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Odd fish abandon mixed-species groups when threatened

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Summary. In a field experiment, two juvenile size classes of striped parrotfish (*Scarus iserti*), stoplight parrotfish (*Sparisoma viride*), and ocean surgeonfish (*Acanthurus bahianus*) were threatened by a model of a common predator (the trumpetfish, *Aulostomus maculatus*) while alone and in mixed-species groups of 3–100 members. Striped parrotfish, which usually constitute the majority of a group, used the groups for protection. Stoplight parrotfish, present in very low numbers, hid in the coral. Individuals of both species left a group sooner if it had fewer conspecifics. Small surgeonfish sought protection in groups, while larger individuals, too big to be consumed by the trumpetfish, swam away alone. These results may be explained by differences in the protection derived from mixed-species groups, and particularly, by the high predation risk suffered by odd individuals.

Introduction

Predator avoidance is considered a major force promoting formation of groups in vertebrates (reviewed in Morse 1977, 1980; Bertram 1978; Hobson 1978). Compared to solitary individuals, groups detect predators earlier (Powell 1974; Siegfried and Underhill 1975) and attacks directed at groups are less successful (Neill and Cullen 1974; Kenward 1978; Major 1978). Each member has a lower risk of capture as one of many possible prey (Hamilton 1971), provided that all individuals appear similar to the predator (Hobson 1969, 1978). Sometimes individuals that belong to rare or minority species are overlooked by predators with a search image for more common prey (Krebs 1978). Often, however, when an animal in a group differs in some way from most others, this odd individual has a greater predation risk (Hobson 1969; Mueller 1971, 1975; Milinski 1977; Ohguchi 1978). Thus, although membership in mixed-species groups connotes improved protection (Ehrlich and Ehrlich 1973; Alevizon 1976; Buskirk 1976; reviewed in Morse 1977), participants with few conspecific members might suffer a disproportionately high risk of predation (Hobson 1963; Mueller 1977; Barnard 1979). For these minority individuals, protection may improve as number of conspecifics increases and oddity declines (Mueller 1977). The present study reports supporting evidence: in a field experiment, coral reef fish abandoned mixed groups when threatened, leaving sooner if a group had fewer conspecific members.

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Methods

Study site and population. Experiments were conducted in a shallow (3–5 m) back-reef area at Buck Island (BI) National Monument, St. Croix, US Virgin Islands. The densely-branched coral *Acropora prolifera* dominates the area, with interspersed patches of sand and rubble. Because the BI reef is legally protected, natural predators are abundant and fishes are accustomed to SCUBA divers. Foraging groups of juvenile parrotfishes (*Scarus iserti* [formerly *croicensis*], *Sparisoma atomarium, S. aurofrenatum, S. radians, S. viride*), young surgeonfish (*Acanthurus bahianus*), and various wrasses (*Halichoeres bivittatus, Halichoeres maculipinna, Thalassoma bifasciatum*) are a prominent feature of the area. The groups are in constant flux, changing in size and species composition as fishes join or depart (Wolf 1983; see also Itzkowitz 1977).

Experimental procedure. I used a model of the trumpetfish (*Aulostomus maculatus*), a diurnal predator common to the area, to threaten juvenile striped parrotfish (*Scarus iserti*), stoplight parrotfish (*Sparisoma viride*), and ocean surgeonfish (*Acanthurus bahianus*). The model was made by preserving a 43 cm (stan-

Table 1. a Number of focal individuals tested with a trumpetfish or grunt model while alone or in mixed-species groups of different sizes. **b** Typical proportion of each species in the groups studied

a

Group size	Trumpetfish model			Grunt model
	Scarus iserti	*Sparisoma viride*	*Acanthurus bahianus*	*Sparisoma viride*
1	10	20	20	20
3–9	12	14	13	10
10–19	12	8	9	10
20–39	9	11	6	8
40–59	9	8	10	12
60–100	2	1	4	0
Total	54	62	62	60

b

Group size	Mean percentage of members					No. of groups
	Scarus iserti	*Sparisoma viride*	Other species of *Sparisoma*	*Acanthurus bahianus*	Other species	
3–9	29	29	12	23	7	49
10–19	52	15	10	19	4	39
20–39	78	7	5	8	2	34
40–59	75	6	5	8	6	39
60–100	70	3	5	8	14	7

