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## **Competitive ability and the potential for lotteries among territorial reef fishes**

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**Abstract** *Stegastes diencaeus* and *S. dorsopunicans* are mutually territorial Caribbean damselfishes. *S. diencaeus* is larger, grows faster and lives longer than *S. dorsopunicans*. *S. diencaeus* is a habitat specialist that shares its primary habitat mainly with *S. dorsopunicans*. Field manipulations show that both *S. diencaeus* and *S. dorsopunicans* readily take over living space from smaller, but not larger, heterospecific neighbors. Natural changes in the use of living space by both species occur frequently and adult *S. diencaeus* often aggressively usurp the living areas of smaller *S. dorsopunicans*. Lunar and seasonal patterns of juvenile recruitment by *S. diencaeus* and *S. dorsopunicans* are similar. Large size bestows competitive superiority on *S. diencaeus* by giving its adults a superior ability to aggressively acquire living space, and by enabling its juveniles to quickly escape the period when they lack a size advantage. Hence they spend much of their lives as competitive dominants. There is no evidence that competitive advantages arising from large size are offset either by other adult attributes or by differences in temporal patterns of recruitment that affect priority of access to space. The lottery hypothesis for species coexistence relies on patterns of abundance being determined by patterns of recruitment to vacant space because different species have equal space-holding abilities. These data show that the existence of such a mechanism is doubtful.

**Key words** Coral reef fish · Lottery coexistence · Competitive ability

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## Introduction

When field work began on the community ecology of coral reef fishes, competition was thought to be an important factor affecting their abundances, distributions and coexistence (reviewed in Sale 1980). Early work showed that, in many cases, closely related species that use the same types of food resources have extensively overlapping habitat distributions (Talbot et al. 1978; Anderson et al. 1981; Williams 1991 for review). In particular, many benthic feeding, territorial damselfishes (Pomacentridae) share habitats and defend living areas that, over time, often change ownership between different species. These observations stimulated the "Lottery Hypothesis", which proposes that mutually territorial species compete for living space and that their coexistence is mediated by chance events rather than by mechanisms such as resource partitioning. That hypothesis asserts that such species have equal abilities to hold space against each other, and hence that occupancy of a living site is determined by whichever species arrives first when the site becomes vacant, and abundances of species are determined by patterns of recruitment into vacant space (Sale 1974, 1975, 1976, 1977, 1978, 1979, 1982, 1991; Abrams 1984a; Chesson and Warner 1981; Comins and Noble 1985; Chesson 1991).

A considerable amount of theoretical work has developed on the mechanics of competitive lotteries since the original presentation of the hypothesis. This has examined effects of environmental variability (Chesson and Warner 1981; Chesson 1985; Warner and Chesson 1985; Chesson 1994), longevity (Chesson 1984, 1994; Warner and Chesson 1985), intra- and interspecific competition among larvae (Abrams 1984a, b), frequency-dependent reversals in relative competitiveness (Chesson and Warner 1981; Sale 1982; Warner and Chesson 1985), and compensatory reversals on the competitive ability of different life history stages (cf. Loreau and Ebenhoh 1994). Empirical work has lagged

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behind these developments. Soon after the lottery hypothesis was presented, studies of the population biology of reef fishes revealed that recruitment dynamics have major limiting effects on the population dynamics and community organisation of reef fishes (Sale and Dybdahl 1978; Williams 1980; Doherty 1983; Victor 1986; Doherty and Williams 1988; Doherty and Fowler 1994). As a result, much of the field research on the organization of reef fish communities became oriented towards the "recruitment question" (reviews in Doherty 1991; Sale 1991; Williams 1991) and interest waned in the role of interspecific competition among benthic populations (but see Ebersole 1985; Robertson and Gaines 1986; Clarke 1989).

This paper presents the results of an empirical test of the original, central assumption of the lottery hypothesis – that mutually territorial species using the same habitat and living sites have equal abilities to hold living space, and that occupation of a living space is determined by whichever species arrives first when that space becomes vacant. I use empirical data to examine how relative competitive abilities of two such species are affected by size-dependency in space-holding ability and patterns of growth, longevity and population structure, and whether there might be compensatory reversals in competitiveness of different life history stages that could lead to overall equality in species competitiveness. Aspects of the lottery hypothesis that were developed after its initial presentation, such as frequency-dependent fluctuations in relative competitiveness, are beyond the scope of this study.

For this test I used a guild (sensu Root 1967) of benthic-feeding Caribbean damselfishes that is a close analog of the damselfish guild studied by Sale (1974 and later papers) in the West Pacific. Adults of members of both guilds defend exclusive, general purpose territories against conspecifics and other guild members. In both guilds some species have habitat "refuges" in which they are virtually the only species present, although they may also occur in other, shared habitat. Other species lack such refuges and occur only in shared habitat (Robertson and Lassig 1980; Waldner and Robertson 1980). The lottery hypothesis is relevant to species of the latter type and both Sale's and the present study focused on space use by such species. The species Sale examined belong to different genera, while those studied here are congeners. If interspecific competitive equality exists it seems likely to occur in a guild of congeners, because the highest levels of similarity in ecological characteristics tend to occur among congeners.

This paper examines the following questions about relations between *Stegastes diencaeus* and *S. dorsopunicans*, the main species that co-occurs in *S. diencaeus*' primary habitat:

1. How much overlap in habitat and microhabitat use is there between *S. diencaeus* and its congeners, and does *S. diencaeus* have a habitat refuge?

2. Does interspecific variation in body size produce interspecific asymmetry in space-holding ability and hence competitiveness?

3. How much natural short-term flux is there in the occupancy of space in shared habitat, and does some of that flux result from asymmetric interspecific behavioral dominance interactions?

