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Direct male-male competition can facilitate invasion of new colour types in Lake Victoria cichlids

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Abstract The possibility that disruptive sexual selection alone can cause sympatric speciation is currently a subject of much debate. The initial difficulty for new and rare ornament phenotypes to invade a population, and the stabilisation of the resulting polymorphism in trait and preference make this hypothesis problematic. Recent theoretical work indicates that the invasion is facilitated if males with the new phenotype have an initial advantage in male-male competition. We studied a pair of sympatric incipient species of cichlids from Lake Victoria, in which the red (*Pundamilia nyererei*) and blue males (*P. pundamilia*) vigorously defend territories. Other studies suggested that red phenotypes may have repeatedly invaded blue populations in independent episodes of speciation. We hypothesised that red coloration confers an advantage in male-male competition, assisting red phenotypes to invade. To test this hypothesis, we staged contests between red and blue males from a population where the phenotypes are interbreeding morphs or incipient species. We staged contests under both white and green light condition. Green light effectively masks the difference between red and blue coloration. Red males dominated blue males under white light, but their competitive advantage was significantly diminished under green light. Contests were shorter when colour differences were visible. Experience of blue males with red males did not affect the outcome of a contest. The advantage of red

over blue in combats may assist the red phenotype to invade blue populations. The apparently stable co-existence of red and blue incipient species in many populations of Lake Victoria cichlids is discussed.

Keywords Cichlids · Lake Victoria · Sexual selection · Speciation · Male-male competition

Introduction

The possibility of sympatric speciation, in which reduction of gene-flow between emerging species occurs in the absence of geographical isolation, has become increasingly accepted in the past decade (Bush 1994; Seehausen and Van Alphen 1999; Schluter 2001; Via 2001; for recent review, see Coyne and Orr 2004). There is now broad consensus that reproductive isolation can arise as a pleiotropic consequence of disruptive natural selection on traits associated with competition for resources. In this view of sympatric speciation, reproductive isolation results mainly from ecological causes, and sexual selection only plays a supporting role (Panhuis et al. 2001; van Doorn and Weissing 2001; Arnegard and Kondrashov 2004). A growing number of speciation models, many of which were motivated by the explosive speciation of haplochromine cichlids in Lakes Victoria and Malawi, suggest that divergent sexual selection alone can cause sympatric speciation (Lande and Kirkpatrick 1986; Turner and Burrows 1995; Payne and Krakauer 1997; van Doorn et al. 1998; Higashi et al. 1999; Kawata and Yoshimura 2000; van Doorn and Weissing 2001). These models are inspired by comparative studies, which indicate that closely related species often differ markedly in their secondary sexual characteristics and mate preferences, and only little in ecology (Bouton et al. 1997; Seehausen and Bouton 1997). However, empirical studies are few (Endler and Thery 1996; Wells and Henry 1998; Seehausen et al. 1999) and it is difficult to say whether sexual selection is the primary cause of their phenotypic divergence, or whether sexual selection exerting mate

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choice was recruited by disruptive natural selection (Turelli et al. 2001; Arnegard and Kondrashov 2004; Kirkpatrick and Nuismer 2004). A fundamental problem in sympatric speciation driven by sexual selection is the initial hurdle for a novel rare male phenotype to invade a population against the predominant female mate preference (Seehausen and Schluter 2004; van Doorn et al. 2004). Successful invasion requires a fitness advantage for a new morph, but maintenance of polymorphism requires that this advantage is negative frequency-dependent (van Doorn et al. 2004). When exerting selection on the same traits that determine female mate choice, male-male competition for access to spawning territories could generate such frequency-dependence in sexual selection. An advantage could emerge if the new morph induces submissive behaviour in opponents, e.g. by being more brightly coloured. This would generate negative frequency-dependent selection, because as the frequency of the new morph increases, the proportion of fights of new morphs with ancestral morphs as opposed to new morph males decreases. The symmetry of frequency-dependent selection may be modulated if the ancestral type males change their behaviour as a result of social experience with, or genetic adaptation to, males of the new morph. Here we experimentally investigate whether the invasion of a new morph may be facilitated by direct male-male competition, using two closely related incipient species of rock-dwelling cichlids from Lake Victoria.

