



Aggressiveness, Boldness and Parental Food Provisioning in Male House Wrens (*Troglodytes aedon*)

Craig A. Barnett*, †, Charles F. Thompson* & Scott K. Sakaluk*

* Behavior, Ecology, Evolution and Systematics Section, School of Biological Sciences, Illinois State University, Normal, IL, USA

† Department of Life Science, Rikkyo University, Tokyo, Japan

Correspondence

Craig Barnett, Department of Life Science, Rikkyo University, Nishi-ikebukuro 3-34-1, Toshima-ku, Tokyo 171-8501, Japan.
E-mail: optimalforager@hotmail.com

Received: March 5, 2012

Initial acceptance: April 22, 2012

Final acceptance: July 10, 2012

(S. Foster)

doi: 10.1111/j.1439-0310.2012.02092.x

Abstract

Behavioural syndromes have been identified in a large number of species, yet our understanding of them in an ecological context remains poor. Specifically, there are few data that relate behavioural syndromes to other biologically important behaviours and, ultimately, to reproductive success. In this field study, we examined the aggressiveness and boldness of free-living male house wrens (*Troglodytes aedon*) and found a statistically significant positive relationship between these two behaviours (i.e. a behavioural syndrome). When we examined the two axes of this behavioural syndrome in relation to the male's share of provisioning, we found a negative relation between a male's aggressiveness and his provisioning rate, but no relationship between male boldness and provisioning behaviour. These differences in provisioning behaviour among males with different levels of aggression may reflect differences in reproductive strategies or different life-history trade-offs among males. Moreover, these results indicate that while some behavioural traits may be correlated, this does not mean that traits that compose the behavioural syndrome cannot evolve independently of one another.

Introduction

Behavioural syndromes are correlations in a population that occur within individuals when two behaviours are compared or when the same behaviour is compared at different times (see Sih et al. 2004; Sih & Bell 2008; Sih et al. 2010 for reviews). Many authors use the terms 'personality' and 'behavioural syndrome' synonymously. However, there are two subtle differences between personalities and behavioural syndromes: (1) personalities have a demonstrable heritable element and (2) personalities are correlations between behaviours in different contexts and at different times (they are repeatable). Conversely, behavioural syndromes assume no genetic relation, and a syndrome can be either a correlation between two behaviours in different contexts or in the same behaviour at different times (Sih et al. 2010). Behavioural syndromes have been described in many taxa (Wilson et al. 1994; Boissy 1995; Gosling & John 1999; Koolhaas et al. 1999; Gosling 2001; Sih et al.

2004; Groothuis & Carere 2005; Réale et al. 2007; Logue et al. 2009; Cain et al. 2011; Conrad et al. 2011), and avian models have contributed extensively to this research. However, the majority of studies have been laboratory based, so behavioural syndromes in ecological contexts need more study (e.g. Hollander et al. 2008; Garamszegi et al. 2009; but see van Overveld & Matthysen 2010).

The correlation between aggressiveness (e.g. an individual's response to a conspecific competitor) and boldness (e.g. an individual's reaction to a nest predator; see Réale et al. 2007 for a discussion of our interpretation of aggressiveness and boldness) is one of the most widely studied syndromes in animals (see Sih & Bell 2008 for a review). However, there have been no studies that have examined this behavioural syndrome in relation to parental care in birds, although some studies have examined aggressiveness in relation to parental care (or some other measure that relates to reproductive success). Duckworth (2006) examined aggressiveness in two contexts in

western bluebirds (*Sialia mexicana*) in relation to male provisioning behaviour. She found that male aggressiveness was negatively correlated with the number of feeds the male made to the female during incubation, but not with the number of feeds he made to his young during the nestling period. Wingfield et al. (1990) has shown that testosterone (T) can, under some circumstances, increase male aggressiveness and concomitantly reduce parental care, which has been confirmed in other species (e.g. Ketterson & Nolan 1999). Similarly, there have been a small number of studies that have examined boldness in relation to parental care and reproductive success. Budaev et al. (1999) examined boldness in relation to paternal care in convict cichlids (*Amatitlania nigrofasciatum*) and found that bold and active males tended to provide more care to their offspring. Kontiainen et al. (2009) examined the nest defence behaviour of female Ural owls (*Stryx uralensis*) in response to human intruders (boldness). Bolder females recruited more offspring into the breeding population than females with less obvious defence behaviour. Therefore, parental care could be related to personality types and could lead to different parenting styles (Roulin et al. 2010).

Behavioural syndromes need not be adaptive (see Sih & Bell 2008; Sih et al. 2010 for discussion), although much personality research (and an increasing amount of research on behavioural syndromes) has focussed on understanding the life history and fitness benefits of different behavioural types (Dingemanse et al. 2004; Smith & Blumstein 2008). For example, in great tits (*Parus major*), exploration has been used as an index of personality, and evidence suggests that it is related to other ecologically important behaviours (e.g. Hollander et al. 2008; van Overveld & Matthysen 2010). Birds that explore new environments quickly (fast explorers) have also been shown to invest more in nest defence than slow explorers (Hollander et al. 2008), and there are links between exploration rate and fitness (Dingemanse et al. 2004; Quinn et al. 2009). Therefore, these differences in fitness could be explained by differences in behavioural type leading to different parental care strategies. Patrick & Browning (2011) examined this suggestion in great tits and found that there was no association between exploration behaviour and parental care. However, the relationship between parental care and different behavioural types requires further research.

