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Time–Place Learning Based on Food but not on Predation Risk in a Fish, the Inanga (*Galaxias maculatus*)

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Abstract

Time–place learning, or the ability to learn to be in different places at different times of day, is already known to occur in response to daily spatio-temporal patterns of food availability. However, the ability to learn daily patterns of predation risk and move between areas at the right time of day in order to avoid predation has never been tested. This study asked whether inangas, *Galaxias maculatus*, are capable of time–place learning based on food availability only, predation risk only, or the antagonistic combination of food availability and predation risk. Shoals of five inangas were kept in aquaria partially divided into a right and left section. Every day they were exposed to a stimulus on one side in the morning and on the other side in the afternoon. Depending on the experiment, the stimulus could be two deliveries of food, two simulated heron strikes, or both of the above within the same hour. After 14 d the stimuli were not given and the position of the fish was noted in both the morning and the afternoon. The majority of the fish learned to switch sides at the correct daily time in order to get food, but they remained on the same side at both daily times in response to either predation risk alone or the combination of predation risk and food. It seems that the potential for time–place learning based on predation risk is less than that based on food, and that predation risk can even curtail the expression of time–place learning based on food. Fish may resort to other tactics, such as shoaling and reduced movement, in response to predation risk. Daily habitat shifts could still be present in nature and rooted in the avoidance of predation, but instead of being the direct result of learning they would be mostly innate.

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Introduction

Time–place learning is the ability to associate different places with different times of day (here and throughout the paper, day means the interval between

sunrise and sunset; day–night shifts in habitat are larger-scale phenomena that will not be considered until the discussion). For example, an animal that is trained to be in place A in the morning and then in place B at noon can be said to have learned a time–place association. Such an ability has already been demonstrated for a number of species in various laboratory studies (honey bees: Wahl (1932), Gould (1987), Moore et al. (1989); ants: Schatz et al. (1994); fish: Reebbs (1996); birds: Daan (1981), Biebach et al. (1989, 1991), Krebs & Biebach (1989), Wenger et al. (1991), Falk et al. (1992), Saksida & Wilkie (1994); rats: Boulos & Logothetis (1990), Mistlberger (1994), Carr & Wilkie (1997)). It has also been inferred from a few cases of daily spatio-temporal routines observed in the wild (Daan 1981; Daan & Koene 1981; Rijnsdorp et al. 1981).

In all studies to date, animals have been trained to associate time and place with food as a reward. This is a reasonable approach, given that food supply in nature can vary spatio-temporally throughout the day but predictably from day to day, the best example being the pollen and nectar sought by bees (Saunders 1982). But what is true for prey items could also apply to predators. The activity of some predators can also follow predictable diel patterns (Rijnsdorp et al. 1981). Moreover, multiple predators with different activity cycles and habitat preference could prey on the same species. For the prey, this could translate into a daily spatio-temporal pattern of predation risk. It would be advantageous for the prey to be able to learn such predation patterns and to avoid some places at specific daily times. This, however, has never been tested; up to now there have been no reports of time–place learning based on the avoidance of a stimulus rather than on the search for food.

This study provided such a test with the inanga, *Galaxias maculatus*, a common freshwater fish of New Zealand. Like the only other fish species for which time–place learning has been demonstrated (the golden shiner, *Notemigonus crysoleucas*; Reebbs 1996), the inanga is a shoaling species that can be found in a variety of habitats with open, gently flowing or still waters (McDowall 1989). It is abundant in estuaries, coastal rivers, streams and lakes. It is prey for a variety of piscine and avian predators, including the whitefaced heron (*Ardea novaehollandiae*; Carroll 1967) which was used as a predator in this study. However, little is known of the inanga's daily patterns of activity in the wild, and before this study nothing was known of its potential for time–place learning. In this study, time–place learning in inangas was investigated based on: 1. food only; 2. predation risk only; and 3. concurrent food and predation risk.

