.33	-0.08	0.62	0.70	1.65	41.4
PC2 chromatic	0.62	0.70	0.33	0.08	1.40	35.0
PC achromatic	0.41	0.47	0.55	0.55	2.24	56.0
Females (n = 13)						
PC chromatic	0.66	0.67	-0.33		1.58	52.7
PC achromatic	0.65	0.70	0.31		1.70	56.6
Absolute colour of focal bird						
Males (n = 18)						
PC1 chromatic	0.38	0.46	0.67	0.45	1.58	39.6
PC2 chromatic	0.64	0.33	-0.13	-0.68	1.11	27.7
PC1 achromatic	0.53	0.23	0.57	0.58	2.10	52.5
PC2 achromatic	-0.23	0.93	0.11	-0.27	1.00	24.7
Females (n = 10)						
PC1 chromatic	0.56	0.77	0.31		1.51	50.2
PC2 chromatic	-0.59	0.11	0.80		1.24	41.3
PC1 achromatic	0.73	0.62	-0.27		1.32	44.0
PC2 achromatic	-0.11	0.50	0.86		1.07	35.5

Table 2

Factors affecting the aggressive behaviour of Crimson Finch males (n = 18) and females (n = 13) towards (a) conspecific mounts (b) heterospecific mounts. Only models of $\Delta AICc < 2$ are presented here.

	Model	Variable	Estimate	Standardised coefficient	$\Delta AICc$	AICc weight
(a) Conspecific mount						
Males	1	SizeD	-0.44 ± 0.25	-1.71	0.00	0.38
	2	Null				0.29
	3	Age	-0.30 ± 0.24	-1.23	1.53	0.18
	4	SizeD + Age	-0.40 ± 0.25 -0.24 ± 0.24	-1.56 -0.99	1.99	0.14
Females	1	Null			0.00	0.55
	2	C2	-0.35 ± 0.31	-1.01	1.62	0.25
	3	A1	0.28 ± 0.30	0.93	1.98	0.21
(b) Heterospecific mount						
Males	1	Null			0.00	0.11
Females	1	Null			0.00	0.25

C2 = principal component (PC) values for the second PC of chromatic scores from red plumage; A1 = PC1 values for achromatic scores from red plumage areas; Size = body size (tarsus length); SizeD = difference in body size between focal bird and mount (relative size); Age = age of the focal bird (first year or 2+).

Table 3

Summary of model averaging for the predictors of aggressive behaviour in Crimson Finches towards conspecific mounts. Only models of $\Delta AICc < 2$ were included in model averaging. High relative importance indicates that the variable is more likely to be in the best fitting model.

	Variable	Estimate	Adjusted SE	Confidence interval	Relative importance
Males	Intercept	-1.48	0.13	-1.23, 1.73	
	Relative size	-0.43	0.28	-0.97, 0.12	0.52
	Age	-0.27	0.27	-0.79, 0.25	0.32
Females	Intercept	-1.21	0.15	-0.88, 1.55	
	Chromatic	-0.35	0.32	-1.05, 0.35	0.25
	Achromatic	-0.28	0.30	-0.38, 0.95	0.21

and their age. Female aggressive behaviour was influenced by plumage colouration, but the relationship was weak. None of the variables examined predicted aggression towards heterospecific intruders in either sex. Focal birds were equally aggressive to conspecific and heterospecific mounts. However, we found no links between aggression, and sex of the focal bird or context (conspecific/heterospecific), and no evidence of individual consistency in aggression across context.

