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Foraging among cannibals and kleptoparasites: effects of prey size on pike behavior

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The northern pike (*Esox lucius*) is an important and selective piscivore that chooses smaller prey than predicted from energy/time budgets. In a laboratory experiment, we investigated pike predatory behavior to explain this selectivity. Northern pike feeding on different prey sizes in aquaria were observed when foraging alone, when in the presence of chemical cues from similar-sized or larger conspecifics, and when in the presence of conspecifics that were allowed to interact with the focal pike. The results show that prey handling time increases with prey size and that the duration of manipulating and handling prey inflicts a risk of exposure to cannibals and kleptoparasites on the pike. Therefore, the risk of falling victim to cannibals or kleptoparasites increases with prey size. Attracting and experiencing intraspecific interactors can be regarded as major fitness costs. Chemical cues from foraging conspecifics have only minor effects on pike foraging behavior. Furthermore, the ability to strike and swallow prey head first improves pike predatory performance because failing to do so increases handling time. Our findings emphasize the increasing potential costs with large prey and explain previous contradictory suggestions on the underlying mechanisms of behavior, selectivity, and trophic effects of northern pike predation. *Key words:* cannibalism, *Esox lucius,* foraging, kleptoparasitism, northern pike, predation, trade-offs. *[Behav Ecol 10:557–566 (1999)]*

Foraging and avoiding predation may act as conflicting demands (e.g., Sih, 1980). Although any forager should maximize its energy intake, predation may indirectly or directly decrease foraging efficiency and therefore lifetime fitness in the forager (Lima and Dill, 1990). Foragers under the risk of predation should adjust habitat use, diel activity, or diet, for example, to minimize reductions in fitness (e.g., Godin, 1990; Hughes, 1997; Lima and Dill, 1990; Mittelbach, 1986). Predators, too, may be subject to predation threat, and if prey selection affects predation risk, predators should choose prey that minimize risk (Gilliam, 1990).

In many predators, intraspecific predation, or cannibalism, is an important mortality factor that acts as a density-dependent population regulator (Elgar and Crespi, 1992; Fox, 1975; Polis, 1981). Cannibalism may affect population densities and year-class strength through direct, lethal effects, but it may also have indirect, behavioral effects such as changes in habitat use or activity patterns (e.g., Smith and Reay, 1991). Cannibalism may occur at different life stages, from eggs to adults, and between siblings or nonrelated individuals. It has also been shown that the frequency of cannibalism is dependent on factors such as population density, hunger level, and availability of alternative prey (Polis, 1981; Smith and Reay, 1991). Another interaction that may be important among predators is kleptoparasitism (i.e., the stealing of food items from other foragers). The prevalence of kleptoparasitism depends on a number of factors, including, for example, size or dominance differences between foragers, prey size and abundance, forager group size, host aggregation, and risks or costs involved with the behavior (e.g., Bélisle, 1998; Cangialosi, 1991; Elgar, 1989; Higgins and Buskirk, 1998; Hockey and Steele, 1990; Whitehouse, 1997). Both cannibalism and kleptoparasitism are taxonomically widespread behaviors that impose risks and costs on foragers (e.g., Barnard, 1984; Elgar and Crespi, 1992). Mortality through cannibalism and lost foraging opportunities through kleptoparasitism should thus be considered costly in terms of fitness (Barnard, 1992; Elgar and Crespi, 1992), and the risk of such interactions should affect foragers in the same way as risk of predation. In this study we investigated how prey size affects the risk of falling victim to cannibals or kleptoparasites in piscivorous fish. Changes in the probability of intraspecific attacks with changes in prey size should affect prey choice in piscivores; low-risk prey that minimize the risk of cannibalism and kleptoparasitism should be preferred.

Cannibalism is common among piscivorous fish (Smith and Reay, 1991). The northern pike (*Esox lucius*) is an important piscivore in many north temperate freshwater systems, and it is well known that cannibalism is a common feature of pike populations (e.g., Grimm and Klinge, 1996), both within (e.g. Bry et al., 1992; Giles et al., 1986) and between (Craig and Kipling, 1983; Grimm, 1981) cohorts. Further, kleptoparasitism has been observed among pike individuals (Grimm and Klinge, 1996). Pike is a selective predator that feeds on prey sizes well below its upper size-limit (e.g., Hart and Hamrin, 1988; Nilsson and Brönmark, 1999). Pike also prefer shallow-bodied over deep-bodied prey, both within (Nilsson et al., 1995) and between (Hambright et al., 1991; Wahl and Stein, 1988) species. Different aspects associated with handling time, foraging time, and energy gain have been suggested to account for prey selectivity in piscivores, including pike (e.g., Hart and Connellan, 1984; Hart and Hamrin, 1988, 1990; Hoyle and Keast, 1987; Nilsson et al., 1995). However, when given a choice, pike prefer prey that are smaller than predicted by optimal foraging models. These previous studies have used time as currency when evaluating the costs in foraging success with changes in diet. However, pike is an efficient ambush predator (Webb and Skadsen, 1980) that spends relatively little time foraging (e.g., Breck, 1993). Thus, it is somewhat of a paradox that some seconds or, at the most, minutes in manipulation and handling time would make pike prefer small prey instead of larger, energetically more profitable prey. A plausible explanation is that some external factor, acting on handling time, affects prey selectivity (see Gilliam, 1990). Risk of cannibalism and kleptoparasitism may be such factors. Pike are attracted to their prey by visual, chemical, and mechanical cues (Raat, 1988). When pike handle their

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Table 1

Total length, body depth, and mass (means ± SD) of the four prey-size classes (1–4) of crucian carp used in the experiments

	Prey-size class				
	1	2	3	4	4b
Body length (mm)	54.2 ± 1.8	66.1 ± 1.9	75.4 ± 1.4	86.5 ± 1.9	84.3 ± 0.8
Body depth (mm)	14.2 ± 1.8	18.5 ± 1.1	21.4 ± 0.9	24.6 ± 1.3	23.7 ± 0.5
Body mass (g)	2.0 ± 0.3	3.9 ± 0.6	5.5 ± 0.8	8.2 ± 1.0	7.1 ± 0.4

Prey-size class 4b indicates the measures of crucian carp used in an additional experiment with size class 4 prey.

prey, they elicit such signals themselves, through erratic movements and odors released from injured prey. Therefore, long handling times (associated with large and/or deep bodied prey; Nilsson et al., 1995) should incur a risk if conspecifics are within sensory distance of the foraging pike (see Chivers et al., 1996). Consequently, adapting predatory behavior to the presence of potential conspecific interactors should be beneficial.

