Title

Maintaining a Competitive Edge: Dominance Hierarchies, Food Competition and Strategies To Secure Food in Green Anoles (Anolis carolinensis) and Firemouth Cichlids (Thorichthys meeki)

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Maintaining a Competitive Edge: Dominance Hierarchies, Food Competition and Strategies To Secure Food in Green Anoles (*Anolis carolinensis*) and Firemouth Cichlids (*Thorichthys meeki*)

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We explored whether the opportunity to learn about the arrival of food, a scarce resource, might facilitate subordinates' food-stealing attempts—and dominants' strategies to prevent stealing—in two species, namely green anole lizards (*Anolis carolinensis*) and firemouth cichlid fish (*Thorichthys meeki*). Following establishment of a dominance hierarchy, each group was randomly assigned to one of two treatment conditions, either a learning treatment in which a signal preceded the appearance of food, or a control treatment in which both signal and food appeared at randomly determined times. Dominants and subordinates of both species learned to anticipate food arrival using learned cues, which in turn changed their social dynamic. In anoles, learning enabled subordinates to steal food more effectively, and both dominants and subordinates to capture it more quickly. Alternatively, learning enabled dominant cichlids to protect their food more successfully by mounting a more aggressive defense. These results suggest that learning could play an important role in the competition for a scarce resource amongst many animals that form dominance hierarchies.

Many animals that defend the exclusive use of territories during the breeding season live together in groups at other times of the year; winter flocks of birds are a common example. Other animals live together in groups permanently. Although group living confers many advantages on animals, whether it is temporary or year-round, a nearly universal cost is competition for scarce resources, such as food, mates, nest sites or safe refuges (Huntingford & Turner, 1987; Krebs & Davies, 1993). Such competition often results in the formation of dominant-subordinate social structures in which dominant individuals garner more of a scarce resource through the use of aggression (Huntingford & Turner, 1987; Pusey & Packer, 1997). Unable to compete aggressively, subordinates are forced to rely on alternative strategies to secure resources (Adams et al., 1998; Schmidt & Hoi, 1999; see Gross, 1996, for a review). Stealing is common. However, depending on the scarcity of the stolen resource, subordinate thieves risk attack, and potentially

serious injury, if caught (Gross, 1982). Thus, stealing often is accompanied by functionally deceptive behavior—what some have called "sneaky" tactics (Clutton-Brock et al., 1979; Gross, 1982)—that is, actions that deceive a dominant but which are not necessarily performed intentionally by the deceiver (for reviews see Cheney & Seyfarth, 1991; Shettleworth, 1998).

These sneaky tactics include occupying a position behind physical objects ("hiding"), darting to and from the protected resource, or attempting to steal only when the dominant is engaged in another activity (Clutton-Brock et al., 1979; Gross, 1982). How, then, do subordinates decide when and where to steal? Alternatively, given that subordinate thieves sometimes are caught by dominants, what mechanisms help dominants protect a resource from thieves?

A voluminous literature on Pavlovian conditioning documents animals' use of learned cues to locate food, water and mates, as well as to avoid predators and repel rivals (Hollis, 1984, 1997; Domjan, Cusato, & Villarreal, 2000; Domjan, 2003). Foraging behavior, which is perhaps the most widely studied behavior amongst animal learning researchers, appears to be easily modified by learned cues that provide information about food's location, availability, and suitability. Countless vertebrates (Macphail, 1982), as well as a growing number of invertebrates (Macphail, 1993; Papaj & Lewis, 1993), approach cues that herald the arrival of food and actively move away from cues that signal its absence (Timberlake & Silva, 1995; Hearst & Jenkins, 1974). In addition, as this same body of literature reveals, animals of many different species respond to learned cues with behavior that anticipates the impending arrival of food (Hollis, 1982). For example, archer fish, *Toxotes chatareus*, not only learn to approach cues that signal the arrival of food items above the water, but also direct a stream of water at those cues, mimicking behavior that they use to capture actual prey items (Waxman & McCleave, 1978); this anticipatory behavior most likely helps them to capture the fast-moving, flying insects upon which archer fish feed. Similarly, if laboratory rats are presented with a small, moving but inedible, object on several occasions immediately prior to the arrival of food, the signal object itself soon begins to elicit predatory behavior, of exactly the sort used to capture moving insects (Timberlake, Wahl, & King, 1982). In some animals, most notably junglefowl, *Gallus gallus*, and ring doves, *Streptopelia risoria*, Pavlovian food cues also are thought to play an important role in food recognition, the process wherein the young learn to recognize what is edible and what is not (Hogan, 1984; Balsam, Graf, & Silver, 1992). Likewise, learned cues inform foraging Norway rats, *Rattus norvegicus*, which foods are safe and which are poisonous (Galef, 1990). Adaptively speaking, then, cues associated with food appear to enable animals to forage efficiently, budget their time effectively, select nutritious food items, avoid poisonous foods, and, thus, maximize caloric intake (reviewed in Hollis, 1982).

Intrigued by the idea that the use of learned cues also might be used to improve the effectiveness of sneaky food-stealing strategies in subordinate animals, we tested this possibility in two species, both of which have been studied for many years and which form dominant-subordinate social structures in the wild, namely green anoles (*Anolis carolinensis*), a lizard native to the Southeastern United States, and firemouth cichlids (*Thorichthys meeki*, formerly *Cichlasoma meeki*), an indigenous freshwater fish of Mexico and Central America. Although the social behavior of green anoles and firemouth cichlids differs in many ways, dominant-

subordinate interactions in these species, as in others that form similar social structures, share many features. For example, dominant individuals use aggressive tactics to secure most of a scarce resource for themselves. Nonetheless, as in other species, subordinate males manage to obtain some of the resource some of the time (Alcock, 2001; Forrester, 1991; Krebs & Davies, 1993). Often, subordinates use "sneaky" maneuvers. For example, in North American sunfish (*Lepomis*: Centrarchidae), subordinates manage to fertilize some of the nesting females' eggs by hiding close to the nesting pair and, from these hiding places, darting into the nest while attempting to avoid the parental male (Gross, 1982). Although some of these attempts to steal are successful—at obvious cost to the dominant male—some attempts are not and, thus, the cost to subordinate thieves is retaliation from dominants. We wondered how cues that heralded the arrival of a scarce resource would affect the competition between dominant and subordinate males.

To answer this question, we formed small groups of males—green anoles in Experiment 1 and firemouth cichlids in Experiment 2—and forced them to compete for food in a semi-naturalistic situation. Following a short period in which groups of males established dominant and subordinate status, each group received one of two treatments, either an associative learning (Pavlovian conditioning) treatment, in which a cue signaled the arrival of food at a particular location, or a control treatment, in which animals had equal experience with the cue and with food but food was not signaled. During this treatment phase, or in a subsequent test phase, we looked for differences in the ability of dominant animals to protect the food resource from thieving subordinates, as well as the ability of subordinates to steal food from the dominant animal.

