Foraging costs drive female resistance to a sensory trap

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Male ornaments can evolve through the exploitation of female perceptual biases such as those involved in responding to cues from food. This type of sensory exploitation may lead to confusion between the male signals and the cues that females use to find/recognize food. Such interference would be costly to females and may be one reason why females evolve resistance to the male ornaments. Using a group of species of viviparous fish where resistance to a sensory trap has evolved, we demonstrate that females exposed to an ornament that resembles food have a diminished foraging efficiency, that this effect is apparent when foraging on a food item with which the ornament shares visual attributes, and that not all species are equally affected by such confusion. Our results lend support to the model of ornamental evolution through chase-away sexual conflict.

Keywords: sensory traps; foraging efficiency; feeding response; chase-away sexual conflict; viviparous fish

1. INTRODUCTION

It is increasingly clear that male ornaments can be attractive because they exploit perceptual biases of the females [1]. If the biases exploited are adaptive in other contexts, such as food detection or recognition [2–6], they are termed ‘sensory traps’ [7]. Males benefit from the display of ornaments that constitute sensory traps because they increase both the rate at which they are approached by females and the time females spend in their vicinity, regardless of what motivation (e.g. feeding) is driving the females [8]. Females thus drawn into the males’ vicinity are consequently exposed to courtship and mating attempts more often and for longer periods than would be optimal for them. As elevated mating rates are often costly to females [9], and so is being exposed to persistent courtship [10–12], natural selection should favour the evolution of female resistance to the male sensory traps [13]. This can be achieved by increasing the threshold to respond to the male signals, which in turn selects for more conspicuous/salient ornaments that then become elaborated through a ‘chase-away’ process [13].

The chase-away model of ornament evolution assumes the existence of costs for females such as those derived from an increased exposure to males (see above), a heightened probability of mating with suboptimal males [14], and a reduction in the adaptive responses of the females to the cues from the environment that are being imitated and subsequently exaggerated by the male ornaments [6,15]. This may be detrimental for the females if their increased response threshold leads them to ignore relevant environmental cues, such as when the original model of the ornament is a prey item [14,15]. Here, we propose another potential cost: that deriving from the interference between the male ornament and the cues that it mimics, and which are used by females to respond adaptively to their environment. We provide evidence that females exposed to a male ornament that resembles food experience a reduction in their foraging efficiency that is explained by the distraction caused by responding to the male signals when searching for the cues from prey. This was investigated in a group of fish species in which there is variation in both the expression of the male ornament and the level of female resistance to the sensory trap that it represents [6].

In several species of the viviparous Goodeidae, a family of North American fish, the males have a vertical band of yellow colour at the end of their tail fin (terminal yellow band; TYB), which resembles a damselfly larva. Where present, the intensity of this band varies, from a faint, pale stripe at the end of the tail in some species (e.g. Xenopoma captivus) to an intense yellow band flanked by a black stripe that enhances its conspicuousness (Ameca splendid) [6]. Goodeid females are attracted to males displaying a TYB, either naturally (in species with a TYB) or when experimentally painted (all species tested) [6]. Females also respond to the TYB with feeding behaviour (nibbling), but these foraging behaviours are less common in species with a conspicuous TYB (measured as the reflectance in the yellow range of the spectrum in relation to the colour of the adjacent section of the tail; see [6]) than in species with a faint one or with none at all. This was interpreted [6] as evidence that females of species with conspicuous TYB have escaped this sensory trap, as they remain interested in males with a TYB—a behaviour related to mating success in goodeid fish [16]—but are less likely to treat the TYB as food than females of the other species. The evolution of such signal discrimination [6] suggests that it is costly for females to mistake the TYB for food, presumably because it reduces their foraging efficiency [14,15]. We evaluated the assumption that visual exposure to a TYB reduces foraging efficiency of females, by exposing pregnant females of six...
goodeid species, which vary in the degree of male TYB conspicuousness (figure 1), to heterospecific males with conspicuous TYB in adjacent tanks. The species selected were the same used by Macías García & Ramirez [6]. *Carachodon audax* is a representative of the ancestral condition, as it belongs to the basal genus of the Goodeinae (viviparous goodeids) and lacks a TYB. It inhabits a series of spring-fed pools at the headwaters of El Tóboso River. The other five species are mostly found in lakes and dams. They belong to an eight-species clade (clade I of Webb et al. [17]) where the species possessing a TYB predominate. ‘*Xenotoca* eiseni’ was included as a representative of the two species that, within this clade, lack a TYB (it is uncertain whether this represents a secondary loss) [6]. *Xenoophorus captivus*, *Xenotoca variata*, *Chapalichthys pardalis* and *Ameca splendens* were included to represent increasing degrees of conspicuousness of the TYB (figure 1). The predominant mode of speciation in this family has been allopatric [17]; thus, reproductive character displacement is unlikely to explain any species difference in the nature of their responses to the TYB. Quantitative information on the diet of goodeids is scant; there is one main piscivorous species (*Alloophorus robustus*) in clade I, and *A. splendens* appears to consume large amounts of plant material [18], but although small amounts of algae are sometimes found in the stomach contents, these may be ingested secondarily while preying on algae-dwelling invertebrates [19], and most species are regarded as generalists, ingesting mainly aquatic invertebrates [20]. We expected that females should be distracted by the TYBs because they look like their major source of food (aquatic invertebrates).

