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Animal behaviour

Escaping peril: perceived predation risk affects migratory propensity

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Although migratory plasticity is increasingly documented, the ecological drivers of plasticity are not well understood. Predation risk can influence migratory dynamics, but whether seasonal migrants can adjust their migratory behaviour according to perceived risk is unknown. We used electronic tags to record the migration of individual roach (*Rutilus rutilus*), a partially migratory fish, in the wild following exposure to manipulation of direct (predator presence/absence) and indirect (high/low roach density) perceived predation risk in experimental mesocosms. Following exposure, we released fish in their lake summer habitat and monitored individual migration to connected streams over an entire season. Individuals exposed to increased perceived direct predation risk (i.e. a live predator) showed a higher migratory propensity but no change in migratory timing, while indirect risk (i.e. roach density) affected timing but not propensity showing that elevated risk carried over to alter migratory behaviour in the wild. Our key finding demonstrates predator-driven migratory plasticity, highlighting the powerful role of predation risk for migratory decision-making and dynamics.

1. Introduction

Billions of animals annually migrate between discrete habitats to enhance foraging, reproduction and survival success [1]. This phenomenon surely ranks among the most spectacular of animal behaviours, with important consequences not only for the fitness of individual migrants but also for structure and functioning of entire ecosystems [2,3]. A key question when studying animal migration is to what degree individual migratory behaviour is obligate versus facultative [4,5]. Flexibility in migratory behaviour has been demonstrated in a number of species in response to various ecological factors. For instance, newts change migratory behaviour in response to population density and sex ratio [6], and the migratory propensity of tropical manakins is influenced by storm events [7]. Recent experimental work also highlights the flexibility of a range of migratory traits in fishes in response to feeding conditions [8–11]. However, few studies explicitly focus on predation risk shaping patterns of seasonal migration, and how migratory decision-making responds to controlled experimental manipulation of perceived predation risk has yet to be tested. Partially migratory populations, composed of both seasonal migrants and year-round residents, offer a unique opportunity to test whether

migratory animals are responsive to changes in perceived predation risk. The roach (*Rutilus rutilus*) is a common freshwater fish and a partial migrant, with migrants making seasonal journeys from shallow lakes into connected streams [9,12,13]. Theoretical work suggests that seasonal changes in a predation/growth (P/G) trade-off between the two habitats shapes migratory dynamics in this species [14], where migrants benefit from a reduced predation risk from piscivorous fish and avian predators by refuging in the low-risk streams during winter [14,15], while paying a foraging cost by migrating to a relatively food-poor habitat [16]. Moreover, translocation experiments with roach have highlighted that individuals can shift their migratory behaviour in response to environmental factors [17], and hence show some plasticity in migratory behaviour. These factors, along with our ability to precisely track migration in individual roach [14] make this an ideal model system for testing novel hypotheses on the role of perceived predation risk on migratory decision-making in the wild. Here, we test the hypothesis that roach exposed to an elevated perceived predation risk prior to migration show a greater propensity to migrate, as compared to roach experiencing experimentally decreased risk. To achieve this, we combined controlled experiments, where we manipulated individuals' perceived predation risk, with monitoring of their subsequent post-exposure migratory behaviour under natural field conditions.

2. Material and methods

(a) Study animals and treatments

We transported wild-caught roach from Lake Krankesjön, southern Sweden, to outdoor experimental facilities at Lund University. We set up 20 cattle-tank mesocosms (volume 1000 l), each comprising two compartments, one large (75 × 100 cm) to hold the experimental roach, and one smaller predator compartment (45 × 100 cm). For the experimental manipulation of perceived predation risk, we crossed direct risk (presence/absence of piscivorous pike *Esox lucius*) with two levels of density-dependent indirect risk (high: 24 roach, low: five roach) in a 2 × 2 factorial design. Group size was manipulated as individual perception of risk is expected to be greater in smaller shoals in strongly gregarious species such as roach [18,19]. The experiment was initiated 20 September 2013 when roach were randomly allocated to the larger of the tank compartments, and single pike (size range 50–63 cm) allocated to the other compartment in tanks used for manipulation of direct predation risk. Each treatment combination was replicated five times (roach: $n = 290$).

(b) Electronic tagging and migration

On 29 October, all experimental roach were temporarily removed from the tanks and anaesthetized before being measured for length (total length: 127.6 ± 0.6 mm; mean \pm s.e.) and tagged with passive integrated transponder tags [20]. The exposure experiment was terminated on 8 November (49 days exposure). Some post-tagging mortality occurred and we also excluded individuals with external injury. Excluded individuals (*ca* 9.7%) were similarly distributed across treatments. Remaining individuals (24 and 24 reared at low density, and 108 and 106 reared at high density, with or without pike, respectively) were then transported back to Lake Krankesjön. Fish were released at the same location (within 50 m of each other) in a haphazard order. We monitored migratory propensity and timing of released individual fish using paired, fixed-location antenna stations in all three streams (two inlets and one outlet) connected to the study lake

Table 1. GLMM output testing the effect of experimental manipulation of perceived predation risk and body length upon migratory propensity in roach.

	estimate \pm s.e.	z-score	<i>p</i>
full model			
intercept	-4.154 ± 2.401	-1.73	0.084
predator	1.837 ± 0.853	2.154	0.031
density	0.316 ± 0.801	0.395	0.693
predator × density	-1.272 ± 0.939	-1.354	0.176
body length	0.014 ± 0.018	0.771	0.441
reduced model			
intercept	-2.12 ± 0.284	-7.45	<0.001
predator	0.845 ± 0.354	2.40	0.016

(see [20,21] for details). Data were collected from time of release until 1 June 2014.

