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Species recognition in the blackbordered damselfish *Dascyllus marginatus* (Rüppell): An evaluation of computer-animated playback techniques

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Dedicated in memory of Dr. William N. McFarland

Abstract

Blackbordered damselfish, *Dascyllus marginatus*, were presented with computer animations of varying backgrounds, with and without moving stimuli of conspecifics and sympatric heterospecifics. When subjects were released into the test tank their initial escape response was nearly always towards a fish stimulus, independent of species identity, rather than towards a background stimulus, even when the former were presented in the open and the latter displayed a coral shelter. Subjects did, however, show distinct preferences according to species with regards to the total time spent with each animation. *D. marginatus* significantly preferred conspecifics over *Dascyllus trimaculatus*, but did not prefer conspecifics over *Dascyllus aruanus*, a species with which they frequently shoal in nature. These results demonstrate that computer animations can be used in ethological studies of coral reef fishes and to isolate critical visual signals. Results also show that reef fishes can use visual signals to make sophisticated discriminations among species that can be modulated according to the task at hand.

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1. Introduction

Visual information is critical in guiding the behavior of most diurnally active coral reef fishes. Finding potential mates, interacting with conspecifics and heterospecific competitors, detecting prey, and evading predators are all likely to have important visual components.

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Among the most striking visual stimuli on the reef are the complex and diverse body patterns of many fish species. These patterns have long been assumed to function in species recognition (Lorenz, 1962). Patterns are often stereotypical within a species, but remarkably divergent among closely related taxa. Surprisingly, few studies have provided empirical tests of the role of body patterns in species recognition in reef fishes (Brockmann, 1973; Thresher, 1976; Katzir, 1981a,b), and some of these have been limited in their ability to control for motor, acoustic, or olfactory cues.

The damselfish genus *Dascyllus* (Pomacentridae) may serve as a useful model for testing the effects of pattern on species recognition. Adults of most *Dascyllus* live in small groups centered on a single coral head (Sale, 1971; Fishelson et al., 1974). These habitats are frequently shared with other species of solitary and shoaling fishes. Although they spend the majority of their time around a single coral head, fish may wander among neighboring corals or shelters (Sale, 1971). Recruitment to the coral and to the group is at the settlement stage, shortly after the larvae have metamorphosed from their planktonic phase. When threatened, individuals dart to the nearest available shelter, which may not necessarily be their home coral head. It is very likely that the choice for such an escape would be visually guided.

Blackbordered damselfish, *Dascyllus marginatus* (Rüppell), frequently share a coral head with other species of solitary or shoaling fishes. In the Red Sea, these frequently include other species of *Dascyllus*, *Chromis*, *Pseudanthias*, and *Neopomacentrus*. Other coral heads, in the vicinity of the home coral, may also shelter schools of these and other planktivorous fishes. Hence the presence of any of these species could potentially provide a distinctive visual cue of an appropriate shelter. In the Gulf of Aqaba, *D. marginatus* inhabit branching corals, predominantly *acroporids*, *pocilloporids*, and *Stylophora pistillata* (Fishelson et al., 1974). In some cases *D. marginatus* are not the only damselfish that occupy a coral head, and they may share it with *Dascyllus aruanus* L. and young stages of *Dascyllus trimaculatus* (Rüppell). In observations performed at water depths of 0–12 m, in front of the Interuniversity Institute for Marine Sciences (IUI), Eilat, 146 of 198 (74%) of branching corals

measuring 10–73 cm in diameter, were inhabited by *D. marginatus*. Of these, 35 corals (24%) were co-inhabited by *D. aruanus*, and only 8 corals (6%) by the threespot damselfish *D. trimaculatus*.

The sympatric damselfish of the Red Sea comprise a particularly appealing study system because their body markings are limited to variations of black and white but are highly divergent among species. Using presentations of dummies and live fish as stimuli, Katzir (1981a,b) showed that both *D. aruanus* and *D. marginatus* used visual cues of body coloration pattern and body shape, to discriminate between conspecifics and heterospecifics. Isolated individuals in a two-stimulus forced choice situation showed preferential first choice and subsequent longer duration spent near conspecifics over heterospecifics.

We were interested to examine these visual cues in a fashion that would allow exact control of distinct visual parameters, while maintaining constant other parameters, namely motion and body shape. Further, we wanted to test the feasibility and suitability of computer-animated stimuli for behavioral studies of reef fishes.

