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Potential feedback between coral presence and farmerfish collective behavior promotes coral recovery

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Stable between-group differences in collective behavior have been documented in a variety of social taxa. Here we evaluate the effects of such variation, often termed collective or colony-level personality, on coral recovery in a tropical marine farmerfish system. Groups of the farmerfish *Stegastes nigricans* cultivate and defend gardens of palatable algae on coral reefs in the Indo-Pacific. These gardens can promote the recruitment, growth, and survival of corals by providing a refuge from coral predation. Here we experimentally evaluate whether the collective response of farmerfish colonies is correlated across intruder feeding guilds – herbivores, corallivores and egg-eating predators. Further, we evaluate if overall colony responsiveness or situation-specific responsiveness (i.e. towards herbivores, corallivores, or egg-eaters in particular) best predicts the growth of outplanted corals. Finally, we experimentally manipulated communities within *S. nigricans* gardens, adding either macroalgae or large colonies of coral, to assess if farmerfish behavior changes in response to the communities they occupy. Between-group differences in collective responsiveness were repeatable across intruder guilds. Despite this consistency, responsiveness towards corallivores (porcupinefish and ornate butterflyfish) was a better predictor of outplanted coral growth than responsiveness towards herbivores or egg-eaters. Adding large corals to farmerfish gardens increased farmerfish attacks towards intruders, pointing to possible positive feedback loops between their aggression towards intruders and the presence of corals whose growth they facilitate. These data provide evidence that among-group behavioral variation could strongly influence the ecological properties of whole communities.

Keywords: aggression, collective behavior, coral reef resilience, damselfish, personality, *Stegastes*

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Introduction

Intraspecific trait variation has far-reaching ecological consequences. For instance, the mixture of genotypes in a foundational species can determine community biodiversity and composition (Crutsinger et al. 2006) and resilience to disturbance (Hughes and Stachowicz 2004, Ladd et al. 2017). Or, individual variation in behavioral innovation can be associated with the performance of individuals in human-altered environments (Tinker et al. 2008). Within behavioral ecology, temporally consistent individual differences in behavior are often studied under the conceptual umbrella of 'animal personality' (Dall et al. 2004, Sih et al. 2004). A plethora of studies have linked animal personality with ecological outcomes, including invasion success (Cote et al. 2010), the presence and magnitude of trophic cascades (Griffen et al. 2012), the outcome of competitive interactions (Webster et al. 2009), community succession and stability (Pruitt and Modlemeier 2015), landscape patterns of animal movement (Speigel et al. 2017, Sih et al. 2018), and various aspects of population dynamics (Sih et al. 2012, Wolf and Weissing 2012). Together, such studies provide compelling evidence that the ecological impacts of intraspecific behavioral variation can be profound.

Social animals provide a unique backdrop for animal personality studies, because temporally consistent intraspecific variation in behavior can occur at not only the individual level but also the group level (Jandt et al. 2014). At the individual level, group members may differ from one another along any number of behavioral axes (Modlmeier and Foitzik 2011, Modlmeier et al. 2012, Segev et al. 2017, Barbasch and Buston 2018). Likewise, entire groups may differ from each other in their collective attributes, such as their collective aggressiveness whilst hunting, their tendency to forage in risky situations, or their movement behavior (Wray et al. 2011, Gordon 2013, Aplin et al. 2014, Jolles et al. 2018). Several recent studies on 'collective personality' or 'colony-level personality' have linked variation in group behavior with group growth rates (Pruitt 2012), productivity (Modlmeier et al. 2012), and resource allocation strategies (Bengston et al. 2017). Some studies have revealed that the relationship between group behavior and success can differ situationally (Pruitt et al. 2018a). However, the broader ecological consequences of such between-group variation have not been rigorously evaluated, despite the fact that animal social groups often have large impacts on their environments (Human and Gordon 1996, Goheen and Palmer 2010, Sih et al. 2011).

We evaluate the community level consequences of variation in collective behavior using a tropical marine farmerfish system. *Stegastes nigricans* (Perciformes, Pomacentridae) is a territorial group-living fish that inhabits coral reef habitats from eastern Africa to western South America. Individual *S. nigricans* occupy territories that contain gardens of palatable turf algae, which the residents cultivate, feed on, and defend (Hata and Kato 2002). Territories are organized into large clusters on hard substrates such as dead coral heads or reef pavement, and individuals within such clusters cooperatively mob intruding fish that attempt to feed within their garden (Johnson et al. 2011). Corals located within farmerfish gardens can experience negative effects such as increased competition with the garden's algae, resulting in partial mortality (White and O'Donnell 2010). A nominal increase in the incidence of coral disease within farmerfish gardens has also been documented (Casey et al. 2014). However, these negative impacts are likely minimal compared to the positive effects of farmerfish gardens for corals – corals that establish in farmerfish gardens enjoy reduced corallivory, because *S. nigricans* mob corallivores that attempt to feed on corals within their territories (Gochfield 2010, White and O'Donnell 2010, Johnson et al. 2011, Pruitt et al. 2018b). Particularly on reefs with high levels of coral predation, territories of *S. nigricans* groups provide an important ecological function by serving as protective nursery habitats for branching corals and potential reservoirs of coral repopulation following large disturbances (Done et al. 1991, Gleason 1996, Suefuji and van Woesik 2001).