Experiment 1

Green anoles are diurnal lizards that inhabit trees and low bushes and prey on a variety of small insects (Crews, 1980). During the four-month breeding season, individual males defend exclusive home ranges that overlap the home ranges of 2-3 females, with which they mate (Orrell & Jenssen, 2002). Males defend their territories, as well as attract mates, with a combination of striking and colorful displays: The displaying male bobs up and down with the forepart of his body, elevates his head, and extends a red throat fan called the dewlap (Greenberg & Noble, 1944; Greenberg, 1977; Crews, 1980). Although the headbob and dewlap display often occur in the context of patrolling the territory, with no apparent recipient, these same behavioral patterns are used to challenge male intruders (Decourcy & Jenssen, 1994). If the intruder does not retreat, or immediately perform a submissive display in which it nods its head rapidly, the territory owner's body becomes greatly compressed laterally, the throat region becomes engorged, and it develops a dark, protruding ridge along its back, all signs of imminent chase and attack. Similar, albeit less frequent, displays occur outside the breeding season, when males are more likely to live in small groups (Jenssen et al., 1996). During this time dominant males appear to compete for food and perch sites, chasing away subordinates. The role of learning in this competition for food was the focus of the current investigation.

Method

Subjects and Apparatus. The subjects were 36 adult male green anoles (*Anolis carolinensis*) obtained from local suppliers. Lizards ranged in body weight from 2.04 g to 5.67 g. An additional 12 females were used to simulate naturally occurring groups of individuals. Prior to selection, all lizards were kept in large communal tanks (91 cm wide x 48 cm high x 46 cm deep) in a room maintained at 25 °C, with a 12:12 h light:dark cycle.

Lizards were removed from the large communal tanks, weighed, and marked with dots of paint on their back for easy identification. Groups of three males were chosen such that, within each group, one male was at least 35% heavier than both of the other two males, which were as similar in weight as possible. This selection process guaranteed that one male, the heavier individual, became the dominant male (D) and the other two males became subordinate males (S). Dominants were distinguished easily from subordinates: Only dominants performed headbob and dewlap displays and only subordinates performed submissive displays. Together with one female, each group of three males was placed into a standard 10-gallon aquarium (51 cm wide x 30 cm high x 25 cm deep). Each tank contained gravel, a large rock, and a log for perching. A warming light was placed on the wire mesh tank cover, directly over the log. The back and side exterior walls of the tank were covered with construction paper. To aid the experimenters in scoring movement, the front exterior wall was marked with a grease pencil, dividing the tank into six sections, two horizontal (top and bottom of the tank) and three vertical (left, middle and right of the tank). The room in which the tanks were located was maintained at 25 °C with a 12:12 h light:dark cycle.

A food delivery device, which consisted of a narrow strip of plywood, was built into the wire mesh cover of each tank. The plywood strip ran from the front to the back of the tank top; it was placed on the far left side of the mesh tank cover for half the tanks and on the far right side for the remaining half. Each plywood strip had a small hole in its center, directly underneath of which was a small acrylic square on which food rested. This square was attached to the plywood by a single hinge pin at one of its corners. Attached to the opposite corner of this square was a line of clear monofilament. When the line was pulled toward the experimenter, the acrylic square pivoted on its hinge pin, moving away from the hole in the plywood, and allowing the food to fall into the tank. A light box, the illumination of which served as the food cue, was placed flush against one side of the tank, the same side as the food delivery device. Each light box contained two 60-W bulbs, connected to a timer set to provide intermittent power, allowing the light to flash at the rate of 150 times per min (time on = time off). One side of each light box was covered with black poster board except for a small rectangular cut-out (5 cm wide x 2 cm high), covered in white tissue paper, 8 cm above the bottom of the tank; a similar cut-out was made in the construction paper that covered the exterior of the tank on that side. The light box and food delivery device were placed opposite the log and warming light; tank arrangement was counterbalanced across treatment conditions.

Procedure. The experiment consisted of two phases, a 2-day Pre-training Competition Phase, which permitted males to establish dominant-subordinate status, followed by a 12-day Training Phase. The Pre-training Competition Phase began the day after lizards were introduced to their tanks. Once each day for 2 days, the feeder was used to drop a small quantity of food (4 mealworms, *Tenebrio molitor*) into each tank at a randomly chosen time between 03:00 and 08:00 h following light cycle onset. Food presentation was not signaled during this phase. Any worms that were not consumed within 1 h were removed.

During the subsequent Training Phase, each group of males received one of two randomly assigned treatments. For groups that received the associative learning treatment (LRN), food (4 mealworms) was delivered at a randomly selected time between 03:00 and 08:00 h following light-cycle onset, once per day, immediately following a short food signal, namely a 10-s presentation of the flashing light. For groups that received the "truly random" control treatment (CTL), mealworms also were delivered at a randomly selected time between 03:00 and 08:00 h following light-cycle onset, once per day. However, the appearance of the 10-s flashing light also appeared at a randomly selected time once per day between 03:00 and 08:00 h following light-cycle onset. Thus, for CTL subjects, the light stimulus was not reliably paired with food.

Each group of lizards was fed mealworms according to the 12-day experimental procedure from the food delivery device. However, to provide subjects with a varied diet, anoles also were fed live crickets on the day following every fourth day of training. Crickets were dropped into the center of the tank by the experimenter and neither LRN nor CTL training occurred on these days. Tanks were sprayed with water twice daily to provide lizards with drinking water and moisture.

Data Collection and Analysis.. During the Training Phase, lizards of both treatment conditions were videotaped for 10 s prior to, as well as during, each light presentation. In addition, each feeding encounter was videotaped, from 20 s prior to food delivery to 3 min following its appearance. Videotapes later were scored for movement toward the flashing light or food (using the zones marked on the outside of the tank), the identity of each anole obtaining food, and the number of worms consumed by each individual. Four individuals, all trained in scoring techniques, analysed the videotapes. To ensure the reliability of their behavioral measurements, inter-observer agreement was calculated for independent scoring of three separate training sessions (including both LRN and CTL treatments); agreement was 100% for all three dependent measures. Observers also noted the latency of each individual to feed (i.e., make mouth contact with a mealworm), obtained by referring to a timer on the videotape record.