Video and computer graphic animation playbacks were used to study a variety of fish behaviors, including perception (e.g. Orger et al., 2000), species and individual recognition (e.g. Balshine and Lotem, 1998), and sexual selection (e.g. Bakker et al., 1999; Nicoletto, 1999; Rowland, 1999; Rosenthal et al., 2002; Kingston et al., 2003). The main strengths of using synthetic animations are twofold: repetitively displaying well-defined, complex moving stimuli, and precisely manipulating specific portions of the visual scene (Rosenthal, 2000; Oliveira et al., 2000). A main drawback of this method, however, is that video output is tuned to the human visual system, in terms contrast, flicker rates, color, etc. It is most likely that for a fish observer a stimulus will appear very different than it is perceived by the human experimenter. However, responses by fish to animated computer graphic images are documented (e.g. Clark and Stephenson, 1999; Rosenthal, 1999). Additionally, the achromatic nature of the visual signal in *Dascyllus* allows us to minimize concerns about color fidelity.

We used presentations of synthetic animations to *D. marginatus* to evaluate their response to conspecifics, heterospecifics, and salient habitat features.

2. Materials and methods

2.1. Experimental animals

Twenty adult *D. marginatus* were collected from the shallow waters (4–7 m deep) of Palm Beach, Eilat, Israel. Fish were placed in running seawater aquaria with a dead coral head positioned in each. After 1–2 days of acclimation, each fish was transferred to the experimental setting and was examined individually. An experimental session lasted up to 1.5 h (typically 1 h) after which the fish was returned to its original aquarium overnight or longer. Each fish was tested in up to 3 such daily sessions for a maximum of 3 h. In preliminary tests, the fish were to be less active after natural timing of sunset, even when tested under artificial illumination. Therefore testing was conducted between 7 AM and 5 PM, when the fishes are active in nature. After testing, individuals were measured and returned to their original site and coral head in nature.

2.2. Experimental setup

Experiments were carried out in an isolated room, under artificial illumination and with unfiltered running seawater, hence keeping temperature and water quality similar to those of the natural and acclimation conditions. The experimental aquarium (L50×D32×H40 cm) was placed between two identical computer screens powered by identical CPUs and other computer settings and properties. Monitors were 17", flat CRT screens (786PF by MAG Technologies Co. Ltd. with a 0.25 mm DPI resolution), which filled the entire field of view on each side of the aquarium. The experimental aquarium was lined with gravel and maintained at a water level in line with the top of the computer screen. The back of the experimental aquarium was with a opaque white paper and the front of it was left exposed for video recording (Fig. 1).

A video camera provided a full view of the fish's movement and recorded the experiment on a remote video deck. The video camera and the monitor displays were controlled from a neighboring room. With the exception of the computer animations there was no moving stimulus in the experimental room and acoustic noise levels were kept to a minimum.



Fig. 1. Experimental setup included an experimental aquarium placed between two computer monitors on which the fish animations (Fig. 2) were displayed. The aquarium was observed via a video camera from a separate room, from where the computer animations were controlled as well. Prior to each testing the fish was held in a small transparent acclimation box at the center of the tank for 10 min with animations of the coming experiment running, after which it was released by remotely raising the box out of the tank.

2.3. Computer animations

Computer animations were generated using 3D Studio Max 4 (Discreet®) software based on extensive observations of fish behavior in nature and of video recording taken underwater, in the horizontal plane of the focal fishes. Digital images of real underwater scenes were used for stationary segments such as background and coral. Special care was taken to replicate the swimming speed and body motions of undisturbed *D. marginatus* in the wild. Animated fish in all clips had identical body shapes (that of *D. marginatus*), sizes (52 mm total length, 39 mm body length), and movement paths. Animation clips were displayed on the entire screen and were looped to run continuously and seamlessly unless stopped.

The experimental animation clips employed are shown in Fig. 2: (i) Background only (abbreviated B) did not include a coral or any fish (a static image), (ii) Coral (C)—same as B but containing half a *Stylophora pistillata* coral sphere (also a static image), (iii) A group of *D. marginatus* swimming in the background above (abbreviated M), (iv) A group of *D. marginatus* swimming in and around the coral in C