Farmerfish mobbing behavior begins with individuals emerging from their shelters in the reef matrix in response to an intruder (which we describe here as a group's 'responsiveness'). This response is often followed by more directly aggressive behavior, including chases, strikes, and bites (Johnson et al. 2011, Pruitt et al. 2018b). Groups of farmerfish that respond more strongly to intruders appear to have a particularly large protective effect on corals within their territories (Pruitt et al. 2018b). However, previous work has focused largely on responsiveness towards heterospecific marauding herbivores, although Johnson et al. (2011) found certain species of corallivorous fishes and egg-eating predators also elicited aggressive responses. This prompts the question of whether the level of colony responsiveness is consistent across intruders from these different feeding guilds, and if situational responsiveness towards particular intruders is a more informative predictor of the ecological interactions of farmerfish with coral than their overall responsiveness. We evaluate these topics here and, further, probe the role of local community structure (corals versus macroalgae) in driving inter-colony differences in colony behavior.

In this paper, we combine observations of farmerfish collective behavior with two long-term habitat manipulation experiments to address the following questions (Table 1): 1) are inter-colony differences in the collective response of farmerfish correlated across different types of intruders? 2) Do colonies respond more strongly, on average, towards particular intruder types? 3) Which kind(s) of group responsiveness (overall responsiveness and/or specific responsiveness towards herbivores, egg-eating predators, or corallivores) best predict the growth of corals experimentally outplanted into the territories of *S. nigricans*? 4) Is there evidence of a positive feedback between the collective behavior of *S. nigricans* and the presence of corals in their territories?

Table 1. Summary of the questions asked and the methods used in the two experiments presented in this paper.

	Experiment 1	Experiment 2
Aim	Examining the consistency of collective responses of farmerfish colonies to different types of intruders, and assessing associations between responsiveness and coral growth	Understanding the impacts of habitat characteristics (coral and foliose algae) of farmerfish territories on their collective behavior
Question(s)	1. Is responsiveness by *Stegastes nigricans* to intruders repeatable across intruders from different feeding guilds? 2. Does responsiveness differ across intruder types? 3. Does intruder-type-specific responsiveness to intruders predict coral growth?	4. Does the addition of coral and/or macroalgae to a *Stegastes nigricans* garden alter the behavior of the fish?
Approach	Addition of coral outplants to measure associations between coral growth and natural variation in *S. nigricans* responsiveness	Addition of coral and macroalgae to measure shifts in *S. nigricans* responsiveness and attacking behavior
Control	Measuring response to an empty container	Measuring changes in behavior for unmanipulated gardens with and without naturally occurring coral
Duration	One year between initial and final measurements of coral branch length	Three months between initial and final measurement of farmerfish collective behavior
Analyses (R package; see text for citations)	1. Repeatability estimation (rptR) 2. Mixed effects models (lme4; lsmeans) 3. Structural equation modeling (lavaan)	4. Mixed effects models (lme4; lsmeans)

Material and methods

Study site and colony selection

We selected 29 farmerfish colonies inhabiting 29 bommies (small patch reefs) located in the mid-lagoon on the north shore of Moorea, French Polynesia (17°30′S, 149°50′W) in July 2016 for long-term behavioral observation (Pruitt et al. 2018b). A large mounding coral (*Porites* spp.) formed the base of each bommie; each contained a *Stegastes nigricans* colony of subadults and adults and its associated garden of at least 2 m^2 of turf algae. Bommies occurred in depths ranging from 1.6 to 2.1 m and a matrix of white sand separated neighboring bommies. The number of *S. nigricans* within each colony (which ranged from two to 26 individuals) was enumerated by a trained observer (A. J. Brooks). The behavioral assays described below were conducted in 2017.

Experiment 1. Consistency of collective responses of colonies to different types of intruders and associations between responsiveness and coral growth

Prior research has shown that the short-term (six months) growth rate of small outplanted coral nubbins is enhanced, and corallivory rates are reduced, in the territories of more aggressive *S. nigricans* colonies (Pruitt et al. 2018b). In that study, responses of *Stegastes* colonies towards the herbivorous fish *Zebrasoma scopas* were quantified, and the conclusions of that study were based on the assumption that responsiveness towards herbivores would be correlated with responsiveness towards other intruder types. Here, we use data on growth of outplanted corals after one year and colony responsiveness towards different types of fish intruders to test these assumptions. Specifically, we explore whether farmerfish colony responsiveness is correlated across intruder types (question 1), whether the magnitude of the response differs across intruders (question 2), and whether responsiveness towards any particular intruder type is more informative for predicting coral performance than overall responsiveness (question 3). Our research in this experiment builds upon in our earlier findings (Pruitt et al. 2018b) in several ways. First, we extended the period during which coral growth was assessed to the one year mark, having previously reported growth after six months. Second, we quantified responses of farmerfish to a variety of fish intruder types, not just the herbivorous *Z. scopas*. And third, we conducted a habitat manipulation experiment to explore responses of collective behavior to habitat features. The overlap between the datasets analyzed in these two studies is restricted to measurements of the responsiveness of farmerfish in response to *Z. scopas* in 2017 (referred to as aggressiveness in Pruitt et al. 2018b).

