Female preference and male nuptial colouration in the freshwater fish *Gobiomorphus breviceps*: geographic variation among populations

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Abstract: Geographic variation in the strength or direction of sexual selection acting on different populations has been documented before but has not been the subject of intense study. We examine covariation among sexually selected traits and environmental factors for five stream populations of a small New Zealand freshwater fish, the upland bully, *Gobiomorphus breviceps* (Eleotridae). Levels of infection by a trematode parasite and some aspects of female behaviour and male colouration varied significantly among populations. Among individual fish we found that female mate choice behaviours and male colouration did not correlate similarly with other traits, or with parasite load, in the different populations studied. We also determined whether average population values correlated among the different stream populations. Whereas environmental factors such as water clarity and substrate colouration appeared to be unimportant, average parasite load correlated with some components of male colouration, and female preferences appeared to be correlated with male colouration. These results illustrate both the variability among populations that prevents results obtained from one population from being generalized to the entire species, and the plasticity of sexually selected traits in relation to local conditions.

Résumé : La variation géographique de la force et de la direction de la sélection sexuelle qui agit sur différentes populations a été étudiée antérieurement mais n'a jamais fait l'objet de recherches en profondeur. Nous avons étudié la covariation entre des caractéristiques déterminées par sélection sexuelle et des facteurs environnementaux chez cinq populations de ruisseau d'un petit poisson dulcicole de Nouvelle-Zélande, *Gobiomorphus breviceps* (Eleotridae). La gravité des infections par un trématode parasite et certains aspects du comportement des femelles et de la coloration des mâles varient significativement chez les populations. Nous avons constaté que le comportement de choix d'un partenaire chez les individus femelles et la coloration chez les individus mâles ne sont pas reliés de la même façon avec d'autres caractéristiques ou avec le fardeau de parasites chez les différentes populations étudiées. Nous avons également examiné si les valeurs moyennes des populations étaient reliées chez toutes les populations de ruisseau étudiées. Alors que certains facteurs écologiques comme la transparence de l'eau et la coloration du substrat ne semblent pas importants, le fardeau moyen de parasites est relié à certaines composantes de la coloration des mâles et les préférences des femelles semblent reliées à la coloration des mâles. Ces résultats illustrent la variabilité entre les populations, ce qui fait que les résultats obtenus chez une population ne peuvent être généralisés à l'échelle de l'espèce, et ils illustrent aussi la plasticité de certaines caractéristiques soumises à la sélection sexuelle en relation avec des conditions locales.

[Traduit par la Rédaction]

Introduction

Different populations of the same species often experience different selective pressures, as several environmental factors vary on a geographic scale. This may result in covariation between some characters in one population but not in others, or in different mean values for a character between populations. In the context of sexual selection, for instance, there is often much geographic variation in female mate preference and male nuptial colouration (e.g., Reimchen 1989; Houde and Endler 1990; Hill 1994; Endler and Houde 1995; Morris et al. 1996). This variation has at least two

important implications. First, the generality of the results obtained in studies focusing on single populations may be questionable. Second, geographic variation allows comparative tests across populations of the same species, an approach that can yield more insight about the operation of sexual selection than interspecific comparisons (Houde 1993).

In fish, it has been found that variation in female mate preference or male nuptial colouration is associated with geographic variation in certain variables, particularly predation pressure (Endler 1980), water clarity (Reimchen 1989), and water spectral composition (Endler and Houde 1995; McDonald et al. 1995). These factors can contribute to determining which female preferences and male colouration are favoured in a given population. The visual environment and the risk of predation are not the only pressures modulating sexual selection. Parasitism may also be important (Hamilton and Zuk 1982) if different populations exhibit different levels of parasitic infections. By extending Hamilton and Zuk's (1982) interspecific prediction, we can expect that

