

## COMPETITIVE COEXISTENCE OF CORAL-DWELLING FISHES: THE LOTTERY HYPOTHESIS REVISITED

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**Abstract.** Evidence for competitive lotteries among reef fishes has remained elusive despite this being the group of organisms for which the lottery model was first developed. I used a combination of laboratory and field experiments to test the mechanisms of coexistence between two closely related species of coral-dwelling goby, *Gobiodon histrio* and *G. erythrospilus*, that occur in similar abundance at Lizard Island on the Great Barrier Reef. These two species exhibited similar patterns of habitat use and nearly identical ability to compete for vacant corals. Furthermore, there was a priority effect where the first species to occupy a vacant coral excluded an interspecific intruder of similar body size. The relative abundance of recruit and juvenile *G. histrio* and *G. erythrospilus* in the field matched the relative abundance of adults, as expected where there is no post-recruitment displacement by a competitive hierarchy. Finally, a reciprocal competitor-reduction experiment confirmed that *G. histrio* and *G. erythrospilus* compete for vacant space, with the removal of either species leading to an increase in the abundance of the other species. Therefore these two species are nearly ecologically equivalent and appear to coexist by means of a competitive lottery for vacant space.

**Key words:** competition; competitive coexistence; coral-reef fish; Gobiidae; *Gobiodon*; habitat specialization; lottery hypothesis; priority effect; recruitment.

### INTRODUCTION

Understanding the mechanisms by which similar species coexist is a central goal of community ecology and has become increasingly important as we attempt to predict the consequences of habitat destruction on patterns of species diversity (Nee and May 1992, Pacala 1997, Yu and Wilson 2001). Traditional niche-based models of competition (Colwell and Fuentes 1975, Diamond 1978) propose that competing species coexist through resource partitioning, where one (or both) of the competing species contracts its resource use to reduce competition with the other species. An alternative suite of models, such as the lottery hypothesis (Sale 1977, 1978), propose that competing species coexist through demographic mechanisms, without the need for resource partitioning. Despite the extensive body of theory dealing with coexistence of competing species (see Chesson 2000), the mechanisms by which similar species actually coexist in nature are still not well understood.

According to the lottery hypothesis, species with similar patterns of resource use can coexist through chance recolonization of vacant space, provided there are temporal or spatial fluctuations in the relative abundance of recruits available to occupy vacant habitats (Chesson and Warner 1981). The lottery model assumes that space is a limiting resource, that vacant

space is recolonized by the first-available recruit (analogous to a winning lottery ticket), and that once recolonized there is no displacement through competitive hierarchies (i.e., there is a strong priority effect). Coexistence is favored if the birth rate is higher for one species at some times or places and higher for the other species at other times or places. This idea was expanded by Warner and Chesson (1985), who demonstrated that coexistence by a lottery was enhanced in long-lived species because episodes of successful recruitment were maintained in the age structure and could buffer the population against periods of poor recruitment (the “storage effect”).

The lottery hypothesis was an important milestone in competition theory, but it has received relatively little empirical or experimental support. There is some evidence for the existence of competitive lotteries in plant (Henri et al. 1997, Lavelle 1999) and parasite (Janovy et al. 1992) communities, but there is almost no support for them in reef fish assemblages (Robertson 1995), the group for which the model was first developed (Sale 1977, 1978). Munday et al. (2001) suggested that a lottery for space determines the relative abundance of two coral-dwelling fishes (*Gobiodon histrio* and *G. axillaris*) at a scale of 10's of meters within reefs at Lizard Island on the Great Barrier Reef (Australia). However, they concluded that habitat partitioning at larger spatial scales was also important for the continued coexistence of these species. Where interspecific competition has been demonstrated to influence the distribution and abundance of reef fishes, the

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competitive ability of the species is usually highly asymmetric and resource partitioning appears to play a role in species coexistence (Hixon 1980, Larson 1980, Ebersole 1985, Holbrook and Schmitt 1985, Robertson and Gaines 1986, Schmitt and Holbrook 1990, 1999, Robertson 1996, Munday et al. 2001)

