

Observational Learning and Predator Inspection in Guppies (*Poecilia reticulata*)

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Abstract

Prior work has demonstrated that, following a predator inspection visit of their own, guppies prefer to associate with individuals who inspected a predator most closely. Based on this work, as well as studies of social learning in the context of mate choice, we predicted that male guppies that observed but did not participate in an inspection trial would subsequently choose to associate with the closer of two inspectors. Our experimental protocol consisted of three treatments: a control test in which an observer watched two fish consecutively, only one of which was exposed to a predator, a sequential test in which an observer watched two fish consecutively, both of which were exposed to the predator, and a social test in which an observer watched two fish inspect simultaneously. We found no preferences by the observer for either of the fish in any of the trials. Our results suggest that direct interaction is a critical component to the development of preferences in male guppies. We discuss our findings in light of game theoretical treatments of cooperation.

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Introduction

Predator inspection behavior entails the breaking away of a small group of individuals from a shoal to investigate potential predators at close range and presumably to determine, among other things, if a predator is satiated or hunting (Pitcher et al. 1986; Magurran & Higham 1988). In guppies (*Poecilia reticulata*), predator inspection is a social phenomenon insofar as two or more guppies often participate in the inspection bout. In addition, guppies that have participated in an inspection bout prefer to associate with more cooperative co-inspectors, that is,

those that approach the predator more closely (Dugatkin & Alfieri 1991). However, inspection is a perilous behavior, as there is a 50% risk of predation associated with close-range predator inspection for the lead fish, and this risk increases as the distance separating them from fellow inspectors increases (Milinski et al. 1997). In fact, this asymmetry in predation risk, combined with the cooperation necessary to successfully inspect and the costs inherent in inspection behavior, means that predator inspection fits all of the inequalities required to be modeled as a prisoner's dilemma (Milinski et al. 1997). Thus, it might benefit an individual to assess the cooperative nature of other individuals in the group prior to accruing the potential costs of inspecting with these individuals.

Dugatkin & Alfieri (1991) demonstrated that guppies prefer co-inspectors that approached the predator more closely in an inspection bout in which they themselves participated. Three guppies were allowed to inspect a predator together, but each fish was separated from the other two by clear partitions that divided the tank into three lanes. Either immediately following the inspection trial or 4 h later, the guppy from the middle lane was given a preference test between the other two inspectors. In both cases, the middle fish preferred to associate with the inspector that had approached the predator more closely.

These experiments indicate that guppies keep track of the behavior of their co-inspectors and that they subsequently draw on this information to discriminate between cooperative and non-cooperative co-inspectors. Dugatkin & Alfieri (1991), however, did not examine whether individuals demonstrate a preference for one inspector over another after watching an interaction in which they did not actually participate. Observational learning has previously been demonstrated in guppies derived from natural populations in the context of female mate choice. In these cases, females preferred to mate with males who apparently had been more successful at attracting females, i.e. mate copying (Dugatkin 1992b, 1996a,b, 2000; but see Brooks 1996; Lafleur et al. 1997 for experimental evidence that mate copying does not occur in pet-store and feral populations of guppies).

The notion that animals gather information about their social environs by watching interactions between others has most recently been cast in terms of communication networks and eavesdropping (McGregor & Peake 2000). Eavesdropping can be considered a special case of observational learning that entails gathering information by watching *interactions* between conspecifics. Much of the recent empirical work in this area has focused on whether fishes eavesdrop on aggressive contests, a context in which the participants likely accrue more costs than the observer (e.g. Oliveira et al. 1998; Earley & Dugatkin 2002).

Generally speaking, the more costly a particular behavior is to those performing it, the greater the benefits accrued via observation (as opposed to direct experience). Predator inspection, which can have direct negative effects on the inspectors' survival (Dugatkin 1992a, 1997; Milinski et al. 1997; but see Godin & Davis 1995a,b; Milinski & Bolthauser 1995), would seem to fit these criteria. Individuals who can assess which group mates are more likely to cooperate in the future without risking the costs associated with predator inspection should have an advantage over those who learn only through interaction. Hence, predator

inspection behavior may be ideal for investigating whether individuals can learn about the behavior of conspecifics observationally.

