Social interactions among grazing reef fish drive material flux in a coral reef ecosystem

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In human financial and social systems, exchanges of information among individuals cause speculative bubbles, behavioral cascades, and other correlated actions that profoundly influence system-level function. Exchanges of information are also widespread in ecological systems, but their effects on ecosystem-level processes are largely unknown. Herbivory is a critical ecological process in coral reefs, where diverse assemblages of fish maintain reef health by controlling the abundance of algae. Here, we show that social interactions have a major effect on fish grazing rates in a reef ecosystem. We combined a system for observing and manipulating large foraging areas in a coral reef with a class of dynamical decision-making models to reveal that reef fish use information about the density and actions of nearby fish to decide when to feed on algae and when to flee foraging areas. This "behavioral coupling" causes bursts of feeding activity that account for up to 68% of the fish community's consumption of algae. Moreover, correlations in fish behavior induce a feedback, whereby each fish spends less time feeding when fewer fish are present, suggesting that reducing fish stocks may not only reduce total algal consumption but could decrease the amount of algae each remaining fish consumes. Our results demonstrate that social interactions among consumers can have a dominant effect on the flux of energy and materials through ecosystems, and our methodology paves the way for rigorous in situ measurements of the behavioral rules that underlie ecological rates in other natural systems.

collective behavior | ecological rates | critical transition | functional response | Allee effect

Our understanding of the ecology of the natural world is rooted in the study of pairwise interactions between individual consumers and their resources. Reducing ecological dynamics to individual consumer–resource interactions provides a powerful way to derive fundamental ecological rates, such as the fluxes of energy and materials from resource to consumer populations (1). This approach, however, often neglects correlations between the behaviors of individual consumers. Studies of natural (2–5) and human (6–8) systems have documented widespread behavioral coupling, whereby the presence or action of one individual generates cues that influence the actions of other individuals. In the context of an ecosystem, behavioral coupling among consumers has the potential to induce feedbacks that can increase [e.g., via behavioral Allee effects (9)] or decrease [via consumer interference or false alarms (10)] the rate at which consumer communities harvest resources, and thereby affect how the ecosystem functions, fluctuates, and responds to environmental change (11, 12).

The population- and ecosystem-level consequences of behavioral coupling are typically inferred from demographic data, for example, by fitting models with and without behavioral Allee effects to population time series (9, 13). However, relying on demographic data alone can severely mischaracterize dynamics when data are limited: for example, in cases where observed population dynamics occur in a regime where behavioral coupling has little effect on population growth and death rates, but unobserved regimes exist where effects of coupling are dominant (13).

In principle, behavioral coupling and the feedbacks it induces could be measured directly, by quantifying the rules consumers use to respond to one another and linking these rules to rates of resource consumption (14). This approach has been successfully used to characterize ecological rates in laboratory systems (11, 15) but has not been applied in natural ecosystems. Here, we measure how behavioral coupling influences resource consumption in a coral reef ecosystem by combining field experiments with a method for fitting and comparing dynamical decision-making models.

We focused on a vital consumer–resource interaction in coral reef ecosystems: the consumption of benthic algae by fish. When unchecked, algae can harm foundation coral species and cause catastrophic changes to reef ecosystems (12, 16). We studied mixed-species aggregations of nonschooling reef fish [primarily herbivores in the families Acanthuridae and Scaridae; (17)] in the coral reefs of Mo'orea, French Polynesia. These species face a trade-off between foraging in open reef flats, rich in algae but exposed to predators (Fig. S1), or remaining close to the reef structure, where algae are less available (18). Because fish feed in shared foraging areas, they have the opportunity to base their decisions to forage or flee foraging areas, at least in part, on the presence and actions of other nearby fish (3).

If reef fish interact primarily by interfering with one another during foraging (14), or if copying one another's actions causes frequent false alarms (2, 10), we might expect behavioral

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Significance

Social behaviors pervade natural ecosystems, but their effects on ecosystem processes have been difficult to measure. Here, we demonstrate that coral reef fish base decisions to feed on algae or flee from predators on the density and actions of other fish in the landscape, inducing strong temporal correlations in foraging behavior. Using field experiments and a modeling framework, we show that these behavioral interactions can strongly affect the ecological function of reef fish, including the amount of algae fish consume, and the resulting rate at which fish move energy and materials through the reef ecosystem. More generally, our results illustrate that behavioral correlations can exert a dominant effect on ecosystem processes.