Our study had two aims: (1) to determine whether there was a relationship between male aggressiveness and boldness (i.e. a behavioural syndrome) and (2) to relate any such syndrome to male nestling

provisioning behaviour. Assuming that a behavioural syndrome between aggressiveness and boldness exists, there are two complementary hypotheses that we can test. The first hypothesis is that an individual's behavioural type might relate to its share of nestling provisioning with more aggressive and bold individuals valuing reproductive events more than less bold and aggressive individuals, leading the former to invest more than the latter in each reproductive event (Roulin et al. 2010; Patrick & Browning 2011). This is because aggressive and bold individuals may achieve higher reproductive success per breeding attempt, but have shorter lifespans than less bold and aggressive individuals (e.g. Benus & Rondigs 1996). The second hypothesis is that behavioural type might relate to nestling provisioning behaviour with more aggressive and bold individuals investing less in provisioning than less bold and aggressive individuals. This is because there is a trade-off between the investment in provisioning and levels of aggressiveness (e.g. Ketterson & Nolan 1999; but see Class & Moore 2010). Therefore, males that provide a lower share of the total provisioning effort may invest more in other forms of parental investment (e.g. nest defence). Moreover, aggressiveness and boldness have been found to be correlated (Sih & Bell 2008) and may have a common physiological basis (see Koolhaas et al. 2010 for a review), which suggests that boldness may relate to parental investment in a similar manner to aggressiveness. To test these hypotheses, we examined the aggressiveness (reaction to a simulated territory intrusion by a conspecific male) and boldness (reaction to a human intruder) of a free-living population of male house wrens. We then explored whether a male's share of nestling provisioning was related to either of these behavioural traits to determine which hypothesis better explained these data.

Material and Methods

Study Species and Site

The house wren is a small (10–12 g), migratory, insectivorous passerine that breeds throughout much of temperate North America. Both sexes provision the nestlings, but only females incubate the eggs and brood the nestlings. Our study was conducted at the Mackinaw study site in McLean County, Illinois (40° 40'N, 88°53'W), which has 700 nestboxes distributed in a grid pattern (density 5.4 boxes/ha) in secondary deciduous forest surrounded by cultivated fields (see appendix 1 of Lambrechts et al. 2010 for dimensions

and other details of nestboxes). Males arrive before females near the end of April, and immediately begin placing twigs in a nestbox and singing to attract mates. Pairs typically raise two, occasionally three, broods of between four and eight nestlings each breeding season (for additional information, see Johnson 1998).

We used only males in this study for a number of reasons. First, males respond more readily to simulated conspecific territory intrusions (SCTIs) than females, and they are behaviourally more conspicuous than females (C. A. Barnett, pers. obs.). Second, it is difficult for a single person to observe a pair of birds simultaneously. Finally, males exhibit much greater variation in their provisioning behaviour among individuals than females (i.e. the coefficient of variation in provisioning is greater in males than in females; see DeMory et al. 2010; Barnett et al. 2011 for examples), making it easier to detect whether either aggressiveness or boldness is correlated with parental care.

Breeding Phenology

We assessed the behavioural syndrome of males within breeding attempts during the 2009 breeding season. The egg-laying period was defined as the time from when the first egg was laid in the nest (egg-1 day) to when no further eggs were laid. Although we did not always observe the actual egg-1 day, we were able to extrapolate the date that the first egg appeared because females typically lay one egg/day near dawn until the clutch is complete (Johnson 1998). Once the female had stopped laying and the eggs were warm to the touch, we considered incubation to have begun. Females normally incubate eggs for 12–13 d before they hatch. To determine the day on which the first egg hatched (brood-day 0), we began checking the nests daily after the tenth day of incubation.

Capture and Ringing of Birds

Males were captured the day before the SCTI took place (brood-day 2) using a sample of conspecific song to draw them into a mist net placed near the nestbox. Captured birds were ringed with a numbered US Fish and Wildlife aluminium band (both sexes) and three colour bands (on males) to aid in individual identification. We weighed adults and nestlings to the nearest 0.1 g (Acculab Pocket Pro 250, Acculab, 8 Pheasant Run, Newtown, PA, USA) and measured their tarsus (tarsometatarsus) to the nearest 0.1 mm with vernier callipers. Wing length and tail length of adults were

measured to the nearest 0.5 mm with a stopped rule. After processing, we released adults near where they had been captured.

Behavioural Assays

We assayed the aggressiveness and boldness of male birds, which enabled us to build behavioural profiles for each individual. We achieved this using two assays: (1) the SCTI to assess aggressiveness and (2) the human territorial intrusion (HTI) to assess boldness. While there might be similarities in how birds respond to these different threats, we used a well-established dichotomy between boldness and aggression (Huntingford 1976; Sih et al. 2004; Réale et al. 2007; Johnson & Sih 2007; but see Duckworth 2006; Cain et al. 2011 for alternative interpretations). Boldness is an individual's reaction to a risky situation (such as a predator or a human), whereas aggressiveness is an individual's agonistic response to a conspecific.

