Cooperation under predation risk: experiments on costs and benefits

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SUMMARY

Two fish that cooperatively inspect a predator may have negotiated the share of the risk that each takes. A test of both the costs of predator inspection dependent on the distance from which the predator is approached and the potential benefits of cooperation was carried out strictly experimentally. We made either singletons or pairs of dead sticklebacks, *Gasterosteus aculeatus*, approach hungry pike, *Esox lucius*, by remote control according to an algorithm that mimicked natural inspection. The predation risk of both single inspectors and parallel inspecting pairs increased with closer inspection distances. A member of an inspecting pair had only about half the risk of that of a single inspector. In pairs, a companion diluted the lead fish's risk of being caught, depending on its distance behind the leader. The absolute risk difference between leader and follower was greatest for close inspection distances and decreased further away from the predator. The leader's relative risk increased with its distance ahead of the laggard. However, for a given distance between leader and laggard, the relative risks to the two fish remained similar with distance from the predator. The cost side of the inequalities that define a 'Prisoner's Dilemma' has thus been measured for this system. In a second experiment the 'attack deterrence hypothesis' of predator inspection (i.e. inspection decreases attack probability) was tested. The pike was offered a choice between two sticklebacks, one of which had carried out a predator inspection visit. There was no indication of attack deterrence through predator inspection.

1. INTRODUCTION

Small fish often approach a detected predator to obtain information about the pending risk (Magurran & Girling 1986; Pitcher *et al.* 1986; Magurran 1990; Pitcher 1992). Although inspecting predators appears risky there is no direct evidence that inspectors are at risk of being attacked (Magurran 1990; Magurran & Seghers 1990; Dugatkin 1992; Pitcher 1992); it is claimed that they may even gain from pursuit deterrence (Magurran 1990; Vega-Redondo & Hasson 1993; Godin & Davis 1995; but see Milinski & Boltshauser 1995). Since inspectors prefer to have a companion nearby and make their further approach conditional on the other one's continued cooperation (Milinski 1987; Dugatkin 1988; Milinski *et al.* 1990; Dugatkin & Alfieri 1991) the companion potentially dilutes the risk (Milinski 1987). The causal relationship between inspection distance and risk of death remains to be determined experimentally both for single inspectors and for pairs in which one fish lags behind at various distances.

The pike is a perfectly designed sit-and-wait predator that strikes at its prey with high powered and hydrodynamically efficient bursts of acceleration (Webb 1982; Frith & Blake 1995). The hunting behaviour of pike can be reliably studied under lab conditions (Webb 1982; Frith & Blake 1995; Hart & Hamrin 1988). Its prey has evolved counteradaptations such as vigilance, fleeing ability, seeking information about the predator's current state, or, possibly, pursuit deterrence (Webb 1982; Magurran & Girling 1986; Pitcher *et al.* 1986; Magurran & Pitcher 1987; Magurran 1990; Pitcher 1992; Vega-Redondo & Hasson 1993). Individual fish carry out predator inspection visits, probably to seek information, either singly or jointly with one or a few companions (Magurran & Girling 1986; Pitcher *et al.* 1986; Magurran 1990; Pitcher 1992). Cooperative predator inspection could be a model case for understanding the negotiations by partners in a 'Prisoner's Dilemma' (Milinski 1987; Dugatkin 1988; Milinski *et al.* 1990; Dugatkin & Alfieri 1991). To measure the benefit of cooperation the predation risk of single inspectors has to be compared with that of pairs at different inspection distances. Lagging behind by one partner may be either a deceptive strategy that diverts the risk towards the lead fish, or a cooperative result of negotiations.

In order to determine whether and when the inequalities that define a 'Prisoner's Dilemma' (Axelrod & Hamilton 1981) are fulfilled for inspecting pairs, a test of the costs of predator inspection and the potential benefits of cooperation must be carried out strictly experimentally. Individuals with higher fleeing ability that approach the predator more closely because they can flee better may be caught less frequently than more cautious fish that flee less well. Such correlational evidence cannot uncover the causal relationship between predation risk and inspection distance (Milinski 1997). Randomly chosen individuals have to be assigned to different approach and partner distances. The aim of the first experiment was to compare the risk of single inspectors being attacked with that of pairs in relation to their inspection distance from the pike. If inspectors in pairs have a lower per capita risk (through confusion or dilution effects), the experiment should determine how this benefit is shared by the two fish when one fish lags behind the other fish by various distances.

