



Reproductive isolation among closely related Lake Malawi cichlids: can males recognize conspecific females by visual cues?

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Little is known about mate recognition systems among the species-rich cichlid flocks of the African Great Lakes. Such knowledge is critical to our understanding of how evolutionary processes have brought about the current diversity. In the present study we focused on three anatomically similar species of rocky shore cichlid fish *Pseudotropheus* (*Maylandia*) spp. from Lake Malawi. We scored male responses to heterospecific and conspecific females which were enclosed in separate watertight transparent chambers. Any male behaviour we observed was therefore due to visual cues alone. Although males of some species could clearly identify conspecific females on visual cues alone, others could not. In cases where conspecific and heterospecific females were phenotypically similar, males could not consistently distinguish between them. Further experiments are required, however, to see whether males can recognize these females using alternative means, such as olfactory cues.

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The breeding systems of the African Great Lake cichlid flocks are of particular interest since they may tell us something of the means by which the vast numbers of species endemic to these lakes (e.g. Ribbink et al. 1983; Seehausen 1996) may have arisen over such a short time period (an estimated 700 000 years in Lake Malawi; Meyer et al. 1990; probably considerably less in Lake Victoria; Johnson et al. 1996). Sexual selection by female choice has been suggested as one of the potentially important mechanisms fuelling this rapid speciation (Dominey 1984; Turner 1994), particularly within Lakes Malawi and Victoria. Male coloration is a trait that often varies strikingly among closely related taxa in these lakes, whereas females in contrast are often phenotypically similar. Male coloration has therefore been hypothesized as a key trait upon which female choice operates, which may subsequently lead to the divergence of populations, a scenario supported by theoretical modelling (e.g. Lande 1981; Turner & Burrows 1995). Several recent studies demonstrating female preferences for male characteristics (Hert 1991; Taylor et al. 1998), and notably for male coloration (Seehausen & van Alphen 1998), have lent this suggestion some credence.

The existence of female choice for male colour does not, however, suffice as evidence for the importance of sexual selection during the evolution of these taxa (e.g. Ryan & Rand 1993). Solid support for such a proposition

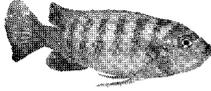
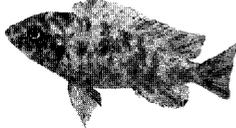
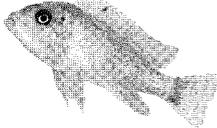
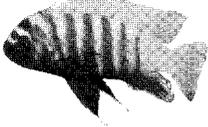
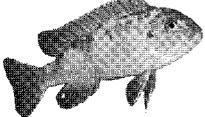
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must also include evidence that such sexually selected traits are also used as cues in mate recognition (Boake et al. 1997). Few studies to date, however, have addressed mate recognition systems within the Great Lake cichlids and little is known of the cues that maintain reproductive isolation among closely related species.

The *Pseudotropheus* (*Maylandia*) species complex belongs to the mbuna, a group of genera occupying the shallow rocky fringes of Lake Malawi. (Stauffer et al. 1997 recently proposed *Metriaclima* as a new genus name for this complex.) Three members of this complex occur sympatrically at Nkhata Bay, Malawi: *P. zebra*, *P.* 'zebra gold' and *P. callainos*. Males of these species differ strikingly in coloration. *Pseudotropheus zebra* males are blue with six or seven black vertical bars, *P.* 'zebra gold' males are yellow with brown vertical bars, and *P. callainos* males are plain blue (Table 1). Females of each of these species occur as two or three colour morphs (Table 1): 'barred' (*P. zebra* and *P.* 'zebra gold'); 'blotched' (*P. zebra*, *P.* 'zebra gold' and *P. callainos*); and 'plain' ('orange' in *P. zebra* and both 'blue' and 'white' in *P. callainos*). The 'barred' and particularly 'blotched' females of *P. zebra* and *P.* 'zebra gold' are very similar in colour and pattern and can often be distinguished only by small differences in head and body shape (e.g. Konings 1995). Males of these different morph types can be found in the field but are extremely rare.