4. Are interspecific differences in patterns of aging and growth likely to affect relative competitiveness of those species?

5. Do temporal patterns of recruitment differ in ways that indicate recruits of either species have an advantage in establishing themselves in the benthic population?

6. Could reversed asymmetries in different abilities compensate for each other and produce overall competitive equality between *S. diencaeus* and *S. dorsopunicans*?

## Materials and methods

### Study Site

The study was done on reefs at Punta de San Blas, on the eastern Caribbean coast of Panama. Reef numbers used here follow Robertson (1987). Data were collected between 1978 and 1994.

### Study organisms and their general biology

There are six species of *Stegastes* on Caribbean coral reefs (Allen 1991): *S. diencaeus*, *S. dorsopunicans*, *S. leucostictus*, *S. partitus*, *S. planifrons* and *S. variabilis*. *S. partitus* feeds on both benthic and planktonic algae, while the remainder feed mainly on benthic microalgae (Emery 1973; Robertson 1984). Adults and large juveniles of *S. diencaeus*, *S. dorsopunicans*, *S. leucostictus* and *S. planifrons* individually defend small (~1 m<sup>2</sup>) territories against conspecifics, congeners and certain other fishes. In these species a territory is an exclusive-use living area that provides food, shelter and, for males, a nest site. Neighboring living areas are often contiguous but are essentially non-overlapping (<1% of feeding bites by individuals with contiguous territories are in overlap areas: Robertson (1984) for *S. dorsopunicans* and *S. planifrons*, and >100 h of observation on >100 *S. diencaeus* during the present study).

### Overlap in habitat use by *S. diencaeus* and its congeners

#### Between habitats

To assess the degree of overlap in habitat use between *S. diencaeus* and its congeners, I examined their distributions on 5-m wide transects that were run perpendicular to the long axis of a large reef (Aguadargana 1, 800 m in largest dimension) that supported the largest population of *S. diencaeus* (several hundred individuals) on any reef in the study area. *Stegastes* species are non-cryptic, sedentary fishes that usually stay within the bounds of their living areas. All individuals of each species with living areas partly or wholly within each 5 × 5 m section of a transect were included in the counts that I used to define their distributions.

One transect ran across the eastern tip of reef Aguadargana 1, from the bottom of the reef slope on one side across the top of the reef and down the reef slope on the other side. The other two

transects were placed about 100 m apart in the center of the reef, and were situated to include the type of microhabitat used by *S. diencaeus* (Waldner and Robertson 1980). They ran from the inner limit of the backreef, over the reef top and down to the lower limit of the reef slope. I use these data to compare the population densities of each species in three habitats: (1) the backreef (1–1.5 m deep, the shallow inner limit of reef development where reef substrate interface with sand, rubble and seagrass); (2) the reef top (uniformly 1–2 m deep, continuous reef substrata); and (3) the reef slope (the sides of the reef, grading from 2–25 m depth).

#### Within habitat

To assess interspecific similarities in microhabitat use by the various species of *Stegastes* in the primary habitat of *S. diencaeus* I followed Sale (1974, 1975, 1976, 1978), and measured levels of change over time in occupancy of living areas used by *S. diencaeus*.

To determine the utility of the living areas of adults and large juveniles of *S. diencaeus* for other species I removed, by spearing, all *S. diencaeus* (27 juveniles and 122 adults) from one section of the backreef of reef West Barrier 4, after marking the location of each living area on a map and with a masonry nail hammered into the substratum. Each living area was then checked at monthly intervals over the following year for occupancy by other *Stegastes* species. A similar set of observations at monthly intervals ( $n = 9$ ) was made on the use by other congeners of naturally vacated living areas of small juveniles of *S. diencaeus* on reef Aguadargana 1. These included both new recruits (fish that had settled from the plankton during the month in which they were first recorded; see Robertson 1992) and slightly older (2–3 months post-settlement) juveniles.

#### Population size structure

To assess the size structures of populations of different species I made population collections (by spear) of virtually all adults of each species that I found in either randomly chosen patches of appropriate habitat, or on line transects placed across the centers of reefs. These damselfishes are non-cryptic in their behavior and all adult size classes are readily visible. The collections were done on randomly chosen reefs representative (in terms of habitat) of the range of types present in the study area. *S. diencaeus* was collected from two large reefs and each of the other species from four to five reefs. The fish were weighed and sexed (by macroscopic examination of their gonads) while fresh.

I also compared the size structures of a population of *S. diencaeus* that I removed to assess use of their living areas by congeners (see above), and the population of congeneric occupants (all species) that I removed from a random subsample of those living areas 11 years later.

#### Short-term dynamics of space use

To estimate the natural frequency of change in the occupation of living space by *S. diencaeus* and *S. dorsopunicans* in shared habitat, I compared maps made at 1 month intervals of the distributions of living areas of these fishes in three  $6 \times 6$  m quadrats scattered along the backreef of Aguadargana 1. Those maps were based on 10-min observation of the movements, feeding and defense of each fish in the quadrat, plus indirect observations on it while I focused in turn on each of its neighbors. Mapping was done in the afternoon, when the fishes feed most intensively throughout their living areas (Robertson 1984). One month after the initial mapping I recorded any change in the occupant of a living area and any changes of  $>10\%$  in the size or shape of each

area. Fish were not tagged and I used the relative sizes of each set of neighbors in the two observation periods to assess whether there had been a change in the occupant of a feeding area. Because multiple changes may have occurred between successive observation periods and I would not have detected replacement of one fish by another of equal size these data provide a conservative estimate of change in space use.

