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Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*)

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Abstract. Acoustically mediated individual recognition has been demonstrated in the field by males of the bicolor damselfish *Pomacentrus partitus* Poey. Playbacks of non-resident sounds from a given fish's territory elicited a greater response from its nearest neighbour than playbacks of the resident's sound—in accordance with the predictions of the 'dear-enemy' effect. Testing also included switching the sounds of the two nearest neighbours relative to each respective male's territory. Results demonstrated that all males in the colony individually recognized the sounds of their two nearest neighbours.

Recognition processes at the level of the individual were largely ignored by ethologists until the beginning of the last decade (Beer 1970). Primarily stimulated by the resurgence of the individual as the unit of selection, interest in the precise nature of inter-individual behaviour has grown steadily ever since. Yet, despite that renewed interest, little information exists on individual recognition and its sensory mediation in one vast group of vertebrates—the fishes.

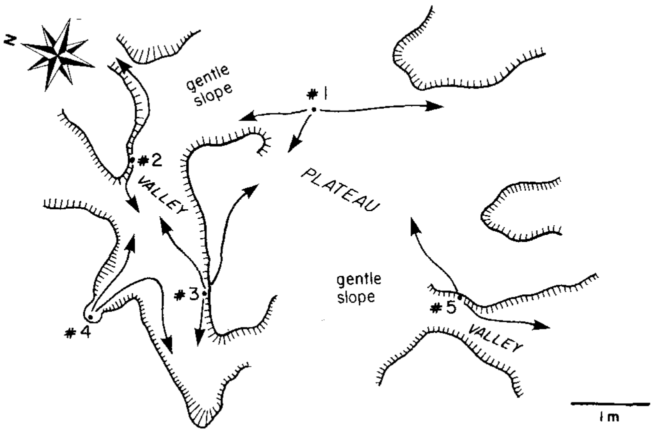
Acoustical recognition is unknown among fishes, although many species are vociferous (Fine et al. 1977; Myrberg 1981). The existence of this capability could lead to a substantial revision of the possible functions of sound production and reception in the aquatic medium. The present investigation was undertaken to determine if members of a highly soniferous species, the bicolor damselfish (*Pomacentrus partitus*) can recognize one another solely by acoustical means. The chosen methodology required that the resulting data should stand independent of sound-source location (direction) per se, and rule out binary patterns of recognition, e.g. familiar versus unfamiliar.

METHODS

The bicolor damselfish is a small (70–90 mm total length), highly territorial resident of the coral reefs off southern Florida. Its behavioural ecology and acoustical biology have been extensively studied (Myrberg 1972a, b; Stevenson 1972; Emery 1973; Spanier 1979; Myrberg & Spires 1980; Schmale 1981). Members of this species are typically found in colonies which consist of isolated groups of closely interacting individuals. Throughout their extensive spawning season, males produce characteristic chirp-sounds in their territories as they simultaneously perform diving displays of courtship termed 'dips'. Investigations involving sound playback have established that only adult males of the species produce the distinctive chirp-sounds as well as responding, in turn, rapidly to the transmission of such sounds during daylight hours (Myrberg & Spires 1972; Myrberg et al. 1978; Spanier 1979).

Experiments were conducted directly on the reef, at a depth of 10 m, near Fowey Rocks Light (25°35′N, 80°06′W), 11 km southeast of Miami, Florida, during late May, when males were frequently interacting and actively courting. A moderate-sized colony, consisting of five adult males and a similar number of adult females and juveniles, was selected for study. The choice of colony was based on the activity of the males, their proximity to one another, and the absence of any large, intervening object that might have interfered with sound transmission. Only the behaviour of adult males was monitored.

