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TRIBUTE TO STANLEY DODSON

Temporary intermissions in capturing prey (*Daphnia*) by planktivorous fish (*Rutilus rutilus*): Are they due to scramble competition or the need for antipredation vigilance?

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Abstract Capture rates in planktivorous fish may differ in individuals foraging alone or in a group, and this may result either from the altered risk of predation due to vigilance sharing in the group, or from a difference in the intensity of scramble competition for encountered prey items. Changes in capture frequency and the feeding pattern observed in young roach (*Rutilus rutilus*) feeding alone and in a group of three on a high density prey (*Daphnia*), in the presence and in the absence of predator odor, were used to determine which of these two alternate explanations is more likely. Earlier studies revealed that a foraging roach captures *Daphnia* prey in uninterrupted sequences of captures occurring every 1–3 s. Such multiple captures are separated by intermissions of 10–20 s, with their duration being likely to determine the overall capture rate. An experiment was performed to examine whether feeding in a group of three permits higher capture rates (hypothesis 1), and whether the intermittent foraging pattern is due to the need to invest more time for vigilance when foraging alone (hypothesis 2). Video recordings were made of many series of subsequent prey captures by roach feeding on high *Daphnia* densities, alone or in a group, and in the presence or absence of predator odor. Analysis of these data revealed that the mean duration of intermissions between bursts of feeding activity was significantly greater in the presence of predator odor, which resulted in a significant decrease in the capture rate. Furthermore, when the roach were feeding in a group, these intermissions were reduced to a greater extent in the presence of predator odor than in its absence, implying that the intermission intervals represent an investment for vigilance as an effective antipredation defense that permits increased food intake regardless of whether or not it is enhanced by the resource or the interference competition.

Keywords Aggregating · Antipredation defenses · Capture rate · Feeding rate · Fish impact · Handling time · Temporal–spatial distribution · Vigilance sharing · Zooplankton

Introduction

Stanley Ivan Dodson was a pioneer in the observation of prey characteristics and deduced how these characteristics impact on the efficiency of predators such as planktivorous fishes. The notion of the importance of fish predation for zooplankton arose from his early renowned paper with John Langdon Brooks (Brooks & Dodson, 1965). However, he

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ignored this lead into the ‘thrust and parry in the pelagia’ (O’Brien et al., 1976; O’Brien, 1987) to focus on the ecology and evolution of prey anti-predation defenses, to become the author of the first papers on morphological defenses in *Daphnia* (Krueger & Dodson, 1981; Havel & Dodson, 1984) and the first review on predator-induced reaction norms (Dodson, 1989).

For this reason, our contribution to this volume celebrating Stanley’s work does not follow the line of our recent papers on predation of *Daphnia* by planktivorous fish. Instead, we examine anti-predation defenses in fish, which may weaken their impact on their *Daphnia* prey, thus indirectly reinforcing *Daphnia*’s defenses. In planktivorous fish, as in *Daphnia*, antipredation defenses may be manifested as morphological and life-history adjustments, but they are most commonly displayed as modifications of group behavior (schooling of Pitcher & Parrish, 1993), and careful depth selection related to light intensity. Optimal illumination selected by fish is just sufficient to see planktonic prey, but at the same time is low enough to prevent detection by visually feeding piscivores, i.e., predatory fishes and fish-eating birds (anti-predation window of Clark & Levy, 1988). The behavior of vigilance and its sharing between the members of a group, so common in birds and mammals, is another potential antipredation defense that has received little attention in fish.

The phenomenon of greater time investment for vigilance in solitary animals than in individuals within a group has been recognized since early observations on birds such as the wood pigeon (Isaacson & Westwood, 1971), great tit (Krebs et al., 1972), and bar-tailed godwit (Smith & Evans, 1973). However, the notion that intermissions in food collection by animal croppers or harvesters stem from the need for vigilance, and the hypothesis that vigilance might be shared among the members of a group to allow more effective feeding, were developed later, following studies on the feeding behavior of the great blue heron (Krebs, 1974), ostrich (Bertram, 1980), and many other species of birds and mammals, reviewed by Elgar (1989), Bednekoff & Lima (1998), and Beauchamp (2003), and summarized in textbooks on behavioral ecology by Krebs & Davies (1993, 1997) and Lima (1998).

Although it has long been known that planktivorous fish locate prey faster in shoals than when alone (Pitcher et al., 1982), this phenomenon has rarely been attributed to the possibility of vigilance sharing between the members of a group. It was generally recognized as a result of scrambling competition between individuals in the shoal rather than as an effect of more eyes available to scan the environment for an approaching predator. This notion was the dominant interpretation in reports on coral reef fishes (Forrester, 1990; Booth, 1995); and on freshwater planktivorous species such as coho salmon (Grand & Dill, 1999) and rainbow trout (Johnsson, 2003). However, White & Warner (2007) showed that the bluehead wrasse, a coral reef fish, did not have higher capture rates and had lower growth rates when foraging in a group, even though they spent more time foraging in the water column than the solitary fish; thus demonstrating that an increase in foraging time within an aggregation reflects resource competition rather than risk reduction due to vigilance sharing. The results of their meticulous study provide some of the strongest evidence that the cost of the antipredation behavior of aggregation, lies in reduced feeding rates due to intra-specific competition for resources (for reviews see Lima, 1998; Bednekoff & Lima, 1998; Beauchamp, 2003).