Collective response to intruders

We evaluated colony responsiveness by observing each colony's response to staged intruders in their garden. Each colony was subjected to a variety of intruder species, twice each, over the course of two weeks. Intruder fish species were selected to include two representatives from each of three guilds: corallivores (porcupinefish: *Diodon hystrix* [response measured only once per colony]; ornate butterflyfish: *Chaetodon ornatissimus*), herbivores (brushtail tang: *Zebrasoma scopas*; brown surgeonfish: *Acanthurus nigrofuscus*), and egg-eating predators (sixbar wrasse: *Thalassoma hardwicke*; checkerboard wrasse: *Halichoeres hortulanus*). All of these intruder fish frequent *S. nigricans* territories to pilfer from the garden (herbivores), consume resident corals (corallivores), or prey on *S. nigricans* eggs (egg-eaters) (Johnson et al. 2011). These feeding-guild classifications were made based on the most likely effect of the intruder species on *S. nigricans* and their gardens, even though some species can have more generalist diets (e.g. wrasses can be generalist benthic invertivores).

Farmerfish have been observed to respond with high levels of aggression (e.g. chasing, striking) when these intruders enter their territories (Johnson et al. 2011).

For all species except the porcupinefish, for which only one adult individual was available for use as a stimulus, we used between three and ten adult individuals for each species, with a gap of at least one day between the repeated use of an individual as the stimulus. Additionally, we ran one control trial per colony, in which the response to an empty container was measured. Two trials were performed on each colony per day. Intruder species order was determined haphazardly, and a minimum of three days elapsed between consecutive measures for any particular intruder species. Trials were ceased if a free-living intruder (e.g. shadow hunting wrasse) entered the garden, though this happened rarely.

Intruders were placed within a transparent plastic sphere (radius = 18 cm) with a series of vent slits that allowed the movement of seawater into and out of the enclosure. Farmerfish could therefore see the intruders as well as perceive any olfactory cues. A spherical container was preferable because it prevented the stimulus fish from becoming trapped in a corner. This chamber was then placed on the edge of the *S. nigricans* garden; its orientation in the water column was maintained by tying a transparent float to the top of the container and a 2.27 kg dive weight to the bottom with fishing line. An observer was positioned at least 5 m away from the stimulus, at a 90° angle to the experimenter positioning the stimulus. The experimenter placed the container on the edge of the *S. nigricans* territory and the observer monitored the number of *S. nigricans* that emerged to observe the intruder every 30 s for two min, i.e. four measurements per trial. We calculated colony responsiveness to a particular intruder (including the empty container control) as the average number of fish that responded to that intruder. The emergence of fish from retreats within the coral to inspect intruders is a consistent precursor to escalated aggression, e.g. chases, strikes, and is repeatable across colonies in response to an herbivore stimulus (Pruitt et al. 2018b). This metric of collective responsiveness is thus closely associated with colony aggression. This metric is also highly correlated with the number of individuals in a colony, and the association between number of farmerfish in a group and colony responsiveness to intruders was accounted for statistically in all analyses.

Coral outplant setup and assessment

Five small fragments (‘nubbins’) of the staghorn coral *Acropora pulchra* were outplanted into the garden of each of the 29 focal *S. nigricans* colonies. Coral nubbins were placed at least 10 cm apart within the central portions of the gardens. *Acropora pulchra* is highly favored by corallivores (including the porcupinefish *Diodon hystrix*), and forms thickets that are occupied and defended by farmerfish in Moorea (Johnson et al. 2011). Each transplanted coral consisted of a primary branch with an intact apical tip, collected from a nearby *A. pulchra* thicket. Each nubbin was affixed vertically on a uniquely-numbered PVC plate (~80 × 35 mm) using epoxy to anchor the base of the branch to the plate. Each numbered fragment was then photographed and measured (tip to edge of the epoxy; mean ± SE initial length 4.5 ± 0.7 cm; range 3.0–6.5 cm). Each coral plate was affixed to the substrate using a pre-installed stainless-steel bolt that fit through a hole in the PVC base plate and was secured with stainless steel nuts. During the one-year long duration of the outplant, turf algae from the *Stegastes* garden grew over the PVC plates and onto the base of the coral branch. However, turf was not observed to overgrow entire branches; rather, partial and complete mortality that we observed resulted from consumption (breakage) by excavating corallivorous fishes. We used the change in the length of coral branches between July 2016 and July 2017 (as a proportion of initial branch length, and averaged across five nubbins per bommie) as an estimate of coral growth.

Experiment 2. Impacts of habitat characteristics (coral and foliose algae) of farmerfish territories on collective behavior

Prior work (Pruitt et al. 2018b) has shown that more responsive *S. nigricans* colonies tended to contain a larger number of naturally-occurring colonies of branching coral, whereas less responsive colonies harbored a higher percentage of macroalgae (mostly *Turbinaria ornata*). In this study, we evaluate a possible cause–effect relationship between farmerfish colony behavior and the presence of two types of habitat structure – branching corals and the large macroalga *Turbinaria*, by adding one or the other of these to a new set of *S. nigricans* colonies. Branching corals and macroalgae compete for space on Moorea (Gleason 1996) and throughout much of the Indo-Pacific (Done et al. 1991). Much of the marine literature on ecological thresholds and community tipping points considers competition and supremacy between these two players (Hoegh-Guldberg et al. 2007). We examine how these competitors impact colony behavior in *S. nigricans*, which could in turn influence the quality of defense provided to each competitor by the farmerfish. In addition, this experiment allowed us to explore whether there is a positive feedback between farmerfish collective behavior and the presence of corals in their gardens.