We examined whether guppies prefer individuals that approached a predator more closely after observing, but not participating in, a predator inspection session. Our goal was to determine whether guppies learn about the cooperative tendencies of other inspectors through observation alone, rather than through personal experience. Our experimental design differed from Dugatkin & Alfieri (1991) by the inclusion of initial preference tests (see below) to control for any pre-existing preferences in the guppies, and by visually isolating inspectors via a one-way mirror to separate interaction and observation as the causes of preference formation. For our study, one observer guppy was allowed to watch two other individuals in three different conditions. In the first condition, one of the observed individuals inspected while the other did not, to control for the effect of inspection behavior on the observer's preference. In the second and third conditions, the observer guppy watched two conspecifics inspect either sequentially or simultaneously, respectively. We predicted that observer guppies would prefer inspectors over non-inspectors, and prefer inspectors that approached the predator more closely.

Methods

General Methodology

All experimental guppies were male descendants of wild stock caught in 1997 from a high-predation region of the Guanapo River, Trinidad, West Indies. A total of 90 observers (30 per treatment) and 180 inspectors (30 pairs per treatment), were used. Prior to testing, guppies were housed in mixed-sex groups of approximately 350 in two 151 l holding tanks lined with gravel. The subjects were all kept on a 12 h Light:12 h Dark photoperiod and the water temperature was maintained at 23°C. Three guppies were removed from the holding tanks and their standard length was measured (mm). The three guppies in each trial (one observer and two inspectors) were matched for standard length to within 1 mm (i.e. <5% of their total body length). All guppies used were naïve to predators, however predator-naïve guppies in previous experiments have demonstrated inspection behavior (Dugatkin & Alfieri 1991), indicating that previous experience with predators is not a prerequisite for normal inspection behavior.

Between preference testing and inspection sessions, guppies were isolated in breeders placed in 76 l aquariums to minimize preferences based on interactions. The breeders were small, clear holding tanks which afforded physical, but not visual, separation between individuals; visual contact was maintained to reduce stress on the fish. After testing, inspectors and observers were housed in separate 76 l aquariums lined with gravel. Because so many male guppies were required (270), approximately 10% of the previous inspectors were re-used, but only as inspectors (never observers), never <3 wk after their first test, and never for a

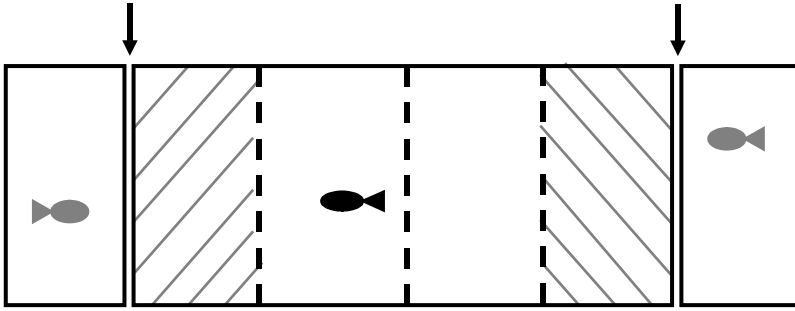


Fig. 1. The apparatus used for initial preference testing. A preference was demonstrated when the observer fish (black) spent more time in the preference area (gray hatched lines) adjacent to one or the other of the side fish. The opaque partitions, which were removed when preference tests commenced, are depicted with arrows

third time. Observers were used in only a single trial over the course of the experiment and were never re-used as inspectors.

A Texas cichlid (*Cichlasoma cyanoguttatum*), 12.9 cm in standard length, was purchased from a pet store and used as the predator in all inspection trials. *C. cyanoguttatum* is similar in general body shape and form to *Crenicichla alta*, a natural predator of guppies found in the Northern Mountain ranges of Trinidad and Tobago. In addition, the attack behavior displayed by *C. cyanoguttatum* (e.g. lunges) is similar to that of *C. alta*, and the guppies clearly responded to such attacks as if they were predatory in nature. Our *C. cyanoguttatum* was fed a diet consisting exclusively of guppies and exhibited lunging and attack behavior in the experimental setup.

Before observing two conspecifics inspect a predator, the observer's preference for these two fish was determined in an apparatus similar to that of Dugatkin (1992b) (Fig. 1). This initial preference test allowed us to examine the possibility that observers were choosing to associate with others based on intrinsic preferences rather than what they observed during the inspection bout. The observer was placed in a 9.5 l aquarium and the two remaining fish (inspectors in the subsequent inspection trial) were each randomly placed in one of the smaller compartments on each end. After 15 min of acclimatization time, removable opaque partitions between the observer and each side fish were lifted to allow visual contact for 5 min. The quarter of the observer's tank closest to each side fish was designated as a 'preference area'. The total number of seconds the observer spent in each preference area was recorded on two stopwatches from behind a black curtain. Preference was designated if the observer: (1) spent more than half of the preference period in the preference areas and (2) spent > 60% of this time in one of the preference areas. Immediately following the preference test, the guppies were transferred to the breeders for 48 h of isolation to minimize the influence of their prior choice on subsequent choices in the post-inspection preference test.

