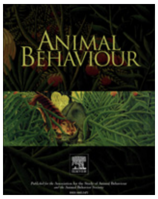
Animal Behaviour 82 (2011) 619–625

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Articles

Something smells fishy: predator-naïve salmon use diet cues, not kairomones, to recognize a sympatric mammalian predator

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ARTICLE INFO

Article history:
Received 27 May 2010
Initial acceptance 13 August 2010
Final acceptance 17 June 2011
Available online 31 July 2011
MS. number: 10-00371R

Keywords:
antipredator behaviour
Atlantic salmon
conspecific alarm cue
diet
generalization
otter
predation
Salmo salar

The ability to recognize predators is one of the most important lines of defence in a prey's arsenal, but the detection of novel predators poses a particular challenge. Novel predators provide few or no visual cues to inexperienced prey, which may have to rely on complementary chemical mechanisms to identify predators and survive the first encounters. We examined the role of diet-released chemical cues in facilitating predator recognition and promoting antipredator responses in predator-naïve juvenile Atlantic salmon, *Salmo salar*, presented with blank water or with diet cues from a common sympatric predator (the Eurasian otter, *Lutra lutra*) fed either salmon or a nonsalmon diet. No antipredator behaviour was found among individuals tested with blank water or with water scented with cues from an otter fed on a nonsalmon diet, suggesting that Atlantic salmon do not innately recognize the sympatric predator as a threat. In contrast, strong spatial avoidance, reduced activity and increasing ventilation were observed among salmon tested with water scented with cues from an otter fed on a salmon diet. We propose that juvenile salmon use diet-released conspecific alarm cues, and not predator-specific kairomones, to label novel predators as a threat chemically, thereby achieving generalized predator recognition and avoiding sensory overload.

In the evolutionary arms race, prey stand to lose more than predators. As a result, prey that competently determine the risk and intensity of predation will be able to devote sufficient time to other fitness-related behaviours, such as foraging or courtship (Brodie & Formanowicz 1991; Lima & Bednekoff 1999; Brown et al. 2009), gaining a selective advantage (Abrams 2000). Predator detection and recognition present prey with the first line of defence against predators and thus represent a pivotal stage in the repertoire of antipredator behaviours (Kelley & Magurran 2003), which are often innate (Blumstein et al. 2002a; Berejikian et al. 2003). However, spatial and temporal shifts in predation pressure throughout an animal's life may require an element of learning to regulate threat-sensitive predator recognition adaptively (Blumstein et al. 2002b; Griffin et al. 2001; Ferrari et al. 2007a).

Visibility is limited in many aquatic systems, and chemical alarm signals such as conspecific alarm cues (Chivers & Smith 1995, 1998) and predator-specific kairomones (chemicals emitted by predators that allow eavesdropping by prey without benefitting the predator, Kats & Dill 1998) are prevalent means of obtaining information about predation risk (Brown 2003) when visual cues are unreliable. Perhaps the best studied chemical signals are capture-released conspecific alarm cues, that is, chemical cues released by prey upon mechanical damage through predation (Brown & Godin 1997), which have been identified in several aquatic taxa (amphibians: Peterson et al. 1992; Chivers et al. 2001; invertebrates: Ferrari et al. 2007b: fish: reviewed in Wisenden et al. 2003).

A further means of obtaining information about predation risk in aquatic systems is the use of conspecific cues released in the diet of predators (i.e. diet-released alarm cues, Chivers & Mirza 2001). Unlike capture-released alarm cues (released following direct, mechanical damage; Brown & Smith 1997), diet-released alarm cues are released in the faeces of a predator following the consumption of conspecifics (Brown et al. 1995). Diet-released cues have received much less attention than capture-released cues, and although it is unclear to what extent these represent different antipredator systems, both cues tend to elicit similar antipredator responses in prey (Ferrari et al. 2007c).

The use of diet-released alarm cues in predator recognition has previously been demonstrated in a few fish species, but only using other fish as predators. For example, Arctic charr, *Salvelinus alpinus*, recognize conspecific cues in the diet of brown trout, *Salmo trutta*, and pikeperch, *Stizostedion lucioperca* (Vilhunen & Hirvonen 2003), while goldfish, *Carassius auratus*, and fathead minnows, *Pimephales*

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doi:10.1016/j.anbehav.2011.06.019

promelas, recognize alarm cues in the diet of pike, *Esox lucius* (Zhao et al. 2006) and brook trout, *Salvelinus fontinalis* (Ferrari et al. 2007c). Most fish are at risk from a wide diversity of predators, and not just from fish predators. Diet-released alarm cues could represent a reliable and relatively low-cost (compared to capture-released cues or kairomones) means of effectively mediating learned predator recognition without sensory overload. For example, Ferrari et al. (2007a) found that fathead minnows exposed to conspecific alarm cues paired with lake trout, *Salvelinus namaycush*, can generalize the recognition of predators to other, novel salmonids. Yet, the extent to which diet-released conspecific cues can also be used for chemical labelling and recognition of phylogenetically distant predators has not been tested.

Aquatic birds and mammals represent important predators of fish, but it is not known if these also elicit chemical recognition by prey. The Eurasian otter, *Lutra lutra*, is a common predator of stream fishes, which make up the bulk of its diet (Kruuk 1995). Therefore it would be advantageous for fish to distinguish otters as a threat. To ascertain whether diet-released alarm cues can be used to recognize a sympatric predator without the need for learning, we exposed predator-naïve juvenile Atlantic salmon, *Salmo salar*, to diet-released cues from a Eurasian otter fed either a salmon or a nonsalmon diet. The aims of this study were twofold: first, to determine whether predator-naïve juvenile salmon were able to recognize innately a sympatric mammalian predator as a threat using chemical cues alone, and second to assess whether this was accomplished by recognition of the predator's scent itself (kairomones, Schoeppner & Relyea 2009), or by detection of conspecific diet-released cues, thereby adding support to the 'predator recognition continuum hypothesis' (Ferrari et al. 2007a) across nonfish taxa. This proposes that there is a continuum in antipredator behaviours from 'innate predator recognition' to 'learned predator recognition without generalization' and finally to 'learned predator recognition with generalization'.