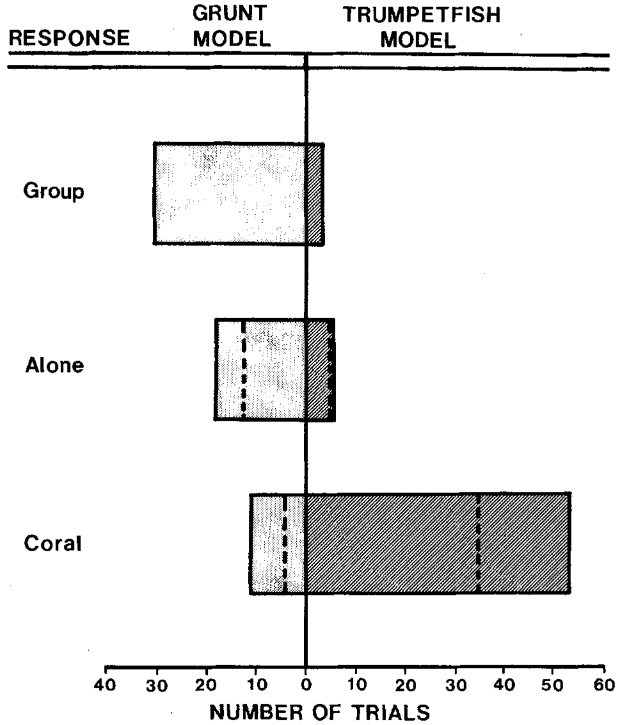

Fig. 1. Absolute frequency of different responses of *Sparisoma viride* to predator (trumpetfish) and control (grunt) models. *Group* includes fish that stayed with their original group, solitary fish that joined a group, and fish that left their original group to join another, larger one. *Alone* includes fish that left their group to swim alone, and solitary fish that swam away alone. *Coral* includes fish that left a group to hide in the coral, and solitary fish that entered the coral. The broken lines indicate values for only the fish that left a group. Responses to the two models are significantly different ($G = 33.83$, 2 *df*, $P < 0.001$)

dard length) trumpetfish in formalin and coating it with a thin layer of fiberglass (Helfman 1983). When fastened to the end of a 1 m rod of transparent plexiglass, the model could be moved in a lifelike manner by a diver. Because of time constraints and a large barracuda that repeatedly attacked the models, I used a control model (the non-piscivorous French grunt, *Haemulon flavolineatum*) only in trials testing stoplight parrotfish. In these control trials, however, I was able to note the behavior of striped parrotfish and ocean surgeonfish in the groups.

For each prey species, two size classes of individuals were tested while alone or in groups of 3–100 members (Table 1). The lengths of the small and medium parrotfishes were 25–40 mm and 60–75 mm respectively; for the surgeonfish, these values were 25–30 mm and 60–75 mm. In each trial, while holding a plexiglass rod and model behind me, I approached within approximately 2 m of a randomly-chosen focal individual. I estimated its standard length by comparison with freely-swimming tagged individuals of known size (Wolf 1983), noted its species, and recorded the size and species composition of its group. The trumpetfish model was then presented in a vertical, head-down, stalking position. In control trials, the grunt model was presented in a normal swimming position. Fleeing fish were pursued for 20 s and the response of the focal individual was recorded. To prevent fish from habituating to the models, I moved to different areas in the study site between trials, and never presented a model to the same group twice.

Results were analyzed using tests described in Sokal and Rohlf (1981): an approximate t-test that allows unequal variances (two-sample t-test in Minitab statistical package), the Mann-Whitney U-test, the G-test for contingency tables (using log-likelihood ratios), and stepdown multiple regression. Parametric tests were used only when assumptions of normality were met.

Results

Trial results indicate that fish responded to characteristics of the models and not to the diver manipulating them. In preliminary studies, fish behaved normally in the presence of a diver and no model. Although stoplight parrotfish continued to forage and swim normally when approached by the control model, they stopped foraging and usually hid in the coral when threatened by the predator (Fig. 1). In the presence of the control model, stoplight parrotfish in groups were equally likely to continue foraging in the group or to leave it to forage elsewhere ($G = 2.49$, 1 *df*, $P > 0.05$), but far more likely to stop foraging and abandon the

