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Editor's choice

Original Article

Collective aggressiveness of an ecosystem engineer is associated with coral recovery

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The ecological impacts of animal groups may be different and predictable depending on their collective behavior. Farmerfish (*Stegastes nigricans*) live in social groups and collectively defend gardens of palatable algae. These gardens also serve as settlement and nursery habitats for corals because farmerfish mob corallivores that attempt to forage on corals within these gardens. We detected large among-colony differences in farmerfish collective aggression towards intruder fish that persisted across years. We further found that the territories of aggressive groups and territories containing larger farmerfish provided greater protection to corals: territories of aggressive groups naturally harbored more branching corals than nonaggressive groups, and experimentally outplanted branching corals experienced 80% less skeletal loss and grew larger over 25 weeks in aggressive territories than in nonaggressive territories. These findings hint that factors that increase farmerfish group aggressiveness (e.g., higher temperatures) could enhance the protective value of farmerfish territories for the replenishment of coral populations.

Key words: **animal personality, behavioral syndrome, mobbing, temperament.**

INTRODUCTION

It is now well established that intraspecific variation can have significant ecological impacts (Bolnick et al. 2003; Bolnick et al. 2011; Sih et al. 2012; Wolf and Weissing 2012). Studies over the past decade have shown that community succession (Dickie et al. 2012; Pruitt and Modlmeier 2015), the presence and magnitude of trophic cascades (Griffen et al. 2012; Toscano and Griffen 2014), invasion success (Fogarty et al. 2011), population viability (Hughes and Stachowicz 2004), extinction risk (Pruitt 2013), and myriad other ecological processes can be influenced by intraspecific variation. Such effects can arise either by altering the average phenotype of the individuals involved in the process, or by the magnitude of individual variation (variance) itself, e.g., via intraspecific portfolio effects (Sih et al. 2012; Wolf and Weissing 2012). In the most extreme cases, studies have suggested that trait diversity within a species can have larger impacts on ecological outcomes than interspecific variation (Keiser and Pruitt 2014b). Within behavioral ecology, temporally consistent individual differences in behavior are referred to as temperament (Réale et al. 2007), behavioral syndromes (Sih et al. 2004), behavioral types, or personalities (Sih and Bell 2008). Recent years have seen an increasing number of studies aimed at documenting the presence of such individual differences and assessing their ecological impacts.

Social animals provide a special case study for examining the ecological effects of intraspecific behavioral variation because stable differences in behavior can occur at both the individual and group level (Jandt et al. 2014). At the individual level, group members may differ from one another in traits like sociability, aggressiveness, and so on (Keiser et al. 2014; Keiser and Pruitt 2014b). Likewise, at the group level, whole groups may differ from each other in their collective behavior (Gordon 2013; Hui and Pinter-Wollman 2014). Such intergroup differences may arise because of the relative ratios of different phenotypes within the groups (Modlmeier et al. 2014), differences in the average behavioral phenotypes of group members (Keiser and Pruitt 2014a), the presence or absence of one or a few individuals with extreme behavioral phenotypes (Chang and Sih 2013), or as a consequence of differences in the environment in which groups reside (Pinter-Wollman et al. 2011; Pinter-Wollman et al. 2012). This variation in collective traits, in turn, can drive collective outcomes, like the rate at which information spreads through a group (Aplin et al. 2015) or the collective defenses exhibited

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towards rival groups (Modlmeier and Foitzik 2011). Only recently have investigators begun to examine the broader ecological effects of such intergroup differences. However, the evidence available suggests that stable intergroup differences in collective behavior are a taxonomically widespread phenomenon and commonly determine group success (Wray et al. 2011; Pruitt 2012; Hui and Pinter-Wollman 2014).

Here, we evaluate the effects of intergroup behavioral variation on community-level processes using a farmerfish-coral system. The dusky gregory (*Stegastes nigricans*) is a group-living farmerfish (hereafter "farmerfish") occurring on tropical reefs from the western Indian Ocean to the eastern Pacific (Randall 2005). Both males and females maintain individual territories where they cultivate lawns of palatable microalgae that they then defend from intrusion by foreign conspecifics and heterospecifics (Hata and Kato 2002; Gobler et al. 2006; Hata et al. 2010). Groups of territories are organized into clusters where fish collectively attack would-be intruders, potentially to their shared benefit (as in: Jungwirth et al. 2015). Because of a pelagic larval phase, like most marine fishes (reviewed in: Taborsky and Wong 2017), relatedness among group constituents is predicted to be low in farmerfish groups. Most farmerfish defend their unique subterritories and reproduce (Hata and Kato 2002; Hata et al. 2010), and therefore, overt reproductive suppression does not appear to occur in these societies.

Prior studies have shown that branching corals (e.g., *Pocillopora*, *Acropora*) that settle into farmerfish territories enjoy reduced mortality and faster growth rates relative to corals that recruit outside of farmerfish territories (Done et al. 1991; Gochfeld 2010; White and O'Donnell 2010). This occurs because farmerfish harass corallivores, and virtually all other fishes, that attempt to consume branching corals located within their territory (Haley and Muller 2002; Gochfeld 2010; Johnson et al. 2011; Vullioud et al. 2013; Ros et al. 2014). As a result, farmerfish gardens may serve as nursery habitats for branching coral and reestablishment nuclei following coral die-offs in lagoons (e.g., from cyclones, outbreaks of crown-of-thorns sea stars). Some investigators have therefore referred to farmerfish, and other territorial damselfish, as ecosystem engineers (Ceccarelli et al. 2001; White and O'Donnell 2010).

We examine here whether farmerfish colony aggressiveness is associated with enhanced protection for corals. We first test whether colonies exhibit temporally stable differences in their aggressiveness. We then explore possible associations between intercolony differences in aggressiveness and the presence of naturally-occurring branching corals. Finally, we investigate the fate of small coral fragments ("nubbins") experimentally outplanted into farmerfish territories with contrasting levels of aggressiveness to evaluate whether more aggressive groups confer increased protection.

METHODS

Study site and colony selection

The farmerfish colonies used in this study were located at <3 m depth in the mid-lagoon region of the north shore of the island of Moorea, French Polynesia (17°30′ S, 149°50′ W). During the Austral winter of 2016, we haphazardly selected a set of farmerfish colonies, each situated on a discrete patch reef ("bommie") formed by massive coral (*Porites* spp.) and surrounded by sand. For each colony ($N = 29$), the size of the host bommie (height, length, width, and circumference) was recorded, and the percent of the bommie surface covered by the macroalga *Turbinaria ornata*, living *Porites* coral, and the colony's garden were estimated visually by S.J.H. and R.J.S. We also recorded the number and size (cm length, width) of each naturally-occurring branching coral (in the genera *Pocillopora* and *Acropora*) and encrusting coral (*Montipora* spp.) in the garden. For our analyses here, we elected to focus on the number of corals within farmerfish territories, as this represents the number of successful recruitment and establishment events. The number of the farmerfish in each colony was enumerated and total body lengths estimated to the nearest cm by a trained observer (A.J.B.). All behavioral assays were conducted in the morning or early afternoon each day (0830–1400).

