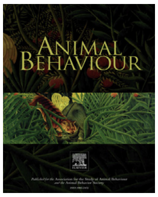
Animal Behaviour 128 (2017) 51–60

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Effects of early life adversity and sex on dominance in European starlings

Tom Bedford, Caitlin Jade Oliver, Clare Andrews, Melissa Bateson, Daniel Nettle*

Centre for Behaviour and Evolution & Institute of Neuroscience, Newcastle University, Newcastle, UK

ARTICLE INFO

Article history:
Received 19 December 2016
Initial acceptance 9 February 2017
Final acceptance 9 March 2017

MS. number: 16-01083

Keywords:
birds
dominance
early life adversity
individual quality
resource competition
starlings

Dominance in socially foraging animals may be related to sex and to variation in individual quality. Individual quality may in turn reflect conditions during early development. We studied dominance in a cohort of adult European starlings, *Sturnus vulgaris*, that had been subject to experimental manipulations of food supply and begging effort when they were nestlings. We measured dominance in two different contexts, contests over a food resource and relative position on a sloping perch, over the course of 3 weeks. Dominance in food contests was extremely stable over the 3 weeks and relative perch position somewhat stable. Males were dominant over females in contests over food and perched in higher positions. These sex differences were not explained by males' greater size or body weight. Food dominance and perch position were uncorrelated. Neither early life food supply nor early life begging effort affected food dominance; nor did an alternative measure of developmental stress, developmental telomere attrition. Birds that had been made to beg more as nestlings perched in higher positions than those that had begged less. Our results did not support the hypothesis that early life adversity leads to lower adult dominance rank in the context of feeding, and we suggest that relative perch position may have measured individual preference rather than competitive ability.

Socially foraging animals of many species form dominance hierarchies in which each individual can be characterized by a social rank (Chase, Tovey, Spangler-Martin, & Manfredonia, 2002). Dominant or higher-ranking individuals are able to displace subordinate or lower-ranking individuals from sought-after resources, and dominance is typically positively related to reproductive success (Ellis, 1995). Attained positions in dominance hierarchies are often, although imperfectly, related to variation in individual attributes such as size, age or individual quality (Chase et al., 2002). For example, in birds, dominance rank often correlates with plumage ornamentation, which, in both sexes, can function as an indicator of quality (Rat, van Dijk, Covas, & Doutrelant, 2015; Santos, Scheck, & Nakagawa, 2011; Senar, Camerino, Copete, & Metcalfe, 1993; Swaddle & Witter, 1995).

Individual quality may partly reflect genetic variation (Ryder, Tori, Blake, Loiselle, & Parker, 2010), but it is also likely to be influenced by developmental history. The evidence for developmental history affecting dominance rank is indirect. In passerine birds, dominance has been shown to correlate with traits such as song repertoire size (Spencer, Buchanan, Goldsmith, & Catchpole, 2004); song repertoire size in turn has been shown to reflect developmental history, with more adverse histories leading to smaller song repertoires (Buchanan, Spencer, Goldsmith, & Catchpole, 2003; Nowicki, Searcy, & Peters, 2002). Thus, the hypothesis that adverse developmental experience would lead to lower dominance rank in adulthood is a reasonable one. It has not, however, been directly tested experimentally.

In recent studies in the European starling, *Sturnus vulgaris*, we have found that individuals that experience more early life adversity (due to competition during the nestling phase) show a number of behavioural differences in adulthood from those that experience less adversity. For example, they are less selective in what they eat (Bloxham, Bateson, Bedford, Brilot, & Nettle, 2014), and they tend to be hyperphagic and heavier for their skeletal size (Andrews et al., 2015). Accumulating fat reserves is a strategy used by subordinate individuals in the starling (Witter & Swaddle, 1995), and other passerines (Ekman & Lilliendahl, 1993), as insurance against their risk of exclusion from food resources. The reduced dietary selectivity might also reflect a foraging strategy appropriate for subordinate individuals, which may be restricted to lower-preference food resources and at risk of displacement from feeding sites by dominants.

---

* Correspondence: D. Nettle, Centre for Behaviour and Evolution, Newcastle University, Newcastle Upon Tyne NE2 4HH, UK
E-mail address: daniel.nettle@ncl.ac.uk (D. Nettle).

http://dx.doi.org/10.1016/j.anbehav.2017.03.026
0003-3472/

Thus, one simple explanation for the behavioural differences we have found between adults that experienced early life adversity and those that did not is that the early adversity birds are socially subordinate as adults, and therefore display the behavioural traits typical of subordinates. This explanation garners plausibility from the fact that forms of early life deprivation and insult have been shown to predict subordinate status in adulthood in primates and rodents (Bastian, Sponberg, Suomi, & Higley, 2003; Benner, Endo, Kakeyama, & Tohyama, 2015). To establish whether the explanation is correct, it is first necessary to determine whether early life adversity does indeed affect adult dominance in the starling.

In the present study, we investigated the relationships between early developmental history and adult dominance in a cohort of starlings previously hand-reared and subjected to an early adversity manipulation (Nettle et al., 2017). The 32 birds consisted of eight sets of four siblings. Within each sibling set, one bird was assigned to each of four experimental groups from day 5 to day 15 posthatching. The groups were composed of the factorial combinations of a high or a low amount of available food (henceforth, Plenty versus Lean Amount treatments), and a high or a low level of begging required per day (henceforth, Hard versus Easy Effort treatments). The four experimental groups were thus: Plenty-Easy, Plenty-Hard, Lean-Easy and Lean-Hard. After day 15, experimental groups were mixed together and kept in uniform conditions until adulthood. We then assembled them into their sibling quartets to measure dominance relative to their siblings from the other experimental groups at around 1 year old.

