Environmental Biology of Fishes (2005) 73:163–170
DOI 10.1007/s10641-004-5561-y

The effect of community on the territorial behavior of the threespot damselfish

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Received 18 February 2004 Accepted 10 October 2004

Key words: coral reefs, ecological complexity, *Stegastes planifrons*

Synopsis

I examined the hypothesis that animals alter their behavior in response to changes at the community scale of organization, rather than simply reacting to a sequential set of independent interactions with other organisms. The focal species was the threespot damselfish, *Stegastes planifrons,* a territorial coral reef fish that experiences a high degree of variation in community composition. Field observations of individual threespot damselfish showed a significant increase in the amount of time spent on active territorial defense when the community contained greater proportions of food competitors. Territorial behavior also increased concurrently with higher species diversity in the community. However, no behavioral change was observed in response to the total number of fish entering the defended territory, suggesting that threespot damselfish are responding to more complex environmental cues associated with community structure rather than simple density.

Introduction

Very little is known about the way community influences behavior. Animals clearly alter their behavior in response to encounters with other individual organisms, and although interactions between two individuals are relatively predictable in isolation, observation suggests that behavior patterns are also simultaneously influenced by other organisms in their environment. This is seen, for instance, in predator-prey interactions (e.g., Milinski et al. 1990; Mauck & Harkless 2001), foraging strategies (Rubenstein et al. 1977, Vahlburg 1992), and territorial defense (Foster 1985). Such variation in behavioral interactions suggests that animals respond to cues from larger scales of organization, and yet we know little about the composite effect of the community (i.e., the community acting as a discrete unit) on the behavior of the animals inhabiting it. This study represents an initial effort to examine whether the non-additive, emergent properties of the community influence the general behavior patterns exhibited by an individual in a way that would not be predicted by the sum of its encounters with other organisms.

The focal species I used to address this question was the threespot damselfish, *Stegastes planifrons*, a coral reef-dwelling fish whose behavior patterns have been studied extensively. Threespot damselfish, like many of their congeners, are strongly territorial, defending areas of the reef surface containing algal mats as a food source, shelter sites against predators and, for males, nest sites for demersal egg masses (Myrberg & Thresher 1974, Thresher 1976, Robertson et al. 1981). The level of territorial defense exhibited by threespot damselfish toward another individual is species-specific, such that those species representing a greater potential competitive threat to the defended resources elicit more aggressive responses at larger distances from the center of the territory (Myrberg & Thresher 1974, Thresher 1976, Ebersole 1977, Harrington & Losey 1990, Itzkowitz 1990). Three characteristics in particular make the threespot damselfish an ideal species for examining the influence of the community on behavior. First, their primary habitat provides a dynamic community structure with an abundance of species, such that any one individual may encounter extreme variation in the density and identity of species in its territory. Second, their ability to distinguish among species and their relative competitive impact on the territory holder suggests that this species may respond to more subtle variation in community structure, rather than simply overall fish density. Lastly, their territorial nature, provides an opportunity for discrete observation of individuals in a limited space, while also acting as a mechanism for identifying individuals without the need for tagging or otherwise disrupting normal community conditions.

The objective of this study was to test the hypothesis that the threespot damselfish alters its territorial defensive behavior in response to changes at the level of the community. I identified three parameters as representative of the community: (1) number of fish in the community, irrespective of species, (2) total number of species, and (3) percentage of the community presenting a high potential competitive impact on the food resources of the threespot damselfish. If damselfish respond to changes at the community scale, then changes in the proportion of competitors in the community were expected to elicit a clear modification in the intensity of territorial defense. A greater number of species in the community was also expected to increase territorial defense, as the probability of encountering potential competitors rises. Conversely, an increase in territorial defense in response to sheer number of intruders, regardless of identity, would suggest that the damselfish are not sensitive to community composition and instead simply utilize fish density as a trigger for territorial defense.

Materials and methods

Data collection

I conducted field observations during 1996 and 1997 on a 450 m^2 patch reef approximately 300 m off the west coast of Elbow Cay, Bahamas. The reef ranged in depth from 1.5 to 5 m at high tide, and supported an abundance of fish species, including high densities of threespot damselfish.