#### Ability to aggressively acquire and hold space

##### Induced takeovers of occupied living areas

To assess the ability of *S. diencaeus* and *S. dorsopunicans* to acquire and hold space, I used experiments in which I reduced the size of an individual's living area with an exclusion cage, and determined whether it responded by aggressively usurping the living space currently used and defended by one of its contiguous neighbors. Size is an important determinant of social dominance in fishes (Kodrick-Brown 1990) and the three experimental treatments were organized around patterns of difference in the relative sizes of neighbors: (1) "exclude" a *S. diencaeus* having a smaller ( $\sim$  two-thirds size) *S. dorsopunicans* neighbor; (2) "exclude" a *S. dorsopunicans* having a smaller ( $\sim$  two-thirds size) *S. diencaeus* neighbor; (3) "exclude" a *S. dorsopunicans* having a larger ( $\sim$  one-third greater) *S. diencaeus* neighbor. I did not do a treatment with an "excluded" *S. diencaeus* versus a larger *S. dorsopunicans* neighbor because *S. diencaeus* is relatively uncommon, most individuals were larger than their heterospecific neighbors and I could not find appropriate situations.

For each replicate I chose a group of fish with apparently stable spatial and social relations, i.e., with low levels of aggressive interaction and no evidence (abrasions, shredded fins) of recent fighting. After the living areas of the experimental fish and all its contiguous neighbors were mapped I reduced the size of the experimental fish's area by covering about 50% of its substratum with a galvanized steel wire cage (1 cm mesh size) that excluded the owner. The cage was arranged so that the manipulated fish had normal access to its refuge(s) and the uncaged portion of its living area abutted the living area of an appropriately sized neighbor. After installing the cage I visited the site daily for up to 10 days and recorded any changes in use of space and aggressive interactions between the participants. For each of those treatments there were concurrent uncaged controls with appropriate combinations of fishes of different sizes and species.

These experiments were performed in the primary habitat of *S. diencaeus* (backreef – see results).

#### Constraints on space use and takeovers of vacated space

I used experimental removals to assess whether fish were constrained from obtaining living space by surrounding neighbors, and if the level of any constraint depended on the relative sizes of those fish. There were three treatments in this experiment:

1. Remove an adult *S. diencaeus* having smaller ( $\sim$  one-half size) *S. dorsopunicans* neighbors.
2. Remove an adult *S. dorsopunicans* having a larger ( $\sim$  one-half greater) *S. diencaeus* neighbor.
3. Remove an adult *S. dorsopunicans* having smaller ( $\sim$  one-half to one-third size) conspecific neighbors. The latter treatment was done to identify whether responses were due to size effects or species effects. The rarity of appropriate situations precluded a treatment in which I would have removed a small *S. diencaeus* that had larger *S. dorsopunicans* neighbors. In each replicate the living areas of the "removal" fish and its surrounding neighbors was mapped during  $\sim 45$  min of observations, then it was speared. The site was visited daily thereafter for 3–5 days, then 1 month hence and occupation of the vacated living area was recorded.

Recruitment dynamics

Data have been presented elsewhere on the lunar periodicity and seasonality of settlement of pelagic juveniles of *S. diencaeus* and *S. dorsopunicans* (Robertson 1990; Robertson 1992), and inter-annual and intermensual variation in recruitment strength (Robertson et al. 1993). Settlement of pelagic juveniles is minimal around full moon and I censused new recruits just before each full moon in a set of permanent plots scattered around the study area (details in Robertson 1990; Robertson 1992). The analyses presented here, which expand on those of Robertson (1990) and Robertson et al. (1993), are based on 11 years (1983–1993) monitoring of recruitment of *S. diencaeus* and *S. dorsopunicans*.

Data analyses

I used the computer package SYSTAT (Wilkinson 1990) for time series analyses of recruitment dynamics. When examining the degree of correlation between intermensual variation in recruitment by the two species I first seasonally adjusted each time series to remove autocorrelations (Chatfield 1984). I used the mean level of recruitment in each month as the seasonal factor for these adjustments. Remaining analyses followed Sokal and Rohlf (1981).

Results

Overlap in habitat use

*Between habitats*

*S. diencaeus* was restricted almost entirely to backreef habitat on a large reef on which it was relatively abundant. However, *S. diencaeus* was substantially less common in that habitat than *S. dorsopunicans* and about equally as common as *S. planifrons* (Table 1). Other *Stegastes* species were rare in that backreef (Table 1).

*Within habitat*

Removal of all 149 resident *S. diencaeus* from a section of backreef on reef West Barrier 4 resulted in

takeovers of their vacant living areas by other species of *Stegastes* in almost all cases (Table 2): only 2% of those vacated areas were unoccupied 1 month after the removal and only 1.6% were never occupied at least once during the year following the removal. Most of those takeovers, particularly of the living areas of adults of *S. diencaeus*, were by *S. dorsopunicans*. *S. planifrons* was the other main species involved in such takeovers.

Naturally vacated living areas of newly settled and slightly older juveniles of *S. diencaeus* became occupied mainly by recruits and older juveniles of *S. dorsopunicans* and, to a lesser extent, *S. planifrons* and *S. partitus* (Table 3). All 25 vacated sites of recruits of *S. diencaeus* were occupied by congeners and only 8 of 82 sites of older juveniles were unoccupied consistently (although of these latter, 3 were “available” for only the last 3 months, and 4 for only 1 month).