Lake Victoria's flock of endemic haplochromine cichlid fishes is among the most rapidly speciating groups of vertebrates (Johnson et al. 1996; Seehausen 2002), and is considered an outstanding example of explosive evolution and adaptive radiation (Greenwood 1981; Kaufman 1997; Seehausen et al. 2003). Sexual selection by female choice on conspicuous male colour patterns has been proposed as an important factor in the rapid speciation (Dominey 1984; Seehausen et al. 1997; Seehausen and Van Alphen 1998; Kocher 2004). Males of many of the speciose genera of cichlid fish in Lake Victoria vigorously defend territories to secure mating opportunities, and it appears that possession of a territory is a prerequisite for access to spawnings. The genus *Pundamilia* is a good example of this pattern. Females provide extensive mouth broodcare and preferentially mate with males that hold large territories (Maan et al. 2004). Hence, competition over territory sites is likely intense, and may play an important role in sexual selection (Fryer and Iles 1972; Seehausen et al. 1998a).

We experimented with a pair of hybridising or incipient species of the genus *Pundamilia*, consisting of a *Pundamilia nyererei* (Witte-Maas and Witte 1985)-like form with red, and a *P. pundamilia* (Seehausen et al. 1998b)-like form with blue male nuptial coloration. Incipient species refers to two populations which are not reproductively isolated, representing an early stage of speciation. We used a population (Kissenda Island) in which red and blue phenotypes are undifferentiated at neutral microsatellite loci (M. Taylor et al., unpublished data). In this population, therefore, red and blue males have a largely homogeneous genetic background except for traits that appear

to be under disruptive selection. This makes them a suitable system to investigate the effects of nuptial coloration on behaviour. Assortative mating among *Pundamilia* sp. is based on female mating preferences for male nuptial coloration, but is constrained by water clarity (Seehausen and Van Alphen 1998). Kissenda Island has turbid water, probably explaining the porous reproductive isolation between the red and blue forms.

Blue phenotypes have a wider and more continuous geographical distribution than red phenotypes. Red always co-occurs with blue, and the latter has the highest record of sympatric occurrences with other members of the *Pundamilia* complex (Seehausen 1996; Seehausen and Van Alphen 1999). This suggests that it is likely that blue populations have been invaded repeatedly by red forms during independent episodes of speciation (Seehausen 1997; Seehausen and Van Alphen 1999; Seehausen and Schluter 2004). If the red nuptial phenotype tends to be the invading phenotype, it requires an initial selective advantage. This advantage would diminish as the frequency of red males increases, because the proportion of fights between blue and red contestants drops. The advantage would also diminish when the behaviour of blue males changes with more frequent experience with red males. Such negative frequency-dependent selection could promote a stable colour polymorphism. To test the effect of nuptial coloration on the outcome of competitive interactions, we staged contests between red and blue males under white and under green light. Green light effectively masks the differences between red and blue coloration. To test if prior experience with red males affects competitive ability in blue males, blue males were either given experience with red males or not.

Methods

Fish

P. nyererei and *P. pundamilia* are morphologically highly similar haplochromines that at many places in Lake Victoria behave like behaviourally isolated sibling species (Seehausen 1997; Seehausen and van Alphen 1998). Where the lake waters are extremely turbid though, single populations of *Pundamilia* are found, with variable male coloration but no well-differentiated red and blue phenotypes. At intermediate turbidity, differentiated red and blue nuptial phenotypes co-exist as incipient species with less frequent intermediate phenotypes. Such is the population from Kissenda Island in the central Mwanza Gulf in Tanzania. Males of both phenotype classes have blackish under parts and blackish vertical bars on the flanks. Males of the red (*P. nyererei*-like) phenotype, however, are crimson dorsally, yellow on their flanks, and have a crimson dorsal fin. We refer to them as "red males". Males of the blue (*P. pundamilia*-like) phenotype are greyish-white dorsally and on the flanks, and have a metallic-blue dorsal fin. We refer to them as "blue males". At Kissenda Island, blue and red occur sympatrically and syntopically (Seehausen 1997).