Planktivorous fish are typical ‘harvesters’ that are able to capture tiny zooplankton prey with a frequency as high as one prey per second (Gliwicz et al., 2001; Rygielska-Szymanska, 2009; Gliwicz et al., 2010). Moreover, like granivorous birds and insectivorous mammals, they are also capable of fast detection of unexploited patches of prey in the process of optimal patch exploitation and optimal patch choice, described by McNamara & Houston (1985). Also, as in mammal and bird harvesters, their feeding is usually under stress that stems from the never ending risk of predation, which is even higher in the water column far away from deep-water dark refuges where zooplankton prey cannot be seen, and even further away from the safety of dense littoral vegetation where prey is constantly overexploited (Gliwicz, 2003).

This never ending risk from visual predators in the water column would be expected to make vigilance sharing among the members of a group a common strategy in planktivorous fish, affording an increase in individual capture rates within a foraging group. According to Beauchamp (2003), such an increase may have an alternate, equally viable, albeit difficult to prove, explanation in contest or scramble competition, whereby fish in a group tend to feed faster to capture the subsequent prey before it is taken by a nearby competitor. The relative importance of this alternate explanation has been questioned by Lima et al. (1999) and Bednekoff (2003) who state that the effects of the predation risk and competition can be separated from one another. We believe such a separation is possible in a two-factorial experiment in which the sequence of prey captures is registered in fish feeding alone or in a group of three, in the presence and absence of an immediate predation risk or chemical information indicating such a risk.

To test whether foraging in a group permits higher individual capture rates than when feeding alone (hypothesis 1), and—if it does—whether the intermittent foraging pattern is due to the need to invest more time for vigilance when foraging alone (hypothesis 2), we have video recorded many series of subsequent prey captures by roach (*Rutilus rutilus* L.), a common European freshwater planktivorous fish, feeding on *Daphnia*, either alone or in a group, in both the presence and absence of predator odor. We assumed that a greater difference in capture rate, between the fish feeding alone and in a group, in the presence of predator odor, rather than in its absence, would indicate that vigilance sharing is more important than scramble competition for fish when joining a group of foraging conspecifics.

Materials and methods

The animals

The prey, *Daphnia pulex* × *pulicaria*, originating from a single female isolated from Crooked Lake (Indiana, USA; courtesy of William R. DeMott). *Daphnia* were grown in batch cultures at 20 ± 0.1°C in 3 l jars filled with 1 μm Millipore mesh-filtered lake water (Janówek Lake, Jabłonna, Poland). Each day the animals were transferred to a new jar containing *Scenedesmus obliquus* at a concentration of 1 mg C L^{-1}. *Daphnia* neonates, collected within 12 h of their release from brood chambers, were grown under the same conditions, and offered to experimental roach when 3 days old and 1.08 ± 0.09 mm long (mean ± SD body length from the upper edge of the eye to the base of the tail spine, measured in 50 individuals). Thus, in each experiment the same number of captures meant the same consumption rate in energy units per time unit.

The predator-harvester, 9 roach (*Rutilus rutilus*) of more than 1-year old and 9-14 cm in length (1 +) netted in a small (1 ha), shallow (5 m deep) lake with rich emergent and submerged vegetation (Sznajder's Pond, Warsaw; N 52 13.072 E 20 54.676). Each fish was acclimated to the experimental conditions in a separate 5 l tank with black painted walls for 30 days. They were fed daily with the same *Daphnia* instar as that used in experiments, but supplemented with a standard flaked fish food (Ichtiovit). The five fish observed to most actively feed on the *Daphnia*, were used in the experiments (roach **A**, **B**, **C**, **D** and **E**), their subtle differences in the relative length of caudal and tail fins and coloration allowing to tell them apart even when they were used in groups of three.

The piscivore, five perch (*Perca fluviatilis*) of 14–18 cm in length were used as a source of the predator odor. They came from the same habitat as the roach, where perch is the primary piscivore. They were kept in a 100-l tank in the same conditions as the roach and were fed frozen chironomid larvae. Two weeks before the start of each experiment, their food was supplemented for 1 week with small-bodied 3–4 cm sunbleak (*Leucaspius delineatus*) used as a substitute for the equivalent sized roach that were unavailable at the time when the experiments were performed. When the predator-odor treatment was performed, a single perch was transferred to an annex aquarium of the experimental system by net to prevent importation of any chemical information from its earlier prey. The annex aquarium was left empty for the no-predator-odor treatment. Each experiment was run in freshly prepared medium.

