

Well-informed foraging: damage-released chemical cues of injured prey signal quality and size to predators

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Abstract Predators use a variety of information sources to locate potential prey, and likewise prey animals use numerous sources of information to detect and avoid becoming the meal of a potential predator. In freshwater environments, chemosensory cues often play a crucial role in such predator/prey interactions. The importance of chemosensory information to teleost fish in marine environments is not well understood. Here, we tested whether coral reef fish predators are attracted to damage-released chemical cues from already wounded prey in order to find patches of prey and minimize their own costs of obtaining food. Furthermore, we tested if these chemical cues would convey information about status of the prey. Using y-maze experiments, we found that predatory dottybacks, *Pseudochromis fuscus*, were more attracted to skin extracts of damselfish, *Pomacentrus amboinensis*, prey that were in good condition compared to prey in poor body condition. Moreover, in both the laboratory and field, we found that predators could differentiate between skin extracts from prey based on prey size, showing a greater attraction to extracts made from prey that were the appropriate size to

consume. This suggests that predators are not attracted to any general substance released from an injured prey fish instead being capable of detecting and distinguishing relatively small differences in the chemical composition of the skin of their prey. These results have implications for understanding predator foraging strategies and highlights that chemical cues play a complex role in predator-prey interactions in marine fish.

Keywords Predator foraging cues · Chemical alarm cue · Secondary predators · Coral reef fish · Kleptoparasitism

Introduction

Many organisms rely on odor cues for crucial information. Chemical cues may determine where they live, what or when they eat, and whether they should fight with, run from or mate with the individuals surrounding them (Debose and Nevitt 2008; Hay 2009). In both terrestrial and aquatic ecosystems, predators frequently rely on olfactory cues to detect, localize and identify their prey. Indeed, chemical information can afford a richer source of information than visual cues, providing information on location, ontogenetic stage, diet, gender, reproductive condition and level of stress (Stowe et al. 1995; Hay 2009; Ferrari et al. 2010). This chemical information is particularly useful at night or in structurally complex habitats where visibility is limited.

Chemical information cannot only be used in the initial detection of a prey by a predator, but can also be used to capitalize on instances where the defenses of a prey are compromised. Escaped or otherwise wounded prey items would present an easier target for a hungry predator. Similarly, predators can enhance their foraging by disrupting the predation sequence of a subordinate or less capable

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predator once this predator has captured a prey item. Areas containing an abundance of prey present ideal hunting grounds for roving predators. If alarm chemicals released from the skin of injured prey trigger a search and hunting response in predators, patches containing higher concentrations of good quality prey fish (with correspondingly higher capture rates) are likely to 'mark' prey territories. Predators should therefore develop mechanisms that enable them to detect the presence of compromised or injured prey as this would allow them to make informed foraging decisions. Many teleost fish predators are gape limited, and are expected to have dome-shaped size selective profiles (Rice et al. 1997), so the prey they are able to consume is a function of their size (Jones and McCormick 2002). Predators therefore select prey with particular phenotypic characteristics (Nilsson and Bronmark 2000; Holmes and McCormick 2010), and the most successful predators in search of potential prey items will be those that are best informed with respect to the characteristics of the potential prey item. In the aquatic environment, chemicals released when prey are captured could provide an important source of information about the prey. While it is known that some marine piscivores use chemical information to inform foraging decisions (Debose and Nevitt 2008; Hay 2009), the use of chemical cues to inform hunting behavior, and the information content of these olfactory cues, is currently unknown.

The information content of the chemicals released when a fish is captured by a predator is potentially high. In both marine and freshwater environments, fish prey are warned that predators are in the vicinity by chemical alarm cues released from the epidermis of injured conspecifics (McCormick and Larson 2008; Ferrari et al. 2010). When released, these alarm cues elicit species-specific anti-predator behaviors, and hence promote the survival of conspecifics within the vicinity of the cue donor (Ferrari et al. 2010). Moreover, prey modify the intensity of their anti-predator behavior in relation to the concentration of the cues; fish in better body condition liberate more cues than those in poor condition (Brown et al. 2004; McCormick and Larson 2008), and these chemicals may be modified depending on gender, breeding status and ontogenetic stage of the cue donor (see Ferrari et al. 2010 for review). From a predator's perspective, not only are these cues reliable indicators that a prey item has been caught but they may also provide vital information concerning the appropriateness of prey items, on which to base foraging decisions. Whether predators are preferentially attracted to the cues of their prey when locating a food source is largely unknown, although Lailo et al. (2004) showed that the structure of distress calls of the short-toed lark (*Calandrella rufescens*) signaled quality of prey to predators allowing the predators to optimize their foraging choice. Other studies from freshwater ecosystems have found that predatory fish