Analysis of microsatellite loci in sympatric populations has shown these taxa to be reproductively isolated in the field (van Oppen et al. 1998). Captive studies report the

Table 1. Appearance of males and intraspecific female colour morphs of *P. zebra*, *P. 'zebra gold'* and *P. callainos* (see also [Konings 1995](#))

| Species | Sex | Appearance | Colour |
|------------------------|-------------------|---|---------------------|
| <i>P. zebra</i> | Male 'barred' |  | Bright blue/black |
| | Female 'barred' |  * | Brown/light brown |
| | Female 'blotched' |  | Orange/black |
| | Female 'orange' |  | Orange |
| <i>P. 'zebra gold'</i> | Male 'barred' |  | Bright yellow/brown |
| | Female 'barred' |  * | Brown/light brown |
| | Female 'blotched' |  | Orange/black |
| <i>P. callainos</i> | Male 'blue' |  | Bright blue |
| | Female 'blue' |  | Blue |
| | Female 'blotched' |  | White/blue |
| | Female 'white' |  | white |

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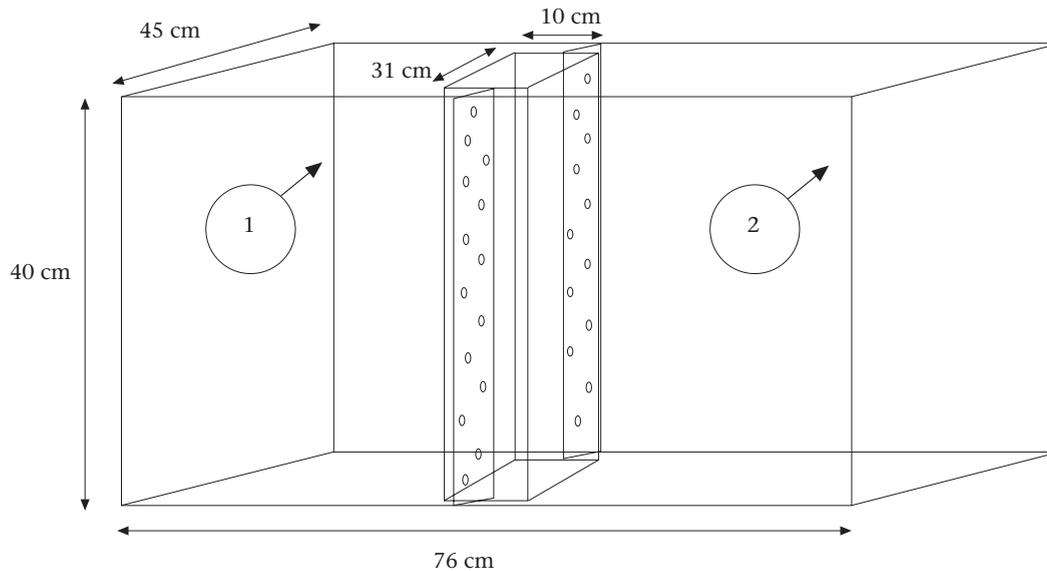


Figure 1. Experimental set-up showing two end male compartments and a central sealed female compartment.

persistence of this assortative mating under laboratory conditions and conclude that reproductive isolation among these three species can be maintained by direct mate choice alone (Knight et al. 1998). Whether, however, mate recognition is a function solely of female choice or whether males also play a role is as yet untested. In this study we investigated the ability of males to discriminate between conspecific and heterospecific females, thereby testing the potential male role in the maintenance of reproductive isolation in these taxa.

METHODS

Fish Maintenance

Both males and females were a mixture of wild-caught adults (from Nkhata Bay, Malawi) and first-generation offspring bred from this stock. Eight male pairs of each species were wild-caught individuals that had been kept in captivity for a minimum of 12 months; the remaining eight pairs were from F1 generation stock. Males had previously been kept in stock tanks housing both conspecific and heterospecific males and females.

