



Novel strategies of subordinate fish competing for food: learning when to fold

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In group-living animals, competition for a scarce resource often results in the formation of dominance hierarchies. Dominant individuals garner more of that resource for themselves through the use of aggression, forcing subordinates to rely on nonaggressive strategies to secure it. Stealing from dominants is common, but subordinate thieves can risk attack if caught. How, then, do subordinates decide when and where to steal? We explored whether the opportunity to learn about the location and availability of food might facilitate food-stealing attempts by male blue gouramis, *Trichogaster trichopterus*, a freshwater tropical fish. Our results show that subordinates were able to use learned cues to mount highly effective 'sneaky' tactics. By anticipating food location and availability, subordinates reduced the number of attacks they received as well as the amount of time they spent fleeing from dominants. More importantly, however, our results revealed unexpected plasticity in the cognitive mechanisms underlying this learning: like privately trained dominants, privately trained subordinates learned to approach food cues directly; however, on the very first occasion that subordinates were tested with a dominant present, they dramatically altered their previously learned direct approach to food cues, immediately adopting a different, sneaky tactic instead. Thus, subordinates were able to combine information about previous learning, namely an 'expectancy' of food, with the probability of future attack and adjust their food-getting strategy accordingly.

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Many potential benefits accrue to animals living in a group, among them a decrease in the risk of predation (Pulliam 1973; Bertram 1980) and an increase in the ability to find food (Ward & Zahavi 1973) or to defend it from others (Bertram 1978; Wrangham 1980). None the less, a nearly universal cost of group living 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 dominance hierarchies, social structures in which dominant individuals garner more of a scarce resource through the use of aggression (Huntingford & Turner 1987; Pusey & Packer 1997). To obtain a greater share of

the limited resources, subordinates may depend on non-aggressive strategies, such as stealing (Adams et al. 1998; Schmidt & Hoi 1999); 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 what some have called 'sneaky' tactics (Clutton-Brock et al. 1979; Gross 1982, 1996). 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; Adams et al. 1998). The success of subordinates' sneaky strategies is highly dependent on the ability to locate the resource efficiently and to escape detection. But how do subordinates decide when and where to steal?

A voluminous literature documents animals' use of learned cues to locate food, water and mates, as well as to avoid predators and repel rivals (Hollis 1982, 1997; Pear 2001). Foraging behaviour, which is perhaps the most widely studied behaviour among learning researchers,

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appears to be easily modified by cues that provide information about food 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, especially when hungry, actively move away from cues that signal its absence (Hollis 1982; Macphail 1993; Timberlake & Silva 1995; Shettleworth 1998; Pear 2001; Wynne 2001). In addition, as this same body of literature reveals, animals of many different species respond to such cues with behaviour that anticipates the impending arrival of food. 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 behaviour that they use to capture actual prey items (Waxman & McCleave 1978); this anticipatory behaviour most likely helps them to capture the fast-moving, flying insects upon which archer fish feed. Similarly, if Norway rats, *Rattus norvegicus*, 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 behaviour, of exactly the sort used to capture moving insects (Timberlake et al. 1982). In some animals, most notably junglefowl, *Gallus gallus spadiceus*, and ring doves, *Streptopelia risoria*, food cues 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 et al. 1992). Likewise, learned cues inform foraging Norway rats which foods are safe and which are poisonous (Galef 1990). Adaptively speaking, then, cues associated with food enable animals to forage efficiently, budget their time effectively, select nutritious food items, avoid poisonous foods, and, thus, maximize energy intake (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 hypothesis in blue gouramis, *Trichogaster trichopterus*, a species of freshwater tropical fish. Previous research with blue gouramis in our laboratory has shown that they are capable of using learned signals to great advantage in several seminatural situations. For example, learned cues of a rival's impending intrusion enable males to mount a more aggressive defence of their territories than males that do not have the benefit of such cues (Hollis 1984; Hollis et al. 1995); learned 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 defence typically requires large energy expenditures (Miller 1964; Frey & Miller 1972), this enhancement of territorial defence, 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 et al. 1989). More importantly, however, 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). Because of blue gouramis' seemingly large capacity to learn both about the location and availability of biologically important events such as the appearance of rivals and mates, and to use cues to their advantage in seminatural situations, they presented an excellent opportunity to test the hypothesis that learned cues might also afford benefits in the competition for food.

