

INDIVIDUAL RECOGNITION IN A COOPERATIVELY BREEDING CICHLID: EVIDENCE FROM VIDEO PLAYBACK EXPERIMENTS

by

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Summary

Most theories of social behaviour and cooperation assume that animals can recognise other individuals, but this is rarely tested. Using *Neolamprologus brichardi*, a cooperatively breeding cichlid fish, we monitored behavioural responses to (1) real fish *versus* video images of fish; (2) mate *versus* neighbour and (3) video images of mate *versus* video image of neighbour. All tests were controlled for size and sex. Fish reacted appropriately to the playbacks, although responses to videos were not as strong as to real fish. Both males and females fought against the images of stranger and neighbour fish and they courted images of mates. These results confirm that the cooperatively breeding fish, *Neolamprologus brichardi*, recognises individuals based on vision and that video playbacks contain sufficient information to facilitate recognition.

Keywords: cooperative breeding, cichlid, individual recognition, playback, video.

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Introduction

In 220 bird species (Brown, 1987; Stacey & Koenig, 1989), 120 mammal species (Reidman, 1982) and seven fish species (Taborsky, 1994), young delay dispersal, remain in well-organised social groups or 'families' and help other individuals to breed. Animals with such complex social systems need to respond in particular ways to particular individuals. For example, they need to behave sexually with their mates, aggressively towards strangers and submissively to dominant group members. Variation of behavioural responses in these species is presumably based on recognition of individuals. Moreover, some level of individual recognition is a prerequisite for many models of helping evolution (*e.g.* reciprocity: Trivers, 1971; social prestige: Zahavi, 1976, 1995; pay-to-stay: Gaston, 1978; enforcement: Clutton-Brock & Parker, 1995). Although cooperatively breeding animals are assumed to have individual recognition abilities, this assumption is rarely tested and the mechanisms of recognition are mainly unknown (Hert, 1985).

Cooperatively breeding species live in long-term, stable groups so there are ample opportunities for individuals to become familiar with one another. In such species strong selection pressure should operate on the ability to distinguish individuals, or at least to identify one's own group. Hert (1985) showed that in the cooperatively breeding cichlid fish, *Neolamprologus brichardi*, breeders can distinguish their own helpers from other conspecifics. For this fish, it is also vital to distinguish between individual helpers, because some helpers occasionally act as reproductive parasites or cannibalise eggs and larvae (Dierkes, 1995; Taborsky, 1985). These unreliable helpers are punished by the breeders (Taborsky, 1985), so breeders must be able to distinguish them from reliable helpers who never hinder reproduction.

A number of studies have investigated individual, kin and mate recognition in mammals, birds, insects and fish (Noble & Curtis, 1939; Lamprecht, 1973; Fricke, 1974; Zayan, 1974; Thresher, 1979; Falls, 1982; Caldwell, 1992; Dhondt & Lambrechts, 1992; Hooper, 1995; Stoddard, 1996; Sherman *et al.*, 1997). A common problem with recognition studies is that it is unclear whether individuals would be recognised in the absence of feedback. By 'feedback' we mean information (behaviour, smells or sound) that is provided by an individual and reinforces recognition by others.

One way to test visual recognition while controlling for behavioural feedback is to use a one way mirror. A second approach is playback. Audio playbacks have been used to investigate acoustic individual recognition in birds (Brooks & Falls, 1975; Stoddard *et al.*, 1991, 1992), lions (McComb *et al.*, 1994; Grinnell & McComb, 1996), monkeys (Cheney & Seyfarth, 1990) and fish (Myrberg & Riggio, 1985). Recently, video playbacks have been used as experimental stimuli in several behavioural studies (*e.g.* Clark & Uetz, 1990, 1992, 1993; Evans & Marler, 1991; Evans *et al.*, 1993; McKinnon, 1995; Roster *et al.*, 1995; Rowland, 1995; Rowland *et al.*, 1995a, b; Rosenthal *et al.*, 1996). So far this technique has been mainly applied to study female preference of particular male traits, or predator-prey interactions (but see Macedonia *et al.*, 1994). The video playback technique is potentially a powerful tool because videos can be edited to produce almost any sequence of behaviours and therefore allows the experimenter to examine animal responses in a variety of situations. Nevertheless, before using video playback as a manipulative tool to study social behaviour, one should verify that the species in question can recognise the images presented on the video screen.