Our main question of interest was whether the experimental treatments (Amount and Effort) predicted dominance. We also aimed to test whether the attrition of erythrocyte telomeres over the developmental period (days 5–56) predicted dominance. Telomeres are the repetitive DNA caps on the ends of chromosomes that shorten with age, and the extent of developmental telomere attrition has been proposed as an integrative measure of the impact of developmental stressors (Boonekamp, Mulder, Salomons, Dijkstra, & Verhulst, 2014; Herborn et al., 2014). The experimental treatments both affected developmental telomere attrition, and did so additively (Nettle et al., 2017). However, developmental telomere attrition potentially provides a better measure of developmental stress than experimental treatment. First, developmental telomere attrition may capture variation within experimental groups in how severe the impact of the treatment was. Second, developmental telomere attrition also integrates sources of developmental stress other than those stemming from our experimental design. In several previous studies we have found that developmental telomere attrition is a better predictor of adult phenotype than experimental group (Bateson, Brilot, Gillespie, Monaghan, & Nettle, 2015; Nettle et al., 2015). Thus, a secondary objective was to test the possibility that developmental telomere attrition would be an additional, or perhaps better, predictor of adult dominance than the experimental treatments.

Previous studies of dominance in the European starling have performed one or more bouts of observation on a set of birds, and used the outcomes of all the competitive interactions over resources to derive a single dominance score for each individual within the group (Feare & Inglis, 1979; Spencer et al., 2004; Swaddle & Witter, 1995; Witter & Swaddle, 1995). Thus, these studies assume that dominance within a given group is stable over time, so that either a single observation bout suffices, or that data from different times can be amalgamated. However, no study has tested the assumption of stability over time. Moreover, while the contested resource is usually food, one study also included competitive interactions over perching sites in the calculation of dominance (Swaddle & Witter, 1995). Combining food and perch contests into a single dominance score assumes that the dominance ranking is the same for these two situations. This is an assumption that is untested in the starling, although there is evidence from the chaffinch, *Fringilla coelebs*, that food and perch contests produce the same hierarchy (Marler, 1955). Given that early life adversity may change the motivational salience of food (Andrews et al., 2015; Bloxham et al., 2014), it was particularly important for our current purposes to be able to separate out dominance in food-related interactions from those in other contexts, as the experimental treatments may have affected each in different ways. Thus, in our study we aimed to measure dominance in food contests separately from the ability to defend a preferred perch position; and to measure dominance in both contexts over 3 successive weeks, to establish whether each of these rankings was in fact stable over time.

The predictions of our study were as follows. First, we predicted that both dominance in competition over a valued food resource (since this is the typical way dominance is measured, we henceforth refer to it simply as ‘dominance’) and ability to defend a desirable perch position (henceforth ‘perch position’) would show stability over time, with scores in successive weeks correlated with one another. Second, we predicted that dominance and perch position would be correlated with one another, on the assumption that both reflect the same underlying ranking of competitive ability. Third, we predicted that greater early life adversity (either Lean Amount, Hard Effort or their combination) would be associated with lower adult dominance rank and lower perch position. If this prediction was supported, we aimed to further explore whether the dominance differences were mediated by differences in adult skeletal size or weight. Fourth, we predicted that greater developmental telomere attrition would be associated with lower adult dominance rank and perch position, and that developmental telomere attrition would provide greater explanatory power for adult dominance and perch position than experimental treatment alone. Fifth and finally, since in nonbreeding starlings, adult males tend to dominate females at feeding sites (Feare, 1984; Feare & Inglis, 1979), and occupy safer and more central positions in roosts (Feare, 1984), we predicted that females would have lower dominance ranks and perch positions than males in our cohort.

METHODS

Study Subjects and Housing

Subjects were 31 hand-reared European starlings (16 male, 15 female) from eight natal families. Birds were between 11 and 13 months old at time of testing. After fledging, and prior to the current experiment, birds were housed in groups of up to 24 in an indoor ‘home’ aviary (220 × 340 cm and 220 cm high; ca. 18 °C; ca. 40% humidity; 15:9 h light:dark cycle), apart from shorter periods of individual caging to take part in behavioural experiments not described here. Each home aviary always contained complete families; hence, the quartets of birds in which dominance was measured were familiar to one another. The home aviary was provided with environmental enrichment (foraging substrate, water baths, multilevel rope perches, suspended cardboard boxes as cover), clean drinking water, and an ad libitum diet of domestic chick crumbs (Special Diets Services ‘Poultry Starter (HPS)’), cat biscuits (Royal Canin Ltd. ‘Fit32’), dried insect food (Orlux insect patée), live mealworms and fruit. Owing to the unchanging light:dark cycle of long days, the birds remained in nonbreeding condition. Birds were individually identified by unique colour ring combinations.

For the present experiments, the four birds from each family were moved for testing to one of two large experimental cages (90 × 183 cm and 183 cm high) fitted with four rope perches (horizontal perches at heights 66 cm, 121 cm, 132 cm and a sloping