

Threat-sensitive predator avoidance in damselfish-trumpetfish interactions

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Summary. Predatory threat can vary during a predator-prey interaction as an attack escalates or among predators at different times. A Threat-sensitivity hypothesis is presented which predicts that prey individuals will trade-off predator avoidance against other activities by altering their avoidance responses in a manner that reflects the magnitude of the predatory threat. This hypothesis was tested in the field by presenting prey (threespot damselfish, *Stegastes planifrons*) with models of foraging predators (Atlantic trumpetfish, *Aulostomus maculatus*). During a presentation, damselfish displayed progressively stronger avoidance as predator models were brought nearer; response waned rapidly once predator models passed overhead. Larger predator models and those oriented in a strike pose evoked stronger avoidance reactions than smaller and non-attacking models, intermediate responses were evoked by size and orientation combinations that were intermediate in threat, and habituation was more common to weakly-threatening presentations. Smaller damselfish showed stronger avoidance of models than did larger damselfish. Non-avoidance activities, such as feeding and territorial defense, were curtailed during presentations or were more common during weakly threatening presentations. Approaches to the models, equated with mobbing, were more common among large damselfish, again reflecting degrees of vulnerability among different size prey individuals. These initial results indicate that damselfish threatened by predators respond in a graded manner that reflects the degree of threat posed by the predator, in accordance with the Threat-sensitivity hypothesis.

Introduction

The concept of the trade-off is central to the thesis that behavioral traits are a product of natural selection (e.g. Jaeger et al. 1983; Davies and Hous-

ton 1984; Dill and Fraser 1984; Lucas 1987). During predator-prey interactions, prey often trade-off time and energy available for other activities, such as feeding, courtship, and territorial defence, against the need to avoid predators (Sih 1980; Lima et al. 1985; Helfman 1986; Milinski 1986; Ydenberg and Dill 1986; Dill 1987; Gilliam and Fraser 1987; Power 1987). Work in this area has usually involved experimental protocols testing prey responses to the presence or absence of predators (e.g. Milinski and Heller 1978; Sih 1980; Martindale 1982; Cerri and Fraser 1983; Godin and Smith 1988; Holbrook and Schmitt 1988), or investigators have focused on responses of grouped prey, or on ontogenetic or sexual differences in response (e.g. Stein and Magnuson 1976; Zaret and Suffern 1976; Sih 1982; Werner et al. 1983; Gilliam and Fraser 1987).

Individual prey, however, commonly face a spectrum of trivial to powerful influences on survival, and ultimately on fitness. For example, potential predators may vary continuously in the degree of threat that they pose due to differences in body size, hunger, food preferences, and foraging strategy, and the threat posed by a predator may vary during an interaction as the predator escalates its attack. In balancing predator evasion against other activities, natural selection would presumably favor prey individuals capable of recognizing the degree of threat represented by a particular predator. Such prey should take evasive action appropriate to the magnitude of threat, rather than avoiding any predator encountered regardless of degree of threat. Progressively greater threat should produce progressively stronger avoidance responses, which in turn would entail greater relative costs in the time, energy, or activity budget of the potential prey (e.g. Sih 1982, 1987; Fraser and Huntingford 1986; Magurran and Pitcher 1987).

This cost-benefit approach to predator-prey interactions can be formulated into a preliminary

Threat-sensitivity hypothesis that describes the actions of prey individuals faced with a series of predatory threats that differ in magnitude. The hypothesis is based on the assumptions that animals (1) face conflicting demands on their time and energy, (2) must trade-off predator avoidance against other activities that influence fitness, and (3) will do so in an appropriate, graded manner.

In the present study, I have attempted an initial test of the Threat-sensitivity hypothesis by presenting prey individuals (threespot damselfish, *Stegastes planifrons*) with simulated threats of varying degree as represented by models of "foraging" Atlantic trumpetfish (*Aulostomus maculatus*). Threespot damselfish were chosen as the test species because they are near-benthic, sedentary, territorial fish that are relatively undisturbed and easily observed by divers (e.g. Williams 1980; Robertson et al. 1981). Trumpetfish were chosen because they are easily observed, common, diurnal, stalking-lurking predators that swim just above the reef surface and feed on small fishes and invertebrates, including the threespot damselfish (Eibl-Eibesfeldt 1955; Randall 1967; Kaufman 1976; Aronson 1983). Trumpetfish foraging behavior, described below, is easily and realistically mimicked by the model presentation technique used here.

After initial observations of trumpetfish-damselfish interactions in the field which focused on possible threat-sensitive behavior, I conducted a series of model presentations in which I provided a graded threat by varying trumpetfish size, orientation, and proximity to prey and then measured the distance at which damselfish reacted to models, the duration of avoidance responses, and which of a hierarchy of avoidance and nonavoidance responses were elicited. Five predictions, based on threat-sensitivity, were tested:

1. Strength of avoidance response is a function of changing threat during a presentation, with greater avoidance elicited as the distance between prey and predator model decreases;
2. Strength of avoidance response is also a function of presentation type, with more threatening presentations evoking stronger responses;
3. Response strength is mediated by relative size of predator and prey, with larger trumpetfish eliciting stronger responses and smaller damselfish showing a stronger avoidance response;
4. Nonavoidance activities, including territorial attacks on competitors and predators, are more common during less threatening presentations; and
5. Habituation, if present, is more likely in response to less threatening presentations.

Methods

Study area

This investigation was conducted in the lagoon and forereef of Teague Bay, St. Croix, U.S. Virgin Islands, at depths of 2–10 m; additional observations of trumpetfish behavior were made in Salt River Canyon, St. Croix, at depths of 15–40 m.