Like many other territorial species, blue gouramis abandon their territories outside of the breeding season and live together in groups (Forselius 1957). Although males display less aggression when living in groups than when defending territories, they quickly establish dominance hierarchies when forced to compete for food. Dominant individuals typically garner more food for themselves by bullying subordinates. None the less, subordinate males manage to obtain some of the food some of the time (Forrester 1991; Krebs & Davies 1993; Alcock 2001). Often the manoeuvres they use are 'sneaky'; for example, subordinates sometimes hover in the background, keeping out of the way of dominant males, and quickly rush in to steal food away before dominant animals appear to notice that food has arrived. In this regard, subordinates' behaviour resembles the sneaky strategies of many animals competing for mates (reviewed in Alcock 2001). For example, in North American sunfishes (*Lepomis*: Centrarchidae), subordinate males manage to fertilize some of nesting females' eggs by hiding close to nesting pairs and, from these hiding places, darting into the nests while attempting to avoid the parental males (Gross 1982). In both sunfishes and blue gouramis, subordinates attempt to flee when detected by the dominant male; however, subordinates are not always successful at escaping detection and, thus, they sustain multiple attacks from the dominant male. We wondered whether cues that heralded the arrival of food, especially if such cues were learned in the absence of dominants, would permit subordinates to adopt strategies that reduced the amount of aggression they received, increased the amount of food they obtained, or both.

To answer this question, we formed pairs of males, placing each pair in a single aquarium, and gave them the opportunity to establish dominant and subordinate status. Following this phase, pair members were separated into the right and left end compartments of their aquarium, where they received one of two treatments, either a learning treatment, in which a cue signalled the arrival of food at a particular location, or a control treatment, in which animals had equal experience with the 'cue' and the food but food was not signalled. Subsequently, we tested the ability of the subordinate of each pair to steal from the dominant. 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 appearance of food, if only one of them learned about food's appearance, or if neither of them could predict the appearance of food.

METHODS

Subjects and Apparatus

The subjects were 52 adult male blue gouramis provided by EKK Will Waterlife Resources (Gibsonton, Florida, U.S.A.). Prior to selection as subjects, fish were transferred from large stock tanks, where they had been maintained, to individual compartments of smaller aquaria. All fish then were screened carefully over a period of 4–5 days for vigorous eating behaviour and normal activity levels, both reliable indicators of good health. From this larger pool of healthy individuals, 26 pairs of males were chosen such that, within each pair, both the weight and body length of the two pair members matched each other as closely as possible; within-pair body weights did not differ by more than 10%. Although such close matching of pair members was not essential to the experimental design, it effectively guaranteed that each pair member would attempt to establish dominance over the other.

One member of each pair was randomly assigned to the left compartment of a standard 20-gallon aquarium (75 cm wide × 30 cm high × 30 cm deep) that had been divided vertically into three compartments of equal size (i.e. 25 cm wide × 30 cm high × 30 cm deep). Its partner was assigned to the right compartment.

Tank compartments, each of which contained a gravel bottom, a box filter, and a few plastic plants, were separated by dividers. Each divider consisted of an opaque acrylic barrier (19 × 30 cm) that could be raised and lowered by means of a string and pulley system. The back and sides of the tank were covered in opaque, adhesive

paper. Aquaria were maintained at 27–30°C with a 14:10 h light:dark cycle.

A small light fixture, the illumination of which served as the food cue, was placed above the centre of each of the three tank compartments. It 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 narrow strip of plywood that was placed across the top of the tank; the other end of the tube, suspended a few centimetres above the water surface, was covered with red acetate. Alongside each light fixture was a feeder, also consisting of a narrow strip of plywood that rested on top of the tank. The plywood strip had a small hole in its centre, directly underneath of which was a small acrylic square on which the 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 the square was a ‘string’ made of clear monofilament line. When the string was pulled towards 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.

Procedure

The experiment consisted of three phases (Fig. 1), a pretraining competition phase (3 days), a training phase (8 days), and a post-training testing phase (3 days). The pretraining competition phase, which began approximately 3 days after fish were introduced to their tanks, commenced with the lifting of barriers separating pair members. Pair members were permitted to fight until they

Pretraining competition (3 days)	Training (8 days)	Post-training testing (3 days)
<ul style="list-style-type: none"> • Barriers open (pair members interact) • Establishment of hierarchy: dominant (D) and subordinate (S) males • Food competition (1/day × 3 days): Unsignalled food only 	<ul style="list-style-type: none"> • Barriers closed (pair members separated) • Males receive separate training: LRN or CTL • Four treatment combinations: $D^{LRN} + S^{LRN}$ $D^{LRN} + S^{CTL}$ $D^{CTL} + S^{LRN}$ $D^{CTL} + S^{CTL}$ 	<ul style="list-style-type: none"> • Barriers open (pair members interact) • Re-establishment of hierarchy: dominant (D) and subordinate (S) males • Food competition (1/day × 3 days): Light → Food

Figure 1. Experimental procedure. D: dominant male; S: subordinate male; LRN: the learning treatment condition in which males, either D or S, received paired presentations of a food cue and food; CTL: the control treatment condition in which males, either D or S, received random presentations of the food cue and food.