Here, we measured the effects of prey size and indirect and direct presence of conspecifics on pike predatory behavior and subsequent intraspecific interactions. We hypothesized that increased prey sizes lead to increased handling times and increased exposure to both cannibalism and kleptoparasitism, which should both constitute major costs to the pike. Given that intraspecific interactions are costly, northern pike should alter predatory behavior in the presence of conspecifics. We also examined what effects intraspecific interactions and prey size have on frequency of cannibalism, kleptoparasitism, and prey survival, as well as the drawbacks of nonoptimal striking of prey (i.e., failing to strike and swallow prey head-on).

MATERIALS AND METHODS

The experiments were performed in 300 l aquaria (L×H×D: 120×50×50 cm), that were divided into three compartments: two holding compartments (50×25 cm each) in one end, and an experimental arena (70×50 cm) in the other end. Gray PVC walls separated the compartments, and remotely controlled doors (20×20 cm) were installed between each of the holding compartments and the experimental arena. The bottom of each aquarium was covered with sand. The aquaria were kept at constant light (9:15 h light:dark) and temperature (12±1°C) regimes. Twelve wild-caught focal pike [219.8±13.8 mm (±SD) total length: TL] were each assigned one aquarium and placed in one of the holding compartments. We quantified pike predatory behavior in five different treatments: (1) control; chemical cues from (2) similar-sized or (3) larger conspecifics; and direct interaction with (4) similar-sized or (5) larger pike. The treatments were performed with four prey-size classes (Table 1), each replicated six times with separate pike. Half of the pike participated in treatments 1, 2, and 4, and half in the other. The treatments were completed in numerical order in order to avoid learning, recognition, and subsequent changes in focal pike behavior over the experiment. All trials were filmed using VCR equipment, and the recordings were checked for pike predatory behavior (Table 2).

Control

The focal pike were starved 3–4 days before each trial. At the start of an experiment, one crucian carp (*Carassius carassius*) from a randomly chosen prey-size class was put in a remotely controlled plastic net cylinder (18 cm diam; mesh size: 1.2×1.2 mm) in the center of the experimental arena. The door to the pike was opened, and when the pike had entered the experimental arena, the door was closed and the net cylinder removed, allowing the pike to attack the crucian carp. When the pike had completely swallowed its prey, the trial was over, and the pike was returned to the holding compartment. Predatory behaviors 1–11 in Table 2 were recorded.

Chemical cues

We ran the chemical cues treatments in the same way as the control, but with a conspecific, either larger (382.3±13.7 mm

Table 2

Definitions of predatory behaviors in northern pike recorded in the experiment

Behavior	Definition
1. Enter	Time until the pike had completely entered the experimental arena
2. Inactive	Time spent resting and motionless in the tank, not oriented toward the prey
3. Search	Time spent moving around in the tank, not oriented toward the prey
4. Follow	Time spent following a particular prey after observing it
5. Observe	Time spent motionless, but oriented toward, aiming at a particular prey
6. Miss	Number of unsuccessful attempts to strike the prey
7. Secure time	Time between capture and securing the prey head or tail first into the mouth
8. Hold	Inactive holding of the prey during secure time
9. Manipulation time	Secure time minus hold
10. Handling time	Time between capture and complete ingestion of prey
11. Distance	Distance moved during secure time (DST) and handling time (DHT), respectively
12. Approach	Secondary-pike approaches toward the focal pike
13. Attack	Secondary-pike attacks on the focal pike
14. Lose	Focal pike lost its prey after an attack by the secondary pike

TL) or similar-sized (213.2±15.0 mm TL), in the remaining holding compartment of each aquarium. The secondary pike were not allowed access to the experimental arena at the same time as the focal pike, but were fed crucian carp in the experimental arena before and between trials, allowing for the focal pike to recognize the scent of a foraging conspecific.

Interaction

In the interaction treatments, the focal pike were held in the experimental arenas, while secondary pike (the same as in the chemical cues treatments) were held in one of the holding compartments in each aquarium. In these experiments, the crucian carp were simply dropped into the experimental arena, and as soon as the focal pike had successfully struck its prey, the door to the secondary pike was opened, and the two pike were allowed to interact. A trial was completed when either of the pike had swallowed its prey. Behaviors 7–14 in Table 2 were recorded. After a trial, the secondary pike were changed between aquaria (within each treatment) so that any focal pike did not meet the same conspecific twice. In seven experiments with larger conspecifics, the focal pike were attacked and eaten and thus replaced with similar-sized pike (232.7±12.5 mm TL).

In the trials with large pike interacting with focal pike handling prey from size class 4, half of the larger pike had by chance been cannibalistic in the previous trial. The 3–4 days between trials did not allow for complete digestion of such large prey (Nilsson and Brönmark, personal observations). Because gut fullness generally decreases foraging motivation (e.g., Hart and Hamrin, 1988, 1990), the cannibalistic pike should have been less motivated to feed in the subsequent trial. Therefore, we performed an additional experiment with new pike that had not been feeding on large prey (i.e., other pike) prior to the experiment. In this experiment, focal (242.2±12.0 mm TL) and large (381.2±10.3 mm TL) pike were starved for 3 days before trials, and interaction experiments were run with prey from size class 4 (Table 1).

Prey orientation

We recorded the effects of the orientation of prey in the mouth of the pike after a strike on postcapture predatory behaviors. The results from all treatments were pooled, and behaviors related to handling time (behaviors 7–11 in Table 2) were compared between prey struck and swallowed head-on or other (tail-on or sideways).

Statistical analyses

There was no difference in behavior between pike individuals (Table 3). Thus, pike individuals were pooled in the analyses of effects of treatment and prey size. We analyzed the effects of prey size, chemical cues, and interactions from conspecifics on precapture (behaviors 1–6, Table 2) and postcapture (behaviors 7–11, Table 2) behaviors with MANOVAs with prey-size class and treatment as fixed factors and behaviors as dependent variables. The analyses of precapture effects included data from treatments ‘‘control’’ and ‘‘chemical cues’’ from large and small conspecifics, while analyses on postcapture effects included data from all treatments. However, data from focal pike that did not complete their predatory sequence due to interactions from conspecifics were excluded from analysis. We analyzed the number of approaches and attacks from larger and similar-sized secondary pike during focal pike hold, manipulation, and handling time with *t* tests. Number of approaches and attacks in the interaction treatments were compared between prey-size classes with ANOVAs. Effects of prey orientation in the mouth of the pike on handling-time–related events were evaluated with *t* tests with head first or other direction as independent and each separate behavior as dependent variables. Differences in size class between lost and retained prey, as well as between prey swallowed head first or in other directions were analyzed with Mann-Whitney *U* tests. We conducted all statistical tests using Systat 5.2.1 for the Macintosh (Wilkinson, 1992).

Table 3

MANOVAs of differences in behavior between individual northern pike and the effects of treatment (T) and prey-size class (P) and their interaction (T × P) on pre- and postcapture behaviors of the pike

	Wilks's λ	Hypothesis df	Error df	*F*	*p*
Pike individual	0.007	12	7	7.471	.338
Precapture behaviors					
T	0.705	12	110	1.794	.066
P	0.716	18	156	1.088	.369
T × P	0.567	36	244	0.937	.576
Postcapture behaviors					
T	**0.66**	**20**	**246**	**1.596**	**.054**
P	**0.589**	**15**	**204**	**2.887**	**<.001**
T × P	0.473	60	350	1.011	.458

Significant effects are shown in bold.