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Fig. 1. Locations of bully populations sampled in Otago province, South Island, New Zealand. G, Garden Bush stream; H, Garden Bush High stream; L, Linnburn stream; S, Shag tributary stream; T, Trotter's Gorge stream.
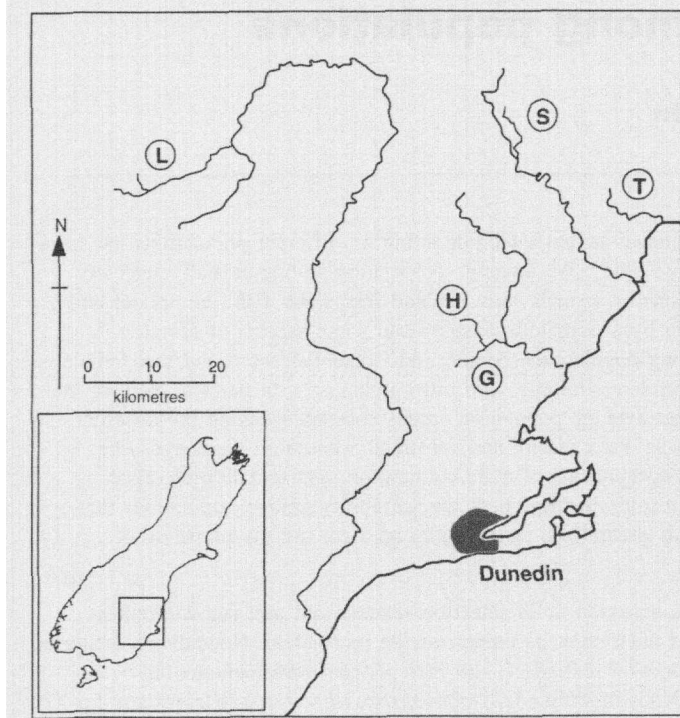
males, on average, should be brighter and that females, on average, should prefer brighter males in heavily parasitized populations than in lightly parasitized populations of the same species. The influence of parasites on intraspecific geographic variation in sexual selection has yet to be examined empirically.

The upland bully, *Gobiomorphus breviceps* (Eleotridae), is a freshwater fish native to New Zealand and common in streams, rivers, and lakes east of the alps on the South Island (McDowall 1990). Bullies are sedentary, and different stream populations can be considered distinct and isolated. The upland bully is a sexually dimorphic species. Males establish nests under flat rocks and provide parental care to the eggs they obtain from one or several females. Males have yellow–orange stripes along the tip of the first dorsal fin and along the base of the pectoral fins. These stripes are displayed during both courtship displays addressed at females and aggressive encounters with other males. To the human eye, the nuptial colouration of male bullies varies considerably among stream populations in the Otago province of New Zealand's South Island (W.J. Hamilton and R. Poulin, personal observation). In this region, bully populations are all infected to some extent by the trematode parasite *Telogaster opisthorchis*; it is the only parasite found in bullies. Metacercarial cysts of *T. opisthorchis* are located in the muscles, visceral organs, and body cavity of bullies. Fish become infected when free-swimming infective stages (cercariae) penetrate their skin after leaving the first intermediate host, the snail *Potamopyrgus antipodarum*. The parasite reaches adulthood after infected bullies are ingested by eels (*Anguilla australis* or *Anguilla dieffenbachii*), which act as definitive hosts for the trema-

tode (MacFarlane 1945). Evidence from two populations suggest that parasite loads vary among streams but not from year to year (Hamilton et al. 1997). Bullies harbouring large numbers of *T. opisthorchis* cysts exhibit a reduced physical condition, impaired predator avoidance, and altered parental-care behaviour (Poulin 1993; Stott and Poulin 1996). This suggests that the parasite can be an environmental pressure on sexual selection in bullies.

This study used laboratory mate choice tests and video-image computer analysis to achieve two main objectives. First, we determined whether population values for sexually selected traits covaried with environmental factors across five bully populations. More specifically, we related average male colouration and female preference to one another and to variation in water transparency, substrate colour, and levels of parasitism. Second, we determined whether variation in female preference or male colouration within populations was associated with individual variation in parasite load, and whether the relationship differed among populations. For these analyses, we also took into account fish length or age and the size of the female's current clutch of eggs, since these are potentially confounding factors. This study is one of only a handful to provide data on whether trends in sexual selection observed in one population can apply to other populations. In addition, the results can provide clues regarding which sexual-selection model (i.e., good genes or Fisher's runaway selection) provides the best explanation of geographic variation.