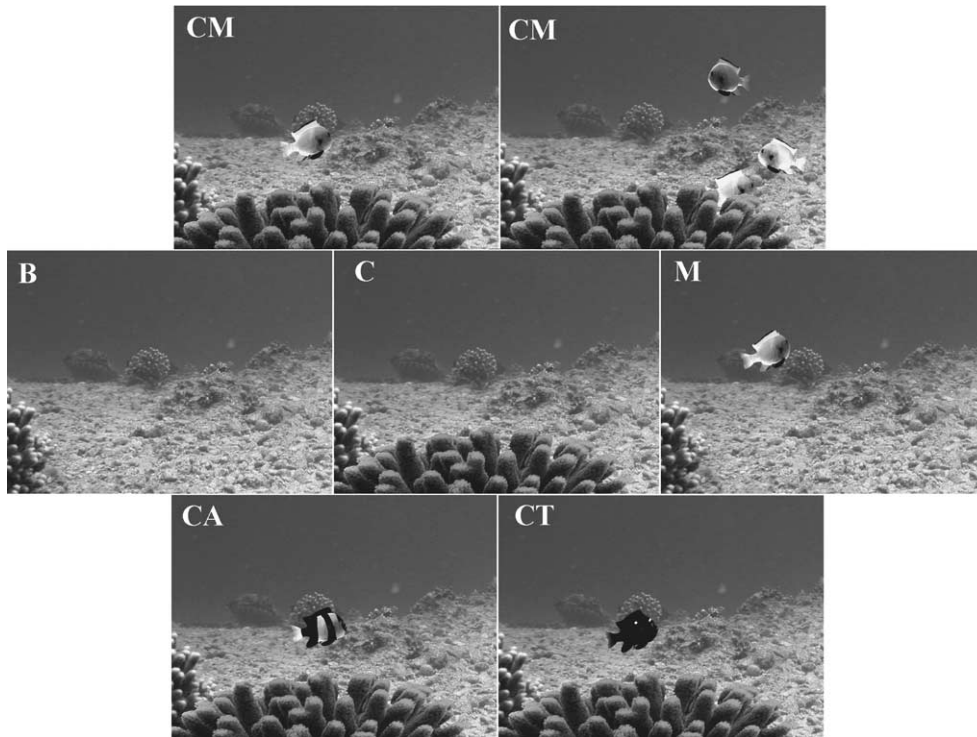


Fig. 2. Representative still images from the computer animations presented to individual *D. marginatus* fishes. B—background only, C—*Stylophora pistillata* coral head on background without any fish. M—*D. marginatus* fishes on the background but without a coral. CM—coral with *D. marginatus* images. CA—coral with *D. aruanus* fishes, CT—coral with *D. trimaculatus* fishes. In the fish animations (M, CM, CA, CT) 3 fishes swam one after the other out of the coral, onto the background, made a looped path in it (top left and center panels), and back into the coral.

above (CM), (v) A group of *D. trimaculatus* fish (juveniles) or *D. aruanus*, swimming in an identical form and surroundings as in CM (abbreviated CT and CA, respectively). In each of the fish animations (M, CM, CA, CT), three fishes were swimming out of the coral, into the background and back into the coral along a set path. Animated fishes entered or left the coral asynchronously. In the case of animation M, the fishes arrived at the bottom center of the screen, where the coral was displayed in other treatments, and swam down out of view. Fish trajectories did not overlap or interact with each other.

2.4. Experimental procedure

Stimuli were played simultaneously, but not in synchrony, on the monitors flanking the test aquarium. Subjects were acclimated inside a clear Perspex box in the test tank, with both stimuli of the following pre-

sentation in view, for 10 min prior to the start of each test. Subjects were then released from the box using a specially designed lever, keeping the fish's contact with humans during the experiment to a minimum. Once the box was lifted the subject fish's movements in the tank were recorded for 5 min. We recorded the fish's first choice in approaching either side of the aquarium, the number of approaches and the total duration of time spent within 5 cm each computer screens.

To test whether fish attended to visual cues when seeking coral heads, we presented a choice between background only and a coral head (B vs. C). To test how fish weighted seeking shelter versus shoaling with a conspecific, we presented a choice between a coral head and a *D. marginatus* with and without a coral head (C vs. M, and C vs. CM). Finally, to evaluate the role of body patterns in conspecific recognition, we tested *D. marginatus* with a coral head versus an identically shaped and moving stimuli having

D. aruanus and *D. trimaculatus* body patterns (CM vs. CA, and CM vs. CT). As an additional control for unknown computer affects the same animation (CM) was also examined on both sides.

A total of 10 individual fishes were tested on each animation pair; with each animation running once on the right and once on the left sides of the experimental aquarium, for each fish. Animations were presented in a random order, and the order of presentation did not affect fish's choice ($p > 0.4$ for both a fish's first choice and time spent near animation).

2.5. Data analysis

First choice for each fish at each situation ($n=20$ presentations for each of animation pair) was analyzed using the sign test (Sokal and Rohlf, 1995).

For each trial, we computed the total duration that the subject stayed within 5 cm of the monitor. With the exception of the presentation of the same animation (CM) on both sides, the two settings in which the animations were presented once on the left and once on the right were summed for each presentation to each subject ($n=10$ combined presentations per fish). The amount of time spent with each stimulus was analyzed with a Wilcoxon signed-rank test (Sokal and Rohlf, 1995).

