Predator density and competition modify the benefits of group formation in a shoaling reef fish

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Predation risk experienced by individuals living in groups depends on the balance between predator dilution, competition for refuges, and predator interference or synergy. These interactions operate between prey species as well: the benefits of group living decline in the presence of an alternative prey species. We apply a novel model-fitting approach to data from field experiments to distinguish among competing hypotheses about shifts in predator foraging behavior across a range of predator and prey densities. Our study provides novel analytical tools for analyzing predator foraging behavior and offers insight into the processes driving the dynamics of coral reef fish.

Studies of predator foraging behavior typically focus on single prey species and fixed predator densities, ignoring the potential importance of complexities such as predator dilution; predator-mediated effects of alternative prey; heterospecific competition; or predator–predator interactions. Neglecting the effects of prey density is particularly problematic for prey species that live in mixed species groups, where the beneficial effects of predator dilution may swamp the negative effects of heterospecific competition. Here we use field experiments to investigate how the mortality rates of a shoaling coral reef fish (a wrasse: *Thalassoma amblycephalum*), change as a result of variation in: 1) conspecific density, 2) density of a predator (a hawkfish: *Paracirrhites arcatus*), and 3) presence of an alternative prey species that competes for space (a damselfish: *Pomacentrus pavo*). We quantify changes in prey mortality rates from the predator's perspective, examining the effects of added predators or a second prey species on the predator's functional response. Our analysis highlights a model-fitting approach that discriminates amongst multiple hypotheses about predator foraging in a community context. Wrasse mortality decreased with increasing conspecific density (i.e. mortality was inversely density-dependent). The addition of a second predator doubled prey mortality rates, without significantly changing attack rate or handling time – i.e. there was no evidence for predator interference. The presence of a second prey species increased wrasse mortality by 95%; we attribute this increase either to short-term apparent competition (predator aggregation) or to a decrease in handling time of the predator (e.g. through decreased wrasse vigilance). In this system, 1) prey benefit from intraspecific group living though a reduced predation risk, and 2) the benefit of group living is reduced in the presence of an alternative prey species.

The importance of prey density in modifying predator foraging behavior, and hence community dynamics, has a rich history in ecology (Nicholson and Bailey 1935, Holling 1959). For example, shifts in a predator's foraging behavior can affect the stability of predator–prey dynamics (Deangelis et al. 1975), spatial distribution of predators (Van Der Meer and Ens 1997), food chain length (Schmitz 1992), and the strength of species interactions in complex food webs (Novak and Wootton 2008). The functional response represents mechanisms underlying the prey–predator interaction; thus, quantifying changes in functional response parameters is a natural way to test hypotheses about these mechanisms. Shifts in predator foraging response can occur due to predator–predator interactions (e.g. intraguild predation, interference competition, or cooperative hunting by predators) (Skalski and Gilliam 2001) as well as common or conflicting behavioral responses

of prey to multiple predators (Sih et al. 1998). Predator-induced benefits of group living are common for a number of taxa, from caribou (Wittmer et al. 2005) to cliff swallows (Brown and Brown 2003) to queen conch (Ray and Stoner 1994), and active group formation by prey in the presence of predators (e.g. schools of fish and herds of savannah ungulates) or group formation of predators hunting prey can stabilize predator–prey dynamics by modifying the functional response (Fryxell et al. 2007). Below we describe a first experiment where we estimate how two components of a predator's functional response (attack rate and handling time) vary under different predator densities, and link these changes to mechanistic hypotheses.

Functional responses can also be used to study the effect of multiple prey species on predator foraging behavior (Murdoch 1973, Golubski and Abrams 2011). For example, an alternative prey species can increase predator

attack rates on focal prey by competitively excluding a focal species from refuges. Alternatively, the presence of alternative prey could drive short-term aggregation of mobile predators, again increasing rates of focal prey mortality (Holt and Kotler 1987). Shifts in attack rate and handling have conventionally been examined at fixed predator densities, whereas short-term aggregative responses of predators are often studied by documenting short-term shifts in predator abundance (Schmitt 1987, Overholtzer-McLeod 2006). It can be difficult to document short-term aggregative response of highly mobile predators and to distinguish an aggregative response from a shift in attack rate or handling time of sedentary predators. In a second experiment, we quantify mortality rates of a focal prey species in the presence and absence of an alternative prey that is also a likely space competitor (Carr et al. 2002, Almany 2004). We develop and apply an explicit statistical framework that combines predator functional response curves and short-term aggregative response of predators by estimating shifts in attack rate, handling time, and effective predator density as alternative mechanistic models explaining variation in mortality rates of prey. For each experiment, we take both a 'predator-centric' (examining feeding rate of a single predator, as a function of prey density) and 'prey-centric' approach (examining per capita prey mortality rate, as a function of prey density).

Methods

Study system and species

We conducted all fieldwork during the austral summer of 2007 on two arrays of patch reefs within the shallow (3–7 m deep) northern lagoon of Moorea, French Polynesia (17°30′S, 149°50′W). The array used in experiment 1 consisted of 12 replicate artificial patch reefs separated by 20 m within a sand flat (for a detailed description see Supplementary material Appendix A1). The array used in experiment 2 consisted of 16 reefs randomly selected from 28 patch reefs that had been translocated to a large sand flat. Patch reefs were separated by a minimum of 15 meters. Each patch reef was a monospecific colony of *Porites lobata* to which we attached one colony of *Pocillopora verrucosa* to provide additional structural complexity (for specific details on the array see Geange and Stier 2009). Each of our experimental reef arrays closely mimic the size and spatial arrangement of patch reefs in Moorea, where the lagoon is interspersed with patch reefs within a matrix of sand, fine coral rubble and coral pavement with individual patch reefs separated by less than a meter, to tens of meters (Galzin and Pointer 1985). These patch reefs are regularly occupied by a variety of wrasse, damselfish and hawkfish species.