Forty bommies containing *S. nigricans* colonies were selected on the north shore of Moorea in July 2017. Colonies were assigned to one of four treatment groups (n = 10/treatment): coral added (four *Pocillopora* added), *Turbinaria* added (four clumps of *Turbinaria* added), control without coral (bommie naturally lacked branching coral), and control with coral (bommie naturally contained branching coral). *Pocillopora* corals added to territories ranged from 17–22 cm in length and 12–19 cm in width; *Turbinaria* clumps were 15–20 cm in diameter and contained 10–15 large stipes (each 20–25 cm length). Control colonies with corals contained three to 10 naturally-occurring branching corals in the genera *Pocillopora* and *Acropora*. Added corals were harvested

12 h prior to outplanting from the fore reef at depths of 3 to 4 m and were stored in a flowing seawater table in the laboratory overnight. *Turbinaria* clumps were harvested from the mid lagoon near our study site at depths of 1–3 m and outplanted within two hours of collection. *Pocillopora* corals and *Turbinaria* clumps were affixed to bommies inside *S. nigricans* colonies using Zspar with U-shaped fencing nails and cable ties to temporarily secure them while the underwater epoxy set. The nails and cable ties were removed after 24 h. Colony responsiveness towards *Z. scopas* was evaluated for each colony prior to the addition of corals or *Turbinaria* and again three months later in October 2017, using the methods described above. We also recorded the number of times the farmerfish struck at the stimulus fish (number of attacks). We observed no instances where any farmerfish struck at an empty control stimulus. All but two of the experimentally added corals and all of the transplanted *Turbinaria* patches remained alive within each territory over the three-month period.

Statistical methods

All analyses were conducted in R ver. 3.41 (<www.r-project.org>). We used the package rptR (Stoffel et al. 2017) to estimate the repeatability of *S. nigricans* colony responsiveness across all intruder types (including the empty container control; question 1), where repeatability is defined as the proportion of variance attributable to between-colony variation (note that repeatability varies from 0 to 1, where higher values indicate higher repeatability; Nakagawa and Schielzeth 2010). The model to estimate repeatability included fixed effects of the number of fish in the colony and intruder fish type, and random effects of trial number and intruder fish species, in addition to colony ID. Confidence intervals were calculated by 1000 bootstrap replicates, and a likelihood ratio test was used to assess if models with and without the colony ID effect were significantly different. To examine if, on average, colony responsiveness differed between intruder types (question 2), we compared AIC scores for linear mixed effects models (*lme4* package; Bates et al. 2015) with and without a fixed effect of intruder type (herbivore, egg-eater, corallivore); models additionally included a fixed effect of the number of *S. nigricans* in each colony and random effects of trial number, intruder fish species, and colony ID.

We used structural equation modeling (SEM) to investigate the drivers of coral growth in the one-year long coral outplant experiment (question 3). Structural equation modeling allows for the specification and simultaneous evaluation of multiple linear relationships among variables in a dataset. It also allows for the designation and estimation of 'latent' variables, which are defined as variables that have not been, and likely cannot be, measured directly but that are potentially important to understanding relationships within the system under consideration (Grace 2006). We specified and compared a series of models, described below and in Table 2, to understand the behavioral predictors of coral growth within farmerfish gardens. Some of our models included a latent 'reactivity' variable that was described as causing the specific responsiveness of colonies to each intruder type (Fig. 2). The designation of this variable allowed us to evaluate if a colony's underlying propensity for responding to intruders helps to explain variation across colonies in their responses to intruders as well as the growth of corals within their gardens. Models were fit, and parameters estimated, using maximum likelihood, and standard errors were estimated from 1000 bootstrap replicates. We compared AIC scores to discern the best fitting models and checked overall model fit of the best-fitting models using a chi-square test. Best fit

Table 2. Structural equation models to discern predictors of coral growth in a one-year outplant experiment. Models included one or more of the following predictors of coral performance: *Count*: number of *Stegastes nigricans* in the colony, *Herb*, *Egg* and *Coral*: mean observed responsiveness towards herbivores, egg-eating predators, and corallivores, respectively. *React:* latent 'reactivity' variable. The best-fit models are indicated in bold text.

Model	Latent 'reactivity' variable included?	Predictors of coral growth	No. of parameters	AIC score
1	no	Count	21	701.5
2	no	Herb	17	742.0
3	no	Egg	17	712.6
4	no	Coral	17	735.7
5	no	Count + Herb	18	740.8
6	no	Count + Egg	18	714.5
7	no	Count + Coral	18	733.1
8	yes	Count	15	706.0
9	yes	Herb	15	703.1
10	yes	Egg	15	703.7
11	**yes**	**Coral**	**15**	**699.0**
12	yes	Count + Herb	16	705.1
13	yes	Count + Egg	16	705.7
14	**yes**	**Count + Coral**	**16**	**699.1**
15	yes	Count + React	16	704.2
16	yes	Count + React + Herb	17	703.3
17	yes	Count + React + Egg	17	706.2
18	**yes**	**Count + React + Coral**	**17**	**698.2**

models had the lowest AIC scores (ΔAIC >2 were considered significant differences) as well as low chi-square values, and correspondingly high p-values (greater than 0.05), in a test of model fit comparing the observed variance–covariance matrix with that estimated by the model. Analyses were conducted with the *lavaan* package (Rosseel 2012).