had established a winner and loser. In anabantid species, which include gouramis (genus *Trichogaster*), paradise fish, *Macropodus opercularis*, and Siamese fighting fish, *Betta splendens*, rival males of similar size engage in reciprocal aggressive behaviour until one fish, often quite suddenly, signals its subordinate status by assuming the submissive posture (see Table 1). Fights are typically brief (i.e. less than 20 min) and submissive behaviour is unmistakable: the loser folds its fins, blanches in colour, and tilts its body upward along the median axis (Forselius 1957; Miller 1964; Frey & Miller 1972). Although the winner, which now assumes dominant status, occasionally displays aggressive behaviour towards the subordinate male, the loser ceases altogether to engage in any aggressive behaviour; indeed, it attempts to flee or hide. Dominant-subordinate status does not reverse itself; rather, it remains relatively permanent (Frey & Miller 1972). Later that day, day 1, and for an additional 2 days, through day 3, the feeder was used to drop five 'TetraBits' food pellets (TetraWerke, Melle, Germany) into the centre compartment of each tank once per day at a randomly chosen time between 0600 and 0900 hours following light cycle onset. Food presentation was not signalled during this pretraining competition phase. Approximately 1 h following the presentation of this unsignalled food on day 3, pair members were separated into their respective left and right end compartments, where they remained throughout the subsequent training phase.

During the training phase, each dominant (D) and subordinate (S) member of the pair received one of two individual treatments. For males that received the learning

treatment (LRN), food was delivered at a randomly selected time between 0600 and 0900 hours following light cycle onset, once per day, at the top centre of their respective end compartments immediately following a short food signal, namely the 10-s illumination of the small overhead light. For males that received the control treatment (CTL), food also was delivered at a randomly selected time between 0600 and 0900 hours following light cycle onset, once per day, at the top centre of their respective end compartments. However, the illumination of the 10-s light appeared at a randomly selected time once per day between 0600 and 0900 hours following light cycle onset and, thus, light illumination was not reliably paired with food. Each D and S member of a pair received either the LRN or CTL treatment based on the random assignment of pairs to one of the four possible treatment combinations: (1) both D and S received the learning treatment ($D^{LRN} + S^{LRN}$); (2) D received the learning treatment but S received the control treatment ($D^{LRN} + S^{CTL}$); (3) D received the control treatment but S received the learning treatment ($D^{CTL} + S^{LRN}$); and (4) both D and S received the control treatment ($D^{CTL} + S^{CTL}$). Separate training of each pair member commenced on day 4 and continued for an additional 7 days thereafter for a total of 8 days of training.

On day 12, the first day of the post-training testing phase, the barriers separating pair members again were lifted, allowing pair members to re-establish their dominance hierarchy. Approximately 6 h later, the light above the centre compartment was illuminated for 10 s, immediately followed by the appearance of five food pellets, dropped from the centre feeder. This light-plus-food presentation occurred on each of the 3 days of this final phase at a randomly selected time between 0600 and 0900 hours following light cycle onset.

Table 1. Behavioural patterns and operational definitions

Behavioural pattern	Operational definition
Approach	Fish moves to a position within 2 cm of the water surface, oriented towards either the light stimulus or the food delivery device
Biting	Fish makes an abrupt forward lunge and contacts opponent with open mouth
Fleeing	Fish darts quickly in a direction opposite that of a pursuing opponent; fleeing is maintained usually for 1–5 s but sometimes longer
Nipping	Fish skims the surface of the water, rapidly opening and closing its mouth, oriented towards either the light stimulus or the food delivery device*
Orienting	Fish assumes a position in which its longitudinal body axis, from mouth to tail, points towards either the light stimulus or the food delivery device
Submissive posture	Fish assumes a body angle of 15–60° with the horizontal (usually head up but occasionally head down), with all fins in a folded position; this display is accompanied by a rapid blanching of colour until the fish appears pale grey to silver

*Although *T. trichopterus* is an air-breathing fish, and also goes to the surface to breathe occasionally, nipping and air-breathing are easily distinguished. Compared to air-breathing, nipping involves much more rapid movement along the surface and the snaps at the surface are faster. Air-breathing often is followed by the release of bubbles.

Data Collection and Analysis

Data were collected from three replications of the experiment; each replication was conducted identically by the same principal observer and contained equal numbers of each of the four pair types. During both pretraining competition and post-training testing phases, feeding encounters were videotaped for 30 s before food was dropped into the tank and for an additional 3 min thereafter. The camera was positioned approximately 1.25 m from the tank. Three of the experimenters (K.L.H., K.S.L.-L. and L.A.B.) later scored the videotapes for the latency to feed, the amount of food consumed, the duration of feeding, and the occurrence of agonistic behaviour in dominant and subordinate fish, namely biting, fleeing and submissive behaviour (see Table 1). In addition, during presentation of the food cue in the final post-training testing phase, we noted the occurrence of behaviour recorded during training (described below). For all dependent measures, interobserver agreement ranged between 88% and 100%, which is typical for dependent measures in our laboratory (see Hollis et al. 1995 for further details).