The aim of this study was to determine whether *N. brichardi* can recognise individuals from video playbacks. We investigated the following questions: (1) Do *N. brichardi* respond to video playbacks as if they were real fish?; (2) Do *N. brichardi* recognise and respond differently to known *versus* unknown conspecifics, using (a) live stimuli and (b) video playbacks.

Methods

Laboratory protocols

Neolamprologus brichardi, endemic to Lake Tanganyika, inhabits the rocky sublittoral zone from 3-45 m depth (Hert, 1985). Its biology and ecology have been well described by Brichard (1978) and Limberger (1983). Fish used in this study came from laboratory stock of the Vulcani Institute, Israel. Fish were sexed, measured and placed in pairs (one male and one female) in aquaria. Pairs were housed for at least one month in aquaria with a neighbouring pair (matched for total length and weight) in view. Each aquarium (60 × 30 × 30 cm) contained: two ceramic flower pot shelters, a water heater (70 volts), an electrical filter and a 10 cm air stone attached to an air supply. The light:dark regime was kept at 13 hours light to 11 hours dark throughout the three experiments. Water temperature ranged between 26.6-28.6°C and pH was maintained between 8.2-8.5. Fish were fed (dry flake food, frozen tubifex worms and daphnia) twice a day.

We used an ethogram for *N. brichardi* based on Coeckelberghs (1974) and Kalas (1975) and assigned specific behaviours to one of the following four broad categories: courtship, aggression, submission or maintenance (locomotion and feeding) behaviour. Position in the aquaria and behavioural responses were recorded using the Observer (Noldus Information Technology) and a psion organiser. In our experiments, we defined 'close' as the half of the aquarium near the stimuli and 'far' as the other half (away from the stimulus).

Experiment 1: responses to real fish versus video stimuli

In total 18 fish (nine of each sex) were tested. Fish were placed in a test aquarium which was flanked on one side by a second aquarium 'the live stimulus aquarium' and on the other by a video monitor (see Fig. 1). The monitor (14 inch screen, 250 lines, Sony Trinitron KX-1410QM) was connected to a Sony Hi 8 camera (CCD TR 750E) placed near a third aquarium (the 'video aquarium') in which additional fish were held. All aquaria were lined with light blue backgrounds to minimise reflection. *N. brichardi* live in social groups, therefore, pairs were placed in the test aquarium to reduce stress and enhance normal responses to the video, although only one fish from each pair was tested per trial.

Experimental fish could see both fish in the 'live stimulus aquarium' and fish on the video monitor but stimuli fish (in the video aquarium and in the live stimulus aquarium) were prevented from seeing the experimental fish or the camera (by one way mirrors). The one way mirrors ensured that stimuli fish in the live stimulus and video aquaria would

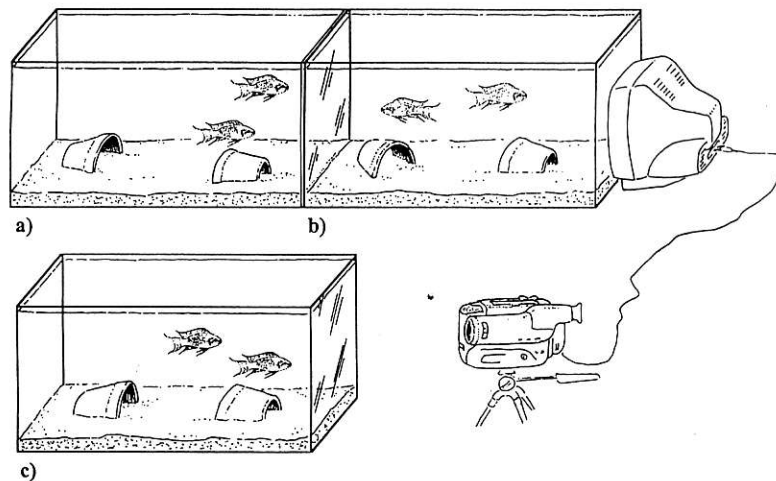


Fig. 1. A schematic diagram of the experimental set up: (a) the live stimulus aquarium, (b) the test fish and (c) the video stimulus fish. The two stimulus aquaria (a) and (c) were identical, containing two fish, two half flower pots and a one way mirror. The one way mirrors prevented the live stimuli fish from seeing the test fish in (b), and the video stimuli fish from seeing the camera in (c). The mirrors also ensured that the test fish would receive a similar response from both kinds of stimuli fish; aggression.