Between 11 and 16 chirps were recorded from each of the colony males. All recordings were made with a Clevite CH-17 hydrophone and an Ithaco 144 L preamplifier onto a Uher 4000 Report L tape-recorder at a tape speed of 19 cm/s. Sounds were analysed using the same tape-recorder, a Krohn-Hite 3100 band-pass filter and a Tektronix 5103n memory oscilloscope. The analysis showed greater inter-individual variation in the dominant frequencies (i.e. those frequencies within 3 dB of the frequency of greatest intensity) than the corresponding intra-individual variation. Differences in



	Nearest Neighbour		2nd N.N.		3rd N.N.		4th N.N.	
Subject	Indiv.	Distance (m)	Indiv.	Distance (m)	Indiv.	Distance (m)	Indiv.	Distance (m)
1	2	2.5	3	2.8	5	3.1	4	4.0
2	3	2.0	4	2.2	1	2.5	5	4.7
3	4	1.5	2	2.0	1	2.8	5	3.3
4	3	1.5	2	2.2	1	4.0	5	4.9
5	1	3.1	3	3.3	2	4.7	4	4.9

Figure 1. Topography of the test site near Fowey Rocks Light. The central region of the plateau is only a few centimetres higher than the valleys. Areas of preferential movement by the five colony-males are depicted by arrows; residences are depicted by dots. The table provides the distances separating the residences of each numbered subject within the colony. Since each subject usually had a different individual (Indiv.) as its nearest neighbour, second nearest neighbour, etc., this order is also shown.

the temporal patterning of the pulse intervals of the various individuals, on the contrary, showed only slight inter-individual variation of ±3 ms. After scrutinizing the recordings for possible distortion or transients, we selected a representative three-pulse chirp-sound with a high signal-to-noise ratio from each of the five males, and used them to make five tape loops, each with a repetition rate of 25 per min.

The playback system consisted of the tape-recorder used during the recording periods, a Schober TR-2 power amplifier, and a J-9 underwater loudspeaker. Playback levels were set on the day prior to the start of the experiments to equal those of the initially recorded signals. Sound levels were verified during each test by divers on the site. The loudspeaker was carefully moved to a given location within the first 45 s of a 5-min 'rest' period preceding the test at that location. A preliminary study showed that such movement produced no measurable effect during subsequent control and playback periods. The sound repetition rate chosen for playback, 25 per min, was that previously determined to be optimal for eliciting the primary response by males (dipping) monitored during this study (Ha 1973).

We tested for individual recognition of one another's sounds by the colony males using what has become known as the 'dear enemy' phenomenon (Wilson 1975). Briefly stated, territorial residents respond less intensively to certain activities when performed by their near neighbours within their respective territories than to strangers performing the same activities nearby, or to near neighbours performing such activities beyond their territorial boundaries. The latter condition provided the crucial test of individual recognition since it precluded a more simple model of recognition, i.e. familiar versus unfamiliar (Beer 1970; Wiley & Wiley 1977; Falls & McNicholl 1979).

The experimental design involved transmitting one of the five tape-loops for 2 min from a loudspeaker located 30 cm from one of the male-residences (i.e. near the centre of the territory) (Fig. 1). This transmission was bracketed by 2-min silent control periods, with the 5-min 'rest' period following each post-playback control. The order of playbacks followed the Latin-square design, with both the tape-loops and the position of playback changing relative to one another for each succeeding test. A series was complete when all five sounds had been played back in each of the five territories. Three such series were completed, each taking approximately 2 days. Particular attention was given to testing at comparable times of the day. To ensure that responses were not due to possible differences in equipment, only one playback system was used throughout the study. Chirp-sounds from non-colony males, i.e. strangers, were not used in the investigation, so as to preclude complications due to possible differential attention by the colony males (Wiley & Wiley 1977).

A series began after three divers had positioned themselves so that they had unobstructed views of the males for which each had responsibility. Activities were recorded on hand-held slates, with emphasis directed at the occurrence of dipping (a courtship action) and chasing by the respective males. Only dipping was subsequently found to have occurred often enough for statistical analysis.

Although transmitting chirp-sounds within a colony of bicolor damselfish readily elicits competitive courtship displays by the resident males, motivational differences among such males are often apparent, judging by the presence or absence of egg-batches within their nests on any given day. Such differences could not be manipulated or experimentally equated in any direct way without seriously confounding the natural situation. To reduce the effects of such differences relative to a specific male throughout the period of testing, the number of responses by that male during the playback of a particular sound at a specific location during a given series was expressed as a fraction of the total number of responses shown by it during all playbacks at that position for that series. This fraction was then multiplied by the actual number of responses elicited during that particular playback to de-emphasize possible cumulative effects of low response levels throughout that series. Since a particular sound was transmitted at each position three times (i.e. once per series), these three values were summed to obtain the 'weighted' response by a given male at that location for the sound in question. Considerable variation in the response levels of the males, except at the nearest neighbour's position, could not be eliminated by transforming the data without presupposing some a posteriori conclusion. In order not to do so, the weighted responses for each male were analysed using Fisher's exact test, which allowed us to test the hypothesis of individual recognition without making direct comparisons between the responses of the different males.

