Migration confers survival benefits against avian predators for partially migratory freshwater fish

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The importance of predation risk in shaping patterns of animal migration is not well studied, mostly owing to difficulties in accurately quantifying predation risk for migratory versus resident individuals. Here, we present data from an extensive field study, which shows that migration in a freshwater fish (roach, \textit{Rutilus rutilus}) that commonly migrates from lakes to streams during winter confers a significant survival benefit with respect to bird (cormorant, \textit{Phalacrocorax carbo} spp.) predation. We tagged over 2000 individual fish in two Scandinavian lakes over 4 years and monitored migratory behaviour using passive telemetry. Next, we calculated the predation vulnerability of fish with differing migration strategies, by recovering data from passive integrated transponder tags of fish eaten by cormorants at communal roosts close to the lakes. We show that fish can reduce their predation risk from cormorants by migrating into streams, and that probability of being preyed upon by cormorants is positively related to the time individuals spend in the lake during winter. Our data add to the growing body of evidence that highlights the importance of predation for migratory dynamics, and, to our knowledge, is one of the first studies to directly quantify a predator avoidance benefit to migrants in the field.

1. Introduction

Each year billions of animals migrate between different habitats [1]. This spectacular phenomenon has important consequences for the fitness of individuals, the population dynamics of migratory animals, and the structure and function of entire ecosystems ([2] and references therein). Hence, understanding the ecological factors that shape patterns of migration in wild populations of animals is critical. Migration is thought to evolve in response to seasonal changes in food availability, weather conditions or predation risk [1]. There is much support for the importance of changes in food availability and weather conditions for migratory behaviour [1]. However, owing to the logistical challenges in collecting field data on predation risk for migratory species, studies that have addressed this question are scarce (with important exceptions; [3,4]). Even fewer studies have directly quantified the predation risk associated with migration versus residency.

Perhaps the most prevalent form of migration is known as partial migration, which occurs when just a fraction of a population migrates and the remainder are resident [5,6]. Partial migration is widespread and has been documented in a range of vertebrate [1,7,8] and invertebrate taxa [9]. Partially migratory...
animals offer a unique opportunity to assess the costs and benefits associated with migration versus residency, and can hence provide an insight into the factors involved in the evolution of migration itself. For example, recent work on partially migratory freshwater fishes has provided understanding of the role of piscivorous fish predators in shaping patterns of migration and residency [3,10]. These studies highlighted the importance of predation risk from predatory fish, such as pike (*Esox lucius*), in influencing the migratory dynamics of cyprinid fishes, which commonly migrate from lakes into streams during winter, and suggests that migration has an anti-predatory function. However, as with many other migratory species, cyprinid fishes are at risk of being eaten by numerous predators, including piscivorous birds. Birds may present a significant risk during the winter migratory period, as unlike fish predators they are endothermic and require a high food intake throughout the cold period. Hence, a full test of the hypothesis that predation risk is important in shaping the migratory dynamics of cyprinid fishes, and that migration can reduce the risk of predation, needs to incorporate the effect of bird predation.

Here, we present a multi-year field study from two Scandinavian lakes where we quantify predation upon migratory and resident individuals of roach (*Rutilus rutilus*), a freshwater fish, by a key avian predator, cormorants (*Phalacrocorax carbo* spp.). Cormorants are predatory birds with a variety of space use strategies that include movements inland from coastal breeding habitats in the spring and summer to freshwater wintering grounds, where they feed on a variety of lake and river fishes, including roach [11]. Cormorants that prey upon tagged roach excrete these tags in their pellets, enabling the identification of fish eaten by cormorants. Hence, by individually tagging over 2000 fishes with passive integrated transponder (PIT) tags and subsequently recovering tag data from areas where cormorants roost and excrete, we are able to address the question of whether migration confers survival benefits against bird predation by relating predation probability to individual migratory behaviours.

2. Material and methods

We individually tagged a total of 2219 roach (total length: 120–350 mm) in two lakes in Denmark, Lake Viborg and Lake Loldrup (figure 1), during the 4 year study period using PIT tags (see the electronic supplementary material, table S1 for details about capture and tagging and for site details). Using PIT tags allowed us to identify which individuals were preyed upon by cormorants, the habitat these fish were captured in (lake versus stream) and the number of days spent in the streams. Fish were sampled from the lakes in September to early October, prior to migration, before being tagged and returned to the lake (following [12]). We monitored migratory patterns using paired, fixed-location antenna stations in all streams connected to the study lakes [3], enabling continuous evaluation of whether tagged individuals resided in the lakes or migrated into the connected streams (see the electronic supplementary material, table S1 for details). Estimates of mortality from cormorant predation were calculated by recovering PIT tag data of fish eaten by cormorants from pellets at a number of sites in the surrounding area (see the electronic supplementary material, table S1). Data from PIT tags were mostly recovered from two primary locations: the cormorant roost at Lake Viborg and at a nearby cormorant breeding colony 5 km from Lake Viborg and 12 km from Lake Loldrup: (figure 1). PIT tag scans at these locations were carried out several times each year during the study period (see the electronic supplementary material, table S1 for details). All tags recovered during the migratory period (September–May) were included in the analysis.