Methods

Territorial male and gravid female bullies were collected from five stream populations (Fig. 1) during the 1994–1995 breeding season. All streams flowed through similar high-country catchment, with native tussock, scrub, and exotic grasses growing on the banks. They were similar in width (2–4 m), depth (average <0.5 m), and substrate (gravel and boulders). Predator species were also the same in all five streams: brown trout (*Salmo trutta*), eel (*Anguilla* spp.), and crayfish (*Paranephrops zealandicus*). Territorial males were also captured from a sixth stream population, geographically remote from the others, for use in mate-choice experiments. This sixth population was chosen because the colouration of its males was not extreme and was within the ranges of the five study populations.

All holding conditions and experimental procedures have been approved by the University of Otago's Committee on Ethics in the Care and Use of Laboratory Animals. Fish were segregated by sex and stream of origin and kept for a few days under laboratory conditions, i.e., water temperature 18–20°C, photoperiod 15 h light : 9 h dark. Following all experiments, fish were killed by an overdose of anaesthetic (2-phenoxy ethanol), measured to the nearest millimetre (total length), and dissected. The number of *T. opisthorchis* cysts found in each fish was recorded. Scales and otoliths were removed from each fish for age determination, as in Staples (1975).

Female-choice tests
The test aquaria were divided into three sections, with a middle "female" section (40 × 45 cm) located between two "male" sections (30 × 45 cm). The test female could see both males simultaneously through a one-way glass partition, whereas males could not see the female or one another. This design prevented interactions between fish and left only male physical appearance as a cue for mate choice. A nest site was provided in each male section,

consisting of a ceramic tile (10 × 10 cm) supported 2.5 cm off the gravel bottom by a U-shaped wooden bracket, with the opening facing the female section.

Pairs of similar-sized males from the sixth population were selected by an independent observer, who matched a brightly coloured male with a dull one. The contrast in brightness between two males in a pair was the same for all pairs, at least to the human eye. Males of each pair were placed at separate ends of a test aquarium and given 2 days to resume territorial behaviour prior to mate-choice tests; the end of the aquarium receiving the bright male was always chosen at random.

Gravid females (n = 20–21 per population) were used in two sequential choice tests. For each test, a single female was placed under a glass jar in the centre of the middle section of the aquarium, from where it could see both males. After 30 min, the jar was gently lifted and the trial begun. At the end of the trial, the female was isolated in a separate tank for 2 h before being used in a second trial with a different pair of males in a different test aquarium.

For each trial, the following behaviours were recorded: (i) time taken to make the first visit to a male following removal of the jar; (ii) percentage of time spent with males, or total time spent within 10 cm of either male section, facing the male, during the first 10 min following the female's initial visit to a male; (iii) number of visits to males, i.e., the total number of approaches to within 10 cm of either male section during the 10 min beginning with the first visit; and (iv) identity of the preferred male, or the male with which the female spent at least 60% of her time. Measure i may represent willingness to mate and measures ii and iii may serve as an index of investment in mate assessment; all were obtained by averaging the results from both mate-choice tests. In a previous study on bullies (Poulin 1994), females spending >60% of their time with a male would initiate spawning with it if allowed to do so. Also, in this study, the first male visited by a female was also the one with which she spent >60% of her time in 127 out of 165 choices observed (χ^2 = 48.01, P < 0.001). Therefore, measure iv is a good indication of female preference. Females not spending at least 60% of their time with a male were deemed to have made no choice. The number of times during the two trials that an individual female chose the bright male (0, 1, or 2 times) was divided by the number of choices she made in those two trials (again 0, 1, or 2) to give a brightness-preference ratio for each female. For comparisons among populations, the above measures were averaged across females to obtain population values.

Male colouration

Males from the five populations sampled were allowed to establish a nest individually in modified aquaria (16 × 12 cm) equipped with a moveable glass partition that allowed us to position each male at a standard distance from the front of the tank. This facilitated videotaping (Hi-8 mm Canon Canovision EX1 camera with a zoom (8–120 mm) lens) of each fish from a set distance with standard illumination provided by tungsten lights. Calibration of the camera using a white standard ensured consistency of colours; the autogain option on the video camera was disabled to ensure consistency of colours during videotaping. Still frames of the males were captured by computer and their colours were analyzed using the Adobe Photoshop software package.