act in a similar way: both attacked themselves in the mirror (see below). Between trials, opaque barriers covered the mirrors. The stimuli fish were filmed (shutter speed: 50-100/s) through the mirror and played back to experimental fish. The image of the fish varied in size, depending on how far the fish was from the video recording camera. The camera lens focal length was adjusted so that the image obtained on the surface of the monitor was life size or smaller (as the fish swam away from the camera).

Experimental fish were given 24 hours to habituate to the test aquaria. Observations were then conducted for 30 minutes in total. Each of the following was presented for 10 minutes: (1) control (video playback of an empty aquarium), (2) real fish (the fish in the live stimulus aquarium in view) and (3) video playback (the fish in the video aquarium in view). The order of trials (empty aquarium video, real fish, fish playback) was controlled by alternating the sequence of presentation in each trial.

We provided each experimental fish with a different pair of fish in the live stimulus aquaria and video aquaria to avoid pseudoreplication or preferences for any particular fish. All fish used as stimuli (in the live stimulus and video aquaria) were unknown (strangers) to the test fish. End preferences were controlled for by switching the side of the live stimuli aquarium and the video monitor halfway through the trials.

When opaque barriers were removed and one way mirrors were exposed, the fish in the live stimulus aquaria and the video aquaria began to fight their own images. This aggression together with the presence of neighbours elicited a strong territorial response in the experimental fish. However, the behaviour of the experimental fish did not affect the behaviour of the flanking fish since the one way mirror prevented them from seeing the experimental fish.

Experiment 2: testing individual recognition of mates versus familiar neighbours of the same sex and size

A. Using real fish

Ten males and ten females were tested. In this experiment, each aquarium was divided into three sections using a double barrier (a fixed one-way mirror covered by an opaque sheet of PVC) (see Fig. 2). The test fish was left in the middle chamber. Its mate was placed in

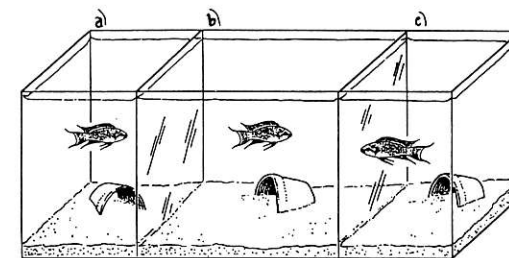


Fig. 2. A schematic diagram of a test aquarium set up for experiment 2a. (a) One end chamber for the mate or the familiar neighbour, (b) the test fish chamber, (c) second end chamber for the mate or the familiar neighbour. Each chamber contained a flower pot. Both end chambers had one way mirrors preventing the end fish from seeing the test fish.

one of the two side chambers and a neighbour (matched in size and sex to the mate) in the other side chamber. After an hour of habituation, the opaque barriers were removed and the test fish could see both its mate and its neighbour simultaneously. The one way mirror ensured that the test fish's response was not a reaction to the behaviour of the stimulus fish (see above). Each test fish was tested once by monitoring position and all behaviours in the aquarium for 10 minutes. Side preferences were controlled by alternating the side on which mate *versus* neighbour were presented between trials. In half the trials the mate was presented on the right side of the test aquarium and in half the trials the mate was presented on the left.

B. Using video playbacks

Ten males and females (all from the previous experiment) were tested. Each fish was given one hour to habituate to the presence of the video monitor placed next to the aquarium (see Fig. 3), after which a video recording of an empty aquarium was shown for one hour. Finally, two sequential 10 minute video recordings were shown of: (1) the test fish's mate and (2) its neighbour of the opposite sex. The order of trials (mate *vs* neighbour playback) were controlled by alternating the presentation. We recorded all responses to video playbacks of mates and neighbours.