We were also conscious that parents' nest defence behaviour may change over the course of the breeding attempt (Montgomerie & Weatherhead 1988). Therefore, we standardized the age of the nestlings for each assay among nests. We also examined the relationships between the birds' behavioural profiles and the share of provisioning that males provided at their primary nest.

We designed the experiment to standardize the stimuli between individuals so that individuals' responses were not affected by differences in stimuli. This intentional standardization is common in the studies of behavioural syndromes and personality in relation to exploration (e.g., Patrick & Browning 2011).

Simulated Conspecific Territory Intrusions

We performed this assay using a bespoke mount of a conspecific male in concert with a playback of the species' song, which was recorded at our study site over 15 yr before this study. This method has been shown to elicit a more extreme stress response from birds than the use of live and caged conspecifics (Scriba & Goymann 2008). We conducted SCTIs on brood-day 3, an age at which nestlings are still vulnerable to being killed by intruding conspecifics and predators. The day before the SCTI (before they were captured and banded), the male's territory was watched to determine where they were active. This prior mapping was important to eliminate the possibility that the SCTI was conducted in an area not used by focal males. Before the trial began, we stripped a suitable branch of obstructing leaves and branches so

that the focal bird had an unrestricted view of the simulated intruder from within his territory. This branch was between 5 and 7 m from the nestbox and at a height of between 1.2 and 2.0 m. We fastened the mount to the stripped branch using fine galvanized steel wires that were attached to the mount's tarsi. We also broadcast a sample of song (which was the same for all birds) from an MP3 player with a built-in speaker to simulate a singing conspecific intruding into the focal bird's territory (playback amplitude was 75 dB at 1 m from the speaker). When the MP3 playback was initiated, the observer retired a further 10–15 m from the nestbox to observe the male's response (placing the observer 15–23 m from the nestbox). The focal male had 10 min from the time the observer was in place to respond to the intruder. Once the focal male had been spotted, we noted the time and visually identified him using binoculars. The response time (the time at which the male was first recorded) was normally within two minutes of the trial start ($\bar{x} \pm \text{SE}$: 48.1 \pm 8.23 s). He was then observed using binoculars for up to a further 10 min and every hop, jump, flight, alarm call, song, approach, wing flutter and attack was noted. Periods of time during which the male was out of view were excluded from the analysis (even when he could be heard singing or calling). In addition, the minimum approach distance (to the nearest 1 m) and the number of approaches the male made towards the mount were recorded. Although we attempted to watch the birds for a similar amount of time, this was not possible in all cases, so we standardized the values among individuals to actions noted while the bird was observable/total time the bird was in view (expressed as actions/min). We censored the data after 7 min because males normally responded most vigorously within the first 7 min of the start of the trial, after which their agitation declined (C. A. Barnett, pers. obs.).

Human Territorial Intrusions

We conducted HTIs (method modified from Hollander et al. 2008) on brood-day 6, which is approximately one-third of the way through the nestling period. The assay began when the observer walked through the territory to the nestbox, opened the lid of the nestbox to peer in, closed it and then stepped back 1 m. At this stage, the trial started, and the male was given 15 min to respond. The female usually responded before the male. Indeed, her alarm calls probably alerted the male that there was a threat in the territory. The time at which the focal male was first seen or heard was noted, and he was visually identified using binoculars.

The male was then watched and every hop, jump, flight, alarm call, song, wing flutter and attack was noted for a further 6 min. Males that did not respond after 15 min were classified as having no response.

Provisioning

On brood-day 6 (directly after the HTI was completed), we filmed the nest so that we could calculate the male provisioning rates and share of the total number of provisioning visits. Twenty-four hours before filming the nest, we erected a dummy camera on a 1.5-m steel pole at a distance of 2 m and at 45° from the perpendicular plane of the nestbox opening hole to habituate the birds to the presence of a camera-like object close to the nest (see DeMory et al. 2010 for further details). At the completion of the HTI, we replaced the dummy camera with a pocket video camera (Kodak Zx1, Eastman Kodak Company, Rochester, NY, USA). We filmed nests for approximately 120 min to ensure that we obtained at least 60 min of footage of the males from when they started visiting the nest again after the disturbance of setting up the camera. Females normally returned to the nest within 5 min of human departure and males normally visited the nest at the same time or shortly after the first female visit. Therefore, we calculated the male visit and provisioning rate from either the first male visit or when he was heard singing at or around the nest on the recording. A male's singing could be determined because the amplitude of his song was much greater than those of his neighbours, and from this time, we scored all male provisioning and nest visits. These data were standardized between individuals as hourly rates for later analysis. This method has been used successfully in the previous studies to generate significant effects and is a good indicator of relative male parental effort in this species (see DeMory et al. 2010; Barnett et al. 2011).

Statistics

We used Wilcoxon matched-pairs signed-ranks tests to compare the frequencies of an individual's behaviours between the contexts. We then tested the hypothesis that the overall behaviours between contexts were different by conducting a transformed-*z* test. To correlate aggressiveness with boldness in association with a male's provisioning contribution, it was first necessary to reduce the data using a principal components analysis. We conducted within-assay principal components analyses on both the aggressiveness and boldness data. For the aggressiveness analysis, we included the

following behaviours: (1) attacks, (2) approaches, (3) wing flutters, (4) songs, (5) flights and (6) hops. Attacks, approaches, wing flutters and songs tended to indicate aggressiveness. Flights and jumps were included as measures of activity. For the boldness analysis, we included the following behaviours: (1) attacks, (2) approaches, (3) wing flutters, (4) alarm calls, (5) flights and (6) hops. We interpreted attacks, approaches, wing flutters and alarm calls to indicate boldness, whereas we interpreted flights and hops to indicate activity.