Our studies focused on three species of coral reef fish: a focal prey species, the bluntnose wrasse *Thalassoma amblycephalum*, an alternative prey species, the sapphire damsel *Pomacentrus pavo*, which competes with the bluntnose wrasse for space on the reef (Almany 2004), and a predator, the arc-eye hawkfish *Paracirrhites arcatus*. All three species use *Pocillopora* spp. (a structurally complex coral) for shelter. The bluntnose wrasse (hereafter 'wrasse') is a

habitat generalist that feeds diurnally on zooplankton; recently settled individuals shoal above coral colonies in aggregations of approximately 5–15 individuals (McDermott 2006). The sapphire damsel, like the wrasse, is a diurnally feeding planktivore and habitat generalist, often forming loose shoaling aggregations on live coral or coral rubble. The sapphire damsel ('damselfish') settles at densities from 1–35 individuals per m² (Stier and Geange unpubl.), and is known at adult sizes to be territorial and aggressive towards heterospecifics inhabiting the same habitat patch, inhibiting the recruitment of newly settled fishes (Almany 2004). The arc-eye hawkfish ('hawkfish') is an abundant, diurnally active, territorial predator. Individuals scan the surrounding reef from atop coral colonies of *Pocillopora* spp. or *Acropora* for small fishes and invertebrate prey. Hawkfish live in loose harems, with large dominant males accompanied by 4–6 females on neighboring coral heads. Within a given *Pocillopora* colony, the abundance of hawkfish in Moorea ranges from 0–2 individuals (Kane et al. 2009). Notably, the focal wrasse described here can be loosely described a Pacific analogue to a well-studied congener wrasse, *Thalassoma bifasciatum*, found in the Caribbean. Previous studies of *T. bifasciatum* have documented both direct and inverse density dependent mortality for recently settled fish (Caselle 1999, White 2007, White and Warner 2007); therefore the formation of loose shoaling aggregations is an important phenomenon governing the dynamics of this well-studied group of reef fish (White et al. 2010).

Fish handling and tagging

We collected experimental fishes from the lagoon using hand nets and anesthetic clove oil. Collected fish were transferred to holding tanks for 24 h. After 24 h, fish were randomly assigned to treatments and tagged with subcutaneous Visible Implant Elastomer (VIE) tags slightly anterior to the caudal peduncle. VIE tags do not have adverse effects on other fishes (Beukers et al. 1995, Imbert et al. 2007, Simon 2007) and mortality after tagging was less than 2% for 330 wrasses tagged in our study. To allow the assessment of immigration and emigration between reefs, different colored tags were used for each reef. After tagging, we returned fish to aerated aquaria for 6–12 h before measuring them to the nearest 0.1 mm SL and deploying them in the field. VIE tags were readable through the skin of the fish by observers in the field, so it was not necessary to recapture individuals to determine their identity. We therefore assumed that tagging and handling effects were minimal.

Our visual recapture of fishes on experimental reefs and nearby natural reef found no evidence for immigration or emigration of experimental fishes (wrasses, hawkfish or damselfish). Therefore the loss of a wrasse from a reef was assumed to be due to predation and not emigration. First, previous experimental studies of *T. amblycephalum* (wrasse) congeners of similar size on the array used in experiment 2 detected zero immigration or emigration of tagged individuals between reefs over a seven day experiment (Geange and Stier 2009). Second, another six day study manipulating shoals of recently recruited *Thalassoma* wrasses on reefs separated by as little as 5 m have found no immigration of tagged individuals (White and Warner 2007).

Experiment 1

Effects of predator and conspecific density on prey survival

We assessed the interacting effects of shoal size of the wrasse (4 levels: 3, 5, 10 or 15 wrasses per reef) and predator density (3 levels: 0, 1, or 2 hawkfish per reef) on the per capita survival of wrasses (12 treatments randomly assigned to 12 reefs).

We removed all resident predators (including sandperch, groupers, stonefish and eels) from the reef array prior to deploying experimental fishes to the reefs. We allowed wrasses to acclimate by deploying hawkfish 1 h after wrasses. The standard length of wrasses and hawkfish used in the experiment were 13.8 ± 2.0 mm and 72.0 ± 3.5 mm (mean $\pm$ SD) respectively. We replicated our experiment in three temporal blocks (beginning 2, 10 and 21 May 2007), with no within-block replication (i.e. n = 3 temporal replicates for each treatment, which was randomized for each time step). For each temporal block, we maintained predator removals (although immigration of new predators was minimal after initial removals, with 2.0 ± 1.0 (mean $\pm$ SD) predators removed per temporal block). Each temporal block was terminated after six days because mortality rates of reef fishes are generally greatest in the first 36–48 h after settlement (Almany and Webster 2006).

To determine whether shoaling behavior was affected by shoal size and/or predator density we quantified the shoaling behavior of wrasses during the second and third temporal blocks. Two divers sequentially visited each reef, allowing ten minutes for fish to acclimate to their presence before beginning observation. Each diver recorded the shoaling behavior of one focal wrasse for five minutes. Shoaling was quantified as the number of seconds out of 300 during which two or more wrasses swam within two body lengths of the focal individual.

Experiment 2

Effect of a heterospecific damselfish competitor on wrasse survival

To test how the presence of an alternative prey species affects the strength of density dependence in wrasses, we crossed wrasse density treatments (3, 5, 8, 12 and 15 individuals per reef) with the presence of damselfish (0 or 20 individuals per reef) on reefs where predators existed at naturally occurring densities and often with heterospecifics (Supplementary material Appendix A2). To improve our estimates of survival we increased the number of replicates at low densities of wrasse: we used three replicates for the 3-wrasse treatment; two replicates for the 5-wrasse treatment; and one replicate each for the 8-, 12- and 15-wrasse treatments. We randomly assigned treatments to reefs, and fish to treatments. We deployed damselfish on the morning, and wrasses on the afternoon of 29 May 2007, and assessed survival of wrasses after six days. Mean sizes of wrasses and damselfish used in the experiment were 14.28 ± 1.61 mm SD and 15.8 ± 1.16 mm respectively. Fish collections and tagging protocols were identical in experiment 1 and 2. Although we attempted similar behavior observations of wrasses as were conducted in experiment 1, we were unsuccessful because damselfish were particularly sensitive to the presence and absence of divers making it difficult to monitor interactions between individual wrasses and damselfish.
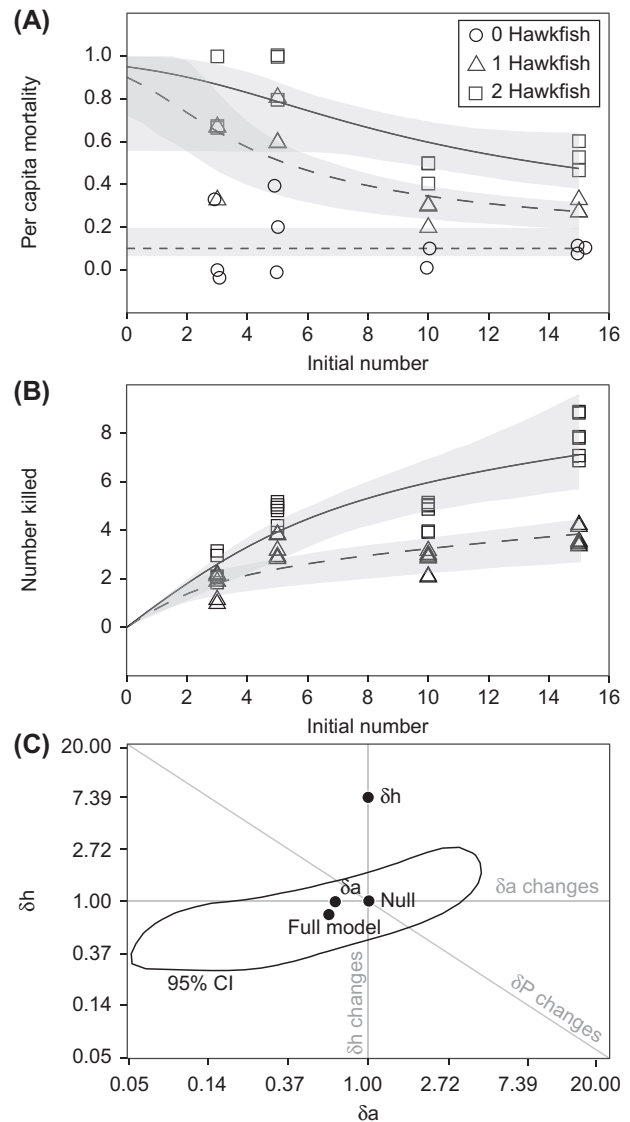