Trumpetfish foraging behavior

Approximately 19 hours were spent observing the foraging behavior of 54 Atlantic trumpetfish prior to conducting the model experiments described below. Scuba or snorkel divers followed individual trumpetfish for 5–90 min, recording fish size (estimated by comparison with a meter stick), coloration (for individual identification), height above bottom, speed of movement and distance moved/time (calculated with a hand-held General Oceanics plankton net flow meter). Species and size of prey oriented to and attacked, attack success, intraspecific interactions, and agonistic behavior of prey toward trumpetfish were also noted. Activities of five trumpetfish were recorded on Super 8 mm movie film.

Model presentations

Eleven territory-holding, threespot damselfish (29–114 mm total length, measured by underwater comparison with drawn outlines of fish) were presented with predator models made from formalin preserved, resin-coated, Atlantic trumpetfish (Helfman 1983, 1986; Fig. 1). Models were lashed with clear Mylar tape to a 75 mm long, 25 mm wide, 20 mm thick block of clear plexiglass. A 1-m long, 13 mm diameter clear plexiglass rod was then pushed into a hole drilled in the face of the block. During each presentation, models were passed in a semi-circle at a relatively constant speed (\bar{X} = 13.6 cm/sec, SD = 1.3 cm/sec; \bar{X} pass duration = 14.6 sec, SD = 1.5 sec; n = 330 passes) and height (snout 25 cm above substrate) above the test fish by a kneeling diver. A 2-m long piece of weighted string with small pieces of flagging attached at 25 cm intervals was placed in an arc centered on the damselfish' refuge hole to facilitate measurement of reaction distances. Refuge holes were located

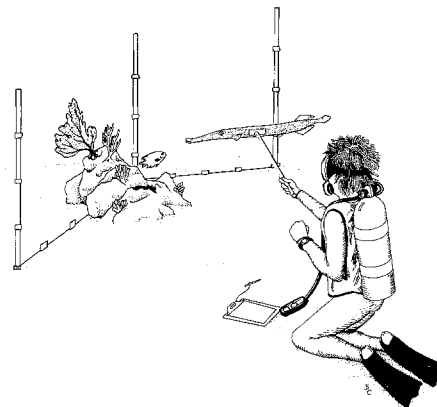


Fig. 1. Testing threat-sensitivity in free-living damselfish using model presentations. The predator model, a resin-coated Atlantic trumpetfish, is attached to the end of a clear plexiglass rod and passed at a constant height and speed through an arc centered above the damselfish' refuge hole. Initial reaction distance between model and damselfish, response duration, and avoidance behaviors of the damselfish are recorded. Damselfish is depicted "orienting" to the predator model

during brief observations of the damselfish prior to testing. Weighted, vertically oriented meter sticks were placed at the middle and two ends of the arc to help maintain constant model height during a pass. All passes were from right to left, were initiated when the damselfish was adjacent to its refuge hole, and were timed with a stopwatch. Behavioral responses of damselfish were recorded visually; three sessions were recorded on Super 8 mm movie film to check the reliability of visual observations.

Five presentation types of models were used: large vertical, large horizontal, small vertical small horizontal, and control. Models were presented during 11 sessions, one per damselfish. A session consisted of five trials, each trial involving six consecutive passes with one of the five presentation types (passes = pseudoreplications). Each damselfish encountered all five presentation types over an 80 min period. Although each session was intended to include 30 presentations (5 types, 6 passes/type, total = 330 passes), some data were discarded because of ambiguity in damselfish response or errors in recording, which lead to differences in sample size for different response measures.

Presentation types were characterized by model size (large or small) and orientation (horizontal or vertical). Size relationships have a strong influence on predator-prey relationships in fishes; small prey are vulnerable to more predators than are large prey, and large predators consume a wider variety of prey sizes than do small predators (e.g. Werner et al. 1983; Werner and Gilliam 1984; Helfman 1986). From this general relationship, coupled with field observations suggesting that large trumpetfish were more threatening than small trumpetfish and that most trumpetfish struck from a head down posture, it was predicted that threat would decrease in the order large vertical (LV) > large horizontal (LH) \geq small vertical (SV) > small horizontal (SH) > control (C). No difference could be anticipated between large horizontal and small vertical presentations because field observations suggested that both large size and vertical orientation constituted strong threat (see Discussion). Large models were either 595 or 610 mm long, small models were either 350 or 390 mm long. Orientation was constant throughout a pass. Controls consisted of passes using only the plastic rod-75 mm block combination. This controlled for experimental artifact induced by the rod, block, and diver; control for predator recognition would have required presentation of non-predatory models with morphologies similar to trumpetfish and was not attempted in the present study (see Thresher 1976). Order of presentation was randomized with respect to trumpetfish models and orientation, except that controls were run as the last trial in seven of the 11 sessions. Sessions were conducted in daylight, between 0915 and 1930 hrs.