Sizes of *Stegastes* species

There were significant differences between the size structures of adult populations of *S. diencaeus* and all other congeners (Fig. 1; Kolmogorov-Smirnoff two sample tests,  $P < 0.01$  in each case). Adults of *S. diencaeus* reached a substantially larger maximum size than those of any other species (Fig. 1) and median adult weight of *S. diencaeus* (23 g) was 2.5 times as great as median adult weight of *S. dorsopunicans* (9 g). Over half the adults of *S. diencaeus* were heavier than the largest *S. dorsopunicans* collected (Fig. 1). Eleven years after the removal of *S. diencaeus* from reef West Barrier 4 *S. diencaeus* occupied 16% of the 148 original sites I was able to find and congeners occupied 82%. Those congeners were considerably smaller than the original owners of those sites: median weight of original *S. diencaeus* owners was 23 g (range 3–45 g,  $n = 149$ ) versus a median weight of congeneric owners in 1994 of 10 g (range 3–15 g,  $n = 60$ ; Kolmogorov-Smirnoff two sample test comparing size distributions,  $P < 0.01$ ).

**Table 1** Population densities of six species of *Stegastes* in three habitats (see methods for description). Backreef was absent on transect 1

Species	Mean (SE) population density (fish/m <sup>2</sup> ) in each habitat								
	Transect 1			Transect 2			Transect 3		
	Backreef	Top	Slope	Backreef	Top	Slope	Backreef	Top	Slope
<i>S. diencaeus</i>	–	0.01 (0.01)	0	0.49 (0.09)	0.02 (0.01)	0	0.36 (0.12)	0.01 (0.01)	0
<i>S. dorsopunicans</i>	–	0.87 (0.05)	0.04 (0.03)	1.06 (0.02)	1.46 (0.12)	0.07 (0.05)	0.80 (0.33)	1.58 (0.12)	0.07 (0.07)
<i>S. leucostictus</i>	–	0	0	0.01 (0.01)	0	0	0.01 (0.01)	0	0
<i>S. partitus</i>	–	0.01 (0.01)	0.05 (0.02)	0.08 (0.03)	0.04 (0.02)	0.26 (0.11)	0.02 (0.01)	0.01 (0.01)	0.16 (0.07)
<i>S. planifrons</i>	–	0.02 (0.01)	0.42 (0.08)	0.45 (0.12)	0.20 (0.15)	0.68 (0.25)	0.65 (0.24)	0.11 (0.10)	0.47 (0.12)
<i>S. variabilis</i>	–	0	0.07 (0.01)	0	0	0.05 (0.02)	0	0.01 (0.01)	0.06 (0.02)
No. 25-m <sup>2</sup> quadrats	0	18	17	4	9	9	4	7	10

**Table 2** Occupation of experimentally vacated living areas of *Stegastes diencaeus* by congeners. Living areas were checked monthly. Percentages are for cumulative total for each species (sum may be >100% because some living areas were divided between two species or occupied by different species on different occasions)

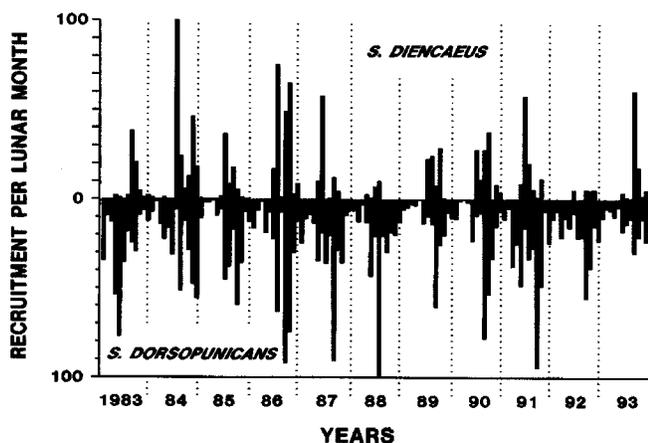
Occupant(s)	Percentage of <i>S. diencaeus</i> ' living areas occupied			
	Juvenile areas		Adult areas	
	After 1 month	At least once over 1 year	After 1 month	At least once over 1 year
<i>S. dorsopunicans</i> adult	40.7	55.5	59.0	69.7
juvenile	18.5	31.8	3.3	3.3
<i>S. planifrons</i> adult	11.1	14.8	19.6	22.1
juvenile	11.1	11.1	11.4	11.4
<i>S. leucostictus</i> adult	0	3.7	1.6	4.1
juvenile	0	0	0	0
<i>S. partitus</i> adult	14.8	22.2	4.9	4.9
juvenile	3.7	3.7	0.7	0.7
Nil	0	0	2.5	1.6
<i>n</i>	27		122	

**Table 3** Occupation of naturally vacated living areas of juveniles of *Stegastes diencaeus* by juvenile congeners

Congeneric occupant		Percent <sup>a</sup> of living areas occupied at least once during 9 consecutive monthly observations	
Species	Age	New-recruit areas	Larger-juvenile areas
<i>S. dorsopunicans</i>	new recruit	40	29
	larger juvenile	68	61
<i>S. planifrons</i>	new recruit	12	2
	larger juvenile	16	21
<i>S. variabilis</i>	new recruit	4	0
	larger juvenile	4	11
<i>S. leucostictus</i>	new recruit	0	0
	larger juvenile	4	6
<i>S. partitus</i>	new recruit	12	12
	larger juvenile	12	18
Never occupied		0	8
<i>n</i>		25	82

<sup>a</sup>Sum exceeds 100% because different species occupied the same site at different times

**Fig. 1** Monthly fluctuations in juvenile recruitment of *Stegastes diencaeus* and *S. dorsopunicans* over 11 years. Recruitment of both species is shown at the same scale – a percentage of the maximum monthly level for each during that period



The population of *S. diencaeus* collected from reef West Barrier 4 in 1983 was composed largely (73%) of adults. Adults were less abundant in populations of *S. dorsopunicans* and *S. planifrons*, representing 45% and 27%, respectively, of 200 individuals of each species censused in that habitat at the same time as the collection (*G* tests for independence, *S. diencaeus* versus *S. dorsopunicans* and versus *S. planifrons*,  $P < 0.001$  in each case).