The data used in the SEM models included mean colony responsiveness towards corallivores, herbivores, and egg-eating predators as well as the empty container control, i.e. all SEM models included four measures of responsiveness per colony. In all models (summarized in Table 2), the number of *S. nigricans* in each colony was designated a predictor of observed measures of colony responsiveness. In model 1, the number of *S. nigricans* was also designated a predictor of coral growth. In model 2–4, we designated observed colony responsiveness towards each of these intruder types (corallivores, herbivores, and egg-eating predators) in turn as a predictor of coral growth, and in model 5–7, we added the number of *S. nigricans* in each colony as a predictor of coral growth. In model 8–18, we added a latent 'reactivity' variable as a cause of all four observed measures of colony responsiveness, constraining this variable to be uncorrelated with the number of *S. nigricans* in the colony. This latent 'reactivity' variable was added as a predictor of coral growth in model 15–18 to ask if the overall response to intruders was a better predictor of coral growth compared to intruder-specific responses.

To assess the effect of habitat manipulations on the behavior of colonies of *S. nigricans* (question 4), we compared AIC scores of linear mixed effects models with and without a fixed effect of treatment (control without coral, control with coral, coral added, and *Turbinaria* added). We calculated differences between pre- and post-treatment behaviors of colonies for both colony responsiveness and number of attacks, standardizing by the number of *S. nigricans* in the colony, and including a random effect of colony ID in both models. We used post hoc Tukey's tests using the *lsmeans* package (Lenth 2016) to compare behavioral differences among treatments.

Data deposition

Data available at the publicly accessible MCR-LTER database (<http://mcr.lternet.edu/data>).

Results

Experiment 1. Consistency of collective responses of colonies to different types of intruders and associations between responsiveness and coral growth

The repeatability of colony responsiveness across intruder types was 0.38 ± 0.07 (mean ± SE; [2.5%, 97.5%] = [0.21, 0.49]; likelihood ratio test: $D_1 = 100$, $p < 0.001$), which is comparable to the mean repeatability of behavioral traits across taxa and traits (Bell et al. 2009) and suggests that responsiveness of *Stegastes nigricans* towards intruders is consistent across the different types of intruders – herbivores, egg-eating predators, corallivores, and the empty container control – and thus across the contexts of different ecological interactions (question 1; Table 1).

After accounting for differences among trials, colonies, and intruder species, as well as variation with colony size, we found that intruder type was a significant predictor of variation in responsiveness (ΔAIC = 43.6, $\chi^2_3 = 49.6$, $p < 0.001$). However, post hoc tests revealed that this was due to, on average, 70% fewer fish responding to the empty container control than to any of the intruder fish types; response levels towards herbivores, corallivores, and egg-eating predators were not significantly different from one another (Fig. 1; question 2, Table 1).

After one year, the performance of the outplanted staghorn coral varied dramatically among the bommies. About half (49%) of the 160 outplanted coral nubbins were alive and had at least one branch; the remaining nubbins were either dead or persisted as a flat nubbin of less than 2 mm height without any branches. Survival of the nubbins was variable among the bommies. For example, after a year, all outplanted corals on five bommies were alive, whereas all were dead on five others. The change in the total branch lengths of the five outplanted corals on a bommie ranged from −100% (i.e. all had died) to an increase of 1284%. On average, coral branch length on bommies increased by 291% ± 420%.

Variation across *S. nigricans* colonies in responsiveness towards herbivores, egg-eating predators and corallivores (measured as number of fish that emerged in response to an intruder), the number of fish in the colony, and coral growth was equally well-explained by three structural equation models (model 11, 14 and 18 in Table 2 and Fig. 2). Moreover, these three models were a good fit to the data, as indicated by chi-square tests (Table 3; note that low χ^2 values and high p-values indicate better model fit). All three best-fit models

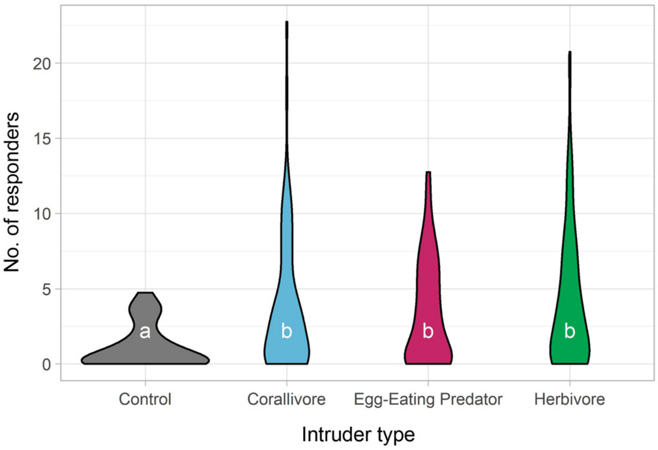

Figure 1. Number of fish from a farmerfish colony that responded to each of the three types of intruders as well as the empty container (control) experimentally introduced into *Stegastes nigricans* territories. Plot shape is a mirrored probability distribution estimate indicating the distribution of data for each intruder type.