Figure 1. The effect of wrasse density on (A) the per capita mortality of wrasses (i.e. proportion lost after six days), (B) functional response of hawkfish, and (C) the functional response parameters log(δa) and log(δh). In (A) and (B), lines and surrounding gray area represent mean $\pm$ 95% CI for each hawkfish treatment: zero ($\bigcirc$, fine dash); one ($\triangle$, medium dash); or two ($\square$, solid) hawkfish. Functional response curves in (B) are adjusted for baseline mortality to isolate the hawkfish effect. Panel (C) represents maximum likelihood estimates for four models of increasing levels of complexity: 1) null model: no flexibility in attack rate or handling time, 2) δh: handling time varies but attack rate is fixed, δa: attack rate varies but handling time is fixed, and 4) Full model: both attack rate and handling time are allowed to vary. Three grey lines (log δh, δa and δP changes) represent the plane over which each estimate of log(δa), and log(δh) change with each of the four models. For the Full model, the 95% CI is plotted for the maximum likelihood combination of log(δa) and log(δh). See results section for significance tests of each of the parameters in the four reported models and Supplementary material Appendix A3 for details on hypothesis tests using likelihood ratio tests.

Estimation of functional response curves

In both experiment 1 and 2 we fit functional response curves to our data, which are represented in Fig. 1 and 3, respectively. To test for changes in predator foraging behavior, we

examined changes in attack rates (a) and handling times (h) estimated using a modified form of the Rogers random predator (RRP) equation (itself a modified version of a Holling type II functional response that incorporates prey depletion: Juliano 2001). In our version of the RRP equation, the expected rate of decrease of the prey population at time t depends both on a baseline extrinsic mortality rate and on instantaneous predation mortality, which we assume can be described using a Holling type II functional response:

$$\frac{dN_j(t)}{dt} = -\left(\mu + \frac{a_i P_i}{1 + a_i h_i N_j(t)}\right) N_j(t) \qquad (1)$$

where μ is baseline mortality, P_i is the number of predators, a_i is the (per-predator) attack rate (rate at which the predator encounters prey) when P_i predators are present, h_i is the handling time (time associated with pursuing, handling, masticating and digesting prey) for P_i predators, and $N_j(t)$ is the number of prey remaining at time t at wrasse density j. For reef fishes where direct consumption is commonplace, the handling time parameter is primarily associated with pursuit and digestion rather than mastication. When $\mu = 0$ equation 1 reduces to the Rogers random predator equation, which can be solved for the total number of individuals eaten by time T either iteratively (Juliano 2001) or using the Lambert W function (McCoy and Bolker 2008); when $\mu > 0$ we integrated (1) numerically from 0 to T because the equation cannot be solved in closed form. For experiment 1, subscript i varies with hawkfish density treatment; thus attack rate and handling time are estimated for treatments with one or two hawkfish, and P is fixed at one or two in each respective treatment. For experiment 2, subscript i varied with damselfish treatment (i.e. control or *P. pavo* present) rather than predator density. Wrasse mortality did not significantly vary among temporal blocks (one-factor ANOVA on model residuals with temporal block as a factor: $F = 0.92$, $p = 0.40$). Notably, we did not observe each component of the functional response (i.e. attack rate and handling time) separately, but rather inferred these processes from the parameters of the fitted models.

Using a general-purpose maximum likelihood estimation function assuming binomial responses to obtain parameter estimates for a_{Hawk} and h_{Hawk}, we used the integrated version of Eq. 1 to address two specific questions about experiment 1. First, we evaluated if per-predator attack rate a_{Hawk} differed between hawkfish densities by parameterizing a_{Hawk} as $a_2 = a_1 \times \delta a$, and testing the null hypothesis that $\delta a = 1$ (or equivalently $\log(\delta a) = 0$). The parameter δa gives the proportional change in per-predator attack rate with two rather than one predators present: $\delta a = 1$ suggests that the attack rate of a predator was independent of predator density, $\delta a > 1$ suggests predator synergism, while $\delta a < 1$ suggests predator interference. Second, we evaluated whether handling time h_{Hawk} differed between the two predator densities by parameterizing h_{Hawk} as $h_2 = h_1 \times \delta h$, and testing the null hypothesis that $\delta h = 1$ (or equivalently $\log(\delta h) = 0$).

We tested for changes in per-predator attack rate and handling time (i.e. whether δa and δh were significantly different from 1) by using two separate likelihood-ratio tests comparing the full model (with both δa and δh different from 1) to (1) to a reduced model with $\delta a = 1$ and (2) to a reduced model with $\delta h = 1$ (see Supplementary material Appendix A3 for model decision tree). This flexible version of the RRP is an appropriate model for our data because: 1) the model assumes type II functional response where handling time produces an asymptotic relationship between the initial number of prey and the number of prey eaten per predator, 2) the model allows for depletion of prey through time by adjusting parameter estimates based on reductions in prey density through time, and 3) the full and reduced models described above are specific nested subsets of existing predator interference models reviewed in Skalski and Gilliam (2001): Beddington-DeAngelis (Beddington 1975), Crowley-Martin (Crowley and Martin 1989), and Hassell-Varley (Hassell and Varley 1969) (Supplementary material Appendix A4). Therefore we take a strong inference approach by offering up a variety of candidate models that are established in the theoretical literature on predator-dependent functional response curves (Skalski and Gilliam 2001).