#### Short-term dynamics of occupancy of living space

Over the course of a month there were changes in ownership of substantial portions of about one-quarter of the living areas of adults and two-thirds of the living areas of juveniles of both *S. diencaeus* and *S. dorsopunicans* (Table 4). Half the changes in space use by *S. diencaeus* and a quarter of those by *S. dorsopunicans*

**Table 4** Change in ownership of living areas of *Stegastes diencaeus* and *S. dorsopunicans* from one month to the next in 1983. Changes included loss of the original occupant of an area and/or an increase or decrease of >10% of the size of a living area (*n* number of individuals per 6 × 6 m quadrat)

Quadrat	Proportion of living areas showing change owned by:			
	<i>S. diencaeus</i>		<i>S. dorsopunicans</i>	
	Adult ( <i>n</i> )	Juvenile ( <i>n</i> )	Adult ( <i>n</i> )	Juvenile ( <i>n</i> )
1	0.38 (8)	0.50 (2)	0.43 (21)	0.40 (5)
2	0.25 (8)	0.60 (5)	0.50 (14)	1.00 (3)
3	0.17 (6)	1.00 (2)	0.55 (20)	0.57 (14)
Total	0.27 (22)	0.67 (9)	0.49 (55)	0.59 (22)

involved the disappearance of the original owner from a living area. In connection with several experiments I also monitored the use of space by another 89 adults of *S. dorsopunicans* that were neighbors of *S. diencaeus*; 31% of their living areas showed similar natural changes in ownership, shape or size from one month to the next.

Ability to acquire and control space

*Induced takeovers of occupied living space*

When an individual of either *S. diencaeus* or *S. dorsopunicans* was excluded from half of its living area by a cage it usually responded by attacking and taking control of defended living space occupied by a smaller conspecific or heterospecific neighbor, which then dis-

appeared (Table 5). In all such situations I observed the “excluded” fish actively fighting with and clearly dominating (forcing into cover) its smaller neighbor, despite aggressive resistance from the latter. This fighting, which included mutual chasing, butting, tail-beating and biting, resulted in obvious physical damage (split fins and body abrasions) to both combatants. Although *S. dorsopunicans* whose living areas were partly caged also attacked and fought with larger *S. diencaeus* (and conspecific) neighbors they did not invade or add space at the expense of those neighbors. In fact in three replicates of this treatment the increased aggressiveness of the “excluded” fish apparently led to the larger neighbor invading and expelling it, then adding the uncaged part of that fish’s area to its own living area. Invasive takeovers occurred more frequently in each of the three experimental treatments than in their respective controls (Table 6; binomial test for goodness of fit, *P* < 0.01 in each case).

In all cases of aggressive takeovers in both the experiments and the controls the invader was distinctly larger than its victim. Despite the availability of situations with appropriately sized neighbors (Table 6) there were no cases in which a fish invaded and took over even part of a larger neighbor’s area.

*Takeovers of experimentally vacated living areas*

Removal of *S. diencaeus* adults that had smaller *S. dorsopunicans* neighbors invariably resulted in those

**Table 5** Responses of *Stegastes diencaeus* and *S. dorsopunicans* to exclusion from parts of their living areas by cages

Response of “excluded” fish	Number of different responses to caging of living area of:					
	Large <i>S. diencaeus</i>		Large <i>S. dorsopunicans</i>		Small <i>S. dorsopunicans</i>	
	Experiment	Control	Experiment	Control	Experiment	Control
Invades living area of:						
smaller heterospecific	9	4	7	3	1	0
smaller conspecific	1	1	0	0	6	1
larger heterospecific	0	0	0	0	0	0
larger conspecific	0	0	0	0	0	0
Does nothing	0	15	0	8	2	13
Disappears	3	1	5	1	3	7
Total	13	21 <sup>a</sup>	12	12	12	21 <sup>a</sup>

<sup>a</sup> The same replicates were used as controls for these two treatments

**Table 6** Relative sizes of *Stegastes diencaeus* and *S. dorsopunicans* that took over occupied living areas during caging experiments (see Table 5; numbers given here for some interactions are higher than those in Table 5 because some takeovers are not relevant to cate-

gories in Table 5). Heterospecific takeover = invasion of *S. dorsopunicans* by *S. diencaeus* or vice versa (*n* number of replicates in which potential invader of the appropriate size was present)

Relative size of invader	No. heterospecific takeovers by:		No. conspecific takeovers by:	
	<i>S. dorsopunicans</i>	<i>S. diencaeus</i>	<i>S. dorsopunicans</i>	<i>S. diencaeus</i>
Larger	11 (34)	19 (45)	8 (44)	2 (12)
Smaller	0 (29)	0 (27)	0 (48)	0 (19)

**Table 7** Takeovers of experimentally vacated living areas of adults of *Stegastes diencaeus* and *S. dorsopunicans* by heterospecific or conspecific neighbors. Temporary takeover were for 1–2 days and then abandoned; permanent takeovers were for at least 1 month

Species removed	Neighbor	No. trials in which neighbor makes each response		
		No. response	Temporary takeover	Permanent takeover
<i>S. diencaeus</i>	Smaller <i>S. dorsopunicans</i>	0	0	12
<i>S. dorsopunicans</i>	Larger <i>S. diencaeus</i>	12	3	4
	Smaller <i>S. dorsopunicans</i>	0	0	19