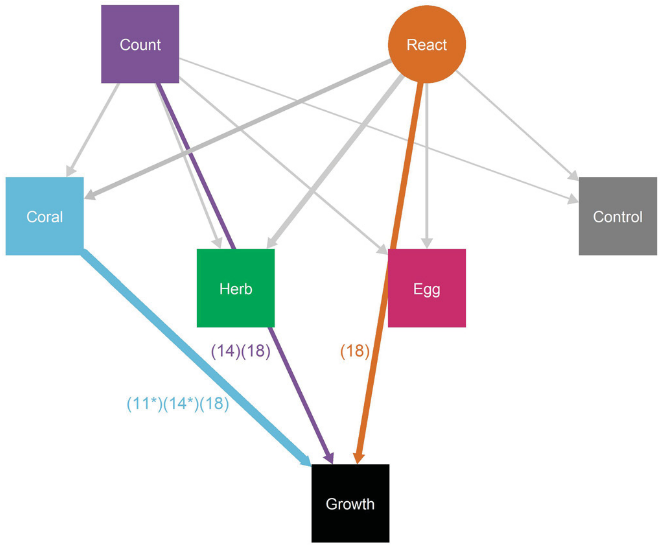

Figure 2. Graphical representation of the best fit structural equation models (model 11, 14 and 18; Table 2) explaining the growth of corals outplanted in farmerfish colonies (experiment 1, question 3). Edges shown in grey were included in all three best fit models and all of these relationships were estimated to be significantly positive (Table 4). All three best fit models include a latent 'reactivity' variable (React) that causes fish type specific responses (mean number of responders) to corallivore (Coral), herbivore (Herb), and egg-eating (Egg) intruders, as well as to an empty container (Control). The number of farmerfish in a colony (Count) was constrained to be uncorrelated with 'reactivity' (React). Colored edges and arrows show variables hypothesized to influence coral growth in these models; edge labels show if the specific relationship was included in the model (number) and asterisks indicate if the relationships were significant (Table 3).

Table 4. Parameter estimates (unstandardized parameters and standard errors, with standardized parameter estimates in parentheses and $p < 0.05$ indicated by an asterisk) from the best fit models for the relationships between the number of fish per colony (count) or the latent 'reactivity' variable and observed number of responders to corallivores (coral), egg-eating predators (egg), and herbivores (herb).

Variable 1	Variable 2	Parameter estimates ± SE (standardized parameter estimate)
React	Coral	1.00 ± 0.00 (0.38)*
React	Herb	1.30 ± 0.27 (0.48)*
React	Egg	0.53 ± 0.17 (0.27)*
React	Control	0.36 ± 0.14 (0.39)*
Coral	Count	0.57 ± 0.08 (0.90)*
Herb	Count	0.57 ± 0.08 (0.87)*
Egg	Count	0.44 ± 0.03 (0.92)*
Control	Count	0.19 ± 0.03 (0.87)*

included a latent 'reactivity' variable as a cause of responsiveness towards each intruder type, where increases in reactivity caused increases in specific responsiveness (Fig. 2, Table 4). This confirms the result from the repeatability estimate described above (question 1) that responses to intruders are correlated across ecological contexts. Larger colonies also had greater responsiveness than smaller colonies (Fig. 2, Table 4).

Model fit and parameter estimates for the three best fit models are reported in Table 3 and 4. In all three best-fit models, farmerfish responsiveness toward corallivores was included as a positive predictor of coral growth, and this relationship was significant in two of the three models (question 3; Table 1). These effect sizes can be interpreted as follows: all else being equal, for an increased responsiveness of one, i.e. the emergence of one additional fish in response to the stimulus intruder corallivore, we expect to see an increase in proportionate coral growth of 64% ± 16% (model 11) or 105% ± 44% (model 14). In model 14 and 18, the number of fish in a colony and the latent 'reactivity' variable (model 18 only) were included as predictors of coral growth, but these relationships were not significant (Table 3).

Experiment 2. Impacts of habitat characteristics (coral and foliose algae) of farmerfish territories on collective behavior

Habitat manipulations did not influence the number of fish that emerged in response to the intruder ($\Delta AIC = 0.75$; $\chi^2_3 = 5.40$; $p = 0.14$). However, the number of attacks made by farmerfish in response to the intruder varied across habitat manipulation treatments ($\Delta AIC = 12.6$; $\chi^2_3 = 18.54$; $p = 0.0003$). Specifically, relative to the start of the experiment, fish in the coral addition treatment attacked 184% more than fish in the *Turbinaria* addition treatment ($t_{80} = 3.3$, $p = 0.008$) and 605% more than fish in the control treatment without naturally occurring coral ($t_{80} = 4.4$, $p = 0.0002$) at the

Table 3. Model fit for the three best-fit structural equation models, including parameter estimates (unstandardized parameters and standard errors, with standardized parameter estimates in parentheses and $p < 0.05$ indicated by an asterisk) for the predictors of coral growth.