Animal care

Pike and crucian carp were caught in the field and directly transported to the Ecology building, Lund University, and acclimatized to laboratory conditions. Before experiments, all pike and crucian carp were kept in large aquaria and fed crucian carp or frozen chironomids, respectively. At the end of the experiments, we returned remaining fish to their natural habitat. The results of the experiment depend on the natural behaviors of the experimental animals. Thus, care was taken to minimize disturbance and stress. The Malmö/Lund Committee for Animal Experiment Ethics examined and commissioned the experimental procedure (permission no. M 32–97) to certify that ethical concerns were complied with.

RESULTS

When the northern pike in our experiments foraged, neither treatment nor prey size had any effects on precapture behaviors (Table 3). Postcapture behaviors, on the other hand, were affected by both treatment and prey size (Table 3). Post-hoc ANOVAs revealed that treatment affected the postcapture behaviors hold and distance moved during handling time (DHT; Table 4, Figure 1c, f). In treatments with chemical cues from both larger and similar-sized pike, as well as during interactions with larger conspecifics, the focal pike decreased holding behavior (Figure 1c). DHT was lower in the control than in the treatments and increased the most in treatments using chemical cues from similar-sized pike and interactions with larger and similar-sized conspecifics (Figure 1f). Prey size affected all postcapture behaviors, generally increasing behaviors with increasing prey size (Table 4; Figure 1a,b,d,e,g,h). There was also a significant interaction effect of treatment and prey size on DHT (Table 4). These results imply that northern pike are reluctant to alter predatory behavior, but that prey size has inevitable effects on the duration of postcapture behaviors.

Table 4

Univariate two-way ANOVA of effects of treatment, prey-size class, and their interaction (T × P) on pike postcapture predatory behaviors

	Treatment		Prey size		T × P	
	p	$F_{4,78}$	p	$F_{3,78}$	p	$F_{12,78}$
Secure time	.103	1.999	**.003**	**5.114**	.254	1.270
Hold	**.037**	**2.690**	**.051**	**2.706**	.732	0.709
Manipulation time	.710	0.535	**.006**	**4.410**	.093	1.659
Handling time	.976	0.118	**.004**	**4.836**	.802	0.639
DST	.272	1.314	**<.001**	**9.306**	.508	0.944
DHT	**.015**	**3.303**	**.003**	**5.180**	**.039**	**1.962**

DST, distance moved during secure time; DHT, distance moved during handling time. Significant effects are shown in bold.

Both large and similar-sized secondary pike approached and attacked foraging focal pike. However, approaches and attacks from larger and similar-sized conspecifics were elicited by different foraging behaviors in the focal pike. Large pike approached and attacked throughout focal pike handling time, as long as the focal pike were active in any way (Figure 2a,b; differing from zero: $p < .01$, df = 23, $t = 2.883$ and $p < .02$, df = 23, $t = 2.638$, respectively). That is, any motion in the focal pike potentially attracted cannibals. When the focal pike were inactive and no motion was detectable, larger conspecifics never approached or attacked (Figure 2a, b). Further, the number of approaches from larger conspecifics differed between prey-size classes handled by the focal pike ($p = .049$, $F_{3,44} = 2.840$), whereas number of attacks did not ($p = .115$, $F_{3,44} = 2.095$; Figure 2c,d). Interestingly, larger pike never approached focal pike handling prey from the smallest