(a) Data processing and statistics

Via tag recovery, we identified fish that had been preyed upon by cormorants, and also where they were eaten (lake versus stream). To evaluate whether individuals can reduce their predation risk by migrating into streams, we tested the hypothesis that the
probability of cormorant predation is negatively related to the time a fish spends out of the lake. Hence, we calculated the total ‘days out of lake’ for each fish from our passive telemetry monitoring of individual movement patterns. This variable is a cumulative measure of the time an individual spends out of lake, and hence includes all migrations within the study period (i.e. in the case that an individual fish moved between the lake and streams multiple times). We had no information about the precise time when a fish was preyed upon by the cormorants. Hence, as a conservative measure to calculate ‘days out of the lake’ for fish preyed upon in the streams, we used the day when the tag was recovered as the final day of migration.

Individual predation risk was analysed using a binomial generalized linear model (GLM) with a logit link function. Predation by cormorant (yes/no) was entered as a dependent variable.

Days out of lake, lake identity, year (factor) and roach length at tagging were entered as explanatory main effects (see the electronic supplementary material, table S2 for data sheet). Additionally, the three two-way interactions involving the explanatory variable of primary interest (days out of lake) were included. Finally, an interaction term (between-lake identity and year) was included to allow for between-lake variation in year-to-year fluctuations in cormorant abundance. Parsimonious model selection was performed by stepwise elimination of non-significant terms. Significance of model terms was tested using analysis of residual deviance from single term deletions according to [13]. Statistical analysis was performed in R v. 2.15.0 [14].

3. Results

Across years and lakes, between 2 and 12 per cent of tags from the fish tagged in autumn were recovered from the cormorant colony and roosts in subsequent months (see the electronic supplementary material, table S1). Overall, the majority of the recovered tags were from fish last positioned in the lake (92.5%). The number of days a fish spent out of lake significantly decreased the individual probability of being preyed upon by a cormorant (GLM, \( \chi^2 = 24.58, p < 0.001 \)). There were no significant interactions between days out of lake and any of the other model terms (\( p > 0.20 \)), indicating that the reduction in predation risk that an individual gains by spending the winter in the streams was consistent between the two lakes, across fish lengths and across the four study years (figure 2). The GLM revealed a significant lake \( \times \) year interaction term (GLM, \( \chi^2 = 10.13, p = 0.018 \)), which reflects the fact that the lake-specific predation risk varied over time (figure 2). Finally, total length significantly influenced the individual probability of being preyed upon (GLM, \( \chi^2 = 21.9, p < 0.001 \)), with larger fish being more vulnerable to predation (figure 2).

Figure 2. (a) Visualization of the GLM results with values predicted by the model for a 150 mm and (b) a 250 mm roach. Each line represents the probability of cormorant predation in different years in Lake Loldrup (LOL) and Lake Viborg (VIB) in relation to the time each fish was out of the lake during the winter period.

4. Discussion

Our data clearly show that migration confers survival benefits with respect to cormorant predators, and that the reduction in risk is related to the time spent out of the lake during winter. Hence, by migrating out of lakes during winter, prey fish such as roach can reduce their probability of predation from cormorants significantly. Precisely why roach are safer in the streams is not known: we speculate that as cormorants hunt by pursuit-diving [15], it is possible that this strategy is less effective in shallow streams than in more open water.

These data support the predation risk/growth potential (\( p/g \)) model of seasonal migration [16], whereby cyprinid fishes migrate from lakes to connected streams to minimize predation risk during the winter when growth potential is low. The model was designed with fish predators such as pike in mind, but our data highlight the possibility that piscivorous birds also impose a significant cost of remaining in the lake. For larger roach (greater than 250 mm total length), the probability of a resident being preyed upon by a cormorant can be up to 40 per cent during the winter period. In addition to cormorant predation, predation from pike is likely to be higher in the lake versus the streams in our two lakes of study, and hence the effects of cormorants are additive to those of piscivorous fish predators. This raises the question of why some fish do not migrate and so spend the entire winter in the lake. The answer is complex: evidence from cyprinids suggests residency is influenced by a number of factors including energetic constraints [17] and individual differences in behaviour (i.e. animal personality: [10]). Our data also highlight the fact that different pressures may come into play at different ontogenetic stages in an animal’s life. We show a positive relationship between size and probability of cormorant predation, indicating that (in the context of cormorant predation) larger fish may benefit more from
migration than smaller roach. In many partially migratory systems, body size correlates with migratory tendency, yet the importance of size-specific predation vulnerability and its role in shaping patterns of partial migration are often overlooked [3].

Evidence for the role of predation in migration is growing [4], as is support for the p/g model of migration across a range of taxa (fishes: [3]; zooplankton: [9]; ungulates: [18]). Our data add further support by highlighting that in multi-predator systems, predation risk from birds can act additively to risk from piscivorous fishes to increase the costs of residency for our cyprinid model species. Given the prevalence of bird predation for a diverse array of migratory fishes, the importance of this force in shaping patterns of migratory dynamics has possibly been underestimated [19]. Incorporating additional predators into studies will clearly be fruitful for a range of migratory animals. Mammalian predators are important in many systems, as are a number of additional piscivorous bird species, such as (in our system) goosander Mergus merganser and grey heron Ardea cinerea. Future work to investigate the ecological trade-offs involved in migration versus residency (for which partially migratory populations provide an excellent and under-used opportunity) has the potential to reveal new insights about the evolution of animal migration more generally.

Experimental animal treatment was performed in accordance to the guidelines described in permission (2012-DV-2934-00007) from the Danish Experimental Animal Committee.

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