Behavior categories and statistical analyses

The following damselfish responses were recorded: (1) initial reaction distance = the distance (cm) between the trumpetfish model's head and the damselfish at which the damselfish first reacted; (2) response duration = time elapsed (sec) from initial reaction until the damselfish ceased responding to the model or engaged in nonavoidance activities; and (3) behavioral response (see Table 1) = avoidance and nonavoidance activities performed during a pass. Avoidance activities were ranked 1 to 10 from weak to strong; "maximum response" elicited (= highest ranking response during a pass) served as the metric of response in most analyses. Rankings were determined prior to analysis of model presentation data and were based on how much time a response took away from other activities, and how visually obvious a response was (see Magurran and Pitcher

Table 1. Common behavioral responses of threespot damselfish when presented with models of predatory trumpetfish, listed in approximate order of strength of response. More than one response often occurred during a pass, and some responses occurred more than once during a pass

Rank	Response (definition)
1.	no response (no overt reaction to model)
<i>Avoidance</i>	
2.	weak drop, hover still, suppressed motion (weak drop = slow sink in water column to near substrate; all occur without orientation to model)
3.	orient (shift in body position to damselfish snout facing model)
4.	strong drop (sudden sink to near substrate)
5.	roll, fin spread (roll = repositioning of body, presenting dorsum, side or ventrum to model; fin spread = obvious spreading of dorsal, anal, and pelvic fins; two actions often occurred simultaneously)
6.	back up (swim backwards toward refuge site by sculling pectoral fins, usually while oriented)
7.	slow swim (normal forward swim away from predator toward refuge site at slow to moderate speed)
8.	fast swim, dive, zigzag (rapid swim down and toward refuge site, often with erratic, zigzag motion)
9.	to refuge entrance (to area at entrance to refuge site but not inside; sometimes with tail inside)
10.	enter refuge (most of body inside refuge, damselfish often out of sight of the observer)
<i>Nonavoidance</i>	
1.	approach (damselfish approaches model slowly)
2.	feed (picking at bottom)
3.	chase (agonistic attacks on territorial intruders)

1987 for a similar ranking of avoidance behaviors). This latter criterion was based on the assumption that overt actions were more visible to a predator and would not be used unless they also provided more protection than less overt responses. Nonavoidance responses were ranked from 1 to 3 according to the presumed difficulty a damselfish would experience monitoring the activities of a predator while engaged in that response.

T-tests were used to assess the effects on response strength of (1) trumpetfish size for all large versus all small presentations, and (2) trumpetfish orientation for all vertical versus all horizontal presentations. Response strength as a function of damselfish size was tested by simple regression analysis. Chi-square values were used to test the frequency of nonavoidance responses as a function of presentation type; a posteriori tests of chi-square analyses were conducted using the subdivided chi-square procedure of Zar (1974). Differences in response strength within a bout were tested with *t*-tests (2-response presentations), and one factor ANOVA followed by Scheffe *F*-tests where differences were indicated (3-response presentations). Only responses elicited before the trumpetfish' head passed over the head of the damselfish were scored, since threat presumably decreased once the trumpetfish had passed the damselfish (see below). Habituation within trials and within sessions was analyzed by regressing response strength against pass number. Multiple comparisons of relative response strength among presentation types were tested with non-parametric Kruskal-Wallis tests, followed by Conover's *T* where differences were indicated (Conover 1980). Autocorrelation of response results within pre-

sensation types may have resulted from consecutive presentations of each model type, but consecutive presentations allowed testing of possible differences in habituation to differently threatening stimuli.

Results

Field observations

Trumpetfish foraging behavior. Trumpetfish typically moved horizontally above the reef, generally 15–100 cm above the substrate at speeds of approximately 10–30 cm/sec; less frequently, trumpetfish swam along the reef while vertically oriented. Swimming was accomplished primarily via undulation of the soft dorsal and anal fins, with little visible body flexion. Trumpetfish frequently stopped and investigated potential benthic or near-benthic prey; intense investigation (=“stalking”) and most actual predatory strikes occurred while oriented vertically to the substrate, as was also found by Aronson (1983). Successful strikes were often obvious because the membranous skin covering the elongate mouth of the trumpetfish is relatively translucent and captured prey could be seen during swallowing movements. Eight of 45 strikes during 156 stalks were successful.

Interactions with damselfish. Damselfish approached by a trumpetfish generally oriented to the predator, sank to the bottom, and then entered a refuge hole in the damselfish’ territory, re-emerging as the predator moved away (Table 1). Cruising trumpetfish were also frequently approached (116 times) and even contacted (32 times) by various prey fishes. Approaches involved generally rapid swimming toward the trumpetfish by a damselfish, were usually directed at the trumpetfish’ tail, and usually occurred after the trumpetfish’ head was past the damselfish. Only one such approach was made to a vertically oriented, head down trumpetfish out of the 156 stalks observed. On two occasions, a damselfish approached a trumpetfish’s tail, the predator turned and oriented head down at the damselfish and the damselfish retreated to its refuge hole.

Occasionally during an approach and usually upon contact by a damselfish, the trumpetfish “jumped” a few cm laterally away from the damselfish and accelerated from the area. Trumpetfish driven away in this manner did not return immediately to the same locale. Trumpetfish failed to respond to such attacks only when stalking another prey individual (three observations). It appeared that larger damselfish were responsible for most

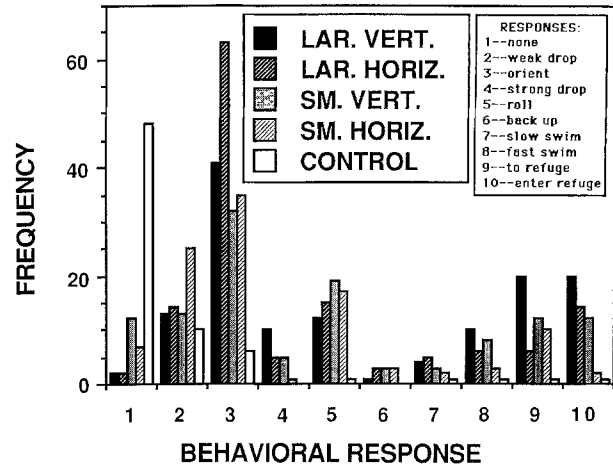


Fig. 2. Frequency of 10 avoidance responses by 11 threespot damselfish as a function of model presentation type. The number of times each response was elicited is shown for each of the five presentation types. Response types are presented from weakest to strongest and defined in Table 1. In general, stronger responses were elicited by more threatening presentation types and weaker responses were more common to less threatening presentation types

approaches, and that larger trumpetfish were approached more often than smaller trumpetfish. On two occasions, damselfish approached the larger of two trumpetfish that were passing by their territory. No obvious sexual differences correlated with agonistic attacks: of six damselfish collected that had attacked trumpetfish and in which gonads could be detected microscopically, four were male and two were female.