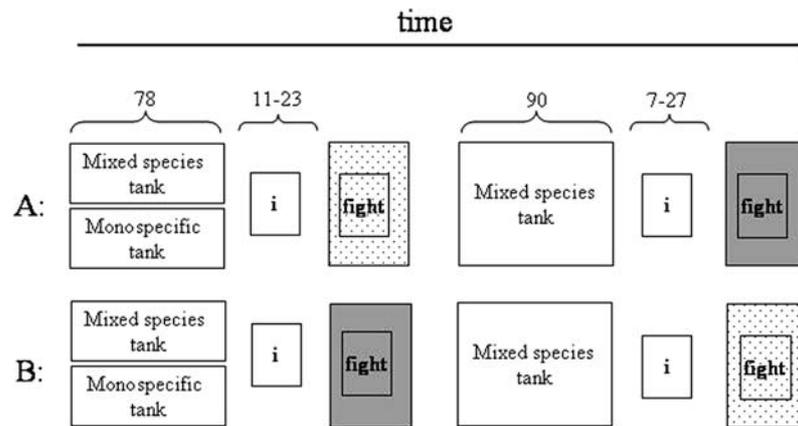


Fig. 1 Scheme of experimental design. Experimental males were divided over two groups: group A experienced their first fight under white light and their second under green light, whereas males in group B experienced their first fight under green light, and their second under white light. White light is shown by *dots*, green light by *grey shading*. Before and between fights males were housed in

large monospecific or mixed species groups. At least 1 week prior to moving males for a fight, they were housed individually (denoted by “i”) to ensure territoriality. Number of days are indicated below the *timeline* to indicate the range of days in which males experienced a particular housing condition

Males and females were collected at the island and brought to the Zoological Laboratory in Haren in June 2001. We used first-generation offspring bred from this stock. For each phenotype, males were bred from five wild-caught females and three wild-caught males. Experimental males were selected from 60 red and 51 blue males. All males were sexually mature and at least 11 months of age.

Housing

Wild-caught males and females were kept in monospecific groups of 13–25 individuals per aquarium (100–300 l). First-generation offspring were bred from this stock, and reared in sibling groups. The sides and the back of all aquaria were covered with black plastic. All aquaria were connected to a central biological filter system and water was circulated continuously. Water temperature was kept at $25 \pm 2^\circ\text{C}$, and a 12:12 h light:dark cycle was maintained. All aquaria contained a substrate of gravel. The fish were fed flake food (TetraMin Tropical Fish Flakes) six times per week.

Experiment

Experimental males were housed in groups of 20–60 individuals in 100 to 300l aquaria. To avoid the effect of previous encounters in the raising tanks, males were individually housed for at least 1 week prior to a contest in tanks of 100 l, divided into eight to ten compartments by PVC sheets. To avoid social deprivation and to encourage territoriality, all males were kept in compartments with another male visible behind a transparent PVC sheet. Each compartment contained a PVC tube that the fish used as a hiding place. They often indulged in boundary fighting with their territorial neighbour.

Experimental pairs were matched for weight, and had never been housed in visually adjacent compartments during the pre-experimental period. To test if coloration determines contest outcome, we conducted the experiment both under white light and under green light (see below). Green light eliminates the colour difference between red and blue males. Figure 1 illustrates the experimental design. For each light treatment, we selected pairs, such that most males experienced one contest under white light and one under green light. To control for possible sequence effects, we used a cross-over design, testing some individuals (group A) first under white light, and thereafter under green light, and the other individuals in reverse sequence (group B). We staged 42 contests under white light, and 42 under green light. Two contests from the white light treatment were excluded because we were unable to assign a winner and a loser. Thus, in group A we ended up with 31 contests under white light, and 27 contests under green light. Group B included 15 contests under green light, and 9 under white light. To further reduce the effect of prior experience, we allowed approximately 3 months between contests, during which males were housed in large mixed-species aquaria, 1 for group A (63 fish), and 1 for group B (24 fish). We ensured that males never fought twice under the same light condition. When composing pairs of males for their second contest, it was possible to choose the opponent of one male from at least five but often more individuals, of which only one could have been the fish that had been the opponent in the previous fight. It is therefore unlikely that re-confrontation with the same male is an important confound in this study. We therefore treated each contest as an independent event.

