Animal behaviour

Bearded ladies: females suffer fitness consequences when bearing male traits

Lindsey Swierk and Tracy Langkilde

Department of Biology, Intercollege Graduate Program in Ecology, and Center for Brain, Behavior and Cognition, The Pennsylvania State University, 208 Mueller Laboratory, University Park, PA 16802, USA

A central assumption in evolutionary biology is that females of sexually dimorphic species suffer costs when bearing male secondary sexual traits, such as ornamentation. Nevertheless, it is common in nature to observe females bearing rudimentary versions of male ornaments (e.g. ‘bearded ladies’), as ornaments can be under similar genetic control in both sexes. Here, we provide evidence that masculinized females incur both social and reproductive costs in nature. Male fence lizards (Sceloporus undulatus) discriminated against ornamented females during mate choice. Ornamented females had lower reproductive output, and produced eggs that were laid and hatched later than those of non-ornamented females. These findings support established theories of the evolution of sexual dimorphism and intralocus sexual conflict, and raise questions regarding the persistence of masculinizing ornamentation in females.

1. Introduction

In sexually dimorphic species, males are usually the more ornamented sex. Although ornaments pose energetic or survival costs, these can be offset by reproductive benefits if ornaments allow males to successfully compete for and attract females [1]. Females sometimes bear rudimentary versions of male sexual ornaments if genetic correlation for the trait exists between the sexes [2–4]. Human females, for example, may experience male-pattern facial hair growth as a result of excess androgen production [5], although usually to a lesser degree than average males. The assumption that females experience fitness costs of masculinization is central to key ideas in evolutionary biology, including the evolution of sex-specific chromosomes and sex-biased gene regulation [6–8], the origin of sexual dimorphism [2,3,7] and maintenance of phenotypic variation in a population [9]. However, whether masculinized females actually experience social and reproductive costs in nature is surprisingly underexplored.

The eastern fence lizard (Sceloporus undulatus) facilitates examination of the fitness consequences of male-pattern ornamentation in females (hereafter ‘female ornamentation’). Males bear bright blue ventral badges outlined in black on both sides of their throats and abdomens (figure 1a). Plasma testosterone drives the production of badges, which have little seasonal variation and appear to be fixed upon sexual maturity [10]. Badges serve as sex-identifiers—females painted with artificial badges are treated aggressively by males, whereas males with obscured badges are courted [11] and females are attracted to males bearing larger badges [12]. Notably, a relatively large percentage (see §3) of females bear rudimentary badges, which are smaller and less vibrant than badges on adult males (figure 1b). Ornamented females are otherwise physically indistinguishable from females without badges (figure 1c), and there is no known function of badges in female fence lizards.

We used fence lizards to test the hypothesis that females bearing a rudimentary form of a male sexual ornament would experience an associated fitness cost (as per [2,3,7]). We expected that these costs could take two forms: (i) since
badges act as sex-identifiers [11], males may preferentially court females lacking badges and (ii) since badges result from high levels of plasma testosterone (in males and females; [10]), they may indicate low female fecundity associated with high testosterone in females (e.g. [13]).

2. Material and methods

(a) Field survey and fecundity estimates
In spring 2006 and 2007, we obtained adult female fence lizards (n = 118) from four field sites in the southeastern USA. Females were measured for snout–vent length (SVL; to the nearest mm), scored for the presence or the absence of badges on their ventral surface (abdomen and/or throat), and palpated to determine reproductive status. We recorded the number, sex and weight (clutch mass, to 0.01 g) of the offspring produced by a subset of these females (n = 34) in the laboratory (see the electronic supplementary material).

(b) Male mate preference
In 2008, we collected 24 gravid females from two of our study sites (see electronic supplementary materials), and raised their offspring to sexual maturity (see [14]; see [14] for detailed description of the trials). We quantified the total time males spent associating with and courting each female, and we recorded the presence or the absence of badges on females.

(c) Statistical analysis
To test whether SVL and mass differed between females with and without badges, we used a MANCOVA with site, date and badge score as predictors. We tested whether females with and without badges differed in reproductive status using a nominal logistic regression, with site as a factor and female SVL as a covariate. We also compared the following parameters using separate ANCOVAs: egg number, clutch mass, hatching success, laying date, hatching date and sex ratio, each with site of origin as a factor and maternal SVL as a covariate. Maternal identity was a random effect in laying and hatching date models to account for between-clutch variation. We used two separate mixed models to test whether a male’s adjusted association and courtship times (see electronic supplementary material) were related to female badges, with male identity as a random effect.