In the second experiment the 'attack deterrence hypothesis' (inspection lowers the probability of the predator's attack) of predator inspection was tested. For such a test one cannot measure the fate of sticklebacks that select inspection distances themselves since this may reflect individual fleeing abilities (Milinski & Boltshauser 1996; Külling & Milinski 1992; Milinski 1997). In a strictly experimental test one has to present the predator with two equal-sized fish, one of which (determined randomly) is made to approach the predator and then returns to the other fish; both then wait side-by-side at the same distance until the predator strikes. The fish differ only in that one of them has carried out a predator inspection visit. If predator inspection has an attack deterrence function the predator is predicted to preferentially attack the fish that had not approached.

This study manipulates distance from predators and distances between inspectors experimentally using dead 'inspecting' sticklebacks with live pike.

2. METHODS

(*a*) *Experiment 1: costs and benefits of cooperative predator inspection*

Figure 1 shows the experimental set-up used. Each of six wild-caught pike (mean length ± s.d.: 32.7 ± 2.3 cm) was acclimatized to the experimental tank (area 156 cm × 50 cm, height 44.7 cm, bottom covered with brown gravel, two parallel fluorescent tubes above the tank over its whole length, 16L:8D illumination) during six weeks and fed as under experimental conditions. Thereafter, each pike was tested with a six-day programme of 'inspections' with dead sticklebacks in a randomized sequence, i.e. on two days 'inspection' by a single stickleback, on one day by a pair that moved in parallel, on one day by a pair of which one fish lagged behind by 2.5 cm, on another day by 5 cm (about one body length), and on another day by 7.5 cm, all repeated weekly for six consecutive weeks. On each day the sticklebacks inspected the pike up to 11 times, each time to a different distance, i.e. 10 cm, 15 cm, 20 cm, etc., to 60 cm, in random sequence until the pike caught a stickleback. The sticklebacks (whenever possible from our own culture) were of a similar length (mean length ± s.d.: 4.6 ± 0.1 cm), were sacrificed just before each trial and mounted (below and along the spinal column) on a thin flexible wire curved sinusoidally in order to fix the fish's position and prevent rotation. The flexible wire was attached to a stiff wire at right angles. This wire was attached to a pressure cylinder which was moved on guide rails above the tank (above the fluorescent tubes) by a motor at a speed of 2.34 cm s^{-1}, i.e. the sticklebacks' natural inspection speed (Milinski, unpublished data). The whole apparatus was attached to the wall and thus had no connection to the tank. Pairs were attached to one cylinder with a lateral distance of 6 cm. The position (left or right trail on each side of the tank) of the leading fish of pairs was randomized. Although the four sticklebacks to be used for each trial with pairs were of a similar size, they were randomly assigned to the roles of leader or laggard.

Single or pairs of sticklebacks were positioned in dark starting chambers with slits for the fish to enter the tank at both ends. Those farthest from the pike were moved towards the pike until the inspection distance was reached (they started when the pike was facing them and stopped whenever the pike moved forward). When they had reached the predetermined inspection distance, they waited between 1 and 3 s (randomized) and then flew upwards (lifted by the pressure cylinder at a speed of 30 cm s^{-1} until above the surface) and were moved back to the start. The procedure mimicked the behaviour of sticklebacks that rush back after an inspection visit (Milinski 1987); sometimes stickbacks swim backwards over the first cm, then turn and rush back, which could not be simulated. If the pike's snout-tip had passed the middle of the tank, the stickleback(s) from the other side were used for the next inspection visit (after the pike had turned so that it could see the approaching prey) so that there was always at least a distance of half the length of the tank between the pike and the starting fish. The procedure was remotely controlled from a video screen that was visually isolated from the set-up. A video camera viewed the tank from the front. One person moved a Plexiglas plate (which had markings for both the stickleback's snout-tip and the inspection distance) on a guide rail on the screen synchronously with the image of the stickleback (or the leading fish of pairs) until the marking for the inspection distance had reached the tip of the pike's snout. There were individual Plexiglas plates for each inspection distance and trail. A second person operated the motors for the movement of the stickleback(s) and the pressure cylinder (which had an oval diameter, so that the stickleback's axis could not deviate from the forward direction). All speeds were preset. All data were taken from a Sony U-matic video record.