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coupling to reduce the amount of algae fish consume. On the contrary, if fish are more likely to enter foraging areas or feed for longer periods of time when other foraging fish are present—for example, because the presence of other foragers reduces perceived risk (19, 20)—behavioral coupling could increase algal consumption, at least across a range of consumer densities where resource productivity is not limiting. These two scenarios have vastly different implications for reef ecosystems. The first scenario induces a negative density dependence that reduces the amount of algae each fish can consume as population densities rise (10, 14). The second scenario can induce a positive density dependence across a range of population densities, potentially causing Allee effects that could make fish populations highly vulnerable to extinction as they become small (9, 11, 13).

Results

Detecting and Quantifying Behavioral Coupling in Situ. To determine whether and how behavioral coupling influences algal consumption, we engineered large underwater camera frames, each equipped with an array of downward-facing video cameras to remotely monitor foraging areas within the reef (*Materials and Methods* and Fig. S1). This setup allowed us to observe continuously all fish that entered or exited foraging areas and to record the timing of thousands of fish foraging decisions.

Our data revealed that fish entered and exited foraging areas in bursts of activity, interspersed among periods of low activity (Fig. 1). Bursts were caused by strong temporal correlations in fish behavior (Fig. S2) that could have been generated by two nonmutually exclusive mechanisms: independent responses of fish to environmental stimuli (e.g., nearby predators) and behavioral coupling (2). To determine how these two mechanisms influence fish foraging decisions, we experimentally manipulated foraging areas by imposing an ecologically relevant threat: an approaching spear fisherman (21) (*Materials and Methods*).

By applying the same threat stimulus in repeated trials ($n = 51$), we could condition observed responses of fish on a known stimulus. In unmanipulated controls ($n = 44$), fish grazed foraging areas continuously, with the exception of sporadic instances when all fish briefly exited (Fig. S3). In the predator treatment, all fish exited the foraging area in nearly 100% of experimen-
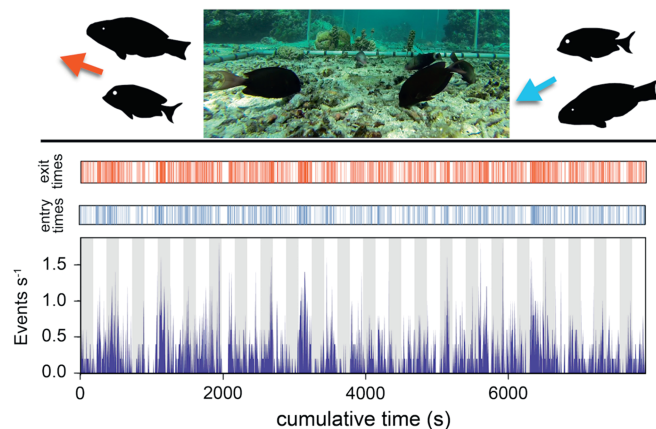
Fig. 1. (*Top*) Reef fish enter and exit foraging areas in bursts of activity. Using overhead camera arrays (Fig. S1), we recorded (*Middle*) the times at which reef fish exited (red bars) and entered (blue bars) foraging areas (bars are exit/entry times from $n = 44$ concatenated time series; gray and white bands indicate distinct time series). (*Bottom*) The rate of events (entries + exits s^{-1}), illustrating bursts of activity. Large bursts of activity occur more frequently than expected if fish foraging decisions were temporally uncorrelated (permutation test, $p = 1 \times 10^{-4}$; Fig. S2).
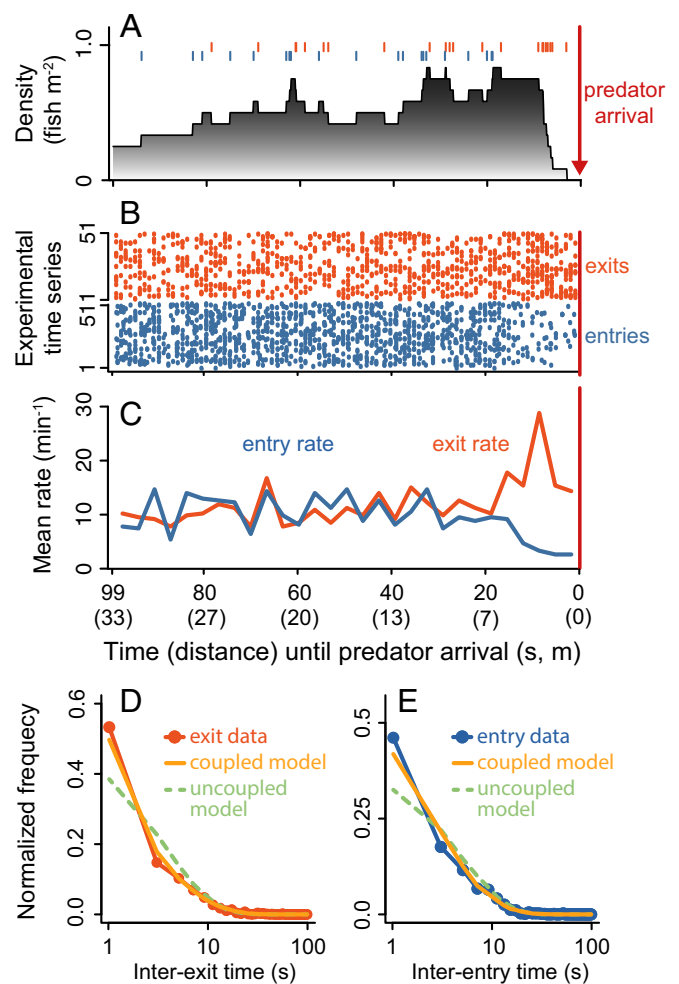