Monospecific and mixed species housing treatment

To test for the effect of prior experience with red males on competitive ability in blue males, we housed the males

before the contest experiment as follows. Prior to the first series of contests under white light (group A, Fig. 1), mature males were removed from their sib groups and housed for at least 78 days in either a monospecific or a mixed-species group in aquaria of 170 l. We created 2 monospecific aquaria: 1 for 36 blue males, 1 for 36 red males. The mixed-species aquarium contained 19 blue and 17 red males. During this period, males were already mature and frequently engaged in aggressive interactions. During the individual housing period prior to the contest, males from the monospecific groups were given a conspecific neighbour, whereas the males from the mixed group were given a heterospecific neighbour.

Males that experienced their first contest under green light were also housed in either monospecific or mixed-species groups. In the present study, we only analysed the effect of social experience on the contests under white light.

Twenty blue males from the monospecific group fought against 20 red males from the monospecific group. Eleven blue males from the mixed group fought against 11 red males from the mixed group.

Light treatment

We used green filters to eliminate the colour difference between red and blue males. Illumination was provided by 58-W fluorescent light tubes (cool white) in metal hoods. White light was created by wrapping two layers of neutral filters (Filter Neutral Density, code 209 0.3ND, Lee Filters) around the hoods. Green light was created with a single layer of green sheets (Filter Primary Green, code 139, Lee Filters). Light intensity did not differ between light treatments (independent sample *t*-test: white light: $X \pm SD = 429 \pm 210$ lx, $N = 40$, green light: $X \pm SD = 373 \pm 153$ lx, $N = 42$, $t_{82} = 1.351$, $P = 0.18$).

Experimental procedure

Males were quickly weighed in air on an electronic pan balance. The weight asymmetry between paired males was calculated as $\ln(\text{weight red male}/\text{weight blue male})$ following Enquist and Leimar (1983). Weight asymmetries were balanced and roughly symmetrically distributed over the two species (absolute weight asymmetry range 0–0.3). We staged contests by placing pairs of males in test aquaria (100 l). Males were separated by an opaque partition in the middle. Each compartment contained a PVC tube that provides a shelter. A mixture of three to four juvenile fish of either one or both species, showing no nuptial coloration, were placed in each compartment to maintain territoriality in the test fish; they were separated from the test fish by a transparent partition. All pairs were placed in the experimental aquarium 1–3 days before the contest took place. At the start of the contest, we removed the opaque partition between the two experimental fish, and the PVC tubes, to avoid hiding behaviour. The contest was videotaped from behind a blind.

After conflicts had been settled, the fish were separated immediately. Males were blotted dry and weighed again to the nearest 0.1 g. These final weight measurements were used in the analysis of weight asymmetry and conflict outcome, because these were closer in time to the conflict. Weight asymmetry did not differ significantly between light treatments (independent *t*-test, $t_{82} = -0.021$, $P = 0.98$), and nor did it differ in favour of either species (white light: $t_{40} = -0.565$, $P = 0.58$; green light: $t_{42} = -1.551$, $P = 0.13$).