METHODS

Test Fish

The fish used in the study were 0+ (fry) predator-naïve, juvenile salmon reared at the Cynrig Fish Culture Unit, Wales, U.K. and derived from the stripping of wild broodstock caught at the River Taff, a system where predatory otters are common (Roberts et al. 2009). For the study, approximately 600 fry (average weight 1.7 g) were transported from Cynrig Fish Culture Unit to Swansea University Fresh Water Research Unit on 20 September 2008. Here they were held in two 1 m circular tanks (approximately 300 fish per tank, loading density 0.5 g/litre) under normal photoperiod and fed at ca. 2.4% body weight on commercial food pellets (TrouW) dispensed through automatic belt feeders for the duration of the experiment. Water temperature was kept between 10 and 14 °C (the normal range in the river of origin for that time of year) with the aid of a chiller.

Manipulation of Predatory Diet

Predator cues were obtained from the spraints (faeces) of an 8-year-old female Eurasian otter, captive reared in an outdoor pen at the Wildwood Nature Reserve, Kent, U.K. Before the diet manipulations began, the otter had been maintained on a nonfish diet consisting predominantly of chicken and rabbit (approximately 1.2 kg/day). One day before the diet manipulations began, the rearing pen was completely cleared of all existing spraints.

On 15 November 2008 the feeding trials began with the otter fed a nonsalmon diet (chicken or rabbit at approximately 1.2 kg/day). This was carried out for 7 days. On 22 November 2008, after 7 days on a nonfish diet, the diet was switched to an Atlantic salmon-only diet. The salmon used to feed the otter were 3-year-old hatchery-reared Atlantic salmon, also originating from Cynrig Fish Culture Unit population. These were humanely killed with a rapid blow to the head and frozen immediately, until use. One day before use, the fish were defrosted at room temperature and gutted, but the skin and head were left intact. The otter was fed one salmon daily (average weight 1.2 kg). During the diet manipulations the otter received the same amount of chicken or rabbit as salmon to keep the food intake standard between trials.

Spraints were collected daily in individual bags, and frozen immediately at −18 °C to prevent degradation. Gloves were used at all times, and spraints collected on the first 2 days of each feeding trial were discarded to reduce potential contamination from previous feeds. Feeding trials lasted for the same length of time (7 days) on each diet.

Preparation of Predatory Cues

Solutions were made from spraints collected when the predator had been fed on either a salmon or a nonsalmon diet. For each cue type, 60 g of spraints were homogenized in a liquidizer and then mixed with 6 litres of distilled water to make a concentration of 10 g/litre. This was made 1 day before the behavioural analysis. The scents were then divided into 12 × 1 litre sealable bottles and kept at 4 °C until use. Six litres of distilled water was also treated in the same manner to serve as blank controls.

Behavioural Analysis

Animals generally demonstrate a range of threat-sensitive antipredator responses depending on the perceived predation risk (Kusch et al. 2004; Brown et al. 2009). These can range from overt, marked changes in behaviour (Brown et al. 2004) to more subtle changes in physiology (Hawkins et al. 2004). Therefore we assessed the following responses in an attempt to capture the full antipredator repertoire: latency to leave shelter, spatial avoidance, number of freezes and opercular beat rate (OBR). We assayed the motivation to leave shelter because it tends to correlate well with measures of boldness (Sneddon 2003; Brown & Braithwaite 2004; Brown et al. 2005), and because we expected latency to diminish under the threat of predation (Wilson & Stevens 2005; Bell & Sih 2007). We then employed a Y-maze to assess the time spent in the odour channel, as well as the first arm chosen after leaving the hide, as a means of quantifying the spatial avoidance of high-risk areas (Hirvonen et al. 2000; Vilhunen & Hirvonen 2003). Many fish rest motionless on the bottom of the tank without moving their fins under the threat of predation (termed 'freezing', Chivers & Smith 1998). This represents a sensitive antipredator behaviour in salmonids, and has been interpreted as a form of crypsis (Vilhunen & Hirvonen 2003). We therefore also recorded the number of freezes in the Y-maze as a measure of the strength of antipredator response. Finally, as detection of predators may not always result in overt antipredator behaviours, we also quantified a sensitive stress response. For this, we measured OBR in a separate experimental chamber to reveal whether individuals increased their ventilation rate when exposed to chemical cues emanating from the predator. The OBR can increase in response to the threat of predation (Metcalfe et al. 1987; Sundstrom et al. 2005) and may therefore reveal predator recognition when overt behaviours are not manifested.

Y-maze Choice Chamber

The Y-maze choice chamber used in this study consisted of a modified hatchery trough (280 × 39 cm and 14 cm deep) with a start box (Braithwaite & Salvanes 2005) as a hide at the outflow end (16 × 39 cm and 14 cm deep). The start box had a remotely operated door and an overhead cover allowing approximately 30% of the light through. The trough was divided into two arms (19 × 162 cm and 14 cm deep) with a central partition to prevent the scents from mixing (Hirvonen et al. 2000; Vilhunen et al. 2005). Opaque barriers were fixed on the outer rim of the trough to prevent disturbance. Experiments were carried out under artificial light and all windows were blacked out. Water was supplied from submerged perforated spray bars that had been modified to produce an even flow to both arms. Average flow was 19 litres/min via the inlets, resulting in a surface velocity of 10–13 cm/s. The water used was dechlorinated tap water which flowed straight through a carbon filter and was not recirculated. Behavioural observations were carried out from 12 January to 21 January 2009 and between 12 and 16 fish were assayed per day. During an individual trial, the scent of conspecific diet-released cues, nonsalmon cues or blank water was dripped into a randomly preselected arm of the Y-maze at the inflow end. For this, 1-litre drip bags (Baxter Saline drip bags, Dealmed Medical Supplies, New York, U.S.A.) containing one of the randomly selected scents were placed at the inflow end behind a screen, 1600 mm upstream of the shelter and the start box. An IV drip (Dynatex, Dealmed Medical Supplies) was attached to each bag, which was used to release the scent into the selected arm of the Y-maze. The scent was released 1 min before the door was opened and the drip rate was set at 0.15 ml/s for the duration of the trial (144 ml per 15 min trial). The use of red dye revealed that the plume took approximately 20 s to reach the shelter, and the fish were therefore exposed to the scent for around 40 s before the gate to the start box was lifted.