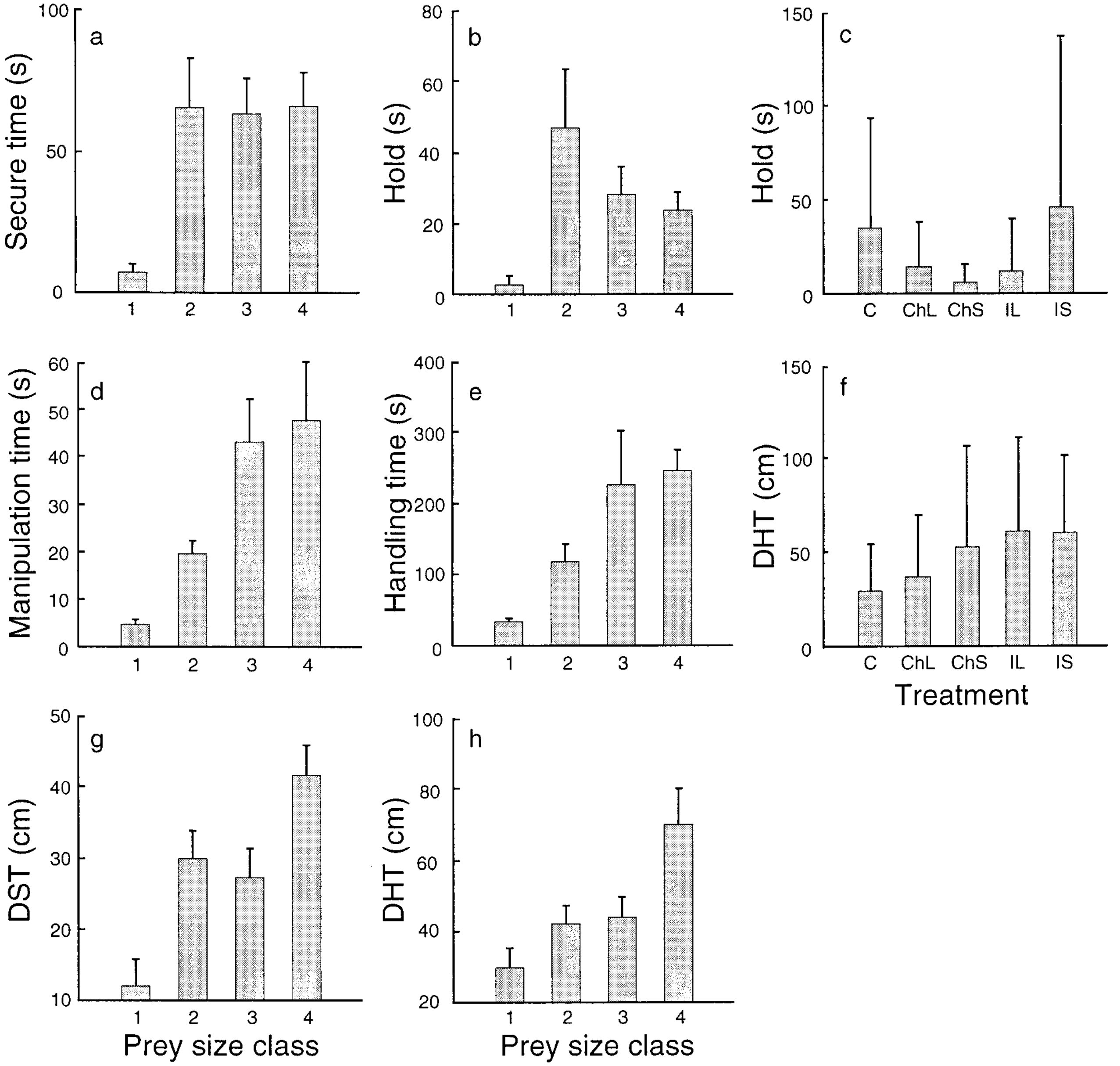

Figure 1

Effects of prey size (four distinctive size classes increasing in size with class number; see Table 1) and presence of conspecifics (C = control, ChL = chemical cues from large pike, ChS = chemical cues from similar-sized pike, IL = interactions with large pike, IS = interactions with similar-sized pike) on northern pike predatory behavior. Error bars denote 1 SE.

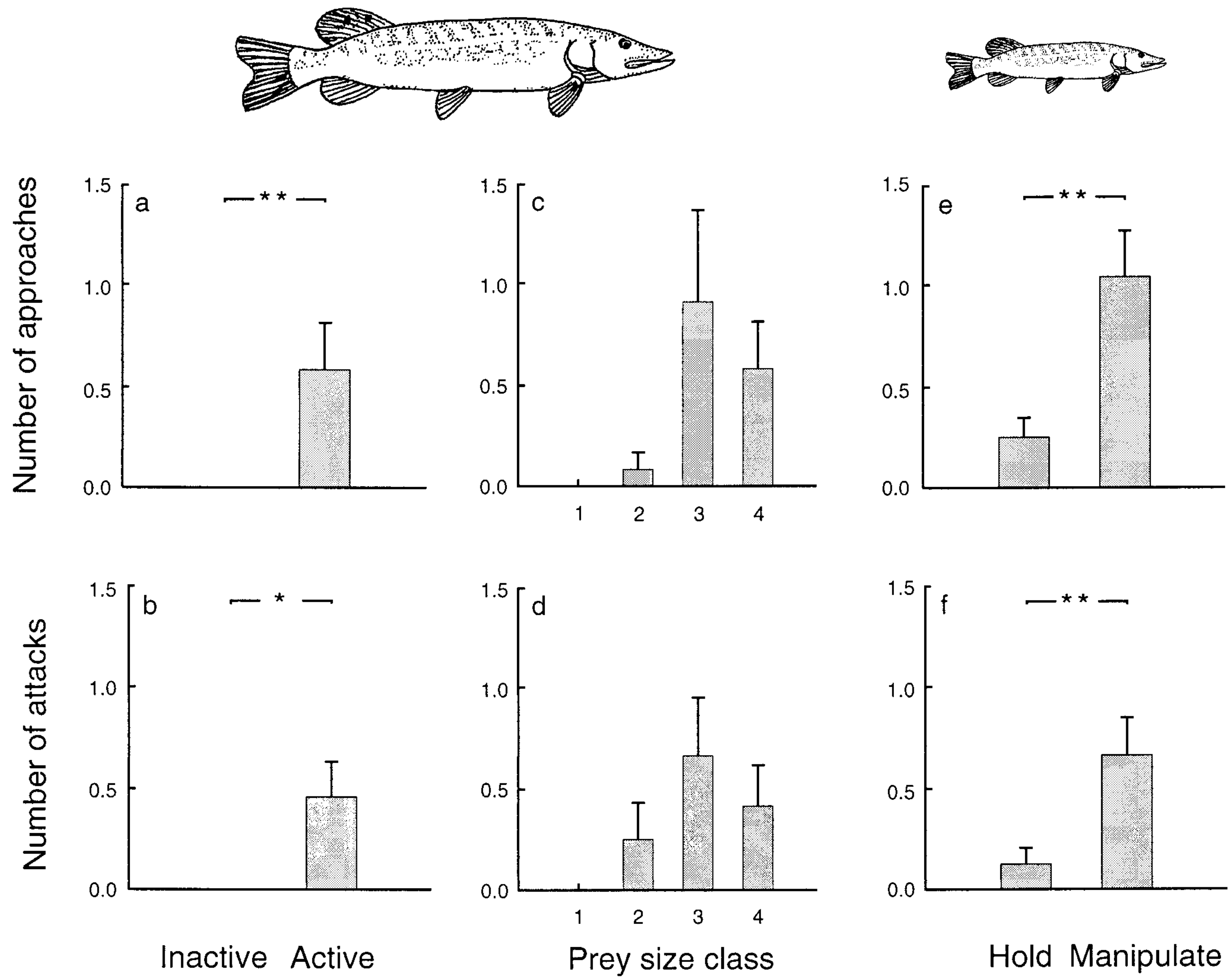

Figure 2
Predatory behavior of northern pike and size of prey handled determine frequency of approaches and attacks from larger and similar-sized conspecifics. Error bars denote 1 SE, and * = $p < .05$ and ** = $p < .01$.

size class (Figure 2c,d). In contrast, for similar-sized secondary pike, there was no effect of prey size on approach or attack frequency ($p = .590$, $F_{3,44} = 0.646$ and $p = .495$, $F_{3,44} = 0.810$, respectively). Showing somewhat different behavioral patterns, similar-sized conspecifics approached ($p = .006$, df = 23, $t = -3.019$) and attacked ($p = .009$, df = 23, $t = -2.849$) focal pike more often when they manipulated their prey (Figure 2e,f), compared to when the prey was held. The larger pike did not show this pattern ($p = .295$, df = 23, $t = -1.071$ and $p = .679$, df = 23, $t = -0.419$, respectively). Further, similar-sized pike never approached focal pike after the prey had been secured head first or tail first into the mouth.

Some of the focal pike lost their prey during interactions with larger conspecifics. There was a tendency that lost prey were larger than those retained, but the difference was not significant ($p = .074$, $n = 24$, $U = 42.0$; Figure 3a). In interactions with similar-sized conspecifics, on the other hand, the difference between lost and retained prey was significant ($p = .006$, $n = 24$, $U = 22.5$; Figure 3b), indicating that the risk of lost foraging opportunity increases with prey size.

The interactions with larger pike led to cannibalism in some cases, and prey size handled by the focal pike affected the risk of cannibalistic interaction. One focal pike was cannibalized when handling prey from size class 1, two when handling size class 2, three with size class 3, and one with size class 4 (Figure 4a). In the additional experiment on interaction with larger pike, where new, nonsatiated pike were used, five of the six small pike were cannibalized when handling prey of size class 4 (Figure 4a). This pattern of increasing risk with increasing prey size also shows in the experiments with similar-sized pike. Focal pike handling prey of size class 1 never lost their prey, while one prey from class 1, four from class 3, and four from prey-size class 4 were lost to kleptoparasites in interactions with similar-sized pike (Figure 4b). In the trials with interactions with larger pike, prey size also had effects on the chance of escape for the prey. One crucian carp from size class 1, one from 2, three from 3, and one from 4, escaped and survived trials with interactions from larger pike because the focal pike let go of them after it was caught (Figure 4c). In the additional experiment, five out of six size class 4 crucians escaped predation after the interaction.