3. Results

Fish spent most of their time (60% for all cases; Fig. 3) in close proximity (i.e. within 5 cm) of one of the screens displaying an animation and rarely in proximity to the back or front glass sides of the aquarium. Subjects often switched from one side to the other, and we did not observe a single case where they remained next to a given animation throughout the trial. Frequently, the fish would swim parallel to an animated fish for some time, and would turn as the animation turned, thus indicating that they reacted to the computer animations. No aggressive interactions (attacks) towards the animations were recorded.

Subjects preferred animations with fish to those without. Using both response measures, first choice and duration next to screen, animations containing conspecifics were preferred over background without fish. This held true even when subjects were given a choice between fish stimuli swimming against in open background vs. a background containing a coral head but no fish (Table 1, Fig. 3, yet it is possible that a larger sample size would have yielded a different conclusion in the first response setting). No side (i.e. left/right) preference was found in the experiments (CMI/CMr, Table 1, Fig. 3) though in when both

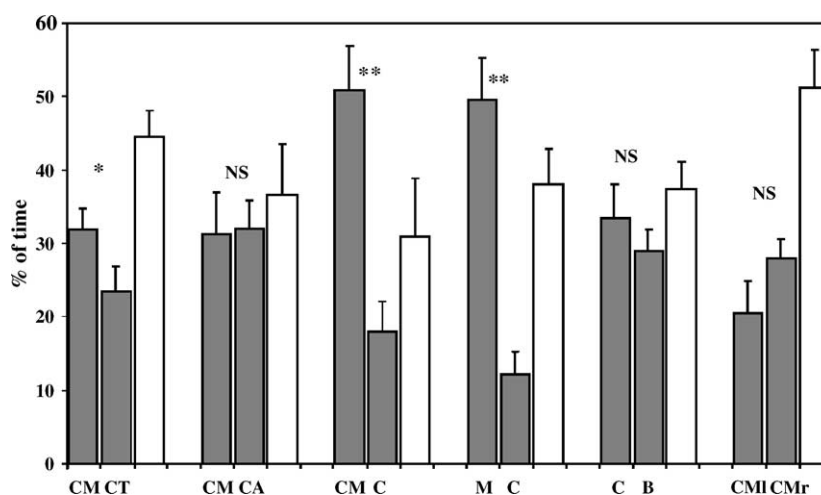


Fig. 3. Mean \pm S.E. percentage of time spent near computer graphic animations (filled bars) or away at a distance of more than 5 cm from any side (white bars). Animations were: B—background only, C—*Stylophora pistillata* coral-head on background without any fish. CM—coral with *D. marginatus* images, M—*D. marginatus* fishes on background but without a coral. CA—coral with *D. aruanus* fishes, CT—coral with *D. trimaculatus* fishes, as in Fig. 2. Individual fish are depicted by different hatching on bars. * $p < 0.1$, ** $p < 0.05$, NS—no significant difference; Wilcoxon signed-rank test. On average fish spent $60 \pm 18\%$ near any one of the animations.

Table 1
Fishes first choices of animations upon release from a transparent holding box

Animations presented	Fish first choices (sign test, $p=$)
Background/coral	6/14 (0.169)
Coral/ <i>D. marginatus</i>	4/16 (0.022)
Coral+ <i>D. marginatus</i> /Coral+ <i>D. trimaculatus</i>	13/7 (0.359)
Coral+ <i>D. marginatus</i> /Coral+ <i>D. aruanus</i>	12/8 (0.646)
Coral+ <i>D. marginatus</i> —left/Coral+ <i>D. marginatus</i> —right	10/10 (1.0)

Subjects preferred animations showing other fish versus animations showing background stimuli, but did not discriminate among species.

animations were identical the fishes swam more from one to the other and spent less time next to the animation (Fig. 3; $p=0.058$). No difference was found between non-identical treatments in the time spent next to animations vs. time spent in other parts of the aquarium ($p>0.185$; one-way ANOVA with LSD Post Hoc tests, after ArcSin transformation on ratios). First choice escape responses did not reveal any additional significant preference between animations (Table 1). Subjects did, however, spend significantly more time with conspecific fish rather than with a coral ($p=0.005$) and with conspecific *D. marginatus* over *D. trimaculatus* ($p=0.09$). Fish did not, however, respond differentially to *D. marginatus* versus *D. aruanus* ($p=0.95$).