Experimental assessment of threat sensitivity: model presentations

Response as a function of presentation type. Avoidance responses to the models were related to presentation type, with presumed greater threats eliciting the strongest responses (Fig. 2). Large vertical presentations received a disproportionately large number of strong responses (responses 6–10; subdivided $\chi^2 = 17.59$, $P = 0.0001$, 1 *df*). The strongest response, “enter refuge”, occurred least frequently to control presentations and increased in frequency progressively along the presumed hierarchy from control to large vertical presentations. Three other strong responses (responses 7–9), and response 4 also tended to increase in frequency as threat increased from control to large vertical presentations.

Weak responses appear to follow the reverse pattern (Fig. 2). “No response” was a relatively rare reaction to large trumpetfish models, more common to small models, and very common to

Table 2. Response strength as a function of presentation type. Presentation types appear in order of mean rank (=sum of ranks/no. of presentations, rounded to nearest whole number); underlining connects responses that were not significantly different ($P>0.05$). Comparisons based on combined data for each presentation type over all trials, analyzed with Kruskal Wallis Tests (H) and Conover's T Multiple Range Test

	Initial reaction distance						Response duration						Maximum response								
	H	response rank					<i>n</i>	H	response rank					<i>n</i>	H	response rank					<i>n</i>
Presentation type	124**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	314	133**	<u>LH</u>	<u>LV</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	316	122**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	330
Mean rank		214	201	171	143	57		216	211	165	148	55		236	195	188	149	66			
Number of presentations		65	64	61	60	64		64	62	63	62	65		66	66	67	65	66			

LV large vertical; *LH* large horizontal; *SV* small vertical; *SH* small horizontal; *C* control; *n* total number of presentations; ** $P\leq 0.01$

Table 3. Strength of avoidance responses of threespot damselfish to resin-coated models of predatory Atlantic trumpetfish. Differences in the strength of an individual's responses as a function of presentation type were analyzed with a Kruskal-Wallis test (H) and Conover's T Multiple Range Test (*= $P<0.05$; **= $P<0.01$). Presentation types appear in order of mean rank within a trial; underlining connects responses that were not significantly different at $P>0.05$. Presentation types involved models of large trumpetfish or small trumpetfish presented vertically or horizontally, or clear plastic block controls (LV, LH, SV, SH, C)

Damselfish Length (mm)	Initial reaction distance						Response duration						Maximum response					
	H	relative response strength					H	relative response strength					H	relative response strength				
29 ^a	15.2**	<u>LH</u>	<u>SH</u>	<u>SV</u>	<u>LV</u>	<u>C</u>	16.8**	<u>LH</u>	<u>SH</u>	<u>SV</u>	<u>LV</u>	<u>C</u>	16.9**	<u>LH</u>	<u>SV</u>	<u>LV</u>	<u>SH</u>	<u>C</u>
38 ^a	16.2**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	18.4**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	18.3**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>
51	20.1**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	15.6**	<u>LH</u>	<u>LV</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	15.7**	<u>LV</u>	<u>SV</u>	<u>LH</u>	<u>SH</u>	<u>C</u>
55	18.5**	<u>LH</u>	<u>LV</u>	<u>SH</u>	<u>SV</u>	<u>C</u>	14.7**	<u>LH</u>	<u>LV</u>	<u>SH</u>	<u>SV</u>	<u>C</u>	16.1**	<u>LV</u>	<u>LH</u>	<u>SH</u>	<u>SV</u>	<u>C</u>
64 ^a	16.7**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	15.1**	<u>LH</u>	<u>LV</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	10.3*	<u>LV</u>	<u>SV</u>	<u>LH</u>	<u>SH</u>	<u>C</u>
64 ^a	18.3**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	20.8*	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	10.7*	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>
70	14.8**	<u>LH</u>	<u>LV</u>	<u>SH</u>	<u>SV</u>	<u>C</u>	10.1*	<u>LH</u>	<u>LV</u>	<u>SH</u>	<u>SV</u>	<u>C</u>	4.4 ^{NS}					
89	15.8**	<u>SV</u>	<u>LH</u>	<u>LV</u>	<u>SH</u>	<u>C</u>	18.3	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>LV</u>	<u>C</u>	16.0**	<u>LH</u>	<u>LV</u>	<u>SV</u>	<u>SH</u>	<u>C</u>
102	7.1 ^{NS}						6.5 ^{NS}						7.6 ^{NS}					
108	16.6**	<u>LV</u>	<u>SV</u>	<u>LH</u>	<u>SH</u>	<u>C</u>	16.6**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	23.4**	<u>SV</u>	<u>LV</u>	<u>LH</u>	<u>SH</u>	<u>C</u>
114	10.3*	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	19.4**	<u>LV</u>	<u>LH</u>	<u>SV</u>	<u>SH</u>	<u>C</u>	15.6**	<u>LV</u>	<u>SV</u>	<u>LH</u>	<u>SH</u>	<u>C</u>

^a sessions when controls were run in other than last position (see Methods)

controls. Controls elicited progressively fewer of the three weakest responses and almost none of the stronger responses. Small horizontal and control presentations elicited disproportionately fewer strong (responses 6–10; subdivided $\chi^2=5.99$, 17.6, $P=0.01$, 0.0001, $df=1,1$ for small horizontal and control respectively). “Orient”, the most common response, was elicited more often by large than by small models ($\chi^2=8.39$, $P<0.005$, $df=1$).