We first measured the average colour of a particular area as the grey-scale value, which ranges between 0 (black) and 256 (white). In our analyses, the actual range of values obtained went from 20 (grayish brown, almost like the rest of the body) to 190 (bright orange), with yellow colours at around 150. We calculated (i) the colour score of the dorsal fin stripe, (ii) the colour score of the left pectoral fin stripe, and (iii) the overall colour score. This last measure was obtained by summing the product of stripe colour and the relative surface area of the fin occupied by the stripe, for all stripes.

We then calculated the optical density for all three primary colours, red (wavelength 700 nm), green (546.1 nm), and blue (435.6 nm). We were only interested in the relative intensity of the red component in the colour of each fin stripe, which was computed as follows using density values: red / (red + green + blue). This index is independent of the brightness of a colour; it is only sensitive to increases in hue or saturation of the colour (Frischknecht 1993; Bakker and Mundwiler 1994).

Water clarity and substrate colour

Water samples from all five streams were collected at the time of fish capture. They were taken 10 cm off the stream bed in opaque bottles. Vigorous shaking of the samples before analysis ensured resuspension of any settled particles. The relative transmittance of light for wavelengths between 380 and 700 nm (20- to 50-nm intervals) was determined using a spectrophotometer, with recalibration to distilled water (100% transmittance) before each reading.

Photographs of the stream bed, taken through a glass-bottomed float, were used to determine substrate colour in all five streams. Lighting was provided by a ring flash calibrated to the amount of ambient light at each site for each exposure. An orange disk placed on the substrate at each site and appearing in all photographs provided a colour standard during computer analysis. Photographs were scanned into a computer colour analysis program, Adobe Colour Shop. Substrate colour was calculated from the pixel score of the scanned substrate area (0 for black, 256 for pure white), standardized against the colour of the disk to remove any biases in colour reproduction due to film processing or ambient light conditions.

Data analysis

We used parametric statistics after $\log_{10}$ transformation (parasite load, female clutch size, time of first visit, number of visits to males, and all male colour scores) or arcsine (percentage of time spent with male) transformation of the data requiring normalization. Fish length and fish age were highly correlated (females: r = 0.384, n = 90, P < 0.001; males: r = 0.358, n = 85, P < 0.001), and only fish body size was used in the analyses. The effect of the population of origin on variation in parasite load among fish was examined with analyses of covariance (ANCOVA) in which fish body size was the covariate. ANCOVAs were also used to assess variation among populations in female behaviour and male colouration, with fish parasite load, body size, and female fecundity as covariates. We also examined relationships among variables in each population separately. Multiple regressions were used for these within-population analyses. Each of the measures obtained during female-choice tests was regressed against female clutch size, body size, and parasite load. Each measure of male colouration was regressed against male body size and parasite load.

For analyses of geographic variation among populations, we used mean scores obtained by averaging values from individual fish. Because of the small sample size (only five populations) and because no interactions among our predictor variables were apparent in preliminary multiple regression analyses, we used simple correlations to assess the relationship between variables. Since the power of the analyses is limited, we did not adjust probability values using the Bonferroni procedures (Rice 1989). The results are therefore meant to indicate potential trends and do not provide definitive answers.

Results

Within populations

Parasite load varied significantly among the five populations (ANCOVA: females, $F_{[4,93]}$ = 5.18, P = 0.001; males,