Results

Two tanks were excluded from analysis because of death or illness. Five LRN groups and five CTL groups remained for a total of 30 subjects.
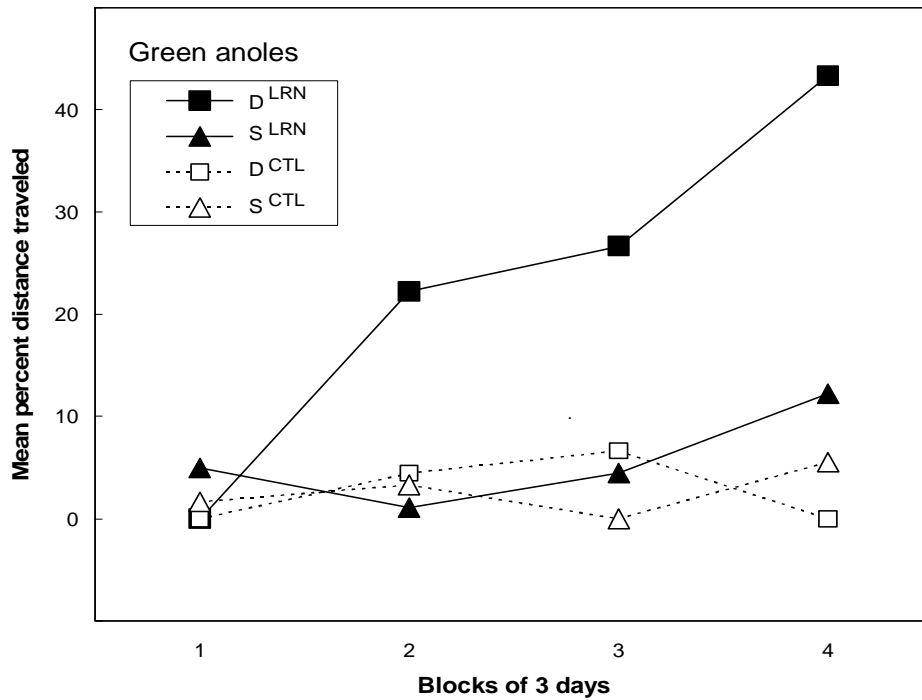

Figure 1. Mean percent of distance travelled toward the food cue by subordinate and dominant male anoles over twelve days of training (four blocks of three days). D^{LRN}: dominant males that received the associative learning treatment during training; S^{LRN}: subordinate males that received the associative learning treatment during training; D^{CTL}: dominant males that received the control treatment during training; S^{CTL}: subordinate males that received the control treatment during training.

Although movement toward the light box did not occur in any animals during the 10 s prior to onset of the food cue, D^{LRN} males learned to approach the food cue, and thus the site of impending food delivery, prior to presentation of food. The acquisition of this learned approach response is illustrated in Figure 1. As that figure also suggests, males receiving the control treatment, namely D^{CTL} and S^{CTL} males, exhibited no such change in behavior over the course of training. The performance of S^{LRN} males, however, is more difficult to interpret. Although Figure 1

shows that they did not approach the cue to anywhere near the same extent as D^{LRN} males, it suggests that they might be moving, ever so slightly, toward the cue by the end of training. Statistical analysis supports these interpretations of the data. A repeated measures analysis of variance (ANOVA), which included two between-subjects variables, namely treatment condition (LRN or CTL) and male status (D or S), and one within-subjects variable (four blocks of three days of training), revealed significant main effects of treatment, $F(1, 26) = 14.972$, $p < 0.001$, and status, $F(1, 26) = 8.421$, $p < 0.01$, and a significant interaction of treatment and status, $F(1, 26) = 8.159$, $p < 0.01$. Thus, D^{LRN} males differ from S^{LRN}, D^{CTL} and S^{CTL} males. However, a significant interaction of treatment and blocks, $F(3,78) = 3.874$, $p < 0.05$, combined with a marginally *non*-significant interaction of treatment, status and blocks, $F(3,78) = 2.680$, $p = 0.0527$, suggests that S^{LRN} males may be behaving differently than males receiving the control treatment, namely D^{CTL} and S^{CTL} males.
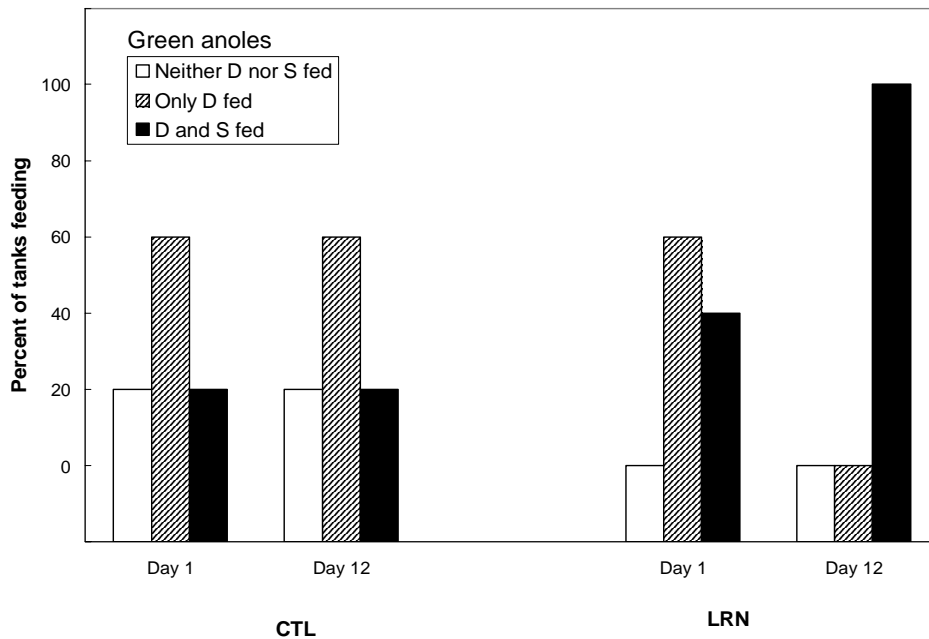

Figure 2. Percent of tanks in which feeding took place by neither the single dominant male in each tank nor the two subordinate males sharing that tank (Neither D nor S fed), by the dominant male only (Only D fed), or by the dominant male plus *at least* one of the two subordinate males (D and S fed) on the first day (Day 1) and last day (Day 12) of training. LRN: tanks of three males (one D and two S males) that received the associative learning treatment during training; CTL: tanks of three males (one D and two S males) that received the control treatment during training.