(*b*) *Experiment 2: does predator inspection have an attack deterrence function?*

This experiment was done with the same set-up and the same six pike from the first experiment. Between experiments 1 and 2 there was a pause of several weeks during which the pike were fed dead sticklebacks that were offered as in experiment 1 except that they were not made to inspect the pike (only moved into the tank to wait until the pike struck). The pike attacked these fish readily. In experiment 2, two dead sticklebacks of similar size were moved in parallel (attached to different cylinders on different guide rails) out of the starting chamber from which the pike was farthest away. They started when the pike faced that chamber. At a distance of 10 cm from the chamber one fish automatically stopped

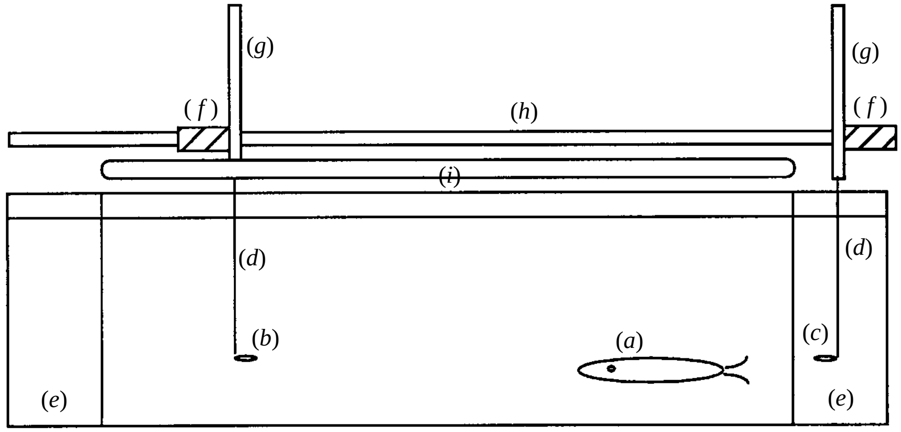

Figure 1. Set-up for singleton inspection experiment (pike (a), stickleback moving toward pike during trial (b), stickleback in starting chamber (c), stiff wire (d), starting chamber (e), machinery for moving along guide rail (f), pressure cylinder (g), guide rail (h), fluorescent tube (i)); see text for further explanations.

(there was a stopping device on the guide rail) and the other continued to approach the pike further either for 5 cm (when the pike was between 63 and 78 cm away from this end), for 7.5 cm (when the pike was between 78 and 93 cm away), for 15 cm (when the pike was between 93 and 125 cm away) or 20 cm (when the pike was more than 125 cm away). By using these relatively long inspection distances (the distance between the inspector and the pike) we wanted to reduce the probability of capture of the inspector during inspection or on its way back to its waiting companion. After the inspection distance had been reached the inspector was moved backwards at the same speed at which it had been moved forward. Live sticklebacks often swim slowly backwards over short distances until they finally rush back. The inspector was automatically stopped (by a stopping device that was attached to the pressure cylinder above the waiting fish) when it was exactly parallel to its waiting companion. Both fish waited for 1 min (when the pike was further than 63 cm away from this end), for 2 min (when the pike was between 63 and 30 cm away), or for 5 min (when the pike had come closer than 30 cm), thereafter they were moved back into the starting chamber. When the pike had turned to face the other end a new trial started with the pair of sticklebacks from the other starting chamber. This was repeated until the pike caught a stickleback, but at most for 15 times (which rarely occurred). Which of the two fish became the inspector was determined randomly on each day. This was repeated on six days per week for three consecutive weeks with each pike.

3. RESULTS

(*a*) *Experiment 1*

The pike caught sticklebacks by acceleration strikes at a speed that was similarly high (mean ± s.e. speed during the last 10 cm: $0.68 \pm 0.12\ \mathrm{m\,s^{-1}}$) as in other studies (Webb 1982; Frith & Blake 1995). Their attack behaviour did not seem to change during the experiment (correlation between mean speed during last 10 cm of a strike and day in experiment: $r_s = -0.05 \pm 0.09$, mean ± s.e., $n = 6$, n.s.). The strike occurred usually during the first five inspections and was unpredictable for the observer. Pike stalked without obvious fin movements and struck suddenly without obvious warning. Strikes sometimes covered 50 cm.

