

Growth trades off with habitat specialization

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How differences in niche breadth evolve and are maintained remains largely unknown. The ‘jack of all trades is master of none’ model of resource specialization has been widely considered, but, to our knowledge, never before supported empirically. It invokes performance trade-offs associated with specialization. Specialists should outperform generalists on a subset of resources, but be unable to maintain high performance over a broader range of resources. By contrast, generalists should perform less well, on average, using a greater diversity of resources. We report such trade-offs among four coral goby species in the wild. Habitat specialists grew faster than generalists in one of two habitats. Average growth rates of generalists were less than that of specialists, but more consistent between habitats. Performance trade-offs associated with resource specialization could influence the evolution and maintenance of narrow niche breadth.

Keywords: genotype–environment interaction; growth; coral-reef fishes; niche breadth; specialization; trade-offs

1. INTRODUCTION

Niche breadth differences among species are commonly thought to be underpinned by genetic trade-offs between the capacity of species to exploit a range of resources and their performance using each one (Lynch & Gabriel 1987; Futuyma & Moreno 1988; Kawecki 1994; Van Tienderen 1997; Scheiner 1998). Accordingly, a specialist species may outperform a generalist on a subset of resources, but be unable to maintain that greater performance on a broader range. Alternatively, a generalist species may be able to perform on a greater range of resources but never achieve the performance of a specialist on any one (figure 1). An extensive search for such trade-offs with specialization has been largely unsuccessful (Futuyma & Moreno 1988).

We investigated under field conditions, trade-offs with specialization among four species of coral-dwelling gobies that vary widely in their degree of habitat specialization (Munday *et al.* 1997; table 1). Specifically, we tested for growth trade-offs in two habitat-specialized and two habitat-generalized goby species in two species of coral host. In the presence of performance trade-offs with resource specialization, habitat specialists should exhibit faster growth than generalists on one or more of the resources they exploit compared with the maximum growth rate of generalists on any of their broader range of resources (figure 1).

2. MATERIAL AND METHODS

This experiment was conducted in the lagoon of Lizard Island (14°40' S, 145°28' E) on Australia's Great Barrier Reef between January and April in 1997 and 2001. We translocated onto colonies of two coral species (i.e. *Acropora nasuta* and *A. loripes*) juveniles of four goby species (i.e. *Gobiodon brochus*, *G. histrio*, *G. quinquestrigatus* and *G. oculolineatus*) and estimated their subsequent growth. These goby species were classified as either habitat specialists or habitat generalists based on the total number of coral species they occupy at this location in proportion to their availability, or more frequently than expected by chance, compared with the number they either avoided (used less than expected based on availability) or did not use at all (Munday *et al.* 1997; table 1). The range of coral species used by the specialist species is nested within the range occupied by the generalists (Munday *et al.* 1997). Such nesting of resource use facilitates a very reliable estimate of specialization (Futuyma & Moreno 1988).

Acropora nasuta and *A. loripes* were chosen as experimental hosts because they are both used naturally at this location by these *Gobiodon* spp. (Munday *et al.* 1997); growth rates of gobies in these two hosts can vary substantially (Munday 2001) and they are the most morphologically divergent of the coral species (Veron 2000) used by these gobies. Growth rates of *Gobiodon* spp. are correlated with coral morphology (Munday 2001) and by using these morphologically divergent coral species we hoped to sample the maximum variation in growth rates of gobies associated with their use of different habitats at this location. The design of this experiment is illustrated by the left-hand half of figure 1a–c.

Juvenile gobies were collected from corals, measured (standard length (SL) ± 0.1 mm) and individually marked with a small fluorescent intramuscular tag. Each coral from which a goby was collected was individually tagged with a numbered metal washer and cleared of all other gobies. Tagged fishes were released 24 h after capture on these corals, one fish per coral, and never on the coral from which it was collected. Three to four months later, the fishes were recaptured and their growth estimated. Variances of growth estimates were homogenized using a log($x + 1$) transformation (Bartlett's test, $p > 0.12$).