Despite the failure of S^{LRN} males to approach the food cue to the same extent as the D^{LRN} males, Figures 2 and 3 reveal that these males not only learned something as a result of their associative training, but also derived some benefit from that learning. Figure 2 illustrates that by Day 12, at least one subordinate in 100% of tanks receiving the associative learning treatment, each of which contained one D and three S males, managed to obtain some food; that is, referring to Figure 2, "D and S fed" in 100% of tanks receiving the LRN treatment. The ability of at least one S^{LRN} male in each tank to obtain food on Day 12 represents a sig-

nificant change from Day 1 of their training in which dominants were able to prevent *both* subordinates from gaining access to the food source in 60% of the tanks (i.e., "Only D fed"). This change in the ability of dominants to control the food source did not occur in tanks receiving the control treatment; indeed, there was no change whatsoever from Day 1 to Day 12 in CTL tanks. Chi-square analyses (based on a tank of males as the individual unit of analysis) supported these observations, revealing that tanks receiving LRN and CTL treatments did not differ on Day 1, χ^2 (2, N = 10) = 1.33, $p > 0.05$, but did differ significantly on Day 12, χ^2 (2, N = 10) = 6.67, $p < 0.05$. Furthermore, chi-square analyses that excluded tanks in which none of the males obtained food during the 3-min interval (i.e., "Neither D nor S fed" in Figure 2), or in which Block 1 and Block 4 data were analysed, instead of Day 1 and Day 12, yielded virtually identical results.
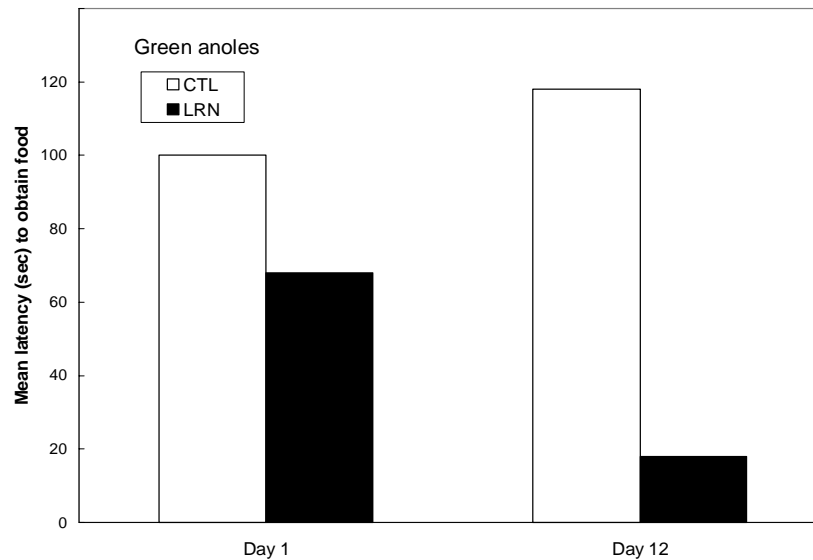

Figure 3. Mean latency (sec) to obtain food on the first day (Day 1) and last day (Day 12) of training by groups of male anoles receiving the associative learning treatment (LRN) and by groups of males receiving the control treatment (CTL).

Additional evidence of S^{LRN} males' ability to benefit from the treatment condition is illustrated in Figure 3: Although LRN and CTL tanks did not differ on Day 1 of training, Mann-Whitney U = 17.5, $p > 0.05$, by the last day of training the *combined* latencies to capture food by both dominant and subordinate males within each tank was significantly different between tanks receiving associative training and tanks receiving the control treatment condition, Mann-Whitney U = 24, $p < 0.05$. D and S latencies were collapsed for these analyses because of the changing dynamic in the tanks, a dynamic that was different for LRN and CTL tanks: Because the anoles moved about the tank, and because food was provided at random times during the day, sometimes a subordinate reached food first and sometimes the dominant male was first. Moreover, by the end of training, the dynamic in LRN tanks was quite different than in CTL tanks, as Figure 2 illustrates. However, once one male obtained food, the remaining animals followed its lead (or attempted to do so, in the case of S males). Thus, analysing D and S separately would introduce a confound, namely that the scores are differentially influenced by who reached

food first, D or S, and that the first to feed tended to be different between treatment conditions near the end of training. Nonetheless, by summing the latencies, we show that tanks of LRN males behaved differently than tanks of CTL males. Although one might be tempted to argue that the difference between LRN and CTL tanks illustrated in Figure 3 is entirely the effect of learning on dominant males, chi-square analyses revealed that dominant males were not always the first to feed in either treatment condition, whether at the beginning of training on Day 1 or at its end on Day 12, both χ^2 s(2, N = 10) = 1.33, $p > 0.05$. Finally, as expected, dominant males in both treatment conditions obtained more worms than did subordinates, $F(1,26) = 10.891$, $p < 0.05$.

Discussion

In our experiment, lizards spent long periods of time basking in the heat, either perched on the log or sitting on the gravel substrate. Our 10-s food cue was, perhaps, too brief to allow these rather sedentary animals to reach the site of food delivery before food was dropped into the tank and, thus, D^{LRN} males may not have reaped the full benefits of their associative training. However, D^{LRN} males, together with the subordinates with which they were housed, did reach the food faster than males receiving the control treatment.

Subordinate males, on the other hand, managed to compete more successfully as a result of associative learning. Although an alternative explanation of our results is that S^{LRN} males did not themselves learn an association between the cue and food but merely became alert to the anticipatory conditional approach response of D^{LRN} males (Figure 1), and then followed them to the food source, we think this explanation is unlikely for two reasons: One, as mentioned earlier, dominant males were not first to reach the food source more often than were subordinates in either treatment condition and, thus, following behavior, per se, cannot explain the results. (A variant of this same argument is that S^{LRN} males did not follow, per se, but were alerted to impending food delivery by D^{LRN} males' anticipatory conditional locomotory response. However, this behavior in itself would be a form of associative learning in which the behavior of another individual served as the food cue and, thus, this explanation does not alter our associative interpretation in substantive ways.) Two, research with blue gouramis (Hollis et al., in press), which we review in the General Discussion, demonstrates that when subordinates are trained privately, both the rate of acquisition and its asymptote are identical to dominants. Together with the results of our experiment with firemouth cichlids, presented in Experiment 2, the behavior of subordinate anoles seems more likely a failure of performance, rather than a failure of learning.

Clearly our experiment would have benefited from a procedure in which males were separated for private training, enabling us not only to assess directly the ability of subordinates to learn but also to explore how the group behaved if only one of the individuals had the benefit of a learned cue. However, pilot work demonstrated that anoles do not respond well to either isolation or handling. Nonetheless, our procedure mimics conditions in which both dominants and subordinates learn simultaneously about the arrival of food. Our results suggest that, at least in anoles, conditions like these would appear to favor the ability of subordinates to steal food from dominant males.