We conducted a Spearman correlation analysis between aggression and boldness to examine the relationship between these two factors. To examine the relationship between the males' contributions to provisioning, we ran a generalized additive mixed model (GAMM). We used a binomial distribution and a logit link function in the model. We included the male's share of provisioning as the dependent variable and their boldness and aggressiveness scores as smoothed factors. We also included clutch size, start time of provisioning recording and egg-1 day in the model to control for these effects on male provisioning. Bird identity was included as a random factor to control for the non-independence of data. We conducted analyses using the 'gamm' command in the mgcv package of R (R Development Core Team 2010). We also examined the relationship between structural body size and behavioural type by conducting regression analyses of male tarsus length as a predictor variable, and aggressiveness scores, boldness scores and proportion of male feeds/h ($\sqrt{x + 0.5}$) as the dependent variables. All analyses were performed using SPSS version 15.0 for Windows® (SPSS Inc., Chicago, IL, USA) and R version 2.11.1 (R Development Core Team 2010).

Results

Behavioural Differences Across Contexts

Comparisons of behaviour between contexts that we assayed (aggressiveness and boldness) revealed significant differences in five of seven behaviours that we examined and a non-significant trend in another (Table 1). These results suggest that birds construed the two assays differently and responded in different ways in each assay. Moreover, it suggests that the birds were not responding to the human observer in the SCTI as they did in the HTI. Although the birds' behaviour was different between contexts (Table 1), individual levels of response were similar between contexts. We combined the probabilities for all the

Table 1: Median (minimum–maximum) frequencies/min for the behaviours measured in the aggressiveness and boldness assays that were obtained from the behavioural assays and Wilcoxon tests for differences across contexts

Behaviour	Aggressiveness	Boldness	Statistics
Attacks	0 (0–14.77)	0 (0–1.18)	$W = 10, p = 0.061$
Approaches	0.38 (0–1.5)	0 (0–0.70)	$W = 4, p < 0.001$
Wing flutters	0.63 (0–8.31)	0 (0–3.24)	$W = 56, p < 0.001$
Flights	2.4 (0.39–8.86)	2.97 (0.81–8.54)	$W = 181, p = 0.195$
Hops	1.2 (0–4.15)	3.06 (0–9.87)	$W = 61, p < 0.001$
Songs	4 (0.13–8.99)	0 (0–6.89)	$W = 12.5, p < 0.001$
Alarm calls	0.58 (0–8.33)	6.14 (0–15.25)	$W = 62, p < 0.001$

comparisons made in Table 1 to test the overarching hypothesis that there are differences in behaviour between contexts and found that there were differences in the behaviours expressed between contexts (transformed- Z : $Z = 7.416, p < 0.001$). The differences in behaviours noted in Table 1 led to them loading differently for the factors in the principle component analyses that we used to obtain our index of aggressiveness and boldness (Table 2).

Principle Components of Aggression and Boldness

We extracted three principal components from the SCTI data and two principle components for HTI data with eigenvalues >1 . The way in which the measured behaviours loaded for each first principle component was consistent with aggressiveness for SCTIs and boldness for HTIs (Table 2). This is because the behaviours that were related to aggressiveness and boldness (e.g. attacks, approaches and wing flutters) loaded more strongly than would be expected if the factors

Table 2: Factor loadings for measures of aggressiveness and boldness extracted using PCA from our behavioural assays. Figures in brackets are the amount of variation that each factor explains. Behaviours that loaded above 0.6 are emboldened. Dashes (–) indicate that behaviour was not included in the factor

Behaviour	Factor	
	Aggressiveness (36.0%)	Boldness (47.2%)
Eigenvalue	2.162	2.834
Attacks	0.556	0.831
Approaches	0.909	0.858
Wing flutters	0.684	0.314
Flights	0.613	0.930
Hops	0.081	0.232
Songs	0.420	–
Alarm calls	–	0.624

represented another behavioural context. Therefore, we used the first principle components extracted from the SCTI and HTI data as our indices of aggressiveness and boldness, respectively. All behaviours that were included in the PCA loaded positively onto our factors for aggression and boldness (Table 2). The factor that was used for aggressiveness explained 36.0% of the variance in the data, and the factor for boldness explained 47.2% of the variance in the data (Table 2).

Relationships Among Aggressiveness, Boldness and Provisioning Behaviour of Males

There was a significant positive relationship between aggressiveness and boldness in male house wrens ($r_s = 0.583$, $N = 31$, $p = 0.001$, Fig. 1a). This result confirms the behavioural syndrome between aggressiveness and boldness in house wrens. We then ran a GMM on parental care to examine its relationship with boldness and aggressiveness while controlling for brood size, time of day and egg-1 day (as an indicator of time within the breeding season). There was a significant negative relationship between aggressiveness and male provisioning behaviour ($r = -0.391$, $N = 31$, $p = 0.0371$, Fig. 1b). Individuals that were more aggressive reduced their share of provisioning visits that they made to nests. However, males' boldness scores were not related to their share of provisioning of nestlings ($r = -0.145$, $N = 31$, $p = 0.3726$, Fig. 1c). None of the co-variables included in the model explained a significant amount of variation: brood size ($p = 0.4200$), time of day ($p = 0.9518$) or egg-1 day ($p = 0.7010$). Finally, structural body size (tarsus length) was not a significant predictor for neither aggression ($F_{1,28} = 0.055$, $p = 0.816$, $r^2 = 0.002$), boldness ($F_{1,28} = 0.014$, $p = 0.917$, $r^2 = 0.001$), nor the male share of provisioning behaviour ($F_{1,28} = 1.586$, $p = 0.218$, $r^2 = 0.064$).