Observations

In 82 of the 84 contests that we staged, males engaged in territorial fighting, defined as at least 1 aggressive interaction in which both contestants performed threat display and/or overt aggression. In all these pairs, we could clearly identify a winner and a loser. Males showed the common behavioural repertoire found in cichlid wrestling (Baerends and Baerends-Van Roon 1950; Turner and Huntingford 1986). They usually commenced a fight by raising their fins. This was then followed by several noncontact displays, such as lateral display, gill display, quivering and tail beating. In several interactions, one of the males initially performed courtship display, usually presentation of egg dummies on the anal fin, and the courted male responded to this by showing female mimicry behaviour. This was always rapidly replaced by agonistic behaviour. Instances of courtship in male-male interactions followed by agonistic behaviour have been found in previous cichlid contest studies (Oliveira and Almada 1998). Escalated fighting began abruptly in the form of biting, mouth locking and circling. At the end of each contest, one fish would abruptly break from the interaction and flee, accompanied by paling in coloration; this fish was defined as the loser. The contest duration was quantified from the videotapes in seconds. It was defined as the time period between the start of the aggressive interaction, when both fish started to display, and the time the loser started to flee, minus the duration of any pauses and courtship. Pauses were defined as interruptions in contests during which males did not interact with each other. In such cases, they showed non-aggressive behaviour, such as exploring the tank environment.

Analysis

We tested for the effect of light treatment on contest outcome using binomial, chi-square and Fisher-exact probability tests.

In addition, we used general linear models (GLM), with contest duration as response variable, and logistic regressions, with outcome of contest (red wins or blue wins) as response variable to test the effect of light treatment and monospecific or mixed-species housing condition (social experience). Independent variables also included weight asymmetry and contest duration. Models are specified in the results section. We used backward stepwise selection procedures to determine which variables accounted best

for the variation in the dependent variable. The criterion to remove a variable was set at $P=0.05$. In the logistic regression, we used the Wald test to evaluate the significance of a variable. The fit of a candidate model was tested by comparing the deviance (D) of this model with a “saturated” model that contained as many parameters as data points (Hardy and Field 1998).

The variables contest duration and average weight of opponents were $\ln(x+1)$ transformed to meet the assumptions of parametric analysis.

All tests were two-tailed, and all statistical tests were performed in SPSS 11.0.1 or Statistix.

Results

Contest outcome

The saturated logistic model for conflict outcome consisted of light treatment, WA, contest duration and all interaction terms. The stepwise selection procedure yielded a final model with light treatment (Wald=4.233, $P=0.04$) and weight asymmetry (Wald=8.059, $P=0.005$) as significant predictors of contest outcome. The overall fit of the final model was good ($D_{79}=81.59$, $P>0.1$). Figure 2 illustrates the probability curve for this final model. This curve shows that the probability that red wins was higher under white light than under green light, and that the outcome was in favour of the heavier fish.

To ask whether males of either colour type won more contests, while taking into account weight disparities as well as light condition, we examined contests in which contestants were weight-matched (absolute weight asym-

Table 1 Outcome of weight-matched contests with a weight asymmetry (WA) of less than 0.02 for each light treatment. P -values are given for binomial tests, comparing the number of fights won by each species

Light	Blue wins	Red wins	P -value
White	3	11	0.029
Green	6	7	0.5

metry less than 0.02, see Table 1). Weight-matched red males won significantly more contests than blue males under white light (binomial, $P=0.03$). Under green light, the chance of winning was similar for red and blue males (binomial, $P=0.50$). However, the effect of the light treatment on the proportion of contests won by red males in weight-matched contests was only significant at the 10% level (chi-square: $\chi^2=3.04$, $P=0.08$).

Contest duration

Figure 3 shows the contest duration under white and green light. The saturated GLM model for contest duration included the variables light treatment, winner’s colour (red or blue), weight asymmetry and all interaction terms. The stepwise procedure selected a final model ($F_{2,79}=3.108$, $P=0.050$), with the variables light treatment ($F_{1,79}=4.533$, $P=0.036$) and winner ($F_{1,79}=2.914$, $P=0.09$) as best predictors of contest duration. Contests under green light were longer than under white light (Fig. 3). The winner of the contest was not significantly related to contest duration but we retained this effect in the model because it accounted for some variation (variation within winners of the same colour smaller than between winners of different colour, as

