ANIMAL BEHAVIOUR, 2008, **75**, 509–517
doi:10.1016/j.anbehav.2007.06.007

Risk-taking behaviour in foraging perch: does predation pressure influence age-specific boldness?

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*(Received 24 April 2007; initial acceptance 28 May 2007;
final acceptance 5 June 2007; published online 22 October 2007; MS. number: 9374R)*

In fish, predation risk is often size-specific due to gape limited piscivores and visibility constraints. We have investigated whether risk-taking behaviour in perch varies in accordance with size-specific predation risk in their natural habitat. In our two study lakes, the risk of cannibalism was estimated from fishing survey data. In Lake Fisksjön, the relative risk for juvenile perch was much higher than in Lake Ängersjön in the early stages, but after reaching a body length of approximately 70 mm the situation was reversed, with higher predation risk in Ängersjön than in Fisksjön. Groups of perch, from either of the two lakes and of two age classes (0+ or 1+ years), were given the choice of foraging in an open area or hiding in the vegetation in the presence of a predator. Three measures of boldness were estimated: proportion of time spent in the open area, latency to start feeding and duration of first feeding bout. A principal component analysis was used to calculate individual boldness scores from a combination of the behaviour estimates. Differences in boldness scores within age classes corresponded well with the relative attack rates in the two lakes. In the youngest age class, perch from Fisksjön were less bold than those from Ängersjön. In the older age class, the Fisksjön perch were bolder than those from Ängersjön. Within lakes, boldness differed between age classes. Seemingly, perch adjust risk-taking behaviour to perceived predation risk.

Keywords: boldness; *Perca fluviatilis*; perch; population differences; predation risk; size-specific risk-taking

For a foraging animal, there is often a trade-off between feeding and watching out for potential threats (Elgar 1989). When vigilance reduces feeding rate it would be beneficial to adjust behaviour to the actual conditions, for instance, regarding density of predators in the feeding area and food availability. Accordingly, animals commonly adapt their behaviour to local conditions and behavioural traits can thus vary between populations of the same species (Foster & Endler 1999). In many fish species, antipredator behaviour is found to vary in populations with different predation risks (e.g. Giles & Huntingford 1984; Magurran 1990; Magurran & Seghers 1991; Brown et al. 2005). Differences in response to predators have also been found to be connected with habitat complexity (Brown & Warburton 1997). Furthermore, food availability can affect the trade-off between foraging activity and risk avoidance (Biro et al. 2003).

Variation in antipredator behaviour, found within and between animal populations, could depend on the selection for different degrees of boldness (Drent et al. 2003; van Oers et al. 2004; Sundström et al. 2004), phenotypic response to the environment (Wilson et al. 1993), individual learning, either from conspecifics (Dugatkin & Alfieri 2003; Kelley et al. 2003; Galef & Laland 2005) or from early experience (Hilakiviclarke et al. 1991; Kelley & Magurran 2003a). Learning seems to play an important role in the development of antipredator responses in a variety of fish species, although population differences in learning ability can have an underlying genetic basis (reviewed in Kelley & Magurran 2003b). The consistency of behaviour across ontogeny has been found in some studies, both for individuals (Dingemanse et al. 2002) and when comparing differences between populations (Salonen & Peuhkuri 2004). In contrast, inconsistent behaviour patterns over

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0003–3472/08/$34.00/0

age suggested that ecological and developmental circumstances may favour behavioural plasticity (Bell & Stamps 2004). In fish, the vulnerability to predators changes with size (e.g. Werner & Hall 1988; Lundvall et al. 1999; Claessen et al. 2002). A high feeding rate, leading to fast growth is predicted to minimize the time spent in a vulnerable size window. However, since feeding activity can increase the risk of being eaten (Elgar 1989; Lima & Dill 1990), costs and benefits of different foraging behaviours in different situations must be considered when trading off between feeding activity and predator avoidance.

