

Effect of ornament manipulations on following relations in male bearded reedlings

Z. TÓTH^{1,5}, D. BALDAN², C. ALBERT³, H. HOI⁴ and M. GRIGGIO^{2,4}

¹ *Lendület Evolutionary Ecology Research Group, Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, 15 Herman Ottó, 1022 Budapest, Hungary*

² *Department of Biology, University of Padova, 58/B U. Bassi, I-35131 Padova, Italy*

³ *Faculty of Sciences of Orsay, Université Paris-Sud University, 15 Georges Clemenceau, 91400 Orsay, France*

⁴ *Konrad Lorenz Institute of Ethology, Department of Integrative Biology and Evolution, University of Veterinary Medicine of Vienna, 1/A Savoyenstrasse, A-1160, Vienna, Austria*

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Several studies have investigated how individuals' social status or behavioural and physiological traits affect social organisation in group-living species, but the potential role of ornamental traits has been rarely studied. Here, we analysed initiator–follower interactions in relation to experimentally manipulated sexually selected ornaments in captive flocks of male bearded reedlings (*Panurus biarmicus*). We manipulated beard length or tail length on the most and least frequently followed individuals in unisex flocks and examined how trait manipulation affected social prestige (i.e. frequency of being followed) and centrality (i.e. frequency of following others) of these individuals. We found that prestige/centrality after manipulation was significantly positively associated with their before-manipulation measure, whereas body condition did not affect social position within flocks. Similarly, the manipulation of the ornamental traits had no significant effect on the social positions of the manipulated individuals. Both social prestige and centrality were significantly positively correlated with the frequency of allopreening interactions, but not related to fighting success, i.e. the number of won/total fights in the flocks. Our findings indicate that the level of influence male bearded reedlings exert on social cohesion is not related to ornamental traits, and birds are likely to have a consistent social position, at least in the short term, within their flocks.

KEY WORDS: social network position, within-group following, sexually selected ornaments, *Panurus biarmicus*, regression to the mean.

⁵ Corresponding author: Zoltán Tóth, Lendület Evolutionary Ecology Research Group, Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, 15 Herman Ottó, 1022 Budapest, Hungary (E-mail: toth.zoltan@agrar.mta.hu).

INTRODUCTION

Living in groups is known to be advantageous in terms of increased likelihood of finding food, or detection and avoidance of predators (KRAUSE & RUXTON 2002). Although larger group size is expected to cause more intense competition between group-mates (GIRALDEAU & CARACO 2000), it may also contribute to achieving a higher individual feeding rate (SULLIVAN 1984; FANSHAW & FITZGIBBON 1993; CREEL & CREEL 1995) or to having an ‘increased pool of competence’ which may help in solving foraging problems (LIKER & BÓKONY 2009; MORAND-FERRON & QUINN 2011). However, it is less obvious how heterogeneity between individuals due to variation in morphology, physiology and/or behaviour (in short, group composition) shapes the structure and efficiency of animal social aggregations. Previous theoretical studies suggest that various traits can be influential depending on the environmental, cognitive and social constraints that act on group formation (CONRADT et al. 2009; BODE et al. 2011, 2012; SUEUR et al. 2012).

Gaining a better understanding of the process of how leaders and followers emerge in animal societies can greatly improve our knowledge about how social units evolve and function (reviewed in KING & COWLISHAW 2009; KING et al. 2009; KING 2010). In this context, we know very little about how ornaments operate in leadership relations and contribute to social cohesion in most species, especially in birds, despite their recognised role in dominance and sexual signalling (ANDERSSON 1994; HILL & MCGRAW 2006; SENAR 2006; BLOUNT & MCGRAW 2008). Different feather ornaments represent visual cues for conspecifics, and can serve as honest indicators of individual quality whenever they are constantly used during costly agonistic interactions (‘badge of status’; ROHWER 1975, 1982; SENAR 1999; GRIGGIO et al. 2007; HOI & GRIGGIO 2008) and/or are costly to produce and maintain (JAWOR & BREITWISCH 2003; MCGRAW 2003; GRIFFITH et al. 2006; SERRA et al. 2007). It is also well established that individuals in many species base their mating preferences on such ornamental traits, so they are often sexually selected (ANDERSSON 1994). However, it has been rarely studied whether these ornaments are also associated with particular positions within the social organisation of avian aggregations. Social positions in this sense are indicators that reflect the level of influence different individuals exert on maintaining cohesion in their group. Recently, TÓTH & GRIGGIO (2011) found in a non-manipulative study that a yellow breast patch, a carotenoid based trait which reflects dominance status and is sexually selected by both sexes (GRIGGIO et al. 2005, 2007, 2009), was the best predictor of leadership in free-living rock sparrows (*Petronia petronia*). Indeed, birds with bigger patches exerted greater influence in the foraging groups and were followed by more group-mates than less elaborate individuals were. Also, OH & BADYAEV (2010) showed that in a wild population of house finches (*Carpodacus mexicanus*), less elaborate males were socially more labile and visited more social groups than more elaborate males, most probably to increase their attractiveness as mates relative to local conspecifics. These findings indicate that sexually selected ornamental traits can be related to individual social positions in passerine flocks, but experimental evidence supporting this idea is still lacking.