Fig. 2. Reef fish make foraging decisions by combining direct information about predators with social cues. (*A*) An experimental time series from the predator treatment, showing the density of foraging fish (gray) and sequence of fish entries (blue) and exits (red) from the foraging area. (*B*) Sequence of entries and exits for all $n = 51$ time series from the predator treatment. (*C*) Mean entry and exit rates calculated from time series shown in *B*. (*D* and *E*) Normalized frequency distribution of (*D*) interexit and (*E*) interentry intervals calculated from the time series shown in *C* and from simulations using best-fit model (orange solid line) and best-fit model without behavioral coupling (green dashed line; see *SI Text, Multimodel Inference and Model Comparisons*).

tal trials, and fish did not return for an average of 34 s (Fig. S3), indicating that the predator treatment elicited a community-wide flight response. Fig. 2*A* shows a typical time series of fish entries and exits from the predator treatment (blue and red bars), along with the density of foraging fish (gray density plot). When the predator was far from the foraging area, fish entered and exited individually or in short bursts of several entries or exits (Fig. 2*A*, time >20 s). As the predator came near the foraging area, fish ceased to enter, and all remaining fish exited (Fig. 2*A*, time <20 s). This pattern was consistently observed across predator trials (Fig. 2 *B* and *C*).

The timing of entry and exit events (Fig. 2*B*) and changes in event frequency are driven by underlying changes in fish behavior. To infer the behavioral rules fish use to decide when to enter and exit foraging areas, we modeled latent entry and exit rates using a dynamical decision-making model.

Dynamical Decision-Making Model. To infer decision rules from behavioral time series, we derived a dynamical decision-making

model based on the theory of self-exciting random walks (22, 23). The model described the timing of fish entries into and exits from the foraging area (Fig. 2 *A* and *B*) as a stochastic process, with latent entry and exit rates that could depend on the predator stimulus, socials cues, or both (*Materials and Methods* and Eq. **1**). The predator experiment served to provide a known stimulus, which allowed us to distinguish effects of predator forcing from effects of behavioral coupling among fish.