Examining shifts in attack rate and handling time in the presence of a competitor allows us to test three different hypotheses about why the number of wrasses eaten can change with the addition of damselfish. 1) The presence of damselfish increases competition for refuges, which decreases wrasses' ability to hide. This competition increases encounter rates (i.e. attack rates) with predators, leading to $\delta a > 1$. 2) Handling time decreases in the presence of damselfish due to decreased wrasse vigilance or exploitative competition for refuges from damselfish, leading to $\delta h < 1$. 3) Damselfish attract predators, which then also forage on wrasses (i.e. apparent competition): i.e. $P_{Damsel} > P_{Control}$. To test these three hypotheses we used a suite of modified functional response models to evaluate prey per capita mortality rates in experiment 2, but fixed the baseline mortality estimate (μ) from experiment 1. To test hypotheses 1 and 2, we parameterized a_i, and h_i, as $a_{Damsel} = a_{Control} \times \delta a$ and $h_{Damsel} = h_{Control} \times \delta h$, respectively, where once again δa and δh give the proportional change in per predator attack rate and handling time. However, unlike experiment 1 where predator densities were fixed as an experimental treatment, in experiment 2 we did not manipulate predators directly. Therefore to test hypothesis 3, we allowed P to vary with damselfish treatment as well by fitting a third model to ask whether differences in the number of predators could explain observed shifts in a_i and h_i in the presence of damselfish. We could not allow a_i, h_i and P_i to vary simultaneously (they are jointly unidentifiable); therefore, in the models where we explored variation in a_i and h_i we fixed $P = 1$, and in the model where P_i was allowed to vary with damselfish treatment, a and h were held at a constant ratio and we parameterized P_i as $P_{Damsel} = P_{Control} \times \delta P$. We again used likelihood ratio tests to test our three hypotheses. To test the attack rate (or handling time or apparent competition) hypothesis we compared the model parameterized with $\delta a \neq 1$, $\delta h \neq 1$ and $\delta P \neq 1$ with the reduced models parameterized with $\delta a = 1$ (or $\delta h = 1$ or $\delta P = 1$). The $\delta P = 1$ model restricts changes in δa to be inversely proportional to changes in δh (i.e.

$\delta a \times \delta h = 1$); therefore, it is nested within the full model where both δa and δh differ from 1.

To test the hypothesis that mortality of wrasses in experiment 1 and 2 was inverse density dependent we used a likelihood ratio test to compare each of the fully parameterized models to reduced models with handling time fixed at zero.

Behavioral analysis

Reefs with fewer than three wrasses at the time behavioral observations were conducted were dropped from the analysis (this occurred on a single reef in each of the second and third temporal block). We modeled the proportion of time wrasses spent shoaling using a generalized linear model with a quasibinomial family to account for over-dispersion (residual deviance = 1249.3, residual DF = 37) and a logit link function. We included hawkfish density as a categorical fixed factor, wrasse shoal size as a continuous covariate, and used a series of F-tests (Venables and Ripley 2002) to test for an interaction between hawkfish density and shoal size and main effects of hawkfish density and shoal size. Because our habitat units were a fixed area, the amount of time a focal fish shoaled should increase with density. To generate a null model, we calculated the expected number of neighbors within a range of shoaling radii (r): 0.05, 0.15 and 0.30 meters as $\lambda = \pi \times r^2 \times (N-1)/A$, where A is the area of the reef and N is the number of individuals on the reef. Thus if the neighbors were distributed at random on the reef, the probability of finding > 1 fish in the shoaling radius would be $1 - \text{Poisson}(0, \lambda) - \text{Poisson}(1, \lambda)$, where Poisson(n, λ) is the Poisson probability of observing n individuals at a mean rate of λ.

All statistical analyses were conducted in R ver. 2.9.2 (R Development Core Team).

Results

Experiment 1

Effects of predator and conspecific density on prey survival
From a prey perspective, mortality of wrasses was inversely density dependent in both experiment 1 and 2 (experiment 1: $\chi^2_3 = 14.399$, p = 0.002; experiment 2: $\chi^2_3 = 12.373$, p = 0.002). From a predator perspective, hawkfish foraged independently from one another. The proportional change in attack rate and handling time did not differ significantly from one (mean and 95% CI: $\delta a = 0.66$ (0.10, 4.00) prey per predator day: $\chi^2_1 = 0.164$, $p = 0.686$; $\delta h = 0.83$ (0.27, 2.82) prey per predator day: $\chi^2_1 = 0.161$, $p = 0.688$, Fig. 1c), providing no evidence for risk enhancement or risk reduction with increasing hawkfish density. In other words, the increased wrasse mortality with two hawkfish (relative to one) was entirely explicable by an increase in predator density and not by shifts in attack rate or handling time. Parameter estimates for the full model (mean and 95% CI) were: attack rate (a) = 0.367 (0.080, ∞) per predator day, handling time (h) = 1.989 (0.501, 4.181) prey per predator day, and baseline daily mortality rate (μ) = 0.017 (0.009, 0.031). The attack rate estimate has an

infinite upper bound because of high depletion. Thus, it is not possible to distinguish between a wide range of attack rates, because even predators with arbitrarily large attack rates cannot kill more prey than are available. We observed low (but non-zero) levels of mortality in the absence of hawkfish ((μ) = 0.017 (0.009, 0.031) per day, Fig. 1a), which we attribute to predation by transient predators that are known to increase mortality rates of fish (e.g. Carangids and Lethrinids) (Schmitt et al. 2009) and that we occasionally witnessed near experimental reefs (Stier and Geange unpubl.).

Shoaling behavior of wrasses was not affected by an interaction between predator density and shoal size (F = 0.027, p = 0.870) or the main effect of predator density (F = 0.050, p = 0.825); however, the incidence of shoaling significantly increased with increasing conspecific density (F = 154.84, p < 0.001, Fig. 2). The observed proportion of time focal individuals spent shoaling greatly exceeded the predictions of the null model for shoaling radii of 0.05 and 0.15 m, but were similar to null expectations for the large 0.3 m (Fig. 2).

Experiment 2

Effect of a heterospecific competitor on *T. amblycephalum* survival
Of the 20 *P. pavo* outplanted to each reef, the mean number surviving across all *T. amblycephalum* treatments was 10.13 ± 4.63 (mean $\pm$ SD); this effect was independent of wrasse density (ordinary least-squares regression: $t = 0.30$, $p = 0.77$). From a prey perspective, the per capita mortality of *T. amblycephalum* was inversely density-dependent in the presence of *P. pavo* (Fig. 3). From a predator perspective, the proportional change in attack rate did not significantly differ from zero ($\delta a = 0.66$ (0, 4.31) per predator day: $\chi^2_1 = 0.330$, $p = 0.566$) with the addition of damselfish. In contrast, the data do suggest increases in either
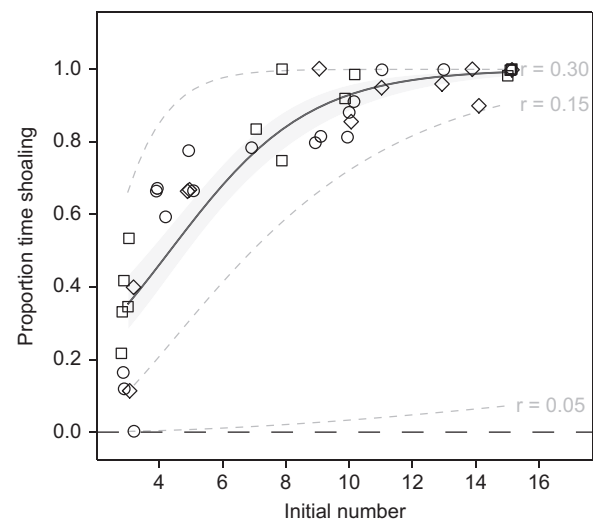