4.1. Aggression towards conspecifics

Body size, relative to an opponent, is likely more important than absolute body size in aggressive contests where mutual assessment is used, as individuals are expected to be able to overpower only relatively smaller opponents (Arnott and Elwood, 2009; Logue

et al., 2011). In support of this hypothesis we found that male Crimson Finches showed higher levels of aggressive behaviour toward mounts that were a similar body size to themselves. Males that were smaller relative to the mount were less aggressive, meaning they showed a higher latency to approach, maintained some distance and were relatively quiet when body size disparity was large. In addition, we found evidence that older males showed higher levels of aggression than younger males (those in their first breeding season). The AICc values for the top four models were very close together and included the null model (see Table 2) meaning these effects are weak, however this is most likely due to the low sample size. There is currently no published evidence relating to age based dominance in Crimson Finches. However, age related dominance structures are well known in birds and have been recorded across many species, with older males commonly dominating younger

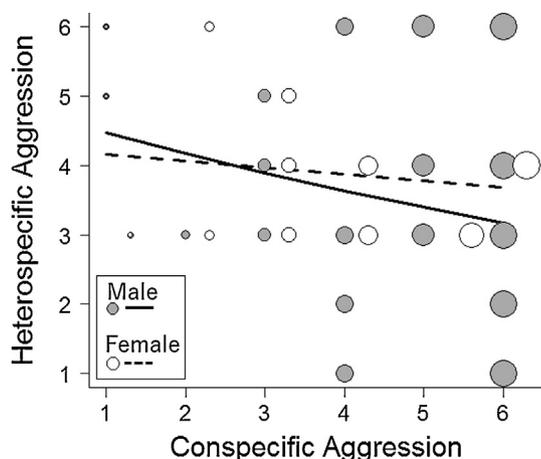


Fig. 3. Scatter plot demonstrating the lack of relationship in aggression across context for each sex. Overlapping points have been jittered for clarity. The grey circles and dashed line represent females while the black circles and solid line represent males. The lines represent predicted values from the model.

conspecifics (e.g. Enoksson, 1988; Edler and Friedl, 2010). The influence of prior fighting experience has been shown to have a large influence on contest outcome (e.g. Ratner, 1961; Beacham and Newman, 1987) and may further explain the higher levels of aggression observed in older birds. Because our mounts were reared in aviaries with unlimited food, they were on average larger than the focal birds. Thus we were unable to test whether the relationship between relative size and aggression persists when the focal bird is larger than the intruder.

Within female Crimson Finches we found some evidence that red plumage colouration (chromatic and achromatic) was an indicator of aggressive behaviour. Less bright and ‘redder’ individuals were shown to have higher levels of aggression. Female colour often indicates dominance or quality (e.g. Murphy et al., 2009; López-Ildiáquez et al., 2016). In particular, red plumage is considered a signal of dominance, for example Pryke (2007) found that in female Gouldian Finches, naturally red-headed females and naturally yellow-headed individuals manipulated to have red plumage dominated other colour morphs (yellow and black-headed). Nevertheless, caution is warranted as the top model was the null model, while the variables in the two models that followed (PC2 of chromatic colour (hue), $\Delta AICc$ 1.62 and PC1 of achromatic colour (brightness), $\Delta AICc$ 1.98), received very low importance scores in the model averaging (<0.30). The importance value gives an indication of how likely each variable is to appear in the best model. However, it is interesting to note that the only values that appeared in the top models were the female’s absolute colouration, not their colouration relative to the mounts. A number of studies have suggested that females ignore the traditional signals of fighting ability such as relative size and colouration (Draud et al., 2004; Elias et al., 2010). Instead, for females, resource value may be a stronger motivator for aggressive behaviour than physical traits and ornamentation of either themselves or their opponent (Dale and Slagsvold, 1995). For example, Elias et al. (2010) found that in *Phidippus clarus* jumping spiders, females rarely participated in displays and differences in resource valuation rather than size or weight predicted the outcome of contests, a pattern repeated in other species (see Draud et al., 2004; Arnott and Elwood, 2009).