The trials consisted of four treatments: (1) blank (distilled water) versus predator fed salmon diet; (2) blank versus predator fed nonsalmon diet; (3) predator fed salmon diet versus predator fed nonsalmon diet; and (4) blank versus blank (control). For each treatment 40 fish were sampled, except for the blank versus blank controls where 20 fish were sampled. In each trial, an individual fish was randomly selected by gently netting it from the rearing tank, and was allowed to acclimatize for 15 min in the start box of the Y-maze. One minute before the end of the acclimatization period (i.e. after 14 min) the scent was added, and a minute later the door was lifted. The latency to leave shelter was recorded as a measure of boldness, and the time spent in each arm was calculated for a total of 900 s as a measure of spatial avoidance. We also recorded the arm that was chosen when the fish first left the hide (first arm choice) and the number of times each individual froze. All fish were measured and weighed under anaesthesia (2-phenoxyethanol) after each behavioural observation and were held in a separate holding tank to avoid duplication. Following every trial, the trough was drained and washed with 90% ethanol.

Opercular Beat Rate

To measure OBR we employed five identical transparent tanks (21 × 13 cm and 13 cm high) isolated with opaque barriers and fitted with small observation holes. Each tank held 2.73 litres of dechlorinated water and had an air stone. Odour cues were administered remotely without disturbing the fish by means of 10 ml syringes and plastic tubing placed out of sight of the fish. Trials were conducted from 14 to 26 April 2009 (12 days). Five fish were randomly selected and placed singly into each of the observation tanks at 1700 hours and left to acclimatize overnight for 15 h. We had found previously that 15 h was sufficient time to allow salmon to reach basal respiration rate (data not shown). At 0800 hours the following day, the basal OBR was recorded as the number of opercular beats/min (this was initially recorded as the time taken to reach 60 beats and then transformed to number of beats/min for the analysis). After 5 min, we added 6 ml of odour cues or blank water via the syringe. The type of odour cue (blank water, predator fed salmon or predator fed nonsalmon) was randomly preselected for each fish. After 5 min, OBR was recorded for 60 s every 5 min for 1 h, and then once every hour for another 4 h (total of 5 h of recordings). Recordings were staggered between each tank to allow five fish to be assayed per day. All fish were measured and weighed under anaesthesia (2-phenoxyethanol) following the experiment and returned to a separate holding tank to avoid duplication.

Data Analysis

Juvenile Atlantic salmon were tested singly in each trial in the Y-maze and also in the OBR aquaria, and were tested only once. We employed ANCOVA to analyse variation in latency among odour cues (predator fed conspecifics, predator fed nonsalmon diet and blank water) with body size (measured as fork length, from the tip of the snout to the fork of the tail) as a covariate, as previous studies have suggested that boldness increases with body size (Brown & Braithwaite 2004). Data were log (latency) or arcsine (avoidance) transformed to meet normality and homogeneity of variances, as needed. As in most studies of boldness (e.g. Brown et al. 2005), we assigned a maximum latency ceiling value (900 s in our case) to those fish that did not come out of the shelter in the allocated test time. To test for avoidance behaviour, we compared the proportion of time spent by each fish in the scented arm; fish that did not leave shelter provided no data on spatial avoidance. We employed one-way ANOVA and the Dunnett post hoc test (Zar 1996) to examine whether time spent in the scented arm differed between cues from a predator fed salmon ($N = 39$) and one fed nonsalmon ($N = 31$) compared to controls ($N = 16$). The Dunnett test serves to identify those groups whose means are significantly different from those of a control or a reference group; it is hence well suited for this type of comparison (Zar 1996; Vilhunen & Hirvonen 2003). A paired t test was employed to test for avoidance behaviour in trials that involved comparing cues from a predator fed salmon in one arm versus cues from one fed nonsalmon in the other arm ($N = 32$). Linear regression was used to test for an association between boldness, measured as latency to leave shelter (log transformed), and avoidance behaviour, measured as proportion of time spent in the scented arm (arcsine transformed). This was carried out separately for treatments with cues from a predator fed salmon, cues from a predator fed nonsalmon and controls. Repeated measures ANOVA was used to compare OBR between treatments, using odour type as a fixed factor and fork length as a covariate to control for variation in body size. For each fish, we used beats above basal rate in the analysis, obtained by subtracting the OBR recording taken at 0800 hours (after the fish had been held overnight) from each recording taken following the introduction of the scent. Where Mauchly's test for sphericity could not be met, Greenhouse–Geisser-corrected probability values were used. All statistical analyses were carried out in SPSS version 16.0 (SPSS Inc., Chicago, IL, U.S.A.).

Ethical Note

The research described here was approved by Swansea University Research Ethics Committee and conducted in consultation with the U.K. Home Office. Fish subjected to odour cues were able to hide in refuges when alarm cues were released and no fish were harmed, as no predators were present. Measuring and weighing took place under anaesthesia to reduce stress, and survival rate was 100% over the study. At the end of the study, the fish were returned to Cynrig Fish Culture Unit for use in their stocking programme. The otter used in the study was under the expert care of trained staff at Wildwood Nature Reserve, who fed the otter and collected the spraints.

RESULTS

Boldness

We found no statistical difference (ANCOVA: $F_{2,94} = 0.56$, $P = 0.57$) in mean latency to leave shelter between treatments (untransformed means ± SE: control: 208 ± 80 s; salmon diet cues: 125 ± 37 s; nonsalmon diet cues: 238 ± 58 s). Boldness was unaffected by body size ($F_{1,94} = 1.99$, $P = 0.16$) and there was no interaction between body size and treatment ($F_{2,94} = 0.61$, $P = 0.55$). However, the proportion of fish that left the shelter differed significantly between treatments ($\chi^2_2 = 8.97$, $P = 0.01$) as more fish left the shelter when tested with conspecific diet cues (39/40) than when tested with blank water (16/20) or nonsalmon diet cues (31/40), possibly reflecting qualitatively different responses to blank versus scented water.

Avoidance Behaviour

There was no bias in the proportion of time spent in the arms of the Y-maze in the absence of predator cues (mean ± SE: left arm: 0.45 ± 0.07; right arm: 0.55 ± 0.07; $t_{15} = -0.84$, $P = 0.41$). However, avoidance of the scented arm differed significantly between treatments when predator cues were added ($F_{2,83} = 4.03$, $P = 0.02$; Fig. 1a). Dunnett's post hoc tests (two-tailed, *q*) show that juvenile salmon significantly avoided the arm scented with conspecific diet-released cues compared to controls ($q_{2,83} = -2.87$, $P = 0.01$), but not the arm scented with odour from a predator fed on a nonsalmon diet ($q_{2,83} = -0.20$, $P = 0.16$). Bonferroni-corrected post hoc pairwise comparisons gave similar results (control versus conspecific diet-released cues: $P = 0.02$; control versus nonsalmon: $P = 0.30$), and indicated that there was no difference between the two treatments (nonsalmon diet cues versus conspecific diet-released cues: $P = 0.55$). When juvenile salmon were confronted with conspecific diet-released cues in one arm and nonsalmon diet cues in the other, they strongly avoided the conspecific diet-released cues (paired *t* test: $t_{31} = -5.44$, $P < 0.001$; Fig. 1b). Latency to leave shelter was unrelated to time spent in the scented arm for both blank controls (linear regression: $F_{1,15} = 0.23$, $P = 0.64$) and fish tested with nonsalmon diet cues ($F_{1,30} = 1.68$, $P = 0.21$). However, for fish tested with conspecific diet-released cues, a strong inverse relationship was found between latency and avoidance behaviour (linear regression: $F_{1,38} = 5.99$, $P = 0.02$), so that individuals that were quick to leave shelter were also those most likely to show strong avoidance behaviour.