Discussion

We examined the aggression/boldness syndrome in males in association with their proportion of the total number of feeds they made. We found a significant correlation between aggressiveness and boldness, which we interpret as a behavioural syndrome for these two behavioural traits. We also found that aggressiveness was negatively related to the share of provisioning that the male provided. Therefore, these data suggest that there may be a trade-off between male aggressiveness and the share of provisioning that he provides, as suggested by Ketterson & Nolan

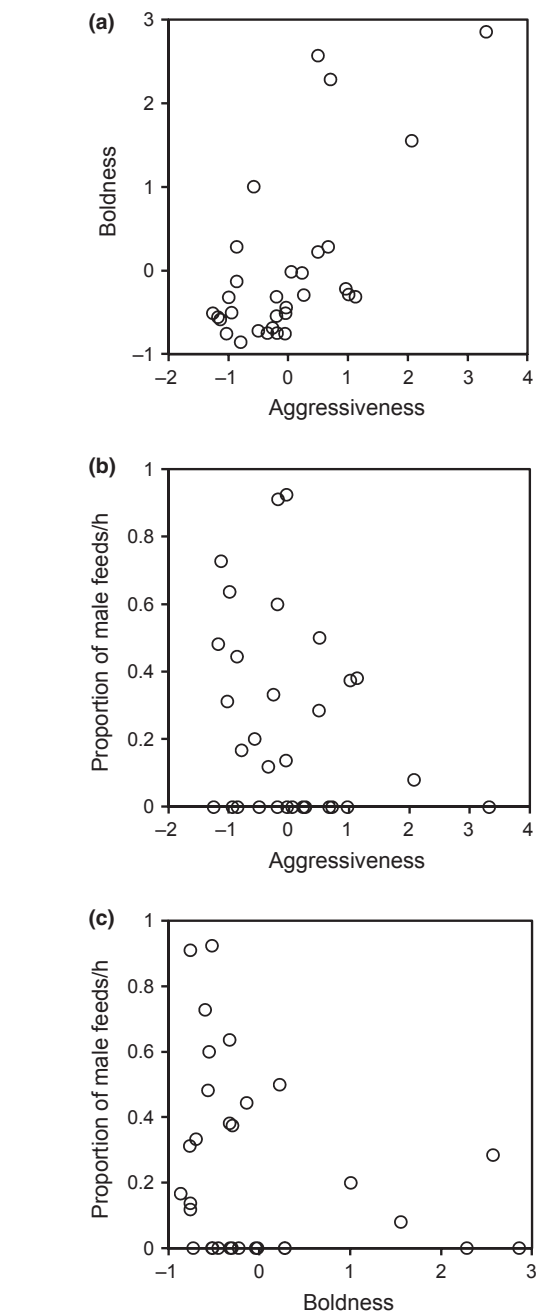


Fig. 1: The correlation among aggressiveness, boldness and provisioning rates: (a) boldness versus aggressiveness, (b) male share of provisioning versus aggressiveness and (c) male share of provisioning versus boldness.

(1999), but not found in all bird species (e.g. Class & Moore 2010). However, there was no relation between boldness and the male's share of provisioning. This is despite the possibility that the significant relationship we found between aggressiveness and boldness derives from common physiological

processes involved in these behavioural responses (Koolhaas et al. 2010).

This is among the first studies that have examined provisioning effort in relation to personality and behavioural syndromes in birds despite suggestions that there may be links (Roulin et al. 2010). A recent study found that there was no relationship between exploration behaviour and provisioning behaviour in great tits (Patrick & Browning 2011). Other studies suggest that boldness and exploration behaviour are positively correlated in many species (e.g., Grootuis & Carere 2005). However, we do not know how boldness relates to exploration behaviour in house wrens. Therefore, more research is required to examine the links between provisioning contributions towards offspring and links with other aspects of birds' behaviour.

It has also been recently suggested that trade-offs between behavioural and life-history traits could lead to correlational selection where traits are selected together, thus leading to behavioural syndromes (Stamps 2007). Aggressiveness and boldness may facilitate faster development and younger age of reproduction at the cost of higher mortality (Wolf et al. 2007), although empirical evidence for this is lacking. Another way this trade-off might be manifested is in the mating strategies that males of different behavioural types employ.