Experimental design

The experiments were performed in an experimental system used previously to study *Daphnia* predation by planktivorous fish (Rygielska-Szymanska, 2009; Gliwicz et al., 2010). This was composed of a main experimental aquarium (800 × 450 × 150 mm, breadth, height and width, respectively) where the foraging roach was video recorded, and an annex aquarium (200 × 300 × 150 mm), where the piscivore perch could be placed – the two being separated by a net fence of 0.1 mm mesh size. The experimental aquarium was illuminated from above by a pair of halogen lamps (20 W, 12 V) shining through a glass diffuser to produce a light intensity of 9 μmol m^{-2} s^{-1}, equal to that at 1 m depth 2 h before sunset on a sunny day in a mesotrophic lake when cyprinid fish such as roach feed on zooplankton (Gliwicz & Wrzosek, 2008). All sides of the aquarium apart from the front were painted black to preclude any penetration of light other than from the top. The front of the main aquarium faced into a dark room in which two CCTV cameras (TAYAMA 1/3'' B/W) had been set up to record fish behavior in the two halves of the aquarium, with one camera covering the left half and the second covering the right half. The width of the main aquarium was restricted to 15 cm to ensure that the captures predominantly occurred in the plane perpendicular to a line projecting along the center of each camera's field of view. Fine, thicker and thinner black lines marked on the front of the aquarium in the form of a grid (squares of, respectively, 1 and 10 cm) assisted the viewer of the video recording in tracking the fish under observation. The bottom edges of the aquarium were rounded to improve mixing, thus preventing *Daphnia* from aggregating in the corners. Before the start of each experiment, the aquarium was filled with tap water conditioned with Aqua Safe (*TetraAqua*). All procedures were performed at room temperature (20 ± 1°C).

The configuration was modified by adding a small water pump to the aquarium's annex (separated from the main aquarium by a fine mesh) on the left, and a funnel connected to a 1.5 m plastic tube used for *Daphnia* additions to maintain a constant prey density in the course of each experiment. The water pump produced a current to ensure even prey distribution throughout the system. The fine mesh separating the annex from the main aquarium prevented *Daphnia* from being sucked into the pump. During the observation period in each experiment, the roach were foraging on a constant *Daphnia* density of 2.5 ind. l^{-1}, which produced maximum capture rates (Rygielska-Szymanska, 2009). Prior to the start of each experiment, a sufficient number of 50 ml beakers filled with filtered lake water containing 10 *Daphnia* prey were prepared. Following ten subsequent prey captures by the roach during the observation period, the contents of one beaker was manually added (via the tube) to the aquarium to replace the ten captured *Daphnia*. To further ensure even *Daphnia* distribution, the tube exit was situated near to the outflow from the annex. Each observation period lasted for 5 min. A black curtain was used to separate the experimental aquarium (as well as the CCTV cameras) from the computer receiving the images.

A 2 × 2 factorial design was applied, with roach foraging alone or in a group of three, in either the presence or the absence of predator odor. For each treatment a total of twenty-five 5-min observations were made (for each of the 5 experimental fish × 5 replicates). The roach were acclimated to the experimental conditions for 2 weeks before the first session. This was done by placing the fish in the experimental aquarium every day and allowing them to forage (without predator odor) on *Daphnia* at a density of 2–4 ind. l^{-1} for 4–5 h, replenishing the prey every hour.

Each roach was starved for 10–12 h prior to each experimental session, and placed into the experimental aquarium, free of *Daphnia* prey, 2 h before the start of the observations. For the experimental observations in which roach were subjected to predator odor, two randomly chosen perch were put into the annex 10 min before the start, as in the studies of Magurran (1989) and Jachner (1996). Experimental observation of each roach in each of the four treatments was repeated five times, with only one fish at a time being observed, regardless of whether it was feeding in a group or alone. This resulted in a total of 100 video clips, each of 5-min duration. The roach foraged alternately in the presence and in the absence of predator odor to exclude the possibility that they might recognize the deception and ignore the "risk". As the film of the foraging roach was viewed, the time of each successful attack was marked using the software stopwatch SnapTimePro (Measurement and Conversion Software, MAC, http://www.measureandconvert.com), an application similar to the split/lap control of a conventional stopwatch in which times were marked by hitting a computer mouse button. All timings were marked by one person to prevent errors due to differences in the reaction times of individuals. The software then automatically assigned percentage weights to the time of subsequent capture which continuously adjusted as new times were recorded. Comments could be added to the SnapTimePro report to indicate the meaning of each time. A setup comprised of two

CCTV cameras, video quad, and Pinnacle PCTV card was used for all video recordings.