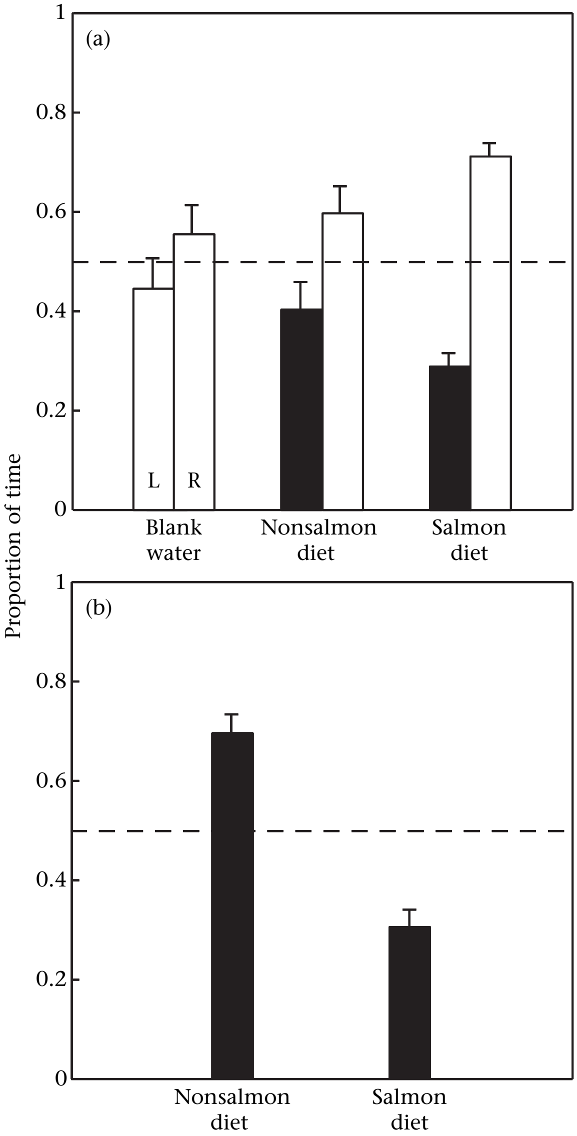

Figure 1. Proportion of time spent by juvenile Atlantic salmon in unscented (□) and scented (■) arms of the Y-maze in (a) control versus scented trials (L = left arm; R = right arm of the maze) and (b) scented trials. In scented trials, the water contained odour from a predator fed a nonsalmon diet or a salmon diet. Means + SE are shown.

First Arm Choice

Upon leaving the shelter, juvenile salmon chose the unscented arm first significantly more often ($\chi^2_1 = 10.54$, $P = 0.001$) when the other arm was scented with conspecific diet-released cues (33 of 39 or 85% of cases) than when it was scented with nonsalmon diet cues (16 of 31 or 52% of cases). When the two arms were scented, juveniles were much more likely ($\chi^2_1 = 12.50$, $P < 0.001$) to choose first the arm scented with nonsalmon diet cues (26 of 32 or 81% of cases) than the arm scented with conspecific cues (6 of 32 or 19% of cases).

Freezing Behaviour

The number of individuals that froze differed significantly between treatments ($\chi^2_2 = 23.18$, $P < 0.001$). Thus, while no individuals froze when they were tested with blank water, 14 of 40 individuals (35%) froze when the arm was scented with nonsalmon diet, and 23 of 40 fish (58%) froze when tested with conspecific diet-released cues. Analysis of the frequency of freezing behaviour gave similar results, and indicated that there were significant differences between treatments in the number of freezes (mean values ± SE; control: 0.00 ± 0.00; nonsalmon diet cues: 0.37 ± 0.08; conspecific diet-released cues: 0.70 ± 0.11; Kruskal–Wallis test: $\chi^2_2 = 19.02$, $P < 0.001$). Post hoc pairwise Bonferroni-corrected comparisons revealed that freezing behaviour differed between controls and the two scent treatments (Mann–Whitney *U* test: control versus nonsalmon diet cues: $U = 540$, $N_1 = N_2 = 40$, $P = 0.01$; control versus conspecific diet-released cues: $U = 170$, $N_1 = N_2 = 40$, $P < 0.001$), which in turn did not differ between themselves (conspecific diet-released cues versus nonsalmon diet cues: $U = 603$, $N_1 = N_2 = 40$, $P = 0.10$).

Opercular Beat Rate

Repeated measures ANOVA showed that OBR differed significantly over time depending on the type of scent (within-subjects effects with Greenhouse–Geisser correction: time*scent type: $F_{12.19,351.06} = 2.66$, $P = 0.002$; time: $F_{6.09,351.06} = 0.49$, $P = 0.82$; time*fork length: $F_{6.09,351.06} = 0.46$, $P = 0.76$). Fish maintained elevated ventilation rates over the 5 h of the trial when they were exposed to the scent of conspecifics in the predator's faeces (Fig. 2). In contrast, fish exposed to blank water, or to the scent of the predator fed a nonsalmon diet, quickly reached basal levels within 5 min of exposure (between-subjects effect for scent type: $F_{2,56} = 12.72$, $P < 0.001$). The OBR increased on average by 9.13 beats/min (SE = 2.14) over basal level following exposure to the scent of the predator fed conspecifics, but remained within or below basal levels following exposure to blank water (mean ± SE = −5.70 ± 2.13) or to the scent of the predator when fed on a nonsalmon diet (−1.75 ± 2.13). Pairwise comparisons indicated that it was the scent of conspecifics in the predator's faeces, and not the scent of the predator itself, that caused an increase in ventilation frequency (Bonferroni-corrected pairwise comparisons of mean differences and SEs: blank versus nonsalmon diet: −3.95 ± 3.01; $P = 0.59$; blank versus salmon diet: −14.83 ± 3.03; $P < 0.001$; salmon diet versus nonsalmon diet: 10.88 ± 3.03; $P = 0.002$).

