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Predation on females or males: who pays for bright male traits?

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Bright colour patterns are found on male guppies, *Poecilia reticulata*, in regions of low predation but not on males in regions of high predation (Haskins et al. 1961). These data have been used to make the claim that bright male guppies get more matings, but are consumed more often by predators, thereby suggesting that coloration results from a balance between natural and sexual selection (Endler 1980). Female preference for male coloration also varies with the local intensity of predation: females from risky locales prefer duller males (Breden & Stoner 1987). It is assumed that female preference evolved through indirect, rather than direct selection on female behaviour (Breden & Stoner 1987; Stoner & Breden 1988; Houde & Endler 1990). Male animals are often the focus of work in behavioural ecology, with females relegated to less important roles. However, new insights may be gained by looking at the effects of a trait on the fitness of both sexes (Rosenqvist & Berglund 1992; Ahnesjo et al. 1993; Berglund et al. 1993).

Although bright male guppies are frequently detected by predators (at long range), this need not lead to more male deaths. Guppies are commonly found in mixed-sex groups (Haskins et al. 1961) and predators that detect bright males from a distance might not necessarily attack them once they are closer. *Crenicichla alta* (a pike cichlid) is a stalking/ambush predator that can detect guppies from at least 1·2 m, but attacks at distances of 5–40 cm (Seghers 1973). Thus, detection and attack will often be separated in time and space. Once a group has been detected by a predator we would expect females to suffer a higher attack rate, because they are larger, and hence more profitable, given equivalent capture rates and handling times. We performed the following experiment to see which sex pike cichlids attack when within striking distance of pairs of female and male guppies.

We presented pairs of guppies to three commercially purchased pike cichlids (10–15 cm standard length, SL) that had experience capturing guppies. The predators used were all identified as members of the *C. saxitalis* species complex (W. Liebel, personal communication), of which *C. alta* is a member. We used only 39 pairs of guppies in the experiment as we wished to use the fewest number of fish possible because the experiment resulted in the death of the prey. The guppies were from a Quare River population that is sympatric with pike cichlids introduced by J. Endler (personal communication) in the 1970s. The experiments were performed in a small climate-controlled room. The temperature remained at approximately 21°C and the lights were set on a 12:12 h light:dark cycle, providing 800 lx illumination at the water surface during the day. The female guppies used ranged from 20 to 26 mm SL (mean = 23 mm), and the males ranged from 13 to 19 mm SL (mean = 17 mm). The females weighed 0·23–0·54 g (mean = 0·35 g) and the males weighed 0·06–0·18 g (mean = 0·12 g). Mixed-sex pairs of fish were removed from stock tanks and placed in a circular, white, Plexiglas arena (22 cm diameter, 10 cm deep) to acclimatize. After 2 h we opened an opaque gate between the attack arena and an adjoining predator holding compartment (20 × 10 × 10 cm) remotely, and videotaped interactions between predator and prey from above. In 29 of 39 trials, the predator left its compartment and attacked one or both of the guppies. When given a choice, pike cichlids first attack female guppies (Fig. 1). We found both sexes were captured with equal facility (mean attacks/kill were 2·22 and 2·18 for females and males, respectively; ANOVA: $F_{28} = 0{\cdot}004$, $P > 0{\cdot}1$), while handling times were unmeasurably short. Thus, with equivalent capture rates and handling times, we conclude that females were the more profitable prey because they were on average three times as

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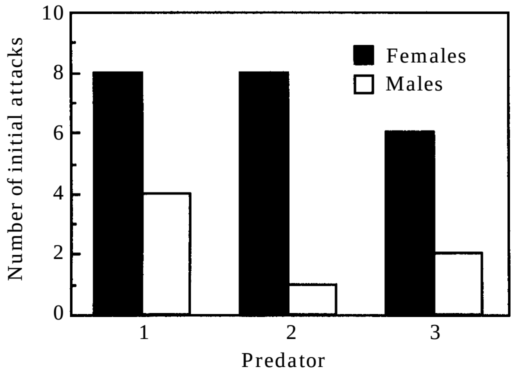

Figure 1. The number of times pike cichlids first attacked female and male guppies when presented with a mixed-sex pair. Using a binomial test we calculated *P*-values for each predator's behaviour ($P=0{\cdot}194$, 0·020, 0·145) and then found the combined probability of three fish behaving in this manner ($P<0{\cdot}025$; Sokal & Rohlf 1981).

massive as males (see above). Size selectivity of the predators combined with female/male size dimorphism produces female-biased predation risk (but see Mattingly & Butler 1994).

Because predators selectively attack females in mixed-sex pairs, nearby male courtship displays and participation in mating activity may pose a predation risk to female guppies. If so, females may prefer to associate with dull-coloured males. Thus, indirect selection against bright males may be sufficient to explain geographic variation in both male coloration and female choice.

Magurran & Nowak (1991) showed that male guppies exploit female vigilance and attempt to forcefully inseminate females reacting to a predator. Female guppies in regions of high predation risk may be forced to choose between mate choice (avoiding forced copulation attempts) and anti-predator vigilance (allowing males to force copulations; Magurran & Seghers 1994). Thus, there may be a direct cost, in terms of increased risk of predation, to mate choice. Predation risk causes female crickets, *Gryllus integer*, to choose mates that they would otherwise ignore (Hedrick & Dill 1993), whereas male pipefish, *Syngnathus typhle*, cease to be choosy in the presence of a predator (Berglund 1993). Pomiankowski (1987) has shown that if there is any cost to female choice it cannot be maintained in a system driven by Fisherian runaway sexual selection. Even if a non-runaway process is responsible for female preference, a slight cost to choice can greatly reduce the maximum stable expression of the male trait.

Pomiankowski's (1987) result is important because it demonstrates that the expression of a male trait may be affected more by predation risk on choosy females than by predation risk on males with the trait. This suggests that the standard explanation, 'Colour patterns of natural populations . . . are a compromise between sexual selection and predation avoidance' (Endler 1991) may not fully describe how predators affect conspicuous male traits. Recent work suggests that the evolution of male coloration is not simply a result of a trade-off between costs and benefits to the male. Dawkins & Guilford (1991) proposed that some of the costs of signalling may be borne by the receiver. Gotmark (1992) has shown that despite their bright coloration, male pied flycatchers, *Ficedula hypoleuca*, are attacked less often than the larger, dull-coloured females, and Olsson (1993) found that sand lizard, *Lacerta agilis*, models painted to resemble the male's bright nuptial coloration were not at greater risk than those without such bright colours. Hypotheses positing direct links between visibility and mortality (Endler 1980) leave out many important steps in predator–prey interactions (Lima & Dill 1990).

Although predation risk is an oft-cited counterbalance to the evolution of sexually selected traits, there is little empirical evidence concerning how the two forces interact. This experiment shows that in guppies, the situation is not necessarily simple. Without understanding the details of how predators interact with both sexes of prey, we are unlikely to understand how anti-predator considerations influence the evolution of sexually selected traits.

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