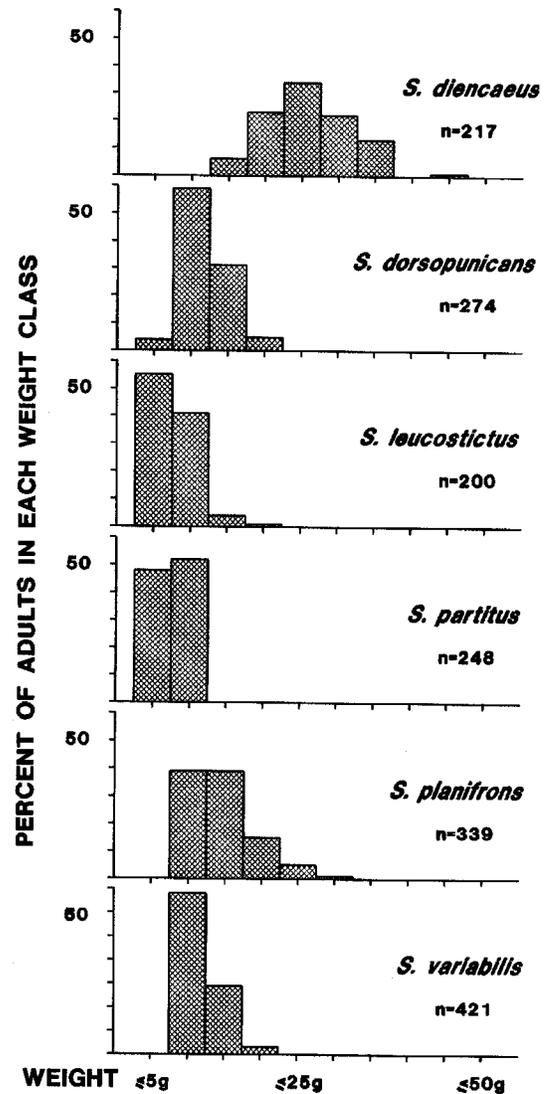
neighbors taking over the vacated living space by the following day and retaining it for at least a month (Table 7). In contrast, the removal of a smaller *S. dorsopunicans* neighbor of an *S. diencaeus* resulted in no change in the latter's living area in two-thirds of the cases (Table 7). In a few trials of this latter experiment there were temporary (1–2 days only) occupations of part of the vacated area by the *S. diencaeus*, which then retired to its original area. In one-fifth of the trials, the *S. diencaeus* took over and permanently added about half that vacated area to its own living area. Smaller conspecific neighbors of those removed *S. dorsopunicans* invariably added vacated space permanently to their feeding areas.

#### Natural takeovers of living space

Each of 33 control sites used in the caging experiments described above was monitored for 5–10 days. Natural aggressive takeovers of living areas were observed in eight of those replicates. Those takeovers included cases in which an *S. diencaeus* took over space from a smaller *S. dorsopunicans* (4 of 21 *S. diencaeus* did so) or smaller conspecific ( $n = 1$ ), and cases in which an *S. dorsopunicans* took over space from a smaller *S. diencaeus* (3 of 12 *S. dorsopunicans* did so). During the course of those observations on control areas four other aggressive takeovers of living areas of adults of *S. dorsopunicans* by larger adult *S. diencaeus* also occurred within several meters of the control fish. In three of the eight takeovers by *S. diencaeus* the invading fish usurped the area of an *S. dorsopunicans* several meters distant rather than the area of one of its immediate neighbors. The 12 natural takeovers by *S. diencaeus* followed the same behavioral pattern as takeovers induced by caging, and the displaced owner disappeared from the vicinity of its original site.

#### Age and growth

Both *S. diencaeus* and *S. dorsopunicans* live for only a few years. Maximum age of *S. diencaeus* is about one-third greater than that of *S. dorsopunicans* and the median age of adults of *S. diencaeus* is about 25% greater than that for *S. dorsopunicans* (Table 8). The absolute growth rate of *S. diencaeus* is about 40% greater than that of *S. dorsopunicans* over the first 2



**Fig. 2** Size structures of the adult populations of six species of *Stegastes*

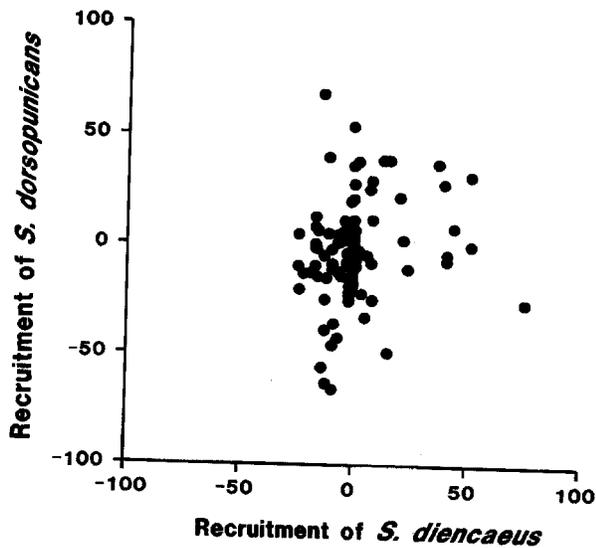
years, by which time *S. diencaeus* has reached median adult size (Table 8).