DISCUSSION

This study shows that predator-naïve juvenile Atlantic salmon exhibit a range of antipredator responses when they are exposed to the faecal scent of an otter, a top mammalian predator, but only when the predator has eaten conspecifics. No antipredator responses were detected when the predator was fed a nonsalmon diet, suggesting that salmon do not chemically perceive the predator as a threat. This is perhaps surprising considering that prey and predator have coevolved together and that the Eurasian otter represents one of the most important predators of salmonids in many rivers (Kruuk 1995), including our study system (Roberts et al. 2009). However, whether fish possess the innate ability to recognize predators through chemosensory information alone and without the help of conspecific alarm cues (i.e. through predator kairomones) has received conflicting evidence in past studies. For example, Mathis & Smith (1993a) found that fathead minnows do not respond to sympatric predatory pike in the laboratory, but learn to detect and respond to it in the wild. In contrast, predator-naïve Arctic charr respond to chemical stimuli from sympatric brown trout and pikeperch (Vilhunen & Hirvonen 2003), which is not mediated by learning. Thus, it appears that while some fish can recognize some predators as a threat without the need for conspecific alarm cues, that is not the case for all potential fish prey or predators.

In this sense, our study indicates that diet-released conspecific cues may provide Atlantic salmon with an efficient way of generalizing predator recognition that is independent of predator identity. Only when conspecific alarm cues were present in the diet of the predator were salmon able to display a full range of antipredator responses, including spatial avoidance, freezing and increased ventilation rates. This suggests that the detection of diet-released alarm cues may have evolved (perhaps from capture-released cues) as a generalized means of responding to novel, diverse predators. We found an inverse relationship between latency to leave shelter and avoidance behaviour, but only among fish tested with conspecific cues in the predator's diet. Fish can use diet-related alarm cues to initiate inspection without sight of a predator (Brown & Godin 1999), and as visual cues were absent in our test arena, this may have resulted in increased willingness to leave shelter and move to the relative safety of the unscented arm. We have recently shown that juvenile salmon react to the presence of chemical alarm cues in the water by leaving shelter sooner, rather than later, possibly as a startle response to the threat of predation (Roberts et al. 2011).

Previous studies have shown that some aquatic prey are able to recognize diet-released conspecific alarm cues in the faeces of predators and that this enhances survival (e.g. Mirza & Chivers 2003a, b). For example, predator-naïve damselfly larvae, *Enallagma* spp., recognize pike only when pike are fed conspecifics (Chivers et al. 1996). Likewise, juvenile western toads, *Bufo boreas*, avoid cues from red-spotted garter snakes, *Thamnophis sirtalis*, fed conspecifics, but not snakes fed larval toads or earthworms (Belden et al. 2000), and marine gastropods respond to crabs but only when they had been fed conspecifics (Jacobsen & Stabell 2004). However, to our knowledge, such a generalized antipredator response has not been described in relation to any piscivorous mammalian predator before.

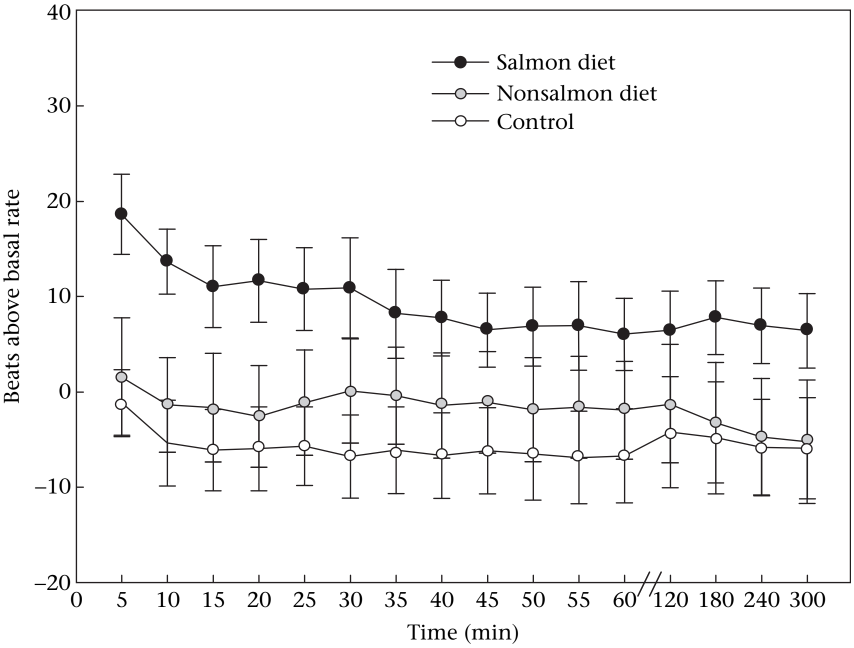

Figure 2. Mean ± SE opercular beat rate above basal level for juvenile Atlantic salmon tested with blank water ($N = 20$), water scented with odour from a predator fed a salmon diet ($N = 20$) and water scented with odour from a predator fed a nonsalmon diet ($N = 20$) over a 5 h observation period. Scent was added at time = 0.