Data analysis

Earlier work on roach feeding using this experimental system (Rygielska-Szymanska, 2009; Gliwicz et al., 2010), revealed that *Daphnia* prey were collected by roach in prolonged sequences of individual captures, with minimum handling times of 3 s or less, half of which was taken up by prey search and capture, and the other half by prey handling. The start of a pause between sequential captures that exceeded 3 s was considered to be the end of a series. After recording captures using SnapTimePro, this flexible and 0.01 s resolution digital stopwatch automatically measured the duration (±0.01 s) of the pause between successive attacks. Attacks from 25 first series were counted to determine the average number of attacks in a sequence. The capture rate was calculated from the number of *Daphnia* prey ingested in each of the 5-min observation periods (mean ± 1SD). Two-way ANOVA with post-hoc Tukey test was used to compare the intermission duration and the number of captures per minute in each sequence. This permitted calculation of the capture rate of a roach foraging alone or in a group of three, in either the absence or the presence of predator odor. Regression analysis was applied to determine whether the capture rate increased with time elapsed. The frequency distribution (%) of pauses between attacks was calculated, with all pauses longer than 10 s shown on a separate axis. IBM SPSS Statistics (2008, www.statsoft.com) was used for the repeated-measures ANOVA and STATSOFT's Statistica 8 (2008, www.statsoft.com) for one-way ANOVA, Friedman's ANOVA, ANCOVA, and regression analysis.

Results

The capture rate of a roach foraging in a group was nearly twice that (in the absence of predator odor) or more than twice that (in the presence of predator odor) of a roach foraging alone (Fig. 1a, b, respectively), attaining a maximum value of 1.30 prey s^{-1} and an average of 0.65 prey s^{-1} for roach foraging in a group in the absence of predator odor. The repeated-measures ANOVA for the four treatments revealed a significant difference in capture rate between roach feeding alone and in a group of three (Fig. 2a), either in the presence ($P < 0.001$) or the absence of predator odor ($P < 0.001$, Table 1). Three independent groups were identified within the four treatments (post-hoc Tukey test) indicating that capture rate was significantly lower for single fish foraging in the presence of predator odor (group 1), significantly higher for fish foraging in a group in the absence of predator odor (group 3), and intermediate in the two remaining treatments (group 2). The difference in the percentage reduction in capture rate between fish feeding alone and in a group of three was only significant ($P < 0.048$) in the presence of predator odor (Fig. 2b).

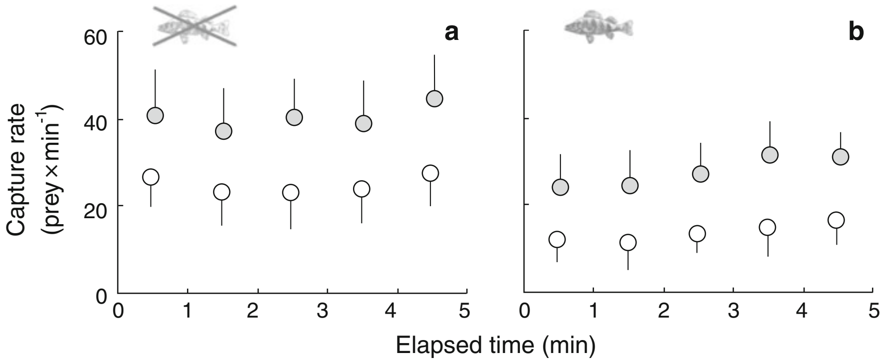

Fig. 1 Capture rate of young roach fed *Daphnia* prey (*D. pulex-pulicaria*) at high constant density of 2.5 ind. l^{-1} shown as the mean (± 1SD) number of prey captured in each sequential minute of the observation period (5 min) when foraging alone (*open circles*) or in a group of three (*filled circles*), in the absence (**a**) or in the presence (**b**) of predator odor. Repeated-measures ANOVA indicated a significant ($P < 0.001$) difference in capture rate between roach foraging alone and in a group of three, in both the absence and presence of predator odor

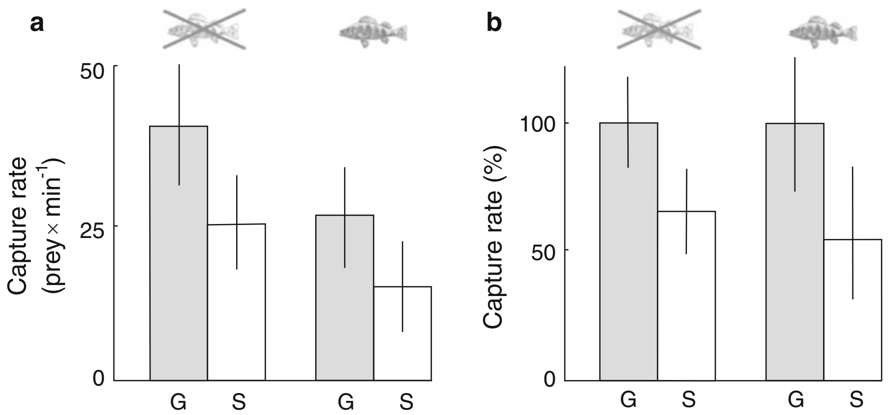

Fig. 2 Mean (± 1SD) capture rate of young roach fed *Daphnia* prey when foraging alone (*unshaded*, also denoted by *S*) or in a group of three (*shaded*, also denoted by *G*), shown as the number of prey captured per minute (**a**), and as a percentage of the capture rate attained when foraging in a group of three (**b**) in the absence or in the presence of predator odor. The difference between fish feeding alone and in a group of three in the percentage reduction of the capture rate in fish feeding alone was significant ($P < 0.048$) only in the presence of predator odor ($F = 3.8$, df = 24, one-way ANOVA)