Northern pike predatory performance was affected by the direction of prey in the mouth after a strike. Failing to strike and swallow prey head first significantly increased manipula-

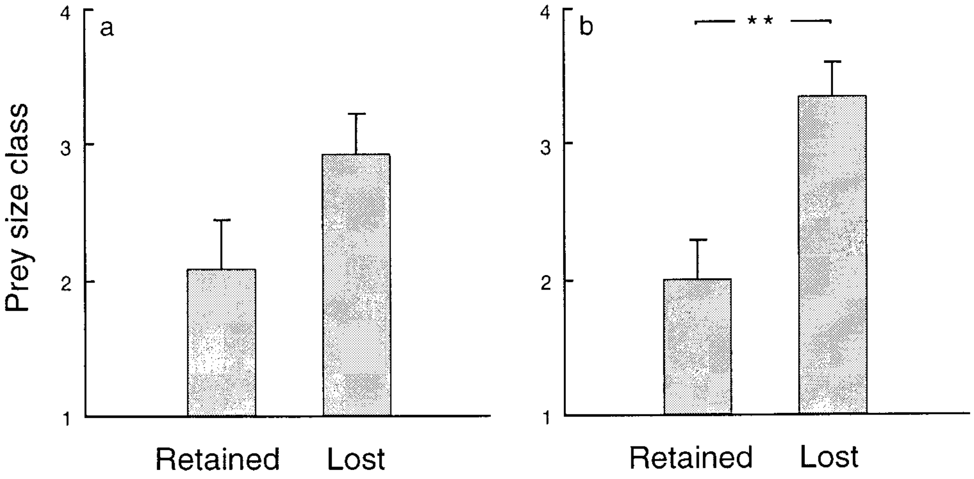

Figure 3
Prey size affects risk of losing prey for northern pike during interactions with larger (a) and similar-sized (b) conspecifics. Error bars denote 1 SE, and ** = $p < .01$.

tion time ($p = .005$, df = 121, $t = -2.862$), handling time ($p = .015$, df = 121, $t = -2.476$), and the time to swallow the prey after securing it ($p = 0.038$, df = 121, $t = -2.098$; Figure 5). Nonoptimal striking and swallowing of prey occurred in about 15% of the trials and was not significantly related to prey-size class ($p = .171$, $U = 1525.5$, $n = 144$).

DISCUSSION

Behavioral interactions

Cannibalism and kleptoparasitism are common in pike populations (e.g., Bry et al., 1992; Grimm, 1981; Grimm and Klinge, 1996; Mann, 1982). To minimize the risk of cannibalism and kleptoparasitism, pike may, for instance, use habitats that lack large conspecifics, forage in patches with low pike density, and generally avoid any behavior that may attract conspecifics. In our experiments, treatments had only minor effects on focal pike predatory behavior, and then only on postcapture events. Chemical cues from conspecifics and interactions from larger pike decreased the time holding the prey. These changes may be due to focal pike avoiding potential competition or risk of cannibalism through minimizing handling time. Treatment, prey size, and their interaction all affected distance moved during handling time. Here, the effect of treatment originates in behavioral interactions and chases from conspecifics that may have made the focal pike increase DHT. Increasing prey size increased the struggle and time elapsed during handling and swallowing, therefore potentially increasing DHT. Thus, both treatment and prey size affect DHT, and because conspecific interactions are more likely with increasing handling time (i.e., increasing prey size), there was also a significant interaction between treatment and prey-size class. Apart from the effects above, treatment did not affect focal pike predatory behavior. However, pike predatory performance diminished when pike were unable to strike and swallow prey head first. Swallowing prey sideways or tail first significantly increased manipulation, handling, and swallowing time. These events are crucial considering the risk of attracting potentially cannibalistic or kleptoparasitic conspecifics. Thus, striking and swallowing prey head first should be advantageous to pike.

Generally, risk of predation and/or chemical cues from potential interactors elicit behavioral changes in prey animals, including behaviors such as escape, avoidance, reduced activity, habitat change, or altered life-history traits (Kats and Dill, 1998; Lima and Dill, 1990). Because there is a trade-off between avoidance of risks and foraging efficiency, any of these behavioral changes should minimize the risk per energy intake (see Gilliam, 1990; Krebs, 1980). Animals that expose themselves to predation when foraging (e.g., while searching or hunting for prey) should optimally choose to minimize this exposure (i.e., decrease foraging intensity or exposure to the risk). Intuitively, pike should therefore adapt foraging strategy to the presence of chemical cues from foraging conspecifics because potential cannibals and kleptoparasites constitute a risk during foraging. However, no such changes in behavior were observed. In nature, pike often live closely together in dense populations (e.g., Raat, 1988) and continuously smell and see conspecifics. Thus, under natural conditions, changing foraging behavior in the presence of other pike may not be optimal regarding foraging efficiency. Because pike with their sit-and-wait foraging behavior already minimize exposure time to conspecifics, changing predatory behavior in response to continuous chemical cues from neighboring pike individuals may not be adaptive.

Cannibalistic and kleptoparasitic pike interact with focal pike during different foraging events. Large pike approach and attack when focal pike emit mechanical and visual cues through motion, whereas similar-sized pike approach and attack primarily when focal pike manipulate their prey while securing it in the mouth. This is probably explained by the fact that large pike do not distinguish between the crucian carp and the smaller pike, but regard them both as a potential package of prey, whereas the similar-sized pike do not have this choice. The similar-sized pike must rely on their ability to steal the prey from the focal pike, and thus approach and attack when the chance of succeeding is the greatest (i.e., when the focal pike manipulates its prey). This phenomenon may also explain why focal pike maintain relatively long holding times during interactions with similar-sized pike, even though this behavior potentially increases handling time. Holding the prey in the presence of similar-sized conspecifics momentarily minimizes the amount of attractive signals emitted and thus decreases the risk of kleptoparasitism. Foragers may thus change and adapt handling time according to the current circumstances, balancing different demands. That is, in the absence of predators, foragers should maximize energy gain per handling time (i.e., generally minimize handling time). While in the presence of a predator, on the other hand, foragers should minimize mortality rate per foraging rate, if necessary by increasing handling time (see Gilliam, 1990). There may also be digestive constraints or demands in the handling time equation. Birds feeding out of cover may minimize handling time to minimize exposure to and risk of predation (Valone and Lima, 1987). When able to handle their food in cover, however, they choose to increase handling time,