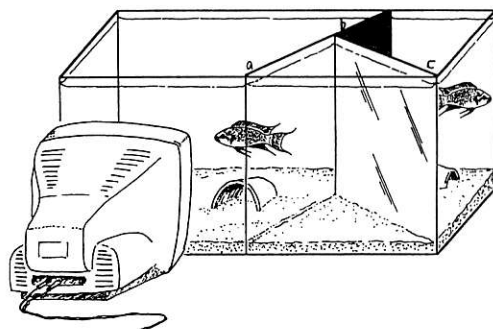


Fig. 3. A schematic diagram of a test aquarium set up for experiment 2b. The test fish could not see its mate during this experiment as the mate was isolated using a mirror (c) and an opaque barrier (b). The mirror (c) allowed the observer to have a complete view of the test fish's behaviour. One part of the barrier was opaque (b), preventing the test fish from seeing its mate and the second part of the barrier (a) was transparent and placed at an angle which prevented the test fish from getting close enough in the mirror to see its own reflection.

Results

Experiment 1: responses to real fish versus video stimuli

All 18 individuals performed aggressive displays at close range (< 5 cm from the edge of the aquarium) towards fish in the live stimulus aquarium. None of the 18 fish tested attacked the monitor during control trails (playback of an empty aquarium). However, 14 of 18 fish attacked or performed submissive displays a short distance (< 5 cm) to the monitor during video playback of fish (control *vs* video: G test = 27.8, $df = 1$, $p < 0.001$). These results indicate that the experimental fish were able to see fish on the monitor.

Intensity of different behavioural responses is illustrated in Figs 4 and 5. Fish were equally submissive in all three treatments (Friedman test, $N = 18$, $\chi^2 = 2.677$, $p = 0.26$). There were differences in aggression, courtship rates and the length of time test fish spent near the stimulus between control, real fish and video trials (Friedman test $N = 18$, courtship $\chi^2 = 20.873$, $p < 0.0001$; aggression $\chi^2 = 20.111$, $p < 0.0001$; time $\chi^2 = 9.294$, $p = 0.01$). Fish were most active in real fish trials (courtship, aggression and time spent near stimulus) (Figs 4 and 5).

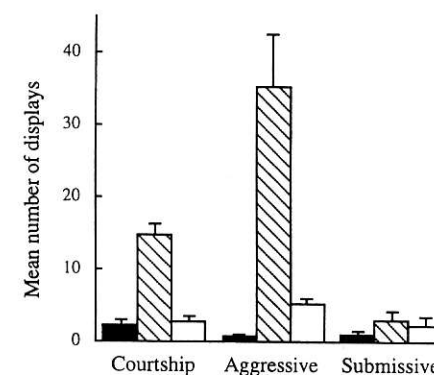


Fig. 4. The mean number of courtship, aggressive and submissive displays performed during each stimulus treatment (10 minutes). The error bars shows standard errors. Black bars are the number of displays performed during the control trials, hatched bars the number of displays performed during real fish trials and the white bars show the number of displays during the video playback trials.

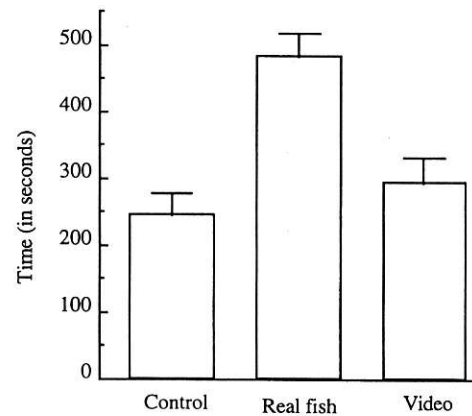


Fig. 5. The mean time experimental fish spent near on the side of the stimulus (monitor or real fish) in the three different treatments (trial time was 10 minutes).

Multiple comparisons between treatments (following the Friedman test, Siegal & Castellan, 1988, p. 181) indicate that the results above represent a much stronger response to real fish compared to videos and controls. Difference in courtship, aggression and time near the monitor were not significant between control and video trials (critical value = 14.36, courtship $|R_c - R_v| = 4.5$; aggression $|R_c - R_v| = 12.5$; time $|R_c - R_v| = 4.0$). However, aggression rates were higher in the video compared to control trial. The multiple comparisons revealed a value for aggression extremely close to a significant value. Since some multiple comparison tests can be overly conservative (see discussion in Sokal & Rohlf, 1995, p. 240-242) we also tested the difference using a Wilcoxon signed rank test and a Bonferroni correction to account for the multiple comparison. The result of this test (Wilcoxon signed ranks test, $N = 18$, $z = 3.110$, $p = 0.001$) remains significant after a Bonferroni correction has been applied ($k = 3$, corrected $\alpha = 0.05/3 = 0.02$). This suggests that fish had a tendency to attack the monitor more often when there was an image of a fish on it *versus* an image of an empty aquarium.