When the three measures of response are considered separately, additional evidence of the predicted threat hierarchy is found (Table 2). For both initial reaction distance and response dura-

tion, large models were differentiated from small models, although no discrimination was made between horizontally- and vertically-presented, large models. In the maximum response category, large vertical presentations elicited significantly stronger responses than all other types. For both initial reaction distance and maximum response, small horizontal presentations elicited the weakest responses of the model presentation types, although small horizontal and small vertical were not differentiated in terms of response duration. Controls elicited the weakest responses for all measures of reaction.

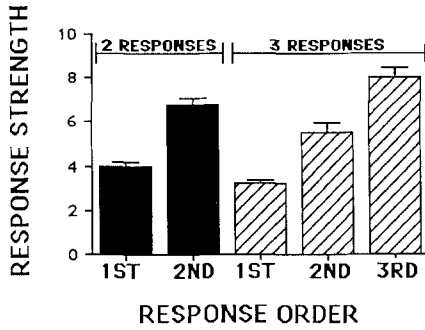


Fig. 3. Changes in strength of avoidance response by damselfish as a function of predatory threat during a presentation. Comparisons are between-responses for presentations during which a damselfish gave two responses, and among-responses for presentations eliciting three responses. Means and standard errors of response strength are shown. For both two- and three-response presentations, response strength increased with order of response, suggesting stronger responses to increasing threat ($P < 0.001$ for all comparisons)

When analyzed at the level of individual behavior, the null hypothesis of no difference in response to the five different presentation types was rejected in 29 of the possible 33 response categories (11 damselfish, 3 response types per fish), suggesting discrimination between threatening and non-threatening stimuli (Table 3). Discrimination among

models was most evident with respect to the strongest and weakest threatening stimuli. Large vertical presentations were ranked highest most frequently, whereas small horizontal presentations generally ranked lower than other non-control presentation types. Small horizontal was the only category to occur alone in lowest rank and occurred more frequently tied for lowest ranking than any other presentation type. Intermediate responses, involving large horizontal and small vertical presentations, received equal ranking, or large horizontal outranked small vertical. Controls received a consistent, weak response, indicating that response strength was not simply an artifact of the experimental procedure.

Within-bout responses. Changes in response as a function of threat strength during an interaction were measured by comparing presentations during which a damselfish gave two or three responses (four responses occurred on only six occasions). During both two- and three-response presentations, mean response strength (as per Table 1) increased significantly with later responses (Fig. 3): first responses were weaker than second responses, or first were weaker than second which were

Table 4. Damselfish responses as a function of size and orientation of predator models. Asterisks indicate significant differences in response to large versus small models or to vertical versus horizontal presentations (t -tests: *** = $P < 0.001$; NS = $P > 0.05$). For all three response measures, stronger avoidance was shown to large than to small models, whereas only maximum response differed with respect to vertical versus horizontal presentations. Responses pooled over all presentations, e.g. "large models" = all large vertical + all large horizontal presentations, "vertical models" = all large vertical + all small vertical presentations, etc.

	Initial reaction distance (m)				Response duration (sec)				Maximum response (scaled 1–10)			
	\bar{X}	SE	n	t	\bar{X}	SE	n	t	\bar{X}	SE	n	t
Response to												
Large models	0.35	0.05	123	5.26***	5.6	0.32	120	6.37***	6.8	0.26	128	4.74***
Small models	0.01	0.04	120		3.1	0.24	124		5.0	0.28	131	
Response to												
Vertical models	0.16	0.04	126	0.085 ^{NS}	4.5	0.33	127	1.23 ^{NS}	6.6	0.28	132	4.41***
Horizontal models	0.16	0.05	124		4.0	0.28	124		5.0	0.26	132	

Table 5. Strength of avoidance responses in threespot damselfish as a function of damselfish size. Correlation analysis indicates an inverse relationship for horizontal presentations, suggesting progressively stronger responses in smaller damselfish. Probability levels (P) for correlation coefficients (r) are based on one-tailed tests ($- = P \geq 0.10$)

Presentation type	Initial reaction distance			Response duration			Maximum response		
	r	P	df	r	P	df	r	P	df
Large vertical	-0.214	<0.05	63	-0.013	-	62	0.062	-	64
Large horizontal	-0.251	<0.025	62	-0.338	<0.01	60	-0.237	<0.05	66
Small vertical	-0.158	-	59	-0.140	-	61	-0.041	-	65
Small horizontal	-0.524	<0.001	58	-0.359	<0.005	60	-0.459	<0.001	63
Control	0.170	<0.10	62	0.147	-	63	0.067	-	65

weaker than third (*t*-test for between-response comparison, 1st response < 2nd response, $t=8.13$, $P<0.0001$, $n=94$ in each category; ANOVA for among-response comparisons, $F=35.29$, $P<0.0001$, $n=22$ in each category; Scheffe-F multiple comparison test, $P<0.001$ for 1st response < 2nd response and 2nd < 3rd, $F=8.6$, 9.0 respectively; $P<0.0001$ for 1st < 3rd, $F=35.3$).

