



## Original Research Article

## Goby–shrimp mutualism: Costs and benefits of obligate versus facultative strategies

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## ARTICLE INFO

## Keywords:

Obligate mutualism  
 Facultative mutualism  
 Cost-benefit  
 Tradeoff  
 Explicit resource accounting

## ABSTRACT

We model the mutualism interactions between gobies and shrimp based on recent experimental work on the shrimp *Alpheus floridans* and the facultative and obligate gobies *Ctenogobius saepepallens* and *Nes longus* in the Bahamas. We show that the model is consistent with observations, and suggest that obligate mutualism may favour rapid speciation in gobies due to their restricted spatial range. We calculate the resilience of the goby–shrimp systems to evaluate the robustness of the mutualist interactions to parameter choices. While experimental evidence has noted the ubiquity of obligation in gobies, our theoretical investigation predicts the ubiquity of facultative mutualism in shrimp despite the many obligate mutualism strategies open to them. Future experimental work might be usefully directed at evaluating the ubiquity of facultative versus obligate interactions of shrimp in goby–shrimp mutualist populations, and examining whether facultative and obligate strategies are correlated with food availability.

## 1. Introduction

We consider the dynamics of a goby and a shrimp population based primarily on the field study of Lyons (2013) in the Bahamas, but see also Thompson et al. (2006). The goby and shrimp engage in a mutualist relationship, that may be facultative or obligate, where each shrimp constructs a burrow that can accommodate both the shrimp and its goby partner. The shrimp provides protection for the goby from its predators (mainly groupers), allowing the goby to forage for food with a refuge in close proximity. The goby provides warnings to the shrimp, signalling when it is unsafe to leave the burrow to forage for food due to the presence of predators. In certain cases the shrimp may utilise the goby's faeces as its sole source of food, and then the goby exclusively defecates inside the burrow. Lyons speculated that the increased costs of an obligate lifestyle must be balanced by the significant advantages enjoyed by both the goby and the shrimp populations. We investigate that speculation in this study.

A key to understanding mutualisms is to understand the cost/benefit payoff or tradeoff involved in the interaction between the mutualist partners. Lyons (2013) measured the improved life expectancy of gobies when they behave in an obligate manner. He also notes that they spend a majority of their time hiding in burrows, but does not quantify this. Lyons also asks what is the cost/payback to the goby for becoming obligate, i.e. is the significant reduction in mortality for obligate gobies

staying close to, and hiding in, a particular shrimp burrow (that is observed by Lyons) offset by a reduction in feeding due to reduced grazing time and range. Lyons (2013) does not measure the costs and benefits that accrue to the shrimp for changes in its behaviour (which appear to be more complex than the options available to the gobies). The shrimp may feed on plankton/detritus outside its burrow, in which case the goby provides a protection; or it may feed both outside and inside its burrow on plankton and goby faeces; or may feed exclusively inside its burrow solely on goby faeces. Each of these options involves different costs and benefits which will have different eco-evolutionary implications.

To robustly consider tradeoffs, we need a measure of costing that is compatible with the benefits of obligate behaviour. The model we propose here is both simple enough to understand, and yet we can compare with data. We use a linear cost/benefit analysis that balances costs and benefits related to the changes in behaviour of the gobies and shrimp spending more time in their burrow versus more time outside and foraging over a larger area. We use this model to examine several aspects of the goby–shrimp interaction, in particular Lyons (2013) suggestion that over 90% of goby species are obligate on their shrimp partners. This raises the question of whether obligate mutualism provides the gobies with an eco-evolutionary advantage that is reflected in the ubiquity of obligate mutualism among gobies, or whether the constriction of spatial movement associated with obligate mutualist

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**Table 1**  
Summary of parameter roles that determine facultative/obligate interactions.

Parameter	Role
$a_{21}$	Rate of goby grazing on plankton - reduced if foraging range is reduced
$a_{23}$	Cost incurred by goby in obtaining a mutualist benefit from the shrimp - metabolic cost of providing warnings to the shrimp or cost of reduced foraging range
$\mu_2$	Maximum magnitude of mortality reduction of gobies due to provision of burrows by shrimp
$\epsilon_2$	Half-saturation constant for mortality reduction due to availability of burrows
$a_{31}$	Rate of shrimp grazing on plankton - zero if shrimp feeds only on goby faeces
$a_{32}$	Cost of obtaining mutualism benefit from gobies or rate of shrimp feeding on goby faeces
$\mu_3$	Maximum magnitude of mortality reduction of shrimp due to warnings from gobies

relationships drives speciation among those gobies that are obligate.

All living populations must resolve the competing imperatives to increase their sustainable population size, by maximising their growth rate and/or minimising their mortality rate, and to ensure the reliable availability of their food supply by “farming” their resources (nutrients or populations) that they rely upon to grow. These imperatives are resolved in an ecosystem in which the equilibrium point where all populations coexist is stable and resilient. Resilience measures the rate at which the system will return to its previous state after a perturbation. Populations in a highly resilient ecosystem will maintain reliable sustainable food supplies even in environments that are subjected to substantial perturbations.