Table 1 Mean (± 1SD) capture rate ($n = 5 \times 25$) of roach foraging alone or in a group of three, and statistics for the difference between the two treatments, both in the absence and in the presence of predator odor (one-way ANOVA with Tukey post-hoc)

Roach	Capture rate (*Daphnia* × min^{-1})					
	Odor absent			Odor present		
	Single	Grouped	*P*	Single	Grouped	*P*
A	26.6 ± 6.1	46.4 ± 6.4	0.001	11.9 ± 1.4	27.9 ± 0.5	0.001
B	21.5 ± 6.9	32.7 ± 8.5	0.001	11.8 ± 1.7	20.0 ± 2.5	0.001
C	20.3 ± 4.4	46.9 ± 6.1	0.001	14.7 ± 1.7	28.0 ± 0.3	0.01
D	25.2 ± 5.9	35.2 ± 7.1	0.01	15.2 ± 1.1	22.5 ± 1.4	0.04
E	33.6 ± 4.3	41.2 ± 9.4	0.04	22.8 ± 2.3	31.5 ± 0.5	0.04
Mean	25.1 ± 5.1	40.3 ± 9.7	0.001	15.6 ± 7.1	26.0 ± 8.1	0.001

The same repeated-measures ANOVA also revealed a weak but clear increase in capture rate of roach during the 5-min observation period ($P < 0.001$). This increase was most apparent in roach feeding in a group in the presence of predator odor, the slope being significant at $P < 0.05$ ($R^2 = 0.15$). The tendency towards an increase in capture rate within the 5 min period for grouped roach in the presence of predator odor was confirmed by the analysis of covariance for three individual fish. The slope and coefficient for roach **A**, **D**, and **E** were 2.11 and 0.38, 2.96, and 0.61, and 2.06 and 0.38, respectively ($P \leq 0.05$, df = 23, ANCOVA).

Although the behavioral responses of all fish were very similar, slight variation could be detected when individuals were compared. Roach **E** exhibited the lowest sensitivity to both analyzed factors, roach **C** showed the highest sensitivity to the predator odor, and roach **A,** the highest sensitivity to the presence of other individuals. Not every fish revealed significant differences in feeding behavior when foraging alone and in a group, when capture rates (Table 1) or feeding patterns (Table 2) were compared.

As might be expected from the model developed by Lima et al. (1999) to study the effect of scramble competition on vigilance, the variations in capture rate (Table 1) clearly reflected differences in the duration of intermissions between series of uninterrupted captures (Table 2). Two examples for each of the two roach exhibiting the greatest difference in their responses to the presence of other individuals (roach **A** and **E**), showed a difference in the duration

Table 2 Mean (± 1SD) duration of intermissions (seconds) between sequential captures ($n = 5{\times}25$), and mean (± 1SD) number of sequential captures between intermissions longer than 3 s in roach foraging alone or in a group of three, and statistics for the difference between the two treatments, both in the absence and in the presence of predator odor (one-way ANOVA with Tukey post-hoc)

Roach	Duration of the intermission (s)						Number of sequential captures					
	Odor absent			Odor present			Odor absent			Odor present		
	Single	Grouped	*P*	Single	Grouped	*P*	Single	Grouped	*P*	Single	Grouped	*P*
A	6.3 ± 1.0	5.0 ± 0.4	0.03	9.0 ± 1.4	6.8 ± 0.5	0.005	6.3 ± 3.0	16.2 ± 7.4	0.001	6.0 ± 3.1	11.4 ± 5.4	0.002
B	9.4 ± 2.7	5.6 ± 0.8	0.01	13.5 ± 1.7	9.2 ± 2.5	0.005	6.1 ± 2.8	10.6 ± 6.5	0.002	5.2 ± 2.4	7.0 ± 3.2	0.007
C	7.5 ± 1.2	4.7 ± 0.3	0.03	10.7 ± 1.7	6.8 ± 0.3	0.009	5.8 ± 2.2	11.3 ± 6.5	0.001	6.8 ± 3.9	8.8 ± 2.9	0.351
D	6.3 ± 0.9	6.2 ± 0.4	0.92	10.1 ± 1.1	7.7 ± 1.4	0.032	6.1 ± 3.0	9.8 ± 4.2	0.001	4.9 ± 1.9	7.0 ± 2.4	0.523
E	5.5 ± 0.5	4.7 ± 0.7	0.61	9.5 ± 2.3	7.0 ± 0.5	0.023	7.8 ± 3.8	12.0 ± 5.1	0.003	7.9 ± 2.9	9.7 ± 3.9	0.541
Mean	6.2 ± 0.9	5.1 ± 0.7	0.03	10.1 ± 2.0	7.0 ± 1.0	0.013	6.4 ± 3.1	12.0 ± 6.2	0.001	6.2 ± 3.1	8.8 ± 4.0	0.017