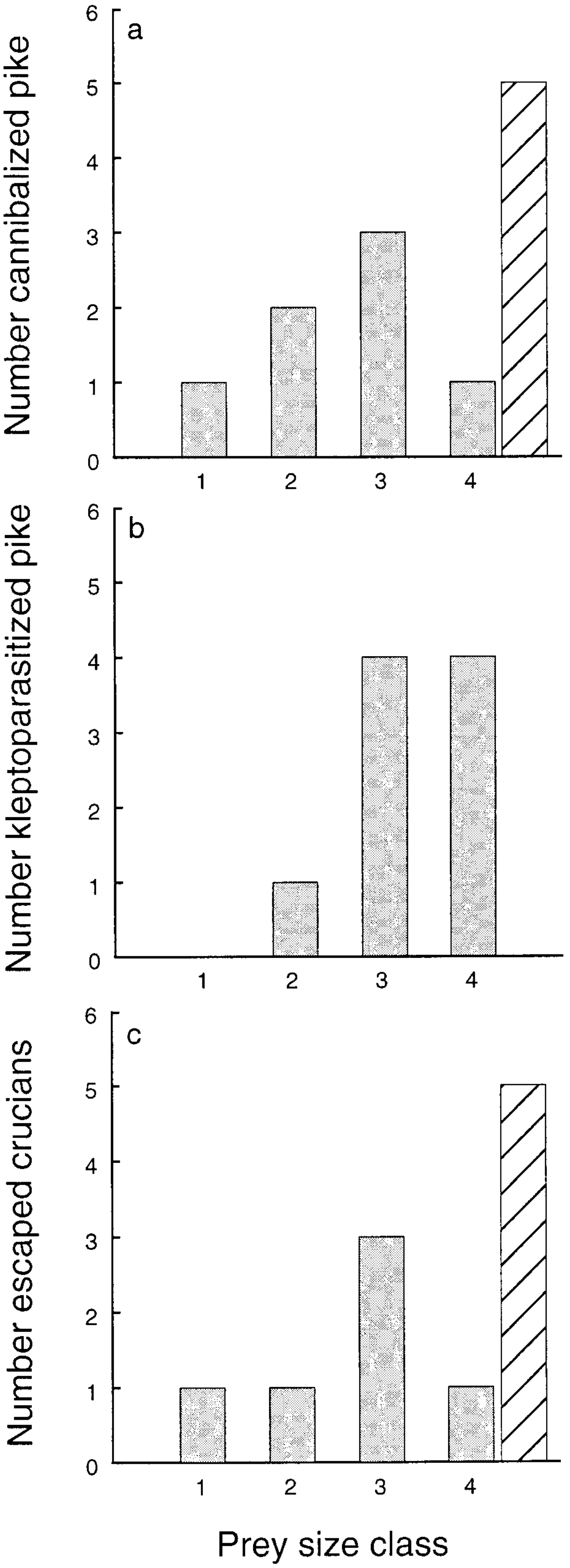

Figure 4
Prey size affects the risk of cannibalism and kleptoparasitism in northern pike and the chances of escape for the prey. Hatched bars indicate results from an additional experiment with prey from size class 4.

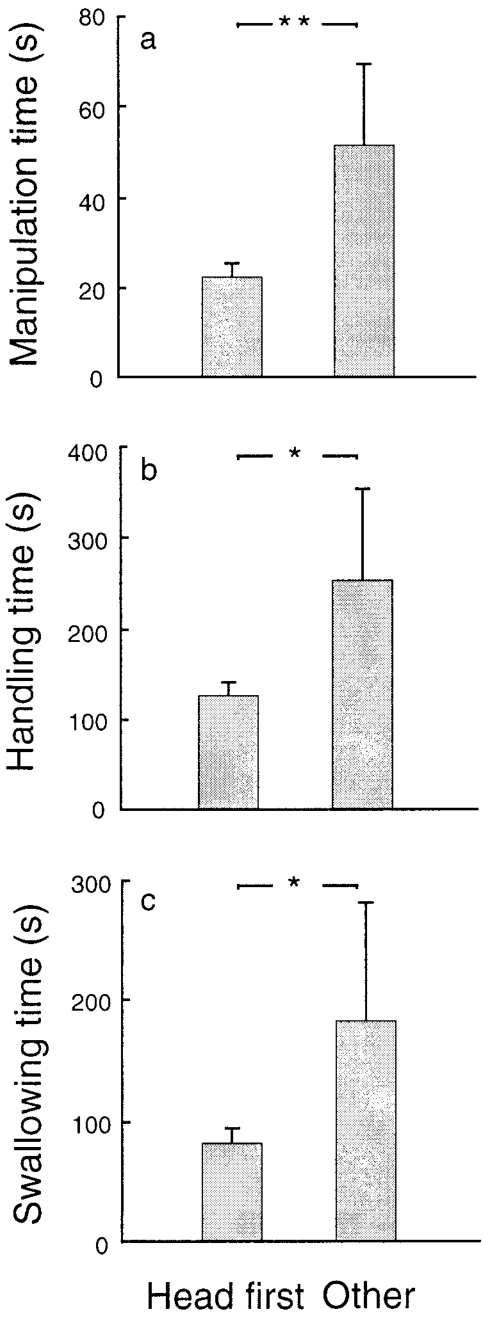

Figure 5
Direction of prey after attack and during swallowing affect predatory performance in northern pike. Error bars denote 1 SE, and * = $p < .05$ and ** = $p < .01$.

breaking up the food in smaller pieces, presumably decreasing digestion time. Thus, optimizing handling time is not always a matter of minimization but is context dependent, and foragers behave accordingly.

In our experiments, we used wild-caught northern pike and crucian carp to experimentally determine effects of prey size on predator behavior and interactions. The experiments were carried out in aquaria, which may confine the behaviors of some animals. However, pike and crucian carp easily adapt to aquarium conditions, and because pike is an ambush predator that moves little during foraging, pike predatory behavior is not seriously constrained by the experimental scale. In natural environments, pike are often associated with the littoral vegetation–open water interface. For logistic reasons, our aquaria did not contain any macrophytes or other structural elements, as any complexity would have seriously interfered with the quantification of behaviors. However, when pike attack their free-swimming prey, they momentarily leave the complex vegetation to forage in open water (e.g., Raat, 1988). Therefore, complexity has little or no effect on the foraging and interactive behaviors measured in this work. Further, cannibalism and kleptoparasitism commonly occur in pike populations in nature (e.g., Grimm and Klinge, 1996). Hence, we conclude that pike behavior was not induced by the experimental setup, rendering our results valid also for natural circumstances.