RESULTS

The responses of the colony males to playbacks at their nearest neighbours' positions indicated that they could distinguish their nearest neighbours' sounds from the sounds of the other males within the colony (Table I). In 16 out of 20 cases ($P < 0{\cdot}05$, Fisher's exact test), playback of the nearest neigh-

Table I. Responses of test males to sounds played back within the territory of their nearest neighbour

	No. of 'dips' to sound of:				
Test males	Nearest neighbour	Second nearest neighbour	Third nearest neighbour	Most distant neighbour	Self
1	0·0	9·3	0·0	4·0	5·3
2	1·3	14·3	0·9	0·3	5·9
3	1·0	4·2	5·1	21·2	9·9
4	0·5	9·8	8·0	5·5	12·1
5	1·9	1·3	6·6	2·8	3·7
Unweighted $\bar{x} \pm$ SD	1·9±2·5	6·1±6·7	4·4±5·8	5·4±8·3	6·0±5·7

In 16 out of 20 cases, greater response was shown to chirps of non-residents than those of residents. The total number of tests conducted was 75; the total number of 'dips' recorded was 358. The difference between the responses shown to nearest neighbours' sounds and those shown to other neighbours' sounds was significant, $P = 0{\cdot}048$, Fisher's exact test (Sokal & Rohlf 1969); analyses were based on weighted data (see text). Refer to Fig. 1 for neighbour relationships.

bour's sound at the nearest neighbour's position elicited less dipping by a given male than did playback of the other sounds. Males also responded to their own chirps, when transmitted from their nearest neighbours' territories, as if they were from another non-resident. The fact that these sounds elicited dips and appeared not to be treated differently from the other non-resident sounds suggested that individuals did not recognize their own self-produced sounds. No significant difference (Student's *t*-test) was found between the mean number of dips performed during the control periods prior to playback of sounds in the territories from which they originated and those performed prior to playbacks in other territories.

To demonstrate conclusively individual recognition rather than simply nearest neighbour recognition, it was necessary, however, to examine the responses of the males in such a way as to preclude discrimination based upon possible habituation to a familiar sound. This was accomplished by analysing the responses of a male when the sounds of its two closest neighbours were transmitted from one another's territories (Fig. 2). Males responded more vigorously ($P < 0{\cdot}05$, Fisher's exact test) whenever a sound not produced by the resident was played back in a neighbouring territory. In all but one case, dipping increased at least two-fold, and usually more than four-fold, when chirps were broadcast under such conditions.

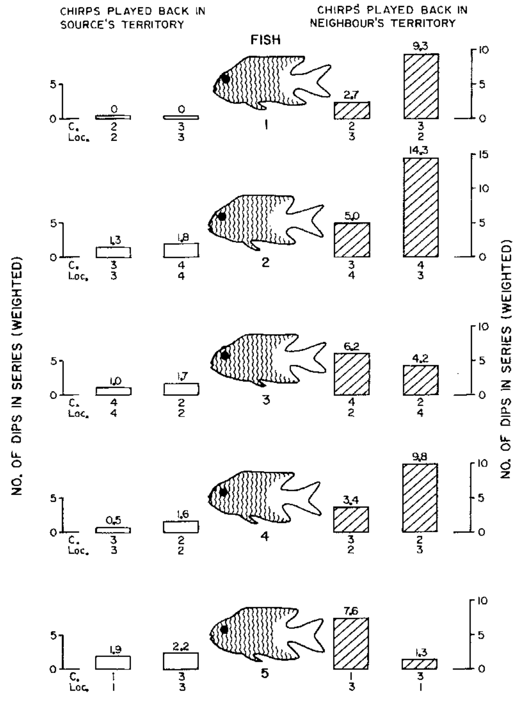


Figure 2. Acoustical recognition of their two nearest neighbours' chirps by the resident male bicolor damselfish. Each male's responses to chirps (C) broadcast from the locations (Loc.) of the actual source (histograms on left) and when the location of the broadcasts was switched (histograms on right) are compared. In 18 out of the 20 comparisons ($P < 0{\cdot}05$, Fisher's exact test), males 'dipped' more vigorously when a test sound was played back in the opposing territory than when it was played back in the source's territory or when the sound of the resident was played back in that opposing territory.