The order of presentation (control, real stimulus and video playbacks) did not affect behaviours examined (Kruskal Wallis test, $N = 6$; courtship: $H = 1.066$, $p = 0.59$; aggression: $H = 0.10$, $p = 0.95$; submission: $H = 1.303$, $p = 0.52$). The side of presentation (right *versus* left) also

did not affect fish behaviour (Mann-Whitney U -tests: $N = 9$; courtship: $z = -0.01$, $p = 0.99$; aggression: $z = -0.627$, $p = 0.54$; submission: $z = -0.273$, $p = 0.78$). The sex of the experimental fish did not affect overall levels of courtship, aggression or time spent near stimuli (Mann-Whitney U -test: $N = 9$; courtship: $z = -0.506$, $p = 0.61$; aggression: $z = -0.05$, $p = 0.96$; time near stimuli: $z = -0.04$, $p = 0.96$). Nevertheless, females were more submissive compared to males (Mann-Whitney U -test: $N = 9$, $z = -2.012$, $p = 0.04$).

Experiment 2: Responses to mates versus familiar neighbours of the same sex and size

A. Using real fish

Fish tended to court mates more often than neighbours (although not significantly so; Fig. 6a. Wilcoxon signed ranks test: $N = 20$, $z = -1.746$, $p = 0.08$) but displayed aggression and submissive behaviours more frequently to neighbours than to mates ($N = 20$; aggression: $z = -3.230$, $p = 0.001$; submission: $z = -2.303$, $p = 0.02$). When males and females were analysed separately these results did not change (see Table 1). However, we found that males courted (mates and neighbours combined) more frequently than females did (Mann-Whitney U -test, $z = -2.309$, $p = 0.02$).

TABLE 1. Male and female displays (number per 10 minute trial) to real fish stimuli (each sex examined separately)

	Mate $\bar{x} \pm SE$	Neighbour $\bar{x} \pm SE$
Courtship		
Male	11.9 \pm 2.3	6.8 \pm 2.1
Female	6.5 \pm 2.7	4.9 \pm 1.5
Aggression		
Male	7.5 \pm 2.1	32.5 \pm 3.2
Female	9.9 \pm 3.2	35.2 \pm 8.2
Submission		
Male	0.8 \pm 0.5	4.1 \pm 2.0
Female	0.6 \pm 1.1	3.6 \pm 4.1

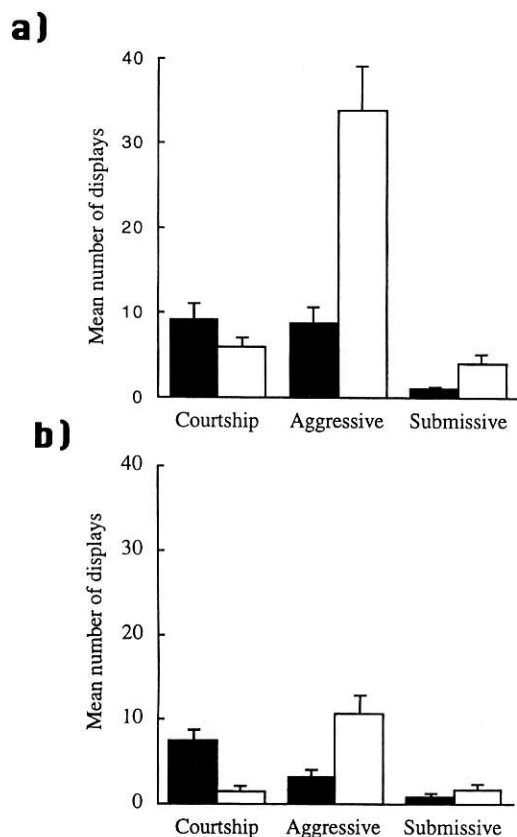


Fig. 6. The mean number of courtship, aggressive and submissive displays performed in ten minutes of observation to (a) real mates *versus* neighbours and (b) video playbacks of mates *versus* neighbours. Black bars are the number of displays performed to mates and the white bars are the number of displays performed to neighbours.