(northern pike, *Esox lucius*) are attracted to chemical substances from fathead minnows (*Pimephales promelas*) (Mathis et al. 1995; Chivers et al. 1996). Currently, no studies have investigated if chemical alarm cues from marine fish attract predators and none have examined whether chemical alarm cues provide information about prey size and quality to predators.

The present study explored whether *Pseudochromis fuscus* (family Pseudochromidae) was attracted to damage-released chemical cues of a common prey item, newly settled ambon damselfish *Pomacentrus amboinensis*. We examined whether predators were differentially attracted to damage released chemical cues from: (1) prey in different body condition and (2) prey that differed in body size. In a final experiment, we investigated whether predators use skin extracts of damaged prey as cues when foraging in their natural environment. We hypothesized that finding prey items using the scent of a wounded prey is a form of flexible foraging present in fish predators. For this type of behavior to be profitable, it requires skills to select the appropriate prey; here, we test if the odor signatures of prey attract and convey information to surrounding predators.

Materials and methods

Laboratory trials

Test subjects and stimulus preparation

The piscivorous dottyback, *Pseudochromis fuscus*, is a common cryptic predator found throughout the Indo-Pacific (Beukers and Jones 1997). It is a gape-limited predator (Holmes and McCormick 2010) and exhibits a strong preference for newly settled damselfish (*Pomacentridae*) recruits in the summer months, being responsible for much of the mortality in the early juvenile life phase of these coral reef fish (Feeney et al. in review). It exists in large numbers at our study site with each individual having a distinct home range site which is readily defended against both conspecific and heterospecific intruders. *P. fuscus* is a very active and mobile diurnal predator, living in the same coral habitats as its much smaller prey, and is therefore an ideal study species. *P. fuscus* were collected around Lizard Island (14°40'S, 145°28'E) on the northern Great Barrier Reef, Australia in December 2008 using a dilute clove oil anesthetic and a fence net. Captured fish were placed in 10-l plastic bags and transported back to the Lizard Island Research Station where they were held in a 30-l flow through sea-water tanks. Newly settling stages of the ambon damselfish were collected using light traps while adult stages were collected using clove oil and fence nets. Cue-donor fish were euthanized by cold shock (in accordance with

the guidelines set by the Lizard Island Research Station) and were subsequently placed into a clean Petri dish (as per Larson and McCormick 2005). A clean scalpel blade was used to make 6 superficial vertical incisions (minor flesh damage) along each flank of the test fish. Cues from adults and recruits were prepared from a similar sized area of skin from the flank of each fish to standardize cue concentration ($66.2 \pm 6.6 \text{ mm}^2$; mean \pm SE). Two recruit fish were used for each stimulus and were rinsed in 15 ml of seawater and subsequently filtered through filter paper (47 mm \varnothing) in order to remove any solid matter prior to being drawn up into a disposable 20-ml syringe for injection into the test aquaria.

