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## The influence of hypoxia on risk of predation and habitat choice by the fathead minnow, *Pimephales promelas*

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**Abstract** Yellow perch (*Perca flavescens*) have a lower physiological tolerance to hypoxic environments than one of its prey species, the fathead minnow (*Pimephales promelas*). These data suggest that environments where dissolved oxygen concentration is lethal to perch, but not fathead minnows, could provide a predator-free refuge. Here, we test the hypothesis that differences in tolerance to hypoxic environments need not be lethal to provide more tolerant prey species with an environment that has a significantly reduced or eliminated predation risk. We predict that moderate hypoxic environments will generate non-lethal stress in predators, rendering them ineffective at capturing their prey. For this hypothesis to operate, we assume that prey are capable of detecting when their predators are stressed and less of a threat, and discount the risk of predation associated with these predators. Fathead minnows were provided with the option of feeding in relatively low- versus high-risk locations or in the presence of a yellow perch under sub-lethal hypoxic and normoxic conditions. Fathead minnows exhibited a significantly reduced response to the predator in hypoxic conditions relative to normoxic conditions. We also observed significant variation in the behaviour of the predator under these two conditions which may provide the cue used by prey to discount the threat associated with the predator.

**Keywords** Physiological exclusion · Dissolved oxygen · Antipredator behaviour · Predation risk · Predator inspection

### Introduction

It is well known that the role of predators extends beyond simply consuming their prey (Sih 1982, 1987;

Werner et al. 1983; Mittelbach 1984). In the presence of a predator, prey will often modify their behaviour, thereby reducing their probability of mortality (see Mittelbach and Chesson 1987). When choosing between habitats, prey must integrate both the costs (risk of mortality) and the energetic benefits associated with available habitats, to select that which maximises their net benefits. For fish, the costs of predation associated with habitat-selection decisions will be determined by morphological characteristics, such as body size (Werner and Gilliam 1984) and possession of body armour (McLean and Godin 1989; Abrahams 1995). Characteristics that change the benefits of energy include hunger level (Dill and Fraser 1984; Godin and Crossman 1994), reproductive status (see Lima and Dill 1990) and sex of the individual (Abrahams and Dill 1989). Furthermore, decisions involving the risk of predation within an aquatic ecosystem are known to be affected by light level (see Lima and Dill 1990), turbidity (Miner and Stein 1996; Abrahams and Kattenfeld 1997) and dissolved oxygen (Kramer et al. 1983; Poulin et al. 1987; Wolf and Kramer 1987; McIntyre and McCollum 2000).

Environmental parameters, such as dissolved oxygen, affect both predator and prey, though their tolerance to environmental stress may not be equal. There appears to be considerable variation among fish species in their tolerance to a reduction in dissolved oxygen (hypoxia) that often results in the segregation of species within fish communities (Doudoroff and Shumway 1970; Gee et al. 1978; Tonn and Paszkowski 1987; Smale and Rabeni 1995). Typically this occurs because individuals avoid the physiological costs of hypoxia in favour of more normoxic (air-saturated) waters (Doudoroff and Shumway 1970; Suthers and Gee 1986). The fathead minnow, *Pimephales promelas*, has a greater tolerance to hypoxia than its predator, the yellow perch (*Perca flavescens*) (T. Robb and M.V. Abrahams, unpublished data). For this predator-prey relationship, the difference is partly due to an inverse relationship between tolerance to hypoxic environments and body size (T. Robb and M.V. Abrahams, unpublished data). As a consequence, in an environment

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of varying dissolved oxygen concentrations, the smaller prey species would be able to use a hypoxic habitat as a predator-free refuge. We term this the physiological exclusion hypothesis.

At or near the critical dissolved oxygen level, fish exhibit behaviours that are not conducive to feeding (Doudoroff and Shumway 1970; Petit 1973; Weber and Kramer 1983). In response to a reduction of dissolved oxygen, fish initially increase activity, increasing their probability of finding more favourable waters, and make increased use of oxygen-rich surface waters (aquatic surface respiration, ASR) (Gee et al. 1978; Kramer 1983). Over the longer term, activity is often decreased, reducing oxygen demand. Therefore, predators less tolerant of hypoxia will manifest more pronounced behavioural changes at greater dissolved oxygen concentrations than the more tolerant prey. Subsequently, prey should be able to take further advantage of moderately hypoxic environments stressful to predators in order to reduce the magnitude of the predation risk.