Under the parental investment hypothesis (Trivers, 1972), aggression is predicted to increase with increasing brood value (e.g. the intensity of nest defence may be positively related to the number of offspring in the nest, their age and survival prospects (Regelmann and Curio, 1983; Redondo, 1989). However, if aggression near the nest is related to nest-site/territory or food-resource

defence, no change or even a negative trend in aggressive behaviour over the nesting period is predicted (Gowaty, 1981). Our results suggest that though Crimson Finches appear to be defending nest sites from competitors, they do not adjust the level of defence according to nest value. We found no relationship between nesting stage (eggs, young nestlings, old nestlings) or brood size and aggressive response to the conspecific mount for either sex. This result is in concordance with Casa (1985), who found no difference in aggression with nesting stage (incubation, hatching, nestlings) in closely related Zebra Finches (*Taeniopygia guttata*). Although we only tested birds at active nests, it is possible that Crimson Finch nest defence against conspecifics in these stages (eggs and chicks), is defence of the nest-site itself, rather than protection of offspring or paternity. We do not know if intraspecific brood parasitism occurs in this species, but nest usurpation through continued harassment was observed twice in the field during this study and has been recorded in aviculture. In addition, a recent study on Crimson Finch nest predation (Young et al., 2017) found that aspects of nest site choice had strong effects on nest success, strengthening the inference that nesting sites may be a valuable resource.

4.2. Aggression towards heterospecifics

Despite the fact that Crimson Finches and Gouldian Finches are not competitors for nest sites (Gouldians use hollow eucalypt branches rather than pandanas) and have a small overlap in diet (both are seed eaters but specialize on separate species in different microhabitats), both males and females responded strongly towards the heterospecific mounts, showing high levels of vocalisations, close physical proximity and physical attacks. Although the mounts represent a realistic bird, their lack of movement may influence the aggressive response of the focal birds and we should consider the fact that wild Gouldian Finches may fly away on seeing an approaching Crimson Finch. There is no apparent advantage for Crimson Finches in displaying high aggression towards Gouldian Finches. Instead, it is potentially costly in terms of energy spent, time taken from other activities (e.g. foraging, feeding nestlings or scanning for predators) and the potential for injury. Possibly there is, or has been, more competition between Crimson and Gouldian Finches for food or habitat, than we currently observe in the wild. Oriand and Willson (1964) proposed that aggression towards heterospecifics suggests that securing a limited resource has selected for the behaviour in the past, although this resource may not be limited in the present (e.g. food or water in times of severe drought). It has also been suggested that heterospecific territorial aggression is simply misdirected conspecific territorial aggression (Murray, 1971) for example where aggression is not plastic or only partially plastic behaviour.

Alternatively, high levels of heterospecific aggression might be advantageous in some cases. For instance, although in our study sites Gouldian Finches were never seen around the nests of Crimson Finches, individuals of another species, the Long-tailed Finch (*Poephila acuticauda*) are commonly observed near Crimson Finch nests and are generally aggressively chased off by nest owners (C.M. Young, pers. obs.). Long-tailed Finches will nest in cavities or open sites and are known to outcompete Gouldian Finches for nest sites (Brazill-Boast et al., 2011). Thus they may also represent a competitor to Crimson Finches. Similarly, many grassfinch species use the same materials for nest construction, and we have observed Crimson Finches taking nesting material from unoccupied nests, suggesting that this is a valuable resource. Thus, aggression towards heterospecific finches may be a generalised response to competition for nest-sites and nesting materials from any potential competitor. Additionally, it may be advantageous to deter any species from being near the nest if their presence could attract predators. Finally, unlike aggression towards the conspecific

mount, none of the measured variables was related to response score, suggesting this behaviour is mediated by different mechanisms and is not simply a maladaptive carryover of aggression towards conspecifics (Duckworth, 2006; Sih et al., 2004b).