Experimental design

All trials were run in a y-maze aquarium ($60 \times 25 \times 11$ cm) with a water depth of 9 cm. The substratum consisted of a 2- to 3-cm-thick layer of sand. A transparent screen permeable to water divided the tank 15 cm from one end of the tank; this area provided an acclimation area for the predator. A shelter, consisting of a plastic tube (6×8 cm), was placed along the back wall of the acclimation area. A plastic opaque barrier impermeable to water divided the tank lengthwise into two equal size compartments. Two identical water flow inlets were placed in the front of the compartments and these were fed aerated seawater from a common reservoir, with the outflows distributed along the back of the tank. A 1.5-m plastic tube, attached just beneath the water level, allowed for rapid dispersal of treatment stimuli into each compartment. Dye trials found the stimulus flow to be even and separated down the center of the tank, even beyond the two compartments. The transparent barrier that separated the acclimation area from the remainder of the tank was slowly removed immediately prior to the start of the trial allowing the dottyback entry to the entire test y-maze. At the commencement of a trial, 15 ml of each treatment stimulus was simultaneously injected into the two compartments, followed by 60 ml of previously collected tank water to flush through each tube. Dye trials had shown that the test stimuli were flushed out after 4 min, so both stimuli were re-injected at intervals of 4 min. Prior to the start of the experiment a single predator [$79.7 \pm 2.5 \text{ mm}^2$; mean standard length (SL) \pm SE] was placed into the acclimation area of the y-maze for 6–12 h to allow for recovery from the stress of capture. Observations commenced immediately after the injection of the two stimuli and lasted for 20 min, during which the observer recorded which compartment the predator was oriented in front of as well as the total time (s) spent inside each compartment. Behavioral observations were conducted from behind a black plastic barrier to minimize disturbance to the focal fish. After each trial, the fish were removed and the y-maze, tubing, shelter and substratum were thoroughly cleaned.

Experiment 1: are predators differentially attracted to skin extracts from prey fish in different body condition?

Prey animals of a given body size often differ markedly in body condition; hence they represent more or less profitable prey items for predators. Predators that are differentially attracted to prey in good body condition have the opportunity to consume a more profitable prey item; however, individual prey in poor body condition may be easier for predators to capture. McCormick and Larson (2008) demonstrated that damselfish held on a restricted diet had a greatly reduced number of alarm substance-containing cells within the epidermis compared to their well-fed conspecifics. We used this fact to test whether *P. fuscus* were more attracted to skin extracts from well-fed prey fish, which possess chemical alarm cues, than to skin extracts from poorly fed prey fish, which have greatly reduced amounts of alarm cues. Since damselfish in better body condition have a significantly higher number of chemical alarm cue cells in their epidermis (Brown et al. 2004; McCormick and Larson 2008), they should be easier for the predators to localize if they are indeed attracted to the alarm cues of their prey. In our experiment, well-fed and poorly-fed fish were obtained by feeding donor fish different amounts of *Artemia nauplii* (as per Lönnstedt and McCormick 2011). Donor fish were placed into 30-L aquaria and fed 320 or 1,600 nauplii l^{-1} per day for 10 days before being sacrificed for use in the experiment. To examine the influence of the feeding levels on fish quality, measurements of body condition [weight (g), SL (mm)] were taken before fish were used to prepare alarm cue extracts. Body condition was then quantified as the residuals of an overall length weight regression. Poorly-fed fish were 60% lighter than well-fed fish for any given length. All were within the size range known to be preferred by the dottyback (Holmes and McCormick 2010). A total of 10 fish from each feeding treatment were pooled and used to prepare the skin extracts in each trial. At the commencement of the experiment, 15 ml of skin extract from well-fed damselfish (*P. amboinensis*) were injected into one compartment, and 15 ml of skin extract from poorly-fed damselfish were simultaneously injected into the other compartment. A total of 15 replicate trials were undertaken and a new predator was used in each trial.

Experiment 2: are predators attracted to chemical cues specific to the size of prey that they can consume?

To examine whether *P. fuscus* are attracted to chemical cues specific to the size of prey that they can consume, we tested whether they were differentially attracted to skin extracts from newly settled ambon damselfish (10–14 mm SL) or to skin extracts from adult *P. amboinensis* (50–70 mm SL).

To standardize the amount of stimulus cue from the 2 ontogenetic stages, fish had the same amount of skin surface area damaged and rinsed in equal amounts of water (15 ml). In this way 6 cuts on each flank (each 1 cm long) were made on the same amount of surface area on each of the two recruits, while 12 cuts (each 1 cm long) were made on a single adult fish. After the acclimation period, 15 ml of solution from the skin extract of light trap collected damselfish (prepared as above) was injected into one compartment, while 15 ml of adult skin extract was injected into the other compartment, and this was then continued every 4 min until the end of the trial. New predators were used for each trial, and a total of 21 experimental trials were undertaken.