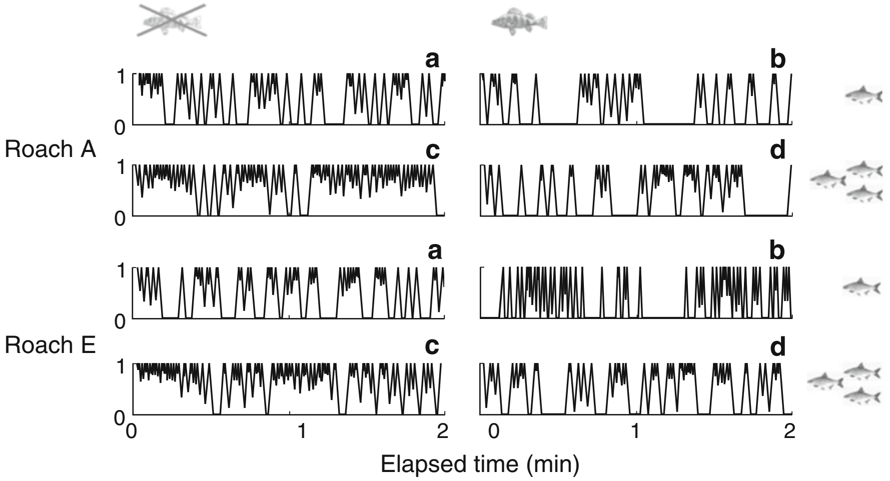

Fig. 3 Examples of recordings of sequential captures made during the first 2 min of each observation period by roach **A** and roach **E**, foraging alone (*a*, *b*) or in a group of three (*c*, *d*), in the absence or in the presence of predator odor. These two fish were selected as the most extreme in terms in their reaction to predator odor. For clarity in distinguishing real intermissions between subsequent captures, we assumed that the duration of each capture equals 3 s, including 1.5 s for prey handling (ascending line 0 → 1), and 1.5 s for the search and capture of the subsequent prey (descending line 1 → 0)

of intermissions when foraging alone (Fig. 3a, b) and in a group of three (Fig. 3c, d), whenever in the presence or in the absence of predator odor.

The longest series, consisting of over 20 captures, were recorded exclusively for roach foraging in a group in the absence of predator odor. The number of captures in a series was more variable in the presence of predator odor and some series were as long as those recorded for roach foraging in the absence of predator odor (Fig. 3; Table 2).

The duration of the intermission between series of sequential prey captures by roach foraging alone or in a group of three was significantly different ($P < 0.003$, Friedman's ANOVA) when analyzed from the % distribution of the duration time of all the intermissions from the entire data set for both situations, irrespective of whether or not predator odor was present (Fig. 4).

The repeated-measures ANOVA with Tukey post-hoc test for the four treatments revealed that the percentage contribution of intermissions longer than 10 s (see Fig. 4) was significantly higher in roach feeding alone than in a group of three, in both the absence and the presence of predator odor

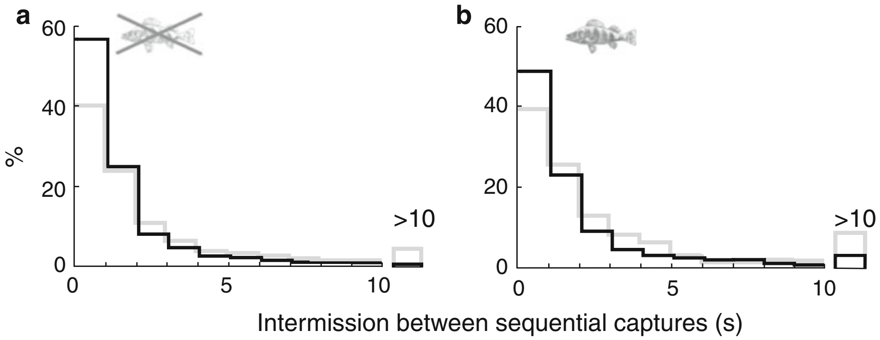

Fig. 4 The difference in cumulative distribution (%) of the duration of intermissions between sequential prey captures in roach foraging alone (*gray line*) or in a group of three (*black line*), in the absence (**a**) or in the presence (**b**) of predator odor. Friedman's ANOVA revealed a significant difference between fish feeding alone and in a group of three at $P = 0.003$. The repeated measure ANOVA with Tukey post-hoc test indicated a significantly greater percentage of intermissions longer than 10 s in roach foraging alone than in a group, in both the absence and the presence of predator odor

(respectively, $F = 10.4$, $\mathrm{df} = 24$, $P < 0.001$, and $F = 18.7$, $\mathrm{df} = 24$, $P < 0.001$). Four independent groups were identified within the four treatments (post-hoc Tukey test) indicating that this percentage was significantly greater in lone fish than in grouped fish when foraging in the presence (mean, respectively, 9.1 and 4.3) or the absence (mean, respectively, 3.3 and 0.6) of predator odor.