Figure 2. Effect of wrasse density and hawkfish treatment (zero (○); one (◇); and two (□) hawkfish) on shoaling behavior of wrasses. Gray dashed lines represent null model predicting increases in the probability of shoaling with increases in density for shoaling radii of 0.05, 0.15 and 0.30 m, and solid line represents mean fit from logistic regression for observed increases in shoaling with increases in density. Shaded region around solid line represents 95% CI of model fit.
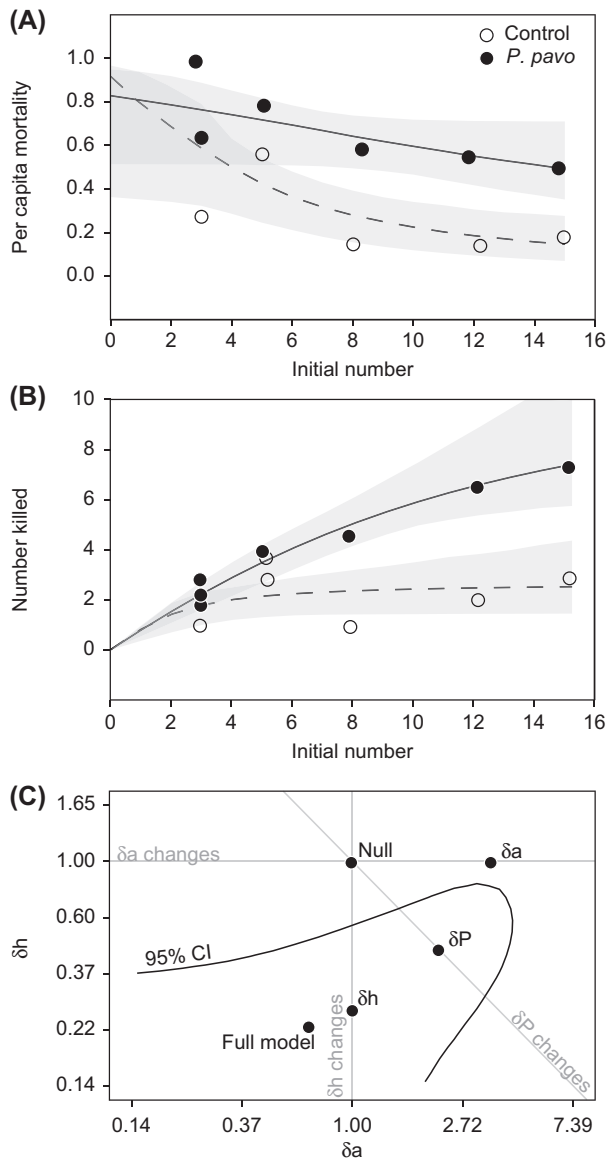
Figure 3. The effect of a competitor, damselfish, and wrasse density on (A) the per capita mortality of wrasses and (B) predator functional response. Solid lines and surrounding gray area represent mean ± 95% CI for each damselfish treatment estimated from maximum likelihood fit. Per capita mortality rates and functional response curves are adjusted for baseline mortality rate. Panel (C) represents maximum likelihood estimates for $\log(\delta a)$ and $\log(\delta h)$ (points) and 95% CI for full model. Note two models, $\log(\delta h)$ and $\log(\delta P)$, fall within the 95% confidence intervals of the full model. The attack rate estimate has an infinite upper bound because of high depletion. Thus, it is not possible to distinguish between a wide range of attack rates because even predators with arbitrarily large attack rates cannot kill more prey than are available (see Fig. 1 legend for further details on plot interpretation and Supplementary material Appendix A3 for further details on hypothesis testing for each model).

handling time or effective predator density. The proportional change in per-predator handling time significantly differed from zero ($\delta h = 0.23$ (0, 0.82) prey per predator day: $\chi_1^2 = 4.888$, $p = 0.027$), and constraining shifts in attack rate and handling time to be proportional did not significantly worsen the model ($\delta P = 2.21$ (1.38, 3.78) predators

per reef: $\chi_1^2 = 1.730$, $p = 0.188$) implying that shifts in effective predator density or shifts in handling time are equally valid explanations for the increased number of wrasses killed in the presence of damselfish. Parameter estimates for the full model (mean (+ 95% CI, − 95% CI)) were: $a = 0.52$ (0.05, ∞), per predator day, $h = 2.10$ (2.98, ∞) prey per predator day. Estimates for the restricted model with proportional shifts in δa and δh were: $a = .20$ (0.08, 0.48) per predator day, $h = 1.40$ (0.73, 2.71) prey per predator day.

Discussion

Despite a rich history in population ecology, the relative strengths of predator and prey density effects on functional responses remain contentious (Arditi and Ginzburg 1989, Abrams and Ginzburg 2000, Fussmann et al. 2005, Kratina et al. 2009). While a variety of predator interference mechanisms have been suggested (e.g. direct interference through group hunting, or indirect interference through common prey antipredator responses) (Abrams and Ginzburg 2000), how much predator interference occurs at the natural densities of predators and prey remains unclear. In our experiment 1 we found evidence for resource (i.e. prey) dependence in hawkfish consumption rates, but no evidence for predator dependence over naturally occurring hawkfish densities. However, we do not conclude predator dependence is unimportant in all reef fish systems. In experiment 1 we implemented a simplified community with only a single predator species (other species were removed), mimicking an isolated patch reef with no other resident predators; other studies have documented predator–predator interactions (Hixon and Carr 1997, Bshary et al. 2006, Stallings 2008) that may lead to predator dependence in more diverse predator communities.