Effects of size and model orientation. Trumpetfish size and orientation and damselfish size affected response strength as would be expected if damselfish were threat-sensitive. Initial reaction distance, response duration, and maximum response were all greater when responding to large rather than to small trumpetfish models (Table 4). Vertical models elicited significantly greater maximum responses than did horizontal models, although no differences in initial reaction distance or response duration occurred as a function of model orientation.

Damselfish size was more strongly correlated with response strength during horizontal than during vertical or control presentations (Table 5). Correlation coefficients were significant and inverse in all six categories for horizontal presentations (3 measures of response \times 2 model sizes), whereas only one of six vertical presentation measures had a significant coefficient (although all six vertical tests had negative signs). The proportion of the variance explained by these correlations was low, never exceeding 28%.

Nonavoidance responses. Damselfish also engaged in nonavoidance activities, although at lower frequencies than avoidance behaviors. A total of 116 nonavoidance acts were seen during the 330 standardized passes, as compared to 493 avoidance acts (neither category includes 71 “no response” observations). The three most frequently observed nonavoidance activities were feeding ($n=51$), approaching the model ($n=43$), and chasing territorial intruders or neighbors ($n=17$); other, infrequent activities included chafing against the bottom and wandering out of the territory ($n=5$).

Frequency distributions of nonavoidance activities relative to presentation type and timing suggest threat-sensitive behavior (Fig. 4). Both approach and feed showed significant, non-random deviations from equal response frequencies (approach, $\chi^2=23.03$, $P<0.0001$; feed, $\chi^2=20.57$, $P<0.0004$, $df=4$ in both cases). Approaches to large horizontal presentations and feeding during control presentations occurred more often than expected (approaches to large horizontal vs. all

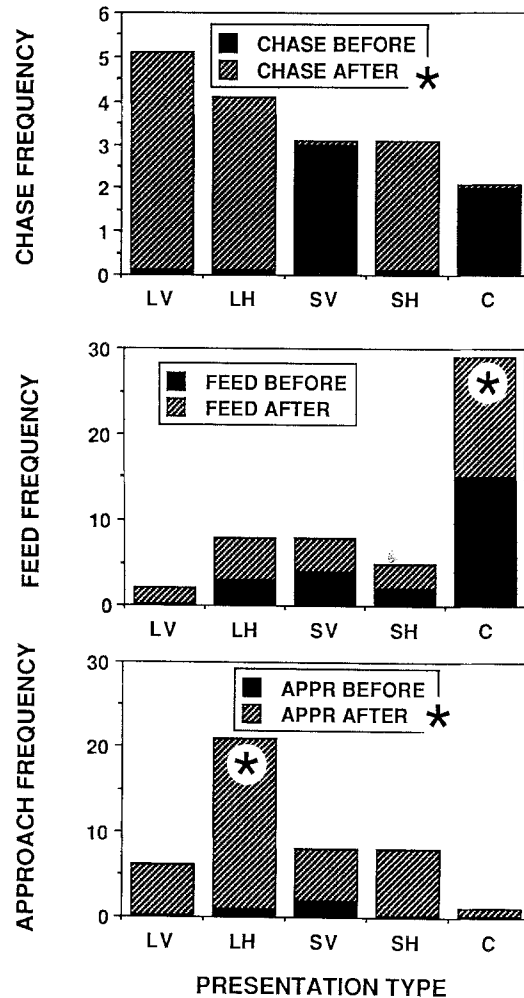


Fig. 4. Frequency of occurrence of 3 nonavoidance behaviors by 11 threespot damselfish as a function of model presentation type and location of the predator model. Predator location is divided into approaching (“before”) versus receding (“after”) models, based on head position of the model relative to the damselfish. Significant deviations from equality of occurrence among presentation types (subdivided chi-square) or between predator locations (chi-square) are indicated with an asterisk (*). Feeding was most common during control presentations, approaches were most common during large horizontal presentations, and both approaches to the model and agonistic chases of territorial intruders were more frequent after the model’s head had passed over the damselfish. Based on 330 model presentations distributed equally among presentation types. *LV* large vertical, *LH* large horizontal, *SV* small vertical, *SH* small horizontal, *C* Control

others, subdivided $\chi^2=19.25$, $P<0.0001$; feeding during controls vs. all others, subdivided $\chi^2=19.4$, $P<0.0001$, $df=1$ in either case). Feeding was as likely to occur before as after the trumpetfish had passed overhead, but both approaches and agonistic chases of intruders were more likely to occur after the trumpetfish had passed overhead (approach, $\chi^2=119.6$, $P<0.0001$; chase, $\chi^2=8.272$, $P<0.004$, $df=1$ in both cases; Fig. 4, controls ex-

cluded from before versus after χ^2 analyses to test for responses to threatening stimuli only). A positive, significant relationship existed between approach frequency and damselfish size for large horizontal presentations ($r=0.647$, $P=0.04$, $df=9$). Approaches to other presentation types showed no such significant relationship, in part because approaches to other presentation types were relatively infrequent (Fig. 4).

Habituation. Evidence of habituation to predator models within trials and within sessions was found. Correlation coefficients of response strength as a function of pass number within trials were significant and negative in 6 of 15 categories (5 presentation types with 3 response measures for each type, $P<0.05$). Strongly significant correlations ($P<0.01$) were found for all three response types to controls, and for initial distance and response duration to small horizontal presentations.

Correlation coefficients between reaction strength and pass number within sessions were significant and inverse in 11 of the 33 possible cases, indicating a weakening response with progressive passes ($P<0.05$, $df=24-32$; 11 sessions, 3 response measures per session). Weak responses to controls, run last in 7 of 11 sessions, accounted for much of this result; when recalculated without controls, only 5 of 33 coefficients were significant. Controls elicited significantly weaker responses than any other presentation type, including all four sessions when controls were presented other than last (see Table 3).