We take as ‘canonical species’ the obligate goby *Nes longus* and the facultative goby *Ctenogobius saepepallens*, together with the shrimp *Alpheus floridans*. We build a computational simulation model for these interactions to see if resilience of the system varies with facultative or obligate behaviours. We examine the ubiquity of obligate and facultative mutualist interactions between gobies and shrimp by examining the properties of ecologically-realistic instantiations of our model, defined with randomly generated parameter values over appropriately defined ranges. We randomly sample large numbers of parameter choices to model our systems, extract the ecologically relevant ones, and then categorise which parameters lead to higher resilience or diversity. Despite constraining the parameter space sampled to minimise unrealistic parameter combinations, only around 8% of the random parameter sets sampled produce valid ecosystems that have positive finite equilibrium populations, of which around 63% have stable equilibriums and 27% have persistent population oscillations. We classify each valid instance of the model according to the type of its mutualist interactions (obligate or facultative). We examine the trade-offs in each case and how they relate to overall properties of the system such as its resilience and the equilibrium partitioning of biomass to identify cost-benefit interactions and consider our results in the context of Lyons (2013) observations that obligate goby species are much more common in the field.

## 2. A mutualist model for gobies and shrimp

Gobies and shrimp are marine shallow water heterotroph populations that have a mutualist relationship which we model by the inclusion and explicit accounting of finite resources for each population. Gobies consume zooplankton such as copepods and utilise shrimp burrows for shelter from grouper, their primary predators. In return, the gobies either provide food for the shrimp by defecating inside the burrow, where the shrimp feeds on the faeces, or alert the shrimp to safe feeding conditions outside the burrow by waving their caudal fins. The shrimp dig and maintain the burrows that provide shelter for both themselves and the gobies.

The goby  $x_2$  and the shrimp  $x_3$  populations and their interactions are modelled in their simplest form consistent with experimental results. We use the Lotka–Volterra models (Lotka, 1925; Volterra, 1925) in the CN framework (Cropp and Norbury, 2015) as the basis for our modelling approach and adopt the standard notation for the parameters and their signs. We accept that this may lead to interactions being

somewhat counterintuitive to some readers, but suggest that the benefits of casting the model in this general framework outweighs the convenience of writing a specific model just for this single application. (Note that using more complicated forms of interactions such as the commonly used saturating Holling Type II and III forms does not qualitatively change our results.)

We reserve  $x_1$  for the aggregated plankton species that the goby, and potentially the shrimp, populations feed on. The goby and shrimp populations may depend upon each other to survive via protection mutualisms, and both populations may feed on a common resource, the plankton  $x_1$ . The goby population  $x_2$  only feeds on the plankton population  $x_1$ , and this is represented by the simplest grazing term  $-a_{21}x_1x_2$  (where  $a_{21} < 0$ ). The shrimp population may also feed on the plankton  $x_1$  or may feed on goby faeces, which are proportional to  $x_2$ . These processes are represented by the terms  $a_{31}x_1x_3$  and  $a_{32}x_2x_3$  respectively, where  $a_{31} < 0$  and  $a_{32} < 0$ .

Either population may receive a mutualist benefit from the presence of the other that reduces its mortality, which we represent with  $r_i(1 - M_i(x_j))x_i$ , where  $r_i$  is the usual density-independent heterotroph mortality coefficient ( $i, j = 2, 3; i \neq j$ ), and  $M_i(x_j)$  is the mutualist protection benefit that  $x_i$  derives from  $x_j$ . We use  $M_2(x_3) = \mu_2(x_3/[x_3 + \epsilon_2])$  for the reduction in goby mortality due to shrimp and  $M_3(x_2) = \mu_3x_2$  for the reduction in shrimp mortality due to gobies. We chose values for  $\mu_2$  and  $\epsilon_2$  consistent with that measured by Lyons (2013) (see Supplementary Material for details). We also include the usual density-dependent mortality terms  $a_{22}x_2^2$  and  $a_{33}x_3^2$  which include predation losses to un-modelled higher trophic levels. The generic interaction term  $a_{23}x_2x_3$  is usually positive, reflecting that the sequestration of a fraction of the total resources by the shrimp population results in fewer resources being available for the goby population (see Table 1 for further details).

Collecting these process terms, and writing them in a per-capita rate form provides the following equations that determine the population sizes:

$$\begin{aligned}\dot{x}_2 &= x_2 f_2(x_1, x_2, x_3) = x_2 [r_2(1 - M_2(x_3)) - a_{21}x_1 - a_{22}x_2 - a_{23}x_3], \\ \dot{x}_3 &= x_3 f_3(x_1, x_2, x_3) = x_3 [r_3(1 - M_3(x_2)) - a_{31}x_1 - a_{32}x_2 - a_{33}x_3].\end{aligned}\quad (1)$$

Our explicit, exact resource cycling and accounting framework requires that we include an equation that describes the availability of resources, in this case plankton  $x_1$ , for the gobies  $x_2$  and shrimp  $x_3$  to feed on, and an equation that describes the availability of nutrients  $N$ , the resource for  $x_1$ . We use  $x_1$  to capture a combined plankton population (i.e. comprising phytoplankton, mixotrophic plankton, and zooplankton). The plankton population dynamics are determined by  $r_1$ , the net growth rate on the limiting nutrient  $N$ , its density-dependent mortality rate  $a_{11}$ , and the coefficients  $a_{12}$  and  $a_{13}$  that represent its losses to grazing by  $x_2$  and  $x_3$  respectively:

$$\begin{aligned}\dot{x}_1 &= x_1 f_1(x_1, x_2, x_3, N) = x_1 (r_1 N - \hat{a}_{11}x_1 - \hat{a}_{12}x_2 - \hat{a}_{13}x_3), \\ &= x_1 (r_1(1 - x_1 - x_2 - x_3) - \hat{a}_{11}x_1 - \hat{a}_{12}x_2 - \hat{a}_{13}x_3), \\ &= x_1 (r_1 - a_{11}x_1 - a_{12}x_2 - a_{13}x_3).\end{aligned}\quad (2)$$

Here we incorporate the plankton population’s growth dependence on the limiting nutrient  $N$ . New interaction coefficients are introduced

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