Collective mobbing behavior

To test whether farmerfish colonies exhibited stable differences in their collective aggressiveness towards intruders, we presented them with an intruder fish: a solitary *Zebrasoma scopas* (brushtail tang) inside a transparent plastic container. Colonies that responded more quickly when an intruder fish was presented, deployed more inspector fish, or delivered more strikes to an intruder were thus deemed to be more aggressive. On Moorea, herbivorous *Zebrasoma* individuals commonly attempt to enter farmerfish territories to forage on the algal gardens and farmerfish respond to these intruders with high levels of aggression (e.g., chasing, striking, etc.) (A.J.B., S.J.H., R.J.S., J.N.P., personal observation).

The open side of the container containing the stimulus fish was covered with black poultry wiring to allow fresh seawater to pass in and out of the container between trials. A snorkeler placed each stimulus fish approximately 1 m from the edge of a colony's garden. This action also resulted in all members of the colony retreating into their shelter crevices within the patch reef. The container was always presented with the black poultry wiring faced down against the substrate to maximize the transparency of the container. We also deployed a paired control container that did not house a fish. Whether the control container or the *Zebrasoma* was deployed first was alternated across days. After placement of the container, we recorded colonies' latency to emerge to investigate the stimulus (with or without the *Zebrasoma*) and the number of individual fish inspecting the stimulus every 30 s for 2 min. An individual was deemed to be inspecting the stimulus if it emerged from its retreat and persistently oriented towards the stimulus. Additionally, we recorded the number of strikes deployed towards the stimulus fish. Strikes were direct contacts with the stimulus. Our estimates of colony aggressiveness were within colonies differences between colonies' responses towards the 2 stimuli (with vs. without a *Zebrasoma*). The positions of the stimuli were varied haphazardly across trials to avoid conflating colony aggressiveness with a specific deployment locality. Colony aggressiveness was estimated 5 times (each separated by 48 h) over 2 weeks. For this study, we focus on the number of responder fish as our metric of colony aggressiveness because this score was the most repeatable metric recovered from this assay.

Colony aggressiveness was reassessed 11 months later (July 2017) using an identical protocol. We measured colonies' collective aggressiveness twice with 8 days between measurements, and then tested for a correlation in colony's average per capita aggressiveness in 2016 versus 2017. Aggressiveness assays were conducted in 2017 merely to evaluate whether short-term repeatabilities identified in 2016 might attenuate with time.

Collective boldness

To assess colony boldness, we recorded farmerfish colonies' latency to emerge following an aversive stimulus. These assays were conducted separately from the collective mobbing assays described above and did not involve the use of a stimulus fish or control container. Boldness assays were conducted on different days than collective aggressiveness assays.

We used the approach of a snorkeler to startle each colony. The same diver (B.T.B.) approached each colony slowly while submerged and then cleared his snorkel immediately above the colony and then swam away. The approach of the diver paired with the noise of clearing the snorkel reliably elicited a flight response where 100% of colony members retreated into crevices within their colonies. Two other observers then watched the colony at a 90° angle from the approach of the diver and recorded colonies' latency to emerge (in seconds) and the number of individuals visible (i.e., outside shelter) 30 and 60 s after the stimulus. Colonies that emerged more rapidly and those with more individuals out at 30 and 60 s after the aversive stimulus were deemed to be bolder. We estimated colony boldness 5 times (each separated by 48 h) over a 2-week period.

Colony boldness was reassessed 11 months later (July 2017) using an identical protocol. We measured colonies' collective boldness twice with 8 days between measurements, and then tested for a correlation in colony's average boldness (latency to emerge) in 2016 versus 2017. Boldness assays were conducted in 2017 merely to evaluate whether short-term repeatabilities identified in 2016 might attenuate with time. Thus, fewer assays were conducted per colony in 2017.

Natural levels of agonistic behaviors

In addition to the 2-staged behavioral assays described above, we also quantified the natural levels of agonistic encounters observed on or immediately around each colony. These data were used to evaluate the degree to which colonies differed in their levels of aggressiveness expressed under natural situations. Each colony was observed for 60 s from a sizable distance, to minimize the impacts of observer presence on fish behavior. The number of chases directed towards conspecific and heterospecific intruders was counted over this time. We performed one such observation per day 5 times over a 2-week duration (48 h between observations). One advisory note for this metric is that the number of chases counted is likely influenced by the number of intrusions which, in turn, are determined by patch size, the quality of the patch, and its position relative to other patches. Thus, while a more naturalistic measure, this metric should be interpreted with caution. Because of a low repeatability of this assays (see Results for details), we did not replicate this procedure in 2017.

Experimental test of colony defense of branching coral

To quantify how variation in collective behavior of farmerfish colonies affected performance of young coral, small fragments of the staghorn coral *Acropora pulchra* were transplanted into the garden of each focal farmerfish colony, and the amount of coral consumed by corallivores was measured after 3 weeks. *Acropora pulchra* has an arborescent growth form with long, cylindrical branches, is highly favored by corallivores, 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 tip that was hand collected by scuba divers from natural colonies growing on a fringing reef located 1.8 km from the Gump Research Station. Collected corals were transported by boat in individual seawater-filled sealed plastic bags to the research station where they were maintained in a shaded outdoor water table supplied by once-through circulated seawater. Within 2 h of collection and while continuously submerged, each coral fragment was affixed vertically on a uniquely numbered PVC plate (~80 × 35 mm) using Z-Spar A-788 Splash Zone 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 44.7 ± 7.0 mm; range 30–65 mm), and the epoxy was left to cure overnight. The following morning the fragments were transported to the experimental site by boat in individual seawater-filled sealed plastic bags. Each coral plate was affixed to the substrate using a preinstalled stainless steel bolt that fit through a hole in the PVC base plate, and secured on the bolt using stainless steel nuts.

Each colony received 5 haphazardly-selected coral fragments that were distributed within the farmerfish-defended garden to span the natural range in height above bottom, cardinal exposure, etc. In addition to the 29 bommies that supported farmerfish colonies, 3 additional bommies that lacked farmerfish received staghorn outplants as negative controls; these additional bommies, which were interspersed among the other focal bommies, were selected based on similarity in their physical characteristics to the farmerfish bommies, except for the presence of farmerfish and their gardens.

