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Green swordtails alter their age at maturation in response to the population level of male ornamentation

Craig A. Walling†,* Nick J. Royle†, Neil B. Metcalfe and Jan Lindström

Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK
†Author for correspondence (c.a.walling@exeter.ac.uk).
*Present address: Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, UK.

Effects of the social environment on age at sexual maturation are assumed to require direct interactions, such as suppression of subordinates through aggression from dominants. Using green swordtails (Xiphophorus helleri), we demonstrate for the first time that females and males adjust their age at maturation in response to visual cues of male sexual ornamentation in the current environment: females matured earlier, whereas males matured later if all the mature males seen had large ornaments. Thus, age at maturation shifted in accordance with the perceived quality of mates (females) or mating competitors (males), demonstrating a capability to use visual cues from the environment to strategically adjust rates of sexual development.

Keywords: life-history strategy; local mate competition; phenotypic plasticity; sexual maturation; social environment

1. INTRODUCTION

The timing of the onset of sexual maturation is an important determinant of fitness and involves the resolution of several trade-offs. For example, in species with indeterminate growth patterns, individuals that mature early trade-off the costs of small size (lower fecundity (Andersson 1994) or reduced offspring quality (Clutton-Brock et al. 1988)) against the benefits of maturing early (e.g. reduced risk of dying prior to reproduction, Roff 1992; Stearns 1992). There are also physiological and other costs associated with being sexually mature (Bentley et al. 1998) and thus individuals should delay maturation until the benefits will be maximized. Given that a number of environmental variables, such as resource availability and predation risk, may alter the costs and benefits of maturing at different ages, the optimal age at maturation should vary among environments. One potential environmental variable that may alter the optimal age at maturation is the availability of suitable mates, since this will depend on factors such as the operational sex ratio and the relative quality of available mates or sexual competitors (Rodd et al. 1997). Therefore, various features of the environment in which an individual develops determine the optimal age of maturation, and perception of these features by juveniles might be expected to influence the timing of maturation. Chemical cues have been shown to affect the timing of maturation in a variety of species (e.g. insects, Pereira et al. 2006; fishes, Aday et al. 2003; mammals, Rekwot et al. 2001). Here, we test a different sensory modality, asking whether juvenile animals can use visual cues in the assessment of their future probability of mating, and test the prediction that the timing of sexual maturation should be sensitive to the perceived quality of mature males (as indicated by sexual ornament size).

We used green swordtails (Xiphophorus helleri), live-bearing Poeciliid fish from sub-tropical North and Central America which have well-documented visual sexual signals and flexible timing of sexual maturation. Direct physical interactions with dominant individuals can cause subordinate male swordtails to delay maturation (Borowsky 1973; Campton 1992), and while such responses may be a physiological stress response as a consequence of social suppression, it is also known that they use visual cues when making other reproductive decisions such as choice of mate (Basolo 1990; Johnson & Basolo 2003). Male green swordtails develop a long, brightly coloured and costly (Basolo & Alcaraz 2003; Basolo & Wagner 2004) sexual ornament at maturity (an extension to the caudal fin; the ‘sword’). Females, in mate choice trials based on visual cues, prefer males of large body size, and among males of similar body size, prefer those with longer swords (Basolo 1990; Rosenthal & Evans 1998). Female preference for longer swords appears to represent a bias for larger apparent size, with investment in sword length representing a cheaper way of increasing the apparent size than investment in body length (Basolo 1998; Rosenthal & Evans 1998). While sexual maturation in males triggers the development of the sword, it also causes a reduction in the rate and eventual cessation of body growth (Basolo 1998; Royle et al. in preparation), and so the timing of maturation has a marked effect on a male’s competitive ability as an adult, since smaller males are usually subordinate (Beaugrand et al. 1996) and although sword length also has an effect on competitive ability, it is less than that of body size (Benson & Basolo 2006).

2. MATERIAL AND METHODS

(a) Creating groups of juveniles

Thirteen breeding females from different families were used to generate the fry used in this study. Breeding females were first generation offspring of wild-caught females from Belize, Central America. Each breeding female was mated to a single mature male and consequently all fry produced by a female were full siblings. Each brood of siblings was separated from the mother on the day of birth and kept as a single brood until the juveniles reached two months of age. At this point, each brood was used to form two sibling groups of three to five juveniles, with one group randomly allocated to the long-sworded treatment and another to the short-sworded treatment. Treatment groups were set up when fry were two months of age in order to avoid the period of high juvenile mortality that occurs early in life. Group sizes did not differ between treatments (mean ± s.e. for long-sworded treatment = 4.69 ± 0.21 fish per group, n = 13 groups; mean ± s.e. for short-sworded treatment = 4.77 ± 0.67, n = 13 groups; paired samples t-test t12 = 1.000, p = 0.337).