Fecundity of coral goby pairs is dependent on the size of both the male and the female (Kuwamura *et al.* 1993). Therefore, we assumed that slow growth is costly in fitness terms for both males and females because a smaller size would be associated with lower fecundity. Growing at the maximum rate possible, however, is not necessarily the fittest strategy either (Mangel & Stamps 2001). Therefore, we also tested whether fast growth was associated with higher mortality in our experiment by examining losses of each goby species from each species of coral. While losses confound emigration and mortality, *Gobiodon* spp. shelter deep in their host corals and are very strongly site attached as adults (Munday 2001). Therefore, losses from these corals should be a reasonable proxy for mortality.

3. RESULTS

These fishes did not differ significantly in initial size, SL, among species (ANOVA: $F_{3,93} = 0.03$, $p > 0.98$). Similarly, their growth rates were unrelated to host volume (least-squares regression: $n = 64$, $r^2 = 0.002$, $p > 0.71$) and year (ANOVA: $F_{1,53} = 0.008$, $p > 0.93$). Therefore, these covariates are not considered further.

On average, specialist species grew faster than generalists (table 2; daily growth rates (given in mm day⁻¹ (mean (s.e.m.)): specialists: *G. brochus* = 0.014 (0.002), $n = 26$; *G. histrio* = 0.018 (0.001), $n = 35$; generalists: *G. oculolineatus* = 0.005 (0.002) $n = 24$; *G. quinquestrigatus* = 0.014 (0.002) $n = 12$; contrast: specialists versus generalists, $p < 0.0005$). Fishes occupying colonies of *A. nasuta* grew faster than fishes occupying colonies of *A. loripes*, but this response to habitat differed between habitat specialist and generalist species (table 2; figure 2). This genotype–environment interaction is evidence of a trade-off between habitat specialization and growth. Specialists displayed higher maximum growth rates than generalists. The average growth rate of both specialist species in one habitat (i.e. *A. nasuta*) was more than 2.6 (s.e.m. = 0.04) times greater than on the other. Growth of generalist species, by contrast, varied between habitats by less than a factor of 1.3 (s.e.m. = 0.39). Therefore, the cost of being