In all, 160 coral fragments were outplanted (32 bommies, 5 nubbins each). To minimize handling time, corals were collected, processed, and outplanted in 3 batches on successive days (i.e., ~53 nubbins at a time). None of the 160 fragments were structurally damaged during the transplantation process (e.g., no axial and radial corallites were broken). Mortality due to handling is readily estimated because over-stressed staghorn fragments first bleach and then lose tissue, leaving an intact skeleton (bleached corals are not consumed). Four outplanted coral fragments bleached (and subsequently died) within a week of deployment and none thereafter, yielding an estimated handling mortality rate of 2.5%.

Based on remote video of outplanted staghorn coral, the primary consumers of *A. pulchra* are excavating corallivores (e.g., barred filefish *Cantherhines dumerilii*; guineafowl puffer *Arothron meleagris*), which in Moorea elicit disproportionately strong aggressive reactions by farmerfish (Gochfeld 2010). These corallivores consume staghorn coral in a distinctive manner by shearing off a portion of the skeleton from the tip of a branch; partially consumed branches are readily distinguished for several weeks afterwards by the sharp end, exposed skeleton, and lack of axial polyp at the branch tip. Thus, in the short term, reduction in length of a coral fragment that shows the characteristic signs of being bitten by an excavating corallivore is an excellent measure of partial predation. Accordingly, the length of each coral fragment was remeasured to the nearest mm in situ after 1, 2, and 3 weeks of its deployment. Here, we only report results for 3 weeks as there was comparatively little change in nubbin lengths between 2 and 3 weeks, suggesting that all bommies had been discovered by corallivores by 3 weeks. The metric used for analyses was the mean proportional reduction in initial branch length after 3 weeks on a bommie, obtained by averaging the proportional change ($[L_{\mathrm{Initial}} - L_{\mathrm{Final}}]/L_{\mathrm{Initial}}$) of the 5 (or 4) replicate coral fragments (excluding the 4 nubbins that died from handling) on each bommie. We elected to focus on proportional change because, despite our careful efforts, there were small differences in the starting size of our outplanted corals.

We remeasured the lengths of each experimental *A. pulchra* nubbin again 6 months later (January 2017) to evaluate the long-term effects of farmerfish aggressiveness on coral performance. Here again, the metric used for our analysis was the mean proportional change in initial branch length across the 4–5 replicate corals on each bommie.

Statistical methods

We first tested whether the collective behavior of each colony was temporally consistent by testing the repeatability of the following responses: 1) the difference in the average number of fish that inspected the stimulus fish (*Zebrasoma*) and the control (Number of Responding Fish), 2) this number divided by the total number of farmerfish in the colony (Per Capita Aggressiveness), 3) the latency for colony members to emerge following the approach of a free diver (Latency to Emerge), 4) the average number of fish out 30 s and 60 s postemergence (Number Out Postemergence), and 5) the number of combined chases exhibited towards conspecific and heterospecific intruders during our scan samples (Total Number of Chases). To assess repeatability, we used the intraclass correlation coefficient (ICC) method in the ICC package (Wolak et al. 2012) of R 3.1.2 (Pinheiro et al. 2014). To improve data fit to a Gaussian error distribution, per capita aggressiveness was arcsine transformed and latency data were not truncated and therefore log-transformed. Repeatabilities and 95% CI are provided here. Repeatabilities were deemed significant if their 95% confidence intervals did not overlap zero. We then tested for correlations across colonies' behavioral responses by averaging colonies' responses across their 5 replicate observations and testing for correlations across these averages (per capita aggressiveness, latency to emerge, number of fish outside after emergence, etc.) using Pearson correlations.

We used general linear models to test for associations between colony attributes and the number of total branching corals (*Pocillopora* + *Acropora*) and total corals present in the farmerfish territory (*Pocillopora*+*Acropora*+*Montipora*). We used colony per capita aggressiveness and the naturally-occurring number of chases exhibited during scan samples as the only predictor variables in our models because all other aspects of colony behavior were highly correlated with each other (Supplementary Information 1) and group size (see Results for details). The average of our 5 behavioral measures for each colony was used to obtain a single metric for per capita aggressiveness and for number of chases per colony. We conducted post hoc pattern exploratory analyses to evaluate possible associations between group size and the body size of group constituents and colony aggressiveness using linear regression models.

To test for associations between colony aggressiveness and the degree of corallivory within farmerfish territories, we averaged the proportional change in length of the 5 *Acropora* coral fragments outplanted into each territory, and then used this metric as our response variable. We then evaluated 4 rival models using AICc model selection criteria, where lower AICc values indicate a more informative model and a difference of AICc >2.0 indicates a notably superior model performance. *Model 1* contained colonies' per capita aggressiveness, time of the census (3 weeks vs. 25 weeks post deployment), and their interaction term. *Model 2* contained the distance of each bommie from the reef crest, times of the census, and their interaction term. Distance from the reef crest is known to be a determinant of coral growth rate in Moorea (Lenihan et al. 2015). *Model 3* contained colonies' per capita aggressiveness, time of census, distance to the reef crest, and all possible interaction terms as predictor variables in the model. Colony per capita aggressiveness was not significantly correlated with distance to the reef crest ($r = 0.11$, $n = 29$, $P = 0.57$). *Model 4* included bommie size (circumference in meters), depth (meters), distance to the reef crest, and all possible interaction terms. All models contained colony ID as a random effect, to account for the fact that data taken from the colony at week 3 and 25 are not statistically independent.

RESULTS

Repeatability of colony behavior

The farmerfish colonies in our study displayed temporally consistent patterns of behavior. Colony identity explained a significant component of the variation in every metric of behavior that we assessed. Our estimates of the intraclass correlation coefficients were as follows, with 95% CI in brackets: number of fish responding to invaders ($r = 0.62$ [0.47, 0.77]), colonies' per capita aggressiveness exhibited towards invaders ($r = 0.35$ [0.15, 0.52]), colonies' latency to emerge in response to invaders ($r = 0.38$ [0.20, 0.56]), the number of fish that emerged following a startle = 0.62 [0.47, 0.77]), and the number of chases colonies exhibited towards foreign fish during natural conditions ($r = 0.15$ [0.01, 0.31]). Per capita colony aggressiveness was not significantly correlated with the number of chases observed at bommies under natural conditions ($r = 0.26$, df = 28, $P = 0.17$), however, per capita aggressiveness was correlated with our metrics of colony boldness (Supplementary Information 1).