It is known that prey are able to assess risk of predation based on the behaviour of their predators through predator inspection behaviour (see Dugatkin and Godin 1992). Although assessment may impose a cost due to increased risk of mortality, prey can obtain valuable information about the predator, such as the predator's intent (Pitcher et al. 1986; Appelberg et al. 1993). Prey can subsequently make a decision based on the perceived risk of predation: If the threat is perceived to be high then prey can react with antipredator tactics to reduce the risk or, if judged as innocuous, prey can resume normal activities (Dugatkin and Godin 1992). We predicted that predators manifesting behavioural responses to hypoxia would probably be judged to be an unlikely threat to prey. Therefore, the physiological exclusion from a habitat may not be necessary to generate a refuge free of predation risk. We would expect prey to sense predators that are stressed due to hypoxic conditions and integrate this into the decision-making process of habitat choice. Here we test the hypothesis that prey are able to assess and exploit moderately hypoxic habitats stressful to the predators but not themselves.

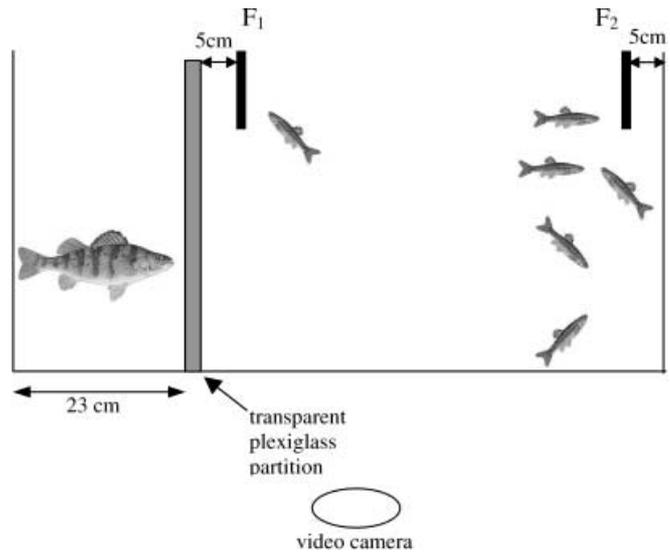
## Methods

### Study animals

The fathead minnows and yellow perch used as prey and predator in this study were collected using minnow traps in September 1998 and 1997, respectively. Both species were collected from Delta Marsh at the University of Manitoba Field Station at the southern tip of Lake Manitoba (50°11'N, 98°23'W). Minnows were held in a 200-l aquarium, fed Nutrafin flakes and kept at room temperature (approximately 22°C) and on a photoperiod of 12 h light:12 h dark. Four yellow perch of similar size (Table 1) were held individually in 50-l aquaria and fed maintenance rations of trout pellets and live minnows. They were held at the same water temperature and photoperiod as the minnows. Three days prior to the experiment, four groups of six similar-sized minnows (Table 1) were randomly chosen. Groups were housed separately for the duration of the experiment in 20-l aquaria. During this

**Table 1** Mean wet weights (g) ( $\pm 1$  SE) of the fathead minnow groups ( $n=6$  for each group) and wet weights (g) of the yellow perch used in the study

| Group | Fathead minnow  | Yellow perch |
|-------|-----------------|--------------|
| 1     | 1.95 $\pm$ 0.28 | 99.78        |
| 2     | 1.77 $\pm$ 0.30 | 86.54        |
| 3     | 2.17 $\pm$ 0.14 | 89.76        |
| 4     | 1.80 $\pm$ 0.35 | 92.85        |



**Fig. 1** Diagram of the experimental apparatus used to determine the effects of hypoxia on response of minnows to a predator.  $F_1$  represents the high-risk feeder,  $F_2$  the low-risk feeder. The transparent Plexiglas partition allowed minnows to view the perch for the duration of the trial while preventing the perch from capturing the minnows (this would be the set-up for the predator location on the left side)

time, the minnows were fed maintenance rations of frozen brine shrimp (*Artemia* sp.), using the same feeding protocol used in the trials.