Experiment 2

Firemouth cichlids (*Thorichthys meeki*), named for their bright red-orange throats, are freshwater fish native to Mexico and Central America, where they are found in abundance in shallow waters, among rocks or vegetation (Miller, 1966). During the breeding season, males actively defend territories against intruders with a colorful display: Males flare their gill covers, which are decorated with iridescent eye spots, and inflate the bright red branchiostegal (gill) membrane inside; if intruders do not flee, territorial males charge, chase and butt them (Baerends & Baerends van Roon, 1950; Neil, 1984). Laboratory investigations of firemouth cichlids reveal that males readily form dominant-subordinate social structures (Baerends & Baerends van Roon, 1950; Evan & Norris, 1996; Radesäter & Fernö, 1979; Neil, 1983) and that, in a foraging situation, subordinate males not only obtain less food but also appear to adopt an "agonistic minimizing foraging strategy" (Frey & Hodapp, 1982) in which they forego opportunities to secure food in an attempt to avoid attack by the dominant male. We asked whether signaling of food would improve the ability of subordinate males to steal food or the ability of dominant males to protect it.

Methods

Subjects and Apparatus. The subjects were 32 male adult firemouth cichlids (*Thorichthys meeki*) obtained from local suppliers and housed in several large colony tanks. Groups of four males were chosen such that, within each group, both the weight and body length of group members matched each other as closely as possible. Although close matching of group members was not essential to the experimental design, it effectively guaranteed that each group member would attempt to establish dominance over the others; however, only one male would emerge as dominant (Baerends & Baerends van Roon, 1950). Group size was determined by pilot research, which indicated that, in smaller groups, fish did not habituate well to the presence of the experimenter and, in larger groups, a more complex hierarchy would emerge.

Each group was transferred to a standard 20-gallon aquarium (75 cm wide x 30 cm high x 30 cm deep) containing a box filter and bubbler, a heater, and four plastic plants; the bottom was covered with gravel. The back and sides of the tank were covered in opaque, adhesive paper. Aquaria were maintained at 22 °C with a 12:12 h light:dark cycle.

A food delivery device, virtually identical to that used in Experiment 1, was placed above the center of each tank. It consisted of a narrow strip of plywood that rested on top of the tank. Two small light fixtures, the illumination of which served as the food cue, were placed alongside the food delivery device, one on each side. Each light fixture consisted of a small 15-W bulb, mounted within a short (5 cm) opaque acrylic tube. One end of the tube was glued to a thin strip of plywood that was placed across the top of the tank; the other end of the tube, suspended a few cm above the water surface, was covered with red acetate.

Procedure. The experiment consisted of three phases, a 7-day Pre-training Competition Phase, an 18-day Training Phase, and a 3-day Post-training Testing Phase. The Pre-training Competition Phase began the day after fish were introduced to their tanks. Each day, at a randomly chosen time between 03:00 and 08:00 h following light cycle onset, the feeder was used to drop a small quantity of food (15 freeze-dried plankton) into the tank; food presentation was not signaled. Although this Pre-training Competition Phase was 5 days longer than the equivalent period used with anoles, the extra time was necessary to allow fish to habituate to the tank conditions and the presence of the experimenter during daily feedings. In addition, fish established dominant-subordinate status during this phase.

During the subsequent Training Phase, each group of males received one of two randomly assigned treatments. For groups that received the associative learning treatment (LRN), food (15 freeze-dried plankton) was delivered at a randomly selected time between 03:00 and 08:00 h following light-cycle onset, once per day, immediately following a short food signal, namely a 10-s illumi-

nation of the paired overhead lights. For groups that received the "truly random" control treatment (CTL), food also was delivered at a randomly selected time between 03:00 and 08:00 h following light-cycle onset, once per day. However, the illumination of the paired overhead lights also occurred at a randomly selected time once per day between 03:00 and 08:00 h following light-cycle onset and, thus, the light stimulus was not reliably paired with food.

During the subsequent 3-day Post-training Testing Phase, all tanks received the same procedure: Food (15 freeze-dried plankton) was delivered at a randomly selected time between 03:00 and 08:00 h following light cycle onset, once per day, immediately following a short food signal, namely a 10-s illumination of the paired overhead lights.

Data Collection and Analysis. During the Training Phase, fish of both treatment conditions were videotaped for 10 s prior to, as well as during, each light presentation; in addition, each feeding encounter was videotaped, from 20 s prior to food delivery to 3 min following its appearance. During the Post-training Testing Phase, each tank was videotaped for 5 min prior to presentation of the 10-s light stimulus, and continuing until 10 min after food was delivered. In addition, on each of the 3 days of the Post-training Testing Phase, each tank was videotaped for another 10-min period at a randomly selected time during the day. Videotapes later were scored for approach to the paired lights or food, the number of feeding bites by each individual, and the number of aggressive bites delivered by the dominant male toward the subordinates in that tank (see Table 1 for operational definitions). Two individuals, trained in scoring techniques, analysed the videotapes; to ensure the reliability of their behavioral measurements, inter-observer agreement was calculated for independent scoring of several training sessions (including both LRN and CTL treatments); agreement was 85%-100% for all dependent measures.

Table 1
Behavioral Patterns and Operational Definitions in Experiment 2.

Behavioral pattern	Operational definition
Approach	Fish moves to a position within 2 cm of the water surface, oriented toward either the light stimulus or the food delivery device.
Aggressive Bite	Fish makes an abrupt forward lunge and contacts opponent with open mouth.
Feeding Bite	Fish snaps at the surface of the water with open mouth, oriented toward a food item.

Results

One tank was excluded from analysis because of illness. Four LRN groups and three CTL groups remained for a total of 28 males.

As Figure 4 illustrates, both D^{LRN} and S^{LRN} males, but not D^{CTL} and S^{CTL} males, learned to anticipate the arrival of food: By Block 6 of training, D^{LRN} and S^{LRN} males were reliably approaching the light stimulus prior to food presentation. Statistical analyses support these observations. A repeated measures ANOVA, which included two between-subjects variables, namely treatment condition (LRN or CTL) and male status (D or S), and one within-subjects variable (first and last blocks of training), revealed a significant effect of treatment, $F(1, 10) = 5.88$, $p < 0.05$, and a significant interaction of treatment and blocks of days, $F(1, 10) = 5.77$, $p < 0.05$. Neuman-Keuls post hoc comparisons indicated that fish did not differ from one another initially (Block 1), all qs(r, 10) < 1.00, $p > 0.05$; however, by the end of training (Block 6), D^{LRN} and S^{LRN} males moved toward the light significantly more than D^{CTL} and S^{CTL} males, qs(r, 10) > 4.53, $p < 0.05$. Finally, D^{CTL} and