Experimental tanks (see below) were filtered with internal box filters in each of the two main compartments, heated to a constant 26°C by an internal 250-W heater and lit with a metal halide (125-W) overhead (white) light on a 12:12 h light:dark cycle. Upon the completion of each male pair trial (see below), tanks were given a one-third water change with tap water (pH 8.0–8.3). All fish were fed daily with a mixture of trout pellets and flake food. After each trial, the fish were returned to separate stock tanks.

Experimental Protocol

We carried out experiments over a year (this period was necessary owing to an initial lack of stock). Experimental

tanks (76 × 45 cm and 40 cm high) were divided into two main compartments by a clear, sealed Perspex box (10 × 31 × 40 cm) which slotted between two (7-cm wide) perforated Perspex runners (Fig. 1). Water could, therefore, flow between the main compartments, but not between the main compartments and the Perspex box. The experimental tanks were surrounded with Roscoscrim 3809 (Teamwork Ltd, London, U.K.). This creates a one-way-mirror effect and thereby minimizes external disturbances to the focal animals. We introduced a single male into each of the main compartments (each pair belonging to the same species) within which terracotta pots were placed as refuges. Males were thus in full visual contact with another conspecific male at all times. This arrangement encouraged males to become territorial. The males were allowed to settle for 3 days. This long period was necessary for males to become territorial towards the neighbouring male (illustrated by 'digging' behaviour around the refuge and aggression towards the neighbouring male). Since the aim of the experiment was to optimize male response, this was of critical importance.

We then introduced a succession of females one at a time into the Perspex box dividing the two main compartments. Females were fully visible to each male during the observation period, but no olfactory communication was possible since the female compartment was sealed. Females were weighed and measured (standard length) before introduction ($\bar{X} \pm \text{SD} = 23.1 \pm 8.4$ g; 85.0 ± 9.8 mm). We presented one female of each morph for each of the three species to each pair of males in randomized order (eight females in total: *P. zebra* 'barred', *P. zebra* 'blotched', *P. zebra* 'orange', *P. zebra* 'gold' 'barred', *P. zebra* 'gold' 'blotched', *P. callainos* 'blue', *P. callainos* 'blotched', *P. callainos* 'white'), one every hour for 8 h. We recorded the response of each male to each female for 5 min, after which we removed the female. Thus, during each trial each male was exposed to the

Table 2. Student–Newman–Keuls post hoc tests comparing the condition of females

| | Z-B | Z-O | Z-BI | G-BI | G-B | C-B | C-W | C-BI |
|------|-----|-----|------|------|-----|-----|-----|------|
| Z-B | — | NS | NS | * | * | ** | * | ** |
| Z-O | | — | NS | * | * | ** | * | ** |
| Z-BI | | | — | * | * | ** | ** | ** |
| G-BI | | | | — | NS | NS | NS | NS |
| G-B | | | | | — | NS | NS | NS |
| C-B | | | | | | — | NS | NS |
| C-W | | | | | | | — | NS |
| C-BI | | | | | | | | — |

Z-B: *P. zebra* 'barred'; Z-O: *P. zebra* 'orange'; Z-BI: *P. zebra* 'blotched'; G-BI: *P. 'zebra gold'* 'blotched'; G-B: *P. 'zebra gold'* 'barred'; C-B: *P. callainos* 'blue', C-W: *P. callainos* 'white', C-BI: *P. callainos* 'blotched'.
* $\alpha=0.05$; ** $\alpha=0.01$.

Table 3. Frequency of male courtship responses to females (16 male pairs)

| | <i>P. zebra</i> | <i>P. 'zebra gold'</i> | <i>P. callainos</i> |
|---|-----------------|------------------------|---------------------|
| No response | 5 | 8 | 3 |
| One male responded only | 8 | 6 | 4 |
| Both males responded but to different females | 1 | 0 | 0 |
| Both males responded to the same females | 1 | 0 | 3 |
| Combination of one and both males responded* | 1 | 2 | 6 |

*Cases where only one male responded to some females and both responded to others (during any one trial of eight presented females).

entire suite of *Pseudotropheus* (*Maylandia*) species complex females present at Nkhata Bay.