### Experimental protocol

Trials were set up to test the relative risk taken by minnows at hypoxic and normoxic conditions. The order of these trials was randomised. Under normoxic conditions and with continuous food input, feeding is expected to follow an ideal free distribution (IFD), as described by Fretwell and Lucas (1970). Under these conditions, the spatial distribution of individuals will match the spatial distribution of resources in their habitat. To achieve this distribution, individuals are assumed to have ideal knowledge of the resource distribution, and each individual is free to enter and compete for this resource in any habitat. Therefore any deviations from the IFD when a predator is present should quantify the response of the minnows to the risk of predation posed by the predator (see Abrahams and Dill 1989 for a description of this technique).

The experimental apparatus consisted of a 40-l aquarium that was divided into 2 unequal sections by placing a transparent Plexiglas divider 23 cm from the end of the tank (Fig. 1). In the smaller section, one yellow perch was placed behind the Plexiglas to prevent contact with the minnows, yet minnows were able to view the predator for the duration of the trial. Predators were positioned behind the divider either on the right or left side of the tank

so as to control for any potential side effect. For control treatments (trials with no predators), the Plexiglas divider was placed randomly on either side of the tank. In the larger section of the apparatus, two automated feeders were set up to provide equal amounts of food to a group of minnows, and were placed at high- and low-risk locations. One feeder was placed 5 cm from the end of the Plexiglas divider (high risk) and the other 5 cm from the opposite end of the tank (low risk; Fig. 1). Each feeder provided 0.5 g frozen brine shrimp over a 25-min time period (see Abrahams 1989 for a description of the feeders).

Approximately 3 h prior to the trial, one group of minnows and, for predator trials, one randomly selected predator (identity was recorded) were placed in the apparatus to acclimate to their new surroundings. To prevent the minnows from becoming habituated to the presence of a predator, a temporary opaque divider was placed in front of the transparent divider for all trials, including predator-free controls. Fifteen minutes prior to the start of trials using hypoxic conditions, the dissolved oxygen was lowered in the tank by bubbling nitrogen gas through perforated Tygon tubing placed at the bottom of the aquarium. By observing these fish in preliminary experiments, this 15-min period provided sufficient time for the fish to become behaviourally acclimated to their new environmental conditions. For trials using normoxic conditions, air rather than nitrogen gas was bubbled through the tubing. The dissolved oxygen was measured using a YSI 53 dissolved oxygen meter (Yellow Springs Instruments, Yellow Springs, Ohio) at the beginning and end of each trial. The presence of groups of foraging minnows and their predator in this apparatus during the time required to conduct these experiments did not generate any measurable change in dissolved oxygen (T. Robb and M.V. Abrahams, unpublished data). Therefore, dissolved oxygen levels were not monitored throughout the trial. The dissolved oxygen was lowered to 2.74 mg/l for all hypoxic trials, as this provided an environment in which perch were compromised but the minnows behaved normally (see T. Robb and M.V. Abrahams, unpublished data). For the normoxic trials, dissolved oxygen was maintained at 8.22 mg/l. For all trials, water temperature was maintained at 22°C. The range of dissolved oxygen values in their natural habitat ranges between 0 and 10 mg/l in late summer (M.V. Abrahams, unpublished data). Once the desired dissolved oxygen levels were attained, the opaque Plexiglas divider was removed and plastic was placed over the water for the duration of the trial to prevent atmospheric oxygen from dissolving into the tank water. Trials began when the feeders were turned on and lasted 25 min. All trials were videotaped and, upon completion, the water was changed and the aquarium cleaned.

At each dissolved oxygen concentration, 6 replicates of each predator location (right and left side) and no predator (controls) were completed for a total of 36 trials. All trials were completed in 9 days with trials being performed twice a day in two aquaria. The first trial began at 1100 hours and the second at 1500 hours. For the duration of the experiment, the feeders were the only source of food for the minnows. The total number of minnows using the feeders and their spatial distribution (number feeding at high- and low-risk feeders) were observed every 30 s. The mean proportion of minnows was calculated for the high-risk habitat adjacent to the Plexiglas. A feeding minnow was considered to be any individual that had or was consuming brine shrimp within 5 cm on either side of the feeder. The mean response to predation risk was calculated as the difference of minnows using feeders in control situations (IFD input matching) and the proportion of minnows using the same feeder in the presence of a predator (means were calculated for predators located on both the right and left side). The behavioural response of the predator to the presence of the minnows was measured as the proportion of the time spent oriented towards the minnows at the Plexiglas divider during the last 20 min of the 25-min trial. The first 5 min were omitted from this analysis due to disturbance associated with the removal of the opaque partition.