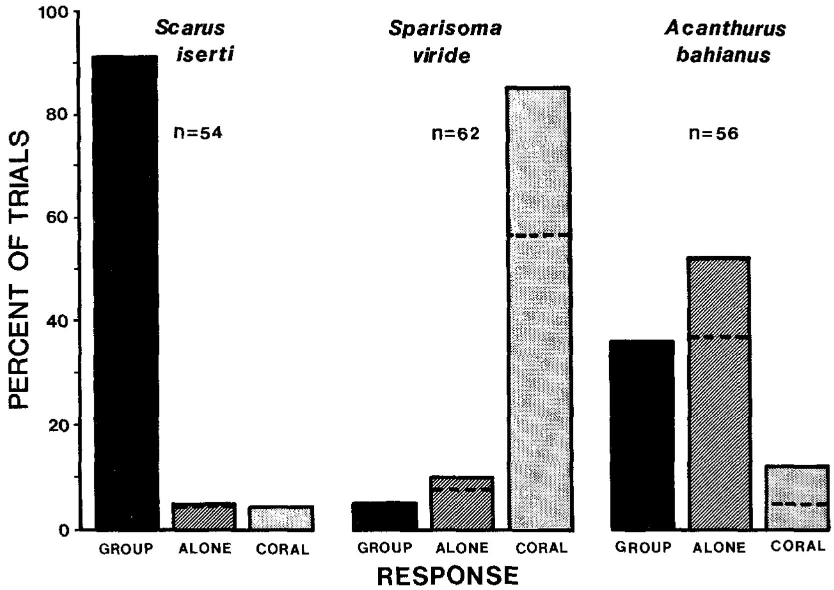

Fig. 2. Relative frequency of different responses of each species to a trumpetfish (predator) model. Response categories as in Fig 1. *Acanthurus* whose groups dispersed are not included (see text)

group when the trumpetfish was present (G= 48.20, 1 *df*, $P<0.001$). Striped parrotfish and surgeonfish in the groups approached by the control model appeared to continue their normal foraging activities.

The three prey species differed significantly in their response to the predator model (Fig. 2; G= 103.53, 4 *df*, $P<0.001$). Striped parrotfish associated with groups when threatened, stoplight parrotfish hid in coral, and surgeonfish had a more varied response. Focal individuals could be classified as either (a) seeking protection in groups (solitary fish that joined other fish, fish that remained in a group, and fish that left a group to join a larger group), or (b) not using groups for protection (solitary fish that did not join nearby groups, fish that left a group to swim alone or hide in the coral). Fish that abandoned a group usually did so early in a trial, although timing was related to group size and species composition, and will be discussed later. Individuals left to join a larger group only if it were very near the original group. Because groups were foraging over coral at the beginning of each trial, fish that left a group to hide in the coral were able to dart directly into a shelter site without increasing their exposure to the predator.

Parrotfish behavior was independent of body size (Fig. 3a, b), but the behavior of surgeonfish was not (Fig. 3c). Small surgeonfish generally avoided the predator in groups while larger individuals swam away alone. On the few occasions when small surgeonfish left groups, their departures were different from those of the other fishes tested. They attempted to stay with the fleeing

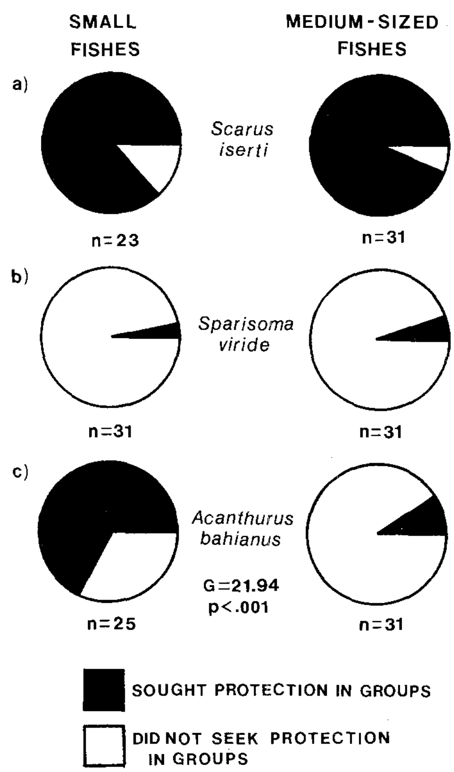

Fig. 3. Proportion of small and medium fishes using groups for protection when threatened. Small *Scarus iserti* and *Sparisoma viride* were 2.5–4 cm; medium sized individuals of these species were 6–7.5 cm. Small and medium sized *A. bahianus* were 2.5–3 cm and 6–7.5 cm respectively. All lengths are estimated standard lengths. Shaded areas include fish that associated with groups to avoid a predator model (*Group* response of Fig. 1. Individuals that did not associate with groups when threatened (*Alone* and *Coral* responses of Fig. 1) are included in the unshaded areas. A G-test indicates no significant interaction between size of individual and use of groups for protection by *Scarus* or *Sparisoma*, but these tests must be viewed with caution because of low expected values