2. MATERIAL AND METHODS

Fish used had been raised in aquaria and were familiar with the aquarium conditions, being the captive-bred descendants of wild-caught fish used in a previous study [6], or of populations established at the aquarium of Universidad Michoacana de San Nicolás de Hidalgo a few years earlier, also from wild specimens. Sexes were kept together in 40 l aquaria with filters and aeration, at 23°C, under a 12 L:12 D cycle, and fed commercial flakes twice daily.

Viviparous goodeids are matrotrophic; the females nourishing the embryos through the roughly eight-week gestation.
period [21,22], during which the offspring weight increases up to 378-fold from a small ovum [23]. The weight of pregnant females in a related species increases steadily until a few days before parturition (A. Valero, A. E. Magurran & C. Macías García 2011, unpublished data). By using only pregnant females (approx. 10 days before parturition), we maximized the opportunity to detect the hypothesized reduction in foraging efficiency both because their food requirements should be especially high, and because they should not have been interested in males. Goodied females neither store sperm for successive broods, nor copulate when pregnant, yet they can be drawn to male courtship and ornaments through their gestation period [24], being thus potentially vulnerable to the effects of sensory traps.

(a) Experiment a: does exposure to conspicuous terminal yellow band reduce the efficiency of females foraging on damselfly larvae?

Female C. audax (n = 7), X. eiseni (n = 14), X. captivus (n = 14), X. variata (n = 10), C. pardinus (n = 11) and A. splendens (n = 12) were food-deprived for 24 h to standardize their motivation to feed. They were tested individually for one week in 40 l tanks containing 12 synthetic plants and a supply of five damselfly larvae replenished twice daily. This was in excess of what female fish were seen to consume during pilot trials, and was designed to minimize the variance in prey density through the experiments and across species. Potentially distracting TYBs were provided by the presence in an adjacent, equally planted tank; we used male C. pardinus, except with females of this species and with three females of X. variata, which were exposed to A. splendens males. Males of both species are prone to swim against gentle water flows. We therefore provided such a flow in order to keep the males swimming, and thus undulating their tails (which gives the TYB its alluring resemblance to a swimming larva), and to prevent the males from approaching the adjacent female tank. We further prevented any male behaviour being directed to the females by preferentially illuminating the male tank, thus reducing the male visibility into the female tank. Males of those two species were chosen as they naturally have the most conspicuous (presumably the most elaborated) TYB, to which females of the six species have been shown to be responsive [6]. This procedure also reduced the variance in the stimulus and thus simplified the comparisons across species. Male size was matched to the female size, so the male TYB represented a realistic stimulus in relation to the size of the ornament to which the female might be exposed to. Also, larva size was matched to the TYB length, so that the hypothesized interference between the male ornament and the food item would be owing to the colour, shape and movement of both, and not to unrealistic size differences.

Daily, at noon, starting on the day of the introduction, we recorded for 15 min frequency and duration of orientations to male/TYB (the female turned towards a male/TYB, approached the adjoining wall and remained oriented to it), frequency of distractions (momentary turns towards a male/TYB not followed by an approach), time spent foraging (inspecting/nibbling at the substrate, artificial plants or larvae), frequency of bites to larvae and number of larvae consumed. Ingested larvae were tallied and replenished twice daily. Females were weighed on days 1 and 7, and their weight change was used as a measure of foraging efficiency. Using a different group of females (C. audax, n = 3; X. eiseni, n = 7; X. captivus, n = 5; X. variata, n = 5; C. pardinus, n = 5; A. splendens, n = 5), we repeated the same procedure but in the absence of males in the adjacent compartment, to control for possible effects of captivity/feeding regime on the reduced efficiency of females when foraging on damselfly larvae. First we used t-tests to perform intra-specific comparisons between experimental and control treatments, except when data failed the normality tests (X. eiseni analysed with a Mann–Whitney U-test). Then we evaluated performance in the experimental condition with pair-wise comparisons between species (Mann–Whitney U-tests) following global Kruskal–Wallis tests on each variable. Comparisons of variables within species were conducted with Wilcoxon signed-rank tests. The significance of correlations across species was adjusted for multiple tests (Dunn–Šidák).

(b) Experiment b: does exposure to the terminal yellow band reduce the foraging efficiency of females when alternative food is available?