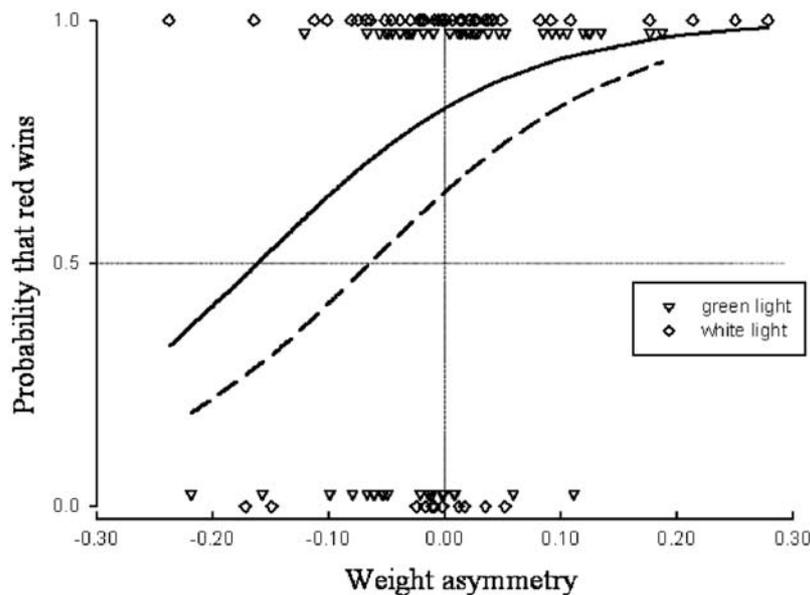


Fig. 2 The relationship between weight asymmetry and the probability that red wins, based on the logistic regression with weight asymmetry and light treatment as variables (— white light treatment; - - - green light treatment). Weight asymmetry is expressed as: $\ln(\text{weight red male}/\text{weight blue male})$. Thus, a negative weight asym-

metry indicates that the blue contestant was heavier, zero means that males were equally matched, and a positive value indicates that the red contestant was heavier. Values (blue winner=0, red winner=1) are slightly displaced for visual clarity

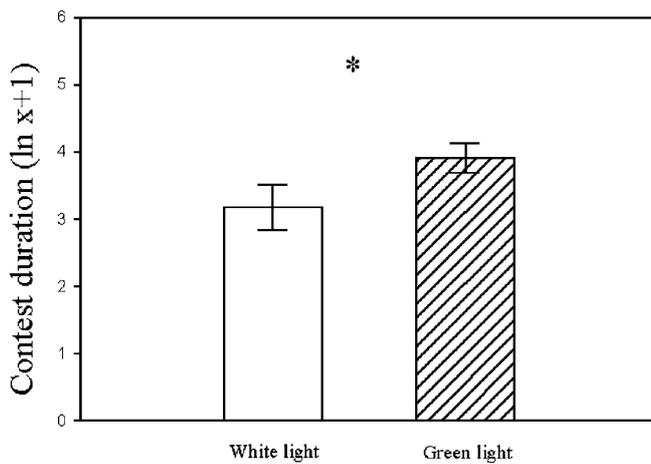


Fig. 3 Contest duration (mean and SD) under white ($N=40$) and green light ($N=42$); $*P < 0.05$

indicated by F -ratio > 1). Contest duration was longer when a red male won the contest.

Social experience

To determine if contest duration and/or outcome under white light were affected by social experience, we used a GLM and a logistic regression, respectively. In the GLM we included, apart from social experience, the variables winner's colour, weight asymmetry and all interaction terms to predict contest duration. To predict contest outcome, we included weight asymmetry, contest duration and all interaction terms in the logistic regression. According to the criteria of the backward selection procedure, social experience was one of the first variables to be removed in both models (logistic regression: social experience $P=0.88$, GLM: social experience $P=0.85$). In addition, a forward regression, starting with social experience did not reveal any significant effect of these variables (logistic regression: social experience $P=0.56$, GLM: social experience $P=0.5$). Thus, social experience is a poor predictor of contest outcome or duration.