Figure 2*a* shows the experimentally determined cost functions (risk of 'death' in relation to inspection distance) of both single inspectors and the average member of a parallel pair. The absolute risk to both single inspectors and parallel inspecting pairs increased with closer inspection distances (table 1). The risk to single inspectors came close to 0.9 for the shortest distances. Due to risk dilution (the pike never caught both fish) the risk per fish of inspecting pairs approached 0.5 for the closest inspections and was significantly lower over all inspection distances than that of single inspectors (figure 2*a*, table 1). With increasing distance between the inspectors the relative risk to the follower decreased at the expense of the leading fish (see figure 2*b*, which shows the effect of the distance between the leader and the follower averaged over all inspection distances): a companion had almost the same risk as the lead fish when it lagged not more than half a body length behind. Lagging behind by 1.5 body lengths (7.5 cm) still reduced the leader's risk (Wilcoxon one-sample test, $z = -2.121$, $n = 6$, $p < 0.035$, two-tailed) although the lead fish had almost 90% of the total risk. At a given strike, pike rarely missed a prey (mean ± s.d. success rate: $90.02 \pm 3.80\%$; although the prey took evasive action by being lifted upwards by the pressure cylinder we do not know whether live sticklebacks are similarly successful).

Did the relative risk to the leader and the follower change with inspection distance? When the relative risk to the leader on the shorter (10–30 cm) inspection distances was compared with its relative risk on the longer (35–60 cm) inspection distances averaged over all the three distances between inspectors (i.e. 2.5 cm, 5 cm, 7.5 cm) there was no obvious difference (mean ± s.e. relative risk to the leader for short inspection distances: 0.732 ± 0.036, for long inspection distances: 0.726 ± 0.059). To enhance the probability

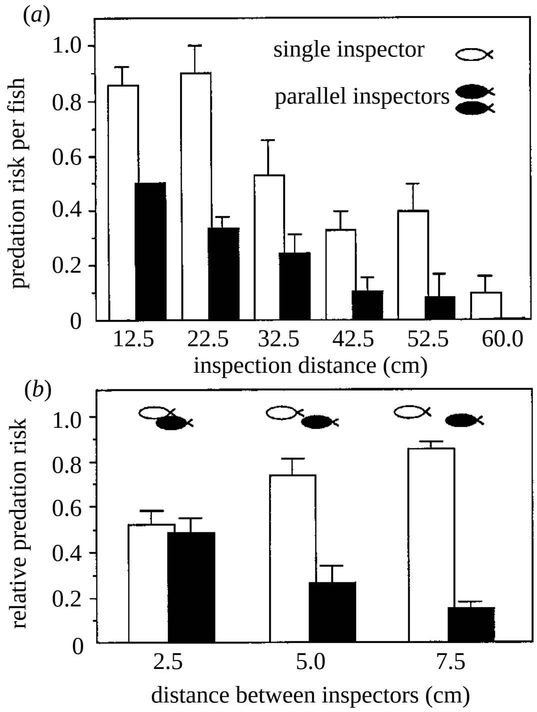

Figure 2. (*a*) Mean (+ s.e.) predation risk per fish of single inspectors (open bars) and two parallel inspectors (black bars) at different distances from the pike predator (distances 10 and 15 cm, 20 and 25 cm, 30 and 35 cm, 40 and 45 cm, 50 and 55 cm, respectively, were pooled). (*b*) Mean (+ s.e.) relative predation risk to the lead (open bars) and the laggard fish (black bars), expressed as (risk to individual)/(sum of risks to both fish), when the distance between inspectors varied between 2.5 and 7.5 cm. At a distance of at least 5 cm from the laggard the lead fish had a significantly higher risk (Wilcoxon signed-rank matched-pairs test, $z = -2.032$, $n = 6$, $p < 0.045$, two-tailed).