During each of the 8 days of training, an observer seated approximately 1.25 m from the tanks noted whether or not the fish oriented towards or approached the light stimulus or food delivery device in the 10 s before, as well as during, each light presentation (see Table 1). Another behavioural pattern, namely nipping at the water surface during the food cue (see Table 1), emerged unexpectedly during the first two replications but was not recorded systematically; it was formally included and recorded during the third replication (and, thus, the analysis of this dependent measure contains fewer degrees of freedom). The observer also noted the latency to begin feeding and the amount of food consumed by each fish. A repeated measures ANOVA was used for each dependent variable to assess differences between the two treatment conditions, as well as between dominant and subordinate fish; these ANOVAs included two between-subjects variables, namely treatment condition (LRN versus CTL) and male status (D versus S), and one within-subjects variable (four blocks of 2 days of training).

Several types of statistical tests were used to assess behavioural differences between groups in the pretraining competition and post-training testing phases: we used ANOVAs to determine whether training altered the feeding behaviour (latency to feed, amount of food consumed, and duration of feeding) and agonistic behaviour (biting and fleeing) of dominant and subordinate fish in each of the four treatment combinations. These ANOVAs included two between-subjects variables, namely treatment combination ($D^{LRN} + S^{LRN}$ versus $D^{LRN} + S^{CTL}$ versus $D^{CTL} + S^{LRN}$ versus $D^{CTL} + S^{CTL}$) and male status (D versus S), and one within-subjects variable, namely phases (pretraining competition, day 3 versus post-training testing, day 12). Days 3 and 12 were selected for analysis because, by day 3, the D and S members of each pair were accustomed to competing for food; day 12 was the first opportunity to compete again following training. In other words, only the experimental manipulation intervened between day 3 and day 12. In addition, we used nonparametric Mann-Whitney *U* tests to analyse post-training testing data directly. Finally, we used chi-square tests to determine whether D and S fish within each of the four treatment combinations responded differently to the food cue during the post-training testing. Statistical analyses ($\alpha = 0.05$) were performed using StatView 5.0 (SAS Institute 1998) and SPSS 10.0 (SPSS 2001).

RESULTS

Five pairs of fish were eliminated from the data analysis: in three pairs, one or both of the pair members became ill; in an additional two pairs, the pair members did not form a dominance hierarchy but, instead, continued to defend a common territorial boundary halfway between their respective end compartments. Forty-two subjects remained. These included five $D^{LRN} + S^{LRN}$ pairs, six $D^{LRN} + S^{CTL}$ pairs, six $D^{CTL} + S^{LRN}$ pairs and four $D^{CTL} + S^{CTL}$ pairs. In each of these remaining pairs, without exception, the dominance hierarchy established in the pretraining

competition phase was re-established in the post-training testing phase.

Training

Response to food presentations

The appearance of food elicited a similar response in all fish, regardless of dominant-subordinate status or assignment to treatment condition: fish quickly approached the food and, as Fig. 2 illustrates, consumed most, if not all, of the pellets within the 3-min observation interval. That is, ANOVAs revealed that fish in the associative learning and control treatments did not differ statistically in the latency to begin feeding ($F_{1,38} = 0.004$, $P = 0.9494$) or the number of pellets consumed ($F_{1,38} = 0.008$, $P = 0.9311$). Similarly, dominants did not differ statistically from subordinates either in the latency to begin feeding ($F_{1,38} = 2.475$, $P = 0.1240$) or in the number of pellets consumed ($F_{1,38} = 0.455$, $P = 0.5040$). As expected, however, over the 8 days of training, all fish, regardless of treatment condition or status, began to feed more quickly ($F_{3,114} = 18.061$, $P < 0.0001$) and to consume more food pellets within the 3-min observation interval ($F_{3,114} = 11.378$, $P < 0.0001$). Neuman-Keuls post hoc comparisons revealed that, for both dependent measures, the change in behaviour occurred between block 1 and block 2, as Fig. 2 illustrates for number of pellets consumed (all $q_{t,114}$: $P < 0.05$).