Coral-dwelling gobies (genus *Gobiodon*) are good candidates for coexistence by competitive lotteries because these fish spend their entire adult life among the branches of small coral colonies that are patchily distributed on the reef. Typically, each coral colony is occupied by just one pair of fish (Munday et al. 1998) and pairs often remain in the same coral colony for most of their adult life (*unpublished data*). Coral colonies are in limited supply (Munday et al. 1997, 2001, Munday 2002) and vacant space is quickly colonized by recruits from the larval pool, or by movement of post-settlement fishes to larger coral colonies (Munday et al. 2001). There is a competitive hierarchy among coral-dwelling gobies, and coexistence of most species is achieved through resource partitioning (Munday et al. 2001). There are, however, at least two species, *G. histrio* and *G. erythrospilus*, that inhabit the same species of coral and occupy the same reef habitats, and therefore must coexist by mechanisms other than habitat partitioning.

I investigated the mechanisms of coexistence between *G. histrio* and *G. erythrospilus* at Lizard Island (14°40' S, 145°28' E) on the Great Barrier Reef, where the two species occur in similar relative abundance (Munday et al. 1999). Specifically, I tested the underlying assumptions of the lottery hypothesis: that *G. histrio* and *G. erythrospilus* (1) use similar resources, (2) have similar competitive abilities, (3) exhibit a priority effect where the first individual to occupy a vacant space excludes interspecific intruders, and (4) compete for habitat space in the field.

#### METHODS

##### *Study species*

*Gobiodon* are small (<60 mm total length [TL]), obligate, coral-dwelling fishes that mostly inhabit corals from the family Acroporidae. Although *G. histrio* and *G. erythrospilus* have previously been regarded as the same species (Munday et al. 1999) they can be distinguished by differences in color pattern and the presence or absence of minute cycloid scales on the side of the body (Suzuki et al. 1995). A recent mitochondrial DNA analysis has confirmed that they are genetically distinct species (P. L. Munday and L. vanHerwerden, *unpublished data*). *G. histrio* and *G. erythrospilus* can be found in neighboring coral colonies, but rarely occupy the same coral colony, and have not been observed to form a breeding pair (*personal observation*).

##### *Habitat use*

To determine whether *G. histrio* and *G. erythrospilus* exhibit similar patterns of habitat use, I estimated the

frequency that each species of goby inhabited the different coral species in the lagoon at Lizard Island (Great Barrier Reef, Australia). Colonies of coral species known to be used by *G. histrio* or *G. erythrospilus* were searched for the presence of gobies and the species identity of the first 70 coral colonies inhabited by each species of goby was recorded. A chi-square test of independence was used to compare the frequency distribution of *G. histrio* or *G. erythrospilus* among the coral species inhabited.

##### *Competitive ability*

The lottery model assumes that vacant space is colonized by the first-available recruit and that once colonized there is no displacement through competitive hierarchies. I used a laboratory experiment to test the relative competitive abilities of juvenile *G. histrio* and *G. erythrospilus* and to determine whether a resident could always exclude an interspecific intruder. Because gobies are small, sedentary fishes, a relatively large aquarium (~50 × 30 × 30 cm) provided a reasonably realistic forum for examining behavioral interactions. To test whether *G. histrio* and *G. erythrospilus* were equivalent competitors, I simultaneously placed one juvenile of each species on a vacant coral colony and recorded which species remained in the coral colony and which species was evicted. *Acropora nasuta* was the coral habitat used in this experiment because it is the preferred species of coral for both *G. histrio* and *G. erythrospilus* at Lizard Island (Munday et al. 1997, 2001). *A. nasuta* colonies of a size inhabited by juveniles (~10-cm diameter) were carefully removed from the reef, transported to the laboratory, and cleared of all infauna (gobies, crabs, and shrimps). One colony of *A. nasuta* was placed in each of 10 glass aquaria. To provide shelter for evicted fish, a similar-sized piece of coral that had been bleached to remove all living tissue was placed at the other end of each aquarium, ~10 cm from the live coral colony. Fresh seawater entered each aquarium from above and an external standpipe controlled water depth.