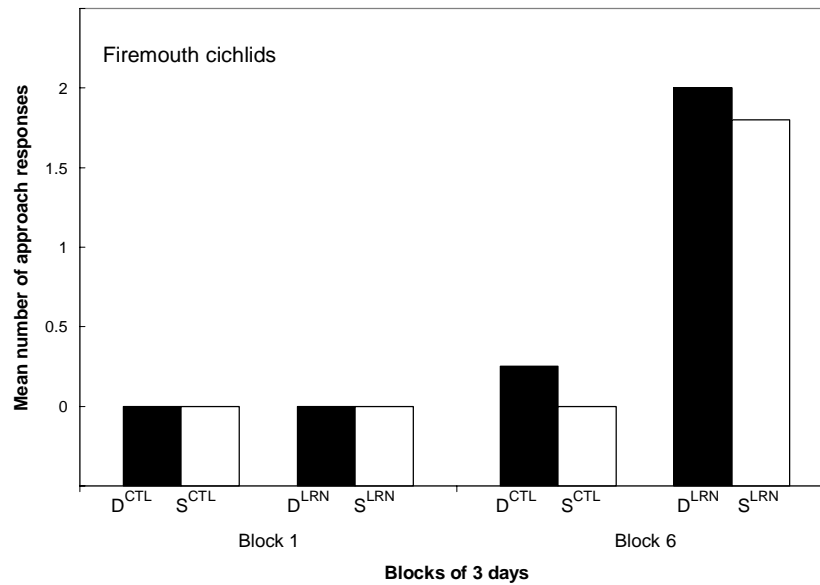S^{CTL} males did not change their behavior from Block 1 to Block 6, qs(r, 10) < 1.00, p > 0.05.

Figure 4. Mean number of approach responses toward the food cue by subordinate and dominant male firemouth cichlids in the first and last block (3 days) of training. Behavior was scored as either occurring or not occurring during each presentation of the light stimulus; thus, a "3" is the maximum score in each block. D^{LRN}: dominant males that received the associative learning treatment during training; S^{LRN}: subordinate males that received the associative learning treatment during training; D^{CTL}: dominant males that received the control treatment during training; S^{CTL}: subordinate males that received the control treatment during training.

Although S^{LRN} males learned an association between the food cue and food, they did so even at the same time that the dominant male in their tank was becoming better at securing more of that food. Figure 5 shows that, during the last three days of training, D^{LRN} males exhibited more feeding behavior than S^{LRN} males, as well as D^{CTL} and S^{CTL} males. Statistical analyses support these observations: A repeated measures ANOVA, which included two between-subjects variables, namely treatment condition (LRN or CTL) and male status (D or S), and one within-subjects variable (first and last blocks of training), revealed a significant effect of treatment, $F(1, 10) = 5.62$, $p < 0.05$, and a significant interaction of treatment, status and blocks of days, $F(1, 10) = 4.93$, $p < 0.05$. Neuman-Keuls post hoc comparisons indicated that fish did not differ from one another initially (Block 1), all qs(r, 10) < 1.00, p > 0.05; however, by Block 6, D^{LRN} males exhibited more feeding bites at the water surface than S^{LRN}, D^{CTL} and S^{CTL} males, qs(r, 10) ≥ 7.23, $p < 0.05$.

In addition to the increase in feeding bites that D^{LRN} males exhibited at the end of training, analysis of their behavior during the extended feeding observations in the Posttraining Testing Phase revealed that associative training enabled D^{LRN} males to defend the food resource more aggressively than D^{CTL} males. As Figure 6 suggests, and statistical analyses confirm, D^{LRN} males exhibited significantly more aggressive biting toward subordinates during signaled food delivery than did D^{CTL} males toward S^{CTL} males, $F(1, 4) = 23.05$, $p < 0.01$.
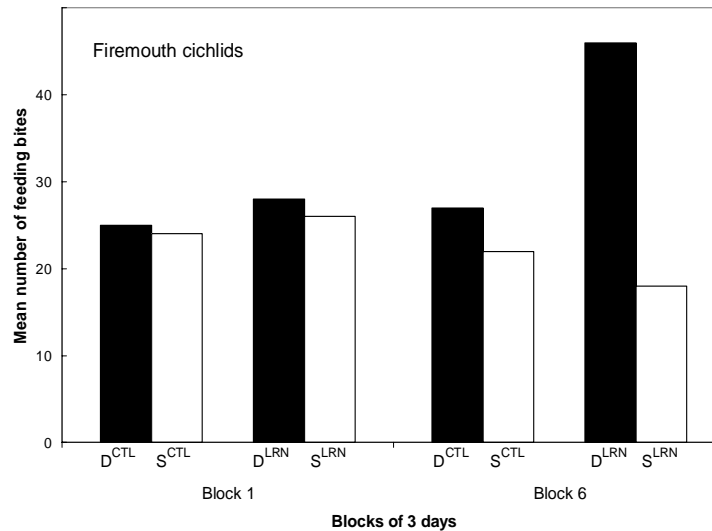
Figure 5. Mean number of feeding bites by dominant and subordinate male firemouth cichlids in the first and last block (3 days) of training. D^{LRN}: dominant males that received the associative learning treatment during training; S^{LRN}: subordinate males that received the associative learning treatment during training; D^{CTL}: dominant males that received the control treatment during training; S^{CTL}: subordinate males that received the control treatment during training.

Discussion

In a procedure that mimics conditions in which individuals in an established dominance hierarchy learn about where and when food will appear, both dominant and subordinate firemouth cichlids learned to approach a cue that signaled the arrival of food. As a result of this learning, associatively trained dominant males were able to mount a more aggressive defence of the food resource, which in turn probably accounted for their increase in feeding behavior. Although associatively trained subordinates also approached the food cue, the increased aggression on the part of the dominant males with which they shared the tank prevented subordinates from reaping any benefits of their associative training.