Fig. 2. Relationship between male pectoral fin colouration and parasite load for five upland bully populations. Values are given as the mean ± SE for each population. G, Garden Bush stream; H, Garden Bush High stream; L, Linnburn stream; S, Shag tributary stream; T, Trotter's Gorge stream.
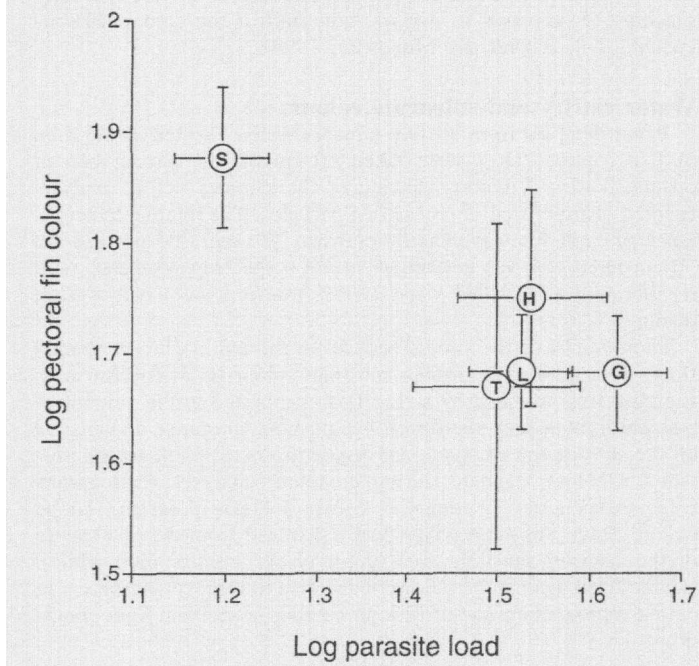
$F_{[4,88]} = 13.94$, $P < 0.001$); this is mainly because fish from the Shag tributary stream harboured much fewer parasites than fish from other streams (Fig. 2). The covariate body size also covaried positively with parasite load (females, $t = 3.774$, $P < 0.001$; males, $t = 3.537$, $P = 0.001$).

ANCOVAs indicated that the only female behaviour that varied significantly across bully populations was the number of visits to males made by females ($F_{[4,82]} = 6.28$, $P < 0.001$), with females from the Trotter's Gorge stream making about half as many visits to males as other females. None of the covariates investigated (female body size, clutch size, and parasite load) showed a significant association with any female behaviour (all $P > 0.15$). However, within a given population, significant and sometimes conflicting trends were found. Parasite load correlated with female mate choice behaviour in two of the five populations. The time taken to make the first visit to a male correlated negatively with parasite load among females from the Linnburn stream (standardized coefficient from multiple regression, $r = -0.873$, $P = 0.013$). However, among females from the Garden Bush High stream, the correlation was positive ($r = 0.429$, $P = 0.022$). Female size and time taken to make the first visit to a male were positively correlated in both these populations (Linnburn stream, $r = 0.987$, $P = 0.014$; Garden Bush High stream, $r = 0.454$, $P = 0.033$), whereas female size correlated negatively with the time taken to make the first visit in the Garden Bush High stream population only ($r = -0.532$, $P = 0.007$). No other significant relationships were found in any other bully population between any measure of female choice and any of the predictor variables.

ANCOVAs showed that some components of male colouration varied significantly among bully populations (dor-

sal colour, $F_{[4,87]} = 3.37$, $P = 0.013$; red index for dorsal fin, $F_{[4,87]} = 2.61$, $P = 0.041$; red index for pectoral fin, $F_{[4,87]} = 2.94$, $P = 0.025$). These components of colouration appeared to vary independently across populations, since no single population ranked as the most colourful according to more than one measure. One covariate, male body size, correlated positively with pectoral fin colour ($t = 2.77$, $P = 0.007$) and the overall colour score ($t = 2.57$, $P = 0.012$), whereas parasite load did not covary with any component of male colouration. However, within a given population, male colouration correlated with parasite load and other variables in different ways in the different streams. Overall male colour correlated negatively with parasite load in the Trotter's Gorge stream population ($r = -0.692$, $P = 0.017$), but surprisingly, in the Garden Bush stream population, male colour correlated positively with parasite load (pectoral fin, $r = 0.560$, $P = 0.013$; dorsal fin, $r = 0.493$, $P = 0.037$; overall, $r = 0.515$, $P = 0.030$). Larger Garden Bush High stream males also showed brighter pectoral fin colouration than smaller ones ($r = 0.610$, $P = 0.025$). No other relationship between measures of male colouration and either predictor variable was found.

Across populations

The relative transmittance of water was very similar for all streams throughout the spectrum tested (380–700 nm), the maximum difference between any two streams being <2%. We therefore excluded this variable from further analyses.

We first tested for a relationship between male colouration and either parasite load or substrate colour (Table 1). Male pectoral colouration was brightest in the most lightly parasitised population, although the relationship is influenced by the outlier point (Fig. 2). Overall male colouration did not correlate with parasite load or substrate colour. However, the males with the brightest overall colouration were from the least-parasitized population (Shag tributary stream), whereas the dullest males were from the population with the heaviest parasite load (Garden Bush stream). Male dorsal fin colour and the red index showed no relationship with either parasite load or substrate colour.