Diet-related cues may allow aquatic prey to react to a wide range of threats without sensory overload or the need for learning, as there is no need to retain information about all potential predators. Also, unlike visual cues and capture-released cues that are only effective if prey are in the close vicinity of an actively feeding predator, diet-released cues are less temporally and spatially bound because they reveal information from the last meal. Such cues can therefore provide information regarding the intensity and frequency of predation, even when the predator is not feeding. For example, knowledge of the last meal provides prey with information that can be used to determine threats from seasonal or novel predators, and may be used by freshwater fishes as an early defence against the threat posed by invasive species. Some prey appear to be able to distinguish between diet-released and capture-released alarm cues and use them in combination to interpret better the intensity of predation risks (Ferrari et al. 2007c; Lautala & Hirvonen 2008). For example, predator-naïve Arctic charr respond more strongly to capture-released cues from previously starved brown trout than to capture-released cues from pikeperch, but the response is equally intense when both predators are fed conspecifics (Vilhunen & Hirvonen 2003). This suggests that chemical alarm cues in the predators' diet can act in an additive or synergistic fashion to provide increasing information during risk assessment, which Ferrari et al. (2008) termed 'sensory complementation'. Yet, the nature of the chemical cues that enable aquatic prey to detect conspecifics in predators' diets remains obscure. In fathead minnows, alarm cues have been traced to alarm substance cells within the epidermis (Schreckstoff alarm cue), and experiments have shown that it is these cues that are also recognized in the diet of predatory pike (Mathis & Smith 1993b). But this has not been determined for most other prey, and the generality of such a response is therefore unclear. To what extent cues released at capture are chemically different from those released in the diet, or if these are indeed different, is not known. Alarm cues in some aquatic species are suspected to consist of small polypeptides, which are highly soluble in water (Fraker et al. 2009), but these may undergo structural changes in a predator's digestive system. If capture- and diet-released cues represent the same type of cues released under different contexts, then our study indicates that these must have remained functionally stable under the extremely low pH of a mammalian digestive system, a much more acidic environment than that found in fishes (Sugiura et al. 2006). Cues that withstood passage through the mammalian digestive tract elicited a repertoire of strong antipredator responses, which was not detected when the predator was shifted to a nonsalmon diet.

In brief, our study illustrates a powerful mechanism that allows juvenile salmon, and presumably other salmonids, to recognize a sympatric mammalian predator by chemically detecting the smell of conspecifics in the predator's faeces. Although the use of diet-released cues has been demonstrated for a few other fishes, our study is the first to extend this mechanism to more distant taxa, such as a mammalian carnivore. It is unclear to what extent detection of conspecific alarm cues remains efficient after passage through the digestive system of other piscivorous predators such as birds and other mammals and this will require further studies. Likewise, as we only used one predator in our experiments, we do not know to what extent individual variation in the predator's scent, perhaps related to gender or stage of maturation, may affect the antipredator response of juvenile salmon. What is clear is that diet-released cues elicited a strong antipredator response across five behavioural traits, providing evidence for the complex way in which prey can use chemical signals to interpret the surrounding environment while avoiding sensory overload. As our test fish had been reared without exposure to predators, this suggests that learning is not necessary for the recognition of such cues. This would suggest that the typically high predation rates sustained by captive-bred fish in restoration programmes (Brown & Day 2002) may not necessarily result from an inability to recognize predators, but perhaps from an inferior ability to escape from them (e.g. Biro et al. 2004). Future studies designed to clarify the generality of diet-released cues across taxa, their relation to capture-released cues, and their integration with visual stimuli during predator recognition would seem to be warranted.

Acknowledgments

Funding for this study was provided by a NERC Ph.D. studentship and the Cardiff Harbour Authority. We are grateful to Dan Forman, John Taylor, Peter Gough and the staff at the Cynrig hatchery for support and help during this project. We also thank Judi Dunn at the Wildwood Trust for collecting the otter spraints, and two anonymous referees for useful comments that have considerably improved the manuscript.

References

Abrams, P. A. 2000. The evolution of predator–prey interactions: theory and evidence. *Annual Review of Ecological Systems*, **31**, 79–105.

Belden, L. K., Wildy, E. L., Hatch, A. C. & Blaustein, A. R. 2000. Juvenile western toads, *Bufo boreas*, avoid chemical cues of snakes fed juvenile, but not larval, conspecifics. *Animal Behaviour*, **59**, 871–875.

Bell, A. M. & Sih, A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, **10**, 828–834.

Berejikian, B. A., Tezak, E. P. & LaRae, A. L. 2003. Innate and enhanced predator recognition in hatchery-reared chinook salmon. *Environmental Biology of Fishes*, **67**, 241–251.

Biro, P. A., Abrahams, M. V., Post, J. R. & Parkinson, E. A. 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society B*, **271**, 2233–2237.

Blumstein, D. T., Daniel, J. C., Schnell, M. R., Ardron, J. G. & Evans, C. S. 2002a. Antipredator behaviour of red-necked pademelons: a factor contributing to species survival? *Animal Conservation*, **5**, 325–331.

Blumstein, D. T., Mari, M., Daniel, J. C., Ardron, J. G., Griffin, A. S. & Evans, C. S. 2002b. Olfactory predator recognition: wallabies may have to learn to be wary. *Animal Conservation*, **5**, 87–93.

Braithwaite, V. A. & Salvanes, A. G. V. 2005. Environmental variability in the early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. *Proceedings of the Royal Society B*, **272**, 1107–1113.

Brodie, E. D. & Formanowicz, D. R. 1991. Predator avoidance and antipredator mechanisms: distinct pathway to survival. *Ethology Ecology and Evolution*, **3**, 73–77.

Brown, C. & Braithwaite, V. A. 2004. Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. *Animal Behaviour*, **68**, 1325–1329.

Brown, C. & Day, R. L. 2002. The future of stock enhancements: lessons for hatchery practice from conservation biology. *Fish and Fisheries*, **3**, 79–94.

Brown, C., Jones, F. & Braithwaite, V. 2005. In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, **70**, 1003–1009.

Brown, G. E. 2003. Learning about danger: chemical alarm cues and local risk assessment in prey fishes. *Fish and Fisheries*, **4**, 227–234.

Brown, G. E., Chivers, D. P. & Smith, R. J. F. 1995. Localized defecation by pike: a response to labeling by cyprinid alarm pheromone? *Behavioral Ecology and Sociobiology*, **36**, 105–110.

Brown, G. E. & Godin, J. G. J. 1997. Anti-predator responses to conspecific and heterospecific skin extracts by threespine sticklebacks: alarm pheromones revisited. *Behaviour*, **134**, 1123–1134.

Brown, G. E. & Godin, J. G. J. 1999. Who dares, learns: chemical inspection behaviour and acquired predator recognition in a characin fish. *Animal Behaviour*, **57**, 475–481.

Brown, G. E. & Smith, R. J. F. 1997. Conspecific skin extracts elicit antipredator responses in juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Zoology*, **75**, 1916–1922.

Brown, G. E., Poirier, J. F. & Adrian, J. C. 2004. Assessment of local predation risk: the role of subthreshold concentrations of chemical alarm cues. *Behavioral Ecology*, **15**, 810–815.

Brown, G. E., Macnaughton, C. J., Elvidge, C. K., Ramnarine, I. & Godin, J. G. J. 2009. Provenance and threat-sensitive predator avoidance patterns in wild-caught Trinidadian guppies. *Behavioral Ecology and Sociobiology*, **63**, 699–706.