In this study, we investigated experimentally how the length of beard, a melanin-based ornament that is a badge of status and sexually selected by females, and the length of tail, a pure sexually selected trait without a dominance-status signalling role, affected within-group following in captive male bearded reedling (*Panurus biarmicus*) flocks. We used unisex flocks to assure that stable pair bonds did not bias the observed patterns of following. By observing following events, we first studied the relationship between social interactions such as fighting and

allopreening and individuals' social position in the following networks. Then, we manipulated these traits on the most and least frequently followed individuals in each flock and examined how the manipulation affected the social positions of these individuals in the flocks. We predicted that if the information signaled by one of these ornamental traits is important in terms of following other group-mates, positions of the manipulated birds in the following networks will be altered in accordance with the applied manipulation.

MATERIALS AND METHODS

Study species

The bearded reedling is a small passerine species typically inhabiting extended areas of reed beds, and breeding colonially. Reedlings are highly social, often forming flocks and exhibiting various activities together during both the reproductive and non-reproductive periods (BIBBY 1983). Previous studies investigating the effect of ornaments in mate choice found that reedlings select their mates according to individual characters like beard length (HOI & GRIGGIO 2008) and tail length (ROMERO-PUJANTE et al. 2002), while HOI & GRIGGIO (2008) showed that beard length also plays an important role in male–male competition, in accordance with the dual utility model (BERGLUND et al. 1996; TAROF et al. 2005).

Bearded reedlings originated from a captive population of 45 individuals, 32 males and 13 females, kept in six outdoor aviaries at the Konrad Lorenz Institute of Ethology (University of Veterinary Medicine Vienna), Vienna, Austria. Males and females were kept separately in unisex flocks and housed in three aviaries prior to the experiments. These aviaries were approximately 2 (width) × 3.9 (length) × 2.6 (height) m in size, equipped with a feeding table, roosting trees, reed bushes and several perches. Ad libitum food was provided, consisting of commercial food for insectivorous passerines, and mealworms. In addition, water provided in a bowl on the ground was also available for drinking and bathing.

Ethical note

We checked the birds' health before allocating them to the flocks. During the experiment, we never observed any sign of injury or stress in the birds, and none of the birds died in the studied flocks. After the experiment, we released individuals back into their original outdoor aviaries, where the birds made several successful breeding attempts in the following breeding season. This suggests that the housing conditions were appropriate and that the experimental birds remained healthy (GRIGGIO & HOI 2011; HOI & GRIGGIO 2011), even though males lost weight during the study (paired *t*-test, $t_{31} = 6.89$, $P < 0.001$). Licenses to take and keep birds from the field were given by the Burgenländische Landesregierung (No. IV-1253/38; IV-1058/39; and 5-N-A1007/178, 5-N-A-1007/367-2009 based on the 'Burgenländisches Naturschutzgesetz': LGBl.Nr. 22/1980). The experiments reported in this paper comply with current laws on animal experimentation in Austria and the European Union. This study was approved by the institutional ethics committee and the national authority according to § 8ff of the Law for Animal Experiments Tierversuchsgesetz – TVG.

Experimental set-up

We observed 12 experimental unisex flocks, each composed of six males, from April to July 2012. For each flock, individuals were randomly taken from the housing aviaries. Each

male flock was transferred to and kept in an indoor aviary measuring 6.60 (width) \times 3.30 (length) \times 2.25 (height) m. This aviary was similarly equipped with reed bushes, a roosting tree, several perches and water basins to simulate the original environment, and a central feeder was the only source of food. Mealworms and commercial food for insectivorous passerines were provided ad libitum throughout the experiment. Natural light from several windows and additional artificial light was provided in a 13:11 hr light:dark period pattern.

Body mass (\pm 0.1 g), tarsus length (\pm 0.01 mm), tail length (\pm 0.5 mm) and wing length (\pm 0.5 mm) were measured prior to the transfer into the experimental aviary. The length of the beards on both sides of the head was also measured (\pm 0.01 mm) and expressed as the average of the right and left beards' length (HOI & GRIGGIO 2008). All birds were individually colour-ringed for identification during the observations. Upon release into the indoor aviary, birds were allowed to become familiar with the environment of the experimental aviary for 1 day, during which we fed them ad libitum. Behavioural observations started on the following day.

Behavioural observations

Each flock was observed in two sessions (session 1 and session 2, henceforward), each composed of 2 consecutive days in which behavioural observations occurred in the morning between 07:15 and 12:30 (mean duration of observation \pm SE: 3.98 ± 0.04 hr/flock) and in the afternoon between 12:30 and 17:00 (1.60 ± 0.05 hr/flock). For nine flocks, the two sessions were separated by 1 day in which one ornament trait was manipulated (see 'Ornament manipulation'). For the remaining three flocks, the second session started on the same day in which birds were released into the aviary and the ornament manipulation was done. This procedure was applied in order to reduce the stress due to higher temperature in the experimental aviaries (please note that these observations were collected in the indoor aviaries in June–July). In both cases, observations started at least 1 hr after the birds were introduced or manipulated, allowing them to become familiar with their environment.