Field assessment

To investigate whether *P. fuscus* was attracted to and could differentiate size of prey fish based on skin extracts in their natural environment, we carried out an underwater experiment at Lizard Island (14°40'S, 145°28'E), northern Australia, in August 2010. All experimental trials were conducted within the reef matrix using SCUBA at depths between 2 and 6 m. Adult test fish were located using SCUBA and their size (estimated to be 70–90 mm SL) as well as home range site were defined from observations prior to the start of each trial. After each trial, the observer (OML) swam at least 20 m up-current from the focal individual ensuring that the predators used were independent of each other. To guarantee that focal fish were not reused, new dive sites was chosen for each dive.

To prepare skin extracts underwater, juvenile fish and adults (*P. amboinensis*) were caught using anaesthetic clove oil, and were placed in a 75 × 125 mm click seal bag which was filled with ~60 ml of sea water. Fish were euthanized by a quick blow to the brain case and the epidermis of the fish was then lightly scratched using a scalpel blade that had been placed in the bag. Cue concentration was calculated according to the surface area of the skin. Due to currents and other diluting factors, we used two juvenile fish for the production of each skin extract imitating concentrations that meso-predators are likely to encounter in nature. A similar surface area was used on each adult fish to prepare skin extracts. A clean scalpel blade was used to make superficial vertical incisions (minor flesh damage) along each flank of test fish. A disposable syringe equipped with a fine needle was used to perforate the bag and extract 60 ml of the stimulus preparation (either juvenile skin extract, adult skin extract, or plain sea water). The donor fish were caught and prepared well away (at least 15 m down-current) from the focal meso-predator to be tested for a response.

A 2-m plastic tube was attached up-current just inside the home range of the focal fish using metal skewers. Behavioral observations were conducted at least 2.5 m from the focal fish to minimize disturbance. Before trials commenced the current speed was estimated from the movement of neutral density particles moving over a 0.5 m distance and did not exceed 0.05 m s^{-1} (range $0.01\text{--}0.05 \text{ m s}^{-1}$). The behavioral response of naïve *P. amboinensis* to 3 different treatments was tested. Treatments were (1) extracts from the damaged skin of juvenile *P. amboinensis*; (2) extracts from the damaged skin of adult *P. amboinensis*; and (3) saltwater (control). If *P. fuscus* were using juvenile skin extracts as a foraging cue, they would be more active and become more attracted to the skin extracts of the recruits than to adult cues or control plumes.

The behavior of focal fish was quantified for 3 min before (pre-stimulus period) and 3 min after (post-stimulus period) the addition of a stimulus (skin extract or saltwater). Immediately following the pre-stimulus period, 60 ml of the experimental stimulus was injected into the tubing, followed by 60 ml of previously obtained saltwater (to ensure that the entire stimulus cue had been flushed through the tubing). All substances were transparent and were not visually detectable by the observer when released. The behavioral response to experimental stimuli was quantified by recording a total of three different behavioral traits for fish during the trials: activity level (quantified as percentage time spent swimming and searching for food), distance from tubing outlet (categorized as % time spent within 10, 20, 30 or >40 cm from the cue release site) and the number of times the focal fish attacked the tubing outlet. We also recorded if any other *P. fuscus* individuals were observed within the focal fish's home range territory.

Statistical analyses

Prior to analysis, data were examined for normality and homogeneity of variance using residual analysis. A one-factor multivariate analysis of variance (MANOVA) was carried out to compare differences in predator behavior among the different stimulus treatments (recruit, adult, poorly-fed and well-fed skin extracts). Variables included in the analysis were the number of times *P. fuscus* spent in front of each compartment and the total amount of time(s) the predator spent inside each compartment. One-factor ANOVAs were then performed to test the equality of means between the y-maze treatments for the 2 variables measured: the number of times spent in front of each treatment compartment, and the total time spent(s) inside each compartment. The equality of changes in overall behavior among treatments in the field experiment was tested using a one-factor MANOVA. Variables included in the analysis were: activity level, distance from tubing outlet and the

number of times the focal fish attacked the tubing outlet. To further explore the significant differences in behavior revealed by MANOVA, one-factor ANOVAs were performed to identify significant differences within individual behaviors of interest, followed by a Tukey's HSD tests. A Bonferroni correction was employed to account for ANOVA tests on non-independent variables.