4.3. Individual consistency and sex differences in aggression

In many species, males generally respond more aggressively towards intruders than females (Pryke, 2013). For example, in a study on White-bellied Antbirds (*Myrmeciza longipes*), Fedy and Stutchbury (2005) found that male birds responded more aggressively than females towards playbacks regardless of season and stimuli (male/female song), however that also found that females matched the aggression of males only in the resource-limited dry season. A number of other studies report sex-specific responses only to same sex intruders (e.g. Mays and Hopper, 2004; Cain et al., 2011), or greater female response (Illes and Yunes-Jimenez, 2009). In the current study, we found no difference in the average aggressive response between male and female Crimson Finches regardless of context (heterospecific vs conspecific intruder); females responded as aggressively as males to a conspecific (male) intruder. However, we did find a difference in the range of aggression scores, with males displaying a larger range of scores than females. This suggests there may be other factors at play in relation to sex specific aggressive behaviour. Additionally, as we did not present a female conspecific intruder we cannot rule out the possibility that sexes would respond differently in this context. Fedy and Stutchbury (2005) suggest that when mate switching is rare, territory defence against all intruders should be equally shared. This is consistent with Crimson Finch pairs in which divorce rates appear to be extremely low, both within and between seasons (Milenkaya et al., 2011). This finding adds weight to our suggestion that in Crimson Finches, aggression near the nest is likely to be predominantly related to nest site defence rather than protection of reproductive investment.

Behavioural syndromes suggest that an individual's response in one context may be tied to what it does in other situations (reviewed in Sih et al., 2004a,b). Although only a small number of studies have investigated aggression across context in birds, many have found consistency in aggressive behaviours (e.g. Duckworth, 2006; Cain et al., 2011). In contrast we found no evidence to support the idea that individual Crimson Finches are consistent in their aggressive behaviour in relation to intruder type, despite all birds tested in this study showing aggressive behaviour in some form towards both conspecific and heterospecific intruders. This suggests that Crimson Finch aggressive behaviour is at least partially plastic and adaptable depending on context.

In conclusion, we found that the aggressive response of wild Crimson Finches to intruders was related to both the sex of the focal bird and the type of intruder. While females were on average, as aggressive as males towards intruders, they also showed a smaller range of scores. Additionally, the different predictors of aggression shown for each sex, suggest there may be other non-sampled sex-specific mechanisms influencing behaviour. The role of sex in nest defence of tropical birds is poorly understood, as are the different factors that may mediate aggressive behaviour in females. Further, investigating aggression at the egg laying stage would draw additional insights into the function of aggressive behaviour in this species. Although all birds responded aggressively to both conspecific and heterospecific intruders, we found no evidence for consistency of aggressive behaviours within individuals. This suggests that although they may not be truly independent, aggression in these two contexts may be mediated by different mechanisms. We suggest that Crimson Finches may assess different situations and adjust their behaviour according to context.

Funding

This work was supported by an Australian Research Council Grant (SRP), an Australian Postgraduate Award (CMY) and a grant from The Australian Bird Study Association, Fund for Avian Research (CMY).

Acknowledgements

We thank Fiona Finch and Sophie Keats for help in the field as well as Save The Gouldian Fund for providing access to their field station. We are grateful to David Hamilton for comments on the manuscript, as well as Thomas Merklings and Liam Bailey for assistance with analysis and R software. We thank anonymous reviewers for their constructive and encouraging comments. All work was conducted under approval from the Australian National University's Animal Ethics Committee (application number A2012/55).