Perch, *Perca fluviatilis*, undergo two ontogenetic niche shifts during its life (Persson 1988). Perch feed on zooplankton as larvae and small juveniles, then shift to benthic macroinvertebrates at intermediate sizes and finally become piscivorous when large enough. One of the most severe threats for a young perch is that of being cannibalized by one of its larger conspecifics (Treasurer 1989; Persson et al. 2000). Perch can become piscivorous at a very early age (Beeck et al. 2002; Borcherding 2006). However, gape limitations restrict the prey size that could successfully be ingested, and visibility constraints give a lower limit for prey detected (Lundvall et al. 1999; Persson et al. 2004). The size relationship between predator and prey determines foraging success of cannibalistic perch (Lundvall et al. 1999; Byström et al. 2003). Thus, in a perch population the risk for cannibalism depends on the size distribution and the density of fish, and will change with growth of the individual perch. Also pike, *Esox lucius*, is an important predator on perch (Treasurer 1989). However, while piscivorous perch are found both in the littoral and pelagic areas (Byström et al. 2003), predation risk from pike would be more severe in perch feeding on benthic prey in the littoral area than those feeding in the pelagic zone (Eklöv & Diehl 1994; Eklöv 1997).

In this study, we wanted to investigate whether perch make trade-offs between feeding and hiding in accordance to size-specific predation risk. We are here considering the fact that the predation risk in the same lake can vary with growth of the potential prey. Previously, differences in risk-taking foraging behaviour have been found in young-of-the-year (0+) perch from lakes differing in predator pressure (Magnhagen 2006). Whether this is due to inherited traits or phenotypic responses to the environment is not known. Here, we study two age classes (0+ and 1+) of perch from two lakes with different size structures of the perch populations to see whether behaviour patterns are persistent over age or change with current predation risk from cannibals in their natural habitat.

METHODS

Study Lakes

We used perch from two populations in this study, from the lakes Fisksjön and Ängersjön, situated close to the city of Umeå (63°47′N, 20°17′E) in northern Sweden. These populations have earlier been investigated regarding population structures, life history (Magnhagen & Heibo 2004; Heibo & Magnhagen 2005) and behaviour (Magnhagen 2006). In Fisksjön, the population consists of a very high density of stunted perch, while in Ängersjön the perch are less abundant, and, on average, of a larger size. The difference in size distribution can partly be explained by a threefold higher density of pike in Ängersjön than in Fisksjön, keeping the density of perch down (Magnhagen & Heibo 2001).

In the end of May 2006, a fishing survey was performed in the lakes of Fisksjön and Ängersjön to look at size distribution and relative densities of the perch populations (J. Borcherding & C. Magnhagen, unpublished data), using Nordic standard survey nets (Appelberg et al. 1995). We used the results of this survey to estimate population-specific predation patterns for different sizes of young perch, using an individual-based model calculating attack rates for cannibalistic perch of different sizes (Persson et al. 2004). The estimated daily attack rate for an individual predator depends both on the size of the predator and victims, and indicates the capacity of the predator to attack prey of different sizes. We estimated attack rates for prey sizes ranging 10–110 mm of total length (TL) corresponding with perch sizes from shortly after hatching and up to the maximum size used in our behaviour study. Individual cannibalistic attack rates (per day) for all perch caught in the 2006 survey were calculated according to their body length (for more information, see Persson et al. 2004; Magnhagen 2006). To illustrate the relative cannibalistic attack rates across size classes in the two lakes, the individual attack rates were added together for each of the two lakes, adjusting for fishing effort (number of nets), and the relative proportions of the summed cannibalistic attack rates for each prey size are shown (Fig. 1). The risk of cannibalism in Fisksjön peaks at a prey size of around 25 mm TL and falls rapidly with increasing size. The risk is lower in Ängersjön than in Fisksjön at smaller sizes, and peaks at 35 mm, but the relative risk switches between the lakes as the potential victims grow larger (Fig. 1). The lake-specific relative risks of cannibalism, averaged for the size ranges of different age classes used in our study, are presented in Table 1. The density of pike could not be estimated in this survey, but earlier fishing surveys showed that the density of pike was about 10% of the density of perch in Ängersjön, while in Fisksjön the number of pike was only 1% of the number of perch caught. Moreover, in Ängersjön the number of pike was three times as high as in Fisksjön (Magnhagen & Heibo 2001).

Behaviour Observations

Perch of two discrete size classes, corresponding to age 0+ and 1+, respectively, were collected on 24 August 2006 with a beach seine, in the lakes Fisksjön and Ängersjön. The fish were transported to Umeå Marine Research Centre, 45 km south of Umeå, where the experiments were performed. In the 100-litre transport vessel, a pump run by a car battery was constantly recirculating and oxygenating the water, and the number of fish never exceeded 120. Before the experiments, the perch were kept in tanks (1 × 1 m and 1 m high) with continuously