Traditional evaluations of density dependent mechanisms often use ANCOVA to explore how the per capita probability of prey mortality changes across a range of prey densities in the presence or absence of a specific ecological process (e.g. resource limitation or predation). This approach provides a qualitative answer of whether or not a specific process is operating. In contrast, our model-based approach allowed us to ask more specific questions about quantitative changes in attack rates and handling times. The ANCOVA and model-based approaches are generally equally parsimonious (they make differing, but similarly strong, assumptions about the nature of the data) but the parameters estimated in the model-based approach can be more directly interpreted in terms of ecological processes – subject, of course, to the usual caveats about the scope and representativeness of the experimental setting and the model used. While model-based approaches do not mitigate the inherent risk in inferring unobserved processes from observed pattern (which ecologists and especially field ecologists must frequently do), they do provide a well-defined framework for testing among a particular set of alternative hypotheses. Similar studies have used model fitting to evaluate density and size effects on prey mortality rates (Vonesh and Bolker 2005, McCoy and Bolker 2008), suggesting the utility of this approach in extracting information from small empirical datasets. Further, the model

fitting approach used here allowed us to test multiple hypotheses regarding the role predator–predator dynamics and competitors play in altering the predator–prey functional responses and/or effective predator density. Prey experienced benefits of intraspecific group living in each of the three predator treatments, and mortality of prey increased with predator density (Fig. 1a). The lack of a significant shift in log attack rate or log handling time in experiment 1 provides no evidence for interference or cooperation among predators, although it is possible that there were interactions between hawkfish and transient predators that were similar in the one and two hawkfish treatments.

Predator–prey interactions can change predator foraging efficacy and result in inverse density dependent mortality for prey in three non-mutually exclusive ways: 1) the confusion effect, whereby organisms living in herds, flocks, or schools make it difficult for predators to single out individual prey; 2) group vigilance or aggression, whereby alarm calls and predator mobbing reduce predation rates; and 3) predator dilution, whereby predator satiation occurs at high prey densities (Courchamp et al. 1999). Although our behavioral observations focused on wrasse shoaling behavior, casual observations revealed no evidence for either predator mobbing or shifts in prey behavior with changes in the size of wrasse groups (though mobbing has been observed in other reef fishes: Sweatman 1984). Hawkfish consume their prey whole (as do most predatory reef fishes), and therefore spend a limited amount of time masticating prey. We speculate that other processes change, likely gut passage time or the amount of time spent pursuing prey. For example, the confusion effect or group vigilance may have produced inverse density dependence in this study, although more detailed observations of each of these behaviors is necessary to identify a concrete mechanism.

The presence of damselfish decreased the survival benefits of intraspecific group formation for wrasses (Fig. 3). A competitor-driven shift in the strength of density-dependent mortality matches the findings of other researchers who have shown increased competition at high densities (Carr et al. 2002, Almany 2004). Notably, the observed competitive asymmetry between damselfish and wrasses mirrors similarly strong competitive asymmetry that also occurs within wrasse congeners (Geange and Stier 2009). Alternatively, it has also been recorded that large adult damselfishes can directly reduce the recruitment of newly settled fishes through aggressive interactions (Sweatman 1985). However, experiment 2 supported two competing models with different mechanisms. The model with differences in handling time but not attack rate suggests that predators may be decreasing their handling times in response to the introduction of an alternative prey. One possible explanation for this decrease in handling time is that exploitative competition by damselfish for refuge space either reduces the vigilance of wrasses or decreases pursuit time by predators (by excluding inferior competitors from refuges). The data also supported a second model where effective predator density varied (i.e. $\delta P \neq 1$), suggesting that effective predator densities may be increasing with the addition of damselfish, leading to increased attack rates and handling times (i.e. short-term apparent competition: Holt and Kotler 1987). No ecological studies have tested apparent competition in reef fish, but aggregative response is known to occur in some predators (Anderson 2001), and short-term apparent competition is widespread in other systems (Holt and Lawton 1994). The parameter estimates for the apparent competition models fall within the confidence limits of the parameter estimates from the handling time model (Fig. 2c); therefore, the data do not discriminate between these two mechanisms. Furthermore, while predator density counts throughout the duration of the study suggest that predator density did not differ between treatments (Supplementary material Appendix A2), apparent competition may still be a plausible explanation because it is difficult to observe aggregative responses of transient predators due to their skittish behavior in the presence of divers (but for an impressive use of time-lapse photography see Overholtzer-McLeod 2006).

Conclusion

The results of our study suggest that predator and competitor density can affect the benefits that intraspecific group formation confers on prey. We develop and implement a model fitting approach that can be applied to small empirical datasets to distinguish among multiple competing hypotheses about shifts in predator foraging behavior. Furthermore, our findings add to a growing body of literature suggesting that predator–predator interactions (Hixon and Carr 1997, Johnson 2006), predator density (Schmitt and Holbrook 2007, White 2007), and competition (Carr et al. 2002, Samhouri et al. 2009) are important in structuring the direction and magnitude of density dependent mortality in benthic marine fishes (White et al. 2010).

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Supplementary material (available online as Appendix O20726 at < www.oikosoffice.lu.se/appendix >). Appendix A1–A4.

Appendix 1: *The construction of Experiment 1 reef arrays*

Individual reefs were constructed of 13 cinder blocks (0.5m X 0.25m X 0.25m), placed on a 1m X 1m sheet of corrugated iron. Blocks were stacked with openings facing outward in three tiers forming the shape of a pyramid. Six blocks (3 x 2) formed the base level, four blocks (2 x 2) the second tier, and three blocks (3 x 1) the third tier. On the top of each reef, four *Pocillopora verrucosa* coral heads (mean surface area 0.011 m^2, SD = 0.004) attached to small cinder blocks (represented here as grey boxes) were placed in a diamond formation on top of reefs to provide shelter for reef fishes.
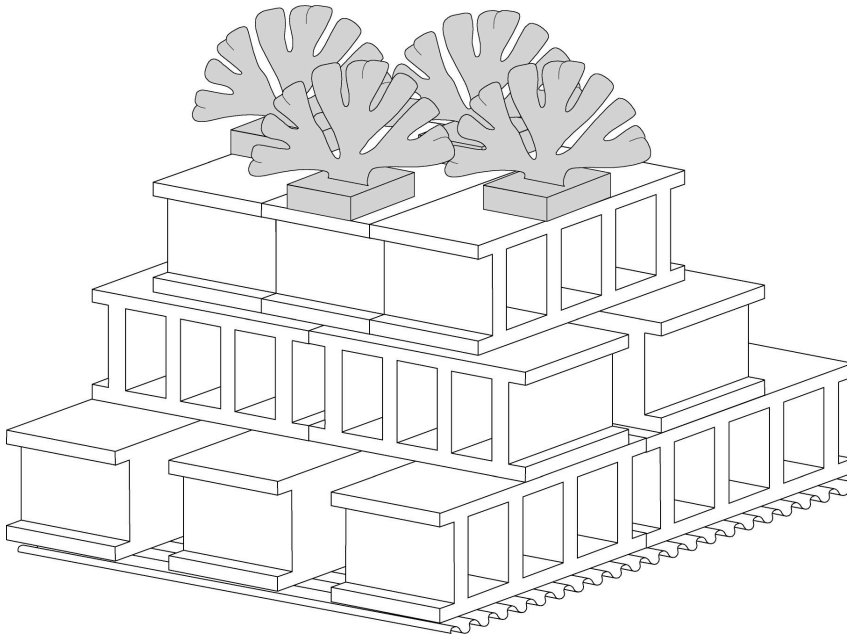
Appendix 2. *Description of predator densities across the natural array*

Predator community on experimental patch reefs for *Experiment Two*. The mean (SE) number of individuals for each species is given for each of our wrasse density treatments (3-15 individuals per reef) in the presence (top) and absence of damselfish (bottom). Averages and standard errors are generated from our surveys conducted incrementally on three days during the experiment (May 30, June 1, and June 4, 2007). Total predator densities in bold represent the mean (SE) of the sum of all predators in each treatment per m^2.