Aquatic arthropods feature largely in the diet of all of the species used in the above experiments except A. splendens, which has been categorized as herbivorous [20] and performed badly in the first experiment. We evaluated whether such reduced foraging could be attributed to the lack of appropriate food during trials, rather than an effect of the TYB on its foraging efficiency. Five female A. splendens were tested as above, except that three 20 cm branches of Elodea sp. were available during trials, and number of bites of these was also recorded. In this experiment, we also included five female X. captivus as a control, as the species has a preference for aquatic invertebrates and was the one whose performance in the previous experiment was most similar to that of A. splendens. We expected that the herbivore A. splendens would not experience a reduced foraging efficiency when allowed to feed on plants because it would not be distracted by the TYBs, whereas X. captivus should perform as poorly as it did in the first experiment. Performance of each species was compared with that of the first experiment using t-tests or Mann–Whitney U-tests, depending on the distribution of data.

3. RESULTS

(a) Experiment a: does exposure to conspicuous terminal yellow band reduce the efficiency of females foraging on damselfly larvae?

Females of all species oriented to the neighbouring males/ TYB and were distracted by them during the trials (figure 2a,c), and all but one species experienced weight loss during the one-week trial (figure 2f). When males were not present, females of all species fared better; they either gained weight or lost less weight than when exposed to males (figure 3). Loss of weight was most likely to be owing to poor foraging, as it was significantly related to the foraging performance (bites directed to larvae; figure 2b) during our recording sessions (see electronic supplementary material), even though weight loss was not related to foraging time nor to time spent orienting towards males/TYB (see electronic supplementary material). Females of four of the six species spent significantly more time orienting towards the neighbouring males than foraging (figure 2a,c).

The amount of weight lost through the week varied across species. Female C. audax, whose males lack a TYB, were unaffected (figures 2f and 3), seemingly because they ingested the largest number of larvae in

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This was probably owing to the fact that *C. audax* was one of the two species that devoted more time to foraging, and it directed more bites at larvae than any other species during our recording sessions (figure 2).

Females of the five remaining species lost weight during trials. In *X. eiseni*, *X. captivus*, *X. variata* and *C. pardalis*, this loss was inversely proportional to the conspicuousness of their male's TYB ($r^2 = 0.92$, $F_{1,4} = 43.6$, $p = 0.003$), which relates to the degree to which females have separated their feeding and sexual responsiveness [6]. However, females of *A. splendens*—the species with the most conspicuous TYB—suffered the largest weight reduction, presumably because of their low larvae intake (figure 1; see §3b). This was due at least partially to the presence of males in the adjacent tank as it lost significantly less weight during the control trials (figure 3). In the remaining four species, the greater the species discrimination between feeding and sexual stimuli (the difference between the mean sexual and feeding responses reported earlier [6]), the better their feeding performance and the less the loss of weight (figure 4).

(b) Experiment b: does exposure to the terminal yellow band reduce the foraging efficiency of females when alternative food is available?

When alternative (plant) food was available, female *A. splendens* spent as much time orienting towards the TYB of males, devoted as much time to foraging, experienced as many distractions and nibbled at (and consumed) as few larvae as when in the presence of males in the first experiment (table 1). They did, nevertheless, lose somewhat less weight (table 1), and nibbled at the offered plants on average 1.5 times per session. The species used as control, *X. captivus*, also performed in this trial
exactly as when exposed to males in the first experiment (table 1): it lost as much weight in both experiments and was never observed nibbling at the plants.

4. DISCUSSION
We found that visual exposure to non-courting heterospecific males with conspicuous TYBs is associated with a reduced feeding performance in females of several goodeid species that have been shown to be attracted to male TYB. Control trials showed a significant improvement of feeding performance when there were no males in the adjacent tank. These results are consistent with the hypothesis that the TYB is a male ornament that interferes with the foraging activities of females, presumably by occupying the same perceptual channel involved in prey search/recognition. It is a tenet of the chase-away theory of ornament evolution [13] that female resistance to male manipulation promotes an increase in the salience of the male signal [13], and the resulting coevolutionary process should produce ornaments that are more efficient at capturing the females’ attention than the original model. As far as we are aware, this is the first demonstration of the maladaptive consequences of this process for females.

We propose that sensory interference was involved in the reduction of foraging efficiency because females were exposed to heterospecific males, were pregnant (and thus sexually unreceptive), and were not courted by the males (see §2). The large effects in X. eiseni and X. captivus are consistent with their reported heightened feeding responsiveness to conspicuous TYB [6] and are further evidence that these species are vulnerable to the sensory trap imposed by conspicuous TYB. Conversely, the small effects in X. variata and in C. pardalis are consistent with their reported separation of feeding and sexual responses to TYB-bearing males. Together, these findings suggest that the costs of facing sensory interference when foraging were the costs that drove the escape of females of the latter species from this sensory trap.

