Field data do not support a textbook example of convergent character displacement

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Experimental evidence supporting convergent character displacement is rare; only one example exists and it is in the form of orientation and territory competition experiments performed in the laboratory. However, outcomes of laboratory experiments involving behaviour or competition can be artefacts of unnatural conditions and, therefore, the results of the previous experiments supporting convergent character displacement are equivocal. In this study, we re-examine the evolution of melanistic nuptial coloration in male three-spined stickleback (*Gasterosteus aculeatus*) inhabiting the Chehalis River drainage in Washington State. This novel nuptial coloration has been thought to have evolved in response to competition for nesting territories with the co-distributed Olympic mudminnow (*Novumbra hubbsi*), which is also melanistic and breeds at the same time. I found that melanistic stickleback males did not have an advantage over their red counterparts from typical populations when competing for nesting territories with Olympic mudminnows. Additionally, competitive interactions between sticklebacks and mudminnows were rare in both cage experiments and naturally breeding sticklebacks. Finally, melanistic coloration in the Chehalis populations did not develop until males were parental, well after the hypothesized territory establishment period. These results refute the only experimental support for convergent character displacement and emphasize the importance of conducting behavioural experiments and observations under natural conditions.

Keywords: territoriality; threat display; competition; nuptial coloration; three-spined stickleback

1. INTRODUCTION

Ecological character displacement is an evolutionary process that results in the modification of morphological, behavioural or physiological traits in populations of one species that are sympatric with those of a second, ecologically similar species (Grant 1972; Schluter 1988; Taper & Case 1993). The result can be convergence or divergence of relevant characters depending on the nature of the interaction (Grant 1972; Taper & Case 1993). For example, divergent character displacement is thought to occur when sympatric populations compete for a common food resource, and leads to the modification of important foraging traits that allow partitioning of the food resource by the overlapping populations (Dunham *et al.* 1979; Schluter & McPhail 1992; Robinson & Wilson 1994). Convergent character displacement is thought to occur when sympatric populations compete for territories and results in the modification of characters associated with territory establishment and maintenance, such as threat display behaviours, markings and vocalization (Cody 1969, 1973; Grant 1972; Arthur 1982).

Character displacement is often inferred on the basis of trait distributions alone. Divergent character displacement is indicated when populations of the two species are similar in allopatry but different in sympatry (Brown & Wilson 1956; Taper & Case 1993), whereas convergent character displacement is suggested when populations of two species are more similar in sympatry than allopatry (Grant 1972; Cody 1969, 1973; Dunham *et al.* 1979).

Although character displacement has generated extensive theoretical debate (Lawlor & Maynard Smith 1976;

Slatkin 1980; Simberloff 1984; Abrams 1986, 1987), and is often invoked to explain trophic polymorphisms (Robinson & Wilson 1994), sympatric speciation (Schluter & McPhail 1992) and community species assemblage (Grant & Abbott 1980; Hendrickson 1981), the existence of well-documented examples has been questioned repeatedly (Strong *et al.* 1979; Connell 1980; Simberloff 1984; Endler 1986; Vadas 1990). This is in part because direct experimental tests of character displacement have rarely been performed. In only three cases is there experimental evidence of character displacement. Two of these involve divergence caused by competition for food resources (Taper 1990; Schluter 1994), and one convergence for threat display between species thought to be competing for space in a restricted habitat (Hagen *et al.* 1980).

Given that there exists only a single apparently well-documented and experimentally tested case of convergent character displacement, it assumes a particularly important role in our understanding of competition as a driving force in the coevolution of interacting species. The example is one in which freshwater three-spined sticklebacks (*Gasterosteus aculeatus*) in the Chehalis River drainage of Washington, USA, are thought to have evolved a derived, melanistic nuptial coloration as a consequence of competition with the endemic Olympic mudminnow (*Novumbra hubbsi*). The interpretation, which is widely accepted and cited (e.g. Cody 1973; Endler 1986; Freeman & Herron 1998) is that the nuptial coloration of sticklebacks converged upon the melanistic colour of mudminnows because the signal enhanced the ability of sticklebacks to hold territories in competition with mudminnows. Here we demonstrate that the melanistic nuptial coloration of the Chehalis River stickleback is unlikely to have evolved as a consequence of

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interspecific territorial competition, thereby leaving us with no well-documented cases of convergent character displacement.