For descriptive statistics, each group of minnows represented a single experimental unit and all means were reported  $\pm 1$  standard error (SE). For statistical analysis, each unique combination of minnows and predator at each dissolved oxygen concentration was considered an independent observation, since observations depended

both upon group identity and the response of the predator to hypoxic manipulation. A single observation for each experiment was determined by taking the mean of all sequential observations within a trial. All statistical analyses used the GLM procedure in SPSS, and data in the form of proportions were arc-sine square-root transformed prior to analysis.

## Results

Preliminary analyses indicated that prey group, predator location (left or right side) and predator identity had no measurable influence on prey behaviour (ANOVA,  $P > 0.05$ ). For simplicity, these parameters have been removed from all subsequent analyses.

There was a visible difference in the behaviour of the perch between the normoxic and hypoxic treatments. Under normoxic conditions, perch were usually positioned against the partition and spent an average of 31% (6% SE) of the time oriented towards the minnows. Under the hypoxic condition, this was significantly reduced to 12% (5% SE) (Table 2).

In conformity with the IFD, the minnows were distributed equally between the two feeders in both normoxic and hypoxic conditions in the absence of predation risk (Table 3). In the presence of a predator, the proportion of minnows using the feeder adjacent to the Plexiglas (high risk) was significantly reduced only under the normoxic treatment (Fig. 2, Table 3). When both predator and prey were in a hypoxic environment, there was no measurable influence of the predator on the spatial distribution of the foraging minnows (Fig. 2, Table 3). This change in minnow-foraging distribution occurred despite no obvious change in the overall number of minnows feeding in both the hypoxic and normoxic treatment (Table 3).

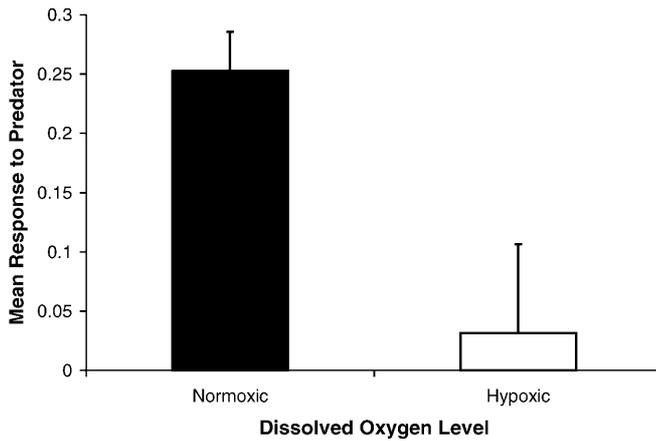
The proportion of minnows feeding at the dangerous location was affected by dissolved oxygen concentration,

**Table 2** Summary of ANOVA results of the influence of dissolved oxygen (hypoxic or normoxic) and predator location on the mean proportion of time a predator spent oriented towards the minnows for the last 20 min of a trial (error  $df=20$ )

| Source of variation   | <i>df</i> | <i>F</i> | <i>P</i> |
|-----------------------|-----------|----------|----------|
| Dissolved oxygen (DO) | 1         | 9.601    | 0.006    |
| Predator location (L) | 1         | 1.305    | 0.267    |
| DO*L                  | 1         | 0.927    | 0.347    |

**Table 3** Summary of mean proportion of minnows ( $\pm 1$  SE) at the high-risk feeder (adjacent to the Plexiglas) and the mean number of minnows ( $\pm 1$  SE) using both feeders at each dissolved oxygen concentration in the presence or absence of the predator

| Dissolved oxygen concentration | Predator | Mean proportion | Mean number feeding |
|--------------------------------|----------|-----------------|---------------------|
| Hypoxic                        | Present  | 0.53 $\pm$ 0.03 | 3.36 $\pm$ 0.51     |
|                                | Absent   | 0.51 $\pm$ 0.05 | 2.97 $\pm$ 0.55     |
| Normoxic                       | Present  | 0.27 $\pm$ 0.01 | 3.34 $\pm$ 0.44     |
|                                | Absent   | 0.56 $\pm$ 0.01 | 3.40 $\pm$ 0.23     |