We derived the likelihood function associated with the stochastic process defined by Eq. **1**, which allowed us to fit and compare models that represent alternative hypotheses about how fish respond to predators and social cues. We compared models that included only direct responses of fish to the predator stimulus to models that also included responses to the density and previous actions of other fish (see *SI Text* and Table S1 for details of model comparison). All models that best described data from the predator treatment included responses to both the predator and social cues, as indicated by the Bayesian Information Criterion (BIC): ΔBIC of the best model without behavioral coupling = 190.8 (Table S1).

As the predator approached, fish lowered the rate at which they entered the foraging area and increased the rate at which they exited (Fig. 2*C*). Models with and without behavioral coupling captured these patterns (Fig. S4), but models without coupling failed to reproduce the large number of brief time intervals between entries and exits that occurred when fish entered or exited in bursts (Fig. 2 *D* and *E*, green dashed line). Models that included behavioral coupling not only fit data far better (Table S1), but these models also reproduced the short intervals between entries and exits (Fig. 2 *D* and *E*, orange solid line), suggesting that rapid bursts of activity occur, in part, because fish use cues from other fish to decide whether to feed or flee.

The model that best described our data revealed that fish increase their entry rate into foraging areas in response to past fish entries, and they increase their exit rate from foraging areas in response to past fish exits (Table S1 and Fig. S4). Furthermore, fish lower their sensitivity to departures of other foragers as the overall density of foragers increases (Fig. S5). Because of this, false alarm cascades are relatively rare, even when the density of foraging fish is high (Fig. S6), and the lengths of foraging bouts increase with fish density (Fig. 3). We did not find evidence that fish change the way they respond to social cues as a predator approaches (Table S1).

Behavioral Coupling Increases Carbon and Nitrogen Flux from Algae to Fish. Because the entry and exit rate models we fitted to data define a stochastic process, we could use fitted models to simulate the number of reef fish in foraging areas over long periods of time. To determine how these behaviors affected algal consumption and consequent elemental fluxes, we used the model that best described our experimental data to simulate foraging by the herbivorous reef fish community over full diel foraging cycles (~10.65 h·d⁻¹; see *SI Text, Simulated Foraging*). To quantify the mean rate at which the herbivorous fish community harvests carbon and nitrogen by consuming algae, we combined these simulations with measurements of consumption rates from our data, predator visitation rate, and published measurements of forager bite size and algal elemental composition (*SI Text, Simulated Foraging* and Fig. S7). We then repeated simulations assuming fish ignore the density of other foragers and the cues generated by past fish entries and exits ("no behavioral coupling," Fig. 4*A* and *Simulated Foraging, Quantifying Effect of Behavioral Coupling on Herbivore Density*).

The model revealed that mean rates of carbon and nitrogen uptake are 68% lower when fish make foraging decisions independently than when they respond to social cues (Fig. 4*A*); this is because fish use social cues to follow one another into foraging areas (Fig. S4), and individual fish feed for longer periods of
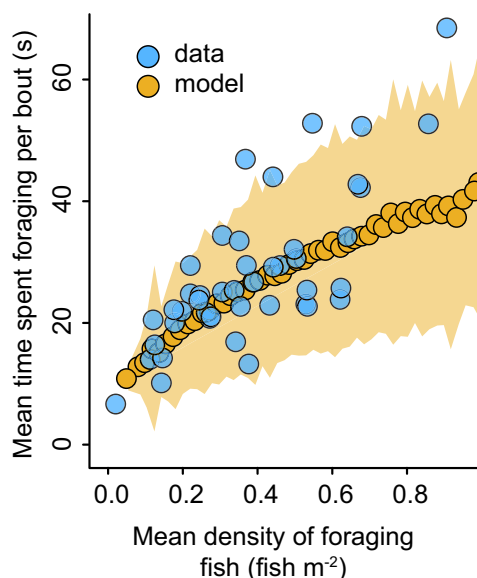

Fig. 3. Fish foraging bouts are longer when the density of foragers is higher. Mean time spent foraging per bout increases with mean fish density (means of individual control trials: blue points, regression with heterogeneous variance $p = 1.7 \times 10^{-5}$; simulated foraging: orange points and 99% prediction envelope). The orange points and prediction envelope were generated by simulating 1,000 180-s intervals using the best-fit model fitted to data from the predator experiments with the predator forcing term set to zero (*Materials and Methods*).

time when more fish are actively foraging (Fig. 3). Foraging rates simulated by the model with behavioral coupling coincide with empirical estimates of foraging rates measured in a Caribbean coral reef ecosystem (Fig. 4*A*, gray band) (24) and algal production at our study site on the north shore of Mo'orea (Fig. 4*A* dashed line) (25). In *SI Text, Robustness of Consumption to Model Assumptions*, we show that these results are unchanged if we more explicitly account for the diversity of herbivorous fish by allowing individual fish to have different bite rates and to consume variable amounts of algae per bite (Fig. S8).