Pearson's correlations testing for an association in colonies' average per capita aggressiveness ($r = 0.67$, df = 28, $P < 0.0001$) and boldness (latency to emerge) ($r = 0.73$. df = 28, $P < 0.0001$) across years (2016 vs. 2017) were both highly significant, conveying a high degree of behavioral consistency across years.

Colony behavior versus coral presence

Our general linear models predicting the number of branching corals and the total number of corals present inside farmerfish territories were both significant: *number branching corals* ($F_{2,26} = 6.42$, $R^2 = 0.33$, $P = 0.005$), *total number of corals* ($F_{2,26} = 7.20$, $R^2 = 0.36$, $P = 0.002$). In both cases, we detected a positive association between colonies' per capita aggressiveness and the number of corals located within the colonies' territories (*number branching corals*: $t = 2.74$, $\beta \pm \mathrm{SE} = 21.24 \pm 7.74$, $P = 0.01$; *total number corals*: $t = 2.91$, $\beta \pm \mathrm{SE} = 25.99 \pm 8.52$, $P = 0.007$) (Figure 1). The number of chases exhibited by colonies under natural conditions displayed a positive, nonsignificant association with both metrics of coral abundance (Supplementary Information 1). Post hoc inspection of the data suggested that these trends were driven by a positive relationship between colony per capita aggressiveness and the number of *Pocillopora* present in the territory (Figure 1) and a positive relationship between the number of chases exhibited and the number of *Acropora* present within the territory (Figure 2) (Supplementary Information 1). *Pocillopora* can represent 30–65% of the annual coral recruits at Moorea and upwards of 85–95% of branching coral recruits (Gleason 1996; Penin et al. 2007). Colony per capita aggressiveness was negatively associated with the percent cover of the dominant macroalga *Turbinaria* ($t = 2.24$, $\beta \pm \mathrm{SE} = -3.32 \pm 2.48$, $P = 0.03$).

Colony behavior versus coral replenishment

All 4 of our models predicting the performance of experimentally outplanted coral contained significant terms: *Model 1* ($R^2 = 0.81$, AICc = 73.63), *Model 2* ($R^2 = 0.85$, AICc = 93.71), *Model 3* ($R^2 = 0.86$, AICc = 99.73), and *Model 4* ($R^2 = 0.66$, AICc = 157.50) (Supplementary Information 1). The highest performing model

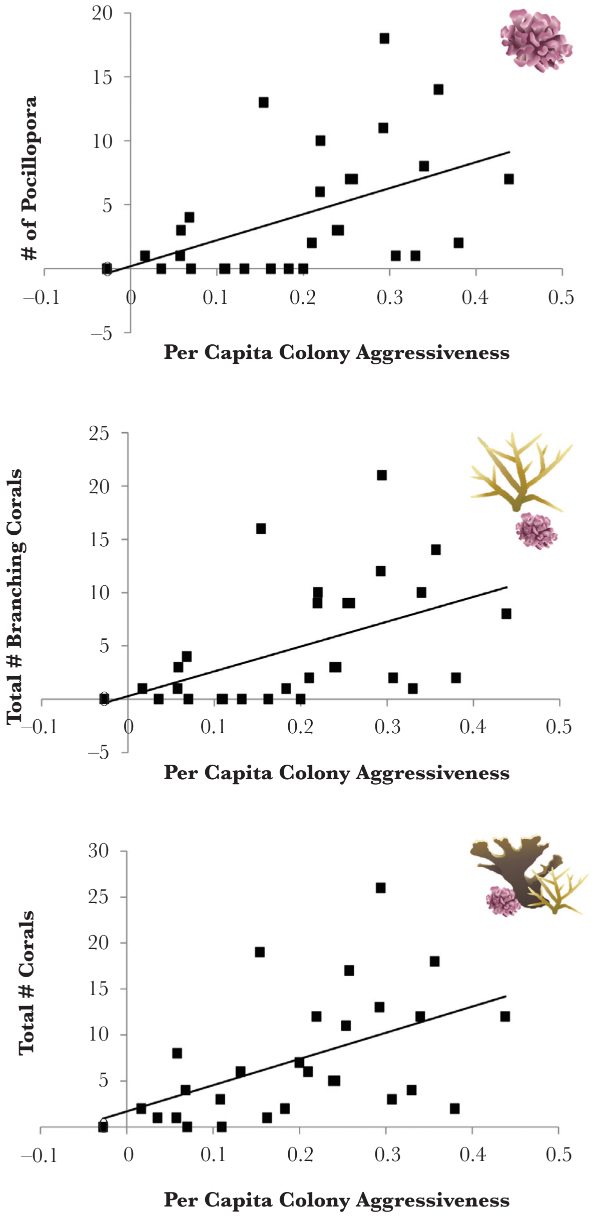

Figure 1
Positive relationships between per capita colony aggressiveness and number of corals in the colony's territory: numbers of *Pocillopora* (top panel), branching corals (middle panel) and total corals (bottom panel) (N = 29). Negative aggressiveness values indicate that a colony was more responsive to an empty container control than a staged herbivore intruder.

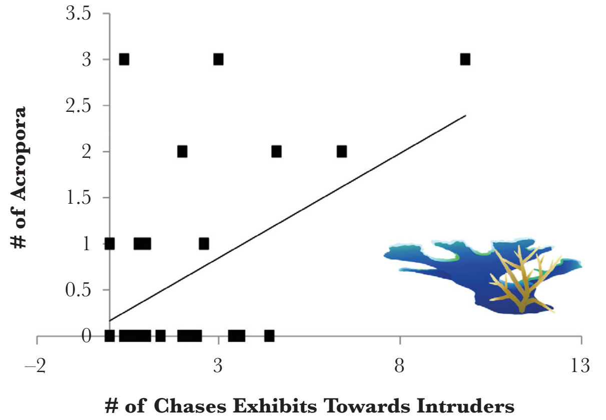

Figure 2
Positive relationship between the number of naturally-occurring chases observed during our scan samples of Farmerfish colonies and the number of *Acropora* found within the colony's territory (n = 29). Note that only 10 bommies contained *Acropora* in our sample.