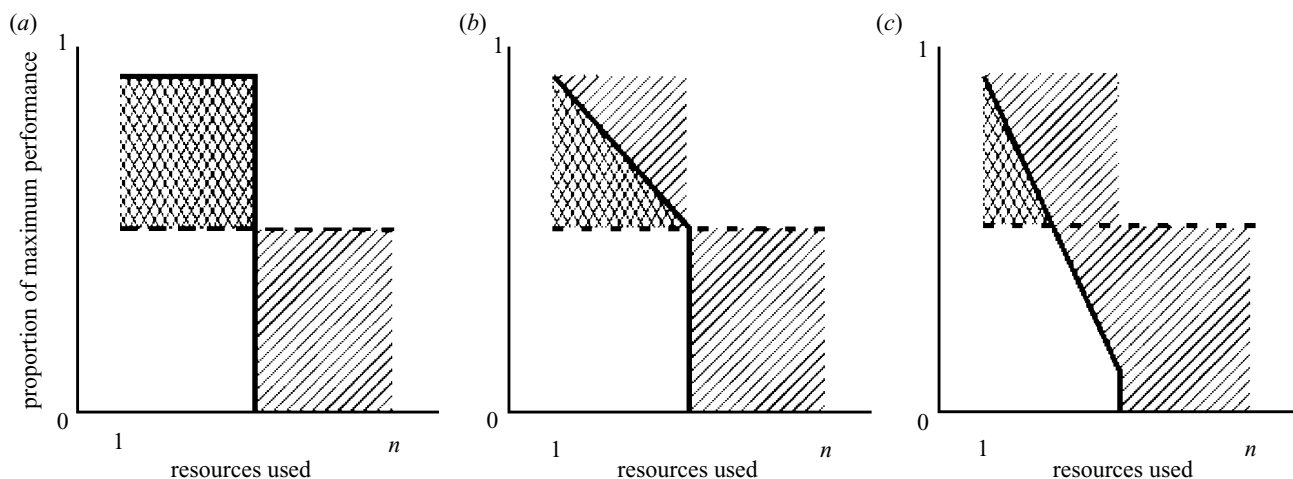


Figure 1. Three fitness trade-off scenarios comparing a generalist (dashed line) and a specialist (solid line) species. The niche breadth of each species is indicated by the width of its resource spectrum associated with a non-zero value of fitness. Along the x-axis resources are ranked from best to worst with respect to the maximum performance of the specialist using each resource. The specialist has a niche breadth half as wide as, and nested within, that of the generalist's niche breadth. The generalist's maximum fitness on any resource is, arbitrarily, half the maximum obtained by the specialist. Hatched area, cost to specialist; cross-hatched area, cost to generalist. (a) The specialist species outperforms the generalist and realizes maximum fitness on all resources it uses. Whereas, the generalist has lower performance across a broader range of resources. The specialist trades greater niche breadth for high performance on fewer resources. The generalist trades high performance on any resource(s) for greater niche breadth. (b) The specialist has higher or equal performance compared to the generalist on all shared resources. In this case, in addition to the cost to the specialist of zero fitness on a range of resources that it does not use, high performance on some of the resources on which it is specialized is associated with an additional cost. Its high performance on some resource(s) trades off against lower performance on some others within the range of resources it exploits. (c) The trade-off for the specialist species between high performance on a subset of its resources and its performance on the rest is greater than in (b) with the generalist outperforming the specialist on some of their shared resources.

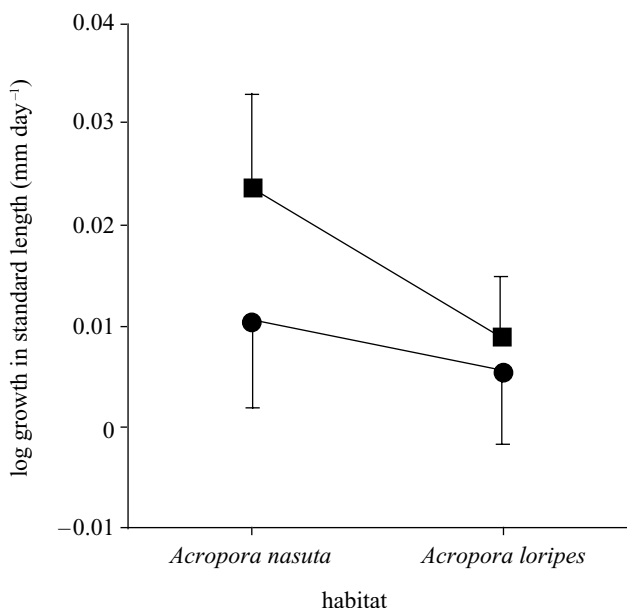


Figure 2. Interaction between growth rates of habitat specialist (squares) and habitat generalist (circles) goby species in two coral habitats. Habitat-specialized species displayed greater differences in growth rates between the two habitats than did habitat-generalized ones. Specialist species were less able to maintain their growth rate in different habitats than generalist species. Generalist species achieved lower maximum growth rates, a cost of plasticity. Plotted values are the mean and standard error of the mean of growth rates. For clarity, the standard error of the mean is plotted in one direction only.

a generalist, in this case, is the trade-off between growth rate and greater niche breadth (i.e. figure 1b).