Discussion

Dominance of red males

We hypothesised that red nuptial coloration provides males with an advantage in male-male competition in the Lake Victoria genus *Pundamilia*, which would facilitate the invasion of blue populations by novel red morphs. We found that when colour differences were visible, red males were more likely to prevail in direct aggressive encounters with weight-matched blue males. Under green light, the chance that red or blue won a contest when weight-matched was equal. The difference in outcome of weight-matched contests between light treatments was only significant at the 10% level, which might be attributed to low sample sizes.

The logistic regression showed a significant light treatment effect, suggesting that red coloration itself confers an advantage in male-male combat. To the human eye, red males appear much more brightly and conspicuously coloured than blue males. If this is also true for the cichlid eye, it is possible that the brightness of red coloration intimidates blue opponents. The observation that contests lasted significantly longer under green light is consistent with this interpretation. It suggests that blue males were more motivated to fight when they could not perceive the red coloration of their opponent.

The advantage of red colour in winning a contest is consistent with studies of intraspecific contests in other cichlids and some other teleosts, where redder males tended to have an advantage (firemouth cichlids *Cichlasoma meeki*: Evans and Norris 1996; sticklebacks *Gasterosteus aculeatus*: Baube 1997). These authors also manipulated colour perception of the males and found a reduction in the chance of winning a contest for redder males when colour differences were masked. Rowland and co-workers (1995) suggested that the conspicuousness of red colour directly intimidates rivals by stimulating a fear response. The same has been suggested for the effect of bright-orange coloration in Midas cichlids, *Amphilophus* ("*Cichlasoma*") *citrinellum* (Barlow 1983).

Co-existence of red and blue species

The competitive advantage of red over blue males offers a potential explanation for how red males can invade blue populations. However, for red and blue forms to stably co-exist in natural communities, it is required that dominant red males are under negative frequency-dependent selection. This could be achieved by blue males becoming less inhibited as a result of fights with the red morph. However, in our experiment, prior social experience with red males was a poor predictor of contest outcome, suggesting that previous encounters with red males did not improve or weaken the competitive ability of blue males. Experience of blue males with red males is thus unlikely to counteract the advantage of red males. However, red males may be subject to negative frequency-dependent selection, because with increasing frequency of red males, red males would be involved in more contests with other red males in which they lack the advantage that they have in red-blue contests. Nevertheless, the advantage of red in male-male combat would then still be frequency-independent, possibly leading to a situation in which red males displace blue males. One possibility that promotes co-existence of both morphs is when contests between red males are more costly than fights between blue males, in terms of fight duration and/or risk of injury. This hypothesis remains to be tested.

We observed that heavier males are more likely to win a fight. This has often been shown in cichlid fish (Turner 1994; Neat et al. 1998) but it could be relevant in the context of sympatric divergence and co-existence. The incipient species with a male coloration that conveys a disadvantage in contests may compensate by growing

larger body sizes. *P. pundamilia* males indeed attain a larger size than *P. nyererei* at several islands in Lake Victoria (Seehausen et al. 1998a).

Several other factors may further counterbalance the advantage of red males. In a separate study, we found that both territorial red and blue males direct more aggressive behaviour to red intruders, whereas under green light males did not discriminate between red and blue intruders (Dijkstra et al., unpublished data). This indicates that redness itself imposes a social cost, and implies that red males are likely to suffer from more aggressive attacks than blue males. Red coloration may also impose a cost due to higher nutritional requirements to maintain red coloration (Candolin 2000), and a higher predation risk of red males to visually guided predators (Endler 1992; Andersson 1994; Godin and McDonough 2003). That red coloration is indeed costly in *Pundamilia*, is suggested by the finding that red colour has almost disappeared in many populations in extremely turbid waters with constrained colour visibility (Seehausen 1997; Seehausen et al. 1997).

It has recently been suggested that competition for breeding sites may promote diversification and possibly sympatric speciation among haplochromine cichlids (Seehausen and Schluter 2004). Here we described an experimental study in a Lake Victoria cichlid genus in which we showed that male-male competition can assist a novel male phenotype to invade. Our study supports the hypothesis that male-male competition can be a significant facilitating force of sympatric speciation.

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