Discussion

From reports on the effect of group size on vigilance sharing (reviewed by Beauchamp, 2003) it is clear that the benefits as well as the drawbacks of foraging in a group alter with the size of the group. Benefits such as higher capture rates due to vigilance sharing and learning are likely to be of greater importance in small groups, whereas the drawback of intra-group competition will be more important in large groups. Thus, the different group sizes encountered in field observations and used in experiments may be responsible for the divergent conclusions of studies on the subject. The small group of three used in our experimental approach may be the reason why, contrary to observations of the behavior of the bluehead wrasse in larger groups made by White & Warner (2007), our experiments on freshwater roach showed that the capture rate is higher in fish foraging in a group than when foraging alone. This was the result of shorter intermissions in the sequential capture of prey rather than an increase in the time allocated for foraging, as was found in wrasse. Capture rates were higher in roach foraging in a group in both the presence and the absence of information on predation risk (Fig. 2a) with the predator odor causing an evident decline in capture rate, as expected from earlier studies on this species (Jachner, 1996; Jachner & Janecki, 1999; Gliwicz et al., 2001; Gliwicz, 2003).

Interestingly, the reduction in capture rate seen in solitary fish compared to fish foraging in a group was significantly greater in the presence of predator odor than in its absence (Fig. 2b). This suggests that at least a part of the difference between the two treatments might be attributed to variation in the time spent on antipredation vigilance rather than increased competition—this time being shorter in the presence of conspecifics, probably due to vigilance sharing. The two alternate explanations for the increased capture rate when foraging in a group could not be separated even for the treatment in the absence of predator odor, since behavioral defenses such as vigilance sharing are constitutive in small planktivorous fish that live in habitats infested by piscivorous fish or intensively patrolled by fish-eating birds (Winfield, 1990). Indeed, the threat of aerial predation has been shown to influence capture rates in the laboratory (Milinski & Heller, 1978) and to act as a 'ghost of predation past' in the field studies (Gliwicz & Jachner, 1992). This is why, even in the absence of predator odor, the difference in capture rate when foraging alone and in a group may result from antipredation vigilance, with the impact of competition being either negligible or even counterproductive, with scrambling leading to a decrease rather than an increase in capture rate.

The vigilance-sharing interpretation seems to be more likely also in light of the pattern of prey collection displayed by our experimental roach. The sequence of *Daphnia* captures shown in Fig. 3 demonstrates that periods of uninterrupted captures occur in each of the four experimental treatments, and that the capture rate within such sequences is very similar. This indicates that the capture rate cannot be higher than that observed within an uninterrupted series, and that any increase may be achieved exclusively by reducing the frequency of intermissions and the mean intermission time. Intermissions in foraging were observed for each experimental roach, in some cases being less frequent but lasting longer (fish **A**) and in others, more frequent but shorter (fish **E**). The same was seen in each of the four treatments (foraging alone or in a group, in the absence or the presence of predator odor), the difference being not in the frequency of intermissions, but rather in their duration, which was clearly greater both in fish foraging alone (compared to those foraging in the group) and in the presence of predator odor (compared to its absence). The same can be seen in the proportion of intermissions longer than 10 s (>10) in Fig. 4.

Although a shorter intermission may theoretically be a product of scramble competition (get the prey before your companion does), there are two reasons why this seems less likely than vigilance sharing.

First, the experimental fish had unlimited food. They were foraging for *Daphnia* prey that was present at densities far greater than those experienced in the field. Moreover, any significant reduction in prey density was precluded by repeated replenishment after the capture of ten prey items, so that the total number of *Daphnia* in the experimental aquarium (225) was never reduced by more than 5%. It is unlikely that such a situation would encourage scramble competition, which is observed when resources are inadequate to meet the needs of all individuals in a group.

Second, the risk of predation is the predominant concern of a foraging fish in the water column where, even in the absence of predator odor, there is always the threat of piscivorous birds. Such a scenario is in accordance with field observations on roach diel habitat shifts between their daytime littoral refuge, where they rest in huge aggregations, and the centre of the lake to which they move in small groups at dusk to feed on more abundant *Daphnia* prey under the cover of reduced illumination (Gliwicz et al., 2006). The fish which chose to move offshore at dusk feed within a short time window where the light intensity is sufficiently low to reduce the risk from piscivores, but is still high enough for them to see the zooplankton prey (antipredation window of Clark & Levy, 1988 in a horizontal plane). In this case, any increase in the potential risk with the distance from the littoral refuge is compensated by increased food gains. Such foraging behavior does not leave much space for interference or scramble competition between the conspecifics moving offshore; the cost of an increase in capture rate is a greater risk of predation rather than interference by other foragers. Moreover, the risk of being away from the littoral refuge, which is directly correlated with the distance from the edge of the reed belt, can possibly be reduced by vigilance sharing among the members of a small group moving offshore, each encountering more and more prey albeit with increasingly poor illumination.