Behavioral Coupling Induces a Correlation Between per Capita Consumption and Total Fish Abundance. For an individual fish to benefit from the effects of behavioral coupling, the total abundance of fish on the reef must be high enough that fish regularly have access to social cues. We simulated foraging with and without behavioral coupling over a range of total abundances of fish on the reef (Fig. 4*B*).

When fish behaviors were uncorrelated, per capita algal consumption was independent of fish abundance (Fig. 4*B*, green points). In contrast, when fish foraging behaviors were coupled, each individual fish consumed more algae as total fish abundance increased (Fig. 4*B*, orange points), because entry cascades were more common when the total abundance of fish was high, leading to higher forager densities and longer bouts of foraging per fish (Fig. 3). One important consideration when interpreting this finding is that we expect this positive density dependence to be most important when total herbivore abundance is low enough that per capita consumption is limited by the amount of time an individual spends foraging rather than by algal supply. Negative density dependence will likely also be important if algal supply is limiting (14).

To generate the per capita consumption shown in Fig. 4*B*, we assume that, regardless of the total abundance of fish on the reef, fish make foraging decisions using the rules we measured by fitting our decision-making models to data. However, it is possible that, when the total abundance of herbivorous fish is low, fish
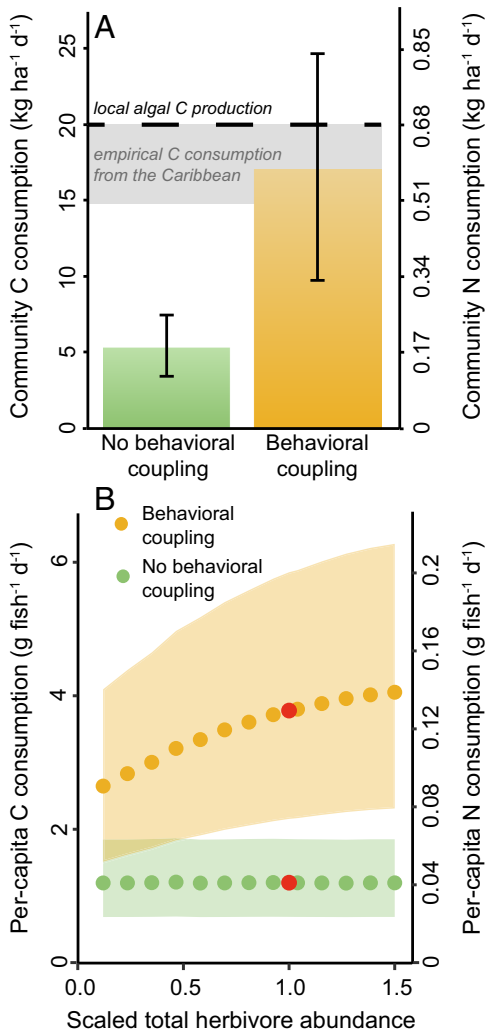
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Fig. 4. Responses to social cues increase algal consumption by the herbivorous fish community. (*A*) Simulations that include behavioral coupling (orange) have mean consumption rates within the range of empirical measurements of carbon consumption by herbivorous fish in a Caribbean reef ecosystem [gray band, mean ±1 SD (24)] and mean biomass production by algal turf at our study site [dashed line (25)]. (*B*) Upper bound on mean per capita daily algal consumption from simulations with (orange) and without (green) behavioral coupling, across a range of total fish abundance (see *Carbon and Nitrogen Uptake by the Fish Community, Per Capita Carbon and Nitrogen Consumption* for details of calculation). Red points are parameter estimates from our data (shown in *A*). Algal consumption is expressed in units of algal carbon or nitrogen based on published measurements from our study site (see *SI Text, Carbon and Nitrogen Uptake by the Fish Community*). Confidence envelopes are computed from empirical variation in predator visitation rate, fraction of the fish community composed of herbivores, bite rate per herbivore, and carbon/nitrogen consumed per bite.