Although our results make clear that associative learning contributed to the benefits derived by dominants, the group training procedure prevents us from teasing apart the separate contributions of associative learning and of the group's own dynamic to that change in behavior. That is, because both dominants and subordinates approached the food cue, the mere presence of subordinates in close proximity probably contributed in some way to the increase in dominant aggression. However, our own extended observations of these animals suggest that proximity, alone, does not result in increased aggression; indeed, in our relatively small tanks, subordinates often were close to the dominant male and, as the baseline levels of aggressive biting in Figure 6 suggest, aggression remained at relatively low and stable levels. Furthermore, as that same figure shows, when food was dropped into the tanks of control group fish, dominants were unable to mount the same high levels of aggressive behavior that associatively trained dominants exhibited, even though dominant and subordinate control fish were feeding alongside one another in close proximity. Thus, an association between signal and food appears to be

necessary to generate the level of aggression exhibited by associatively trained dominants during the food cue.
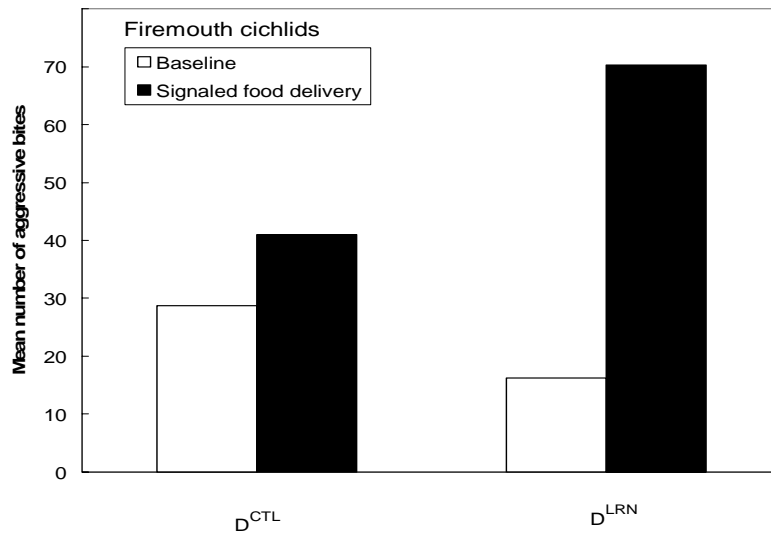

Figure 6. Mean number of aggressive bites directed at subordinates by dominant males during the 10-min period following signaled food delivery and during a 10-min baseline observation period in the Post-training Testing Phase. D^{LRN}: dominant males that received the associative learning treatment during training; D^{CTL}: dominant males that received the control treatment during training.

Although this experiment, too, would have benefited from the ability to separate males for private training, these animals, like anoles, do not respond well either to isolation or to repeated transfer from one tank to another. Nonetheless, our procedure mimics conditions in which both dominants and subordinates learn simultaneously where and when food will appear. Our results suggest that conditions like these would appear to favor the ability of dominants to protect the food resource.

Finally, in a previous study of foraging behavior in firemouth cichlids (Frey & Hodapp, 1982), albeit a study that did not involve associative learning, subordinate males adopted what the authors called an "agonistic minimizing foraging strategy" in which subordinates appeared to ignore opportunities to secure food in an attempt to avoid attack by the dominant male. In contrast, associatively trained subordinates in our experiment continued to approach the food cue and food; moreover, subordinates that received the control procedure did not appear to feed any less than the dominant males with which they shared the tank. Thus, our experiment shows no evidence of an agonistic minimizing foraging strategy.

General Discussion

The experiments described in this paper, like previous research in our laboratory, have focused on the biological function of associative learning: What advantage does an animal gain by responding to environmental cues that signal the appearance of biologically important events? The major goal of this research has been to demonstrate the potentially important—and, as we continue to explore it, very pervasive—role that Pavlovian conditioning might play in the behavior of the

animals under study. In addition, however, because behavioral commonalities abound even among highly divergent species, another goal of this research has been to suggest ways in which other animals, including birds and mammals, might make use of the same benefits (Hollis, 1999; Hollis et al., 1995; Hollis et al., 1997).

For example, previous conditioning research in our laboratory with another species of freshwater fish, blue gouramis (*Trichogaster trichopterus*), has demonstrated that learned cues of a rival's impending intrusion not only enable males to mount a more aggressive defense of their territories than males that do not have the benefit of such cues (Hollis, 1984; Hollis et al., 1995), but these cues also help males to concentrate their efforts at times when the territory is most vulnerable (Hollis et al., 1984). Because female blue gouramis rarely mate with males that do not possess territories (Forselius, 1957)—and because territorial defense typically requires large energy expenditures (Miller, 1964; Frey & Miller, 1972)—this enhancement of territorial defense, tailored specifically to the time and place of likely intrusion, is likely to convey a significant reproductive advantage. In addition, both male and female blue gouramis can learn to anticipate the appearance of a mate (Hollis, Cadieux, & Colbert, 1989), and learned cues that announce a female's impending appearance in a male's territory not only enable him to attenuate his initial aggressive response to her, but also enable him to spawn sooner, clasp her more often, and produce significantly more young than males that do not have the benefit of such cues (Hollis et al., 1997). At a more general level, however, beyond the benefits that appear to accrue to blue gouramis, per se, this same ability to use learned cues in territorial defense, courtship, and reproduction may exist in many other species. Not only are territorial mating systems like those of blue gouramis highly similar across divergent species (Emlen & Oring, 1977), but so, too, are the capabilities of many animals, vertebrates and invertebrates alike, to change their behavior as a result of Pavlovian conditioning (Macphail, 1982, 1993).

Our analysis of food competition in green anoles and firemouth cichlids, presented here, is an attempt to provide some evidence that Pavlovian conditioning may serve analogous functions in divergent animals. Clearly, the results of the two experiments differed—namely in the details of whether, and in what precise ways, subordinates or dominants benefited from signals of impending food—and these results are likely to reflect species differences: Not only are green anoles more sedentary (Jenssen et al., 1996) than pugnacious firemouth cichlids (Radesäter & Fernö, 1979), but also dominant male anoles never maintain exclusive territories (Crews, 1980; Jenssen et al., 1996), even during the breeding season, as do firemouth cichlids (Neil, 1983, 1984; Radesäter & Fernö, 1979). However, at least some of these differences are certain to reflect our experimental conditions. The brief food signal, small amount of food, configuration of the environment, and composition of the group all may have contributed to the results we obtained. For example, subordinate firemouth cichlids, which readily learned to approach cues that heralded food's arrival, may have been more successful at stealing if some protective cover had been available near the food source. This suggestion is based on detailed observations (Gross, 1982) of subordinate North American sunfish males that rely heavily on hiding places from which to mount sneaky mate stealing tactics. Thus, in our view, a summary of the research described in our paper is not, merely, that subordinate anoles (but not dominants) and dominant firemouth cich-