Courtship within these species is highly conserved (McElroy & Kornfield 1990) and consists of a characteristic series of behaviours (see e.g. Baerends & Baerends van Roon 1950; Vodegel 1978). We recorded male courtship behaviour as 'quiver', followed by 'lead'. Only overt behaviours were scored: any behavioural responses where interpretation of motive could be ambiguous (such as 'lateral display') were not included. We analysed the data in two ways: considering simply whether males displayed any courtship behaviour towards the females (i.e. a 'yes' or 'no' recorded for each trial), and then analysing the tallied scores for courtship behaviour displayed by the males towards each female (the number of 'leads' observed).

We tested 32 males (16 pairs) belonging to the common morph of each of the three species (i.e. 32 *P. zebra*, 32 *P. 'zebra gold'* and 32 *P. callainos*) and each male was tested only once. We carried out experiments on two male pairs at a time (i.e. there were two duplicate experimental tanks). These male pairs were always of a different species. Each female was presented only once to any male species, although it was presented twice in total to different species (i.e. one female was presented to, for example, a pair of *P. zebra* males as well as a pair of *P. callainos* males but never to, for example, two pairs of *P. zebra* males). Once used, females were returned to separate stock tanks and not used again. Thus, 24 females of each morph were used (16 male pairs \times 3 species/2; one female used for two different species male pairs). The one exception to this was *P. callainos* 'blotched' females. The morph is rare and only

three individuals were available over the experimental period. These three individuals were individually recognizable and were used eight times each. (All analysis was carried out both including and excluding this female morph to prevent this pseudoreplication affecting our results. In all cases the exclusion of this morph did not alter the significance of the analyses: data available on request.)

RESULTS

Experimental Control

Since males were tested in pairs with the same female, it could be argued that males within these pairs should not be analysed as independent replicates, since the behaviour of one male may influence the behaviour of the other. All results of *G* tests comparing the observed and expected frequencies of the courtship displayed by each of the three male types towards each of the eight female types were nonsignificant, even before a Bonferroni correction of $\alpha=0.05/24$ was applied. (Expected frequency of two males courting, f_{CC} , calculated as: $f_{CC}=P_C \times P_C$; of only one male courting $f_{NC}=P_C \times P_N \times 2$; of neither male courting $=P_N \times P_N$, where P_C =number of trials where courtship was observed/total number of trials, $P_N=1-P_C$.) This indicates that the observed pattern of courtship behaviour displayed by each male was not significantly different from that expected at random. Evidently, males were not merely copying the reaction of the male in the opposite compartment, nor did potential intimidation by dominant males have any significant effect on individual courtship responses. Female

behaviour during the 5-min experimental period was characteristic: they swam back and forth in quick succession in the narrow compartment. Females did not at any time respond to the behaviour of either male that was obvious to the observer, even when males were courting. Regarding each male as an independent replicate in the analysis was, therefore, considered justified.

The order of presentation of each female type (first to last out of eight throughout the 8-h period) was controlled for. Male response was not influenced by the sequence order: no significant differences were found in the courtship responses at stages 1–8 in the sequence of presentation (G test: $G_7=10.76$, $P>0.1$).

Wild-caught and F1 generation males may have differed in their response because of differences in prior experience. For each of the three species, male courtship responses to each female type were summed for wild-caught and F1 generation males separately and compared using a Wilcoxon signed-ranks test. This tested the null hypothesis that wild-caught and F1 generation males did not differ in their courtship responses to each of the eight female morphs. All two-tailed comparisons were nonsignificant (where $N=8$ pairs: *P. zebra*: $Z = -1.02$, $P=0.31$; *P. 'zebra gold'*: $Z = -1.63$, $P=0.10$, *P. callainos*: $Z = -1.60$, $P=0.11$). Wild-caught and F1 generation males of all three species did not, therefore, differ in their courtship responses.