Table 2. Relationship between time with group, and group size and species composition. Results are from stepdown multiple regression. Examination of residuals indicated that no transformations were necessary. No significant relationships were found for *Acanthurus bahianus*

	R^2	F	P
Scarus iserti			
Time = 2.12 + 0.54W	0.58	7.00	< 0.05
W = number of *Scarus* individuals in group			
Time = 4.80 + 0.516X–4.08Y	0.94	24.94	< 0.02
X = group size			
Y = number of *Sparisoma* individuals in group			
Sparisoma viride			
Time = 1.60 + 1.07Z	0.15	6.93	< 0.01
Z = number of *Sparisoma viride* in group			

group, but appeared unable to keep pace with the other members.

Parrotfish responses to the predator were related to group size and species composition, aspects that may influence vulnerability. Groups abandoned by striped parrotfish were smaller than those used for protection ($t = 2.049$, 11 *df*, $p < 0.05$) by about 50%. Most had fewer than 20 members and thus contained a low percentage of striped parrotfish (Table 1b). The tendency of striped parrotfish to remain with a group was positively related to group size while it was negatively related to the number of members in the genus *Sparisoma* (Table 2). Time with group was also positively related to the number of conspecific members. However, number of striped parrotfish was highly correlated with group size ($r = 0.99$), and group size yielded a better fit in the regression. Stoplight parrotfish remained longer in groups with more conspecifics (Table 2). No significant factors were found for small and medium-sized surgeonfish.

In 6 trials, mixed-species groups containing small focal surgeonfish dispersed when threatened, leaving the surgeonfish without a group in which to hide. Each unit had 10 or fewer members, was significantly smaller than groups that did not disperse ($t = -5.04$, 14 *df*, $P < 0.001$), and contained a significantly higher proportion of *Sparisoma* than did non-dispersing groups (Mann-Whitney *U*-test, $p < 0.05$).

Discussion

The general belief that predator avoidance promotes group formation (Morse 1977, 1980; Bertram 1978; Hobson 1978; Shaw 1978; Keenleyside 1979; Schaik 1983; Helfman 1984) is supported by the behavior of threatened groups at Buck Islands (which ceased feeding, tightened ranks, fled, and occasionally merged with other groups), by the strong tendency of striped parrotfish and small surgeonfish to associate with a group in the presence of a predator model, and by the tendency of individuals to stay longer in groups that are larger or have more conspecifics, which presumably confer more protection. Other studies report similar results: in the presence of a simulated or live predator, some fishes form schools (Breder and Halpern 1946; Girsa 1973) while others, already in schools, reduce their 'nearest neighbor' distance (Potts 1970; Rüppell and Gosswein 1972; Radakov 1973; Major 1977). Birds, too, increase group size when a predator is present (Caraco et al. 1980).

A contrary result from the present study is that individuals of some species abandoned groups when threatened (Fig. 2). This paradox may occur because the protective merits of mixed groups differ among species and individuals. Of all the fishes tested, medium-sized surgeonfish would be least susceptible to predation by a large trumpetfish the size of the model. Because their deep bodies and larger size would prevent them from fitting easily into the predator's mouth, they would not need the protection of a group. Larger predators, however, might elicit a different response (Potts 1981).

Distinctive coloration and low numbers (no group had more than 5) make juvenile stoplight parrotfish odd and vulnerable in groups. Their intraspecific agonism may increase risk in a group by attracting the attention of a predator (McFarland and Hillis 1982) and/or limiting the number of conspecific members (Wolf 1983). This species uses the reef, rather than groups, for protection. A small home range (Wolf 1983) and close association with the substrate (Barlow 1975) presumably allow familiarity with safe hiding places.

In contrast to stoplight parrotfish, juvenile striped parrotfish often numerically dominate mixed groups (Table 1b; Itzkowitz 1974; Wolf 1983). Their tendency to roam over large areas (Ogden and Buckman 1973; Itzkowitz 1977; Wolf 1983) may limit familiarity with available shelter sites and, as in pelagic fishes, lead to schooling as a form of cover-seeking (Williams 1964).