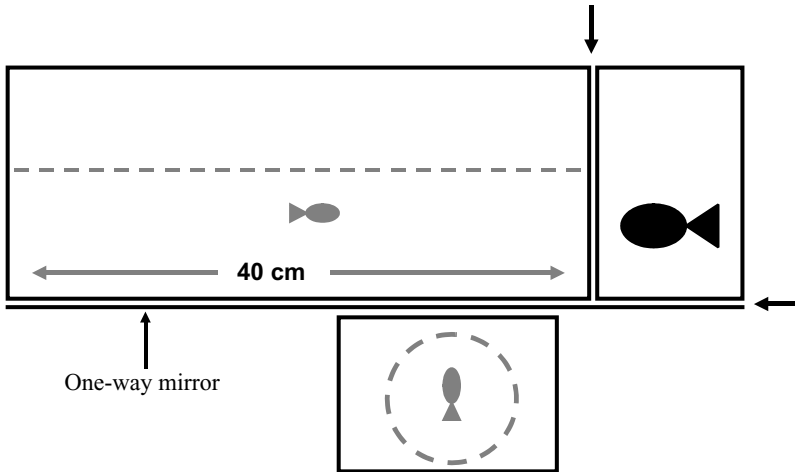


Fig. 2: The apparatus used for inspection trials. An observer fish, sequestered in a clear cylinder (dotted circle), watched one or two inspector fish (grey fish in large tank) engaged in a predator inspection (predator is the large, black fish). The dotted line represents the clear glass partition in place to keep the inspectors physically close to the observer's side of the inspection tank. A one-way mirror separated the observer fish from the inspectors so that preferences were not formed based on interactions between these individuals. The positions of the opaque partitions are depicted with arrows. The panel separating the observer from the inspector(s) and predator was actually two panels that could be removed separately such that the observer could observe the inspectors but not the predator during the control treatment.

After the isolation period, inspection trials were conducted in an apparatus similar to that of Dugatkin & Alfieri (1991) (Fig. 2). The guppies that occupied the side tanks during the initial preference test were allowed to inspect in the longitudinal half of a 76 l tank; the rest of the aquarium was blocked by a clear glass partition to keep the inspectors closer to the observer. The predator occupied a separate tank adjacent to the inspection apparatus. Initially, removable opaque partitions blocked both the inspectors' and the observer's view of the predator as well as the observer's view of the inspector(s). Thus, neither the observers nor the inspectors could see the predator nor could the observer and inspectors see each other prior to the inspection trial.

Each trial began with a 15 min acclimatization period during which both opaque partitions were in place. Following acclimatization, the opaque partitions were lifted and the 2 min inspection trial began. To minimize the observer's inspection behavior, it was sequestered in a clear tube within a 9.5 l aquarium adjacent to the inspection tank. A one-way mirror between the observer's tank and the other tanks allowed the observer to view the inspector(s) and the predator, but not the reverse. The one-way mirror was tinted so that the inspectors could not see their own mirror images and 60 W incandescent lamps were hung at a 45° angle above the aquariums to facilitate viewing. The observers

responded to both inspectors and predators, indicating that the one-way mirror did not hinder their view. This design prevented observers and inspectors from interacting and ensured that the predator would not focus on the observer instead of the inspector(s).

All inspection trials were videotaped from a camera suspended above the inspection tank. The position of the inspector relative to the predator was recorded to the nearest centimeter (from 0 to 40, with 40 being closest possible to the predator) every 5 s for the duration of the trial. For each inspector, a mean distance from the predator was calculated to determine which fish maintained a closer average position to the predator. These data were transcribed from the videotape and calculated using marks on the rim of the aquarium which were invisible to the fish themselves.

Immediately following the inspection session, all three fish were netted and placed back in the original preference test aquarium. After a 5 min acclimatization period, the observer was given a second preference test, with the position of the inspectors switched compared with the initial preference test to determine if the observer's preference had changed. Thirty series consisting of an initial preference test, an inspection trial, and a post-inspection preference test were conducted for each of the three treatments (see below).