#### Temporal patterns of recruitment

Although the bulk of recruitment by both species occurred during the same part of the year (Robertson 1990; Fig. 2), there were some differences in their

**Table 8** Age and size of adults of *Stegastes diencaeus* and *S. dorsopunicans*. These data summaries are from estimates of population age structure of *S. diencaeus* in its primary habitat and *S. dorsopunicans* across a range of habitats (DR Robertson and EB Brothers, unpublished data). Size structures of those populations are shown in Fig. 1

Species	Age of adults (years)		Adult weight (g) at	
	Median	Maximum	1 year	2 year
<i>S. diencaeus</i>	2.0	4.6	10	23
<i>S. dorsopunicans</i>	1.6	3.5	6	11



**Fig. 3** Relation between variation in concurrent, seasonally adjusted, monthly recruitment of *Stegastes diencaeus* and *S. dorsopunicans* over 11 years (1983–1993)

recruitment seasonalities. First, although recruitment by both was minimal during winter, there was relatively more recruitment then by *S. dorsopunicans* than by *S. diencaeus*: the median percentage of the year's recruitment occurring between January and March was 0% (range = 0–0.6%/year) for *S. diencaeus* and 8.8% (range = 4.0–17.6%/year) for *S. dorsopunicans* ( $n = 11$ , Wilcoxon paired sample test,  $P < 0.001$ ). Second, recruitment by *S. diencaeus* tended to occur before recruitment by *S. dorsopunicans* during the main recruitment season. The peak of recruitment (mean angle of the circular distribution: Batschelet 1981) by *S. diencaeus* was earlier than that by *S. dorsopunicans* in 7 years, in the same month in 3 years, and later in only 1 year. A cross correlation of the time series of seasonally adjusted monthly recruitment by the two species showed that there was a weak tendency for recruitment by *S. diencaeus* to occur several months before that of *S. dorsopunicans*:  $r = 0.25$  at a lag of 3 months,  $n = 136$ ,  $P < 0.01$ . There was no correlation between concurrent monthly fluctuations in their recruitment (Fig. 3;  $r = 0.15$  at zero lag,  $P > 0.05$ ).

**Discussion**

Habitat-use relationships between species

*S. diencaeus* is a habitat specialist that shares its primary habitat in San Blas with two congeners, *S. dorsopunicans* and *S. planifrons*, which are the most abundant species in that habitat (Table 1; Waldner and Robertson 1980). The high levels of use by various *Stegastes* species of backreef living sites previously used by *S. diencaeus* of all size classes show that congeners also overlap completely with it in microhabitat use (see also Waldner and Robertson 1980). The few data available indicate that similar habitat overlap between these species occurs elsewhere in the Caribbean (Clarke 1977; Waldner and Robertson 1980, in which *S. diencaeus* was recorded as *S. mellis*). Thus, *S. diencaeus* evidently does not have a habitat or microhabitat that it alone uses and that could act as a refuge from competition with its congeners. Refugia can account for the evolutionary persistence of many species in the guild that Sale studied (Robertson and Lassig 1980), and for the persistence of *S. dorsopunicans* (Waldner and Robertson 1980), but not for the persistence of *S. diencaeus*.

Size structures of populations

*S. diencaeus* has a distinct size advantage over its congeners. In San Blas its adults have substantially greater average and maximum weights than any congener, and the average *S. diencaeus* weighs over twice as much as the average congener that uses the same microhabitat as it. In addition, the population of *S. diencaeus* contains proportionately more large individuals than populations of the main congeners that co-occur in *S. diencaeus*' primary habitat. The patterns of difference in size structures of populations of *Stegastes* species recorded here are similar to those observed elsewhere in the Caribbean (Emery 1973).

Space-holding ability

Size effects

The exclusion-cage experiments show that when a *S. diencaeus* or *S. dorsopunicans* has its access to living space severely constrained it will often successfully attack a smaller conspecific or heterospecific neighbor and invasively take over its living area, despite active aggressive resistance by its owner. However, while fish in such circumstances also become aggressive towards larger heterospecific and conspecific neighbors, they cannot successfully invade their living areas. In fact the increased social friction arising from that constraint may sometimes stimulate a larger neighbor to take over

space from the constrained fish. These experiments show that mutual territoriality among different species of reef fishes does not necessarily imply that they have equal abilities to hold living space. Space-holding ability is size dependent and size effects can override potential species effects and effects of prior residence. The strong size differences between populations of *S. diencaeus* and *S. dorsopunicans* must produce a strong interspecific asymmetry in space-holding ability, with *S. diencaeus* being competitively superior.

### Species effects

Species effects often override size effects and determine space-use relations among reef fishes that are not closely related (Robertson et al. 1976; Foster 1985; Shulman 1985). Species effects also sometimes influence patterns of space use among territorial damselfishes. The large (up to 150 g) damselfish *Microspathodon chrysurus* aggressively dominates and superimposes its living areas on those of adults of *S. dorsopunicans* and *S. planifrons*. Although individual *M. chrysurus* require a large size advantage to dominate either *Stegastes* species, they need a greater size advantage to dominate *S. planifrons*, which is the more aggressive of those two species (Robertson 1984).

Ebersole (1985) proposed that a reversible, habitat-dependent asymmetry in behavioral dominance produces habitat segregation between *S. leucostictus* and *S. planifrons*. His preference tests showed that *S. planifrons* accepted only one of two habitats while *S. leucostictus* readily used both of them. In aquarium tests with equal-sized juveniles of both species *S. planifrons* was aggressively dominant only when fighting for possession of its preferred microhabitat. These results could reflect reversible, habitat-dependent dominance. An alternative explanation is that *S. planifrons* is the more aggressive species, but has more restricted habitat preferences and will fight only for its preferred habitat. In this case competitive dominance by *S. planifrons* would derive from a species effect reinforced by a size advantage (Fig. 1).

Interspecific size differences analogous to those observed here occur among the species that Sale (1974–1979) focused on when developing the lottery hypothesis. Those include two large habitat specialists and a smaller habitat generalist (Robertson and Lassig 1980). There is no reason to expect that size-dependent interspecific asymmetries in space-holding ability and competitive ability do not occur in this guild also.

Interspecific differences in aggressiveness could counter effects of size on dominance capabilities among mutually territorial reef fishes. However, until that has been demonstrated, the simplest assumption is that size-based asymmetries in space-holding ability are the general condition for groups of closely related, territorial reef fishes.