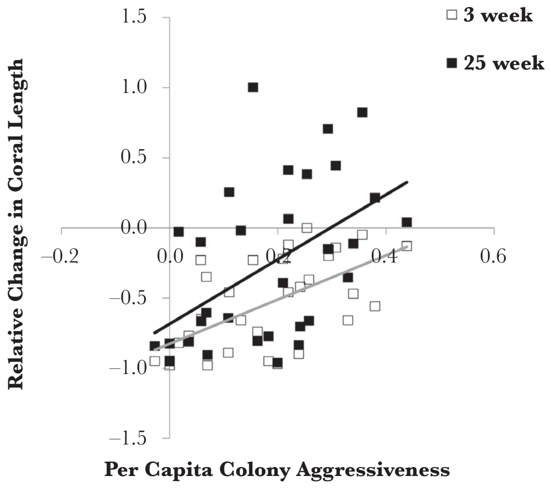

Figure 3
Data are the average relative change in length of outplanted staghorn coral (*Acropora pulchra*) on each *Stegastes* territory 3 and 25 weeks after transplantation vs. colonies' per capita aggressiveness (N = 29). Each territory received 5 replicate branches ("nubbins") of staghorn (mean 44.7 mm tall; range 30–65). Each numbered branch was remeasured periodically in situ until 3 weeks had elapsed and again 25 weeks after outplant. Early decreases in length (week 3) likely represent predation by excavating corallivores. Negative aggressiveness values indicate that a colony was more responsive to an empty container control than a staged herbivore intruder.

in this analysis was the model containing colony aggressiveness, the time of sampling, and their interaction term (*Model 1*). This model contained significant main effects of time of sampling ($F_{1,30}$ = 15.68, $\beta \pm$ SE = 0.13 ± 0.03, P = 0.0004), per capita colony aggressiveness ($F_{1,30}$ = 14.86, $\beta \pm$ SE = 1.94 ± 0.50, P = 0.0006), but not their significant interaction term ($F_{1,30}$ = 1.79, $\beta \pm$ SE = 0.36 ± 0.27, P = 0.19).

Our control corals outplanted on bommies that lacked farmerfish suffered 98% corallivory after 3 weeks, which did not drastically differ from the >80% corallivory experienced by corals in nonaggressive territories in an equivalent amount of time. By contrast, corals outplanted into very aggressive colonies experienced far less (<20%) corallivory (Figure 3). Over 25 weeks, only corals outplanted into moderate or aggressive farmerfish territories grew in length, whereas corals outplanted into docile territories shrank in size (length). Corals were also slightly larger 25 weeks post outplanting, which conveys that corals were on average growing in their new habitats (Figure 3).

Underpinnings of colony aggressiveness

The results above raise the question of why territories differ in their collective aggressiveness. Post hoc pattern exploration using linear regression revealed a positive association between the proportion of colony members that were large in size (10–15 cm FL) and the per capita aggressiveness of the colony ($F_{1,27} = 7.57$, $R^2 = 0.22$, $\beta \pm SE = 0.011 \pm 0.003$, $P = 0.01$). Presumably larger individuals might engage in more aggressive behavior because their size affords them greater safety, and thus, they can more freely engage in risky behaviors, like colony defense. Aggressive demonstrators may also instigate aggressiveness in smaller group mates. Additional studies are required to evaluate these hypotheses.

An association between colony aggressiveness and colony member size raises a question whether differences across colonies in average body size alone might be a stronger predictor of coral recovery rates than our aggressiveness measure. Thus, in a post hoc analysis, we constructed a model containing average colony member size, time point of sampling, and their interaction term as predictor variables and average percent change in coral size at each bommie as our response variable. Bommie ID was again included as a random effect in this model. Although average fish size was a significant term in this model ($F_{1,30} = 10.49$, $\beta \pm SE = 0.014 \pm 0.004$, $P = 0.003$, AICc = 97.12), this analysis did not perform as well as the model containing per capita colony aggressiveness (*Model 1*), suggesting that differences in body size alone are not completely sufficient to explain the observed patterns in coral recovery ($R^2 = 0.80$). To further probe this relationship, we performed another follow-up analysis on just the 25-week data to ask: Does collective aggressiveness tells us anything above and beyond between-colony differences in body size when predicting coral growth? For this analysis we included the average body size of colony members as a covariate ($F_{1,30} = 6.72$, $r^2 = 0.18$, $P = 0.015$) and then tested whether per capita aggressiveness explains a significant component of this residual variation—which is does ($F_{1,30} = 5.14$, $r^2 = 0.15$, $P = 0.03$). We then performed a parallel analysis where we included colony aggressiveness as a covariate ($F_{1,30} = 14.34$, $r^2 = 0.32$, $P = 0.0007$) and evaluated whether body size tells us anything above and beyond colony behavior—which is does not ($F_{1,30} = 0.78$, $r^2 = 0.03$, $P = 0.38$). These results convey that colony aggressiveness is an important driver of coral performance, even when accounting for farmerfish body size, but the reverse is not true.

For most* behavioral metrics considered here, we detected a positive association between colony size (number of farmerfish present) and their collective behavior (All $P < 0.0007$, Supplementary Information 1). However, no such association was detected between colony size and per capita colony aggressiveness ($P = 0.52$).

DISCUSSION

Much of the attention on collective behavior is devoted to understanding how it is organized and executed with imperfect information and a lack of central control (Couzin and Franks 2003; Sumpter 2006). Some studies have explored the functional consequences of collective behavior for social groups (Wray et al. 2011; Gordon 2013) but very few have sought to assess the effects of collective behavior on broader ecological processes. Yet, we reason that the ecological impacts of collective behavior are likely to be sizeable for a variety of systems. Stable intergroup differences in behavior provide us with a convenient tool with which to evaluate such effects. Here, we show that farmerfish groups exhibit stable differences in their collective behavior for every behavioral metric we considered. What is more, our data provide some of the first evidence that these intergroup differences in collective behavior could play a role in shaping the trajectory of ecosystems.

Most coral reefs periodically experience large-scale disturbances. Cyclones (De'ath et al. 2012), outbreaks of crown-of-thorns sea stars (*Acanthaster planci*) (Berumen and Pratchett 2006; Kayal et al. 2012), and bleaching events (Gleason 1993) are some of the most prominent events that result in large-scale die-offs. One challenge for ecologists is to determine the factors that allow some coral communities to rebound from such events and what causes others to transition into alternative persistent states (e.g., algal dominated systems). We propose that intraspecific behavioral variation in coral-associated fishes might help to explain some of this variability on a fine scale. Farmerfish are a highly territorial species with defensive behavior towards intruders including conspecifics, heterospecifics and even novel objects (Vullioud et al. 2013). This species also has a large distribution ranging from east Africa to the eastern Pacific—a region containing many of the world's coral reefs (Roberts et al. 2002). These fish also reach high densities in many reef systems, with many individuals per meter squared (Johnson et al. 2011). These attributes poise this species, and others like them, to have considerable impacts on the dynamics of coral reef systems across large regions, at least at a bommie by bommie level.