Juvenile *G. histrio* and *G. erythrospilus* were collected from colonies of *A. nasuta* in the wild by anaesthetization with clove oil and held in separate aquaria. Juveniles were used in this experiment because their competitive abilities are most likely to closely match that of new recruits and they are the smallest individuals amenable to manipulative experiments. The mean size of juveniles was 25.2 mm TL (range: 16.1–34.0 mm) for *G. histrio* and 24.8 mm TL (range: 17.2–33.9 mm) for *G. erythrospilus*. At the beginning of each trial one juvenile of each species was simultaneously allowed to colonize a colony of *A. nasuta*. Individuals in each trial were matched for size (within 2 mm TL) and transferred to the coral colony via a plastic tube positioned above the coral, which was removed once the fish had colonized the coral. Fish were released onto the corals between 18:00 and 19:00 hours and the

outcome recorded at 07:00 hours the following morning. At the end of the each trial the fish were measured (TL to nearest 0.1 mm) to confirm that they had been correctly matched for size. A chi-square goodness-of-fit test was used to determine whether the observed frequency distribution of wins differed significantly between the species.

Having determined the relative competitive ability of *G. histrio* and *G. erythrospilus*, I then tested whether a resident could exclude an interspecific competitor of similar body size. An identical protocol to that described above was used, except that one juvenile was allowed to be a prior resident of the coral colony for 8 h before the other fish was released. A chi-square goodness-of-fit test was used to determine whether the observed frequency distribution of wins by the resident and intruder differed significantly.

The lottery model assumes that patterns of abundance established by recruits to vacant corals will not be modified by post-recruitment competitive hierarchies. Therefore, the relative abundance of *G. histrio* and *G. erythrospilus* present on reefs at Lizard Island should not differ markedly among recruit, juvenile, and adult stages. In contrast, if the species have unequal space-holding ability then, in the absence of immigration, the relative abundance of the subordinate species should decline in time compared to the relative abundance of the superior competitor. To compare the relative abundances of *G. histrio* and *G. erythrospilus* at different life stages, I censused the abundance of recruits (<25 mm TL) and juveniles (25–30 mm TL) of each species during a haphazard search on reefs on the leeward side of Lizard Island during October 2002. In this census all recruits and juveniles were collected with clove-oil anesthetic, measured (TL to nearest 0.1 mm), and then released back to their home coral. The relative abundance of each life-history stage was then compared to the relative abundance of adults on these reefs recorded during collections made during 2000–2001 in conjunction with other experiments.

#### Competition for space

I used a manipulative experiment to test whether *G. histrio* and *G. erythrospilus* compete for habitat space in the field. Specifically, a reciprocal competitor-removal experiment was used to determine whether competition for space had a similar effect on the abundance of each species in the field. The abundance of *G. histrio* was reduced in four replicate plots of reef and the abundance of *G. erythrospilus* was reduced in another four plots. A further eight control plots were established where neither species was removed. Experimental plots, each ~25 m<sup>2</sup> in area, were established on the reef flat on the leeward side of Lizard Island in January 1998. *G. histrio* and *G. erythrospilus* were removed from their respective treatment plots by anaesthetizing the fish with clove oil and carefully removing them from the corals. Plots were checked again in May 1998