The feeder was inserted into and removed from the aviary at the beginning and at the end of both observation sessions; by doing so, we prevented feeding beyond observation time. Observations were made from a hide 2 m away through a one-way glass, during which we recorded the following events, allopreenings and aggressive interactions among the individuals throughout the aviary. We defined a following event as an interaction during which an individual arrived at the feeding place or water dish, on the ground or on the branches, and was followed by one or more group-mates (TÓTH et al. 2009, 2014; TÓTH & GRIGGIO 2011). The former individual was described as an 'initiator', while the latter was/were described as 'follower(s)'. Only those events in which the initiator and the follower were a minimum of 0.5 m apart were considered as followings. We considered pairwise followings to be movement initiations that facilitated and maintained social cohesion within the flock, and positions within the constructed following networks to be indicators of individuals' influence on that cohesion. We regarded the frequency of acting as an initiator in the flocks to be a measure of social prestige in the following networks, and the frequency of being a follower to be a measure of network centrality. These two prominence measures are in accordance with the definitions of prestige and centrality in directed networks discussed in WASSERMAN & FAUST (1994), and are equivalent to in-strength and out-strength in other works on weighted directed networks (e.g. MIGUÉNS & MENDES 2008; TÓTH et al. 2014).

Allopreening, in which one individual bird preened another (HARRISON 1965), was also recorded after following events to the branch. In all cases, we identified both the preener and the preened individual (HOI & GRIGGIO 2011). For each aggressive interaction, we noted the identity of the participants and the result of the fight (winner vs loser). Appendix I contains the number of observed interactions in each flock and in both sessions.

Ornament manipulation

We used the following events observed during session 1 to rank the birds according to their social prestige, and identified those two individuals that acted the most and least often as initiators during within-group followings. We did so by summing the number of cases when a given bird elicited following from a group-mate. Only one ornament was manipulated in each flock; thus, we had six replicates for each of the two traits (beard and tail length). Among the flocks these traits were manipulated alternately, so there was no seasonal difference in the timing of observations between the two traits.

We performed beard length manipulation in six male flocks ('M/B' flocks). Individuals which most often acted as an initiator in session 1 underwent beard length reduction. This was done by cutting the terminal beard feathers with a scissors to a length of 10 mm and painting with black nail polish. The shortened beard was painted to make its appearance similar to an elongated beard (HOI & GRIGGIO 2008). We detected no substantial differences in reflectance between natural and painted feathers during spectrophotometric measurements (M. GRIGGIO pers. comm.). In the same flocks, the birds which were the least frequently followed by other flock-mates in session 1 underwent beard elongation. The manipulation was done by painting the black and nearby gray feathers with black nail polish to a length of 25 mm. For the remaining four individuals in the flock, beard manipulation was imitated by pretending to paint the original beard with a clean brush. Males' original beard length varied between 17.96 and 22.75 mm (mean \pm SE: 20.58 ± 0.21 , $n = 32$).

We performed tail length manipulation in six male ('M/T' flocks) flocks. Individuals which most often acted as initiators in these flocks in session 1 underwent tail length reduction. Manipulation was done by cutting 20 mm off all the tail feather tips (except the outer tail feathers; ROMERO-PUJANTE et al. 2002, 2005). Under natural conditions, tail feathers can be very short during moult or sometimes even completely missing due to accidental loss (ROMERO-PUJANTE et al. 2005). After the manipulation, the tail length in the shortened groups varied between 63.0 and 67.5 mm in males, whereas it varied between 49.0 and 61.0 mm in females. The individuals which were the least often followed by other flock-mates in these flocks underwent tail elongation. Feather tips 25 mm long were added to the original tail feathers (except the outer tail feathers) using small amounts of a commercial superglue. The overlapping, glued surface was 5 mm; after manipulation the tail was elongated by 20 mm. This treatment resulted in tail lengths varying between 100.0 and 110.0 mm for elongated males. To the remaining four individuals in the flock, a tail manipulation was imitated by pretending to cut the original tail feathers with a scissors. This set-up was made as the unmodified manipulated birds were used more than once during the experiment. Males' original tail length varied between 79.0 and 92.0 mm (mean \pm SE: 85.6 ± 0.6 , $n = 32$).

Statistical analyses

We had only a limited number of birds in captivity; thus, we were forced to allocate individuals before their manipulation (20 males out of 32) randomly into more than one experimental flock (i.e. as non-manipulated birds). In order to control for the pseudoreplication due to this procedure, we included 'flock' and 'individual identity' as random factors into the fitted statistical models, and used randomisation-based correlation tests throughout the study. We ran all analyses in R 3.1.0 Statistical Program (R DEVELOPMENT CORE TEAM 2014). First, we investigated the correlations between initiate/hr and follow/hr, and their relationship with the frequency (event/hr) of other social interactions such as preening and fighting in session 1, using Spearman correlation tests based on Monte Carlo resampling ('coin' R package; HOTHORN et al. 2008). In these tests, 'flock' was used for stratification and *P*-values were calculated from 4999 iterations. Second, we also examined how initiate/hr and follow/hr of the birds changed in session 2 due to the ornament manipulation. In our study, we manipulated the most and least frequently followed individuals from the initial flocks, which raises the problem of the 'regression to the mean'. This statistical phenomenon arises when values are observed with a random error and especially when