Results

Experiment 1: are predators differentially attracted to skin extracts from prey fish in different body condition?

Predators were differentially attracted to skin extracts from prey fish of different body conditions (MANOVA: Pillai's Trace = 0.80, $df_{2,27}$, $P < 0.001$). *P. fuscus* spent significantly more time in front of the compartment containing skin extracts from well-fed damselfish compared to the compartment containing skin extracts from poorly-fed damselfish ($F_{1,28} = 132.4$, $P < 0.001$). In addition, they spent significantly more total time inside the compartment emitting the skin extract from well-fed fish ($F_{1,28} = 10.6$, $P < 0.01$; Fig. 1a).

Experiment 2: are predators attracted to chemical cues specific to the size of prey that they can consume?

There was an overall difference in predator attraction behavior between skin extracts from recruit and adult prey

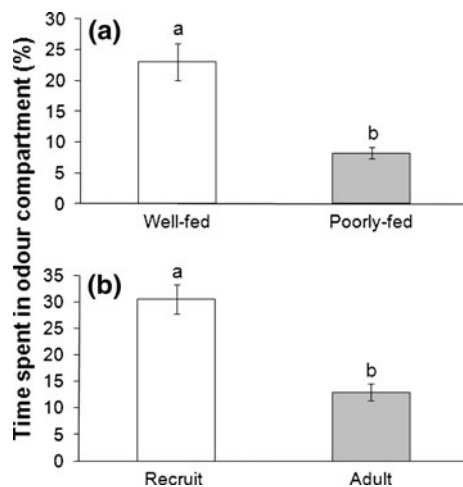


Fig. 1 Percent of time (minutes, mean \pm SE) a predatory fish (*Pseudochromis fuscus*) spent in each odor compartment of a y-maze, given a choice of two cues from skin extracts of damselfish prey (*Pomacentrus amoinensis*): **a** well-fed versus poorly-fed prey ($n = 15$) and **b** recruit versus adult ($n = 21$). Letters above bars represent Tukey's HSD groupings of means. Bars with different letters are significantly different from each other at $\alpha = 0.05$

(MANOVA: Pillai's Trace = 0.89, $df_{2,39}$, $P < 0.001$). *P. fuscus* spent the majority of the experimental period oriented in front of the compartment emitting skin cues from the newly settled damselfish compared to the compartment emitting adult cues ($F_{1,40} = 30.5$, $P < 0.001$; Fig. 1b). The predatory fish also spent more than double the amount of time in the compartment holding the cue from the smaller fish ($F_{1,40} = 100.1$, $P < 0.001$).

Field assessment

In the field, predators were differentially attracted to skin extracts from prey from two ontogenetic stages and the saltwater control (MANOVA: Pillai's Trace = 0.69, $df_{3,23}$, $P < 0.005$). Overall, juvenile skin extracts acted as an attractant to coral reef meso-predators. More specifically, *P. fuscus* adults were seen to respond to skin extracts of *P. amboinensis* juveniles with the predators significantly increasing their activity levels upon the expulsion of the cue ($F_{2,25} = 6.16$, $P < 0.01$; Fig. 2). During the release of the cue, they also spent a significantly higher proportion of their time in close proximity of the cue source compared to when saltwater or adult *P. amboinensis* skin extract were released into the water ($F_{2,25} = 22.84$, $P < 0.001$; Fig. 3). In addition, *P. fuscus* were found to be attracted to the release site only in response to the release of juvenile skin extracts (*P. fuscus* was attracted to within 10 cm of the release site in all the trials). Furthermore, in half of the trials, larger predators (both conspecifics and heterospecifics) were seen to come in and chase the focal animal away upon the introduction of the recruit cue. Predators were also found to repeatedly attack the stimulus injection tubing upon the expulsion of the recruit cue while not exhibiting this behavior when the adult cue or saltwater control was introduced ($F_{2,25} = 6.34$, $P < 0.01$). Interestingly, *P. fuscus* was repeatedly seen to exhibit 'sniffing' behavior as the odor plume of recruit fish was injected into the water. A 'sniffing event' is when the fish spontaneously protrudes its jaw which increases the water flow to accessory olfactory sacs. Nevitt (1991) found that fish sample odors through 'sniffing' (a behavior that resembles a cough in some organisms).