(b) Experience protocol

Each sibling group (n=20) was maintained in its own experimental glass tank (38 cm × 21 cm × 20 cm (L × W × H)) on a 12:12 h L:D cycle and fed Hikari tropical micropellets (Kyorin, Japan) ad libitum twice daily. Stimulus males were from a stock population of males originating from the same wild population as the juveniles used in this study but unrelated to them. Males were introduced singly into a...
small compartment at the front of each experimental tank (12 cm × 21 cm × 20 cm (X × Y × Z)), which allowed the juveniles in that tank visual, but no tactile or chemical communication with that male and vice versa. Tanks were screened so that the only sexually mature fish that each group of juveniles saw from the day that they were born were the single stimulus males placed in the small compartment in front of their tank. Juveniles in the long-sworded treatment saw stimulus males with swords of 18 mm or greater (mean ± s.e. sword length = 22.3 ± 0.4 mm; mean ± s.e. sword as a percentage of body length = 54.6 ± 0.9%), while those in the short-sworded treatment saw males with swords of 12 mm or shorter (mean ± s.e. sword length = 8.0 ± 0.3 mm; mean ± s.e. sword as a percentage of body length = 19.5 ± 0.9%). Each stimulus male remained in its compartment for 3 days before being removed. Juveniles saw the first male at approximately 70 days of age and a subsequent male every 30 days thereafter until they had seen a total of four different males. Ages at maturation for long-sworded and 12/62 for short-sworded; (one-way ANOVA, $F_{1,69} = 1.354$, $p = 0.247$) and stimulus males did not differ in standard length, linear mixed effects model, $t_{12} = -0.601$, $p = 0.599$.

(c) Assessing and measuring size at maturation

Juveniles were checked weekly for the first signs of sexual maturation, defined as the development of the gonopodium for males and the gravid spot for females (Marcus & McCune 1999). Upon maturation, a fish was removed from its experimental tank, weighed (to 0.001 g) and measured (standard length, from the tip of snout to the caudal peduncle to the nearest 0.1 mm), and then placed into a separate tank. A total of 95 fish reached sexual maturity, 36 females and 9 males from the long-sworded treatment and 33 females and 17 males from the short-sworded treatment. Mortality always affected the smallest individuals within a tank and was similar between treatments (16/61 for long-sworded and 12/62 for short-sworded; $\chi^2 = 0.46$, $p > 0.1$). There was no significant difference between the treatments in sex ratio (= number of females/total number of fry) (median (25th, 75th percentile) = 1.0 (0.59, 1.0) long-sworded treatment, 1.0 (0.33, 1.0) short-sworded treatment, Mann–Whitney U-test, $N = 13$, $Z = -0.799$, $p = 0.479$), the order of sexes within the size hierarchy of the group (i.e. whether the largest fish in the group was male or female, etc.) (median (25th, 75th percentile) position of females in the hierarchy = second (1.25, 3.75) long-sworded treatment, third (2.0, 3.0) short-sworded treatment, Mann–Whitney U-test, $N = 69$, $Z = -0.210$, $p = 0.834$) or the order in which males and females matured (median (25th, 75th percentile) = second (1.0, 2.75) long-sworded treatment females, second (1.0, 2.0) short-sworded treatment females, Mann–Whitney U-test, $N = 69$, $Z = -0.122$, $p = 0.903$).

(d) Statistical analysis

All data were tested for normality and homogeneity of variance and treated accordingly. Analyses were carried out using SPSS v. 12.0 or S-Plus v. 2000. General linear mixed effects models were used to analyse the age and the size at maturation, with treatment and sex as fixed factors and family as a random factor.

3. RESULTS

We compared the age and the size at maturation of both males and females maturing from the two treatment groups, while controlling for family identity. Analysis of age at maturation revealed a significant effect of treatment (linear mixed effects model, $t_{129} = 2.59$, $p = 0.01$) and a significant interaction between treatment and sex (linear mixed effects model, $t_{129} = -3.01$, $p = 0.004$; Figure 1). Females reared in the long-sworded treatment matured earlier than those in the short-sworded treatment, but this pattern was reversed in males. Analysis of size at maturation (both standard length and mass) revealed a significant effect of treatment (for standard length, linear mixed effects model, $t_{61} = 3.07$, $p = 0.003$; for mass (ln transformed), linear mixed effects model, $t_{61} = 2.95$, $p = 0.004$), but no interaction between treatment and sex (for standard length, $t_{61} = 1.19$, $p = 0.24$; for mass (ln transformed), $t_{61} = 0.95$, $p = 0.35$; thus, these interactions are not included in the previous models; Figure 2a,b). Females reared in the long-sworded treatment matured at a smaller size than females reared in the short-sworded treatment, whereas there was no significant difference between the treatments in the size of males.

4. DISCUSSION

The results of this experiment suggest that the age and the size at sexual maturation of green swordtails are plastic in response to visual cues, indicative of the current distribution of male phenotypes in the population. Females matured earlier and at a smaller size (whereas males matured later), when all of the mature males that they had seen had longer as opposed to shorter swords.

Earlier maturation of females exposed to visual cues of longer as opposed to shorter swords should reduce the risk of mortality prior to reproduction by reducing the time spent as a juvenile (Streams 1992), and allow females to take advantage of the opportunities for mating with males that have large sexual ornaments. In contrast, the delayed maturation of females that saw only shorter-sworded males should allow females to delay the costs associated with being sexually mature and grow for longer. Therefore, by reaching a larger size at maturation, they have the potential for higher reproductive output. Females that mature earlier and at a smaller size will be at a disadvantage compared to those that mature later but at a larger size, which could lead to a decrease in the current distribution of male phenotypes in the population. Females matured earlier and at a smaller size (whereas males matured later), when all of the mature males that they had seen had longer as opposed to shorter swords.

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