Materials and Methods

Inangas were captured as young-of-the-year in Waitati Creek, north of Dunedin, New Zealand. They were kept as a single group in the laboratory, mostly under a natural photoperiod, for at least 1 yr before being used in the present experiments. They were fed commercial fish food pellets at haphazard times each day. At the time of the experiments they were 7.4–9.8 cm in total length.

The experiments were conducted from Nov. 1997 to Jan. 1998. I decided to

test the inangas in groups because they are a shoaling species and because living in a group creates competition for food, providing an incentive for efficient foraging. Shoals of five inangas, matched for size, were placed in large tanks (125 × 40 × 45 cm), under a constant 12:12 h light:dark photoperiod. This photoperiod was provided by fluorescent tubes which were abruptly turned on and off. The water temperature was set at $16 \pm 1^\circ\text{C}$. The bottom of each tank was covered with coarse gravel. The fish were fed food pellets each day at haphazard times and places within their tanks. They were given 2 wk to habituate to these conditions before the beginning of an experiment. Before the second of these 2 wk, a plastic screen was installed in front of each tank so that I could enter and move within the room without being seen by the fish. Flap-covered slits in the screen allowed the fish to be observed when needed.

On day 0 of an experiment, an opaque partition was placed in the middle of each tank, dividing the tanks into a left and right side. A 5 cm space was left open between the far edge of the partition and the back wall to allow passage from one side to the other. During each of the following 14 d, the stimuli (see below) were presented four times daily. The first two were at haphazard times during the second hour of the day, always on the same side for a given tank (left or right, originally determined at random). This side was called the ‘morning side’. The other two stimuli were given at haphazard times during the seventh hour of the day, always on the opposite side (the ‘afternoon side’).

In the food-only experiment, the stimulus was ≈ 15 mg of food (five to 10 granular pellets) being dropped by hand through a tube permanently fixed in the front corner at the end of the tank. Within a few seconds the pellets sank to the bottom where they remained available to the fish. Because food was delivered through a tube, fish could not see my hand. This experiment tested the ability of inangas to associate time and place based on food rewards. The prediction was that inangas would learn to be on the morning side in the morning, and on the afternoon side in the afternoon, even on test days when food was not given. A weaker prediction was that use of the morning side would at least decrease in the afternoon. The protocol and predictions used here were similar to those of a previous study in which golden shiners successfully displayed time–place learning (Reebs 1996).

In the predation-only experiment, the stimulus was the wooden model of a whitefaced heron’s bill and head being dropped quickly by hand, from over the plastic screen, into the water and then withdrawn. Simulated heron strikes have often been used in studies of predation risk, including some that specifically addressed avoidance learning (e.g. Huntingford & Wright 1992). When exposed to the simulated strikes, inangas in this study swam frantically for several seconds at first, and then froze along the walls. This reaction was observed even after 14 d of exposure. The angle of the strike and the exact place of delivery within the half-tank were varied from day to day in order to prevent habituation. My hand was visible during the strike but did not break the surface of the water. An important modification to the general protocol here was that heron strikes were not given if no fish happened to be present on the scheduled delivery side. Therefore, when on

the correct side (to avoid predation), the fish could not hear and potentially be scared by a strike on the other side, as such strikes were not given. Food (≈ 60 mg) was delivered only once daily, during the tenth hour of the day, over the passage between the two sides. This experiment tested the ability of inangas to learn a time–place association based on the avoidance of predation. The prediction was that inangas would learn to be on the afternoon side in the morning, and on the morning side in the afternoon, even on test days when no strikes were given. A weaker prediction was that use of the morning side would at least increase in the afternoon.

In the food-and-predation experiment, two food deliveries and two heron strikes were given on the same side every morning, and again on the other side every afternoon. The order of presentation of these four stimuli was randomized within each hour. If fish were not present on the delivery side, food was nonetheless given but heron strikes were not. As food availability and predation risk predicted opposite patterns of spatio-temporal activity (for example, in the morning a fish should be on the morning side if it wants to get food before its shoalmates, but on the afternoon side if it wants to avoid predation), this experiment tested whether predation risk could affect the development of time–place learning based on food, or conversely whether food could affect the development of time–place learning based on predation risk.