Although we collected no data on the house wren's breeding system, it is possible that there are different breeding strategies among house wrens with different behavioural types. Duckworth (2006) found that more aggressive western bluebird males did not have higher numbers of extra-pair young compared with less-aggressive males and had lower overall reproductive success than less-aggressive males. This suggests that more aggressive males are less effective at guarding their primary mates during their fertile periods because they may range over larger areas, but are unable to compensate for their poorer mate guarding by increasing their number of extra-pair copulations. Male house wrens are also socially and genetically facultatively polygynous (Forsman et al. 2008), and so, bolder and more-aggressive males may also be attempting to gain secondary females and extra-pair matings. In bighorn sheep (*Ovis canadensis*), there is evidence that bolder males may have greater reproductive success than shyer males, although more docile (i.e. less aggressive) males had lower levels of reproductive success (Réale et al. 2009). Finally, a study of a cooperative breeding cichlid (*Neolamprologus pulcher*) from Lake Tanganyika showed that some helpers invest more in territory defence while others

invest more in territory maintenance. Interestingly, the defending helpers were also more aggressive and explorative than helpers that maintained territories (Bergmüller & Taborsky 2007). These studies all suggest that the aggressiveness/boldness syndrome may be related to reproductive investment in males, but more research is clearly required to establish these links more fully and to determine how the aggressiveness/boldness syndrome relates to other behavioural and life-history traits.

We also found no relationship between a male's boldness and his contribution to nestling provisioning. While it is possible that individuals with different behavioural types were taking food items of differing size back to the nest, we find this unlikely (Wright et al. 1998; Brodmann & Reyer 1999; Schwagmeyer & Mock 2008; Barnett et al. 2011). An earlier study (Barnett et al. 2011) in this population of wrens found that food size was related to seasonal changes in insect abundance rather than the males' investment in parental care. Other studies that have examined the relationship between boldness and parental care and other aspects of parental care have generally found that bold individuals have greater levels of reproductive investment than less bold individuals. For example, bolder (in response to humans) female Ural owls recruited greater numbers of offspring into the breeding population (Kontiaainen et al. 2009). Bold and active male convict cichlids also tended to provide more care to their offspring (Budaev et al. 1999). Such results suggest that aggressiveness negatively affects parental care, whereas boldness has a positive relationship with parental care, and so, these two traits may be antagonistic with one another. Our results also show that aggressiveness is negatively related to provisioning behaviour, but that there was no relation between boldness and provisioning. Therefore, more research is needed to elucidate the relationship between the aggressiveness/boldness syndrome and the rest of the male's behavioural phenotype in house wrens.

In birds, male care is often essential in increasing the condition and survivorship of nestlings (see Ketterson & Nolan 1994 for a review). We found that more-aggressive males tended to reduce their contributions to offspring care, suggesting a trade-off between aggressiveness and parental care that is well documented in avian species (Ketterson & Nolan 1999; Stoehr & Hill 2000; Tuttle 2003). Generally, these studies find that males that invest more in aggressive behaviour have fewer resources to invest in provisioning their nestlings. However, Benus & Rondigs (1996) found that aggressive female house

mice (*Mus domesticus*) tended to nurse their pups more than less-aggressive dams, but that this did not translate to higher masses for pups of the more-aggressive females. Therefore, it is evident that the associations between both aggressiveness and boldness to provisioning effort are complex.

There is growing evidence that the reproductive success of pairs of birds can be related to their personality or the mix of personality of both birds (reviewed by Schuett et al. 2010). For example, a study in great tits found that pairs of birds that were at the extremes for exploration behaviour of a novel environment (i.e. fast and slow parents) raised nestlings that were larger, heavier and had higher levels of nest success than birds with intermediate exploratory levels (Both et al. 2005). Because we did not measure female responses, we were unable to test how different pair combinations of behavioural traits interact with one another. However, females that were paired with aggressive males contributed a greater proportion of the total provisioning. While females do compensate for males that provide little care (DeMory et al. 2010), more research is required to understand how personality is related to mate choice and reproductive success in birds.

Our methods revealed no discrete styles of behaviour as have been found in other studies (e.g. Albers et al. 1999; Carere et al. 2005). This may be because our method of combining many different behaviours may have reduced the apparent differences among individuals so that the behavioural measures were expressed along a continuum. However, it is possible that there are discrete behavioural styles among individuals in our population. Indeed, one reason that drew us to initiate this study in this species was the propensity of a subset of 'hyperbold' individuals to physically strike people as they approached their nests for periodic checks. These hyperbold individuals also tended to be consistent in their behaviour between years, because banded males have been known to strike nest checkers in different years (C. F. Thompson, unpubl. data). Whether these hyperbold males exhibit other behaviours that are unique and may be considered unique behavioural styles requires further study.

Behavioural syndromes might represent constraints on the evolution of plasticity in behaviour (Riechert & Hedrick 1993) or, alternatively, complex integrated suites of behaviours that more fully reflect how behavioural phenotypes are selected (Sih et al. 2004, 2010). Selection acts on the entire behavioural phenotype of an individual, which makes studying behaviours in an integrated manner an important

advance in increasing our understanding of how selection acts on the behaviour of free-living animals. This could lead to significant relationships developing between parents' wider behavioural phenotypes and their provisioning behaviour (correlational selection Price & Langen 1992). Here, we examined the aggression/boldness syndrome in male house wrens in relation to their contribution to provisioning behaviour. Our results show that aggression and parental care also form a syndrome because males' contribution to parental care tended to decline with increased aggressiveness. These data support the hypothesis that there is a trade-off between aggressiveness and a male's provisioning effort. However, more research is needed to elucidate the relationships between boldness and the male's wider behavioural phenotype.