lids (but not subordinates) used food cues to benefit in the competition for food, but rather that subordinates and dominants of both species learned to associate environmental cues with the appearance of food, and that individuals of either status potentially could have used these cues to improve their chances to secure it.
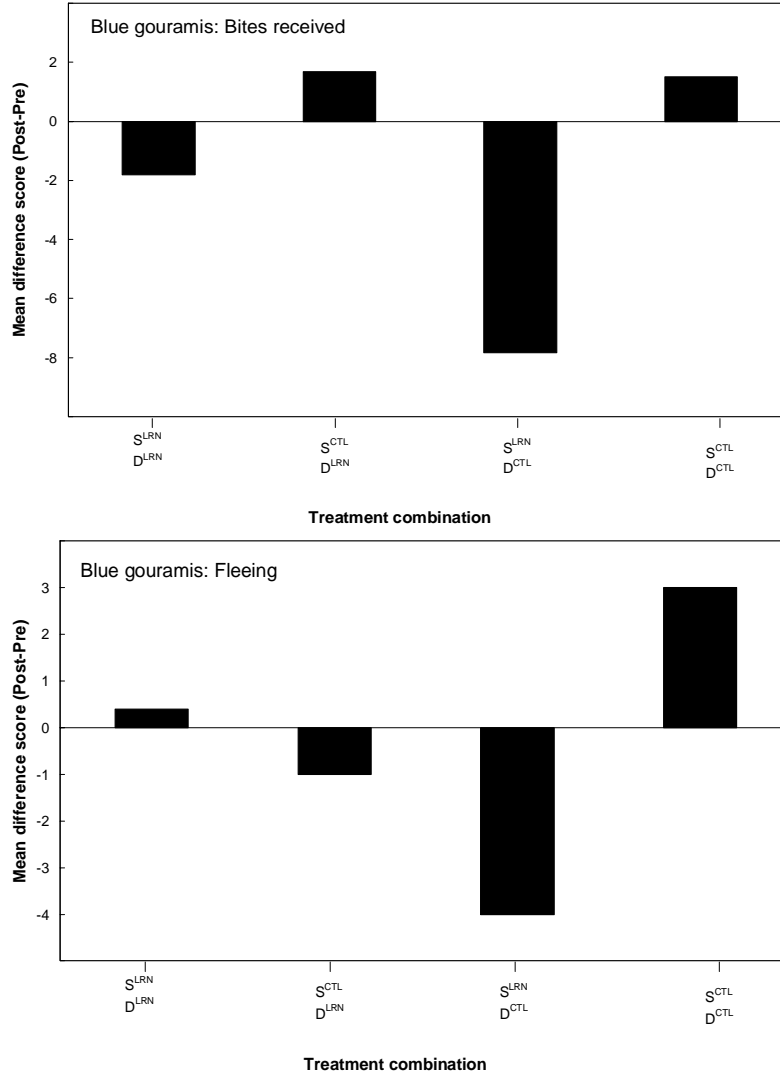

Figure 7. (Top) Mean difference score between the first day of the Post-training Testing Phase and the last day of the Pre-training Competition Phase (only training intervened) in the number of 15-s intervals in which the subordinate male sustained a bite from its dominant partner during food presentation. (Bottom) Mean difference between the first day of the Post-training Testing Phase and the last day of the Pre-training Competition Phase (only training intervened) in the number of 15-s intervals in which the subordinate male spent fleeing its dominant male partner during food presentation. In both figures, the sign of the difference score (+ or –) represents the change (increase or decrease, respectively), if any, resulting from training. S^{LRN}: subordinate males that received the learning treatment during training; S^{CTL}: subordinate males that received the control treatment during training; D^{LRN}: dominant males that received the learning treatment during training; D^{CTL}: dominant males that received the control treatment during training. *Note.* From "Novel strategies of subordinate fish competing for food: Learning when to fold," by K. L. Hollis, K. S. Langworthy-Lam, L. A. Blouin and M. C. Romano, in press, *Animal Behaviour*. Copyright 2004 by Academic Press. Reprinted with permission.

Further evidence of this particular view of our results comes from an experiment with blue gouramis (Hollis et al., in press) that closely resembles the food competition research presented here except in one important detail of animals' training. In that experiment, each of several pairs of males was placed in a single aquarium and, under conditions similar to the two experiments described in this paper, were given the opportunity to establish dominant and subordinate status. Following this phase, however, pair members were trained in isolation. That is, unlike the experiments with anoles and cichlids, gourami pair members were moved into separate end compartments of their tank. Each male then received one of two treatments, either an associative learning treatment or a control treatment, both of which were similar to the treatment conditions we used here. Subsequently, we tested the ability of the dominant and subordinate of each pair to compete for food. Unlike the experiments with anoles and cichlids, then, separate training of each individual permitted us to explore how individuals behaved if both the dominant and the subordinate male had the benefit of a learned cue that predicted the arrival of food, if only one of them learned about food's appearance, or if neither of them could predict the arrival of food.

In that experiment, animals whose partners did not share the benefit of the food cue—that is, associatively trained subordinates whose dominant partners received the control treatment, and associatively trained dominants whose subordinate partners received the control treatment—benefited the most from training. Compared to the two remaining pair combinations with similar treatment histories, associatively trained subordinates with control group partners reduced the number of biting attacks they received (see Figure 7, top panel) as well as the amount of time they spent fleeing their dominant partners (see Figure 7, bottom panel). Moreover, dominants whose subordinate partners did not share their associative training were able to feed significantly longer than pairs with other treatment combinations. In addition, however, the results suggest surprising flexibility in the cognitive mechanisms underlying that learning: Like privately-trained dominants, privately-trained subordinates learned to approach food cues directly; however, on the very first occasion subordinates were tested with a dominant present, they abandoned their previously-learned direct approach to food cues, immediately adopting instead a different, "deceptive", tactic in which they approached the food site while adopting a submissive posture. Thus, it appears that subordinate blue gouramis were able to combine information about previous learning, possibly what learning psychologists call an *expectancy* of the reinforcer (Holland & Straub, 1979; Colwill & Rescorla, 1985), in this case food, with the probability of future attack and adjust their food-getting strategy accordingly.

Like the results of our experiments with anoles and firemouth cichlids, then, both subordinate and dominant blue gouramis seem capable of learning about cues predicting food and, depending upon the circumstances, males of either status are prepared to benefit from that learning. In sum, Pavlovian conditioning is much like other behavioral adaptations that help individuals compete for food, mates, nest sites or safe refuges: Relying on learned food cues will not always be successful, in the same way that other subordinate strategies are not (Clutton-Brock et al., 1979; Gross, 1982; Adams et al., 1998; Schmidt & Hoi, 1999). In addition, at any given time, several competitors may be relying on some of the same multiple weapons, as well as the same strategies to counter weapon use in others, and the

outcome of this competition will depend upon not only the differential competency of the individuals involved but also the prevailing ecological conditions. Learning to use food cues through associative learning does not guarantee successful competition, nor successful stealing; rather, this particular kind of learning may be yet another, heretofore unexamined, mechanism in animals' competition for food.

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