4. Discussion

In the backbordered damselfish, *D. marginatus*, clear, biologically meaningful responses to computer animations were observed, with animations containing other fish preferred over animations of coral heads or background only. This preference was maintained when the simulated fishes swam in an open area without a sheltered coral. Further, there was no preference for a background containing a coral head over an empty background, and subjects did not discriminate among species when making their first choice. These results suggest that for the type of task facing the fish, which resembles finding a refuge when swimming out in the open, rapid aggregation

with shoal mates may be more critical than either habitat type or species identity.

Once subjects had had the opportunity to closely inspect both stimuli, they exhibited more sophisticated responses. Subjects spent significantly more time with conspecific *D. marginatus* than with *D. trimaculatus*, yet did not discriminate between conspecifics and *D. aruanus*. Since both *D. trimaculatus* and *D. aruanus* visual signals are strikingly different from *D. marginatus*, it is unlikely that the difference in response was due to artifacts of stimulus presentation.

Responses towards simulations of conspecifics fishes of heterospecifics varied with task or parameter examined. We interpret the fish first choice as similar to a situation where a fish finds itself, for some reason, in open water and needs to find a shelter as soon as possible. This interpretation is supported by the slight yet not significant preference of the coral head over the open background in the first choice measurements only. The choice as to which animation to spend more time in proximity of is interpreted as being related to the type or quality of a shelter, and could be parallel to a fish in a complex coral environment being already in a protected place and needing to find the next site to go (though it should be noted that, though we have observed fish moving from one coral-head to another in the field, such movements are rare). Katzir (1981b) reported a first choice response in which *D. aruanus* damselfish preferred fishes of conspecifics over heterospecifics. However using criteria of aggression no such preferences were detected (Katzir, 1981a). Our results are well in line with the above in the sense that different tasks require different levels of recognition.

It is likely that when a fish needs to escape to shelter while being in the open (and this is the situation in the experimental aquarium when the holding box is lifted) it will escape to the first/nearest object that might offer shelter. In this regard the existence of damselfish may be good indications of a potential refuge. Subsequently, when able to choose between shelters it is likely that the fish will prefer to associate with species it shares a coral-head in nature (its own species and *D. aruanus*). Our results provide only partial evidence for same species recognition: The tested *D. marginatus* fishes discriminated between their own species and *D. trimaculatus* but

not between their species and *D. aruanus*. This is especially surprising since the body patterns of *D. marginatus* and *D. aruanus* are very different. These result could have originated from one of three sources (a) our animations were not fine or accurate enough and did include markers used by *D. marginatus* to recognize their own species; (b) species recognition in *D. marginatus* involve (also) non-visual cues (e.g. sound; Spanier, 1979); (c) the social situation facing the fish did not require accurate species recognition. This last option is supported by Katzir's (1981a) results on aggression, where the fish were requested to defend a coral-head from other fish that might invade it. In our case the fish were also presented with a non-sexual situation, where they had to choose a proper shelter to find refuge in.

Another option is that the difference in responses towards the two heterospecific species may reflect the relationship that *D. marginatus* has to these two species in nature. While 24% of coral heads inhabited by *D. marginatus* were also occupied by *D. aruanus*, only 6% contained any *D. trimaculatus*. When making decisions about shoaling and/or habitat choice, individuals may be permissive with respect to frequently sympatric congeners. *D. marginatus* may thus not only be able to recognize conspecifics (Katzir, 1981a), but, in the specious environment of the reef, may be able to use a host of visual cues to respond appropriately to heterospecifics.

Computer animations are limited in not being tuned to the visual system of the examined animals but rather to human vision (Fleishman et al., 1998; Fleishman and Endler, 2000). Damselfish for example, are often sensitive to UV, and their visual pigments are more evenly spaced across their visual spectrum as compared to human vision (McFarland and Loew, 1994; Losey et al., 2000; Hawryshyn et al., 2003). Hence it is likely, though not tested, that at least the colors of the animations presented were different from the way real fishes and natural environment appear to these fish. We have attempted to focus on cases that have a large gray scale component (mostly black and white body patterns). But it is not at all clear that this is the way the fishes appear to other damselfish or if they contain any UV patterns (Losey et al., 2000; Marshall, 2000) that cannot be produced on regular computer screens. However, the information provided by our software was apparently suffi-

cient for recognition of the different animated fishes as such and for at least partial species recognition.

Our results also show that computer graphic animations can serve as a powerful tool for studying the complex arrays of visual signals in coral reef fish communities. In our study, we held body shape and motor patterns constant, and were thereby able to show that body patterns alone were sufficient for discrimination among species. Computer animation techniques, coupled with improvements in video output technology, also offer the opportunity to examine the role of body shape, color, temporal patterns, and environmental characteristics in structuring the interaction of reef fishes with their visual environment.

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