References

- Apfelbeck, B., Goymann, W., 2011. Ignoring the challenge? Male Black Redstarts (*Phoenicurus ochruros*) do not increase testosterone levels during territorial conflicts but they do so in response to gonadotropin-releasing hormone. *Proc. R. Soc. Lond. B* 278, 3233–3242.
- Arnott, G., Elwood, R.W., 2009. Assessment of fighting ability in animal contests. *Anim. Behav.* 77, 991–1004.
- Bartoň, K., 2014. MuMIn: Multi-model inference. R Package Version 1.10.5.
- Beacham, J.L., Newman, J.A., 1987. Social experience and the formation of dominance relationships in the pumpkinseed sunfish, *Lepomis gibbosus*. *Anim. Behav.* 35, 1560–1563.
- Bell, A.M., 2007. Future directions in behavioural syndromes research. *Proc. R. Soc. Lond. B* 274, 755–761.
- Bell, A.M., Hankison, S.J., Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis. *Anim. Behav.* 77, 771–783.
- Bennett, A.T.D., Théry, M., 2007. Avian color vision and coloration: multidisciplinary evolutionary biology. *Am. Nat.* 169, 1–6.
- Brazil-Boast, J., van Rooij, E., Pryke, S.R., Griffith, S.C., 2011. Interference from long-tailed finches constrains reproduction in the endangered Gouldian finch. *J. Anim. Ecol.* 80, 39–48.
- Brush, A., 1981. Carotenoids in wild and captive birds. In: Bauernfeind, J.C. (Ed.), *Carotenoids as Colorants and Vitamin A Precursors*. Academic Press, New York, pp. 539–562.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multi-Model Inference – A Practical Information-Theoretic Approach*, 2nd ed. Springer.
- Brunton F.D.H., Evans, B., Cope, T., Ji, W., 2008. A test of the dear enemy hypothesis in female New Zealand bellbirds (*Anthornis melanura*): female neighbors as threats. *Behav. Ecol.* 19, 791–798.
- Cain, K.E., Ketterson, E.D., 2012. Competitive females are successful females; phenotype, mechanism, and selection in a common songbird. *Behav. Ecol. Sociobiol.* 66, 241–252.
- Cain, K.E., Langmore, N.E., 2015. Female and male song rates across breeding stage: testing for sexual and nonsexual functions of female song. *Anim. Behav.* 109, 65–71.
- Cain, K.E., Rich, M.S., Ainsworth, K., Ketterson, E.D., 2011. Two sides of the same coin? Consistency in aggression to conspecifics and predators in a female songbird. *Ethology* 117, 786–795.
- Case, V.M., 1985. Breeding cycle aggression in domesticated zebra finches (*Poephila guttata*). *Aggressive Behav.* 12, 337–348.
- Dale, S., Slagsvold, T., 1995. Female contests for nest sites and mates in the pied flycatcher, *Ficedula hypoleuca*. *Ethology* 99, 209–222.
- Dawkins, R., Krebs, J.R., 1978. Animal signals: information or manipulation? In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*. Blackwell, Oxford, pp. 282–309.
- Draud, M., Macías-Ordóñez, R., Verga, J., Itzkowitz, M., 2004. Female and male Texas cichlids (*Herichthys cyanoguttatum*) do not fight by the same rules. *Behav. Ecol.* 15, 102–108.
- Duckworth, R., 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behav. Ecol.* 17, 1011–1019.
- Endler, J.A., Mielke, P.W., 2005. Comparing entire colour patterns as birds see them. *Biol. J. Linn. Soc.* 86, 405–431.
- Edler, A.U., Friedl, T.W.P., 2010. Plumage colouration, age, testosterone and dominance in male red bishops (*Euplectes orix*): a laboratory experiment. *Ethology* 116, 806–820.
- Elias, D.O., Botero, C.A., Andrade, M.C.B., Mason, A.C., Kasumovic, M.M., 2010. High resource valuation fuels “desperado” fighting tactics in female jumping spiders. *Behav. Ecol.* 21, 868–875.
- Enoksson, B., 1988. Age- and sex-related differences in dominance and foraging behaviour of nuthatches *Sitta europaea*. *Anim. Behav.* 36, 231–238.