I selected focal threespot damselfish territories from all regions of the reef and encompassed the greatest available range in heterospecific density and diversity. The territories of all individuals shared at least two contiguous borders with conspecifics and/or the physical edge of the reef. I mapped the territorial boundaries of each individual during 15 min pre-trial observations, where the maximum distance traveled in any direction was defined as the boundary of the area defended by the individual (unless a territorial display was elicited from a neighboring threespot damselfish, in which case it was assumed that the fish had entered the territory of the other individual). Territory boundaries were noted by existing physical landmarks on the reef. These boundaries served to define the ‘community’ experienced by the focal animal, encompassing all fish that entered the designated space. This method was intended to accurately census those organisms to which the damselfish could respond (Myrberg & Thresher 1974, Thresher 1976), while simultaneously minimizing the possibility of including extraneous fish in the recorded community structure. In addition, the territory location was used to distinguish among individuals, based on the results of previous studies showing that damselfish maintain their territories throughout the year (Thresher 1976, Myrberg et al. 1986). This pre-trial period was also used to identify observation locations of sufficient distance from the territory to avoid influencing the behavior of the fish.

During the observation trials, each focal animal ($N = 20$) was observed for two consecutive observation periods, each 10 min in length, for a total of 20 min. These two periods were separated by a 5 min break, allowing observers to reposition themselves and reducing observational errors due to fatigue. Data were recorded in contiguous 20 s intervals, resulting in a total of 60 observations of each territory holder. Researchers worked in pairs to collect data on (a) behavioral displays and (b) intruder density and identity for each observed subject. Behavioral data were collected using one-zero sampling (Altmann 1974) during each 20 s intervals, recording the presence or absence of each of the following three behavior related to territorial defense: (1) *vigilance* (undirected swimming and hovering at prominent locations within the territory); (2) *chasing* another fish within the territory boundaries; and (3) *hiding* within the structure of the reef. More than one type of behavior could be recorded during each sample interval, but if a behavior occurred more than once during 20 s it was not recorded again.

The community of each focal animal, defined as the number and identity of all fish species observed within the designated territory, was recorded during each 20 s sampling interval. All intruders entering the territory at any point during the sampling interval were recorded, and those fish present for longer than one sample interval were counted for each sample interval present. It was neither feasible nor necessary to census all of the invertebrate species present in each territory and they were not included in the measurements of community structure. No behavioral interactions were observed between the focal species and non-fish inhabitants of the reef, although Williams (1979) reported territorial defense against sea urchins, *Diadema antillarum*.

Data analysis

The frequency of occurrence was calculated for each type of behavior during the observation periods. Defined as the proportion of sample intervals in which the behavior was observed, frequency of occurrence indicated the duration and frequency of each behavior exhibited by an individual. I conducted a principal components analysis to test for a relationship between the frequency of occurrence of the three behavioral categories. If the analysis indicated that the behaviors did not occur independently, then the factor(s) generated from the principle components analysis would be used as a composite variable indicating the overall level of territorial defense exhibited by the individual.

The general density and diversity of each community were characterized by (a) the mean number of fish within the territory during each 20 s interval, regardless of species identity, and (b) the total number of species that entered each territory during the 20 min observation periods. The total number of species in the community, rather than the mean for each interval, was used as it provided a more accurate ecological assessment of the diversity experienced by each territory holder. I conducted a multiple regression analysis (Sokal & Rohlf 1981), regressing the composite territorial behavior estimated by the principle components analysis against these two independent factors. The number of fish in the territory was log transformed to correct for non-linearity of the data. A ridge regression was incorporated into the analysis due to the high level of correlation between the predictor variables, using a tolerance level of 0.01 and lambda of 0.10. The residuals generated from this analysis (hereafter 'PCA residuals') represent the deviation of each individual from the estimated level of territorial defense for a given fish density and diversity in the community.

The potential threat posed by a competitor to the defended food resources of the threespot damselfish varied in accordance with the amount of diet overlap between the two species and the size of the intruder. The value of this threat was quantified as the Potential Competitive Impact (PCI) of each species, as determined by Ebersole (1977):

$$\mathrm{PCI} = \alpha(\nabla_{\mathrm{B}})^{0.75} \tag{1}$$

where α was the amount of food overlap between the damselfish and the competitor based on the based on the diet composition of the two species, and $\nabla_{\mathrm{B}}{}^{0.75}$ was the relative rate of food consumption of the competitor based on its body volume (Table 1) (also see Harrington & Losey 1990, Itzkowitz 1990). For instance, a small fish with little diet overlap with the damselfish would have a PCI value close to zero, while a large benthic algivore may have a PCI greater than the intraspecific value of 1.0. Although this index is not a precise measurement of the amount of resource overlap between two species, it was expected to give a relative value corresponding to the level of competition between the damselfish and an intruder into its territory. Any fish with a PCI value ≥ 1.0 was considered a high competitive threat, as it represented a competitor at least equally as threatening as a conspecific. I calculated the percent of each community that was comprised of these strong competitors, over the entire 20 min observation period, as a measure of the overall competitive pressure on each focal animal. The percentage was then used as an independent variable in a linear regression analysis with the PCA

Table 1. Species present within focal animal territories during the observation periods. The PCI serves as a measure of the relative competitive pressure by each species on threespot damselfish (Ebersole 1977).