	Model 11	Model 14	Model 18
Summary statistic			
Test statistic	9.5	7.6	4.8
Degrees of freedom	6	5	4
p-value (χ^2)	0.15	0.18	0.31
Standardized (absolute ± standard error) residual variance in growth	10.2 ± 2.8 (0.60)	9.6 ± 2.4 (0.56)	8.38 ± 35.7 (0.49)
Predictors of coral growth			
Response to corallivores (Coral)	0.64 ± 0.16 (0.63)*	1.05 ± 0.44 (1.03)*	2.18 ± 32.0 (2.16)
Number of fish (Count)	NA	−0.29 ± 0.25 (−0.45)	−0.94 ± 16.1 (−1.46)
Reactivity (React; latent variable)	NA	NA	−1.48 ± 32.1 (−0.56)

end of the experiment. The change in the number of attacks by fish in the control group with coral did not differ significantly from any other treatments (Fig. 3).

Discussion

Between-group differences in collective phenotypes are important in determining the way that groups function and perform. Yet, the broader ecological implications of this diversity remain largely unexplored. Animal societies can have disproportionately large impacts on their environments. For example, herds of elephants can structurally alter Paleotropical savannas over large geographic scales (Lombard et al. 2001, Kerley and Landman 2006), colonies of leaf-cutter ants in the Neotropical savannas can consume similar amounts of biomass as do African ungulate communities (Costa et al. 2008), colonies of prairie dogs can alter landscapes in ways that increase regional biodiversity in grasslands (Bangert and Slobodchikoff 2006), and colonies of eusocial insects can hold keystone positions in plant-pollinator (Potts et al. 2010) and seed-dispersal networks (Bond and Slingsby 1983). We predict that the effects of social species on population and community outcomes will vary based on their collective phenotypes. Moreover, these effects may be modulated or reinforced based on how these phenotypes change with the environment (collective behavioral reaction norms), due to plasticity or rapid evolutionary dynamics. In the farmerfish *Stegastes nigricans*, groups vary greatly in their collective behavior and these among-group differences persist stably across weeks and months (Pruitt et al. 2018b). In this study, we assess the consistency of *S. nigricans* collective responsiveness across ecological contexts and examine how this collective behavior might not only facilitate but also be facilitated by the presence of corals in the gardens that these fish defend.

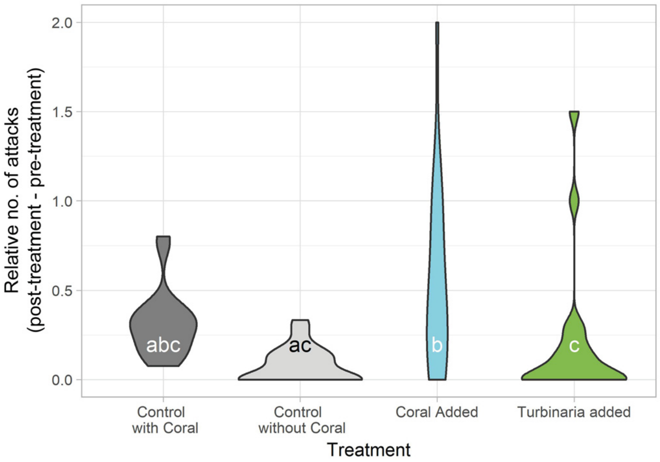

Figure 3. Difference between the number of attacks by *S. nigricans* colonies, corrected for number of farmerfish in a colony, towards an herbivore intruder before and after community structure manipulation treatments. Adding coral to a farmerfish garden increased the number of attacks by residents compared to gardens without coral and gardens with added *Turbinaria*. Plot shape is a mirrored probability distribution indicating the distribution of data for each treatment.

We show that responses to intruders by colonies of farmerfish are repeatable across ecological contexts – colonies that had a greater number of responders towards herbivores also deployed more responders towards egg-eating predators and corallivores, after accounting for group size. Moreover, structural equation models that included a latent 'reactivity' variable as a cause of responsiveness towards herbivores, corallivores, and egg-eating predators (model 8–18 in Table 2) were generally a better fit to the data than comparable models without this latent variable (model 1–7 in Table 2), and the three best fit models all included this latent 'reactivity' variable (Fig. 2). Together, these results suggest that a colony-level behavioral syndrome, defined as cross-contextual correlations in behavior (Sih et al. 2004), contributes to variation in the collective response of *S. nigricans* to fish that intrude into their gardens.

Despite the high correlations across colony responses towards various intruder species, farmerfish responses to some kinds of encounters proved better than others at predicting the growth of corals within their gardens. Specifically, we found that coral growth was better predicted by responses towards corallivores than towards herbivores or egg-eating predators, despite no average difference across colonies in responsiveness towards these three intruder types. For this study, we used two functionally distinct corallivores as model coral predators introduced into the farmerfish gardens. *Diodon hystrix* is a large, excavating facultative corallivore (Rotjan and Lewis 2008), while *Chaetodon ornatissimus* is a considerably smaller, mucus-feeding obligate corallivore that removes coral tissue but not skeleton (Harmelin-Vivien and Bouchon-Navaro 1983). Our findings support the hypothesis that variation in the tendency of farmerfish colonies to mob coral predators such as porcupinefish and butterflyfish underlies the superior performance of corals outplanted into these gardens, compared to corals not defended by farmerfish. Moreover, our results suggest that variation across farmerfish colonies in their response to corallivores could be an important determinant of whether or not corals thrive in their gardens.