Response to the light stimulus

Both D^{LRN} and S^{LRN} males, but not D^{CTL} and S^{CTL} males, learned to anticipate the arrival of food (Fig. 3): by the end of training, D^{LRN} and S^{LRN} males were reliably orienting to the light stimulus within a few seconds of its appearance (Fig. 3a), approaching it (Fig. 3b), and nipping at the water surface (Fig. 3c) just underneath the light, prior to the appearance of food. ANOVAs for each of these three dependent measures confirmed that dominants did not differ statistically from subordinates in the performance of orienting ($F_{1,38} = 0.079$, $P = 0.7799$), approach

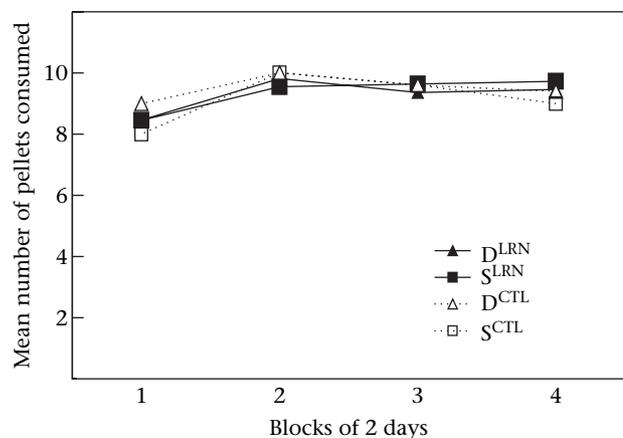


Figure 2. Mean number of pellets consumed by subordinate and dominant males over 8 days of training (i.e. four blocks of 2 days). Treatment categories as given in Fig. 1.

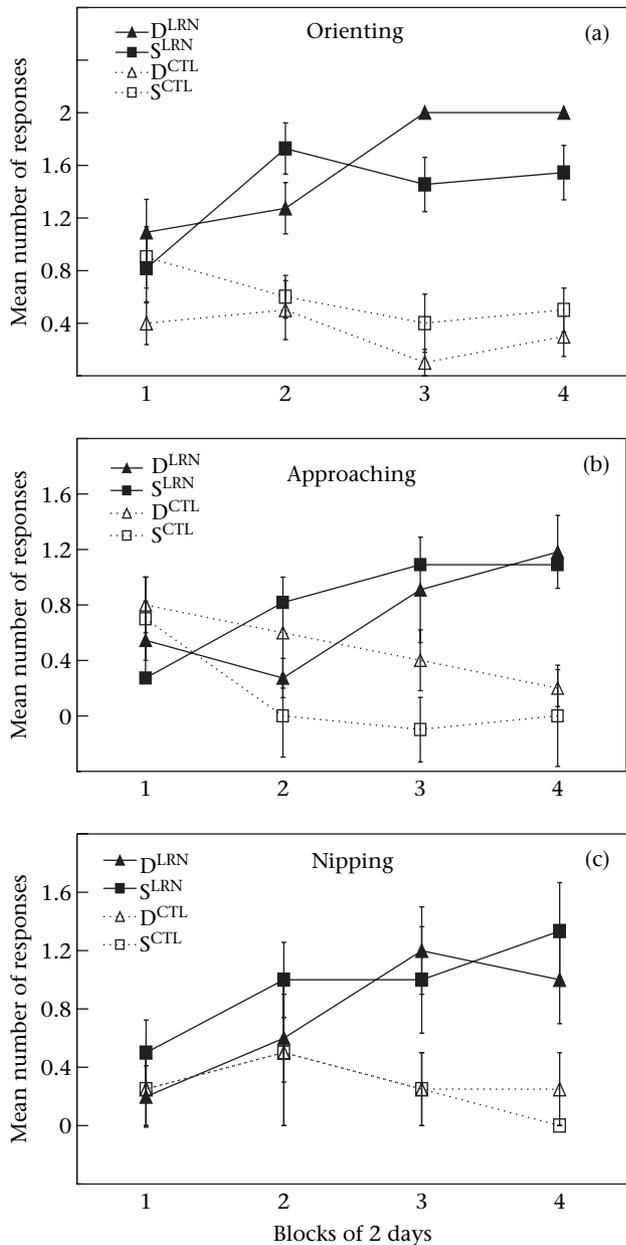


Figure 3. Mean \pm SE number of orienting responses (a), approaching responses (b) and nipping responses (c) during presentation of the light stimulus over 8 days of training (i.e. four blocks of 2 days). Behaviour was scored as either occurring or not occurring during each presentation of the light stimulus; thus, a '2' is the maximum score within each block. Treatment categories as given in Fig. 1.