Adult *S. diencaeus* are sufficiently large to be competitively dominant over any congeners with which they are likely to interact. However, juveniles of *S. diencaeus* may be involved to some extent in space lotteries with congeners because they lack a consistent size advantage, and are likely to be interacting with a set of conspecifics and heterospecifics of a range of sizes. It is also possible that species effects will put juveniles of large species at a disadvantage in interactions with heterospecifics and tend to counter effects of the competitive superiority of their adults. Future work should focus on such potential compensatory mechanisms, as they could have important effects.

### Exercising competitive dominance

Natural changes in occupancy of space by adults and juveniles of both *S. diencaeus* and *S. dorsopunicans* occur frequently. Since both species are short-lived some of that flux presumably results from mortality of residents. However, some of it may have resulted from aggressive takeovers, as adults of *S. diencaeus* exercise their competitive dominance by making natural takeovers of space from smaller heterospecifics surprisingly often (4 of 21 fish did so during 5–10 days of observation). Because they make such takeovers, adults of *S. diencaeus* might be expected to have whatever space they require. The pattern of takeovers of experimentally vacated space largely upholds that expectation: adult *S. diencaeus* take over experimentally vacated space used by smaller neighboring *S. dorsopunicans* much less often than the reverse. However, about one-fifth of adult *S. diencaeus* do add the vacated space of smaller heterospecifics when the opportunity arises. Although this indicates that adults of *S. diencaeus* are constrained to some extent by their smaller neighbors this situation may simply reflect the dynamic state of space use under normal circumstances. If changes are produced frequently by external events fish may tend to wait and take advantage of them rather than fight to precipitate them. Aggressive takeovers may occur when the need for additional space has increased beyond a certain level (e.g., as a result of growth of the owner or habitat disturbance).

### Size, life history characteristics and competitiveness

Juveniles of large species of fishes usually have faster absolute growth rates than juveniles of smaller congeners (Buesa 1987; Legrende and Albaret 1991), and large species tend to live longer than smaller relatives (Blueweiss et al. 1978; Calder 1984). Populations of longer-lived animals also tend to have higher proportions of older individuals (Calder 1984). These differences in patterns of growth, longevity and population structure are evident between *S. diencaeus* and

*S. dorsopunicans*. They should give large species such as *S. diencaeus* a competitive advantage in several ways. Juveniles of larger species should rapidly reach a size at which they become behaviorally dominant space holders. Individuals of larger species should spend larger proportions of their lives as competitively dominant individuals, and a higher proportion of older individuals will mean a higher proportion of competitively dominant individuals in a population. In addition, populations of longer-lived species will be better able to store recruitment influxes (cf. Warner and Chesson 1985) and may have a competitive advantage because they are less susceptible to effects of fluctuations in recruitment. However, because both *S. diencaeus* and *S. dorsopunicans* are relatively short-lived and do not differ greatly in longevity, differences in the storage capacity of their populations may not be as potentially important for coexistence as they could be for long-lived species.

#### Recruitment dynamics and competitiveness

Much of the attention given to how lotteries might function has focused on effects of the temporal and spatial dynamics of recruitment of pelagic juveniles (e.g., Abrams 1984a, b; Comins and Noble 1985; Warner and Chesson 1985). Both similarities and random differences in the dynamics of recruitment of different species at the same site should promote lotteries. Consistent interspecific differences in temporal patterns of recruitment at a site could either produce competitive asymmetries, or reinforce competitive asymmetries that arise from differences in the ecology of adults, or compensate for effects of differences in competitive abilities of adults.

Settlement of pelagic juveniles of both *S. diencaeus* and *S. dorsopunicans* peaks around new moon (Robertson 1992). Although the precise timing of pulses of settlement by *S. dorsopunicans* varies from month to month (Robertson 1992) there are too few data on settlement by *S. diencaeus* to determine whether there are consistent differences in the order of arrival of these two species each month. The bulk of recruitment by both species occurs during the same part of the year and their average seasonal patterns of recruitment are quite similar (Robertson 1990). What differences there are between their recruitment seasonalities are small and should have reverse effects: there is a little more recruitment by *S. dorsopunicans* at the beginning of the year, prior to the arrival of most recruits of *S. diencaeus*. However, during the main recruitment season, influxes of recruits of *S. dorsopunicans* tend to occur several months after influxes of recruits of *S. diencaeus*. There is no indication of asymmetric competition between juveniles of these species prior to recruitment (cf. Loreau and Ebenhoh 1994). If such competition were occurring we would expect to

see a density-dependent relationship between inter-monthly fluctuations in their recruitment, rather than the independent fluctuations that actually occur (Fig. 3). Thus larvae and recruits of *S. dorsopunicans* do not appear to have any advantage that might compensate for the suite of competitive advantages that arise from *S. diencaeus*' larger adult size.

#### Conclusions

The lottery hypothesis is most relevant to territorial reef fishes that lack habitat refuges and always share habitat with other species. This study showed that adults of one such species have superior space-holding and other competitive abilities, and found no evidence that this superiority is offset by inferior competitiveness of its juveniles. This superiority in adult competitiveness derives from differences in body size that commonly occur among guilds of closely related territorial reef fishes and that often produce asymmetries in competitiveness among other animals. Thus there is no convincing empirical support for the central, original assertion of the Lottery Hypothesis concerning the mechanism by which coexistence is achieved – that, because different species have equal space-holding abilities, the patterns of use of space by and abundances of competitors are determined by patterns of juvenile recruitment into vacant space. Hence theory about lotteries needs to be modified to take into account interspecific asymmetries in adult competitive abilities such as those demonstrated here.

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