Chivers, D. P. & Mirza, R. S. 2001. Predator diet cues and the assessment of predation risk by aquatic vertebrates: a review and prospectus. *Chemical Signals in Vertebrates*, **9**, 277–284.

Chivers, D. P. & Smith, R. J. F. 1995. Fathead minnows (*Pimephales promelas*) learn to recognize chemical stimuli from high-risk habitats by the presence of alarm substance. *Behavioral Ecology*, **6**, 155–158.

Chivers, D. P. & Smith, R. J. F. 1998. Chemical alarm signalling in aquatic predator–prey systems: a review and prospectus. *Ecoscience*, **5**, 338–352.

Chivers, D. P., Wisenden, B. D. & Smith, R. J. F. 1996. Damselfly larvae learn to recognize predators from chemical cues in the predator's diet. *Animal Behaviour*, **52**, 315–320.

Chivers, D. P., Kiesecker, J. M., Marco, A., DeVito, J., Anderson, M. T. & Blaustein, A. R. 2001. Predator-induced life history changes in amphibians: egg predation induces hatching. *Oikos*, **92**, 135–142.

Ferrari, M. C. O., Gonzalo, A., Messier, F. & Chivers, D. P. 2007a. Generalization of learned predator recognition: an experimental test and framework for future studies. *Proceedings of the Royal Society B*, **274**, 1853–1859.

Ferrari, M. C. O., Messier, F. & Chivers, D. P. 2007b. Variable predation risk and the dynamic nature of mosquito antipredator responses to chemical alarm cues. *Chemoecology*, **17**, 223–229.

Ferrari, M. C. O., Brown, M. R., Pollock, M. S. & Chivers, D. P. 2007c. The paradox of risk assessment: comparing responses of fathead minnows to capture-released and diet-released alarm cues from two different predators. *Chemoecology*, **17**, 157–161.

Ferrari, M. C. O., Vavrek, M. A., Elvidge, C. K., Fridman, B., Chivers, D. P. & Brown, G. E. 2008. Sensory complementation and the acquisition of predator recognition by salmonid fishes. *Behavioral Ecology and Sociobiology*, **63**, 113–121.

Fraker, M. E., Hu, F., Cuddapah, V., McCollum, S. A., Relyea, R. A., Hempel, J. & Denver, R. J. 2009. Characterization of an alarm pheromone secreted by amphibian tadpoles that induces behavioral inhibition and suppression of the neuroendocrine stress axis. *Hormones and Behavior*, **55**, 520–529.

Griffin, A. S., Evans, C. S. & Blumstein, D. T. 2001. Learning specificity in acquired predator recognition. *Animal Behaviour*, **62**, 577–589.

Hawkins, L. A., Armstrong, J. D. & Magurran, A. E. 2004. Predator-induced hyperventilation in wild and hatchery Atlantic salmon fry. *Journal of Fish Biology*, **65**, 88–100.

Hirvonen, H., Ranta, E., Piironen, J., Laurila, A. & Peuhkuri, N. 2000. Behavioural responses of naive Arctic charr young to chemical cues from salmonid and nonsalmonid fish. *Oikos*, **88**, 191–199.

Jacobsen, H. P. & Stabell, O. B. 2004. Antipredator behaviour mediated by chemical cues: the role of conspecific alarm signalling and predator labelling in the avoidance response of a marine gastropod. *Oikos*, **104**, 43–50.

Kats, L. B. & Dill, L. M. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience*, **5**, 361–394.

Kelley, J. L. & Magurran, A. E. 2003. Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, **4**, 216–226.

Kruuk, H. 1995. *Wild Otters. Predation and Populations*. New York: Oxford University Press.

Kusch, R. C., Mirza, R. S. & Chivers, D. P. 2004. Making sense of predator scents: investigating the sophistication of predator assessment abilities of fathead minnows. *Behavioral Ecology and Sociobiology*, **55**, 551–555.

Lautala, T. & Hirvonen, H. 2008. Antipredator behaviour of naive Arctic charr young in the presence of predator odours and conspecific alarm cues. *Ecology of Freshwater Fishes*, **17**, 78–85.

Lima, S. L. & Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *American Naturalist*, **153**, 649–659.

Mathis, A. & Smith, R. J. F. 1993a. Chemical labelling of northern pike (*Esox lucius*) by the alarm pheromone of fathead minnows (*Pimephales promelas*). *Journal of Chemical Ecology*, **19**, 1967–1979.

Mathis, A. & Smith, R. J. F. 1993b. Fathead minnows, *Pimephales promelas*, learn to recognise northern pike, *Esox lucius*, as predators on the basis of chemical stimuli from minnows in the pike's diet. *Animal Behaviour*, **46**, 645–656.

Metcalfe, N. B., Huntingford, F. A. & Thorpe, J. E. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Animal Behaviour*, **35**, 901–911.

Mirza, R. S. & Chivers, D. P. 2003a. Predator diet cues and the assessment of predation risk by juvenile brook charr: do diet cues enhance survival? *Canadian Journal of Zoology*, **81**, 126–132.

Mirza, R. S. & Chivers, D. P. 2003b. Fathead minnows learn to recognize heterospecific alarm cues they detect in the diet of a known predator. *Behaviour*, **140**, 1359–1369.

Peterson, A. G., Bull, C. M. & Wheeler, L. M. 1992. Habitat choice and predator avoidance in tadpoles. *Journal of Herpetology*, **26**, 142–146.

Roberts, L. J., Forman, D. W., Taylor, J., Gough, P. J. & García de Leániz, C. 2009. Night stocking facilitates nocturnal migration of hatchery-reared Atlantic salmon smolts (*Salmo salar*). *Fisheries Management and Ecology*, **16**, 10–13.

Roberts, L. J., Taylor, J. & Garcia de Leaniz, C. 2011. Environmental enrichment reduces maladaptive risk-taking behavior in salmon reared for conservation. *Biological Conservation*, **144**, 1972–1979.

Schoeppner, N. M. & Relyea, R. A. 2009. Interpreting the smells of predation: how alarm cues and kairomones induce different prey defences. *Functional Ecology*, **23**, 1114–1121.

Sneddon, L. U. 2003. The bold and the shy: individual differences in rainbow trout. *Journal of Fish Biology*, **62**, 971–975.

Sugiura, S. H., Roy, P. K. & Ferraris, R. P. 2006. Dietary acidification enhances phosphorus digestibility but decreases H+/K+-ATPase expression in rainbow trout. *Journal of Experimental Biology*, **209**, 3719–3728.