We then related average population parasite load and male colouration to female mate choice behaviours (Table 1). Females from populations in which males display bright pectoral fin colouration tended to spend less time assessing mates, i.e., less time visiting males, than females from populations with duller males (Fig. 3). The trend is the same when overall male colouration is used (Table 1). Also, females from populations in which male overall colouration was duller were more likely to prefer the brightest male in choice tests than females from populations with bright males (Fig. 4).

Discussion

Comparative studies of vertebrate populations that require testing of individual animals under laboratory conditions are logistically difficult. Constraints on numbers of populations that can be sampled and (or) numbers of individuals per population that can be tested place limits on the statistical power of subsequent analyses. Despite these limitations, our results suggest that the direction and (or) strength of sexual

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Table 1. Relationships between selected independent variables and measures of male nuptial colouration and female choice across five populations of upland bullies.

Dependent variable	Independent variable	Correlation coefficient	P
Pectoral fin colour	Parasite load	−0.892	0.042
	Substrate colour	−0.722	0.169
Dorsal fin colour	Parasite load	−0.476	0.417
	Substrate colour	−0.524	0.364
Brightness-preference ratio	Parasite load	−0.724	0.166
	Substrate colour	−0.525	0.363
	Overall male colour	−0.896	0.039
No. of visits to males	Parasite load	−0.001	0.998
	Male pectoral colour	0.131	0.549
	Male dorsal colour	0.510	0.175
	Overall male colour	0.149	0.522
Percentage of time spent with males	Parasite load	0.733	0.159
	Male pectoral fin colour	−0.890	0.043
	Male dorsal fin colour	0.073	0.907
	Overall male colour	−0.867	0.057

Fig. 3. Relationship between male pectoral fin colouration and the percent spent by females visiting males for five upland bully populations. For details see Fig. 2.
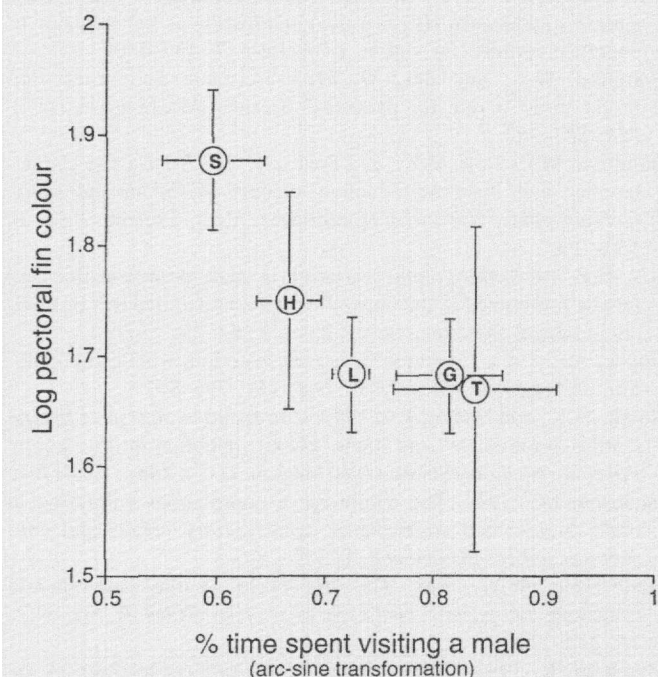
Fig. 4. Relationship between overall male colouration and the brightness-preference ratio for females (see the text) for five upland bully populations. For details see Fig. 2.
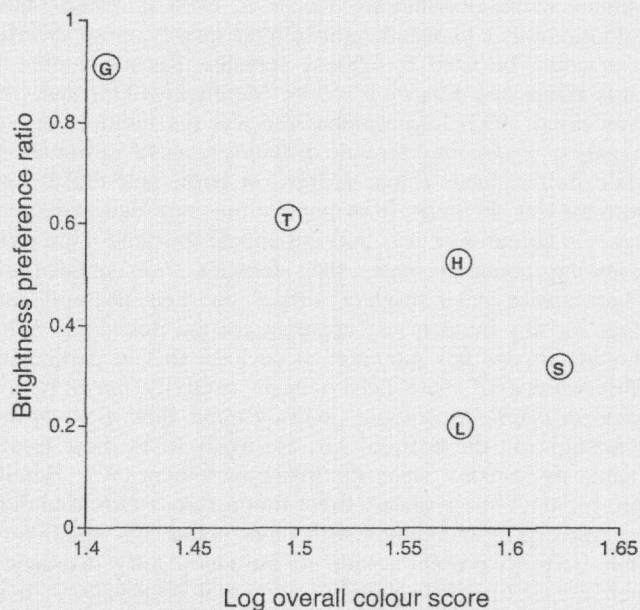
selection operating on upland bullies vary among populations. Indeed, we have shown that different populations have different average trait values and that pairs of traits are associated in different ways in different populations. This has at least one practical implication: results obtained from a single population cannot be generalized or extrapolated to the entire species. This warning has been issued before (e.g., Jamieson 1994) but is generally ignored. Its relevance to the upland bully is obvious. For instance, an earlier study found that heavily parasitized females from the Linnburn stream take less time to first visit males than lightly parasitized or nonparasitized females (Poulin 1994). Here we confirmed