alter their foraging behaviors, thereby affecting their per capita consumption. In *Robustness of Consumption to Model Assumptions, Long-Term Changes in Fish Behavior*, we explore how long-term changes in fish consumption can influence the relationship between per capita consumption and total herbivore abundance. In general, we find that fish can modify their behaviors to maintain high per capita consumption when the total abundance of herbivores is low; however, doing so requires that individual fish become bolder, spending large amounts of time foraging alone or in small groups where the per capita risk of predation is high (*Robustness of Consumption to Model Assumptions, Long-Term Changes in Fish Behavior* and Fig. S9).

Empirically determining precisely how fish balance the trade-off between per capita algal consumption and predation risk will require future studies that measure fish behaviors across a range of total herbivore abundances and predation pressures. However, some herbivorous reef fish have been shown to respond to increased predation pressure and low herbivore density by becoming less bold rather than more bold (26, 27), which could reinforce the pattern of low per capita consumption at low herbivore abundances predicted in Fig. 4*B* (Fig. S10).

Taken together, our results demonstrate that behavioral coupling can impact resource consumption both at the level of the herbivorous fish community and at the level of individual consumers. For example, the model indicated that reducing total herbivorous reef fish abundance to 20% of its current value (e.g., via overfishing) would cause each fish to consume an average of ∼26% less algal carbon and nitrogen per day. If reductions in per capita consumption translate to lower population growth rates, reef fish populations may be particularly susceptible to sudden collapses when they become small (9, 11).

Quantifying the long-term effects of behavioral coupling on algal consumption requires scaling from the behavioral timescale of our foraging area experiments to longer timescales and larger spatial scales. To do this, we made several key assumptions that are important to consider when applying our approach or conclusions to other systems. The first assumption is that, when fish leave foraging areas, they temporarily stop feeding while they transit to another foraging area or hide in the reef structure. Reef fish often cease feeding while hiding or transiting (e.g., refs. 26 and 27), and we regularly observed this behavior in our experiments. Modifying this assumption—for example, by assuming that fish continue to feed outside foraging areas but at a reduced rate—can change the quantitative difference in algal consumption rate between models with and without behavioral coupling. However, the qualitative conclusions that behavioral coupling (*i*) increases total algal consumption rate and (*ii*) induces a positive density dependence in per capita consumption are robust to a wide range of alternative assumptions (*Robustness of Consumption to Model Assumptions, Fish Behavior Outside Foraging Areas*). A second assumption is that the rates at which fish enter and exit a foraging area are independent of one another except through their joint dependence on the predator stimulus (Eq. **1**). Our data support this assumption (*Robustness of Consumption to Model Assumptions, Correlations in Entry and Exit Rates*). However, this need not hold in other systems, and our model could be modified to incorporate correlated entry and exit rates.

Discussion. By combining high-resolution observations of thousands of actions taken by individual foragers with a modeling framework, our analyses reveal that the actions of individual consumers are highly correlated in time, and that these correlations are driven, in part, by behavioral coupling. Social interactions among fish increase the number of fish that are actively foraging and, consequently, the rate at which the herbivorous fish community harvests carbon and nitrogen by consuming algae (Fig. 4*B*).

Through various mechanisms, algae harm corals and can come to dominate reefs when unchecked (28–30). Fish mediate this algal–coral interaction by controlling the abundance of algae, and the loss of fish through overfishing and habitat degradation (28, 31) is emerging as a major driver of global coral reef degradation, with associated losses of biodiversity and ecosystem services (16, 32). Our study expands this paradigm by revealing a potentially fundamental aspect of the alga–herbivore dynamic not yet formally considered: Overfishing and other disturbances that lower fish abundance also reduce the availability of social cues, potentially affecting the ability of remaining fish to control

algae. These findings indicate that reef ecosystems may be more sensitive to reductions in fish abundance than previous analyses have suggested (16, 32). Our results imply that foraging models that do not consider how herbivorous reef fish respond to one another (models that assume ideal-free foraging, random foraging, etc.) could mischaracterize the relationship between fish density and algal consumption, and the consequent dynamics of fish and algal populations.