Risks and costs

The costs involved with experiencing cannibalism and kleptoparasitism are obvious. To stay away from cannibals or at least decrease the risk of attracting them should decrease the risk of mortality. If the risk of being cannibalized increases when taking larger prey, large prey should be avoided. In the initial experiment, the number of cannibalized focal pike increased with prey size in the trials with prey-size classes 1–3. This increasing trend was, however, interrupted with the largest prey-size class, where only one focal pike was cannibalized. We suggest that this latter, somewhat contradictory result is an experimental artifact: in the trials with larger pike interacting with focal pike handling the largest prey, half of the larger pike had cannibalized focal pike in the previous trial. Keeping the original experimental setup with 3–4 days between trials did not allow the cannibals to digest those relatively large prey. Gut fullness generally decreases foraging motivation (e.g., Hart and Hamrin, 1988, 1990), and this resulted in the larger pike taking no notice of the foraging focal pike in the next trial. This artifact should also explain the trend in the number of approaches and attacks on focal pike handling the largest prey, as well as the number of crucian carp escaping predation and surviving trials with interactions with large pike, as chances of escape depend on the focal pike being disturbed by interactions. In the additional experiment, where we reran the trials with interaction from larger pike when focal pike handled prey from size class 4, we used new pike that had been deprived of food for 3 days and thus were motivated to forage. Here, the results clearly show that the largest prey size leads to the greatest risk of cannibalism, as well as the greatest chance of escape for the prey.

Losing an already captured prey is the most direct cost for kleptoparasitized foragers. To avoid this, or any other cost with the interaction, foragers should strive to minimize the risk of kleptoparasitism. Prey size selectivity may be a way of reducing that risk. It has been shown in kleptoparasitic species of birds that the larger the food item, the greater the risk of being parasitized (e.g., Hockey and Steele, 1990). Analogously, the focal pike in our experiments lost prey that were larger than the ones they succeeded in retaining during interactions with kleptoparasites. Further, the frequency of kleptoparasitic events increased with prey size handled. There was also a tendency that focal pike lost larger prey more often in interactions with cannibals. Therefore, large prey items inflict greater risks of losing a meal and should be avoided if the probability of attracting conspecifics is high. Further, when the focal pike were attacked by kleptoparasites, there was often fierce interaction and fight over the prey. Kleptoparasitic pike attack toward the prey in the mouth of the focal pike, and thus risk of contracting injuries to the eyes is prominent. Because pike to a large extent rely on vision when foraging (e.g., Raat, 1988), such injuries may severely decrease future foraging efficiency and ultimately decrease fitness. Fighting with kleptoparasites may inflict further costs. Because fighting increases reaction time and escape reaction distance in case of a predator attack (Jakobsson et al., 1995), engaging in fights over food decreases vigilance and increases risk of attracting and falling victim to predators. Another example of how kleptoparasitism may affect fitness is the wild dog–hyena interactions in South Africa (Gorman et al., 1998). Here, the costs are not necessarily associated with direct injuries, but with energy expenditure. Because wild dogs use a lot of energy when hunting for prey, kleptoparasitism by hyenas not only deprives the wild dogs of their food item, but also of the energy consumed for catching it, thus having large effects on energy budgets.

Prey selectivity

An optimal forager should select prey that contribute the most gain and least cost. Several studies have shown that pike is a selective forager that chooses to feed on small prey (Beyerle and Williams, 1968; Hart and Hamrin, 1988, 1990). Further, pike prefer shallow-bodied prey fish over deeper bodied fish (Hambright et al. 1991, Nilsson et al. 1995, Wahl and Stein 1988). For example, crucian carp may exist in two different morphs, a shallow-bodied morph and deep-bodied morph, where the deep-bodied morph is induced by the presence of piscivores (Brönmark and Miner, 1992; Brönmark and Pettersson, 1994). When given a choice, pike prefer to feed on shallow-bodied, noninduced individuals of crucian carp over predator induced, deep-bodied ones (Brönmark and Miner, 1992; Nilsson et al., 1995). They also prefer shallow-bodied roach (*Rutilus rutilus*) over deep-bodied common bream (*Abramis brama*; Nilsson and Brönmark, 1999). As handling time increases with increasing size and body depth (e.g., Nilsson et al., 1995), pike may be expected to choose prey that minimize handling time per energy input. Yet, pike actually prefer prey fish that are smaller than predicted from optimal foraging models based on energy and time budgets (Hart and Connellan, 1984). The predictions in the models overestimate optimal prey size because they fail to acknowledge that handling time per se does not restrict pike foraging. Pike use an ambush foraging strategy, and the amount of time spent actively pursuing prey is relatively short (e.g., Breck, 1993). However, taking into account that northern pike are exposed to cannibals and kleptoparasites while foraging and that this exposure increases with handling time, which in turn increases with prey size, validates prey size selectivity in pike. The preference for small-bodied prey is thus a result of a trade-off between energy gain and time of exposure to conspecifics (i.e., risk), not in time per se (see Gilliam, 1990; Hughes, 1997; Stephens and Krebs, 1986). Risk of predation has also been shown to affect the food choice of guppies (Godin, 1990). In the absence of predators, guppies fed on prey sizes according to what is predicted from optimal foraging models. Under the risk of predation, however, the guppies changed prey preference to smaller sizes than predicted.

Prey more deep bodied than their neighbors (e.g., induced crucian carp or common bream) benefit from their morphology by being selected against by pike. Also, even if a deep-bodied prey is struck by a northern pike, it may still benefit from its body depth. Postcapture interactions with larger conspecifics made our focal pike lose large prey. Therefore, deep-bodied prey have an increased chance of escape. Out of the total 19 events where large pike actively interacted with focal pike, 13 of the crucian carp escaped and survived. This suggests that being large or deep bodied and thus attracting further pike while being handled is beneficial to the prey. Similarly, Chivers et al. (1996) showed that attacked and injured minnows release alarm substances that attract further predators that may interact with the first. They also showed that these interactions increase the opportunity of prey escape and suggested this as a mechanism behind the evolution of alarm substances in fish.

Effects in natural ecosystems

In natural systems, the risk of cannibalism and kleptoparasitism should vary with density (e.g., Giles et al., 1986) and size structure (Smith and Reay, 1991) of the populations. With increased density, the distance to neighbors decreases, increasing the risk of handling large prey. In stunted populations only the smallest individuals, if any, would risk cannibalism, but kleptoparasitism would be common. In more diversely size-structured populations, cannibalism would be a real risk also for intermediate-sized individuals. One has to bear in mind, however, that the above phenomena should be most prominent in systems with relatively dense populations and somewhat depleted prey abundances. Further, an increased risk involved with handling large or deep-bodied prey should affect prey size selectivity in the predator and subsequently affect population and community dynamics. If predators prefer small prey, prey population size-structure will be skewed. Also, high-cost interference, such as intraspecific interactions in the predator, may have effects on the stability of predator–prey interactions (e.g., Fryxell and Lundberg, 1997). In conclusion, the risk of conspecific attacks may affect predator behavior and therefore behavioral size-refuges for their prey, potentially decoupling top-down impact of predation on trophic interactions (see Hambright et al., 1991).