- Fedy, B.C., Stutchbury, B.J.M., 2005. Territory defence in tropical birds: are females as aggressive as males? *Behav. Ecol. Sociobiol.* 58, 414–422.
- Forshaw, J.M., Shephard, M., Pridham, A., 2012. *Grassfinches of Australia*. CSIRO Publishing, Australia.
- Freed, L.A., 1987. The long-term pair bond of tropical house wrens: advantage or constraint? *Am. Nat.* 130, 507–525.
- Freeman, S., Jackson, W.M., 1990. Univariate metrics are not adequate to measure avian body size. *Auk* 107, 69–74.
- García, J.T., Arroyo, B.E., 2002. Intra- and interspecific agonistic behaviour in sympatric harriers during the breeding season. *Anim. Behav.* 64, 77–84.
- McGlothlin, J.W., Jawor, J.M., Ketterson, E.D., 2007. Natural variation in a testosterone-mediated trade-off between mating effort and parental effort. *Am. Nat.* 170, 864–875.
- Gelman, A., Su, Y., 2014. *arm: Data Analysis Using Regression and Multilevel/Hierarchical Models*. R Package Version 1.7-07.
- Gowaty, P.A., 1981. Aggression of breeding eastern bluebirds (*Sialia sialis*) toward their mates and models of intra- and interspecific intruders. *Anim. Behav.* 29, 1013–1027.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711.
- Hagelin, J.C., 2002. The kinds of traits involved in male-male competition: a comparison of plumage, behavior, and body size in quail. *Behav. Ecol.* 13, 32–41.
- Hart, N.S., Partridge, J.C., Bennett, A.T.D., 2000. Visual pigments, cone oil droplets and ocular media in four species of estrildid finch. *J. Comput. Physiol. A* 186, 681–694.
- Higgins, P.J., Peter, J.M., Cowling, S.J., 2006. *Handbook of Australian, New Zealand and Antarctic Birds*. Vol. 7: Boatbill to Starlings. Oxford University Press, Melbourne, Australia.
- Hill, G.E., 2006. Environmental regulation of ornamental coloration. In: Hill, G.E., McGraw, K. (Eds.), *Bird Coloration, Mechanisms and Measurements*, vol. 1. Harvard University Press, Cambridge, pp. 507–560.
- Illes, A.E., Yunes-Jimenez, L., 2009. A female songbird out-sings male conspecifics during simulated territorial intrusions. *Proc. R. Soc. Lond. B* 276, 981–986.
- JMP®, Version 11.0. SAS Institute Inc., Cary, NC, 1989–2014.
- Jukkala, G., Piper, W., 2015. Common loon parents defend chicks according to both value and vulnerability. *J. Avian Biol.* 46, 551–558.
- Logue, D.M., Takahashi, A.D., Cade, W.H., 2011. Aggressiveness and size: a model and two tests. *Am. Nat.* 177, 202–210.
- López-Idiáquez, D., Vergara, P., Fargallo, J.A., Martínez-Padilla, J., 2016. Female plumage coloration signals status to conspecifics. *Anim. Behav.* 121, 101–106.
- Maia, R., Eliason, C.M., Bitton, P.P., Doucet, S.M., Shawkey, M.D., 2013. Pavo: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.* 4, 906–913.
- Margalida, A., Bertran, J., 2005. Territorial defence and agonistic behaviour of breeding bearded vultures *Gypaetus barbatus* toward conspecifics and heterospecifics. *Ethol. Ecol. Evol.* 17, 51–63.
- Maynard-Smith, J., Harper, D., 1988. The evolution of aggression: can selection generate variability? *Philos. Trans. R. Soc. B* 319, 557–570.
- Mays Jr., H.L., Hopper, K.R., 2004. Differential responses of yellow-breasted chats, *Icteria virens*, to male and female conspecific model presentations. *Anim. Behav.* 67, 21–26.
- Milenkaya, O., Legge, S., Walters, J.R., 2011. Breeding biology and life-history traits of an Australasian tropical granivore, the Crimson Finch (*Neochmia phaeton*). *Emu* 111, 312–320.
- Murphy, T.G., Rosenthal, M.F., Montgomerie, R.D., Tarvin, K.A., 2009. Female American goldfinches use carotenoid-based bill coloration to signal status. *Behav. Ecol.* 20, 1348–1355.