of finding an effect of inspection distance, we omitted the data for the short distance of 2.5 cm between inspectors because it showed no obvious difference in the relative risk to the leader and the follower. Again, there was no obvious effect of inspection distance on relative risk (mean ± s.e. relative risk to the leader for short inspection distances: 0.815 ± 0.046, for long inspection distances: 0.800 ± 0.109; Wilcoxon matched-pairs signed-ranks test, $z = -0.105$, $n = 6$, $p = 0.917$, two-tailed). Thus, relative risks remained similar over different inspection distances, although the relative risk to the leader increased with increasing distance from the follower (figure 2*b*). Since the absolute risk decreases with longer inspection distances (i.e. distance to the predator, see figure 2*a*) we expect that the absolute risk difference decreases with increasing inspection distance. Figure 3*a* shows that the risk difference (the leader's minus the laggard's risk) depended on the inspection distance as expected. Although the risk difference increased with the distance between the leader and the follower, it decreased with the inspection distance: the absolute risk to the leader and the follower became more similar further away from the predator. Both the slopes of the regression lines of the risk difference in relation

Table 1. *Fully factorial ANOVA (arcsine transformed data) for inspection distance (10–30 cm or 35–60 cm) and group size (single or pair) on per capita predation risk, with, in addition, pike included as a factor*

source	sum of squares	d.f.	F-ratio	p
distance	0.159	1	57.743	< 0.001
group	0.194	1	70.672	< 0.001
pike	0.050	5	3.620	= 0.024
distance ∗ group interaction	0.010	1	3.742	= 0.072
error	0.041	15		

to the leader minus the laggard distance (figure 3*b*) and their y-intercepts (figure 3*c*) differed significantly from zero.

(*b*) *Experiment 2*

Although the experimental situation was arranged in such a way (long inspection distances) that the pike is likely to attack only when the inspector has returned to its waiting companion, pike struck during inspections in 33% of cases. In this situation they preferred the inspector in more than 90% of cases (figure 4). This preference was significant (Wilcoxon one-sample test, $z = -2.264$, $n = 6$, $p < 0.025$, two-tailed). When the pike struck after the inspector had returned to its companion (i.e. the test condition for attack deterrence), there was, if anything, a slight tendency to prefer the inspector (Wilcoxon one-sample test, $z = -0.944$, $n = 6$, $p = 0.35$, two-tailed). Thus, there is no indication that predator inspection has any attack deterrence function (figure 4). If we were to regard the 85 cases in which the pike struck after the inspector had returned to its companion as independent cases and perform a power analysis, we obtain (for $n = 85$, $\alpha_2 = 0.05$, medium effect size $g = 0.15$) power = 0.88 (which fulfils the convention of 0.80 for accepting the null hypothesis (Cohen 1988)). Thus, we had enough power to detect an attack deterrence effect if it existed.

4. DISCUSSION

Our experimental results demonstrate that the cost of predator inspection is a deadly risk of predation that increases with closer approach distances. The risk is diluted by a companion even if it lags behind the leader by as much as 1.5 body lengths. The laggard fish's proportion of risk, however, decreases with its distance behind the leader. Since the lead fish's further approach is conditional on the other fish's following (Milinski 1987; Dugatkin 1988), and the laggard's following is conditional on the leader's further approach (Milinski *et al.* 1990; Dugatkin 1991; Külling & Milinski 1992), this scenario appears to be a stage for negotiations. Recent evidence suggests that fish are capable of complex