DISCUSSION

Individual recognition was apparently dependent on the ability of the fish not only to discern the unique characteristics of their neighbours' sounds, but also to detect the proper sound-source directions. The present methodology provided not only a demonstration of such detection, but also a function of such detection, in contrast to those studies which have revealed discrimination based solely on conditioning techniques (see Buwalda et al. 1983).

Of the possible acoustical cues responsible for individual recognition, the temporal patterning and the spectral content of the sounds are the most likely candidates. The temporal patterning of the rapid pulses making up the chirp-sounds has been shown previously to be the basis for species recognition among several sympatric species of pomacentrids possessing extremely similar calls (Myrberg et al. 1978; Spanier 1979). Temporal differences between 5 and 15 ms in the pulse intervals were the requisite cues for such recognition. The smaller differences which characterize intraspecific variability fall below this level of resolution (Ha 1973; Spanier 1979).

Size-dependent variation of dominant frequencies within power spectra has been reported for several species of fishes (Myrberg et al. 1965; Fine et al. 1977; Schwarz 1980) as well as other vertebrates (Davies & Halliday 1978; Clutton-Brock & Albon 1979; Ryan 1980; Fairchild 1981). This same relationship has recently been established for bicolor damselfish sounds (Riggio 1981). Since fishes apparently possess frequency-resolving powers comparable with those of other vertebrates (Fay 1973; Fay & Popper 1980), the size variation among males of a bicolor colony strongly suggests that the acoustical cue for individual recognition rests indeed with the spectral characteristics of a given signal.

Male bicolor damselfish have ample opportunity to learn their neighbours' vocalizations, since they occupy permanent territories and actively compete for the attention of females within the colony. Furthermore, sound production occurs simultaneously with distinctive colour and motor patterns which could readily aid in the learning of specific acoustic signals. Such visual stimuli have been found to enhance responsiveness to species-typical vocalizations in other vertebrates (see Evans 1972). Habituation to the presence and activities of conspecific neighbours within their own territorial boundaries is a well-known phenomenon in fishes. It has not only been demonstrated experimentally for several species in the laboratory (e.g. van den Assem & van der Molen 1969; Peeke & Veno 1976), but has been used in discrimination studies in the field as well, using species closely related to our subjects (Fricke 1973; Thresher 1979).

Individual recognition by acoustical means may well play a significant role in several important contexts. Bicolor damselfish are highly territorial. Each defended area includes a shelter, necessary not only as a refuge but, in the case of males, also as a nest site. If a male is removed from its territory, the area and its associated shelter are invaded by numerous species of fishes within a few minutes—and almost invariably they are taken over by a neighbouring conspecific male. The irregular topography of a coral reef adds to the problems of maintaining secure territories, since residents are often visually cut off from their neighbours. Since it is the neighbours who most often annexe territories, a distinctive and individually recognizable 'keep-out' signal frequently produced throughout the day could substantially reduce the energy costs related to active probing by intruders and to active defence by the residents (Krebs 1976; Krebs et al. 1978).

Individual variation in the chirps of males may also aid females in selecting spawning partners. Male size has been found to be an important determinant of mate choice in bicolor damselfish (Schmale 1981). Since size and dominant frequency are closely related, sound production could well influence mate selection, especially in those regions of the reef where females might hesitate in venturing far from their own shelters to select males prior to sunrise—the time of spawning in this diurnal species. Based on the hearing abilities of these fish (Myrberg & Spires 1980), and the sound-source levels of chirps produced by males (+9 to +11 dB re 1 microbar), these sounds can be heard at least 6–8 m away. This covers an area that will probably include the residential areas of all females within a given colony. Chirp-sounds could thus serve as beacons, leading a female across the reef to the specific location of the mate of her choice.

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