- Murray Jr., B.G., 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* 52, 414–423.
- Olson, V.A., Owens, I.P.F., 2005. Interspecific variation in the use of carotenoid-based coloration in birds: diet, life history and phylogeny. *J. Evol. Biol.* 18, 1534–1546.
- Oriand, G.H., Willson, M.F., 1964. Interspecific territories of birds. *Ecology* 45, 736–745.
- Osorio, D., Vorobyev, M., 2008. A review of the evolution of animal colour vision and visual communication signals. *Vis. Res.* 48, 2042–2051.
- Pryke, S.R., 2007. Fiery red heads: female dominance among head color morphs in the Gouldian finch. *Behav. Ecol.* 18, 621–627.
- Pryke, S.R., 2009. Is red an innate or learned signal of aggression and intimidation? *Anim. Behav.* 78, 393–398.
- Pryke, S.R., 2013. Bird contests: from hatching to fertilisation. In: Hardy, I.C.W., Briffa, M. (Eds.), *Animal Contests*. Cambridge University Press, Cambridge, pp. 287–303.
- Pryke, S.R., Lawes, M., Andersson, S., 2001. Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. *Anim. Behav.* 62, 695–704.
- R Development Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ratner, S.C., 1961. Effects of learning to be submissive on status in the peck order of domestic fowl. *Anim. Behav.* 9, 34–37.
- Redondo, T., 1989. Avian nest defence: theoretical models and evidence. *Behaviour* 111, 161–195.
- Regelmann, K., Curio, E., 1983. Determinants of brood defence in the great tit *Parus major* L. *Behav. Ecol. Sociobiol.* 13, 131–145.
- Rohwer, S., 1975. The social significance of avian winter plumage variability. *Evolution* 29, 593–610.
- Santos, E.S.A., Scheck, D., Nakagawa, S., 2011. Dominance and plumage traits: meta-analysis and meta-regression analysis. *Anim. Behav.* 82, 3–19.
- Senar, J.C., 2006. Color displays as intrasexual signals of aggression and dominance. In: Hill, G.E., McGraw, K.J. (Eds.), *Bird Coloration, Function and Evolution*, vol. 2. Harvard University Press, Cambridge, pp. 87–136.
- Senar, J.C., Domènech, J., 2011. Sex-specific aggression and sex ratio in wintering finch flocks: serins and siskins differ. *Acta Ethol.* 14, 7–11.
- Siddiqi, A., Cronin, T.W., Loew, E.R., Vorobyev, M., Summers, K., 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J. Exp. Biol.* 207, 2471–2485.
- Sih, A., Bell, A.M., Johnson, J.C., Ziemba, R.E., 2004a. Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* 79, 241–277.
- Sih, A., Bell, A.M., Johnson, J.C., 2004b. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372–378.
- Soma, K.K., 2006. Testosterone and aggression: berthold, birds and beyond. *J. Neuroendocrinol.* 18, 543–551.
- Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21.
- Taylor, P.W., Hasson, O., Clarke, D.L., 2000. Body postures and patterns as amplifiers of physical condition. *Proc. R. Soc. Lond. B* 267, 917–922.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man*. Aldine de Gruyter, New York, pp. 136–179.
- Young, C.M., Cain, K.E., Svedin, N., Backwell, P.R.Y., Pryke, S.R., 2016. The role of pigment based plumage in resolving contests. *J. Avian Biol.* 47, 167–175.
- Young, C.M., Cain, K.E., Svedin, N., Backwell, P.R.Y., Pryke, S.R., 2017. Nesting success in crimson finches: chance or choice? *Ethology* 123, 41–50.
- Vorobyev, M., Osorio, D., 1998. Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B* 265, 351–358.
- Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J., Cuthill, I.C., 1998. Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. A* 183, 621–633.
- Westneat, D.F., Stewart, I.R.K., 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annu. Rev. Ecol. Evol. Syst.* 34, 365–396.