treatment groups are selected according to a baseline measurement (BARNETT et al. 2005; KELLY & PRICE 2005). In order to control for the potential confounding effect of the ‘regression to the mean’ phenomenon, we applied linear mixed-effect (LME, ‘lme4’ R package; BATES et al. 2014) models into which the deviance from the mean baseline measurement (i.e. lead/hr and follow/hr in session 1 for each individual minus its mean in session 1, respectively) was included as a covariate, following the recommendations of BARNETT et al. (2005). Into these models, we also added the change in body condition during the observation in the given flock as another confounding variable, and used the initiate/hr and follow/hr measured in session 2 as dependent variables. Body condition was calculated for each individual as a scale mass index from measures of body mass and tarsus length; for a detailed description of the method see PEIG & GREEN (2009). ‘Individual identity’ and ‘flock’ were included into the models as random factors, whereas ‘flock type’ (M/B or M/T), ‘manipulation type’ (shortened, elongated or non-manipulated) and their interaction were included as potential predictors. We applied square-root transformation on both initiate/hr and follow/hr to improve their fit to normal distribution. F -values, denominator degrees of freedom and P -values for the fixed factors were obtained using conditional F -tests with df correction based on Kenward–Roger approximation (‘pbkrtest’ R package; HALEKOH & HØJSGAARD 2013). In both model fittings we used the backward removal procedure, starting with the full models containing all variables, then dropped the predictor with the highest P -value in each step until only $P \leq 0.05$ effects remained (if there were any) in the final models. Eta squares (η^2) as effect sizes and their 95% confidence intervals were calculated to estimate the variance explained by each predictor in the final models (COHEN 1988). Requirements of LME models were checked by plot diagnosis. All tests were two-tailed with α set to 0.05.

RESULTS

Correlations between social interactions in session 1

We found significant positive correlations between the measured prestige/centrality variables and other social interactions in the male flocks: the more often a bird acted as an initiator, the more preening that individual received from its group-mates (Table 1). Similarly, the frequency of followings was positively associated with the frequency of both preening other flock-mates and getting preened by others. This finding indicates that the initiator–follower interactions reflect genuine social relations between birds. The frequencies of initiating and following were not associated with each other, which suggests that these two measures do not describe the same aspect of individuals’ social position in the flocks. The frequency of aggressive interactions and fighting success was not correlated with initiate/hr or follow/hr in either flock type.

The effect of beard and tail manipulation on individuals’ social position

We found that both social prestige and centrality measured in session 2 were significantly positively related to their deviations from the mean in session 1 (social prestige: $F_{1,67.95} = 29.14$, $\eta^2 = 0.30$ [0.13–0.45], $P < 0.0001$; centrality: $F_{1,66.51} = 49.51$, $\eta^2 = 0.43$ [0.25–0.56], $P < 0.0001$), i.e. individuals that elicited more following or followed other group-mates more often than average in the first session acted as initiator or follower more frequently also in the second (Fig. 1a–b). Change in body condition had no significant effect on either response variable in the studied flocks (social prestige: $F_{1,67.45} = 0.63$, $P = 0.432$; centrality: $F_{1,67.59} = 0.484$, $P = 0.489$). Manipulation type and flock type had no significant effect on individuals’ social position either by themselves (effect of manipulation type on social prestige: $F_{2,62.89} = 2.28$,

Table 1.

Spearman correlation tests between initiate/hr and follow/hr, and their relationship with the frequency (event/hr) of other social interactions such as preening and fighting, in session 1. Significant correlations and corresponding P -values are shown in bold.

Variable 1	Variable 2	r_s	Z	P
Initiate/hr	Follow/hr	0.30	1.27	0.211
	Number of fights won/hr	0.02	-0.82	0.416
	Total number of fights/hr	0.06	-0.62	0.550
	Preened/hr*	0.29	3.32	0.001
	Preen/hr*	0.13	1.75	0.077
Follow/hr	Number of fights won/hr	0.17	0.81	0.425
	Total number of fights/hr	0.17	0.77	0.444
	Preened/hr*	0.33	3.83	< 0.001
	Preen/hr*	0.38	4.36	< 0.001

* Outliers (two for preened/hr and one for preen/hr) did not affect the significance of the correlations (all $P \leq 0.001$), except for the relationship between initiate/hr and preen/hr where the omission of the outlier ceased the marginal non-significance of the correlation ($Z = 1.40$, $P = 0.140$). Birds were not manipulated in session 1, so males from M/B and M/T flocks were pooled. Please note that Spearman correlation coefficients were calculated from the unstratified data, whereas test statistics and P -values were obtained from Spearman correlation tests based on Monte Carlo resampling with 'flock' used for stratification ('coin' R package; HOTHORN et al. 2008). Significance levels were computed via Monte Carlo simulation with 4999 iterations.

$P = 0.111$; on centrality: $F_{2,56.34} = 1.22$, $P = 0.302$; effect of flock type on social prestige: $F_{1,10.10} = 0.03$, $P = 0.869$; on centrality: $F_{1,9.98} = 0.01$, $P = 0.937$) or in interaction with each other (social prestige: $F_{5,43.36} = 1.81$, $P = 0.130$; centrality: $F_{5,43.39} = 0.53$, $P = 0.756$).

DISCUSSION

Understanding the basis of social organisation in animal groups requires experimental data on how individual characteristics may play a role in maintaining and modulating social cohesion. We focused here on the role of sexually selected ornamental traits in male bearded reedlings: beard length which also functions as a signal of males' dominance status, and tail length which is purely sexually selected. Our findings indicate that the social position of male reedlings is not related to these sexually selected traits, and individuals are likely to have stable positions within the bearded reedling flocks.

We found that both social prestige and centrality, indicators of social position within the flock, were significantly positively correlated between the two sessions, suggesting that most bearded reedlings had similar positions in the following networks before and after manipulation. This hints that eliciting following and the tendency to follow other group-mates were consistent individual attributes within the investigated period of time. This result is in accordance with the findings of a recent study conducted on house sparrows, *Passer domesticus*, where food reduction was found to have little effect on the following network structure and individuals' position within it (TÓTH et al. 2014).