Residuals were calculated from a logarithmic regression of female body weight on standard length to give an estimate of condition. It was possible that male response was dependent only on the condition of the females presented. A two-way ANOVA, testing whether condition varied significantly with female type ($N=8$) and male type ($N=3$) (and whether there was any significant interaction between the two), showed that while the condition of females presented to each male type did not differ ($F_{2,168}=0.42$, $P=0.656$) and that there was no significant interaction term ($F_{14,168}=0.332$, $P=0.991$), condition did vary between the eight female types ($F_{7,168}=7.65$, $P<0.0001$). Post hoc Student–Newman–Keuls tests examined where these differences lay (Table 2). Female condition varied between species (*P. zebra* females and all other females), but no significant differences were found within any of the three species. We then carried out Student's t tests to test whether male courtship responses to conspecific females only (in light of the above ANOVA result) were dependent on female condition, that is, comparing the condition of conspecific females that were courted and those that were not. All results were nonsignificant (*P. zebra* males: $t_{33}=0.05$, $P=0.96$; *P. 'zebra gold'* males: $t_{16}=1.72$, $P=0.10$; *P. callainos* males: $t_{91}=0.77$, $P=0.44$). There is therefore no evidence that male response was dependent on female condition.

The condition of the females used in the experiment was as variable as that of natural populations. Munthali & Ribbink (1998) calculated a condition factor for *P. callainos* individuals at Nkhata Bay of 0.92 ± 0.11 ($\bar{X} \pm \text{SD}$). The condition factor of the females used here, following Munthali & Ribbink's calculations, was 1.00 ± 0.09 ($N=192$; the condition factor and variance were the same whether the *P. callainos* 'blotched' morph