We show here that, like many other animals (Jandt et al. 2013; Farine et al. 2015), farmerfish exhibit stable between-group differences in their collective behavior. We further provide evidence that their impacts on coral recruitment and population replenishment vary based on a group's behavioral tendencies. Here, we deem recruitment to mean successful establishment in a patch. Specifically, we observed a sizable reduction in incidence of excavating corallivory when corals were experimentally established in aggressive farmerfish colonies, and enhanced relative growth rates over several months. While previous studies have verified that corals experience reduced corallivory inside of farmerfish territories (White and O'Donnell 2010), our data reveal that these effects are not merely binary and vary by more than 400% in association with a colony's behavior (Figure 3). Moreover, more aggressive groups harbor a larger number of branching corals, particularly *Pocillopora*, which often represent the majority of coral recruits in the Moorea system (Gleason 1996). There is thus both correlative and experimental evidence to suggest that the ecosystem effects provided by farmerfish change predictably based on the behavioral tendencies of the colony considered.

One of the limitations of our study's design is the inability to document a cause-effect relationship between farmerfish behavior and coral growth. While aggressive farmerfish territories naturally harbor more branching corals and out-planted corals experience less corallivory in these territories, farmerfish may also behave more defensively because their territories harbor more branching corals. For instance, branching corals may provide greater protection from predators or increased surface area on which to garden turf algae. Farmerfish may therefore behave more aggressively here because coral-rich environments are better territories, and therefore, worth defending more aggressively. To critically decipher whether aggressive groups create coral-rich environments (and not vice versa) one needs to manipulate coral presence in farmerfish territories and observe the effects that this has on farmerfish behavior (corals → behavior). And, one further needs to create experimental farmerfish colonies of contrasting behavioral tendencies, outplant corals within their territories, and then monitor coral performance (behavior → corals). We have data demonstrating that outplanted corals can increase farmerfish colony aggressiveness (Kamath A and Pruitt JN, unpublished data), conveying one direction of causality is present. Unfortunately, the high mobility of farmerfish and the difficulty of creating artificial coral heads, which would weigh hundreds of kilograms, have prevented us from evaluating cause-effect relationships in the opposing direction.

We propose a possible positive feedback loop between farmerfish behavior and community composition in terms of corals versus macroalgae (summarized in Figure 4). Suppose that immediately after a large disturbance that some habitat patches previously dominated by corals come to harbor nonaggressive groups of farmerfish while others come to harbor aggressive groups. If a patch comes to be occupied by an aggressive group, then this is predicted to decrease corallivory and increase coral recruitment and regeneration in that patch. Once the patch becomes coral-dominated, corals are known to inhibit the establishment of macroalgae. Nonaggressive farmerfish groups are predicted to yield higher levels of corallivory and reduced coral regeneration, and therefore may facilitate the establishment of macroalgae competitors. This latter cycle is supported by our finding that nonaggressive groups tend to harbor more *Turbinaria* within their territories. While the directionality of these associations between colony behavior and community composition is uncertain (see above), our data here raise the possibility of such feedbacks.

One significant conclusion from our findings is that overlooking intraspecific variation in key functional traits, like behavior, may prevent us from accurately forecasting the dynamics of future coral reefs. For example, evidence suggests that increasing global temperatures threatens coral reefs by decreasing corals' photosynthetic rates and increasing incidence of bleaching (Glynn 1993; Hoegh-Guldberg 1999; Anthony et al. 2008). However, this prediction becomes more nuanced when one simultaneously considers the behavior of key coral associates, like farmerfish and other territorial fishes. It is well-established in ectotherms that increased temperatures result in an exponential increase in animals' basal metabolic rates (Schmidt-Nielsen 1991; Clarke and Johnston 1999), which leads to large increases in animals' activity, boldness

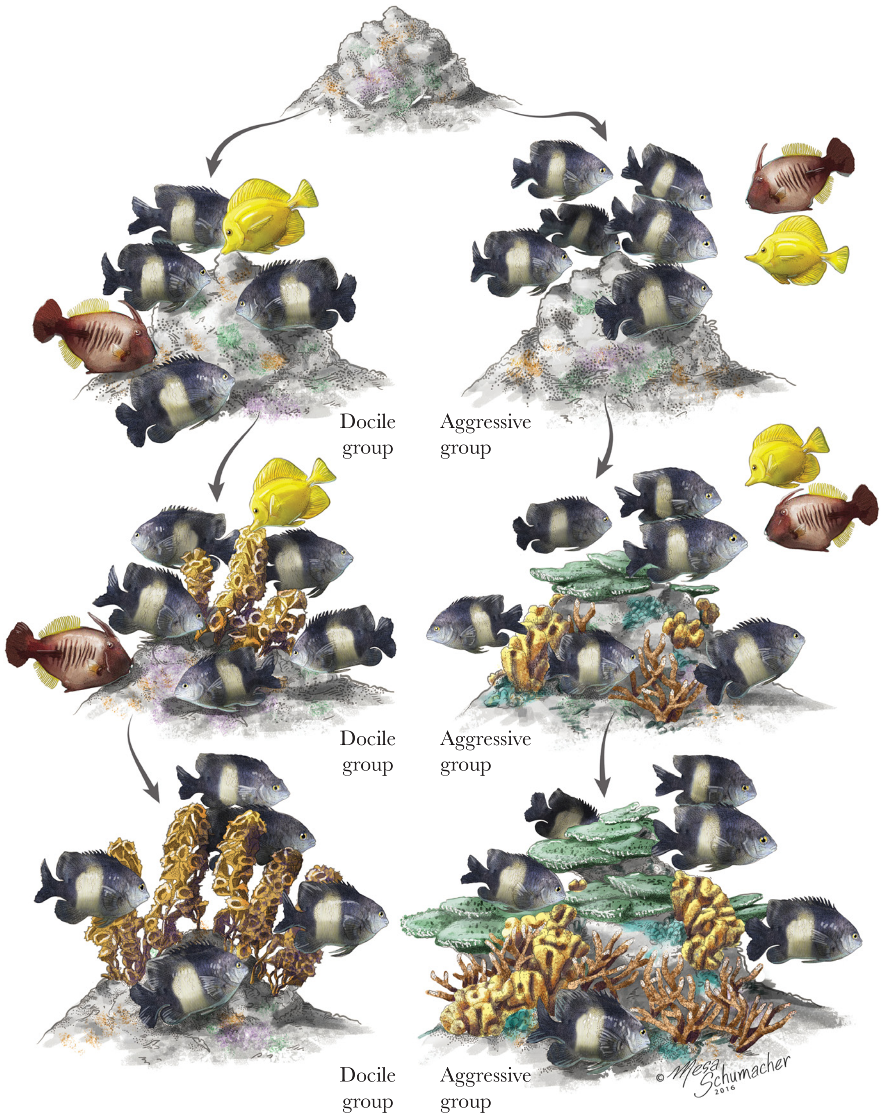

Figure 4
Diagram depicting the predicted successional consequences of docile (left side) versus aggressive (right side) *Farmerfish* groups. Nonaggressive groups are predicted to defend newly-recruited corals poorly, permitting macroalgae (genus *Turbinaria*) to establish in the patch. Aggressive groups are predicted to defend newly-recruited corals more effectively, thus permitting them to reach greater abundances in these patches and prevent the establishment of macroalgae competitors.