3. Results
Of the 118 female fence lizards surveyed from the field, 76% bore badges (ranging from 44 to 95% among populations). Females with and without badges did not differ in mass or SVL (F_{2,107} = 0.045, p = 0.955). Although ornamented females had the same reproductive status (F^2 < 0.001, p > 0.999) and laid the same number of eggs as non-ornamented females (F_{1,30} = 0.936, p = 0.341; figure 2a), ornamented females laid clutches of lower total mass (F_{1,29} = 4.219, p = 0.049; figure 2b) and these were laid on average 13 days later (F_{1,282} = 50.65, p < 0.001; figure 2c). Female ornamentation did not influence hatching success (F_{1,31} = 1.522, p = 0.227; figure 2d), but eggs of ornamented females hatched 8 days later than those of non-ornamented females (F_{1,283} = 38.483, p < 0.001; figure 2e). Clutch sex ratio did not differ between ornamented and non-ornamented females (F_{1,32} = 2.132, p = 0.154; figure 2f).

Ornamented females experienced rejection from males: males spent less time associating with (F_{2,30} = 34.635, p < 0.001; figure 2g) and courting (F_{2,26} = 26.805, p < 0.001; figure 2h) females with male-pattern ornamentation.

4. Discussion
Here, we provide evidence that females with male-pattern ornamentation experience reproductive and social costs in nature. Males discriminated against male-pattern females, even though chemical signals should allow males to correctly determine the females’ sex despite their badges [15]. It is therefore likely that male disinterest was prompted by more than simple sex misidentification (which additionally could exacerbate rejection of ornamented females in the field, [11]). Delayed laying and hatching of ornamented female clutches may reflect delayed mating owing to male disinterest, and may reduce male (and female) fitness owing to lower offspring survival caused by limited time to secure energetic reserves before overwintering ([16], but see [17]).

The opposing fitness optima of ornamentation may be due, in part, to the fact that badges are mediated by high plasma testosterone [10]. Testosterone can cause decreased growth rates and survivorship, and increased levels of parasitism [18]. Benefits of testosterone (including increased home range size, reproductive activity and endurance, [18]) can offset these costs for males [19]. However, females experience costs of high testosterone including delayed laying [20], increased stress and reduced immune function [21] and mating rates [22] and, if testosterone levels are inherited or maternally transferred, females should produce ‘unsexy’ and less fit daughters [23]. As a result, males may benefit from preferentially mating with low testosterone (i.e. non-ornamented) females.

Our findings contrast with other studies that reveal that ornamented females have increased—not decreased—fecundity or condition (reviewed in [24]). In some cases, ornaments serve as indicators of quality in both sexes, with both sexes preferring the same ornaments (e.g. [25]). Male and female fence lizards...
have opposing mating preferences, and the relationship between reproductive output and ornaments is therefore likely to be positive for males but negative for females of this species. This finding represents a natural analogue to experiments testing the consequences of females bearing artificial male traits (e.g. [26]) and could provide evidence of directional selection against a male-pattern trait in females (instead of stabilizing selection, [9], or directional selection for a male-pattern trait in females, [24]).

If female fence lizards experience reproductive costs due to vestigial male ornamentation, and no known associated benefits (e.g. sexy or higher surviving sons, [27]), why are these rudimentary ornaments maintained? Masculinized females of some species adaptively bias offspring sex ratio to produce proportionately more males [27], although we found no evidence of this (see Results). There may be unmeasured benefits to female ornamentation, e.g. enhanced social dominance of ornamented females. Alternatively, it is possible that rudimentary ornamentation in female fence lizards may in fact be functionless and slowly 'going out of fashion'. Opposing fitness optima between sexes for a single trait typically leads to the evolution of sexual dimorphism [7]. However, when males and females share the same genetic drivers of ornamentation, complete sexual dimorphism may be very slow, occurring over a large number of generations, even when the ornament is under negative selection in one sex [2,3]. The presence of vestigial blue badges in fence lizard females may therefore represent a snapshot of the evolutionary process towards complete sexual dimorphism.

Acknowledgements. We thank N. Freidenfelds, K. Boronow, N. Ligon, C. Norjen and M. Goldy-Brown for field and laboratory assistance,
and B. Chitterlings, L. Kruuk, and an anonymous reviewer for valuable comments.

Data accessibility. Data are available through Penn State’s data repository, Scholarsphere, at https://scholarsphere.psu.edu.

References