($F_{1,38} = 0.466$, $P = 0.4991$) and nipping ($F_{1,16} = 0.069$, $P = 0.7964$). However, those same ANOVAs revealed a significant difference between LRN and CTL males in whether or not the light stimulus elicited orienting ($F_{1,38} = 67.221$, $P < 0.0001$), approach ($F_{1,38} = 5.564$, $P = 0.0236$) and nipping at the water surface ($F_{1,16} = 8.947$, $P = 0.0086$) (Fig. 3). A closer examination, using Neuman-Keuls post hoc tests, of the significant interaction between treatment condition and blocks of days in each of the ANOVAs (i.e. orienting: $F_{3,114} = 10.737$, $P < 0.0001$; approach: $F_{3,114} = 5.776$,

$P = 0.0010$; and nipping: $F_{3,48} = 2.591$, $P = 0.0636$) suggests that fish in all of the groups behaved similarly in block 1 of training (all $q_{t,114} \leq 1.98$, NS). In subsequent blocks, however, fish that received the associative learning treatment were increasingly more likely than control fish to display orienting, approaching and nipping behaviour during the 10-s light stimulus; and, by block 4 (if not earlier; see Fig. 3), associatively trained fish (D^{LRN} and S^{LRN}) were orienting, approaching and nipping during the light cue significantly more often than control fish (D^{CTL} and S^{CTL}; $q_{t,114} \geq 4.76$, $P < 0.05$). Finally, orienting, approaching and nipping behaviour rarely, if ever, occurred in the 10 s before the light presentation, suggesting that these responses by D^{LRN} and S^{LRN} males to the light stimulus were due to an association between the light and food.

Post-training Testing

Although S^{LRN} and D^{LRN} males responded identically to the food cue in training, their behaviours diverged abruptly when subordinates were reunited with their dominant partners. On the very first occasion that the light was presented in the post-training testing phase, S^{LRN} males immediately performed a submissive display (Fig. 4), a behavioural pattern that never had emerged in any of the fish during training. Moreover, although 72.7% of S^{LRN} males performed this submissive display in response to the light stimulus, 0% of the S^{CTL} males did so (as did, of course, 0% of both D^{LRN} and D^{CTL} males). A chi-square analysis revealed a significant difference between S^{LRN} and S^{CTL} males in the performance of this submissive display ($\chi^2_3 = 12.38$, $P = 0.0061$). Although this difference between S^{LRN} and S^{CTL} males was characteristic of their behaviour over all 3 days of the post-training testing phase ($\chi^2_3 = 34.29$, $P < 0.001$), the first day of this phase was especially important: the immediate display of submission, a completely novel behavioural response to the food cue, occurred in the absence of any opportunity for subordinates to learn that their previous response to the food cue, namely a combination of

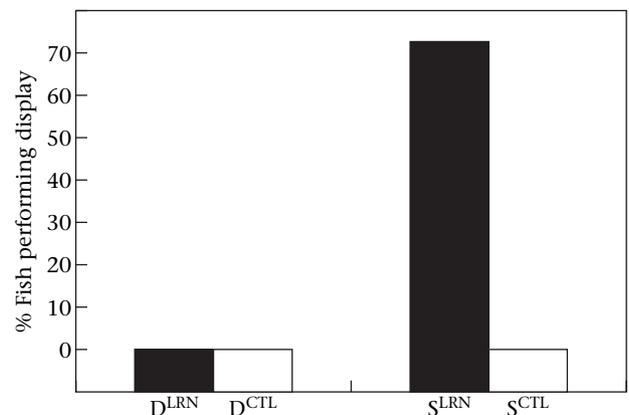


Figure 4. Percentage of males performing a submissive display during presentation of the light stimulus on the first day of the post-training testing phase. Treatment categories as given in Fig. 1.

orienting, approach and nipping, would be punished by dominants. Rather, submission appeared de novo, before food was delivered and before dominants attacked. Moreover, statistical analyses revealed that the performance of orienting, approach and nipping behaviour by S^{LRN} males decreased to such an extent that it was not statistically distinguishable from that of S^{CTL} males at any time in the post-training testing phase ($\chi_3^2 = 5.11$, $P = 0.1639$; $\chi_3^2 = 6.14$, $P = 0.1049$; $\chi_3^2 = 4.40$, $P = 0.2213$, respectively).

Although S^{LRN} males' response to the light cue during the post-training testing phase did not meet the criterion for orienting, approach and nipping (see Table 1), S^{LRN} males did edge closer to the food cue, unlike S^{CTL} males. Thus, they appeared to us to be attempting to use a combination of submission and slow movement to sneak food from their dominant partners. However, only two S^{LRN} males paired with D^{CTL} males were successful at stealing. It is interesting to note, however, that their behaviour was typical of other 'sneaky' male strategies (e.g. Gross 1982): these S^{LRN} males edged towards the location where food was about to appear, their submissive posture successfully appeasing the D^{CTL} male (for which the light did not signal food) and, when food arrived, they quickly grabbed some of it before darting away to safety. Perhaps our experimental conditions, namely a small tank and a small amount of food, together with vigilant dominant animals, especially D^{LRN} males, prevented other S^{LRN} males from being successful. Statistical analyses did not indicate any pre- versus post-training differences in the amount of food that S^{LRN} males obtained, which was little, if any. A statistically significant difference in the latency of S^{LRN} males to reach food was obtained only when the test was one-tailed (Mann-Whitney U test: $U = 9$, $N_1 = N_2 = 3$, $P = 0.05$). Although our predictions are consistent with the use of one-tailed tests, we remain cautious in accepting such a test as reliable.