**Fig. 2** The mean response (+1 SE) of the fathead minnows to the presence of a predator ( $n=4$ ). Mean response of minnows was calculated as the difference using a feeder with no predator and the proportion of minnows using the same feeder in the presence of a predator (large positive values indicate increased avoidance of the high-risk feeder)

**Table 4** Summary of ANOVA results of the influence of dissolved oxygen (hypoxic or normoxic) and predator (present or absent) on the proportion of minnows using the high-risk feeder or adjacent to the Plexiglas (error  $df=32$ )

| Source of variation   | <i>df</i> | <i>F</i> | <i>P</i> |
|-----------------------|-----------|----------|----------|
| Dissolved oxygen (DO) | 1         | 17.07    | <0.001   |
| Predator location (L) | 1         | 17.68    | <0.001   |
| DO*L                  | 1         | 16.27    | <0.001   |

**Table 5** Summary of ANOVA results of the influence of dissolved oxygen (hypoxic or normoxic) and predator (present or absent) on the mean number of minnows feeding (error  $df=32$ )

| Source of variation   | <i>df</i> | <i>F</i> | <i>P</i> |
|-----------------------|-----------|----------|----------|
| Dissolved oxygen (DO) | 1         | 0.268    | 0.608    |
| Predator location (L) | 1         | 0.202    | 0.656    |
| DO*L                  | 1         | 0.312    | 0.580    |

the presence of the predator, and the interaction between dissolved oxygen concentration and predator location (Table 4). The significant interaction between predator location and dissolved oxygen concentration demonstrates that the influence of the presence of the predator on minnow-foraging decisions changes with dissolved oxygen concentration. These parameters did not affect the mean numbers of minnows feeding (Table 5).

## Discussion

Under normoxic conditions in the presence of a predator, minnows were less likely to choose the risky patch in favour of the low-risk habitat. However, under hypoxic conditions, the presence of the predator had little influence on foraging-habitat selection by the minnows. We

also did not observe any change in the mean number of fathead minnows foraging between the normoxic and hypoxic treatment, nor any other obvious change indicating that they were suffering any sort of stress. These data are consistent with our hypothesis that hypoxic stress imposed upon predators, but not their prey, renders them less effective as predators, which then alters habitat-selection decisions by prey species that involve the risk of predation.

Typically, the roles of environmental dissolved oxygen and the risk of predation on habitat-selection decisions have been considered separately. For example, it is known that teleosts generally avoid hypoxic waters in favour of more oxygenated waters (Doudoroff and Shumway 1970; Suthers and Gee 1986). There is also a large literature that demonstrates that prey species integrate the risk of predation into their habitat-selection decisions (Werner et al. 1983; Mittelbach 1984; see Lima and Dill 1990 for a review). But many aquatic ecosystems have dissolved oxygen levels and predation levels that vary both in space and time. Our data indicate that fathead minnows are capable of taking advantage of this heterogeneous environment to exploit physiological differences in susceptibility to hypoxia. If, as in the yellow perch/fathead minnow system, tolerance to hypoxic conditions is inversely related to body size, then these results have implications for many different aquatic ecosystems: hypoxic habitats may provide smaller prey species with some relief from predation by their larger aquatic predators. Such a mechanism is likely responsible for the survival of many haplochromine species thought to be extinct from Lake Victoria after the introduction of the Nile perch, *Lates niloticus* (Chapman et al. 1996a, b). These haplochromine species were limited to the hypoxic wetland areas at the edges of the lake. It is likely that they survived due to the inability of the Nile perch to withstand these hypoxic conditions (Fish 1956) and exploit its prey in these locations.

It is also important to note that the levels of dissolved oxygen used in this study are not lethal to either species, as both the yellow perch and fathead minnow can survive under all experimental conditions described in this paper (T. Robb and M.V. Abrahams, unpublished data). For variation in dissolved oxygen levels to have a significant effect on habitat-selection decisions involving the risk of predation, it must impair the foraging efficiency of a predator more rapidly than its prey. Therefore, ranges of dissolved oxygen need not be lethal to have a significant influence on community structure. However, it should also be noted that refuges created by hypoxia are not necessarily absolute refuges. Rahel and Nutzman (1994) observed central mudminnows (*Umbra limi*) diving into lethal hypoxic regions of a lake to forage. Presumably the stress placed upon the diving predator will incur considerable costs. Unless the foraging rate in this location is high enough to compensate for this cost, it is unlikely to be energetically profitable to use this location.