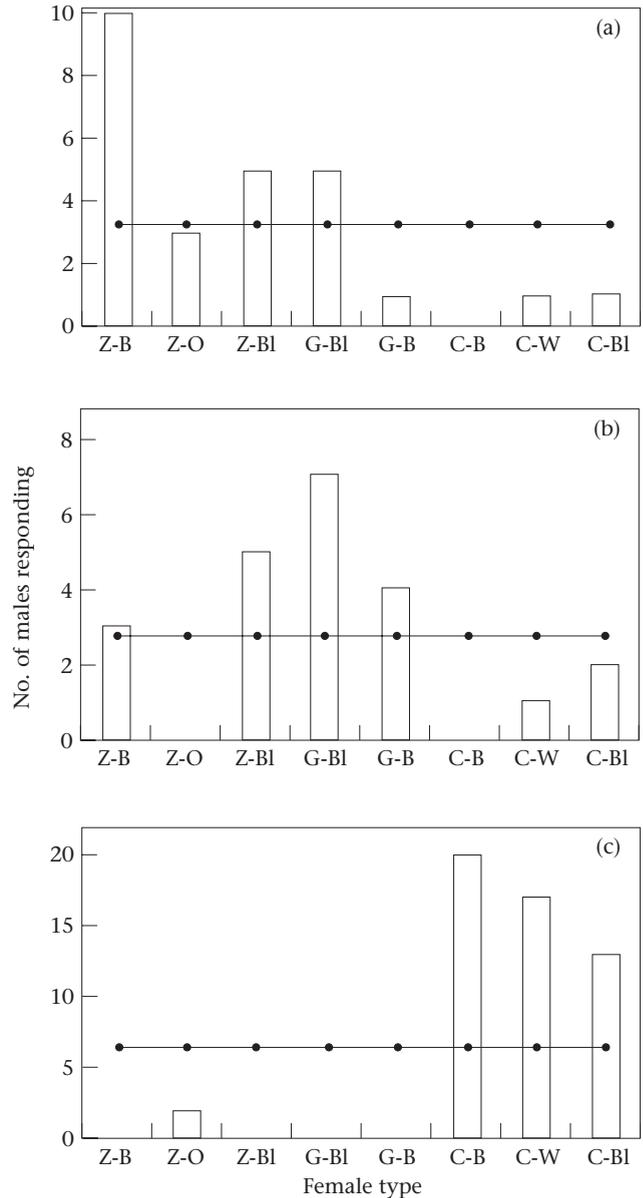


Figure 2. Number of males courting eight different female types. Z-B: *P. zebra* 'barred'; Z-O: *P. zebra* 'orange'; Z-BI: *P. zebra* 'blotched'; G-BI: *P. 'zebra gold'* 'blotched'; G-B: *P. 'zebra gold'* 'barred'; C-B: *P. callainos* 'blue'; C-W: *P. callainos* 'white'; C-BI: *P. callainos* 'blotched'. Bars show the observed values and the horizontal lines the expected values (assuming no preferences between female phenotypes). (a) *P. zebra* males; (b) *P. 'zebra gold'* males; (c) *P. callainos* males.

was kept in the analysis ($N=192$) or not ($N=168$). Finding no differences in the condition of females courted by males was not, therefore, a product of low overall variability in the condition of the females presented.

Male Courtship Responses

Fourteen *P. zebra* males, 10 *P. 'zebra gold'* males and 22 *P. callainos* males showed a courtship response (Table 3). These responses were not randomly distributed among