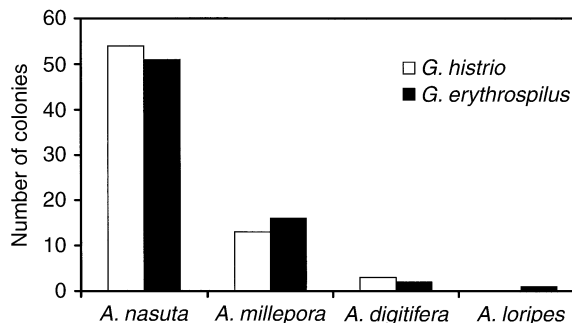


FIG. 1. *Acropora* species inhabited by *Gobiodon histrio* and *G. erythrospilus* at Lizard Island (Great Barrier Reef, Australia);  $N = 70$  coral colonies for both species of goby.

and any *G. histrio* or *G. erythrospilus* that had colonized the respective treatment plots were removed. The abundance of *G. histrio* or *G. erythrospilus* in all plots was recensused in December 1998.

If competition for space limited the abundance of *G. histrio*, it should increase in abundance where *G. erythrospilus* was removed but not in control plots. Similarly, if competition for space limited the abundance of *G. erythrospilus*, it should increase in abundance where *G. histrio* was removed but not in control plots. Therefore, I compared the increase in abundance of each species between the start and end of the experiment in treatment vs. control plots. Because the initial number of *G. histrio* and *G. erythrospilus* varied between plots it was not possible to compare the absolute changes in abundance between control and treatment plots using a parametric test. Mann-Whitney  $U$  tests were used instead to test the rank order of changes in abundance.

## RESULTS

### Habitat use

There was no significant difference in habitat use between *Gobiodon histrio* and *G. erythrospilus* (chi square = 1.6,  $df = 3$ ,  $P = 0.66$ ). Both species mostly occupied colonies of *Acropora nasuta*, used *A. millepora* to a lesser extent, and occasionally inhabited colonies of *A. digitifera* and *A. loripes* (Fig. 1).

### Competitive ability

Juvenile *G. histrio* and *G. erythrospilus* exhibited similar ability to compete for preferred coral habitat. In 32 trials where similar-sized fish were released simultaneously onto a coral colony, one fish was always evicted, with *G. histrio* winning 18 times and *G. erythrospilus* winning 14 times (chi-square = 0.5,  $df = 1$ ,  $P = 0.48$ ). In contrast, where one fish had colonized the coral colony 8 h earlier than the other fish, there was a priority effect where the resident was nearly always able to evict the intruder. In 14 trials, the resident won 12 times and the intruder won only 2 times (chi-square = 7.14,  $df = 1$ ,  $P = 0.008$ ).

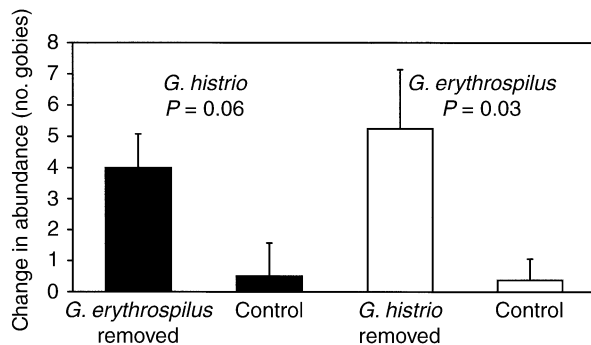


FIG. 2. Change in abundance of *Gobiodon histrio* in plots where *G. erythrospilus* was removed ( $N = 4$ ) and in controls plots ( $N = 8$ ) where no fish were removed, and change in abundance of *G. erythrospilus* in plots where *G. histrio* was removed ( $N = 4$ ) and in controls plots ( $N = 8$ ) where no fish were removed. Data are means + 1 SE.

The relative abundance of recruit and juvenile *G. histrio* and *G. erythrospilus* in the field supported the conclusion that these species have similar space-holding ability. Of 37 recruits (<25 mm TL) recorded during the haphazard search, 15 (40.5%) were *G. histrio* and 22 (59.5%) were *G. erythrospilus*. Of 29 juveniles (25–30 mm TL) recorded during the same search, 12 (41.4%) were *G. histrio* and 17 (58.6%) were *G. erythrospilus*, indicating that there was no post-recruitment displacement of one species or the other through a competitive hierarchy. The proportional abundance of recruits and juveniles was similar to the proportional abundance of adults ( $N = 348$  individuals: *G. histrio* 43.4% and *G. erythrospilus* 56.6%) recorded at the same sites in the previous two years.