To assess learning, a partial test was conducted on day 10, and a final test on day 15. On day 10, the stimuli were given only at the end, rather than during, the second and seventh hours of the day. During these hours (before the stimuli), the number of fish present on each side was noted at 6 min intervals, for a total of nine instantaneous observations per hour. This was a partial test, first because of the short time available for learning (9 d), and second because the stimuli were still given (if only at the end of the hour) and therefore a correct selection of the afternoon side could be attained through the application of a ‘win–shift’ rule of thumb (in the case of food) or a ‘lose–stay’ rule of thumb (in the case of predation) rather than an association between time and place. On day 15, the time that had been available for learning was comparable with other studies (e.g. Huntingford & Wright 1992; Reebbs 1996) and although the position of the fish was noted as before, the stimuli were not given at any time, so that positional shifts could only be based on an internal representation of time and not on direct responses to the occurrence of a stimulus (in its purest form, time–place learning is viewed as an expression of internal clock mechanisms; Gallistel 1990; Biebach et al. 1991; Wenger et al. 1991; Reebbs 1996; but see Carr & Wilkie 1997).

Sample size was seven shoals in each experiment. For each shoal the number of fish present on the morning side was averaged over the nine instantaneous observations of each hour, and expressed as a percentage of the maximum possible (five). Results are given for each shoal individually.

Results

Figure 1 shows the percentage of fish present on the morning side at both daily times, for all three experiments, and for both the partial and the final test. Only the results of the final test are considered further here.

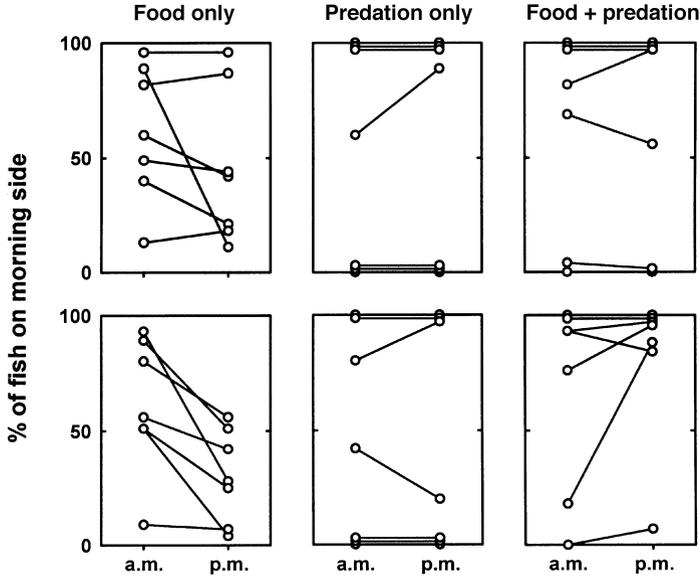


Fig. 1: Mean number of inangas ($n = 9$ observations), expressed as a percentage of the total possible in each of the seven shoals, present on the 'morning side' of an aquarium during the second hour of the day (a.m.) and the seventh hour of the day (p.m.). The morning side is defined as the aquarium half where a stimulus (either food, predation, or both) was delivered every day during the second hour; the same stimulus was given on the other side during the seventh hour. Upper panels: partial test after 9 d of exposure to the stimuli; lower panels: final test after 14 d of exposure. Some data points that would have been superposed at 0% and 100% have been staggered, with some overlap remaining, to render them visible

In the food-only experiment (Fig. 1, bottom left panel), the expectation called for data points at 100% in the morning and 0% in the afternoon. None of the seven groups showed this exact pattern, but all groups showed a decrease in time spent on the morning side from morning to afternoon ($p = 0.008$ for an expected probability of 0.5 on a binomial test). If we accept a criterion of > 50% of fish present on one side as a preference for the side in question, then four shoals out of seven were on the correct side at both daily times ($p = 0.07$ for an expected probability of 0.25 on a binomial test). For clarity, the standard deviations associated with each data point are not shown on Fig. 1, but they ranged from 6.6 to 28.0 (average = 15.5), nonzero values that indicate that the fish were mobile and often switched sides from one instantaneous observation to the next within each hour of observation.