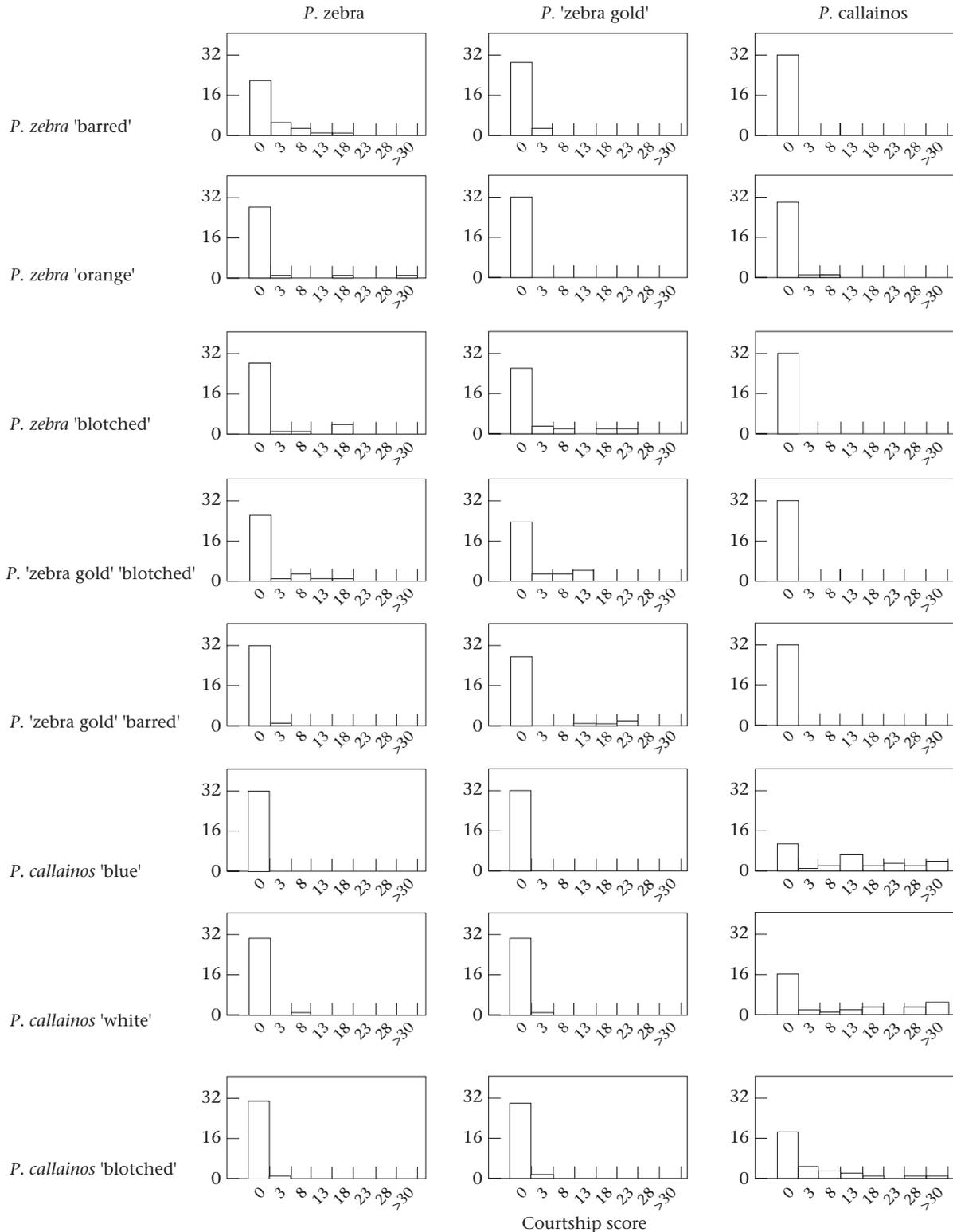


Figure 3. Frequencies of tallied courtship scores for *P. zebra*, *P. 'zebra gold'* and *P. callainos* males towards eight female types. Values on the X axis denote the midpoint bin value (e.g. 3 denotes 1–5 inclusive), with the exception of 0 and >30.

the conspecific and heterospecific female morphs in any of the three species (*G* tests: *P. zebra*: $G_7=23.5$, $P<0.005$; *P. 'zebra gold'*: $G_7=19.3$, $P<0.01$; *P. callainos*: $G_7=91.0$, $P<0.001$; Fig. 2).

Considering the tallied courtship scores, similar trends were found: males differed in the degree of their courtship response depending on female type (Kruskal–Wallis: *P. zebra*: $H_7=26.139$, $P<0.001$; *P. 'zebra gold'*: $H_7=17.550$,

Table 4. Post hoc comparisons of courtship scores of males when presented with eight female morphs

| Female morph | <i>P. zebra</i> 'barred' | <i>P. zebra</i> 'orange' | <i>P. zebra</i> 'blotched' | <i>P. 'zebra gold'</i> 'blotched' | <i>P. 'zebra gold'</i> 'barred' | <i>P. callainos</i> 'blue' | <i>P. callainos</i> 'white' | <i>P. callainos</i> 'blotched' |
|-----------------------------------|-----------------------------|-----------------------------|-------------------------------|--------------------------------------|------------------------------------|-------------------------------|--------------------------------|-----------------------------------|
| <i>P. zebra</i> 'barred' | — | 220 | 200 | 200 | 200 | 400* | 370* | 330* |
| <i>P. zebra</i> 'orange' | 73 | — | 220 | 220 | 220 | 397* | 365* | 310.5 |
| <i>P. zebra</i> 'blotched' | 61 | 59 | — | 200 | 200 | 400* | 370* | 330* |
| <i>P. 'zebra gold'</i> 'blotched' | 66 | 57.5 | 53 | — | 200 | 400* | 370* | 330* |
| <i>P. 'zebra gold'</i> 'barred' | 99.5* | 53 | 62.5 | 62 | — | 400* | 370* | 330* |
| <i>P. callainos</i> 'blue' | 100* | 52.5 | 62.5 | 62.5 | 55 | — | 209 | 342.5* |
| <i>P. callainos</i> 'white' | 93* | 53.5 | 61 | 61.5 | 54 | 54 | — | 306.5 |
| <i>P. callainos</i> 'blotched' | 99.5* | 53 | 62.5 | 62 | 54.5 | 54 | 50.5 | — |

Responses of *P. zebra* males on lower half of matrix (critical value: $U_{0.05(8,10)}=90.9$), *P. callainos* responses on upper half of matrix (critical value: $U_{0.05(8,20)}=325.0$).

* $P<0.05$.