#### Competition for space

Competition for habitat space had similar effects on the abundance of *G. histrio* and *G. erythrospilus*. The abundance of *G. erythrospilus* increased significantly following the removal of *G. histrio* compared to controls where *G. histrio* was not removed (Fig. 2; Mann-Whitney  $U_{4,8} = 3.0$ ,  $P = 0.03$ ). Similarly, the abundance of *G. histrio* increased following the removal of *G. erythrospilus*, compared to controls where *G. erythrospilus* was not removed (Fig. 2; Mann-Whitney  $U_{4,8} = 5.0$ ,  $P = 0.06$ ), although the change was not statistically significant at a probability level of 0.05. The trend for a greater response of *G. erythrospilus* compared to *G. histrio* following the removal of the competitor is consistent with the higher relative abundance of recruits (~60% of total) available to colonize vacant space.

#### DISCUSSION

The lottery model (Sale 1977, 1978) was a key development in competition theory, yet there is almost no evidence for the presence of competitive lotteries among reef fishes (Robertson 1995), the group of an-

imals for which the model was originally proposed. This study supports the existence of a competitive lottery between two coral-dwelling fishes, *Gobiodon histrio* and *G. erythrospilus*, that occur in similar abundance at Lizard Island on the Great Barrier Reef (Australia). These two species exhibit similar patterns of habitat use and juveniles exhibit nearly identical ability to compete for preferred habitat. Furthermore, there is a strong priority effect—the first individual to colonize a vacant habitat is able to defend it against intruders. Finally, these two species compete for vacant space in the field, with the removal of either species leading to an increase in abundance of the other species. In combination, these results demonstrate that coral colonies are a limiting resource and that *G. histrio* and *G. erythrospilus* coexist by means of a competitive lottery where vacant habitat is colonized by the first-available recruit.

The lottery model assumes that species have similar abilities to secure habitat space, and departure from this assumption will lead to competitive exclusion by the superior competitor unless there is a mechanism to compensate for the competitive asymmetry (Chesson and Warner 1981). For example, species with different competitive abilities could coexist in a competitive lottery if the subordinate competitor had higher fecundity than the superior competitor. Under conditions of equal space-holding ability, the relative abundance of each species should not differ markedly among recruit, juvenile, and adult stages. In contrast, if the species have substantially different space-holding ability, then the relative abundance of the subordinate species should decline in time compared to the relative abundance of the superior competitor. The similar relative proportions of recruit and juvenile *G. histrio* and *G. erythrospilus* observed here is consistent with these species having similar space-holding abilities. Furthermore, the correlation between the relative abundance of recruits and juveniles recorded during this study, and the relative abundance of adults recorded during the previous two years, suggests that there is a reasonable stock–recruitment relationship for each species at Lizard Island.

Despite the apparent presence of a stock–recruitment relationship for these species at Lizard Island, stable coexistence in a competitive lottery requires that environmental variability favors the survival of one species at some times or places and the other species at other times or places (Chesson and Warner 1981, Chesson 1985). Temporal or spatial variation in the supply of larvae of *G. histrio* and *G. erythrospilus* to reefs at Lizard Island may be sufficient to prevent one species gaining a numerical advantage that would ultimately lead to the exclusion of the other species. Variations in the relative abundances of recruits could occur due to interannual variation in oceanographic conditions that favor survival of one species over the other in different years. Alternatively, stochastic variation in

TABLE 1. Predictions of different models of competitive coexistence between two species regarding the relative risk of extinction due to habitat destruction.