Species present	PCI value
Caranax ruber (bar jack)	0.00
Holocentrus ascensionis (squirrelfish)	0.00
Mulloidichthys martinicus (yellow goatfish)	0.00
Seriola dumerili (great amberjack)	0.00
Holocanthus tricolor (rock beauty)	0.07
Conodon nobilis (barred grunt)	0.12
Haemulon flavolineatum (French grunt)	0.12
Haemulon plumieri (white grunt)	0.12
Haemulon sciurus (blue-striped grunt)	0.12
Canthigaster rostrada (sharpnose puffer)	0.14
Chaetodon capistratus (four-eye butterfly)	0.15
Thalassoma bifasciatum (bluehead wrasse)	0.28
Pomacentrus leucostictus (beaugregory)	0.97
Stegastes planifrons (threespot damselfish)	1.00
Halichoeres bivittatus (slippery dick)	1.10
Pomacanthus paru (French angelfish)	2.00*
Scarus coelestinus (midnight parrotfish)	3.40
Scarus coeruleus (blue parrotfish)	3.40
Scarus guacamaia (rainbow parrotfish)	3.40
Sparisoma rubripinne (redfin parrotfish)	3.40
Sparisoma viride (stoplight parrotfish)	3.40
Pomacanthus arcuatus (grey angelfish)	3.50*
Abudefduf saxatilis (sergeant major)	4.85*
Acanthurus bahianus (ocean surgeon)	5.70
Acanthurus chirurgus (doctorfish)	5.70
Acanthurus coeruleus (blue tang)	5.70

(*Determined by author, based on body size and food preferences reported by Randall 1967, Boschung Jr. et al. 1983.)

residuals as the dependent variable. This analysis functioned as a direct measure of the behavioral response to the species composition of the community, having removed the effects of fish diversity and abundance. A positive trend in the analysis would suggest that territory holders encountering a large proportion of strong competitors exhibit a greater than expected level of territorial defense given the number of fish and species in the territory, while a lack of a trend would imply that they are not responding to the species composition within their territory.

Results

Threespot damselfish territories covered the majority of available reef surface at the study site, and the observed territories encompassed both edges and central areas on the physical habitat of the reef. Mean focal territory size was 0.56 m^2 (SD $\pm$ 0.10). All observed individuals were adults, 8–10 cm standard body length; the sex of individuals was not determined. No behavioral changes were observed in response to our presence during the observation periods.

The results of this research support those of previous studies indicating that threespot damselfish maintain their territories throughout the year (Thresher 1976, Myrberg et al. 1986); territorial boundaries remained constant throughout the duration of the study and extended territorial disputes were not observed. Furthermore, the territorial boundaries of the focal animal appeared to function as a reasonable limit of community size; no behavioral interactions occurred outside of the areas identified during pre-trial observations.

In addition to the abundance of threespot damselfish, the study reef was characterized by a high density of other species of reef fish; 17 genera and 26 species were recorded within the focal animal territories during the observations (Table 1). The community structure varied considerably among the focal territories (Table 2), with intruder density changing by more than two orders of magnitude among sites and species diversity varying by a factor of four. The community composition, as a percentage of strong competitors in the community, ranged from 0% to more than 75% among sites.

The results of the principal components analysis (PCA) showed a strong correlation among the three measured behavior variables, with a positive relationship between those associated with active territorial defense (vigilance and chase) and a negative relationship with the non-territorial behavior of hiding. The first component had an eigenvalue of 2.55 and explained 64% of the total variance. The second and third components both had eigenvalues less than 1.0, and were excluded from the analysis based on the Kaiser-Guttman criterion (McGarigal et al. 2000). Because the observed behavior did not occur independently, the data were condensed into the single behavioral score for each focal animal generated by the first component of the PCA; a positive value represents an increased proportion of time spent in active defense of the territory and a negative number denotes a greater proportion of time hiding in the reef.