(c) Data analysis

To analyse the effect of experimental treatment and body length upon individual migratory propensity (migrant versus resident), we used a generalized linear mixed model (GLMM) approach fitted with binomial distribution and logit link function (lme4 R package, glmer procedure). Factors pike (presence/absence), density (high/low), their interaction term and body length at tagging were considered as explanatory main effects and tank identity as a random factor: migratory propensity \sim pike + density + pike: density + length + (1 | tank). The final model was obtained by a stepwise backward elimination procedure with selection criteria at $\alpha = 0.1$. Migratory timing (number of days from release until a migratory fish was first recorded on an antenna) was compared between individuals originating from treatments with or without predators and between individuals reared at high or low density with Mann–Whitney *U*-tests. For details on data treatment, rearing and tagging protocols, see the electronic supplementary material.

3. Results

In total, 43 out of the 262 tagged and released individuals migrated during the study period and the majority (*ca* 88%) returned to the lake habitat (i.e. had their last registration on the antenna closest to the lake). There were no differences in return rate between fish from different exposure treatments. The GLMM revealed that migratory probability was significantly influenced by perceived direct predation risk (table 1 and figure 1). However, neither density, the predator × density interaction term, nor individual body length were significant (table 1). Hence, the migratory propensity among individuals experiencing increased predation risk via experimental exposure to a live predator was significantly higher than for individuals originating from experimental environments absent of predators. Finally, fish left the lake throughout autumn, winter and spring (range: 15 November–22 April) but there was no significant difference in migratory timing between individuals exposed to the presence or absence of pike ($U = 175$, $z = -0.726$, $n = 43$, $p = 0.468$). However, fish originating from the low-density treatment migrated

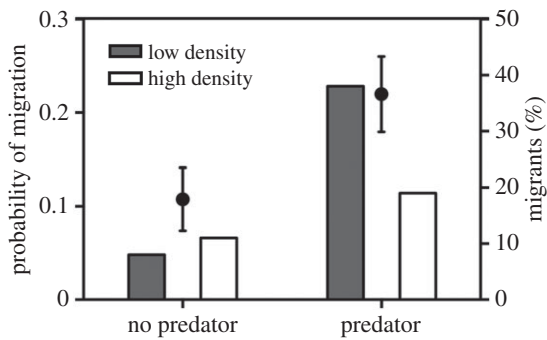


Figure 1. Visualization of the GLMM results with estimated migration probabilities (closed circles, \pm s.e.) for roach following experimental exposure to the absence or presence of a predator. Bars show the percentage of migrants originating from no predator/predator and low/high roach density treatment combinations.

earlier than fish from the high-density treatment ($U = 97.5$, $z = -2.187$, $n = 43$, $p = 0.029$).

4. Discussion

Our results indicate that perceived predation risk can influence migratory dynamics in the wild, and also suggest behavioural flexibility and rapid response to ecological shifts in predator communities in migratory animals such as roach. Roach that experienced exposure to a live predator (elevated perceived direct risk) demonstrated higher migration propensity than fish from treatments without predators, and were thus responsive to prior, experienced predation threat in the decision to migrate or not. Indirect risk (here conspecific density) did not however affect migratory propensity, but instead migratory timing, highlighting that direct and indirect perceived predation risks work in concert to shape migratory decision-making in this species. Our major result was thus in line with our initial prediction: perceived predation risk can be a trigger for facultative migration. We recognize that we have no direct data on the survival of fish in the lake during this period. Thus, one might speculate that fish originating from experimental environments absent of predators suffered a higher mortality in the lake prior to migration than fish in the predator exposure treatment, potentially due to changes in responsiveness to

predators. However, this is unlikely to be the case as a number of studies have shown that exposure to predators increases risky behaviours in a range of fishes [22–24]. Hence, we would predict the opposite effect if premigration mortality rates differed between treatment groups. Recent studies have explored the importance of predation as a dominant force in the evolution of seasonal migration across a range of taxa, including mammals, birds and fish [14,25,26]. Altered migration tactics in both geese and wader bird species have been hypothesized to occur in response to the recovery of avian predators [27,28]. Contemporary studies have also demonstrated that migration confers survival benefits with respect to predation in ungulates and fish, and arctic ground-nesting shorebirds can decrease nest predation by migrating further north [15,25,26]. However, to our knowledge, no studies have hitherto used an experimental approach to investigate how changes in perceived predation risk influences seasonal migratory propensity in the wild, providing mechanistic links between predation risk and migration.

Our data suggest that predators can impact the migratory dynamics of animals, with potential strong ecosystem consequences [3,29]. Understanding changes in migratory behaviour in response to altered landscapes of predation risk is hereby particularly important, given recent losses in apex predators across the globe via changes in climate, harvesting and pollution [30,31].

Ethics. Investigations were performed under ethical permission from the Malmö/Lund Ethical Committee (M165-07, M36-14).

Data accessibility. The data underlying this study are available from Dryad: doi:10.5061/dryad.pr421.

Authors' contributions. K.H. conceived/designed the study with contributions from B.B.C., C.B., P.A.N., L.A.H., C.S. and J.B. K.H. and J.V. performed experimental manipulations and collected field data. K.H., P.A.N. and H.B. analysed the data and prepared figures. K.H. coordinated the study and led the writing and revisions, to which all authors contributed. All authors gave final approval for publication.

Competing interests. We have no competing interests

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