		Wrasse Density Treatment							
		3	**3**	**3**	**5**	**5**	**8**	**12**	**15**
Damselfish Present									
Family	**Species**								
Aulostomidae	*Aulostomus chinensis*	-	0.3 (0.3)	-	-	-	-	-	-
Balistidae	*Balistapus undulatus*	0.7 (0.3)	-	-	0.3 (0.5)	-	-	0.3 (0.3)	0.3 (0.3)
Bothidae	*Bothus pantherinus*	0.3 (0.3)	-	-	0.3 (0.3)	-	-	-	-
Carangidae,	*Caranx melampygus*	-	-	-	-	-	-	0.3 (0.3)	-
Holocentridae	*Neoniphon sammara*	-	2.0	-	0.7 (0.7)	0.3 (0.3)	0.7 (0.3)	1.0 (1.0)	3.7 (0.7)
Labridae	*Cheilinus trilobatus*	-	-	-	-	-	-	0.7 (0.7)	-
Labridae	*Halichoeres trimaculatus*	1.0 (0.6)	-	2.7 (1.3)	3.3 (0.3)	-	-	0.7 (0.7)	1.0 (1.0)
Muraenidae	*Gymnothorax javanicus*	-	-	-	-	-	0.7 (0.7)	-	-

Family	Species								
Pinguipedidae	*Parapercis millepunctata*	0.3 (0.3)	-	-	-	1.0 (0.0)	-	-	-
Synodontidae	*Saurida gracilis*	0.3 (0.3)	-	-	-	0.7 (0.3)	0.3 (0.3)	-	-
	Total	**2.7 (0.3)**	**2.3 (0.3)**	**2.7 (1.3)**	**4.7 (0.7)**	**2.0 (0.6)**	**1.7 (1.2)**	**3.0 (0.6)**	**5.0 (1.5)**

Control

Family	Species								
Aulostomidae	*Aulostomus chinensis*	-	-	-	0.3 (0.3)	-	0.3 (0.3)	-	-
Balistidae	*Balistapus undulatus*	-	1.3 (0.3)	-	0.7 (0.3)	-	-	1.0 (0.0)	-
Bothidae	*Bothus pantherinus*	-	-	-	-	-	-	-	-
Carangidae,	*Caranx melampygus*	-	-	-	-	-	-	-	-
Holocentridae	*Neoniphon sammara*	-	1.3 (0.3)	0.3 (0.3)	2.0 (0.0)	1.3 (0.3)	1.0 (0.6)	-	1.7 (0.3)
Labridae	*Cheilinus trilobatus*	-	-	0.7 (0.3)	-	-	-	-	-
Labridae	*Halichoeres trimaculatus*	1.3 (0.7)	-	1.0 (0.6)	0.7 (0.7)	2.0 (0.0)	-	2.3 (0.7)	0.3 (0.3)
Muraenidae	*Gymnothorax javanicus*	0.3 (0.3)	-	-	-	-	-	0.3 (0.3)	-
Pinguipedidae	*Parapercis millepunctata*	-	-	-	-	-	0.7 (0.3)	-	1.3 (0.3)
Synodontidae	*Saurida gracilis*	-	-	0.3 (0.3)	-	-	-	-	0.7 (0.3)
	Total	**1.7 (0.3)**	**2.7 (0.7)**	**2.3 (0.7)**	**3.7 (0.7)**	**3.3 (0.3)**	**2.0 (0.6)**	**3.7 (0.9)**	**4.0 (0.6)**

APPENDIX 3: *Nested hierarchy of models in Experiment 1 and Experiment 2.*

Table 1. Parameters for type II functional response modified to incorporate both depletion and baseline mortality. Modified functional response was used to examine whether shifts in attack rate, handling time, predator density affected the mechanisms of inverse density dependence in the wrasse for different predator (Experiment 1) and competitor (Experiment 2) densities.

Symbol	Description	Units
μ	Baseline mortality	1/days
a	Per capita attack rate	1/(time*pred/reef)
h	Handling time	Prey/reef/(preda/reef*days)
P	Predator density	pred/reef
T	Time	days
N_0	Initial Number of Prey	prey/reef
N_T	Number of Prey at time T	prey/reef
N_e	Number of Prey Eaten	prey/reef

An estimate of the instantaneous number of prey killed with and baseline mortality can be evaluated using (see text for details):

$$\frac{dN}{dT} = -(\mu + \frac{a_i P_i}{1 + a_i h_i N_T})N_T \tag{1}$$

Equation 1 can be integrated to incorporate prey depletion:

$$N_e = -\int_0^T \frac{dN}{dt} dt$$

In Experiment 1, we use this integrated model to evaluate differences in attack rate (a) and handling time (h) in the presence of a second predator (hawkfish) (Fig. 1). This same model was used in expeiment 2 to evaluate differences in attack rate (a), handling time (h), and effective predator density (P) in the presence of a competitor (damselfish) (Fig 2). Baseline mortality was estimated from Experiment 1 and used to parameterize Experiment 2.

Figure 1: Nested models in Experiment 1 examining the effect of a doubling in hawkfish density on attack rate and handling time of hawkfish. χ^2 values are equal to the difference in the deviance between the two Rogers Random Predator (RRP) models. Significant p values (bold) represent a statistically significant likelihood ratio test (LRT). Significance in the LRT suggests the more complex of the two models is a better fit.