In the predation-only experiment (Fig. 1, bottom centre panel), the expectation called for data points at 0% in the morning and 100% in the afternoon. None of the shoals showed anything close to this pattern. Instead, all seven shoals showed a day-long preference for one side of the tank (either the morning side or the afternoon side, apparently at random). For five of these groups the preference was

absolute (no movement from side to side during either of the two daily observation periods, standard deviation around each data point = 0). For the two shoals that moved from side to side within the hour, the standard deviations ranged from 0 to 26.4 (average = 10.5). Only one of these groups showed the predicted increase in use of the morning side during the afternoon.

In the food-and-predation experiment (Fig. 1, bottom right panel), six of the seven shoals showed a day-long preference for the same side, but in only two cases was this preference as absolute as in the predation-only experiment. The other four groups showed a little more movement from side to side (range of standard deviations = 0–21.8, average = 9.2). For its part, the seventh group was in the correct place at the correct time to avoid predation, not to get food.

Discussion

Inangas seemed capable of time–place learning based on food (four shoals out of seven), although their spatio-temporal distribution was far from absolute, as much sampling took place from side to side within the same hourly period, probably helped by the small cost of travel between areas. Some indication of day-long preferences for the same side was found (the remaining three shoals out of seven), but even in these groups, use of the preferred side decreased at the appropriate time. In contrast, inangas did not show any sign of time–place learning based on predation risk; instead, predation risk induced the fish to stay on the same side throughout the day. When both food and predation risk were present in such a way as to predict opposite effects, the spatio-temporal distribution of the fish was intermediate between the food-only and the predation-only situations, but resembled mostly the predation-only results. This indicates that time–place learning based on food can be prevented by a concurrent pattern of predation risk.

Lack of evidence for time–place learning based on predation risk is a negative result, and negative results are often open to ambivalent interpretations. There is always the possibility that some particular condition of the laboratory test prevented the expression of a behaviour that could nevertheless be present in nature. So, before we can even consider the possible conclusion that inangas cannot learn to use within-day habitat shifts to avoid predators, we need to address a few caveats.

First, in its purest form, time–place learning is based on a circadian clock (to differentiate between times of day) and nothing is known about endogenous clock mechanisms in inangas. Perhaps inangas do not have the internal time sense necessary for hourly time discrimination and can only use shift strategies based on a direct response to the stimuli instead. This seems unlikely, however, as good evidence was obtained for time–place learning based on food, even when the food stimulus was withheld on the final test day.

Second, lack of sophisticated predator avoidance is sometimes rooted in the absence of predatory pressure in populations that have not historically been in contact with predators (Magurran 1990; Huntingford & Wright 1992). For example, oriented escape responses based on the sun-compass (a clock-based ability)

are known to be weaker in fish populations without predators (Goodyear & Ferguson 1969; Goodyear 1973). Did the inangas in this study come from a predator-free population? The answer is no. Predatory birds have been observed near the site of capture, and the fish seemed to react strongly to the simulated heron strikes, and they adopted a consistent tactic of reduced daily movement when so threatened.

Third, fish sometimes disregard predation risk when they are hungry or energetically stressed (Milinski 1993). Were inangas in the predation-only experiment food-deprived? The answer is no. The amount of food provided was in excess of the fish's daily need, and the fish were noticeably fatter by the end of the experiment. Moreover, we would expect hunger to promote efficient foraging in the face of predation risk, and yet in the food-and-predation experiment the outcome was closer to the predation-only than to the food-only results.