and aggressiveness (Biro et al. 2010; Pruitt et al. 2011; Briffa et al. 2013). Thus, as the world's oceans warm, the behavioral tendencies of many marine ectotherms are speculated to shift towards more aggressive phenotypes, at least over some temperature ranges. As documented here, such shifts could increase the defensive efficacy of residential fishes, which could offset some of the costs of reduced photosynthetic performance: a large increase in the aggressiveness of farmerfish could reduce corallivory by 50–80%, based on our estimates. Results like these help to illustrate that much of the diversity in key functional traits, like behavior or physiology, occurs below the level of the guild, the species, or even the population, and that accounting for such variability could be key for predicting the future state of biological systems—terrestrial or marine.

CONCLUSIONS

We establish here that intergroup differences in collective aggressiveness are positively associated with coral establishment and population replenishment in lagoon patch reefs in Moorea. More aggressive farmerfish groups harbor more corals within their territories, and the growth and survival of corals are enhanced when they occur within such territories. These findings suggest that variation in group behavior could play a role in determining the functioning and resilience of entire ecosystems. Many ecosystem engineers are social animals. Elephants are one of the key drivers of structural change in savannah habitats across much of Africa (van Aarde et al. 1999; van Aarde and Jackson 2007). In the Amazon, the ant *Myrmelachista schumanni* turns one of the most diverse forests on the planet into a sparely populated monoculture of one tree species by envenomating all other trees (Frederickson and Gordon 2007, 2009)—termed "Devil's Gardens." Humans have likewise altered the Earth beyond recognition for many of world's most sensitive species. Data like those reported here provide empirical evidence that the impacts of major social organisms on their environments will be different and predictable depending on the collective behavioral phenotype of the specific group considered. Thus, documenting relationships between group behavior and their ecological effects may help us to understand the current and future states of a variety of ecological systems.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Pruitt et al. (2018).

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REFERENCES

van Aarde R, Whyte I, Pimm S. 1999. Culling and the dynamics of the Kruger National Park African elephant population. Anim Conserv. 2:287–294.

van Aarde RJ, Jackson TP. 2007. Megaparks for metapopulations: addressing the causes of locally high elephant numbers in southern Africa. Biol Conserv. 134:289–297.

Anthony KR, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. Proc Natl Acad Sci USA. 105:17442–17446.

Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature. 518:538–541.

Berumen ML, Pratchett MS. 2006. Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. Coral Reefs. 25:647–653.

Biro PA, Beckmann C, Stamps JA. 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. Proc Biol Sci. 277:71–77.

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VH, Schreiber SJ, Urban MC, Vasseur DA. 2011. Why intraspecific trait variation matters in community ecology. Trends Ecol Evol. 26:183–192.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: incidence and implications of individual specialization. Am Nat. 161:1–28.

Briffa M, Bridger D, Biro PA. 2013. How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. Anim Behav. 86:47–54.

Ceccarelli DM, Jones GP, McCook LJ. 2001. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. Oceanography and Marine Biology. 39:355–389.

Chang AT, Sih A. 2013. Multilevel selection and effects of keystone hyperaggressive males on mating success and behavior in stream water striders. Behav Ecol. 24:1166–1176.

Clarke A, Johnston NM. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol. 68:893–905.

Couzin ID, Franks NR. 2003. Self-organized lane formation and optimized traffic flow in army ants. Proc Biol Sci. 270:139–146.

De'ath G, Fabricius KE, Sweatman H, Puotinen M. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci USA. 109:17995–17999.

Dickie IA, Fukami T, Wilkie JP, Allen RB, Buchanan PK. 2012. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. Ecol Lett. 15:133–141.

Done TJ, Dayton PK, Dayton AE, Steger R. 1991. Regional and local variability in recovery of shallow coral communities - moorea, french-polynesia and central great-barrier-reef. Coral Reefs. 9:183–192.

Farine DR, Montiglio PO, Spiegel O. 2015. From individuals to groups and back: the evolutionary implications of group phenotypic composition. Trends Ecol Evol. 30:609–621.

Fogarty S, Cote J, Sih A. 2011. Social personality polymorphism and the spread of invasive species: a model. Am Nat. 177:273–287.

Frederickson ME, Gordon DM. 2007. The devil to pay: a cost of mutualism with *Myrmelachista schumanni* ants in 'devil's gardens' is increased herbivory on Duroia hirsuta trees. Proc Biol Sci. 274:1117–1123.

Frederickson ME, Gordon DM. 2009. The intertwined population biology of two Amazonian myrmecophytes and their symbiotic ants. Ecology. 90:1595–1607.

Gleason MG. 1993. Effects of disturbance on coral communities - bleaching in moorea, french-polynesia. Coral Reefs. 12:193–201.

Gleason MG. 1996. Coral recruitment in Moorea, French Polynesia: the importance of patch type and temporal variation. J Exp Mar Biol Ecol. 207:79–101.

Glynn PW. 1993. Coral-reef bleaching - ecological perspectives. Coral Reefs. 12:1–17.

Gobler CJ, Thibault DB, Davis TW, Curran PB, Peterson BJ, Liddle LB. 2006. Algal assemblages associated with Stegastes sp territories on Indo-Pacific coral reefs: characterization of diversity and controls on growth. J Exp Mar Biol Ecol. 336:135–145.

Gochfeld DJ. 2010. Territorial damselfishes facilitate survival of corals by providing an associational defense against predators. Mar Ecol Prog Ser. 398:137–148.

Gordon DM. 2013. The rewards of restraint in the collective regulation of foraging by harvester ant colonies. Nature. 498:91–93.

Griffen BD, Toscano BJ, Gatto J. 2012. The role of individual behavior type in mediating indirect interactions. Ecology. 93:1935–1943.

Haley MP, Muller CR. 2002. Territorial behaviour of beaugregory damselfish (*Stegastes leucostictus*) in response to egg predators. J Exp Mar Bio Ecol. 273:151–159.