Since C. audax shows a strong feeding response to TYB of heterospecific ornamented males [6], we expected its females to experience a substantial reduction in foraging efficiency in the first experiments. They were distracted by the TYB as often as other species (figure 2), yet managed to devote much time to foraging, during which they nibbled at many larvae, which eventually were consumed. These resemble the results of the previous study, where C. audax was also distracted (it directed bites more readily to the TYB of heterospecific males than to
damsel flies; nevertheless, it attacked all the larvae on offer [6]. We cannot discard the possibility that in nature, the relatively small amount of distractions that they experienced would translate into a sizeable number of food items lost to competitors. There is also some suggestion (figure 3) that its foraging improves when not distracted by males with conspicuous TYBs, but from our evidence it appears that this species is a more active forager than the other species tested, and has a more highly developed capability to detect damselfly larvae (which probably relate to it being the most distinct species of those used here, both phylogenetically and biogeographically [17,25]).

Female A. splendens, evolutionarily exposed to the most conspicuous TYB and known to have separated their feeding and sexual responsiveness to this ornament [6], were in view and somewhat less when plants were available. It seems probable that this loss of weight was not solely owing to the specific interference of the TYB on their performance in experiment b. Mean performance (s.e.) of A. splendens and X. captivus did not differ between trials in which plant material was absent (a; as in figure 2) and present (b), although A. splendens appears to have lost less weight (and did nibble at the plants) when plants were offered (see text). Comparisons were performed using t-test (t) or Mann–Whitney U-tests (z) when normality was not met. z-values are in italics.

We did not measure female fitness, yet weight loss in late-pregnancy females is likely to indicate a reduction in fitness. Maternal investment in matrotrophic species is measured as the ratio of weight of the embryo at birth to the weight of the fertilized egg [29,30]. This ratio is very high in goodeids [31], indicating that embryos grow throughout the gestation period. Consequently, a reduction in weight of late-pregnancy females can only signify that (i) embryos are dying and being incompletely reabsorbed, (ii) embryos are losing weight, or (iii) the mother herself is losing weight. While the first scenario would represent an obvious fitness cost, the other two would also signify a reduction in female fitness, as a low weight at birth compromises offspring survival in viviparous fish [32], and because it is known that future female fitness is a function of past condition in viviparous fish [33].

We predict that similar costs must occur in other cases where male characters exploit female feeding responses, such as the prey-mimicking signals produced by male water mites [2]. It is also possible that female swordtail fish [34,35] and characines [36] face comparable costs, although the foraging nature of the former’s perceptual bias has not been demonstrated. As in our system, not all species that exhibit a perceptual bias are expected to incur costs from responding to such male attributes. Guppy females, for instance, are unlikely to require a constant supply of orange fruits [5], and thus their everyday responsiveness to male orange spots may not interfere with their normal feeding unless competition for food was intense and distractions had deleterious effects.

Table 1. Intraspecific comparisons of foraging performance in experiment b. Mean performance (s.e.) of A. splendens and X. captivus did not differ between trials in which plant material was absent (a; as in figure 2) and present (b), although A. splendens appears to have lost less weight (and did nibble at the plants) when plants were offered (see text). Comparisons were performed using t-test (t) or Mann–Whitney U-tests (z) when normality was not met. z-values are in italics.

<table>
<thead>
<tr>
<th>variable</th>
<th>A. splendens</th>
<th>X. captivus</th>
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<tbody>
<tr>
<td></td>
<td>t or z</td>
<td>p-value</td>
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<tr>
<td>orienting to TYB</td>
<td>1.85 (0.37)</td>
<td>0.758</td>
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<tr>
<td>time foraging</td>
<td>0.64 (0.16)</td>
<td>-0.018</td>
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<tr>
<td>distractions</td>
<td>5.79 (0.70)</td>
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<tr>
<td>bites to larvae</td>
<td>0.07 (0.02)</td>
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<tr>
<td>larvae ingested</td>
<td>3.58 (0.85)</td>
<td>-0.261</td>
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<tr>
<td>weight loss</td>
<td>9.33 (1.45)</td>
<td>1.399</td>
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We thank E. Ávila Luna for logistical support, I. Barbosa Valero for helping recording behaviour, the Lunáticos behaviour discussion group for constructive feedback and A. Valero for providing data on weight of pregnant females. We drew much benefit from the comments of R. Torres, J. Graves and three anonymous reviewers of an earlier manuscript. Rebeca Rueda-Jasso of the Universidad Michoacana de San Nicolás de Hidalgo (UMSNH) kindly lent us fish to complement our stocks. Data were collected as part of Y.S.L.’s BSc thesis under the supervision of C.M.G. and support was given by the Instituto de Ecología, UNAM.