2. THE CASE FOR CONVERGENCE IN THE CHEHALIS SYSTEM

Male three-spined sticklebacks in the Chehalis River drainage, Washington, USA, assume jet-black nuptial coloration rather than the red underside and blue-green dorsum that is typical of the species (McPhail 1969). In typical populations, the red nuptial coloration of males functions in intrasexual territorial interactions and in intersexual selection in at least some populations (Rowland 1982, 1989; Milinski & Bakker 1990; Bakker & Mundwiler 1994; Rowland *et al.* 1995; Bolyard & Rowland 1996). Chehalis drainage sticklebacks are co-distributed with Olympic mudminnows which are also endemic to the Chehalis River drainage and assume melanic nuptial coloration. The two species hold breeding territories synchronously, an observation that led Hagen *et al.* (1972, 1980) and Hagen & Moodie (1979) to examine the possibility that competition for nest sites between the species caused local populations of sticklebacks to evolve threat displays similar to those of the mudminnow.

Although these authors presented evidence that convergence for threat display could be the cause of the derived nuptial coloration in the stickleback, the evidence was not conclusive. Competition was not demonstrated directly, the role of melanic coloration in natural populations was not evaluated, nor was evidence provided that sticklebacks with red nuptial coloration suffered a disadvantage relative to their melanic counterparts when breeding in sympatry with mudminnows. All are essential if character displacement is to be inferred (Connell 1980; Hairston 1980, 1981; Schoener 1983; Diamond *et al.* 1989; Grant 1994).

An additional problem is that all experiments were conducted under laboratory conditions. One experiment used males of the two species, which were in visual but not physical contact. The response variable was direction of orientation by mudminnows, confined to the centre of an aquarium by clear partitions, towards either melanic or red male sticklebacks at opposite ends of the aquarium. Another aquarium experiment examined territory establishment success of red and melanic sticklebacks in the presence of mudminnows but did not include a comparison to sticklebacks nesting alone, a critical control. These methods could not resolve the role of stickleback nuptial coloration in determining success in territory acquisition or reproduction, a crucial element of experiments designed to test the function or selective value of individual features of complex phenotypes (Diamond *et al.* 1989; Reznick & Travis 1996). Here we provide evidence from field experiments and observations on naturally breeding sticklebacks that convergent character displacement is an unlikely explanation for the similarity of nuptial coloration in these two species. This finding is fundamentally important in that we have no other experimentally verified examples of convergent character displacement.

3. METHODS

The presence and/or absence of male Olympic mudminnows was manipulated in field cages to examine the impact of inter-specific territorial interactions on the nesting success of both colour types of three-spined sticklebacks. In addition, we surveyed several natural, monomorphic melanic populations of nesting sticklebacks to determine (i) the frequency and outcome of territorial interactions between sticklebacks and mudminnows, and (ii) the temporal expression of threat coloration.

(a) *Competition experiment*

Competition experiments were conducted in cages in two breeding areas near the mouth of the Humptulips River (McPhail 1969) during the 1995 and 1996 breeding seasons. These sites were chosen because they had large, shallow open areas with sparse vegetation and mud bottoms that permitted cage placement and behaviour observations of the enclosed fish. Cages were constructed of a 1 m × 2 m × 1 m wooden frame covered with fibreglass window screens on the sides. They were placed in position and pushed 20 cm into the sediment. With the exception of juvenile coho salmon (*Oncorhynchus kisutch*), fishes in an area where a cage was placed hid in the sediment. All sticklebacks and mudminnows were removed from the cages with an electroshocker but other fish species (sculpin, *Cottus* sp.; lamprey, *Lampetra richardsoni*) were returned to the cages to produce a natural field experiment (Connell 1983; Schoener 1983). The sides of the cages were cleaned of algal build-up weekly.

We varied male mudminnow presence and male stickleback colour among cages to determine the effects of male mudminnow presence on the reproductive success of red and melanic male sticklebacks. Treatment cages received four male and four female mudminnows and control cages received eight female mudminnows. Male mudminnows typically hold territories of about 1 m² (Hagen *et al.* 1972) so we used four males per treatment cage to ensure saturation of territories by mudminnows. The additional female mudminnows were added to the control cages to maintain constant fish density among cages and thus to avoid the potential confounding effects of density (Bernardo *et al.* 1995). Mudminnows were introduced into the cages in early May and allowed to establish territories and begin courting females. After ten days we added four male and four female sticklebacks from either a red or a melanic population to each of the cages. Mudminnows and sticklebacks were added to the cages at these densities to approximate natural densities observed during visual surveys of nesting areas in five wetlands near the mouth of the Humptulips River. Mudminnows were allowed to begin territory establishment before sticklebacks because that is the order in which reproduction naturally occurs (Hagen *et al.* 1972).