B. Using video playbacks

Fish courted video images of mates more than images of neighbours (Fig. 6b: Wilcoxon signed ranks test: $N = 20$, $z = -3.409$, $p = 0.0007$) but were most aggressive and submissive to playbacks of neighbours (aggression: $z = -3.418$, $p = 0.0006$; submission: $z = -2.14$, $p = 0.03$).

Males and females performed similar amounts of courtship and aggression and spent similar amounts of time near the screen during video play-

TABLE 2. Mean male and female reactions to fish videos (each sex examined separately)

	Males	Females	<i>z</i>	<i>p</i>
Courtship	10.7 ± 2.7	7.4 ± 1.3	-0.380	0.70
Aggression	13.1 ± 3.1	14.7 ± 4.1	-0.303	0.76
Submission	1.0 ± 0.6	4.4 ± 1.6	-2.310	0.02
Time still (s)	40.1 ± 3.3	39.5 ± 3.7	-0.114	0.91
Time near stimuli (s)	323 ± 13	326 ± 24	-0.204	0.84

Mann-Whitney *U*-test performed.

backs (Table 2). However, females were found to be more submissive than males (Mann-Whitney *U*-test: $z = -2.310$, $p = 0.02$) and were more submissive to videos of neighbours than to videos of mates (Wilcoxon signed ranks test: $z = -1.980$, $p = 0.05$).

Although video playbacks elicited a weaker response, the proportional difference in responses to mates *versus* neighbours was similar to responses to real fish (see Fig. 6a *versus* Fig. 6b). The number of fish with 'appropriate' responses (courting their own mate more often and attacking neighbours more frequently) was similar between the real and video stimuli (Fisher exact test, video *vs* real: courtship 18/20 *vs* 15/20, $p = 0.16$; aggression: 19/20 *vs* 18/20, $p = 0.38$).

One way to test for recognition is to determine if there is a difference in response to neighbours *versus* strangers; this is known in bird studies as the 'dear enemy effect' (Fisher, 1954). Although this study was not designed to test this effect specifically, we compared results from all experiments and did not detect a 'dear enemy effect'. Fish were equally aggressive to unknown strangers and known neighbours in both live stimuli and video playbacks trials (Mann-Whitney *U*-test, $N_{\text{strangers}} = 18$, $N_{\text{neighbours}} = 20$, real: $\bar{x}_{\text{strangers}} \pm \text{SE} = 46.5 \pm 8.5$, $\bar{x}_{\text{neighbours}} \pm \text{SE} = 33.9 \pm 5.3$, $z = -0.921$, $p = 0.37$; video: $\bar{x}_{\text{strangers}} \pm \text{SE} = 10.8 \pm 1.6$, $\bar{x}_{\text{neighbours}} \pm \text{SE} = 13.9 \pm 2.5$, $z = -0.762$, $p = 0.45$).

Discussion

The results of this study demonstrate that *N. brichardi* can visually recognise mates. Hert (1985) showed that breeders can visually recognise their own young. Here, we have shown that adults can also discriminate between

mates and non-mates. As fish courted images of their own mates but attacked images of neighbouring fish, it seems likely that *N. brichardi* gain enough information to identify individuals from video playbacks. These results shed light on two related issues that we will discuss in turn: (1) individual recognition and (2) the use of video playbacks as a manipulative tool.

Recognition

Our results demonstrate that *N. brichardi* use visual cues for mate recognition. A number of other studies have reported similar findings. For example, *Amphiprion bicinctus* attack partners rarely compared to strangers but if the partner was dyed green or enclosed in a green plastic jacket, it was not recognised and treated as a stranger (Fricke, 1973). The results of our study do not exclude the possible role of odour in recognition as shown in other fish species (McKay & Barlow, 1976). For example, yellow bullheads (*Ictalurus natalis*) use pheromones to recognise individuals and their rank; subordinate fish avoid areas in which the water from the tank of a dominant fish has been introduced (Bardach & Todd, 1970). Such individual recognition is thought to result from each animal producing a limited number of volatile compounds in different relative amounts (Rasa, 1973; Gorman, 1976). By presenting the real fish stimuli in a separate aquarium we could have reduced the differences between real *versus* video stimuli. However, in our study, the differential responses to videos *versus* real stimuli cannot be explained by the presence or absence of olfactory cues. In the first experiment, pheromones of strangers from the real fish stimulus aquarium could not reach the test fish in the experimental aquarium as the two tanks had completely separated water filtration systems.