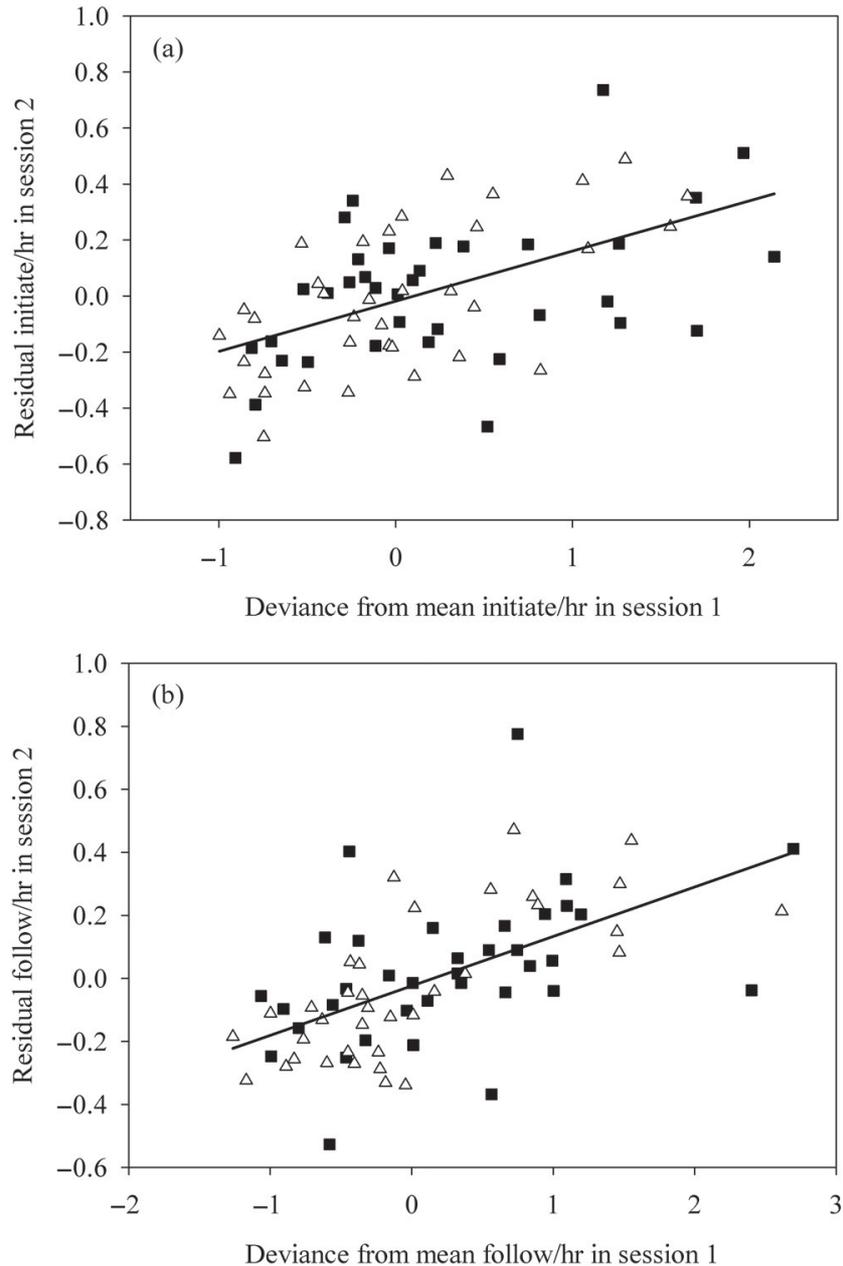


Fig. 1. — The relationship between the initial (session 1) and after-manipulation (session 2) measures of (a) social prestige and (b) centrality in the studied bearded reedling flocks. Social prestige was calculated as the frequency of acting as an initiator in the flocks, whereas centrality was the frequency of being a follower during following interactions. Variables on the x-axis denote deviances from the mean in session 1, whereas variables on the y-axis represents residuals obtained from the null linear mixed-effect (LME) models into which only the random factors were included. Black squares denote the beard-manipulated (M/B) flocks, while white triangles represent the tail-manipulated (M/T) flocks. Regression lines in both cases were fitted to the pooled data of the two flock types.

According to these findings, social positions can be resilient to the manipulations of some individual characteristics and ecological factors in passerine flocks. The idea of similar social positions over time, nevertheless, is in striking contrast to the findings of previous studies, where the removal or replacement of some key individuals induced substantial changes in the social structure in primates and ungulates (FLACK et al. 2006; DELLA-ROSSA et al. 2013). We propose that comparisons of various manipulation types in a single model system could greatly increase our knowledge about the consistency of

individual social positions and the stability of animal social groups when facing a changing (social and/or physical) environment. It is also possible, however, that the observation periods were too short to induce significant changes in social relationships between flock-mates. This may also be the reason why, contrary to some theoretical expectations (e.g. RANDS et al. 2003, 2008), we found no significant effect of individual energy reserves on following and movement initiations.