Acknowledgements

We thank Keith Bowers, Kyle Caron, Megan DeMory, Courtney Kelly, Marion Sakaluk, Jennifer Sutherland, Laura Wig and Beau Williamson, Sr., for their field assistance. The ParkLands Foundation (Merwin Preserve) generously allowed us to use their land for this study. Angelo Capparella provided the male house wren museum specimen from the John Wesley Powell-Dale Birkenholz Natural History Collection at Illinois State University. This research was funded, in part, by grants from the National Science Foundation (IBN-0316580 and IOS-0718140). CAB was supported, in part, by a postdoctoral fellowship from the Program of Excellence in Neuroscience and Behavior, College of Arts and Sciences, Illinois State University.

Literature cited

- Albers, P. C. H., Timmermans, P. J. A. & Vossen, J. M. H. 1999: Evidence for the existence of mothering styles in Guinea pigs (*Cava aperea f. porsellus*). *Behaviour* **136**, 469–479.
- Barnett, C. A., Clairardin, S. C., Thompson, C. F. & Sakaluk, S. K. 2011: Turning a deaf ear: a test of the manipulating androgens hypothesis in house wrens. *Anim. Behav.* **81**, 113–120.
- Benus, R. F. & Rondigs, M. 1996: Patterns of maternal effort in mouse lines bidirectionally selected for aggression. *Anim. Behav.* **51**, 67–75.
- Bergmüller, R. & Taborsky, M. 2007: Adaptive behavioural syndromes due to strategic niche specialization. *BMC Ecol.* **7**, 12.
- Boissy, A. 1995: Fear and fearfulness in animals. *Q. Rev. Biol.* **70**, 165–191.

- Both, C., Dingemanse, N. J., Drent, P. J. & Tinbergen, J. M. 2005: Pairs of extreme avian personalities have highest reproductive success. *J. Anim. Ecol.* **74**, 667–674.
- Brodmann, P. A. & Reyer, H.-U. 1999: Nestling provisioning in water pipits (*Anthus spinoletta*): do parents go for specific nutrients or profitable prey? *Oecologia* **120**, 506–514.
- Budaev, S. V., Zworykin, D. D. & Mochev, A. D. 1999: Individual differences in parental care and behaviour profile in the convict cichlid: a correlation study. *Anim. Behav.* **58**, 195–202.
- 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.
- Carere, C., Drent, P. J., Koolhaas, J. M. & Groothuis, T. G. G. 2005: Personalities in great tits, *Parus major*: stability and consistency. *Anim. Behav.* **70**, 795–805.
- Class, A. M. & Moore, I. T. 2010: Is there a trade-off between caring for offspring and territorial aggression in tropical male rufous-collared sparrows (*Zonotrichia capensis*)? *Behaviour* **147**, 1819–1839.
- Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltz, J. B. & Sih, A. 2011: Behavioural syndromes in fishes for ecology and fisheries management. *J. Fish. Manag.* **78**, 395–435.
- DeMory, M. L., Thompson, C. F. & Sakaluk, S. K. 2010: Male quality influences male provisioning in house wrens independent of attractiveness. *Behav. Ecol.* **21**, 1156–1164.
- Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004: Fitness consequences of avian personalities in a fluctuating environment. *Proc. R. Soc. Lond. B* **271**, 847–852.
- Duckworth, R. 2006: Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behav. Ecol.* **17**, 1011–1019.
- Forsman, A. M., Vogel, L. A., Sakaluk, S. K., Johnson, B. G., Masters, B. S., Johnson, L. S. & Thompson, C. F. 2008: Female house wrens (*Troglodytes aedon*) increase the size, but not immunocompetence, of their offspring through extra-pair mating. *Mol. Ecol.* **17**, 3687–3709.
- Garamszegi, L. Z., Eens, M. & Török, J. 2009: Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. *Anim. Behav.* **77**, 803–812.
- Gosling, S. D. 2001: From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* **127**, 45–86.
- Gosling, S. D. & John, O. P. 1999: Personality dimensions in nonhuman animals: a cross-species review. *Curr. Dir. Psychol. Sci.* **8**, 69–75.
- Groothuis, T. G. G. & Carere, C. 2005: Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.* **29**, 137–150.
- Hollander, F. A., Van Overveld, T., Tokka, I. & Matthysen, E. 2008: Personality and nest defence in the great tit (*Parus major*). *Ethology*, **114**, 405–412.
- Huntingford, F. A. 1976: The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Anim. Behav.* **24**, 245–260.
- Johnson, L. S. 1998: House Wren (*Troglodytes aedon*). In: The Birds of North America, No. 380 (A. Poole and F. Gill, eds). The Birds of North America, Inc., Philadelphia, PA.
- Johnson, J. C. & Sih, A. 2007: Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Anim. Behav.* **74**, 1131–1138.
- Ketterson, E. D. & Nolan, V. Jr 1994: Male parental behavior in birds. *Annu. Rev. Ecol. Syst.* **25**, 601–628.
- Ketterson, E. D. & Nolan, V. Jr 1999: Adaptation, exaptation, and constraint: a hormonal perspective. *Am. Nat.* **154**, S4–S25.
- Kontiaainen, P., Pietiäinen, H., Huttenen, K., Karell, P., Kolunen, H. & Brommer, J. E. 2009: Aggressive Ural owl mothers recruit more offspring. *Behav. Ecol.* **20**, 789–796.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. & Blokhuis, H. J. 1999: Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* **23**, 925–935.
- Koolhaas, J. M., de Boer, S. F., Coppens, C. M. & Buwalda, B. 2010: Neuroendocrinology of coping styles: towards understanding the biology of individual variation. *Front. Neuroendocrinol.* **31**, 307–321.
- Lambrechts, M. M., Adriaensen, F., Ardia, D. R., Artemyev, A. V., Atiénzar, F., Bañbura, J., Barba, E., Bouvier, J.-C., Camprodon, J., Cooper, C. B., Dawson, R. D., Eens, M., Eeva, T., Faivre, B., Garamszegi, L. Z., Goodenough, A. E., Gosler, A. G., Grégoire, A., Griffith, S. C., Gustafsson, L., Johnson, L. S., Kania, W., Keiš, O., Llambias, P. E., Mainwaring, M. C., Mänd, R., Massa, B., Mazgajski, T. D., Møller, A. P., Moreno, J., Naef-Daenzer, B., Nilsson, J.-Å., Norte, A. C., Orell, M., Otter, K. A., Park, C. R., Perrins, C. M., Pinowski, J., Porkert, J., Potti, J., Remes, V., Richner, H., Rytönen, S., Shiao, M.-T., Silverin, B., Slagsvold, T., Smith, H. G., Sorace, A., Stenning, M. J., Steward, I., Thompson, C. F., Tryjanowski, P., Török, J., van Noordwijk, A. J., Winkler, W. & Ziane, N. 2010: The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. *Acta Ornithol.* **45**, 1–26.
- Logue, D. M., Mishra, S., McCaffrey, D., Ball, D. & Cade, W. H. 2009: A behavioral syndrome linking courtship behavior toward males and females predicts reproductive success from a single mating in the hissing cockroach, *Gromphadorhina portentosa*. *Behav. Ecol.* **20**, 781–788.