We did not find sexual differences in visual sensitivities, but such differences have been reported for other species. Female sticklebacks are more sensitive than males to red but only during the breeding season (Cronly-Dillian & Sharma, 1968). Visual sensitivities can vary seasonally (Beatty, 1966), between development stages (Baerends & Baerends-van Roon, 1950) and between individuals (Levin & MacNichol, 1979). Differences detected in male and female responses (males courting more than females and females being more submissive than males) were a con-

sequence of differences in sexual behavioural tendencies, which are well reported in other cichlids (McKay 1991; Balshine-Earn, 1996).

In our study, fish reacted equally aggressively to neighbours and strangers. The lack of the 'dear enemy effect' (Fisher, 1954; Temeles, 1994) may have been a result of (1) using two different set ups; or (2) testing for a response to a neighbour *versus* a stranger out of context. Neighbours were presented to the experimental fish either in the test aquarium itself or on a monitor, both locations where a fish would not normally find its neighbour. Falls & Brooks (1975) have shown that resident male white-throated sparrows respond more strongly to the audio playbacks of strangers compared to neighbours, but when they play the neighbour's song from outside the neighbour's usual boundaries, the resident treated the neighbour's song as a stranger's. In the wild, *N. brichardi* respond differently to strangers *versus* neighbours. Aggression between neighbours usually occurs between two fish matched in size; fights can be prolonged, lasting several minutes. However, conflicts with stranger fish tend to be brief with the entire family unit intensely attacking the stranger (Balshine-Earn *et al.*, in prep.).

Use of video

Recent work has highlighted the ability of various fish species to see and respond to video playback and computer screen animation (Clark & Uetz, 1993; McDonald *et al.*, 1995; Rowland, 1995, Rowland *et al.*, 1995a, b; McKinnon & McPhail, 1996). Our study is the first to show that fish are able to absorb information from video playbacks that facilitates recognition of individuals. The response by fish to video technology developed for human vision is not surprising in light of cichlids' similar visual system. Microspectrophotometric studies show that cichlids have trichromatic colour vision (Fernald, 1984) with three cone pigments which absorb light maximally at about 455, 523 and 562 nm (Fernald, 1984; Loew & Lythgoe, 1978). These values are not very different from our own sensitivity (419, 531 and 558 nm) (Dartnall *et al.*, 1983).

Responses to videos were weaker in magnitude than the responses to real fish. However, the proportion of aggression *versus* courtship displays towards mate and neighbour were similar in both experiments. This suggests that fish obtained accurate information but that they were less stimulated by videos. There are several possible explanations for the weaker video

response. The quality of the video playback may not have been sufficient to highly stimulate the fish. Alternatively, *N. brichardi* may be able to sense that the image on the video monitor was not a real fish. Further studies using monitors with higher resolution or faster critical flicker rates are needed to investigate alternative hypotheses for weaker video playback response. An additional possible reason that the response to video *versus* response to live fish differed could be that individual recognition involves a component of mutual signalling between two fish.

A fourth hypothesis is that response to video was weaker because the video stimuli were presented sequentially while the real fish stimuli were presented simultaneously. Simultaneous presentations are generally thought to be more sensitive in detecting differences in preferences (C. Baube, pers. comm.). Therefore the use of sequential presentations for the video data (exp. 2b) might have accounted for some of the decrease in overall response. However, despite the increased subtlety needed to detect a preference between stimuli presented sequentially, the fish still displayed a similar proportion of courtship behaviours to mates and aggressive behaviours to neighbours. One way to test whether the weaker effect of video was a result of sequential testing would be to create a stereotyped stimuli of both neighbour and mate and play them back simultaneously using two monitors.

In conclusion, our behavioural results suggest that *N. brichardi* visually distinguish between video images of mates *versus* non-mates. Although this study does not rule out the possible role of olfactory cues, it strongly supports the hypothesis that vision is extremely important in recognition in *N. brichardi*. Although caution should be exercised when assessing response to particular stimuli on video, these findings indicate that *N. brichardi* gain enough information to identify individuals from video playbacks.

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