Experimental Treatments

Three different experimental treatments were utilized to more fully examine the effects of order of observation and inspection prowess on the observer's preference. Each treatment consisted of 30 trials, with each trial including one observer and two inspectors, for a total of 30 observers and 60 inspectors. In the control treatment, we examined the effect of sequential viewing of an inspector and a non-inspector. Here, each observer watched two fish sequentially, one for which a predator was visible (inspector) and one for which no predator was visible (non-inspector). For the trials in which the observer viewed an inspector, the opaque partitions were lifted at the commencement of the inspection trial. However, when the observer viewed a non-inspector, the opaque partition between the observer and non-inspector was lifted at the commencement of the inspection trial, but the partitions between the predator and both the observer and non-inspector were not. In this case, neither the observer nor the non-inspector could see the predator but the observer could view the non-inspector. The order of trials was alternated such that, in half of the trials, the observer viewed the inspector first, and in the other half, the observer viewed the non-inspector first. This treatment allowed us to control for the possibility that observers were choosing based on some element of the inspector's movement or some other inherent preference, regardless of whether a predator was present. Trials were separated by 15 min to allow both the inspector and non-inspector to acclimate to the testing apparatus.

In the sequential treatment, the observer watched two inspectors sequentially; again trials were separated by 15 min to allow for the second inspector's

acclimatization period. Each of the inspectors and the observer had full view of the predator during their inspection trials. In the social treatment, the observer watched two inspectors simultaneously; the inspectors could also interact with one another. These inspectors were placed in the inspection aquarium simultaneously and thus had 15 min to acclimatize to each other as well as to the apparatus. Once again, the observer could not see these individuals until the inspection trial commenced.

Statistical Analyses

Chi-square analyses were conducted on all preference data in this study and tested the observed proportions against a null model assuming random preferences. Dugatkin & Alfieri (1991) demonstrated that 80% of the guppies used in their study preferred inspectors that were on average closer to the predator, a difference of 0.3 probability units from the null model of random preferences (50:50). Cohen (1988) describes methods for evaluating power in tests of proportions of this kind, wherein the effect size is equivalent to some biologically relevant difference between the expected and null proportions. Instead of choosing arbitrarily, we used an effect size of 0.3, corresponding to the preference results of Dugatkin & Alfieri (1991), a technique supported by Cohen (1988). Two-tailed tests of proportions yielded a priori power values that ranged from 0.89 to 0.99 depending on the sample size used in the chi-square test (e.g. $n = 29$, $1-\beta = 0.95$; $n = 61$, $1-\beta = 0.99$); these calculations were based on equations in Zar (1996). According to Cohen (1988), 0.3 qualifies as a large effect size in these types of analyses. Despite choosing our initial effect size based on existing data for preference formation in guppies, we also conducted more stringent a priori power analyses with effect sizes of 0.15 ($0.31 < 1-\beta < 0.72$) and 0.25 ($0.73 < 1-\beta < 0.99$) to accommodate the conventions described in Cohen (1988). Overall, these a priori power calculations indicate that our sample sizes were sufficient to detect whether the observer guppies form preferences based on watching predator inspection trials.

Results

Not all observers demonstrated a preference for one of the inspectors. This lack of a preference occurred when the observers spent less than 50% of the test in the preference areas or divided their time between preference areas equally. As a result, not all statistics are based on a sample size of 30.

In both the sequential and the social treatments, the observer did not show a preference for the inspector with the closer mean position to the predator (sequential: 13 of 29 trials, $\chi_1^2 = 0.310$, $p = 0.58$; social: 13 of 25 trials, $\chi_1^2 = 0.040$, $p = 0.84$). These results were not due to an order of presentation effect because, in the sequential treatment, the observer did not show a preference for either the inspector seen first or second (preferred inspector seen first in 14 of 29 trials, $\chi_1^2 = 0.034$, $p = 0.43$).

In the control treatment, the observer preferred the inspector who saw the predator in only 11 of 26 trials ($\chi^2_1 = 0.615$, $p = 0.43$), indicating that there was no effect of predator presence. Furthermore, the observer did not show a preference for either the inspector seen first or second in the control treatment (preferred fish seen first in 15 of 26 trials, $\chi^2_1 = 0.615$, $p = 0.43$).

There was no relationship between the observer's preferences in the initial and post-inspection preference tests. In all three treatments, observers who showed a preference in both the initial and post-inspection preference tests changed their preference as often as they maintained it ($n = 61$, $\chi^2_1 = 0.016$, $p = 0.90$). In addition, observers that changed their preference were not more likely to switch to the better inspector ($n = 31$, $\chi^2_1 = 0.806$, $p = 0.37$) and observers that chose the better inspector in the initial preference test were not more likely to maintain their preferences ($n = 30$, $\chi^2_1 = 0.133$, $p = 0.72$). These results indicate that observers were not forming preferences based on inherent characteristics of the inspectors, nor were they able to predict cooperative tendencies in the predator inspection behavior during the initial preference test.