Thus, the various species differ in their tactics for avoiding predators, while behavioral flexibility allows individuals to tailor these responses as needed. Perhaps, for example, a threshold number of conspecific members is needed before an individual will remain with a group when threatened. Agonistic species, such as stoplight parrotfish, might rarely reach these thresholds, while more sociable species, such as the striped parrotfish, may frequently exceed them. In any particular group, however, individuals of each species behave according to the number of conspecifics actually present.

These results suggest that an individual is at higher risk in groups with fewer conspecific members, and consequently raise the question: why does a potentially odd individual join groups? Studies of single-species and mixed groups suggest many possible benefits of membership. In a group, this individual may detect approaching predators earlier (Powell 1974; Siegfried and Underhill 1975; Lazarus 1979), be less timid in its search for food (Magurran and Pitcher 1983), devote more time to feeding and less time to surveillance (Powell 1974; Berger 1978; Caraco 1979; Barnard 1980; Lipetz and Bekoff 1982), and/or derive other feeding benefits (Robertson et al. 1976; Pitcher et al. 1982). When a predator has been detected, however, such an individual might increase its chance of escape by leaving the group, where it would be the likely target if it remained, and concealing itself in the available shelter (Eshel 1978). Such a tactic would be most appropriate when the abandoning individual could hide immediately, avoiding a prolonged search for shelter that might increase exposure to the predator. The departure might provide an early warning of alarm for remaining group members (Thompson and Barnard 1983), but also may increase their risk by reducing group size (e.g., trials with small surgeonfish) and by removing a more vulnerable target (Eshel 1978). This could be advantageous to the abandoning individual because a predator presented with the remaining members as alternative prey might be less likely to search for the one that departed (Helfman 1978). Thus, odd individuals may derive antipredator benefits from mixed groups despite the oddity effect, if alternative sources of cover are easily accessible.

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References

Alevizon WS (1976) Mixed schooling and its possible significance in a tropical western Atlantic parrotfish and surgeonfish. Copeia 1976:796–798

Barlow GW (1975) On the sociobiology of four Puerto Rican parrotfishes (Scaridae). Mar Biol 33:281–293

Barnard CJ (1979) Predation and the evolution of social mimicry in birds. Am Nat 113:613–618

Barnard CJ (1980) Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). Anim Behav 28:295–309

Berger J (1978) Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. Behav Ecol Sociobiol 4:91–99

Bertram BCR (1978) Living in groups. In: Krebs JR, Davis NB (eds) Behavioural ecology: an evolutionary approach, 1st edn. Blackwell, Oxford, pp 64–96

Breder CM, Halpern F (1946) Innate and acquired behavior affecting aggregations of fishes. Physiol Zool 19:154–190

Buskirk WH (1976) Social systems in a tropical forest avifauna. Am Nat 110:293–310

Caraco T (1979) Time budgeting and group size: a test of theory. Ecology 60:618–627

Caraco T, Martindale S, Pulliam HR (1980) Avian flocking in the presence of a predator. Nature 285:400–401

Ehrlich P, Ehrlich A (1973) Coevolution: heterotypic schooling in Caribbean reef fishes. Am Nat 107:157–160

Eshel I (1978) On a prey-predator nonzero-sum game and the evolution of gregarious behavior of evasive prey. Am Nat 112:787–795

Girsa II (1973) Alteration in the behavior and vertical distribution of certain juvenile cyprinids in relation to illumination intensity and the presence of a predator. J Ichthyol 13:449–454

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Helfman GS (1978) Patterns of community structure in fishes: summary and overview. Environ Biol Fish 3:129–148

Helfman GS (1983) Resin-coated fishes: a simple model technique for in situ studies of fish behavior. Copeia 1983:547–549

Helfman GS (1984) School fidelity in fishes: the yellow perch pattern. Anim Behav 32:663–672

Hobson ES (1963) Selective feeding by the gafftopsail pompano, *Trachinotus rhodopus* (Gill), in mixed schools of herring and anchovies in the Gulf of California. Copeia 1963:595–596

Hobson ES (1969) Possible advantages to the blenny *Renula azalea* in aggregating with the wrasse *Thalassoma lucasanum* in the tropical eastern Pacific. Copeia 1969:191–193