Our results provide no support for our initial prediction that sexually selected ornaments can play a significant role in the social relations between male bearded reedlings, as manipulation of beard or tail length did not alter individuals' social prestige or centrality. Furthermore, network positions prior to the ornament manipulations were not significantly correlated with beard (initiate/hr: $r_S = -0.10$, $Z = -0.37$, $P = 0.699$; follow/hr: $r_S = 0.15$, $Z = 1.92$, $P = 0.055$) or tail length (initiate/hr: $r_S = 0.005$, $Z = 0.08$, $P = 0.931$; follow/hr: $r_S = 0.17$, $Z = 1.56$, $P = 0.129$) either. In bearded reedlings, extra-pair paternity after pair-formation is very high among colonial breeding pairs (HOI & HOI-LEITNER 1997), so following more attractive male group-mates could be advantageous, theoretically, in terms of opportunities for extra-pair copulations. However, HOI & GRIGGIO (2012) showed that females' contact initiations toward potential extra partners are not closely related to these males' attractiveness. Because of that, even if following other males increases the chances of extra-pair mating, social positions of males may not be associated with between-individual differences in ornaments. Instead, we found that social prestige and centrality were both positively correlated with allopreening, but not with aggression, in the initial flocks. This suggests that preening occurred more frequently among dyads that participated in more following, and thus positions in the following networks were related to affiliative relationships, rather than to competition and/or conflict among individuals (similarly to other gregarious species; see e.g. RAMSEYER et al. 2009; DELLA-ROSSA et al. 2013). Social bonds, for instance, can be beneficial if they contribute to better access to food resources or result in lower rates of agonistic interactions (LEWIS et al. 2007), and may indicate family relations among individuals (STAMPS et al. 1990; TÓTH et al. 2009; GILL 2012). Recent studies investigating the potential role of allopreening in various avian species proposed that such interactions may indeed facilitate the establishment and maintenance of social cohesion within mating pairs and between other members of a social group (EMERY et al. 2007; LEWIS et al. 2007; HOI & GRIGGIO 2011; ABBASSI & BURLEY 2012; GILL 2012).

Our study emphasises the lack of influence of sexually selected ornamental traits on social position in male bearded reedlings. Although our findings are based on the observation of a limited number of captive birds, we showed that most individuals' position in the following networks was consistent within the study period despite the applied manipulations and associated with affiliative interactions. These findings shed light on how individual characteristics such as ornament traits can influence social interactions between individuals in animal aggregations. Future studies on initiator–follower interactions may help better understand the origin and adaptive function of the individual heterogeneity in animal societies by using a similar manipulative approach.

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DISCLOSURE STATEMENT

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REFERENCES

- ABBASSI P. & BURLEY N. 2012. Nice guys finish last: same-sex sexual behavior and pairing success in male budgerigars. *Behavioral Ecology* 23: 775–782. doi:10.1093/beheco/ars030.
- ANDERSSON M. 1994. Sexual selection. *Princeton: Princeton University Press*.
- BARNETT A.G., VAN DER POLS J.C. & DOBSON A.J. 2005. Regression to the mean: what it is and how to deal with it. *International Journal of Epidemiology* 34: 215–220. doi:10.1093/ije/dyh299.
- BATES D., MAECHLER M., BOLKER B. & WALKER S. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7. (Available at: <http://CRAN.R-project.org/package=lme4>).
- BERGLUND A., BISAZZA A. & PILASTRO A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* 58: 385–399. doi:10.1111/bij.1996.58.issue-4.
- BIBBY C.J. 1983. Studies of west Palearctic birds: 186. Bearded tit. *British Birds* 76: 549–563.
- BLOUNT J.D. & MCGRAW K.J. 2008. Signal functions of carotenoid colouration, Vol. 4, pp. 213–236. In: Britton G. et al., Eds. Carotenoids. *Basel: Birkhäuser Verlag*.
- BODE N.W.F., FRANKS D.W. & WOOD A.J. 2012. Leading from the front? Social networks in navigating groups. *Behavioral Ecology and Sociobiology* 66: 835–843. doi:10.1007/s00265-012-1331-6.
- BODE N.W.F., WOOD A.J. & FRANKS D.W. 2011. The impact of social networks on animal collective motion. *Animal Behaviour* 82: 29–38. doi:10.1016/j.anbehav.2011.04.011.
- COHEN J. 1988. Statistical power analysis for the behavioural sciences. *Hillsdale: Lawrence Erlbaum Associates*.
- CONRADT L., KRAUSE J., COUZIN I.D. & ROPER T.J. 2009. Leading according to need in self organizing groups. *The American Naturalist* 173: 304–312. doi:10.1086/593129.
- CREEL S. & CREEL N.M. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* 50: 1325–1339. doi:10.1016/0003-3472(95)80048-4.
- DELLA-ROSSA L., CHADŒUF J., BOISSY A. & DUMONT B. 2013. Leaders of spontaneous group movements influence whole-group social organization: an experimental study on grazing heifers. *Behaviour* 150: 153–173. doi:10.1163/1568539X-00003043.
- EMERY N.J., SEED A.M., VON BAYERN A.M.P. & CLAYTON N.S. 2007. Cognitive adaptations of social bonding in birds. *Philosophical Transactions of the Royal Society (B)* 362: 489–505.
- FANSHAWE J.H. & FITZGIBBON C.D. 1993. Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour* 45: 479–490. doi:10.1006/anbe.1993.1059.
- FLACK J.C., GIRVAN M., DE WAAL F.B. & KRAKAUER D.C. 2006. Policing stabilizes construction of social niches in primates. *Nature* 439: 426–429. doi:10.1038/nature04326.
- GILL S.A. 2012. Strategic use of allopreening in family-living wrens. *Behavioral Ecology and Sociobiology* 66: 757–763. doi:10.1007/s00265-012-1323-6.
- GIRALDEAU L.-A. & CARACO T. 2000. Social foraging theory. *Princeton: Princeton University Press*.