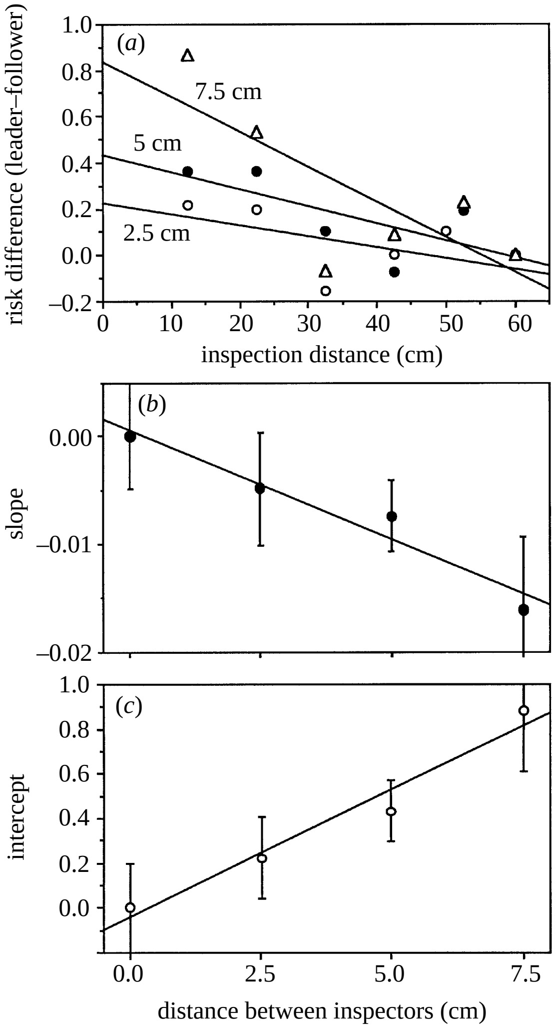

Figure 3. Analysis of risk difference between the leading and the following sticklebacks. (*Caption continued opposite.*)

Figure 3. *Cont.* (a) Risk difference (the leader's probability of capture minus the follower's probability of capture) in relation to the distance of the lead fish from the pike. The three lines are best fit linear regressions to the three distances, d, between the leader and the follower: 2.5 cm (open circles), 5 cm (filled circles), 7.5 cm (triangles). (b) Regression of the slopes of the lines derived in (a) against the distance d between the leading and the following sticklebacks. The best fit line takes account of the standard deviations. In addition, data from the experiment with paired inspectors equidistant from the pike ($d = 0$) were used to generate a comparable standard deviation for the point $d = 0$ with slope $= 0$ (there can be no difference in risk if $d = 0$) in the following way. Working through the data with $d = 0$, each stickleback was randomly assigned to the role of 'leader' or 'follower', and the outcome of the trial noted. The probabilities of capture of the arbitrary leader and the follower at each distance from the pike were then calculated, and the best fit regression obtained as for all the other data in (a). This procedure was repeated ten times, and the average value of the standard deviation calculated. This generated four points with standard deviations, through which the best fit line is plotted. The slope of this regression is significantly different from zero ($t = 7.4$, $p = 0.018$). Thus the slopes of the lines in (a), together with the $d = 0$ data, become significantly steeper as distance d increases. (c) Regression of the intercepts of the lines derived in (a) against the distance between the leading and following sticklebacks. The best fit line takes account of the standard deviations. In addition, data from the experiment with paired inspectors equidistant from the pike ($d = 0$) were used to generate comparable standard deviations for the point at $d = 0$ with intercept $= 0$ in exactly the same way as that explained for the slope in (b). The best fit line is plotted between the four points. The slope of the regression is significantly different from zero ($t = 8.5$, $p = 0.014$). Thus the intercepts of the lines in (a), together with the $d = 0$ data, show a significant increase as d increases.

strategic behaviour (Dugatkin & Sih 1995). In a companion paper (Parker & Milinski 1997) the present data are used in models that seek ESS inspection distances of both single inspectors and pairs. ESS inspection distances existed and were shorter (closer to the predator) for cooperative pairs than for single inspectors. A zone of stable inspection distances was found for pairs behaving non-cooperatively. For two equal fish the best response of a given player in this range is to 'match' the inspection distance played by his opponent. The dynamics are, however, very complex.

In inspecting pairs the follower's share of the risk decreased with its distance from the leader; it approached 50% when this distance was half a body length, and dropped to about 10% at 1.5 body lengths (figure 2b). This implies that the follower is risk-free when its distance behind the leader is greater than two body lengths. This finding has consequences for the definition of 'inspection-group size' (fish that belong to a group that inspects a predator) if the definition is based on the assumption that every group member takes a share of the risk. Thus, our results suggest that for sticklebacks and pike the usual definition 'groups whose members were four body lengths or less apart' (see, for example, Magurran & Pitcher (1987); many other studies used five body lengths) overestimates inspection group sizes. For this and similar systems we propose here that inspection group size should be defined by a distance of at most two body lengths between fish. Any fish that lags behind the leader by more than two body lengths may share benefits (e.g. information) but it does not share the risk. Such fish would be called 'defectors' in a 'Prisoner's Dilemma'.