Table 2. Summary of the variation in community characteristics among observed threespot damselfish territories: mean, standard deviation, minimum and maximum. Intruder density was calculated for each 20 s sampling interval.

Community characteristic	Mean (SID)	Min	Max	*p*-value
Intruder density (20 s^{-1})	4.4 (8.6)	0.2	35	0.18
# Species (20 min^{-1})	7.5 (3.1)	3	13	0.03*
% Strong competitors (20 min^{-1})	23.1 (22.1)	0	77	0.02*

The number of species and percentage of strong competitors in the community were based on the total of each 20 min observation period. Asterisks denote significant predictors on the territorial response of threespot damselfish.

The multiple regression analysis of the behavioral response to (a) the density of fish in each territory and (b) the species diversity was highly significant ($r^2 = 0.52$, df = 2, $p < 0.002$). However, only the species diversity was a significant predictor on the behavioral response ($p = 0.03$, $B = 0.47$), with territorial behavior increasing in response to greater species diversity (Figure 1). The activity level of the focal animals was not significantly correlated to the density of intruders within the territory, once species diversity was accounted for ($p = 0.18$, $B = 0.29$).

The species composition of the community also had a significant effect on the territorial behavior of the threespot damselfish. The PCA residuals increased significantly in response to greater proportions of strong competitors in the community ($r^2 = 0.27$, $p = 0.02$; Figure 2). This implies a greater than expected level of territorial defense as the presence of competitors increased.

Discussion

Animals clearly alter their behavior in response to heterospecifics in their environment. Species-specific responses in communities have not only been recorded in damselfish (Myrberg & Thresher 1974, Thresher 1976, Ebersole 1977, Harrington & Losey 1990), but also in mammals (e.g., Leger et al. 1984), birds (e.g., Rubenstein et al. 1977, Vahlburg 1992), and invertebrates (e.g., Mauck & Harkless 2001). However, little is known about the non-additive effects of multiple species within a community on the behavior of its members.

The results of this study suggest that organisms are capable of altering their behavior patterns in response to cues about the structure and composition of the community. At the most general level, the threespot damselfish does not appear to modify the amount of time allocated to territorial defense simply in response to the number of

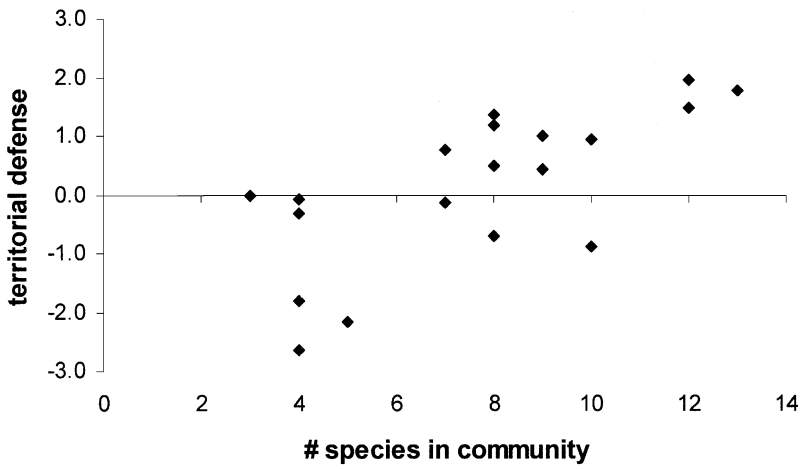

Figure 1. Relationship between the number of species present in the community and the level of territorial activity by the threespot damselfish (multiple regression, (B = 0.47, $p = 0.03$). A higher territorial defense (PCA) score denotes a greater proportion of time devoted to active territorial defense and less time hiding within a shelter.