- GRIFFITH S.C., PARKER T.H. & OLSON V.A. 2006. Melanin- versus carotenoid-based sexual signals: is the difference really so black and red? *Animal Behaviour* 71: 749–763. doi:10.1016/j.anbehav.2005.07.016.
- GRIGGIO M., DEVIGILI A., HOI H. & PILASTRO A. 2009. Female ornamentation and directional male mate preference in the rock sparrow. *Behavioral Ecology* 20: 1072–1078. doi:10.1093/beheco/arp099.
- GRIGGIO M. & HOI H. 2011. An experiment on the function of the long-term pair bond period in the socially monogamous bearded reedling. *Animal Behaviour* 82: 1329–1335. doi:10.1016/j.anbehav.2011.09.016.
- GRIGGIO M., SERRA L., LICHERI D., MONTI A. & PILASTRO A. 2007. Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. *Behavioral Ecology and Sociobiology* 61: 423–433. doi:10.1007/s00265-006-0270-5.
- GRIGGIO M., VALERA F., CASAS A. & PILASTRO A. 2005. Males prefer ornamented females: a field experiment of male choice in the rock sparrow. *Animal Behaviour* 69: 1243–1250. doi:10.1016/j.anbehav.2004.10.004.
- HALEKOH U. & HØJSGAARD S. 2013. pbkrtest: Parametric Bootstrap and Kenward Roger Based Methods for Mixed Model Comparison. R package version 0.3-8 (Available at: <http://CRAN.R-project.org/package=pbkrtest>).
- HARRISON C.J.O. 1965. Allopreening as agonistic behaviour. *Behaviour* 24: 161–208. doi:10.1163/156853965X00011.
- HILL G.E. & MCGRAW K.J. (Eds) 2006. Bird coloration: function and evolution. Vol. 2. London: Harvard University Press.
- HOI H. & GRIGGIO M. 2008. Dual utility of a melanin-based ornament in bearded tits. *Ethology* 114: 1094–1100. doi:10.1111/eth.2008.114.issue-11.
- HOI H. & GRIGGIO M. 2011. Is female mate preference based on the interaction between static and dynamic signals in bearded reedlings? *Ethology Ecology & Evolution* 23: 171–178. doi:10.1080/03949370.2011.554879.
- HOI H. & GRIGGIO M. 2012. Bearded reedlings adjust their pair-bond behaviour in relation to the sex and attractiveness of unpaired conspecifics. *PLOS ONE* 7: e32806.
- HOI H. & HOI-LEITNER M. 1997. An alternative route to coloniality in the bearded tit: females pursue extra-pair fertilizations. *Behavioral Ecology* 8: 113–119. doi:10.1093/beheco/8.2.113.
- HOTHORN T., HORNIK K., VAN DE WEIL M.A. & ZEILEIS A. 2008. Implementing a class of permutation tests: the coin package. *Journal of Statistical Software* 28: 1–23.
- JAWOR J.M. & BREITWISCH R. 2003. Melanin ornaments, honesty, and sexual selection. *The Auk* 120: 249–265.
- KELLY C. & PRICE T.D. 2005. Correcting for regression to the mean in behavior and ecology. *The American Naturalist* 166: 700–707. doi:10.1086/497402.
- KING A.J. 2010. Follow me! I'm a leader if you do; I'm a failed initiator if you don't? *Behavioural Processes* 84: 671–674. doi:10.1016/j.beproc.2010.03.006.
- KING A.J. & COWLISHAW G. 2009. Leaders, followers and group decision-making. *Communicative & Integrative Biology* 2: 147–150. doi:10.4161/cib.7562.
- KING A.J., JOHNSON D.D.P. & VAN VUGT M. 2009. The origins and evolution of leadership. *Current Biology* 19: R911–R916. doi:10.1016/j.cub.2009.07.027.
- KRAUSE J. & RUXTON G.D. 2002. Living in groups. Oxford: Oxford University Press.
- LEWIS S., ROBERTS G., HARRIS M.P., PRIGMORE C. & WANLESS S. 2007. Fitness increases with partner and neighbour allopreening. *Biology Letters* 3: 386–389. doi:10.1098/rsbl.2007.0258.
- LIKER A. & BÓKONY V. 2009. Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences* 106: 7893–7898. doi:10.1073/pnas.0900042106.
- MCGRAW K.J. 2003. Melanins, metals, and mate quality. *Oikos* 102: 402–406. doi:10.1034/j.1600-0579.2003.12513.x.
- MIGUÉNS J.I.L. & MENDES J.F.F. 2008. Travel and tourism: into a complex network. *Physica A: Statistical Mechanics and its Applications* 387: 2963–2971.