It is interesting that although the follower's relative risk increased with its distance from the leader (figure 2b) it did not appear to depend on the inspection distance (i.e. distance from the pike). Since the absolute risk decreases with the inspection distance (it is safer further away from the pike; see figure 2a), the absolute risk difference was significantly influenced by inspection distance: the absolute risks to the leader and the follower became more similar further away from the pike (figure 3). These results have implications for the stability of cooperative predator inspection by pairs (Parker & Milinski 1997). They may make negotiations easier, because the relative

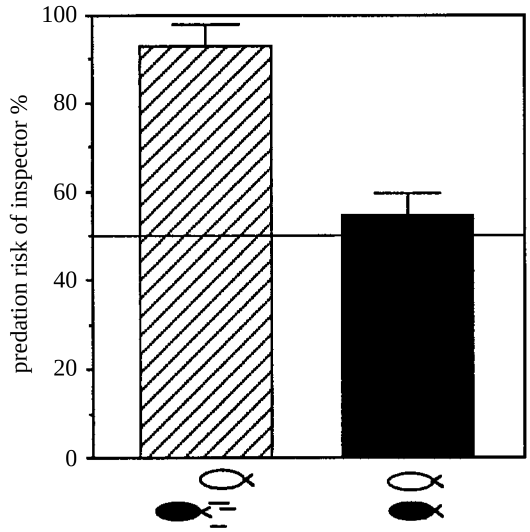

Figure 4. Mean (+ s.e.) % predation risk to the inspector when the inspector was carrying out an inspection visit (hatched column) and when the inspector had returned to the other fish (black column). The inspector's risk differs significantly between the two situations (Wilcoxon matched-pairs signed-ranks test, $z = -2.023$, $n = 6$, $p < 0.05$, two-tailed).

risk to the leader is similar at any inspection distance given that the follower follows at a constant distance.

Are inspecting pairs caught in a 'Prisoner's Dilemma' (Milinski 1987)? To test whether the inequalities that define the 'Prisoner's Dilemma' are fulfilled in the predator inspection scenario, costs and benefits for both single inspectors and inspecting pairs have to be determined experimentally for the whole range of natural inspection distances. Here we have investigated the cost side of the problem: as has been assumed (Milinski 1987), costs of inspection increase with closer inspection distances for both singletons and pairs. Also, as assumed, there is a risk dilution effect that reduces the risk of each member of a parallel cooperating pair to half the risk of a single inspector (figure 2*a*). This is the benefit of cooperation. Now the benefit of inspection needs to be measured experimentally for all inspection distances. There is interesting and suggestive correlational evidence for minnows (*Phoxinus phoxinus*) and guppies (*Poecilia reticulata*) that inspection behaviour is used to collect information about the identity and the motivational state of the predator (Magurran & Girling 1986; Magurran & Higham 1988; Licht 1989; see also Magurran 1990; Pitcher 1992). With these studies one cannot prove, however, that the information was gained through inspection. An experiment is badly needed.

Does predator inspection have an attack deterrence function? This is possible in principle (Hasson & Vega-Redondo 1993) and two empirical studies provided some supporting evidence (Magurran 1990; Godin & Davis 1995; but see Pitcher (1992) and Milinski & Boltshauser (1995) for a discussion of methodological problems). In the present study we offered pike a choice between two (dead) sticklebacks that differed only in that one of them carried out a short predator inspection visit and the other did not. Since both sticklebacks faced the pike, we did not test whether wariness deters attack. We tested whether predator inspection *per se* deters the pike from attacking (and not cues of strength shown by fish that naturally approach predators very closely). If attack inhibition occurs the pike should prefer the non-inspectors. In several trials the pike had already struck during the inspector's approach. In such cases they significantly preferred this fish (figure 4); this is comparable to the results of the first experiment in which the pike preferred the leading fish over the follower when the distance between them was large. However, once the inspector returns to its companion there exists no distance advantage to the pike in striking either stickleback. There was then no indication that the inspector's inspection had deterred the pike's attack. This suggests that if predators tend to avoid natural inspectors (but see Dugatkin 1992) they base their decision on observable traits of the inspector, e.g. size, strength, and not on the inspection behaviour itself. Another result that refutes the attack deterrence hypothesis is our previous finding that the leading fish (more closely inspecting) of an inspecting pair (where leader and laggard roles were randomly assigned) was preferentially attacked. Thus, inspection has been proven to be risky; any benefit would be expected to occur later and not during the inspection visit itself.

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