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REFERENCES

Barnard CJ, 1984. Producers and scroungers. London: Croom Helm.

Barnard CJ, 1992. Parasitic relationships. In: Parasitism and host behaviour (Barnard CJ, Behnke JM, eds). London: Taylor and Francis; 1–33.

Bélisle M, 1998. Foraging group size: models and a test with jaegers kleptoparisitizing terns. Ecology 79:1922–1938.

Beyerle GB, Williams JE, 1968. Some observations of food selectivity by northern pike in aquaria. Trans Am Fish Soc 97:28–31.

Breck JE, 1993. Foraging theory and piscivorous fish: are forage fish just big zooplankton? Trans Am Fish Soc 122:902–911.

Brönmark C, Miner JG, 1992. Predator-induced phenotypical change in body morphology in crucian carp. Science 258:1348–1350.

Brönmark C, Pettersson LB, 1994. Chemical cues from piscivores induce a change in morphology in crucian carp. Oikos 70:396–402.

Bry C, Basset E, Rognon X, Bonamy F, 1992. Analysis of sibling cannibalism among pike, *Esox lucius,* juveniles reared under semi-natural conditions. Environ Biol Fish 35:75–84.

Cangialosi KR, 1991. Attack strategies of a spider kleptoparasite: effects of prey availability and host colony size. Anim Behav 41:639–647.

Chivers DP, Brown GE, Smith RJF, 1996. The evolution of chemical alarm signals: attracting predators benefits alarm signals senders. Am Nat 148:649–659.

Craig JF, Kipling C, 1983. Reproduction effort versus the environment: case histories of Windemere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. J Fish Biol 22:713–727.

Elgar MA, 1989. Kleptoparasitism: a cost of aggregating for an orb-weaving spider. Anim Behav 37:1052–1054.

Elgar MA, Crespi BJ, 1992. Cannibalism: ecology and evolution among diverse taxa. Oxford: Oxford University Press.

Fox LR, 1975. Cannibalism in natural populations. Annu Rev Ecol Syst 6: 87–106.

Fryxell JM, Lundberg P, 1997. Individual behavior and community dynamics. London: Chapman and Hall.

Giles N, Wright MR, Nord ME, 1986. Cannibalism in pike fry, *Esox lucius* L.: some experiments with fry densities. J Fish Biol 29: 107–113.

Gilliam JF, 1990. Hunting by the hunted: optimal prey selection by foragers under predation hazard. In: Behavioural mechanisms of food selection (Hughes RN, ed). NATO ASI Ser G 20:797–819.

Godin J-GJ, 1990. Diet selection under the risk of predation. In: Behavioural mechanisms of food delection, (Hughes RN, ed). NATO ASI Ser G 20:739–770.

Gorman ML, Mills MG, Raath JP, Speakman JR, 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyenas. Nature 391:479–481.

Grimm MP, 1981. Intraspecific predation as a principal factor controlling the biomass of northern pike (*Esox lucius* L.). Fish Manage 12:77–79.

Grimm MP, Klinge M, 1996. Pike and some aspects of its dependence on vegetation. In: Pike: biology and exploitation (Craig JF, ed). London: Chapman and Hall; 125–156.

Hambright KD, Drenner RW, McComas SR, Hairston NG Jr, 1991. Gape-limited piscivores: planktivore size refuges, and the trophic cascade hypothesis. Arch Hydrobiol 121:389–404.

Hart P, Hamrin SF, 1988. Pike as a selective predator. Effects of prey size, availability, cover and pike jaw dimensions. Oikos 51:220–226.

Hart PJB, Connellan B, 1984. Cost of prey capture, growth rate and ration in size in pike, *Esox lucius* L., as functions of prey weight. J Fish Biol 25:279–292.

Hart PJB, Hamrin SF, 1990. The role of behaviour and morphology in the selection of prey by pike. In: Behavioural mechanisms of food selection (Hughes RN, ed). NATO ASI Ser G 20:235–254.

Higgins LE, Buskirk RE, 1998. Spider-web kleptoparasites as a model for studying producer–consumer interactions. Behav Ecol 9:384–387.

Hockey PAR, Steele WK, 1990. Intraspecific kleptoparasitism and foraging efficiency as constraints on food selection by kelp gulls Larus dominicanus. In: Behavioural mechanisms of food selection (Hughes RN, ed). NATO ASI Ser G 20: 679–706.

Hoyle JA, Keast A, 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). Can J Zool 65:1972–1977.

Hughes RN, 1997. Diet selection. In: Behavioural ecology of teleost fishes (Godin J-GJ, ed). Oxford: Oxford University Press; 134–162.

Jakobsson S, Brick O, Kullberg C, Escalated fighting behavior incurs increased risk of predation. Anim Behav 49:235–239.

Kats LB, Dill LM, 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Écoscience 5:361–394.

Krebs JR, 1980. Optimal foraging, predation risk, and territory defence. Ardea 68:83–90.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640.

Mann RHK, 1982. The annual food consumption and prey preferences of pike (*Esox lucius*) in the river Frome, Dorset. J Anim Ecol 51:81–95.

Mittelbach G, 1986. Predator-mediated habitat use: some consequences for species interactions. Environ Biol Fish 16:159–169.

Nilsson PA, Brönmark C, 1999. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. Oikos (in press).

Nilsson PA, Brönmark C, Pettersson LB, 1995. Benefits of a predator-induced morphology in crucian carp. Oecologia 104:291–296.

Polis GA, 1981. The evolution and dynamics of intraspecific predation. Annu Rev Ecol Syst 12:225–251.

Raat AJP, 1988. Synopsis of the biological data on the northern pike, *Esox lucius* Linnaeus, 1758. FAO Fish Synop 30 Rev. 2.

Sih A, 1980. Optimal behavior: can foragers balance two conflicting demands? Science 210:1041–1043.

Smith C, Reay P, 1991. Cannibalism in teleost fish. Rev Fish Biol Fish 1:41–64.

Stephens DW, Krebs JR, 1986. Foraging theory. Princeton: Princeton University Press.

Valone TJ, Lima SL, 1987. Carrying food items to cover for consumption: the behavior of ten bird species feeding under the risk of predation. Oecologia 71:286–294.

Wahl DH, Stein RA, 1988. Selective predation by three esocids: the role of prey behavior and morphology. Trans Am Fish Soc 117:142–151.

Webb PW, Skadsen JM, 1980. Strike tactics of *Esox*. Can J Zool 58: 1462–1469.

Whitehouse MEA, 1997. The benefits of stealing from a predator: foraging rates, predation risk, and intraspecific aggression in the kleptoparasitic spider *Argyrodes antipodiana*. Behav Ecol 8:663–667.

Wilkinson L, 1992. SYSTAT: the system for statistics. Evanston, Illinois: Systat.