Discussion

Response strength as a function of model characteristics: threat-sensitivity

If threespot damselfish responded in accord with the Threat-sensitivity hypothesis, response strength should have diminished in the presentation order: large vertical > large horizontal \geq small vertical > small horizontal > control. This predicted overall ranking was generally supported (Table 2, 3; Fig. 2). Strong threats elicited strong responses, intermediate threats elicited intermediate responses, and weak threats elicited weak responses. Large trumpetfish that were oriented vertically were most threatening. Large trumpetfish oriented horizontally were apparently slightly more threatening than small vertical models. Weak discrimination between large horizontal and small vertical presentations may indicate that a large predator that is searching is as threatening as a smaller

predator that is attacking. Small horizontal presentations and finally controls were the least threatening. Overall, damselfish were sensitive to model presentations in a manner that reflected the magnitude of the predatory threat they apparently perceived.

It is difficult to separate the relative influences of trumpetfish size and orientation since both appeared to influence the strength of avoidance responses. Fairly clear discrimination between large and small trumpetfish existed for all responses, although model orientation was not as clearly discriminated. Vertical passes evoked significantly stronger responses than horizontal passes with respect to maximum response, as would be expected if vertically-oriented trumpetfish represented predators poised to strike. No difference was seen with respect to response duration or initial reaction distance. Response duration is primarily a measure of a damselfish' reaction after the model passes overhead. Since trumpetfish seldom return quickly to a prey locale once past, discrimination between receding horizontal and vertical models may not be important. Lack of difference in initial reaction distance to horizontally versus vertically oriented models may reflect a general level of vigilance on the part of the damselfish. Threat-sensitivity would predict an initial albeit weak response – such as orientation – whenever a potential predator appeared. Assessment of the threat then leads to additional avoidance or no further response, dependent on the degree of threat posed.

Although vertical orientation was an obvious component in the response of damselfish, another important aspect of predator orientation may have been whether or not the head of the trumpetfish was facing the damselfish. Trumpetfish will strike at benthic prey from the horizontal mode, but to do so they must swim closer to the substrate than normal. Preliminary trials varying the height of models indicated that horizontal trumpetfish that were passed lower than the standard 25 cm elicited a stronger response than did models passed higher up. Models held above a damselfish and rotated from horizontal to vertical and back to horizontal elicited a response that increased and decreased as the snout was pointed towards or away from the damselfish (distance from the damselfish was not held constant in these trials and so cannot be discounted as influential). In other studies of predator evasion in fishes, both snout orientation and face recognition were influential. Sticklebacks fed at greater distances from a predatory cichlid fish when the predator was facing toward rather than away from the stickleback (Milinski 1986). An-

other damselfish, *Chromis caeruleus*, showed strongest avoidance of models with the facial characteristics of predators than of non-predators (Karplus et al. 1982).

Changes in avoidance with immediate changes in threat

Threat-sensitivity predicts that a prey individual will adjust its behavior during an encounter with a predator, showing stronger responses as the predator escalates its attack (e.g. Magurran and Pitcher 1987). Threat from the predator model presumably increased as the model was brought closer to the damselfish during a presentation. During presentations, later responses were stronger than initial responses (Fig. 3), suggesting that damselfish increase their avoidance responses as the degree of threat increases. In addition, non-avoidance responses (chases and approaches, Fig. 4) occurred more often after the trumpetfish had passed over the damselfish, suggesting a decrease in response strength once threat began to wane.

Effects of damselfish size

Response strength increased with decreasing damselfish size for horizontal but not for vertical presentations (Table 5). The difference is attributable to uniformly strong responses by all sizes of damselfish to vertically-oriented predators, but to a gradient of responses across damselfish size classes to horizontally-oriented predators. Predator orientation is an important indicator of the phase of the predation cycle (Curio 1976) that a predator has entered. Small damselfish are vulnerable to a broader range of predators and should therefore show stronger avoidance behavior than larger individuals, regardless of predator orientation. Horizontal trumpetfish are searching but not necessarily attacking, hence larger damselfish can be less attentive or engage in weaker avoidance reactions to horizontally moving trumpetfish than can smaller damselfish. Vertical orientation in a mobile trumpetfish is often an immediate precursor to attack; sensitivity to such behavior could be a prudent response for any damselfish, regardless of size.

Nonavoidance responses

Nonavoidance responses were less frequent than avoidance responses, but also showed some threat-sensitivity (Fig. 4). Feeding, the most common nonavoidance activity, occurred significantly more

often during control passes than during all other presentation types, indicating a depression in feeding during presentations of threatening models. In addition, many damselfish fed between passes but ceased feeding when initiating a response to a trumpetfish model. Rather than indicating threat-sensitivity, cessation of feeding in the presence of a predator suggests that vigilance and foraging are incompatible, and that different levels of foraging activity do not occur in response to differing degrees of threat (e.g. Holbrook and Schmitt 1988). Such behavior would be expected if feeding and predator avoidance represent conflicting demands and animals sacrifice time spent foraging to avoid predators (see Fraser and Huntingford 1986; Dill 1987; Gilliam and Fraser 1987; Sih 1987 for reviews).