that result, but we also observed the opposite trend in another population and found no pattern in a further three populations. As these results indicate, considerable variability among populations exists and should never be ignored.

We did not consider all factors that could potentially generate variability among bully populations. For instance, fish cannot synthesize carotenoids, the pigments used to produce their body colouration, so these must be obtained from their diet. However, a survey of invertebrates from our five study streams suggests that the species composition and abundance of prey that can be sources of carotenoids for fish do not differ among streams (R. Thompson, University of Otago, personal communication). In addition, despite all streams having similar communities of fish predators, we did not

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quantify the rate of predation on bullies in our study populations.

Some of the relationships observed within and among populations are puzzling. In the Garden Bush stream, for example, all measures of male colouration except the red index correlate positively with parasite load. Bullies from the Garden Bush stream are, on average, more heavily parasitized than fish from other streams (Fig. 2). Males of this population are, on average, much less colourful than males from other populations, whereas females from this population show a greater preference for bright males than females from other populations (Fig. 4). These results are not compatible with parasite-mediated sexual selection or selection of parasite-resistant males by females. If parasitism was a driving force behind sexual selection in this system, we would expect to find the brightest males and the most discriminating females in the most heavily parasitized populations, with parasite load and male colouration correlating negatively among individual males.

Choosiness is a costly strategy for females, and the fitness benefits it brings them must outweigh the costs (Pomiankowski 1987). Parasites generate variability in quality among males, but if male colouration is a poor indicator of a male's infection status, choosiness may not covary with parasitism across populations. However, even if overall male colouration is a poor indicator of male quality, more specific cues could be used by choosy females. Recent studies in birds (Dale and Slagsvold 1996; Marchetti 1998) and fish (Wedekind 1992) have emphasized that the multiple sexual signals of males may provide different types of information. Male bullies have colour stripes on both their dorsal and pectoral fins. Females from populations in which male pectoral fin colouration was dull did appear to spend more time assessing potential mates than females from populations where males have brighter stripes on their pectoral fins (Fig. 3); this trend is not apparent for the dorsal fin. Why should females pay attention to pectoral fins in particular? Observations of male behaviour in captivity may provide some answers. In aquaria, males extend their fins during courtship, but the pectoral fins are likely to be more easily visible by females, since the males face them (W.J. Hamilton, personal observation). Erect fin posture is also used during aggressive encounters with other males, but males turn their body to present a side to intruders, fully displaying their dorsal fin (W.J. Hamilton, personal observation). It is also interesting to note that pectoral fins are used in egg fanning (Stott and Poulin 1996) and may be a relevant cue to the male's parental qualities.

As suggested earlier, our results are not in agreement with the predictions of parasite-mediated sexual selection, a "good genes" model of sexual selection. At the same time, the lack of a clear covariation between male colouration and female preference does not support Fisherian selection either. We found that the females which chose bright males with the most consistency came from the population with the dullest males (Fig. 4). The forces acting on sexual selection in bullies are therefore unclear. However, sexually selected traits are typically subject to strong and rapid selection (West Eberhard 1983), and we might expect substantial plasticity in these traits in response to environmental changes. What is clear, then, is that the different bully populations have diverged, and this is most likely due to adjustments to local conditions.

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