Hata H, Kato M. 2002. Weeding by the herbivorous damselfish Stegastes nigricans in nearly monocultural algae farms. Mar Ecol Prog Ser. 237:227–231.

Hata H, Watanabe K, Kato M. 2010. Geographic variation in the damselfish-red alga cultivation mutualism in the Indo-West Pacific. BMC Evol Biol. 10:185.

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res. 50:839–866.

Hughes AR, Stachowicz JJ. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proc Natl Acad Sci USA. 101:8998–9002.

Hui A, Pinter-Wollman N. 2014. Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants. Anim Behav. 93:261–266.

Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A. 2013. Behavioural syndromes and social insects: personality at multiple levels. Biological Reviews.

Jandt JM, Bengston S, Pinter-Wollman N, Pruitt J, Raine N, Dornhaus A, Sih A. 2014. Behavioral syndromes and social insects: personality at multiple levels. Biol Rev. 89:48–67.

Johnson MK, Holbrook SJ, Schmitt RJ, Brooks AJ. 2011. Fish communities on staghorn coral: effects of habitat characteristics and resident farmerfishes. Environ Biol Fishes. 91:429–448.

Jungwirth A, Josi D, Walker J, Taborsky M. 2015. Benefits of coloniality: communal defence saves anti-predator effort in cooperative breeders. Funct Ecol. 29:1218–1224.

Kayal M, Vercelloni J, Lison de Loma T, Bosserelle P, Chancerelle Y, Geoffroy S, Stievenart C, Michonneau F, Penin L, Planes S, et al. 2012. Predator crown-of-thorns starfish (Acanthaster planci) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. PLoS One. 7:e47363.

Keiser CN, Jones DK, Modlmeier AP, Pruitt JN. 2014. Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. Behav Ecol Sociobiol. 68:839–850.

Keiser CN, Pruitt JN. 2014a. Personality composition is more important than group size in determining collective foraging behaviour in the wild. Proc R Soc B. 281:20141424.

Keiser CN, Pruitt JN. 2014b. Spider aggressiveness determines the bidirectional consequences of host–inquiline interactions. Behav Ecol. 25:142–151.

Lenihan HS, Hench JL, Holbrook SJ, Schmitt RJ, Potoski M. 2015. Hydrodynamics influence coral performance through simultaneous direct and indirect effects. Ecology. 96:1540–1549.

Modlmeier AP, Foitzik S. 2011. Productivity increases with variation in aggression among group members in Temnothorax ants. Behav Ecol. 22:1026–1032.

Modlmeier A, Keiser C, Shearer T, Pruitt J. Forthcoming 2014. Species-specific influence of group composition on collective behaviors in ants. Behav Ecol Sociobiol. 68:1929–1937.

Penin L, Adjeroud M, Pratchett MS, Hughes TP. 2007. Spatial distribution of juvenile and adult corals around Moorea (French Polynesia): implications for population regulation. Bull Mar Sci. 80: 379–389.

Pinter-Wollman N, Gordon DM, Holmes S. 2012. Nest site and weather affect the personality of harvester ant colonies. Behav Ecol. 23:1022–1029.

Pinter-Wollman N, Wollman R, Guetz A, Holmes S, Gordon DM. 2011. The effect of individual variation on the structure and function of interaction networks in harvester ants. J R Soc Interface. 8:1562–1573.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team. 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1–115.

Pruitt JN. 2012. Behavioural traits of colony founders affect the life history of their colonies. Ecol Lett. 15:1026–1032.

Pruitt JN. 2013. A real-time eco-evolutionary dead-end strategy is mediated by the traits of lineage progenitors and interactions with colony invaders. Ecol Lett. 16:879–886.

Pruitt JN, Demes KW, Dittrich-Reed DR. 2011. Temperature mediates shifts in individual aggressiveness, activity level, and social behavior in a spider. Ethology. 117:318–325.

Pruitt JN, Keiser CN, Banka BT, Liedle JD, Brooks AJ, Schmitt RJ, Holbrook SJ. 2018. Data from: collective aggressiveness of an ecosystem engineer is associated with coral recovery. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.50r4t2p

Pruitt JN, Modlmeier AP. 2015. Animal personality in a foundation species drives community divergence and collapse in the wild. J Anim Ecol. 84:1461–1468.

Randall JE. 2005. Reef and Shore Fishes of the South Pacific. Honolulu (HI): University of Hawaii Press.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. Biol Rev Camb Philos Soc. 82:291–318.

Roberts CM, McClean CJ, Veron JE, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG, Schueler FW, Spalding M, Wells F, et al. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science. 295:1280–1284.

Ros AF, Vullioud P, Bruintjes R, Vallat A, Bshary R. 2014. Intra- and interspecific challenges modulate cortisol but not androgen levels in a year-round territorial damselfish. J Exp Biol. 217:1768–1774.

Schmidt-Nielsen K. 1991. Animal physiology. Cambridge (UK): Cambridge University Press.

Sih A, Bell AM. 2008. Insights for Behavioral Ecology from Behavioral Syndromes. Adv Study Behav. 38:227–281.

Sih A, Bell AM, Johnson JC, Ziemba RE. 2004. Behavioral syndromes: an intergrative overiew. Q Rev Biol. 79:241–277.

Sih A, Cote J, Evans M, Fogarty S, Pruitt J. 2012. Ecological implications of behavioural syndromes. Ecol Lett. 15:278–289.

Sumpter DJT. 2006. The principles of collective animal behaviour. Philos Trans R Soc Lond B Biol Sci. 361:5–22.

Taborsky M, Wong M. 2017. Sociality in fishes. In D. I. Rubenstein and P. Abbot, editors. Comparative social evolution. Cambridge: Cambridge University Press.

Toscano BJ, Griffen BD. 2014. Trait-mediated functional responses: predator behavioural type mediates prey consumption. J Anim Ecol. 83:1469–1477.

Vullioud P, Bshary R, Ros AF. 2013. Intra- and interspecific aggression do not modulate androgen levels in dusky gregories, yet male aggression is reduced by an androgen blocker. Horm Behav. 64:430–438.

White JSS, O'Donnell JL. 2010. Indirect effects of a key ecosystem engineer alter survival and growth of foundation coral species. Ecology. 91:3538–3548.

Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution. Trends Ecol Evol. 27:452–461.

Wolak M, Wolak MM. 2015. Package "ICC". Facilitating Estimation of the Intraclass Correlation Coefficient.

Wray MK, Mattila HR, Seeley TD. 2011. Collective personalities in honeybee colonies are linked to colony fitness. Anim Behav. 81:559–568.