Each cage was monitored for 30–60 min every second day for three weeks from the beginning of the experiment. We recorded the presence of stickleback territories, nests and offspring, as well as the frequency and outcome of interactions between nesting sticklebacks and mudminnows. Fishes were removed from the cages using an electroshocker, euthanized by an overdose of anaesthetic (MS-222) and preserved in 10% formalin at the end of the experiment. More than 90% of fishes introduced into the cages were recovered. Missing fishes were probably removed by piscivorous birds and mammals, or died naturally (carcasses were found occasionally) as the cages were set in the sediment throughout the experiment.

Figure 1. Mean (± 1 s.e.) number of territories established by sticklebacks per 2 m² cage. Solid and shaded bars represent 'mudminnow present' and 'mudminnow absent' treatments, respectively.

(b) Observation of nesting males in the wild

Observations of wild-nesting sticklebacks (melanic populations only) were made at four wetlands near Humptulips River and Conner Creek (McPhail 1969) to document behavioural interactions under natural conditions. Nesting sticklebacks were located from shore and observed continuously for one hour. Male coloration (drab or melanic), the phase of the reproductive cycle (territory establishment, nest building, courtship, the fanning of embryos in the nest, guarding free-swimming young; Wootton 1976), and the frequency and outcome of territorial interactions with other fishes were recorded.

(c) Statistical methods

Mean numbers of males establishing territories in the competition experiment were compared among treatments using a two-factor ANOVA in which both factors were considered fixed effects (Sokal & Rohlf 1995). Variances among treatments were not heteroscedastic (Taylor's power law; Green 1979) and no departures from normality were evident, though no formal test could be performed because of the low sample size in each treatment level. Comparison of the mean number of territorial intruders was compared using single-factor ANOVA (Sokal & Rohlf 1995). Non-significant ANOVAs were followed up with power analyses (Sokal & Rohlf 1995).

4. RESULTS

(a) Competition experiment

The water level in one of the wetlands dropped rapidly during the 1995 breeding season and we removed 12 of the cages before the end of the experiment as a result. The following analyses include data from the remaining 28 cages, seven in each treatment combination. Thirty-six per cent (40 out of 112) of all males in the experiment established nesting territories. There was no interaction between the two experimental factors (male mudminnow presence or absence, or stickleback colour; two-factor ANOVA, $F_{1,27} = 1.2$, $p = 0.3$). Neither factor affected the number of territories established (figure 1; stickleback colour, $F_{1,27} = 0.13$, $p = 0.72$; male mudminnow presence or absence, $F_{1,27} = 0.0001$, $p = 0.999$). The power for each of the factors in the ANOVA was greater than 0.8. The results for nest establishment were identical to those for

Figure 2. Mean (± 1 s.e.) number of territorial intrusions per hour for 54 naturally breeding males from melanic populations observed during four periods of the reproductive cycle. Solid bars represent conspecific intruders and shaded bars represent total intruders.

territory establishment, as all males that established territories also built nests. All cages produced free-swimming offspring, but post-hatching brood mixing occurred so we could not determine which of the males produced which young.

(b) Nesting male observation

We observed 550 interactions between 54 nesting stickleback and other fishes. Of those, 81.8% of the interactions were with other three-spined sticklebacks, 16% were with juvenile coho salmon, and only 0.55% were between a nesting stickleback and a male mudminnow. The number of interactions between nesting males and other fishes increased during the guarding of free-swimming offspring (figure 2; $F_{3,53} = 7.43$, $p < 0.0004$). Twenty-four of the 54 males were observed prior to spawning (13 during territory establishment or nest building and 11 during courtship). Out of those 24, only one had developed melanic coloration; 23 were drab. All 30 of the males observed post-spawning (20 during nest fanning and ten during guarding free-swimming offspring) had developed melanic coloration. Melanic coloration covered most of the ventral surface of males that were fanning a nest and covered the entire body (dorsal and ventral surfaces) of males that were guarding free-swimming fry.

5. DISCUSSION

The threat display convergence hypothesis is clearly an unlikely explanation for the evolution of the derived melanic coloration of Chehalis River drainage three-spined sticklebacks. The hypothesis assumes that male sticklebacks compete for territories with the endemic Olympic mudminnows, yet there exists little evidence of competition between these species during territory establishment. Aggressive interactions were rare between these two species under natural conditions and male sticklebacks of both colour types acquired territories equally often whether mudminnows were present or absent.

A second assumption of the hypothesis, that the nuptial coloration of the stickleback is displayed during territory establishment, proves even more problematic. The melanic nuptial coloration of the Chehalis drainage

three-spined stickleback can have little effect on the probability of territory establishment, through an effect on the aggressive behaviour of mudminnows, because it is rarely displayed during this period under natural conditions. Although melanic nuptial coloration could inhibit attack by mudminnows later in the nesting cycle, interactions were so rare between mudminnows and either red or melanic sticklebacks late in the cycle, that this seems an unlikely function of the signal.