Discussion

Our findings suggest that hunting *P. fuscus* recognize odor signatures emitted from damaged prey, and use these to make informed foraging decisions. Evidence shows that predators use these chemical cues as an indication of prey quality as predators consistently exhibited differential responses depending on the size and condition of the prey. In the field, predators exposed to cues of their potential prey (juveniles) elicited searching behavior and struck at

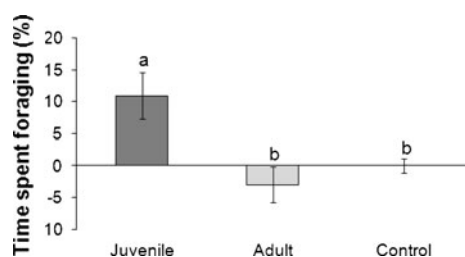


Fig. 2 Percent of time (min, mean \pm SE) *P. fuscus* spent foraging (swimming and searching) in response to the release of juvenile and adult skin extracts from *P. amboinensis* as well as a saltwater control. Percentage time spent swimming and searching in min (mean \pm SE) is plotted on the y-axis while the different treatments is seen on the x-axis. Letters above bars represent Tukey's HSD groupings of means. Bars with different letters are significantly different from each other at $\alpha = 0.05$

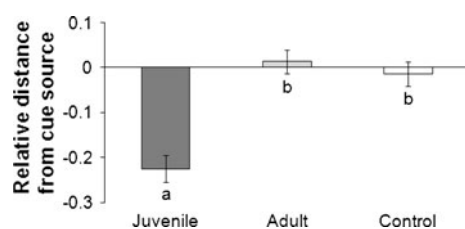


Fig. 3 The relative distance of *P. fuscus* from a cue source (mean \pm SE) in response to either juvenile or adult skin extracts or a saltwater control. Letters below bars represent Tukey's HSD groupings of means. Bars with different letters are significantly different from each other at $\alpha = 0.05$

the cue source. In contrast, cues from same species that were too large to consume (adults) did not elicit a foraging response. The differences in responsiveness to chemical stimuli from various prey sources suggest that the predators are not attracted to any general substance released from an injured prey, but instead are capable of detecting and distinguishing relatively small differences in the chemical composition of the skin of their prey. Predators attempting to find ideal prey patches would benefit from recognizing differences in odor signatures as it would allow them to make optimal foraging decisions. This is the first study to provide direct empirical evidence that a marine fish predator is attracted to damage-released chemical cues, and that they use these cues to distinguish quality of prey both in the laboratory and in the field.

Our findings highlight that damage-released chemical cues from prey play a complex role in predator-prey interactions in *P. fuscus*. The piscivores recognized specific chemicals emitted from skin of their damaged prey and use these to make foraging decisions. Although initially counter-intuitive, producing substances that attract predators could also be highly beneficial for the prey. If the prey releases substances upon being captured that attract additional predators that disrupt the original predator, the prey

gains some chance to escape over an almost certain death. Chivers et al. (1996) found that freshwater minnows escaped from their pike predators in 38% of trials when a secondary predator was present, while no minnows escaped in the absence of secondary predator interference. Our field tests found that the presence of prey chemical alarm cues increases the diversity and number of predators in the vicinity of the cue release, suggesting that these cues may play a predator disruption role in marine systems. In fact, additional meso-predators (especially *P. fuscus* individuals) were attracted to the cue release site and in many instances chased off the focal fish (if this one was smaller).