Finally, in the social inspection test, there were five instances in which the observer did not show a preference for either inspector. All five of these instances occurred in the 13 trials in which the average distance between the inspectors was small (< 4 cm). In contrast, the observer always demonstrated a preference in the 17 instances in which the inspectors averaged more than 4 cm apart ($n = 30$ (17), $\chi^2_1 = 7.850$, $p < 0.01$), but not in any specific direction, indicating that the observers were paying attention to some aspect of the inspector's behavior as they were more likely to show no preference when inspectors stayed close together.

Discussion

Unlike earlier work in which guppies that participated in an inspection trial preferred to associate with others that inspected most closely (Dugatkin & Alfieri 1991), we found that observer guppies displayed no inspection-based preferences. Male observer guppies did not prefer to associate with the inspecting fish in the control treatment, nor did they prefer the closer of the two inspectors in the sequential or social treatments. Furthermore, the observers did not show a preference for either the individual they had seen first or last in the two tests in which they saw the inspectors sequentially (control and sequential treatments). In the social treatment, however, observers often failed to exhibit a preference when the average distance between inspectors was small (< 4 cm), suggesting that subjects in our trials were gathering information about the relative cooperative tendencies of putative inspectors (but not necessarily using this information to demonstrate a preference). If the guppies were gleaned no information by observing an inspection sortie, 'no preference' data should have been evenly distributed throughout trials.

Given earlier work on preference and inspection, as well as studies demonstrating that guppies are capable of using information they gather through observation to form preferences in other situations (e.g. mate choice: Dugatkin 1992a,b, 1996a, 2000) our results are somewhat surprising. Why observers do not display preferences is difficult to say, but we offer a few possibilities here.

It is possible that guppies do not pay attention to inspectors because they are observing these interactions out of context, i.e. they are not directly involved in the inspection bout. In the original study in which guppies did form preferences for better inspectors (Dugatkin & Alfieri 1991), subjects interacted with the other inspectors during the inspection bout. Being involved in the inspection bout may allow the guppies to reliably assess how cooperative other individuals would be with respect to themselves, making it reasonable to show a preference. In our study, an observer could only learn how cooperative another inspector was with respect to some third individual. This type of information may not be relevant to the observer because it does not provide a gauge of how either inspector would cooperate with him. As a consequence, simply watching inspection bouts, without being involved in the interaction, may not be sufficient to elicit preference formation.

The lack of preference following observation alone may be particularly relevant in light of the proposed game theory strategies that the guppies may be following. Several fish species, including guppies, follow a tit-for-tat strategy when inspecting predators (Milinski 1987; Dugatkin 1988; Dugatkin 1991; Dugatkin & Alfieri 1991; but see Stephens et al. 1997). Presumably the cooperative solution to tit-for-tat type interactions develops only in situations where individuals interact repeatedly, recognize each other, and remember previous outcomes (Axelrod & Hamilton 1981). Guppies meet these requirements for predator inspections in which they are a participant (Dugatkin 1988; Dugatkin 1991), and apparently they learn to recognize and prefer to associate with good inspectors (Dugatkin & Alfieri 1991). In our study, however, observers could not interact with the inspectors and did not form preferences for individuals who were better inspectors. This implies that observation alone does not provide accurate information about another individual's cooperative tendencies relative to oneself. These data indirectly support the notion that cooperation via tit-for-tat is most likely to evolve when individuals are allowed to interact directly with one another.

Finally, it may be that in situations where the interactions of the inspectors are of relatively less value, the observer shifts its attention more to the predator. In any predator inspection situation, there are conflicting interests between paying attention to the predator and paying attention to the interactions of fellow inspectors. In our study, the observer was separated from the other inspectors and could not interact with them, so information about the inspectors' behavior may have been less relevant than information about the predator. Thus, after an initial assessment of the situation, the observer guppies may have 'chosen' to focus on the predator rather than the

inspectors. This may also explain the results of Dugatkin & Wilson (2000), who found that, in a group of six inspectors, the guppies did not form preferences for better inspectors. Perhaps here the guppies were unable to assimilate all of the information about their five co-inspectors plus the predator and thus focused most closely on the predator which poses a more daunting threat to fitness.

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