A more plausible function of melanism in this drainage is that it functions as an aggressive signal that deters conspecifics from attacking defended young. In many populations, conspecifics cannibalize embryos and larvae defended by males (Foster 1988, 1994*a,b*; Kynard 1978; Semler 1971; Whoriskey & FitzGerald 1985, 1994; Foster *et al.* 1988; FitzGerald 1991). Aggressiveness of parental males tends to increase dramatically once their offspring become free swimming (Bakker 1994). The changes in aggressiveness and coloration occur as the young near maximum reproductive value to the male (Pressley 1981; Sargent & Gross 1986; Ridgway 1988; Ukegbu & Huntingford 1988), suggesting that the melanic signal may function as a conspecific threat display. The increased rate of conspecific intrusions during the guarding of free-swimming offspring stage (figure 2) observed in this study suggests that cannibalism of free-swimming offspring under parental care may be frequent. Observed instances of cannibalism in wild sticklebacks were infrequent, but this may not be indicative of the actual level of cannibalism since focal individuals in observation bouts were nesting males and not intruders. Therefore, any cannibalism that may have been taking place could have been easily overlooked.

The melanic signal could simply be an extension of the ancestral pattern of coloration observed in typical marine (ancestral) and freshwater populations. Two peaks in the intensity of the nuptial signal are usually described; one during the territorial and courtship phases and a second when offspring are free swimming (Sargent 1985; McLennan & McPhail 1989; Bakker & Mundwiler 1994). The second peak is usually brighter, a change that may reflect both the intensity of the red coloration and the development of deeper black and green shades on the dorsum (McLennan & McPhail 1989). Thus, the question that should be addressed is perhaps why the red signal has been lost, rather than why a melanic nuptial signal has evolved in these populations.

Earlier researchers attempted to explain the presence of the melanic stickleback nuptial coloration in the Chehalis River drainage based on the close concordance of mudminnow and stickleback distributions (McPhail 1969; Hagen & Moodie 1979). Although this pattern of covariation stood out, other potentially causative factors could also covary with the distribution of sticklebacks displaying the melanic nuptial coloration. A second potentially covarying factor is the availability of carotenoids in the Chehalis River drainage (Reimchen 1989). If carotenoid availability is restricted in the drainage it could have favoured the loss of red nuptial coloration, a derived trait that has a genetic basis in sticklebacks in this drainage (McPhail 1969; Hagen & Moodie 1979).

Another possible cause of the loss of the red nuptial coloration is the degree of water staining caused by dissolved organic acids. Many Chehalis drainage sticklebacks are found in streams that are deeply stained (Scott 1999) providing a very different visual environment for signal transmission from that experienced in most typical populations (Lythgoe 1979; Reimchen 1989). This presents the possibility that the red signal has been lost because it presents low contrast in the red-shifted light environment of stained water and thus does not offer a conspicuous signal (Lythgoe 1979; Reimchen 1989; MacDonald *et al.* 1995). Sticklebacks with melanic nuptial coloration are not restricted to stained waters (Scott 2000). Therefore, signal masking does not provide an unequivocal explanation for the loss of red nuptial coloration in the Chehalis drainage.

Regardless of the reason for the evolution of the derived signal expressed by sticklebacks in the Chehalis drainage, the history of research on the signal offers several lessons. The first is that the correlation between the ranges of two potentially competing species is inadequate to indicate a role for character displacement (Strong & Simberloff 1981). Undetected factors that covary with the distribution of the species may instead be responsible (e.g. Endler 1986; Vadas 1990; Reznick & Travis 1996). Equally, if competition is to be invoked as a cause of character displacement, it must be demonstrated directly, preferably in a field situation (Connell 1980, 1983; Hairston 1980, 1981; Schoener 1983; Diamond *et al.* 1989). Finally, this research emphasizes the value of field observation as a means of detecting unexpected laboratory artefacts on behaviour (e.g. Hay & McPhail 1975; Verrell 1990; Fraser & Boake 1997).

The importance of convergent character displacement in evolutionary biology has proven contentious (Grant 1972; Lawlor & Maynard Smith 1976; Arthur 1982). The failure of this research to support a causative role for interspecific competition in the evolution of a melanic nuptial signal in Chehalis River drainage sticklebacks is unlikely to alleviate this situation as this signal was the best supported example of convergent character displacement. This finding calls into question not only the importance of convergent character displacement as a significant cause of evolutionary change, but also the very existence of the phenomenon.

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