- MORAND-FERRON J. & QUINN J.L. 2011. Larger groups of passerines are more efficient problem solvers in the wild. *Proceedings of the National Academy of Sciences* 108: 15898–15903. doi:10.1073/pnas.1111560108.
- OH K.P. & BADYAEV A.V. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *The American Naturalist* 176: E80–E89. doi:10.1086/648327.
- PEIG J. & GREEN A.J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118: 1883–1891. doi:10.1111/oik.2009.118.issue-12.
- R DEVELOPMENT CORE TEAM R. 2014. A language and environment for statistical computing. 2014. *R Foundation for Statistical Computing, Vienna, Austria*. ISBN 3-900051-07-0 (Available at: <http://www.R-project.org>).
- RAMSEYER A., BOISSY A., THIERRY B. & DUMONT B. 2009. Individual and social determinants of spontaneous group movements in cattle and sheep. *Animal* 3: 1319–1326.
- RANDS S.A., COWLISHAW G., PETTIFOR R.A., ROWCLIFFE J.M. & JOHNSTONE R.A. 2003. Spontaneous emergence of leaders and followers in foraging pairs. *Nature* 423: 432–434. doi:10.1038/nature01630.
- RANDS S.A., COWLISHAW G., PETTIFOR R.A., ROWCLIFFE J.M. & JOHNSTONE R.A. 2008. The emergence of leaders and followers in foraging pairs when the qualities of individuals differ. *BMC Evolutionary Biology* 8: 51.
- ROHWER S. 1975. The social significance of avian winter plumage variability. *Evolution* 29: 593–610.
- ROHWER S. 1982. The evolution of reliable and un-reliable badges of fighting ability. *The American Naturalist* 22: 531–546.
- ROMERO-PUJANTE M., HOI H. & BLOMOVIST D. 2005. The importance of tail length for habitat use in the bearded tit *Panurus biarmicus*: an experimental study. *Ibis* 147: 464–470. doi:10.1111/j.1474-919x.2005.00413.x.
- ROMERO-PUJANTE M., HOI H., BLOMOVIST D. & VALERA H.F. 2002. Tail length and mutual mate choice in bearded tits (*Panurus biarmicus*). *Ethology* 108: 885–895. doi:10.1046/j.1439-0310.2002.00821.x.
- SEJAR J.C. 1999. Plumage colouration as a signal of social status. Vol. 2, pp. 1669–1686. In: Adams N.J. et al., Eds. Proceedings of the international ornithological congress. *Johannesburg: BirdLife South Africa*.
- SEJAR J.C. 2006. Color displays as intrasexual signals of aggression and dominance. Vol. 2, pp. 87–136. In: Hill G.E. et al., Eds. Bird coloration: function and evolution. *London: Harvard University Press*.
- SERRA L., GRIGGIO M., LICHERI D. & PILASTRO A. 2007. Moulting speed constrains the expression of a carotenoid-based sexual ornament. *Journal of Evolutionary Biology* 20: 2028–2034. doi:10.1111/j.1420-9101.2007.01360.x.
- STAMPS J., KUS B., CLARK A. & ARROWOOD P. 1990. Social relationships of fledgling budgerigars, *Melopsitticus undulatus*. *Animal Behaviour* 40: 688–700. doi:10.1016/S0003-3472(05)80698-0.
- SUEUR C., DENEUBOURG J.-L. & PETIT O. 2012. From social network (centralized vs. decentralized) to collective decision-making (unshared vs. shared consensus). *PLOS ONE* 7: e32566.
- SULLIVAN K.A. 1984. The advantages of social foraging in downy woodpeckers. *Animal Behaviour* 32: 16–22. doi:10.1016/S0003-3472(84)80319-X.
- TAROF S.A., DUNN P.O. & WHITTINGHAM L.A. 2005. Dual functions of a melanin-based ornament in the common yellowthroat. *Proceedings of the Royal Society (B: Biological Sciences)* 272: 1121–1127. doi:10.1098/rspb.2005.3053.
- TÓTH Z., BALDAN D., HOI H. & GRIGGIO M. 2014. Food reduction has a limited effect on following relations in house sparrow flocks. *Animal Behaviour* 90: 91–100. doi:10.1016/j.anbehav.2014.01.018.
- TÓTH Z., BÓKONY V., LENDVAI Á.Z., SZABÓ K., PÉNZES Z. & LIKER A. 2009. Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. *Behavioural Processes* 82: 173–177. doi:10.1016/j.beproc.2009.06.003.

- TÓTH Z. & GRIGGIO M. 2011. Leaders are more attractive: birds with bigger yellow breast patches are followed by more group-mates in foraging groups. *PLOS ONE* 6: e26605.
- WASSERMAN S. & FAUST K. 1994. Social network analysis: methods and applications. *New York: Cambridge University Press.*

APPENDIX I.

Frequencies of the observed interactions in the studied flocks before (session 1) and after manipulation (session 2). M/B denotes those male flocks in which beard length was manipulated, whereas M/T indicates male flocks with tail length manipulation.

Session	Flock type	Flock	Following	Fighting	Allopreening	Observation time (hr)
1	M/B	1	164	16	1	11.49
		2	90	12	0	11.05
		3	102	8	0	11.52
		4	120	31	0	11.82
		5	92	21	1	11.42
		6	129	16	8	11.15
	M/T	1	108	16	20	12.08
		2	108	7	13	10.08
		3	120	14	3	11.75
		4	99	16	10	11.13
		5	81	18	7	11.63
		6	72	2	11	12.29
2	M/B	1	144	18	9	11.67
		2	99	13	0	12.03
		3	113	12	0	10.60
		4	88	8	1	9.71
		5	98	16	3	11.04
		6	118	15	7	9.36
	M/T	1	109	14	37	11.25
		2	117	13	11	11.04
		3	104	9	0	10.73
		4	86	16	3	10.71
		5	94	12	9	8.35
		6	90	0	33	11.43