Therefore, the results of the present study seem to support the two hypotheses that (1) foraging in a group allows for higher capture rates than feeding alone, and that (2) the intermittent foraging pattern is due to the need to invest more time for vigilance when foraging alone, thus reducing the time of effective foraging and lowering the capture rates. Although it has been appreciated since the early reports of Magurran et al. (1985) and Pitcher (1986), that vigilance sharing may be one of the most important reasons for aggregation or shoaling behavior in fish, the majority of fish ecologists have thought that safety in a shoal could stem from social attributes other than vigilance, such as the confusion effect (Neill & Cullen, 1974) and the dilution effect, whereby the probability of an individual being attacked during an encounter with a piscivore is reduced if it is part of a group (Foster & Treherne, 1981). This explains why, despite the striking similarities between the ecology of food collection in all animal harvesters, fish have not been readily included (so far) among the many examples of vigilance-sharing recorded in mammals and birds.

The results of the present study show a change in feeding behavior that may support the hypothesis that chemical information on a predator's presence, such as its odor, can cause an immediate increase in vigilance behavior and a decline in feeding activity in fish. However, should the fish be able to detect that the information suggesting an imminent risk of predation is false, these are likely to be short-lasting phenomena. Jachner & Janecki (1999) confirmed that such learning ability allows young roach to quickly restore high capture rates, while older fish are not only able to survive longer periods of starvation but are also more cautious, possibly because they represent a more proficient prey to a piscivore and hence are less inclined to take risks (see Fig. 17 in Gliwicz, 2003).

The average capture rate of roach feeding in a group was found to be one prey every 1.6 s (0.6 prey s^{-1}), which is very similar to that determined for roach feeding on *Daphnia* in mesocosm studies (Gliwicz et al., 2001): in the 'plankton towers' at Plön (Lampert & Loose, 1992), the capture rate of 2- to 3-year-old roach (fork length 15 cm) allowed to feed on high densities of *Daphnia hyalina* for 1 h at dusk, was estimated at 0.8 prey s^{-1} or one prey per 1.25 s. Similar values (0.6 prey s^{-1} or one prey per 1.7 s) were obtained from field data on the feeding behavior of another planktivorous fish, *Limnothrissa miodon*. These values were attained when this small clupeid was feeding on unusually high densities of *Daphnia lumholtzi* and *Bosmina longirostris* resulting from the lunar trap: a combination of the sunset and the moonrise one night after a full moon, when the cladoceran prey ascend to the surface during 1 h of complete darkness, only to be illuminated by the rising moon and nearly exterminated by fish (Gliwicz, 1986).

These two examples of high feeding rates come from laboratory and field situations where fish were feeding in a group, and thus could share their vigilance obligations, which may have allowed them to capture more prey. The ability of planktivorous fish to share vigilance may further increase the magnitude of their top–down impact on zooplankton prey populations in the field, particularly their effect on prey aggregations such as those in areas affected by Langmuir spirals, caused by the upwelling current, which carries zooplankton prey such as *Daphnia* upward while they attempt to avoid the high light intensity by swimming downward (George & Edwards, 1973; see Fig. 19 in Gliwicz, 2003). Such aggregations are often subject to intense predation by planktivorous fish, which are known for their optimal patch choice behavior (McNamara & Houston, 1985) and their ability to detect and migrate to locations where *Daphnia* density has increased (McNaught & Hasler, 1961). These characteristics combined with the ability to increase the rate of prey capture due to the possibility of vigilance sharing, could further shorten the time required for planktivorous fish to disrupt or even wipe out any *Daphnia* aggregation, and may be the main reason why zooplankton aggregations are short-lasting phenomena in the field (Gliwicz & Wrzosek, 2008; Gliwicz et al., 2010).

The high capture rate and its further enhancement by vigilance sharing confirm the great power of fish predation in controlling zooplankton populations that was originally pondered by Brooks & Dodson (1965), and which has become one of the most exciting subjects in the study of biomanipulation and trophic cascades in recent decades. It is now widely recognized as a major force of natural selection for the evolution of morphological properties, life histories, or behavioral adjustments to counter the risks of predation and to cope with the challenge of sequestering resources. Sharing the duties of vigilance conveys an advantage in both predation avoidance and the fight for resources: by joining others, you will be both safer and better fed.

The question of whether the ultimate reason for aggregation in fish is the increase in efficiency of antipredation defenses to assure lower mortality risk (Neill & Cullen, 1974; Foster & Treherne, 1981), or the increase in foraging ability to assure faster growth and increased reproduction (McNaught & Hasler, 1961, Magurran et al., 1985), cannot be definitively answered, as the adaptive significance of this behavior apparently lies in both. Vigilance sharing represents an additional reason for aggregation that is distinctly different from both predator confusion (Neill & Cullen, 1974) and the safety-in-a-crowd effect (Foster & Treherne, 1981), where the ecological compromises are between the maximum safety from predation that is greater within an aggregation, and the maximum feeding rate which is greater far away from others, where prey resources have not been overexploited.

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