None the less, for some S^{LRN} males, the submissive response to the food cue was highly advantageous: S^{LRN} males paired with D^{CTL} males (i.e. subordinates belonging to the treatment combination in which only they, and not dominants, had the advantage of being able to predict the appearance of food) sustained significantly less aggression during the 3-min period following food delivery in the post-training testing phase, compared to the pretraining competition phase. These subordinates not only received fewer bites as a result of training (Fig. 5) but also spent less time fleeing dominants (Fig. 6). Supporting these interpretations of the data, ANOVAs revealed significant interactions between treatment combination and phase both for the number of 15-s intervals in which the subordinate was bitten by the dominant ($F_{3,34} = 3.428$, $P = 0.0278$) and the number of 15-s intervals in which the subordinate spent fleeing the dominant ($F_{3,34} = 3.638$, $P = 0.0223$). Moreover, further inspection of these interactions with Neuman-Keuls post hoc comparisons indicated that only S^{LRN} males paired with D^{CTL} males received fewer bites post-training (Fig. 5; $q_{5,34} = 6.25$, $P < 0.05$); likewise, only these same males spent less time fleeing (Fig. 6; $q_{5,34} = 5.31$, $P < 0.05$). However, as Fig. 6 also illustrates, S^{CTL} males paired with D^{CTL} males, neither of which could predict the appearance

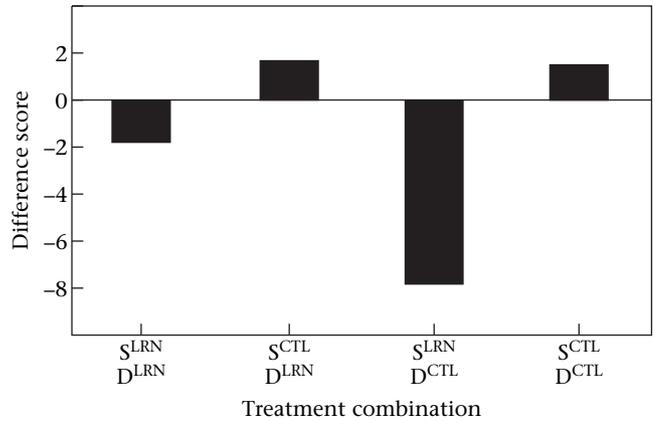


Figure 5. Mean difference between the first day of the post-training testing phase and the last day of the pretraining competition phase in the number of 15-s intervals in which the subordinate male was bitten by its dominant partner during food presentation. The sign of the difference score (+ or -) represents the change (increase or decrease, respectively), if any, resulting from training. Treatment categories as given in Fig. 1.

of food, spent more time fleeing dominants than did other subordinates ($q_{2,34} = 3.98$, $P < 0.05$). Indeed, dominants in these pairs appeared to be in a nearly constant state of vigilance during the post-training testing phase: following a training phase in which the appearance of food never could be predicted, these dominant males pursued their subordinate partners relentlessly, as Fig. 6 suggests. No other comparisons between treatment combinations revealed significant differences (all $q_{r,34} \leq 1.33$, NS).

Finally, although dominant fish fed sooner ($F_{1,34} = 67.164$, $P < 0.0001$), for a longer duration ($F_{1,34} = 46.933$, $P < 0.0001$) and consumed more food than subordinates overall ($F_{1,34} = 457.233$, $P < 0.0001$), exploration of the significant interaction between status,

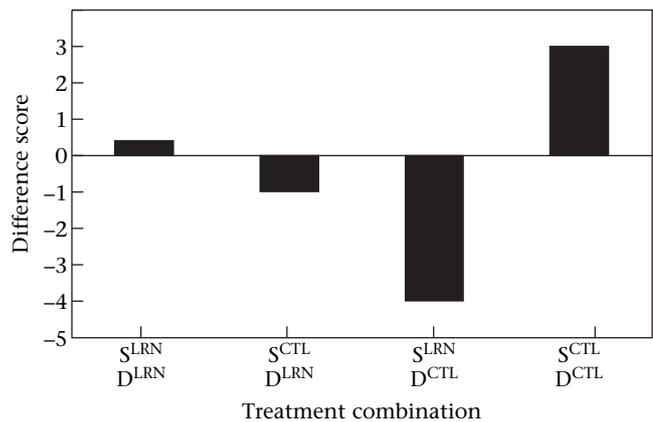


Figure 6. Mean difference between the first day of the post-training testing phase and the last day of the pretraining competition phase in the number of 15-s intervals in which the subordinate male spent fleeing its dominant male partner during food presentation. The sign of the difference score (+ or -) represents the change (increase or decrease, respectively), if any, resulting from training. Treatment categories as given in Fig. 1.