Fourth, if time–place learning exists in the wild, it is likely to involve relatively long-range movements from one habitat type to the next (e.g. shallows vs. open waters, weeds vs. rocks). The tanks used in the present study may not have allowed for the expression of such a behaviour, being relatively small (certainly no bigger than the field of coverage of a single predator) and featuring two sides that were physically similar. However, it would still be difficult to explain why the same set-up allowed the expression of time–place learning based on food but not that based on predator avoidance. Perhaps food availability in nature can vary on a finer spatial scale than predator activity, and, therefore, fish have been selected for more acute discriminatory abilities in their foraging behaviour, resulting in the expression of time–place learning for food even in the restricted and uniform environment of an aquarium. Whether this is true or not, further experiments with more natural set-ups, such as outdoor ponds, would be desirable to provide a better test of time–place learning based on predator avoidance.

Fifth, experimental protocols that involve repeated exposure to a fake predator must always contend with the possibility that experimental subjects can habituate to the threat, especially given the apparent lack of success, over the days, of the predator in question. Care was taken to minimize this possibility (see Materials and Methods), but the possibility cannot be discounted entirely. This points once again to the need for further experiments, this time with more menacing or actual stimuli, such as alarm substance or mild electric shocks.

Notwithstanding the above caveats, the negative results of the present study compel us to at least consider the possibility that inangas simply cannot, or will not, use time–place learning as a way to avoid predation. They may rely on other tactics instead, such as the proven advantages of shoaling (Pitcher & Parrish 1993) and reduced activity (Smith 1997). It is also possible that travel between areas would present its own danger, inasmuch as greater exposure might be involved. The tendency of inangas to remain as a group on the same side of their tank in the present predation experiments is consistent with the use of such alternative tactics. One must also consider the possibility that the original premise of this study, that of a spatio-temporal pattern of predation risk in nature, may be wrong, at least for inangas. Although much is known about the great number of animal species

that prey on inangas (McDowall 1989), the combined spatio-temporal activity pattern of these predators has never been measured. Perhaps inangas are at risk basically all the time and in almost all places, and, therefore, the selection pressure for learning spatio-temporal patterns of predation risk would be weak.

Lack of time–place learning in response to predation risk may be widespread among fish. I have exposed single common bullies (*Gobiomorphus cotidianus*) and groups of golden shiners to spatio-temporal patterns of predation risk, and did not obtain any evidence of time–place learning (unpubl. data). This may not mean much in the case of the bullies, as I could not get them to learn time–place associations based on food either (unpubl. data), but the lack of risk effects on the shiners is more significant, as these fish are known to be capable of time–place learning, at least based on food (Reebbs 1996).

In a recent review, Smith (1997) stated that ‘there is remarkably little direct evidence that timing of prey activity can be altered by predation’ in fish (he gives Helfman (1986a) as an exception, a case of a slight delay in the timing of daily migration by juvenile grunts [Haemulidae], brought about by the regular presentation of a predator model, the lizardfish *Synodus intermedius*, along the migration route). This lack of evidence may reflect a paucity of studies on the topic, or an actual absence of timing plasticity in response to predation risk combined with an unwillingness by researchers to submit negative results for publication (for two examples where negative results were reported, see Tonn & Paszkowski (1987) and MacKenzie & Greenberg (1998)). Interestingly, Smith’s observation could extend to the whole literature on circadian anticipation of daily events, for any animal species. There are many instances of animals that can use an internal representation of time and learn to anticipate the daily arrival of food at precise hours of the day or night (Mistlberger 1994), but none, as far as I know, about the anticipation of unpleasant stimuli, be they completely artificial, like mild electric shocks, or somewhat more natural, like simulated predator attacks. Even when exposed for 30 d to electric shocks at noon, rats fail to show changes in activity or subcutaneous temperature in advance of the daily shock (Bolles et al. 1974). Only when the shock is given 1 h after dusk does anticipation develop (Imada et al. 1985), but this is simply because dusk becomes the conditioned stimulus in a classical conditioning protocol and acts as a warning signal. This is less interesting than a learned association between the risk of predation and the internal representation of a daily time.