Losses of three of the four goby species (i.e. *G. brochus*, *G. oculolineatus* and *G. quinquestrigatus*) did not differ significantly between the two coral species (χ^2 -test of independence, $p > 0.12$ in all cases). By contrast, *G. histrio* translocated to colonies of *A. nasuta* were more likely to be recovered than individuals translocated to *A. loripes* (χ^2 -test of independence, $p < 0.02$). Therefore, rapid growth does not appear to trade-off with mortality for any of these species. Instead, the growth advantage derived by *G. histrio* from residing in *A. nasuta* colonies may actually underestimate the fitness advantage it derives from habitat specialization.

4. DISCUSSION

Habitat specialization traded off strongly against growth; greater specialization was associated with greater growth rates, but a reduced ability to maintain them on different resources (figure 2). Greater generalization, by contrast, was associated with a preference for a wider range of host corals (table 1), but an inability to achieve the high growth rates of the specialists on the two most structurally divergent host species that all four species of gobies inhabit. That specialization on one resource trades off against performance on another, and that there is a cost to being a generalist are fundamental tenets of the 'jack of all trades is master of none' model of the evolution of specialization (Futuyma & Moreno 1988). Such trade-offs have been widely expected because they could prevent the evolution of a single perfect generalist species (Futuyma & Moreno 1988; Van Tienderen 1997), but

Table 1. Patterns of habitat preference exhibited by four species of coral-dwelling gobies among species of acroporid corals in the lagoon of Lizard Island (sources: Munday *et al.* 1997; Munday 2001) classified as generalists and specialists.

coral species occupied	specialist species		generalist species	
	<i>G. histrio</i>	<i>G. brochus</i>	<i>G. quinquestrigatus</i>	<i>G. oculolineatus</i>
preferred or proportional use	3	3	6	6
avoided or unused	5	5	2	2

Table 2. Analysis of variance of log growth rates of four species of coral-dwelling gobies translocated into two species of corals. (Goby species were categorized as either generalist or specialist (table 1). The main effects of habitat and specialization were analysed as fixed effects, and goby (specialization) as a random effect. Therefore, the main effect specialization was tested over a synthesized mean square ($MS_{\text{synthesized}} = 0.774(\text{goby species}(\text{specialization})) + 0.226 \times (\text{residual})$). The remaining factors were tested over MS_{residual} .)

source	d.f.	MS	F-ratio	p
habitat	1	0.0014	22.65	< 0.0001
specialization	1	0.0003	3.60	> 0.29
goby species	2	0.0007	5.55	< 0.005
habitat × specialization	1	0.0008	13.72	< 0.0005
habitat × goby species (specialization)	2	0.00004	0.59	> 0.55
error	89	0.00006		

they have been difficult to demonstrate (Futuyma & Moreno 1988; Jaenike 1990; Via 1990; Fry 1996; Kassen & Bell 1998). Why, then, were these trade-offs evident here?

Our experiment differed in two important respects from previous studies. It exploited interspecific variation in habitat specialization, and it tested for trade-offs under natural conditions. Most previous studies have examined trade-offs within species, among clones or host races, under artificial conditions or following artificial selection for specialization (Futuyma & Moreno 1988; Rauscher 1988; Jaenike 1990; Via 1990; Fry 1996; Van Tienderen 1997; Kassen & Bell 1998). Although the search for trade-offs with host specialization has largely failed, it may be premature to abandon the 'jack of all trades is master of none' model of habitat specialization given our results. Instead, understanding the evolution of niche breadth may require refocusing the investigation of trade-offs on where they would have been important in the evolution of specialization—in the wild, and among rather than within species. If trade-offs between fitness and specialization commonly evolve they are more likely to be detectable in comparisons among species that have had considerable time to diverge.

The trade-offs with host specialization reported here illustrate the potential importance of performance trade-offs in the evolution of niche breadth. In the presence of such trade-offs, habitat specialization may limit the potential of species to respond plastically to environmental change and for the evolution of generalists that can out-compete specialists on all resources. The myriad evolutionary implications of such trade-offs are potentially profound (Holt 1997; Schluter 2000).

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