phase and treatment combination for one of the dependent measures, namely duration to feed ($F_{3,34} = 3.028$, $P < 0.0427$), revealed that D^{LRN} males with S^{CTL} partners (i.e. subordinates that could not predict the appearance of food) fed significantly longer in the post-training testing phase (Neuman-Keuls: $q_{7,34} = 5.48$, $P < 0.05$). No other interactions were statistically significant (all $F_{3,34} < 0.815$, $P \geq 0.4948$).

DISCUSSION

Despite identical behaviours during 8 days of private training, dominants and subordinates that learned to predict the appearance of food did not continue to behave alike when competition for food resumed following training. On the very first occasion that the food signal was presented during the post-training testing phase (i.e. the very first time that subordinates were tested with the food cue alongside their dominant partners), subordinates that were able to anticipate food arrival abandoned their previously learned direct approach to the food signal and immediately adopted a different tactic instead, namely a submissive posture. The special significance of this behaviour is that it emerged in the absence of it being shaped by aggression from dominants, and thus, our results reveal unexpected plasticity in the cognitive mechanisms underlying this learning. That is, when the food cue was presented, subordinates that received the learning treatment did not change their behaviour in response to being punished by dominants. Instead, these subordinates were able to combine information about previous learning, namely an 'expectancy' of food, with the probability of future attack and adjust their food-getting strategy accordingly.

That some animals can form expectancies of biologically important events, and, more importantly, that they can use this information to alter a previously learned response is well known. In the classic demonstration of this phenomenon in the laboratory (Tinklepaugh 1928), monkeys showed evidence of surprise, and objected vociferously, when an otherwise adequate food reward, lettuce, was substituted for the scheduled, and preferred, banana reward. In an experiment that more closely resembles our own, rats learned to associate a signal with food and then, following this training, the food reward was paired with poison (Holland & Straub 1979). Poisoning, of course, served to diminish the value of the food but, more importantly, it also greatly decreased rats' previously learned response to the food cue itself, even though the cue and the poison never were paired directly. This technique has been used to show expectancies in several species, notably laboratory pigeons and rats, as well as to determine which sensory features of biologically important events are encoded in those expectancies (Shettleworth 1998). We believe the de novo performance of a submissive display by subordinates receiving the learning treatment, suggests that fish, too, are capable of using expectancies of future events to alter previously learned behaviour. Although scientists' understanding of the cognitive capabilities of fish recently has expanded

enormously (Johnsson & Akerman 1998; Oliveira et al. 1998), our results, namely our finding of an ability to switch tactics based on a previously acquired expectancy, constitute to our knowledge the first demonstration of this phenomenon in fish. In addition, our results show how animals might use learned expectancies to maximize their interaction with a signalled event.

Because of the pervasiveness of associative learning, both in vertebrates and nonvertebrates alike (Hollis 1982, 1997; Macphail 1982, 1993; Papaj & Lewis 1993; Shettleworth 1998; Pear 2001; Wynne 2001), it may be a mechanism that enables the subordinates of many species to determine when and where to steal successfully. Although our particular signal is not to be found in the natural environment, a plethora of potential learned signals typically accompanies the arrival and location of food for many animals (Hollis 1982, 1999; Shettleworth 1998; Pear 2001; Wynne 2001). Prey species inadvertently produce a variety of such cues, whether chemical, auditory or visual, as they move about their environment, and which their predators are capable of using to gain advantage (Beecher 1988). Indeed, our light signal may not be far removed from the kind of visual stimuli to which fish respond in the wild, such as colour flashes and shadows that signal the appearance of insect prey and other food items on or above the water surface.

In our experiment, only males whose partners were not able themselves to predict the appearance of food seemed to benefit from the use of learned food cues. That is, D^{LRN} males paired with S^{CTL} males used food cues to spend more time feeding; S^{LRN} males paired with D^{CTL} males used the same cues to reduce the number of attacks they received as well as the amount of time they spent fleeing dominants. However, all associatively trained dominants approached the food cue rapidly in the post-training testing phase and all associatively trained subordinates adopted, and thus were similarly prepared to use, the cue-elicited submissive tactic. In naturally occurring situations, in which for example food arrival may not be as clumped as it was in our experiment, the benefits of using food cues to steal, or to secure defended resources, might be more inclusive. None the less, our own view of learning is that it is much like other behavioural 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 will 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 by 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 (see, e.g. Hollis et al. 2004). In other words, 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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