The methodology developed here provides a rigorous way to quantify the behavioral rules consumers use to make foraging decisions in situ, and to link those rules to the ecological rates that are crucial to the dynamics of ecosystems. This approach complements more traditional demographic methods for determining how foraging behavior influences ecological rates (e.g., refs. 14 and 33) and paves the way for future investigations of how animal behaviors scale up in natural ecosystems. More generally, our results suggest that behavioral coupling could be a fundamental but largely unexplored link between collective animal behavior and ecosystem function, with broad implications for environmental management.

Materials and Methods

Camera Array Setup and Study Sites. We used polyvinyl carbonate piping to construct two field-deployable camera frames, each $6 \times 2 \times 2$ m ($l \times w \times h$). In the lagoon off of the north shore of Mo'orea, French Polynesia, we located two foraging areas, separated by $\sim$150 m, each characterized by a shallow (2.5 m depth) reef flat, comprised primarily of pavement and coral rubble habitat. High irradiance and a consistent delivery of new algal propagules by currents yield high algal production across hard-bottom reef flats in the back reef (25). The foraging areas used in our study are representative of foraging areas throughout the ecosystem. Each foraging area was surrounded by abundant and dense reef structures, dominated by live and dead colonies of massive and submassive (mounding and partially branching) *Porites* corals of 0.5 to 1.5 m height, which fish readily used as refuges throughout the study. We mounted one camera frame at each foraging area, using concrete substrate mounts, allowing us to monitor foraging areas from above (Fig. S1).

Experimental Protocol. We randomly assigned the control and predator treatment to each of the two sites at the onset of the experiment and alternated assignments on each subsequent day to control for site effects. At the start of the control and predator trials for a given day, three downward-

facing video cameras (GoPro, Inc.) were mounted to each camera frame. Cameras continually recorded a contiguous field of view of 18 m^2 (Fig. S1) while experiments were being conducted. In each predator trial, a free diver (M.A.G.) holding a pole spear approached the experimental site designated as the predator treatment from a distance of 33 m away (due south) from the center of the video camera array at a pace of 1 m per 3 s. The diver maintained a constant speed by referencing distance markers placed on the substrate before deployment of the camera frames. The diver continued directly through the foraging area, maintaining the same speed, and continued for 5 m beyond the foraging area. The site designated as the control each day was left undisturbed after video camera deployment. At the end of each set of control and predator trials, all cameras were removed. The animal experiments reported in this paper were conducted in full compliance with the policies and procedures of the Institutional Animal Care and Utilization Committee (IACUC) at the University of Florida, and all protocols and procedures involving animals were reviewed and approved by the IACUC.

Inferring Behavioral Rules from Entry and Exit Time Series. We modeled the instantaneous rates at which fish enter and exit foraging areas using the functions

$$\lambda(t) = \lambda_0 + \phi_\lambda(\{X\}_{<t}) + \theta_\lambda(t),$$
$$\mu(t) = N(t)(\mu_1[N(t)] + \phi_\mu[\{Y\}_{<t}, N(t)] + \theta_\mu[t, N(t)]),$$

[1]

where $\lambda(t)$ is the instantaneous rate at which fish enter the foraging area, $\mu(t)$ is the instantaneous rate at which fish exit the foraging area, and $N(t)$ is the number of fish present in the foraging area at time t. The functions ϕ are memory kernels that describe the effect of the history of past fish entries and exits on the current entry and exit rates; the set of entry times that occur up to time t is $\{X\}_{<t}$ and $\{Y\}_{<t}$ is the set of exit times that occurred up to time t. The functions θ are forcing functions that describe the effect of the predator stimulus on entry and exit rates. The terms λ_0 and μ_1 describe the rate of spontaneous entries and exits (i.e., entries and exits that are independent of the past history of entries and exits, and predator forcing). Mathematical details of model derivation, fitting, and model comparison are described in *Supporting Information*.

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