Hobson ES (1978) Aggregating as a defense against predators in aquatic and terrestrial environments. In: Reese ES, Lighter FJ (eds) Contrasts in behavior. Wiley, New York, pp 219–234

Itzkowitz M (1974) Behavioural reconnaissance of some Jamaican reef fishes. Zool J Linn Soc 55:87–118

Itzkowitz M (1977) Social dynamics of mixed-species groups of Jamaican reef fishes. Behav Ecol Sociobiol 2:361–384

Keenleyside MHA (1979) Diversity and adaptation in fish behaviour. Springer, Berlin Heidelberg New York

Kenward RE (1978) Hawks and doves: attack success and selection in goshawk flights at wood pigeons. J Anim Ecol 47:449–460

Krebs JR (1978) Optimal foraging: decision rules for predators. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 1st edn. Blackwell, Oxford, pp 23–63

Lazarus J (1979) The early warning function of flocking in birds: an experimental study with captive quelea. Anim Behav 27:855–865
Lipetz VE, Bekoff M (1982) Group size and vigilance in pronghorns. Z Tierpsychol 58:203–216
McFarland WN, Hillis ZM (1982) Observations on agonistic behavior between members of juvenile French and white grunts – Family Haemulidae. Bull Mar Sci 32:255–268
Magurran AE, Pitcher TJ (1983) Foraging, timidity, and shoal size in minnows and goldfish. Behav Ecol Sociobiol 12:147–152
Major PF (1977) Predator-prey interactions in schooling fishes during periods of twilight: a study of the silverside *Pranesus insularum* in Hawaii. Fish Bull 75:415–426
Major PF (1978) Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. Anim Behav 26:760–777
Milinski M (1977) Experiments on the selection by predators against spatial oddity of their prey. Z Tierpsychol 43:311–325
Morse DH (1977) Feeding behavior and predator avoidance in heterospecific groups. BioScience 27:332–339
Morse DH (1980) Behavioral mechanisms in ecology. Harvard University Press, Cambridge, Mass
Mueller HC (1971) Oddity and specific searching image more important than conspicuousness in prey selection. Nature 233:345–346
Mueller HC (1975) Hawks select odd prey. Science 188:953–954
Mueller HC (1977) Prey selection in the American kestrel: experiments with two species of prey. Am Nat 111:25–29
Neill SR, Cullen JM (1974) Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. J Zool (Lond) 172:549–569
Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54:589–596
Ohguchi O (1978) Experiments on the selection against colour oddity of water fleas by three-spined sticklebacks. Z Tierpsychol 47:254–267
Pitcher TJ, Magurran AE, Winfield IJ (1982) Fish in larger shoals find food faster. Behav Ecol Sociobiol 10:149–151
Potts GW (1970) The schooling ethology of *Lutianus monostigma* (Pisces) in the shallow reef environment of Aldabra. J Zool (Lond) 161:223–235
Potts GW (1981) Behavioural interactions between the Carangidae (Pisces) and their prey on the fore-reef slope of Aldabra, with notes on other predators. J Zool (Lond) 195:385–404
Powell GVN (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim Behav 2:501–505
Radakov DV (1973) Schooling in the ecology of fish. Israel Program for Scientific Translation, Ltd., translated by Mill H. Halsted Press, New York
Robertson DR, Sweatman HP, Fletcher EA, Cleland MG (1976) Schooling as a mechanism for circumventing the territoriality of competitors. Ecology 57:1028–1220
Rüppell G, Gosswein E (1972) Die Schwärme von *Leucaspius delineatus* (Cyprinidae, Teleostei) bei Gefahr in Hellen und im Dunkeln. Z Vergl Physiol 76:333–340
Schaik CP van (1983) Why are diurnal primates living in groups? Behaviour 87:120–144
Shaw E (1978) Schooling fishes. Am Sci 66:166–175
Siegfried WR, Underhill LG (1975) Flocking as an anti-predator strategy in doves. Anim Behav 23:504–508
Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, San Francisco
Thompson DBA, Barnard CJ (1983) Anti-predator responses in mixed-species associations of lapwings, golden plovers and black-headed gulls. Anim Behav 31:585–593
Williams GC (1964) Measurement of consociation among fishes and comments on the evolution of schooling. Publ Mus Mich State Univ 2:349–384
Wolf NG (1983) Behavioral ecology of herbivorous fishes in mixed-species groups. PhD dissertation, Cornell University, Ithaca, NY