In his quote above, Smith (1997) pointedly mentions the lack of *direct* evidence for the effect of predation on the timing of prey activity. Predator avoidance is often suggested as an explanation for what seems to be plastic patterns of diel activity in wild fish (Bowen & Allanson 1982; Hanych et al. 1983; Wurtsbaugh & Li 1985; Tonn & Paszkowski 1987; Reebbs et al. 1995), but direct evidence is either lacking or insufficient to rule out alternative explanations. For example, lake chubs, *Couesius plumbeus*, are known to be diurnal in the laboratory but crepuscular in a natural stream where piscivorous birds are active (Reebbs et al. 1995). The chubs in the stream may be restricting their activity to those times of day when low light levels impede the efficiency of visual predators, but alternative explanations, such

as better food availability for chubs at dawn and dusk, are also possible. Another example comes from the work of Bowen & Allanson (1982), who observed that a rise in the water level of a tropical lake was followed by a night-to-day shift in littoral use by the predatory catfish *Clarias gariepinus*, and a concurrent day-to-night shift in littoral use by the catfish's prey, juvenile *Tilapia mossambica*, such that the prey still avoided the predator. Unfortunately, there was also a change in the prey's diet, and so the true cause of the temporal shift in habitat use (food, predation, or both) cannot be identified with certainty. In such studies then, we are left with the impression that predation risk may very well have altered the timing of prey activity, but that a convincing demonstration of this is still lacking. We should also note that time discrimination in these cases is between broad periods (day vs. night, twilight vs. all other times), something that is presumably easier to do than within-day discrimination.

Even if it was to be shown that the spatio-temporal activity patterns of fish lack plasticity in the face of predation risk, the possibility would remain that they have at least evolved in response to predation. It is quite possible that within-day or day–night shifts in habitat are performed by fish in order to avoid predation, but that they are mostly innate rather than learned. For example, some lake species may be innately predisposed to accept venturing into the open at night or around dawn and dusk, when low light levels may impede prey detection by piscivorous birds, and to move to littoral areas around midday, where structure (weeds, overhanging bank) can provide protection (Hall et al. 1979; Naud & Magnan 1988). In response to predation pressure, such a behaviour might have become hard-wired and proximally based on simple responses to light levels (or internal representations of time) and structure, rather than on predator presence directly.

The same rationale could apply to the very precisely scheduled twilight migrations of many fish species, either vertically (Neilson & Perry 1990) or horizontally (Helfman 1993), the exact timing of which may be an adaptation to minimize predation risk (Helfman 1993) but not necessarily the result of learning. Social learning may be involved in the spatial aspect of twilight migrations (the route taken is socially transmitted, see Helfman & Schultz (1984)), but we do not know whether the same applies to the temporal aspect. Innate responses to changing light levels or to internal representations of twilight time (e.g. Helfman 1986b; Reeb 1994) may be more directly involved in the timing of daily migrations than a learned response to predator pressure or social transmission from conspecifics.

For food, inangas did show evidence of time–place learning. Questions remain, however, about the extent to which such time–place learning is expressed in the wild. It probably depends on the particulars of each situation. For example, the fish may be sensitive to the cost of travel between areas. In the food-only experiment, inangas seemed to take advantage of a low cost of travel and to hedge their bets by frequently sampling each side of the aquarium. How they would react to a greater cost of travel (or sampling) is unclear at this point. One significant cost may be greater exposure to predators. Indeed, in the food-and-predator experiment, exposure to simulated heron strikes prevented the expression of time–place learning based on food. By reducing fish movements, predation risk may curtail the devel-

opment of time–place learning based on food in nature, or at least limit it to small spatial scales.

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