$P=0.014$; *P. callainos*: $H_7=103.151$, $P<0.001$; Fig. 3). Non-parametric post hoc tests for multiple comparisons were calculated (Sokal & Rohlf 1995) to determine where these differences lay (Table 4). Courtship scores for *P. zebra* males were significantly higher towards conspecific 'barred' females than those displayed to heterospecific 'barred' females, or to females of any *P. callainos* morph. Courtship scores for *P. callainos* males were significantly higher towards most conspecific females (*P. callainos* 'blue', 'white' and 'blotched') than they were towards all heterospecific females. The one exception was *P. zebra* 'orange' for which the courtship scores were not significantly different to *P. callainos* 'blotched' but were significantly lower than those for *P. callainos* 'blue' and 'white' females. Post hoc tests on the courtship scores for *P. 'zebra gold'* males were not possible since the sample size (maximum number of females belonging to any one type that males displayed towards) was insufficient ($N=7$, criteria for test: $N>8$).

DISCUSSION

Both analyses (response/no response and tallied scores) recorded similar trends. Males from each of the three species courted some female morphs more frequently than they did others. *Pseudotropheus callainos* males consistently responded to the same female types, courting only conspecific females with the exception of two *P. zebra* 'orange' females. Males of this species can thus recognize conspecific females. The three female morphs of this species are dissimilar to those of the other two species in the sense that they are the most easily distinguished (by the human eye) on coloration alone. Both *P. zebra* and *P. 'zebra gold'* males were less predictable in their responses. Although both of these male types displayed fewer courtship attempts towards *P. callainos* females, they appeared unable to distinguish *P. zebra* and *P. 'zebra gold'* females consistently and particularly those belonging to the 'blotched' morph, which as noted in the Introduction are identical in coloration.

These results suggest that males may be using visual cues to distinguish between conspecific and heterospecific females, since the 'mistakes' that males made were with females that were phenotypically similar to

conspecific females in terms of colour pattern. There were no instances, for example, of *P. 'zebra gold'* males attempting to court *P. zebra* 'orange' females: this morph does not occur within the *P. 'zebra gold'* species. In contrast, *P. 'zebra gold'* males consistently courted both *P. zebra* 'barred' and *P. zebra* 'blotched' females, which are visually very similar to conspecific females.

It is possible, however, that males also use other cues for female recognition (e.g. Nelsson 1991). We consider it unlikely that sound is used: although preliminary investigations of auditory cues suggest that courting males may emit sounds that females may detect (M. C. P. Amorim & G. Turner, unpublished data), there is no indication that females emit similar sounds. The most likely alternative cue that males may be using in the field to recognize conspecific females is a chemical one. Little work has been carried out investigating the use of chemical cues in cichlids, and none on these taxa. Studies focusing on *Astatotilapia burtoni* (a species considered to be related to the ancestral founder of the Malawian and Victorian cichlid flocks; Meyer et al. 1990), however, suggest that chemical cues are important for male recognition of females, whereas females rely primarily on visual cues for male recognition (Crapon de Caprona 1974, 1982). Given that some males are capable of distinguishing females on visual cues alone and others are not, as reported here, we consider it likely that in these species visual cues are used by males, but the possibility of them being used in conjunction with others (such as chemical cues) cannot be ruled out.

The alternative hypothesis to explain the inability of males of some of these taxa to distinguish conspecific females is that males cannot always distinguish between phenotypically similar conspecific and heterospecific females, but females can reliably recognize conspecific males. If females will mate only with recognized conspecific males then the role for male recognition of females may be secondary. Thus, although male recognition of females in such taxa may subsequently arise, it is not a prerequisite for reproductive isolation among closely related taxa and as such need not play a role in the speciation process. Should this be the case then it lends strong circumstantial support to the idea that sexual selection may play a role in speciation in these taxa.

A systematic field study examining male courtship, however, is required to test the feasibility of this hypothesis.

Experiments designed to investigate the potential role of female chemicals as male recognition cues, along with a study focusing on female recognition of males, are in progress. Results from these, taken with the present data, may allow us to gain a far clearer understanding of the evolutionary processes that have brought about such remarkable cichlid diversity within Lake Malawi.

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