- Montgomerie, R. D. & Weatherhead, P. J. 1988: Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* **63**, 167–187.
- van Overveld, T. & Matthysen, E. 2010: Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biol. Lett.* **6**, 187–190.
- Patrick, S. C. & Browning, L. E. 2011: Exploration behaviour is not associated with chick provisioning in great tits. *PLoS ONE* **6**, e26383.
- Price, T. & Langen, T. 1992: Evolution of correlated characters. *Trends Ecol. Evol.* **7**, 307–310.
- Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A. & Sheldon, B. C. 2009: Heterogeneous selection on a heritable temperament trait in a variable environment. *J. Anim. Ecol.* **78**, 1203–1215.
- R Development Core Team. 2010: R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007: Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318.
- Réale, D., Martin, J., Coltman, D. W., Poissant, J. & Festa-Bianchet, M. 2009: Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.* **22**, 1599–1607.
- Riechert, S. E. & Hedrick, A. V. 1993: A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Anim. Behav.* **46**, 669–675.
- Roulin, A., Dreiss, A. N. & Kölliker, M. 2010: Evolutionary perspective on the interplay between family life, and parent and offspring personality. *Ethology* **116**, 787–796.
- Schuett, W., Tregenza, T. & Dall, S. R. X. 2010: Sexual selection and animal personality. *Biol. Rev.* **85**, 217–246.
- Schwagmeyer, P. L. & Mock, D. W. 2008: Parental provisioning and offspring fitness: size matters. *Anim. Behav.* **75**, 291–298.
- Scriba, M. & Goymann, W. 2008: The decoy matters! Hormonal and behavioural differences in the reaction of territorial European robins towards stuffed and live decoys. *Gen. Comp. Endocrinol.* **155**, 511–516.
- Sih, A. & Bell, A. M. 2008: Insights for behavioral ecology from behavioral syndromes. *Adv. Study Behav.* **38**, 227–281.
- Sih, A., Bell, A., Johnson, J. C. & Ziemba, R. E. 2004: Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* **73**, 241–277.
- Sih, A., Bell, A. & Johnson, J. C. 2010: Behavioral Syndromes. In: *Evolutionary Behavioral Ecology* (Westneat, D. F. & Fox, C. F., eds). Oxford Univ. Press, New York, NY, pp. 516–530.
- Smith, B. R. & Blumstein, D. T. 2008: Fitness consequences of personality: a meta-analysis. *Behav. Ecol.* **19**, 448–455.
- Stamps, J. 2007: Growth-mortality tradeoffs and ‘personality traits’ in animals. *Ecol. Lett.* **10**, 355–363.
- Stoehr, A. M. & Hill, G. E. 2000: Testosterone and the allocation of reproductive effort in male house finches (*Carpodacus mexicanus*). *Behav. Ecol. Sociobiol.* **48**, 407–411.
- Tuttle, E. M. 2003: Alternative reproductive strategies in the white-throated sparrow: behavioral and genetic evidence. *Behav. Ecol.* **14**, 425–432.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994: Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M. Jr & Ball, G. F. 1990: The “challenge hypothesis”: theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* **136**, 829–846.
- Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J. 2007: Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581–585.
- Wright, J., Both, C., Cotton, P. A. & Bryant, D. 1998: Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. *J. Anim. Ecol.* **67**, 620–634.