2 attack rates, 2handling times   4 parameters

δh ≠ 1
χ2 = 0.161, p = 0.688

δa ≠ 1
χ2 = 0.164, p = 0.686

2 attack rates   2 handling times   3 parameters

δa ≠ 1
χ2 = 0.025, p = 0.874

δh ≠ 1
χ2 = 0.022, p = 0.882

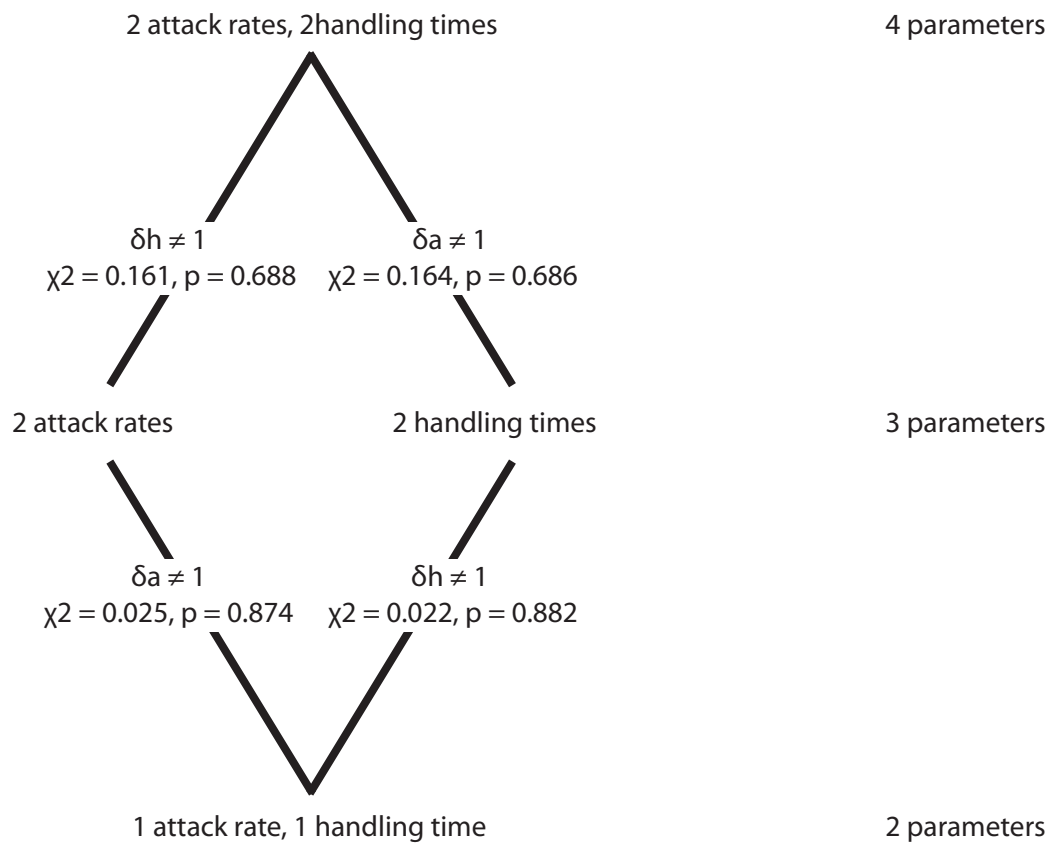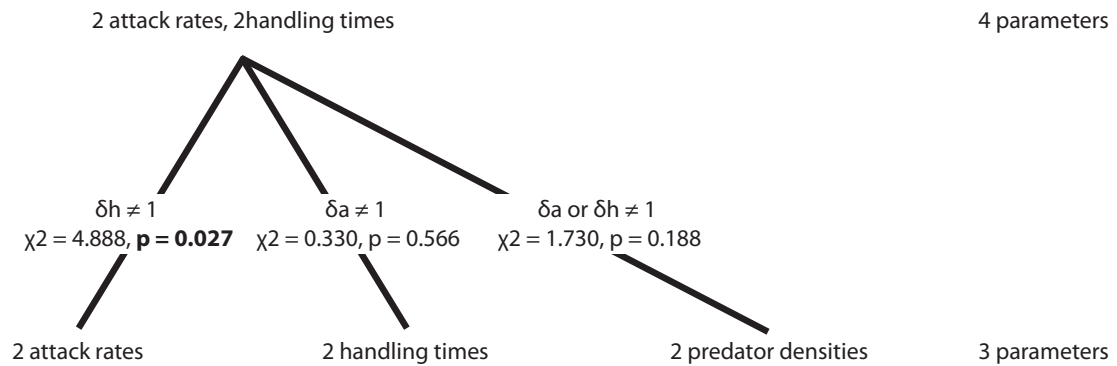1 attack rate, 1 handling time   2 parameters

Figure 2 Nested models in Experiment 2 examining the effect of damselfish addition on attack rate, handling time, and effective predator density. Comparisons among candidate models suggest two appropriate models: 1) the model with different handling times 2) the model with different effective predator densities. See figure 1 legend for more details.

2 attack rates, 2handling times   4 parameters

$\delta h \neq 1$ $\delta a \neq 1$ δa or $\delta h \neq 1$

$\chi 2 = 4.888$, **p = 0.027** $\chi 2 = 0.330$, p = 0.566 $\chi 2 = 1.730$, p = 0.188

2 attack rates   2 handling times   2 predator densities   3 parameters

Appendix 4: *Functional Responses with Predator Density*

Functional response models allowing attack rate (*a*) and handling time (*h*) to vary with each of

the experimental treatments for one and two predators. Our models (far right) are specific

versions of existing functional response models (far left) that explore the role of predator density

5   in affecting predator foraging behavior. Moving from left to right shows how the original

formulation of these models, can be simplified to be identical to our model under scenarios

where there are 1 and 2 predators. Our models are not equivalent to existing models for $P > 2$.

See Skalski and Gilliam (2001) for more details.

10

Model	Original Formulation	1 Predator $f_i(N,P_1)$	2 Predator $f_i(N,P_2)$	2 Predator (simplification)	Our Model
Holling Type II	$f_{H2}(N,P) = \dfrac{aNP}{1+bN}$	$\dfrac{aN}{1+bN}$	$\dfrac{2aN}{1+bN}$	$\dfrac{2aN}{1+bN}$	$\dfrac{aNP}{1+ahN}$
Beddington-DeAngelis	$f_{BD}(N,P) = \dfrac{aN}{1+bN+c(P-1)}$	$\dfrac{aN}{1+bN}$	$\dfrac{aN}{1+bN+c}$	$\dfrac{aN/1+c}{1+bn/(1+c)}$	$\dfrac{(a_1 \bullet \delta a)NP}{1+(a_1 \bullet \delta a)hN}$
Crowley-Martin	$f_{CM}(N,P) = \dfrac{aN}{1+bN+c(P-1)+bcN(P-1)}$	$\dfrac{aN}{1+bN}$	$\dfrac{aN}{1+bN+c+bcN}$	$\dfrac{\dfrac{a}{1+c}N}{1+Nb}$	$\dfrac{aN(P_1 \bullet \delta P)}{1+aNh}$
Hassell-Varley	$f_{HV}(N,P) = \dfrac{aN}{bN+P^m}$	$\dfrac{aN}{1+bN}$	$\dfrac{aN}{bN+P^m}$	$\dfrac{\dfrac{aN}{2^m}}{\dfrac{bN}{2^m}+1}$	$\dfrac{aN(P_1 \bullet \delta P)}{1+aNh}$