The attraction of fish predators to alarm cues of wounded prey could also be an 'overlapping of signals' with the predator intercepting chemical messages that are intended for a different receiver. In fact, many predators are known to exploit the chemical compounds used by their prey for intraspecific communication (Stowe et al. 1995). In this study, fish predators were seen to increase activity levels and directly strike at the cue source when chemicals of their recruit prey were injected into the water column. Chemical alarm cues are used by prey species as reliable indicators of the damage of conspecifics, and the detection of this chemical cue during a predator encounter leads to the increased survival of responsive individuals (Ferrari et al. 2010). *P. amboinensis* elicits typical antipredator behavior when exposed to skin extracts of damaged conspecifics (Lönngstedt and McCormick 2011) and predators may in turn use this source of information to locate potential prey items. The ability to detect a food source is of obvious importance to all animals and one way to forage optimally is to locate areas abundant in high quality prey. The presence of chemical alarm cues may 'label' valuable food patches, as the damage-released skin extracts would suggest that predators are already foraging successfully. Consequently, surrounding piscivores may exploit these cues as a means to locate good foraging grounds.

The attraction of predators to chemical alarm cues could also have evolved as a means of 'kleptoparasitism' (i.e. stealing of already procured food). Food piracy is an opportunistic hunting technique in which the predator only steals the food item if the net energy gained by this behavior exceeds or matches the net energy gained by feeding via other methods. Kleptoparasitism has been well studied and appears to be prevalent among birds (Moraud-Ferron et al. 2007), but has also evolved in a variety of other animals including insects (Vollrath 1984), reptiles (Cooper and Perez-Mellado 2003) and mammals (Gorman et al. 1998). Although marine animals such as sharks are widely recognized as opportunistic predators, stealing food when an opportunity is presented, there are to our knowledge no studies that have investigated how widespread kleptoparasitism is in marine teleost fish (Moraud-Ferron et al. 2007).

However, the ecological conditions present on coral reefs appear to favor the evolution of food stealing. The structural complexity of coral reefs has been found to influence the efficiency of predators, greatly reducing their capture success (Sweatman 1984; Beukers and Jones 1997). In addition, predators that have successfully caught a prey item tend to have long handling times (Sweatman 1984), allowing pirates ample time to sneak in and attempt to steal the food item. By disrupting an initiated capture sequence and pilfering an already caught prey item, the ‘food parasite’ could take advantage of the time and energy investment of primary predators to minimize its own cost of obtaining food. For this type of behavior to be profitable, it requires skills to select the appropriate prey, and piscivores attempting to steal their food would benefit from targeting prey that are of higher quality and the correct size to consume.

One of the most striking changes in skin composition among fish placed under different food regimes (Brown et al. 2004; McCormick and Larson 2008) is a change in alarm cell production, and this is a likely source of variation that the predators could exploit to differentiate among odors. Previous studies have suggested that alarm cues could be a by-product of metabolism (Brown et al. 2004), and, as such, the composition of the cues may change as the individual develops. Alternatively, the differential responses exhibited by the fish to skin extracts may reflect quantitative differences in the concentration of cues in the skin and not necessarily qualitative differences in terms of which chemicals are present in the skin. We found that the predator chose skin extracts from well-fed fish over poorly-fed fish, which suggests that it was the chemical alarm cue within the epidermis of well-fed fish that was most likely the attractant (and not just the general ‘scent of death’). Prey individuals of good body condition either produce more alarm cues per area of skin or alarm cues of better quality (Brown et al. 2004; McCormick and Larson 2008). So it may well be that the predators simply cannot detect the cue released from poorly-fed individuals. This is supported by other studies that found that well-fed prey failed to elicit antipredator behaviors in response to alarm cues from conspecifics in poor condition (Brown et al. 2004; McCormick and Larson 2008).

This is the first study to provide direct empirical evidence that a coral reef fish predator is attracted to prey chemical alarm cues, and the first evidence for any organism of size specificity in its operation. The chemosensory ability to detect the odors of surrounding organisms is important in the arms race between predators and prey; prey use it as a cautionary sign advising them of the presence of predators while predators in turn appear to employ them as a means of finding prey in an attempt to optimize their foraging. Our results likely represent a widespread

phenomenon in aquatic predator–prey systems since many predators appear to use odor in hunting and a diverse range of prey organisms possess chemical alarm cues. Indeed, our findings suggest a new level of sophistication in the use of chemicals in hunting whereby predators track down wounded prey of a particular size and condition.

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