All three of the best supported structural equation models included the response towards corallivores by farmerfish as the direct cause of the growth of corals within their gardens. Two of the three models additionally included the number of fish in a colony and the latent 'reactivity' variable as additional predictors of coral growth. However, these specific relationships were not found to be significant even though their inclusion did not decrease model fit (Table 3). Thus, though colony responsiveness is repeatable across contexts, such that their response to herbivores can predict coral growth (Pruitt et al. 2018b), more nuanced effects in this system may remain undetectable without accounting for how colony behavior varies across ecological contexts. Context-specific expression of personality has likewise been shown at the level of individual animals across both ecological and social contexts (Coleman and Wilson 1998, van Oers et al. 2005). While we did not detect differences in overall responsiveness towards different intruder types, studies on other species of *Stegastes* have shown overall context-specific variation (e.g. towards different intruders, Osório et al. 2006, Johnson et al. 2011, Souza et al. 2011; depending on reproductive status, Souza and Ilari 2014). Moreover, the data we gathered suggest a pattern of more extreme responses to particular intruder types (corallivores and herbivores; Fig. 1), although we did not test this pattern statistically. Thus, measuring context-specific behavioral responses will remain necessary for developing accurate models that describe the ecosystem effects of both individual animals and the collective behavior of animal societies.

The emergence of farmerfish from their shelters in the substrate in response to an intruding fish is a reliable precursor to escalations towards aggressive behavior directed at the intruders, including mobbing, chasing, and striking (Pruitt et al. 2018b). Our results therefore raise interesting biological questions about how corallivores might discern the level of responsiveness of farmerfish colonies when choosing whether to feed on corals guarded by these fish and thereby running the risk of being attacked. Corallivores might enter *S. nigricans* gardens and then retreat based on the intensity of the response they face, or they might make decisions about which gardens to enter based on other behavioral or habitat cues that are correlated with overall responsiveness (e.g. the presence of corals; Pruitt et al. 2018b). Observations of corallivore foraging behavior will help illuminate the mechanisms underlying their foraging decisions, making clearer which ecological contexts and interactions are relevant to the relationships between corals, farmerfish, and corallivores.

The experimental addition of large corals to the gardens of *S. nigricans* revealed the potential for a positively reinforcing feedback between farmerfish aggressive behavior and the presence of corals in their gardens. While the number of responders to an intruder fish (defined as 'responsiveness' in this study) was not influenced by coral addition, the number of attacks made by *S. nigricans* towards intruders increased with the addition of coral compared to gardens without coral, both with and without added *Turbinaria*. This suggests that certain aspects of *S. nigricans* aggressive behavior increase due to the presence of branching corals. It is also worth noting that in experiment 1 we measured responsiveness a year after corals were initially outplanted, suggesting that the presence and growth of corals may have caused increases in corallivore-specific responsiveness (though the responsiveness to the herbivore *Z. scopas* was also measured prior to coral outplanting, and significantly predicted coral growth; Pruitt et al. 2018b). One possible explanation for such causal effects is if the presence of branching corals lowers the risk of predation on *S. nigricans*, either via provision of structural refuges or via reduction of predators' attack success due to the increased structural complexity of the habitat in which these interactions take place. If this higher level of aggressive behavior is maintained, in particular, towards corallivores, then the growth of corals within a farmerfish garden could in turn promote precisely the behaviors that might facilitate coral growth. Positive feedback loops have been described as facilitation when generating and maintaining ecological communities (Wilson and Agnew 1992, Bruno et al. 2003, Holbrook et al. 2008, 2011), and as state–behavior feedbacks in the development of animal personalities (Sih et al. 2015). Our results demonstrate the possibility of synergy between these two seemingly disparate concepts, and their potential joint roles in determining the ecosystem consequences of intraspecific variation in behavior.

Prior research has documented a mix of both positive and negative interactions between farmerfish and coral. For example, farmerfish in general, and *Stegastes* in particular, can prevent the recruitment of juvenile corals into their gardens (Casey et al. 2015, Gordon et al. 2015), are associated with a higher prevalence of coral disease (Casey et al. 2014, Vermeij et al. 2015), and often directly damage corals (Wellington 1982, Rotjan and Lewis 2008, Schopmeyer and Lirman 2015). In contrast, other studies have found reduced predation and higher growth, survival, and diversity of corals within farmerfish territories compared to outside (Done et al. 1991, Gleason 1996, Gochfield 2010, White and O'Donnell 2010). We suggest that examining intraspecific variation in behavior could add an underappreciated dimension to understanding the dynamics of these fish–coral interactions, and help resolve the factors that underlie contrasting findings regarding species-level effects. For instance, the net effects of farmerfish on coral performance may change based on between-population differences in average behavior.

Despite the plethora of papers documenting the existence of animal personality and its role in shaping various ecological processes, there remains active debate regarding the utility of the personality framework (Beekman and Jordan 2017, Jungwirth et al. 2017). However, our findings clearly support the idea that accounting for intraspecific variation at both the individual level and, now, the colony level can enhance our ability to predict, and potentially even manipulate, environmental dynamics at a system level. For *S. nigricans*, shifts in colony behavior as a result of behavioral plasticity or rapid evolution could alter this species' ecological interactions. More broadly, we suggest that such dynamics resulting from intraspecific variation at the group level are unlikely to be restricted to this study system. Instead, we argue that a trait-focused approach could promote our understanding of a variety of systems where social animals are key drivers of environmental change.

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