Agonistic attacks on neighbors were distributed evenly among presentation types. However, such attacks did occur significantly more often after the head of the trumpetfish model had passed over the damselfish, suggesting that damselfish did not direct their attention away from a potential predator until the threat had diminished substantially. Again, this result may be interpreted as a territory holder sacrificing time normally devoted to other activities to monitor the threat posed by a potential predator. Possible depression in attack frequency during passes cannot be tested without baseline information on attack rates of the same damselfish during the period immediately preceding presentations.

Approaches toward the trumpetfish model are difficult to interpret. Damselfishes defend their territories vigorously against a variety of intruders; piscivores are approached and attacked, but less frequently than potential competitors or egg predators (e.g. Robertson et al. 1976; Ebersole 1977). Approaches might represent "predator inspection behaviour" (Magurran 1986; Pitcher et al. 1986), whereby prey individuals swim toward an approaching predator, presumably to assess the degree of threat or to inform the predator that it has been seen (e.g. Woodland et al. 1980; Krebs and Dawkins 1984; Magurran 1986). However, only 3 of 43 approaches occurred as the trumpetfish model was moving toward the damselfish, which essentially negates either suggested function. An alternative is that such approaches were truly agonistic, as is frequently observed during interactions between damselfish and trumpetfish in the field. Such agonism may be analogous to mobbing behavior and may serve to drive predators from an area and increase the interval between predatory bouts (Curio 1978; Donaldson 1984; Ishihara

1987). During field observations, trumpetfish usually fled from the approaching or attacking damselfish. Threespot damselfish also defend their territories vigorously against divers and can occasionally break the skin of a diver. Presumably, trumpetfish flee from an attacking damselfish to avoid injury.

Combining information on the relative frequency of approaches to different presentation types and the direct relationship between damselfish size and approach frequency highlights a potentially interesting aspect of damselfish-trumpetfish interactions. Agonistic attacks are apparently concentrated on large trumpetfish by large damselfish. Assuming trumpetfish are gape-limited, as are most predatory fishes, and only attack prey small enough to swallow (e.g. Helfman and Clark 1986), it is possible that damselfish attack predators that are marginally too small to eat them. Agonistic attacks might therefore serve to inform the predator that it is too small to swallow the damselfish. If this interpretation is correct, agonistic attacks are influenced by the size ratio between predator and prey and should occur over a fairly narrow range of size ratios. Small damselfish should attack smaller trumpetfish than do large damselfish, at least trumpetfish just small enough to be incapable of swallowing the damselfish. Attacks on very small trumpetfish would serve little function as they pose no real threat. Future research along these lines should concentrate on a wider variety of model sizes and a larger number of trials to dissect out a possible size ratio effect during interactions.

Habituation

Damselfish showed little habituation to the more threatening presentation types. Most habituation occurred during control presentations, regardless of when in a session they were presented. Selective habituation, shown here as reduced responses to less threatening stimuli, would be a predictable result of threat-sensitivity (see also Magurran and Girling 1986).

Threat-sensitivity in other species

Although the specific predictions of the Threat-sensitivity hypothesis have not been tested previously, earlier investigations of predator avoidance obtained results suggesting that threat-sensitivity may be widespread. Crayfish (*Orconectes propinquus*) showed differences in time spent in a variety of activities among size classes and between

sexes that varied as a function of liability to predation by fish, with more vulnerable juveniles and females showing relatively suppressed activity (Stein and Magnuson 1976). The copepod *Diaptomus gatunensis* also demonstrated an ontogenetic difference in strength of vertical migration that corresponded to vulnerability to fish predation, whereas the cladoceran (*Daphnia galeata mendotae*) showed a population response in terms of where in the water column it was found relative to light levels and fish foraging abilities (Zaret and Suffern 1976). Among instars of the aquatic insect *Notonecta hoffmanni*, degree of predator avoidance (in terms of differences in the use of space and in movement patterns) correlated with risk of predation, resulting in reduced feeding rates for more vulnerable stages (Sih 1982). Predator avoidance in nest-guarding male threespine sticklebacks *Gasterosteus aculeatus* correlated with vulnerability of the offspring in the nest. Males with eggs returned more quickly to the nest following simulated bird disturbance than did males with less vulnerable fry; males with empty nests returned the slowest (FitzGerald and van Havre 1985). The escape response of the whelk *Buccinum undatum* increased in strength in response to more concentrated chemical extracts from a starfish predator (Harvey et al. 1987). Shoals of the minnow *Phoxinus phoxinus* changed among a dozen evasion behaviors in a progressive fashion that reflected degree of escalation of attack by a predatory pike (Magurran and Pitcher 1987). Finally, Fraser and Huntingford (1986) referred to threespine sticklebacks as "risk-adjustors" because they reduced the time spent foraging as a function of number of predatory trout present. "Risk-adjustment" is an appropriate, descriptive term for the behavioral phenomenon in question but is replaced here with "threat-sensitivity" to avoid confusion with the now-conventional use of "risk" as a descriptor of levels of variance in food rewards that different types of foragers will accept (e.g. Caraco et al. 1980; see Edmunds 1974; Magurran and Girling 1986; Dill 1987; Sih 1987 for other cases of threat-sensitivity).

From this brief summary, it appears that threat-sensitivity can occur as differences in predator avoidance among animals that differ in vulnerability due to ontogenetic, sexual, parental, group, and population characteristics. Largely lacking from previous studies is analysis of changes in the behavior of individual prey animals over the course of a predatory bout, particularly where changes in the behavior of the predator constitute varying degrees of threat. In its preliminary formulation, the Threat-sensitivity hypothesis predicts that prey

animals will balance predator avoidance against other fitness-influencing activities, and will show a graded response that reflects the magnitude of the predatory threat. The present, initial findings, as well as results from studies of other species, are in accord with these general predictions.

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