But how do prey species know that the presence of a predator no longer represents a threat? It is believed that

prey are able to assess the state of the predators, and presumably its probability of attack, through predator inspection (Dugatkin and Godin 1992). Indeed, predator inspection behaviour has been observed in a variety of different species, and has been particularly well documented in fish. For example, Godin and Crossman (1994) demonstrated that hungry three-spine sticklebacks (*Gasterosteus aculeatus*) engaged in a greater amount of predator inspection when actively feeding in the presence of a predator. Eklöv and Persson (1996) observed similar behaviours by juvenile perch (*Perca fluviatilis*) foraging in the presence of a piscivorous pike (*Esox lucius*). Thus, prey species that use this behaviour are able to discriminate between predators that are likely to attack and those that are not. For example, Appelberg et al. (1993) and Christensen and Persson (1993) demonstrated that prey could detect when their predators were satiated or inactive and would then engage in normal feeding behaviour, discounting the risk of predation associated with these predators. Behavioural change is commonly associated with stress due to hypoxia (Doudoroff and Shumway 1970; Petit 1973; Kramer 1983; Weber and Kramer 1983). One specific behavioural change is a reduction in feeding rate or search for more normoxic waters (Doudoroff and Shumway 1970; Gee et al. 1978; Kramer 1987). In our experiments, we observed significant changes in the orientation behaviour of the predators under hypoxic conditions. Minnows in our experiment may have used this or some other cue, to assess the level of threat associated with the predator under our different experimental treatments, and modified their behaviour accordingly.

A common response by many fish species to the hypoxic environment is to obtain air from above the water, or use the relatively more oxygen-rich water at the air/water interface (see Kramer 1987). For prey, however, such behaviour is likely to be very dangerous since they must move from areas of cover, or regions where they are relatively cryptic, to locations where they are more vulnerable to attack. However, the risk of such a response again depends upon how the predator is affected and responds to the same changes in dissolved oxygen. Poulin et al. (1987) found that guppies foraging in the presence of a predatory cichlid, *Astronotus ocellatus*, spent more time near the surface under hypoxic conditions. They also tended to be more active, rather than adopting a more cryptic, and hence less dangerous behaviour of remaining motionless. Although not explained by Poulin et al. (1987), such behaviour is consistent with our results in which the prey are less affected by these hypoxic conditions. Therefore the predator would represent less of a threat, and such behaviour would inherently be less dangerous.

However, there are many species of predatory fish that are well adapted to hypoxic conditions and may actually become more effective predators under such conditions. For example, Wolf and Kramer (1987) studied predator-prey interactions between snakeheads (*Channa micropeltes*) and its prey, the dwarf gourami (*Colisa lalia*). Under hypoxic conditions, the gouramis were

forced to leave cover to move to the surface for air breathing. At this time they were especially vulnerable to attacks from the snakehead. Similar to this study, Wolf and Kramer (1987) concluded that individuals able to tolerate lower levels of hypoxia could reduce predation risk by staying in areas of cover longer.

In summary, we have demonstrated that differential susceptibility to hypoxic stress between predators and their prey may be very important in modifying habitat-selection decisions involving the risk of predation. Our results are probably not restricted only to fathead minnows and yellow perch. Other studies have demonstrated instances in which there is a large degree of variation between predator and prey species in susceptibility to hypoxic stress (Gee et al. 1978; Smale and Rabeni 1995; and a review by Doudoroff and Shumway 1970). In addition, a wide range of aquatic ecosystems exhibit considerable variation in environmental dissolved oxygen levels. Our data indicate that both these parameters will therefore be critical in determining habitat-selection decisions by prey species. As was demonstrated in Lake Victoria (Chapman et al. 1996a, b), and more recently by McIntyre and McCollum (2000), such habitat-selection decisions can even prove critical in allowing prey to survive dramatic shifts in predation pressure.

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