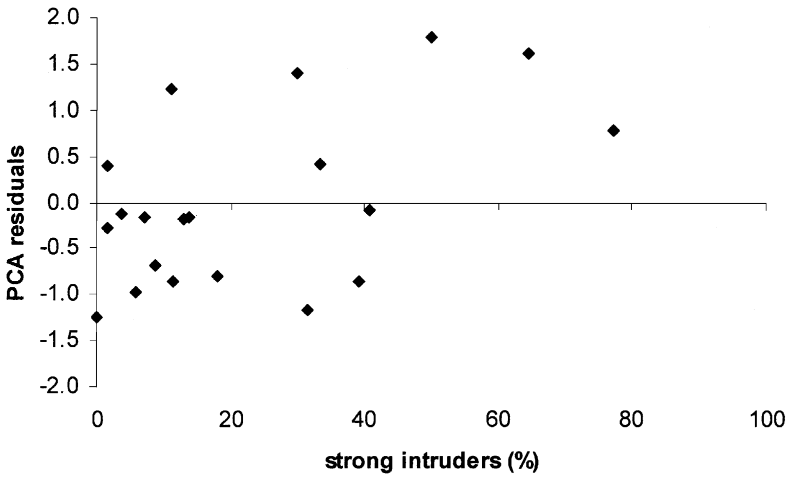

Figure 2. Relationship between the percentage of strong competitors in the community and the PCA residuals by the threespot damselfish. The significant positive trend ($r^2 = 0.27$, $p = 0.02$) suggests that individuals encountering a greater proportion of strong competitors showed a greater than expected level of territorial defense.

individuals encountered – a pattern that would suggest that this species is indiscriminately aggressive to all species entering its territory. Rather, my observations reinforced the results of previous research (Myrberg & Thresher 1974, Thresher 1976, Ebersole 1977, Harrington & Losey 1990), suggesting that this and other species of damselfish are able to differentiate among species within the reef community and alter their level of territorial aggression accordingly. At one level, this was observed as a significant increase in the amount of time allocated to vigilance and chasing intruders as the species diversity in the territory rose. More notably, however, the observed behavior patterns suggest that individuals are sensitive to more complex cues about the composite community structure that they encounter, with individuals increasing their level of territorial defense in response to greater proportions of strong competitors in the community regardless of the overall fish density and species diversity in the environment. This suggests that the distribution of species-types within the community may act as a signal of the overall competitive pressure present in the environment, thus regulating the cost-benefit balance between expending energy on resource defense versus alternative activities, such as feeding or seeking refuge in the shelter. The evolution of this ability to alter behavior patterns in response to community structure may allow individuals to more effectively defend food resources when competitor densities are high (Foster 1985), or alternatively, reduce their risk of predation by spending less time above the reef surface when competitive pressure from the community is low (Robertson & Sheldon 1979. Shulman 1985).

The algal food mats on the reef surface are only one of the resources defended within the territories of the threespot damselfish, although the value of the others tends to vary temporally and among males and females. For instance, territories contain shelters within the reef structure that provide protection from predation, and aggression over securing these locations increases during crepuscular periods as the changeover between diurnally and nocturnally active species occurs (Myrberg & Thresher 1974, Robertson & Sheldon 1979, Shulman 1985). Male threespot damselfish also defend egg masses within their territories, and so are expected to exhibit aggression toward approaching egg predators (Ebersole 1977), whereas females do not defend this resource, The research presented here focuses primarily on the sensitivity of the threespot damselfish to community structure as it relates to competition for algal food resources. As such, the observed patterns emphasize the behavior occurring during daylight hours and without regard to the sex of the territory holder. Clearly, however, the behavioral interactions of this species with the community may well change over a diel cycle, in the immediate presence of predators, or with the presence/absence of eggs within the territory. Further research is needed to better understand the balance of temporally shifting priorities and differences in the response by males and females to community structure.

In the study of ecology, an increasing amount of attention has been focused on the interactions of processes occurring at different spatial and temporal scales and across levels of differing ecological complexity (e.g.,. Maurer 1987, Jones & Lawton 1995); whether considering climate patterns (Francis & Hare 1994), nutrient exchange (Helfield & Naiman 2001), physical perturbation (Jones et al. 1997, Tardiff & Stanford 1998), or community succession (Fishelson 2003). In our understanding and interpretation of animal behavior, the importance of intra- and interspecific interactions at the levels of the organism and the population has been clearly established – as seen in direct competition for resources, mating interactions, predator-prey relationships, etc. (e.g., Noble 1936, Thresher 1976, Leger et al,. 1984). This study provides evidence that a third level of biological complexity, the community, also influences the behavior of animals. These results highlight the complex mechanisms underlying ethology and emphasize the need to consider patterns occurring at multiple ecological scales.

Acknowledgements

Funding for this research was provided by the Duke University International Travel Grant. Significant contributions to the data collection, data analysis, and writing of this study were made by Kate Abrey, Stephanie Carlson, Erin Davis, Dan McShea, Steve Nowicki, Tom Quinn, and Louise Roth. The comments and suggestions of four anonymous reviewers were very helpful and appreciated.

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