Model of competitive coexistence	Mechanism of coexistence	Risk of extinction due to habitat destruction
Resource partitioning (included-niche model)*	Contraction of resource use by subordinate competitor	Greater for subordinate competitor
Lottery	Chance recolonization of vacant space	Equal for both species
Competition–colonization trade-off	Subordinate competitor is better at colonizing vacant space but superior competitor can always displace the subordinate	Greater for superior competitor

\* Hypothesized by Colwell and Fuentes (1975).

the spatial distribution of larvae may produce temporal patchiness in the relative abundance of each species arriving at any reef.

A differential cline in the relative abundance of *G. histrio* and *G. erythrospilus* on a latitudinal gradient from the southern Great Barrier Reef to northern Papua New Guinea (Munday et al. 1999) indicates that variation in environmental conditions may indeed favor the survival of different species at different times or places. The relative abundance of *G. erythrospilus* declines from the southern Great Barrier Reef towards northern Papua New Guinea. In contrast, the relative abundance of *G. histrio* increases along the same latitudinal gradient. This differential cline in relative abundance is correlated with increasing water temperature from the southern Great Barrier Reef to northern Papua New Guinea. If *G. histrio* exhibits better survival than *G. erythrospilus* as water temperature increases and *G. erythrospilus* exhibits better survival than *G. histrio* as water temperature decreases, then inter- and intra-annual variations in water temperature at Lizard Island could lead to temporal variation in the relative abundance of recruits of each species, thereby promoting coexistence. A differential gradient in survival or growth rates related to water temperature could also explain the latitudinal cline in the abundance of these two species. Differences in the relative success of each species at any location along the geographic gradient (i.e., the outcome of competitive interactions on a local scale) could produce a pattern where *G. histrio* tends to dominate in northern regions and *G. erythrospilus* tends to dominate in southern regions.

Coexistence by a lottery for space is favored in long-lived species where successful recruitment events are stored in the population age structure (Chesson and Warner 1981). *G. histrio* and *G. erythrospilus* can live for at least four years (*unpublished data*), therefore, the populations of both species will have a number of overlapping generations. Overlapping generations are important to coexistence in lottery systems involving temporal fluctuations in recruitment (Chesson 1985), because they buffer the population of each species against poor recruitment in some years. Without this buffer, one species may gain a large numerical advantage and consequently produce sufficient reproductive

propagules to swamp any vacant habitat and lead to competitive exclusion of the other species. In contrast to coral-dwelling gobies, many other tropical gobies live for less than one year (Hernaman et al. 2000, Kritzer 2002). Where these short-lived species have very seasonal patterns of reproduction and recruitment, they will tend to have non-overlapping generations and, consequently, be unlikely to coexist by a lottery mechanism that relies on temporal fluctuations of recruitment.

Determining how competing species coexist in nature is important because different models make very different predictions about the relative extinction risk of competing species as a result of habitat destruction (Table 1). Where subordinate competitors use habitats that are less preferred by a superior competitor (i.e., included-niche model of Colwell and Fuentes [1975]), the subordinate competitor is at greater risk of extinction because it may be excluded from these habitats by the superior competitor as preferred habitats become less abundant. In contrast, the superior competitor is at greater risk of extinction in a competition–colonization model because it has lower potential to colonize any new space that becomes vacant (Nee and May 1992). Coral reefs are under increasing stress in many parts of the world and dramatic declines in coral abundance and changes in coral community structure have been reported from numerous locations (Wilkinson 2000). Due to their obligate association with living coral, species of *Gobiodon* are likely to be highly susceptible to population decline as a result of changes in coral abundance (Munday et al. 1997). The ability of each species to secure sufficient habitat space to maintain viable populations will depend on its relationship with competitors. Munday et al. (2001) demonstrated the presence of competitive asymmetries and coexistence by resource partitioning among coral gobies. Under this scenario, subordinate competitors are at greater risk of extinction than superior competitors. This study adds lottery competition as a mechanism for coexistence of these fishes and in this case the probability of extinction for each species will also be a lottery.

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