Sundstrom, L. F., Petersson, E., Johnsson, J. I., Dannewitz, J., Hojesjo, J. & Jarvi, T. 2005. Heart rate responses to predation risk in *Salmo trutta* are affected by the rearing environment. *Journal of Fish Biology*, **67**, 1280–1286.

Vilhunen, S. & Hirvonen, H. 2003. Innate antipredator responses of Arctic charr (*Salvelinus alpinus*) depend on predator species and their diet. *Behavioral Ecology and Sociobiology*, **55**, 1–10.

Vilhunen, S., Hirvonen, H. & Laakkonen, M. V. M. 2005. Less is more: social learning of predator recognition requires a low demonstrator to observer ratio in Arctic charr (*Salvelinus alpinus*). *Behavioral Ecology and Sociobiology*, **57**, 275–282.

Wilson, A. D. M. & Stevens, E. D. 2005. Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, **111**, 849–862.

Wisenden, B. D., Pollock, M. S., Tremaine, R. J., Webb, J. M., Wismer, M. E. & Chivers, D. P. 2003. Synergistic interactions between chemical alarm cues and the presence of conspecific and heterospecific fish shoals. *Behavioral Ecology and Sociobiology*, **54**, 485–490.

Zar, J. H. 1996. *Biostatistical Analysis*. Upper Saddle River, New Jersey: Prentice-Hall.

Zhao, X. X., Ferrari, M. C. O. & Chivers, D. P. 2006. Threat-sensitive learning of predator odours by a prey fish. *Behaviour*, **143**, 1103–1121.

Animal Behaviour 82 (2011) 611–612

Contents lists available at ScienceDirect

Animal Behaviour

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In Focus

Featured Articles in This Month's *Animal Behaviour*

Salmon Use Diet Cues to Recognize a Mammalian Predator

The interaction between prey and predator is one of the classic evolutionary arms races. Predator detection and recognition is the first line of defence for a prey and often combines a big innate component with an element of learning. So how does an animal recognize a predator?

This question is particularly intriguing for animals living in aquatic environments in which visibility is limited and chemical cues may be the main source of information. Such chemical cues are released either by the predator or by other prey from the same (or closely related) species. The best studied cues from prey belonging to the same species are released in the water either upon mechanical damage through predation or in the faeces of the predator after prey consumption. The latter type, called diet-released cues, has been demonstrated in, for example, fish preyed upon by fish and toads preyed upon by snakes. However, the extent to which diet-released cues can be used to recognize predators from distant taxonomic groups has not been tested.

Laura Roberts and Carlos Garcia de Leaniz (Swansea University, U.K.) do just that for the first time in the present issue (pp. 619–625). They carried out experiments to test whether Atlantic salmon (Fig. 1) can recognize diet-released cues from its natural predator, the Eurasian otter. The authors used predator-naïve juvenile fish to eliminate any involvement of learning. The salmon were derived from wild stock from the River Taff, where predatory otters are common, and were reared at the Cynrig Fish Culture Unit, of the Environment Agency Wales, U.K. All fish involved in the experiment survived without sustaining any damage and were returned to the culture unit for their stocking programme. The predator cues were obtained from the faeces of an 8-year-old female Eurasian otter, reared in captivity by trained staff in an outdoor pen at the Wildwood Nature Reserve, Kent, U.K. and fed either salmon or a nonsalmon diet.

Animals generally demonstrate a range of antipredator behaviours. In an attempt to capture the full repertoire in juvenile salmon, the study assessed several responses including willingness to leave shelter (a measure of boldness), spatial avoidance of predatory cues, freezing (or staying motionless as a form of crypsis), and ventilation rate as a measure of stress. The first three responses were tested in a Y-maze choice chamber consisting of two arms with a central partition to prevent any scents from mixing. This allowed two types of scented water to be presented simultaneously to the test salmon in the following four treatment combinations: distilled water versus water scented with faeces from the otter when fed on a salmon diet, distilled water versus water scented with faeces from the otter when fed on a nonsalmon diet, water scented with faeces from the otter fed on a salmon versus a nonsalmon diet, and finally distilled water versus distilled water (the control). Ventilation rate was assessed separately in small fish tanks scented with distilled water (control) and water solutions of faeces from the otter fed on either a salmon diet or a nonsalmon diet. Individual juvenile salmon were tested one at a time, and were tested only once.

Figure 1. Salmon parr. Photo: Pablo Caballero.

Roberts and Garcia de Leaniz found that juvenile salmon strongly avoided the arm scented with the otter's faeces when the otter had been fed salmon. By contrast, they found no evidence that fish avoided the arm scented with predatory odour when the otter had been fed on a nonsalmon diet. None of the salmon froze when they were tested with distilled water while 35% and 58% froze when the arm was scented with nonsalmon diet and salmon diet cues, respectively. Finally, fish exposed to the scent of salmon in the otter's faeces maintained high ventilation rates (above basal levels) throughout the 5 h of the trial, in contrast to fish exposed to distilled water or to nonsalmon diet cues, which reached basal levels within the first 5 min after exposure.

The results of the study provide important evidence that water-borne chemical cues released from the faeces of a predator that has fed on conspecifics provide juvenile Atlantic salmon with an efficient and adaptable means of recognizing a predator. As

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doi:10.1016/j.anbehav.2011.08.003

the test fish had no prior exposure to predators, the results suggest that learning is not necessary for this type of recognition. Therefore, diet-released cues may allow aquatic prey to react to a wide range of threats without sensory overload or the need for learning. Furthermore, while visual or chemical cues released in the water by mechanical damage through predation are effective only when the prey are in the close vicinity of a feeding predator, diet-released cues allow recognition from the safety of a greater temporal and spatial distance because they provide information from the predator's last meal, and not just from the current one. Last but not least, this means of recognizing predators could be used by aquatic prey as an early defence against invasive species and will help inform valuable conservation programmes.

Ana Sendova-Franks
Executive Editor

Love and Harmony In Mosquitoes

Mating occurs in swarms in many flying insects. In the yellow-fever mosquito, swarms consisting mainly of males form in the vicinity of a human host, and females enter the swarm singly to mate. Biologists traditionally have thought that the opportunity for female choice and other mechanisms of nonrandom mating must be severely limited in the apparent chaos of a mating swarm, thus limiting any opportunity for sexual selection. A paper in this issue (pp. 627–633) by Lauren J. Cator and Laura C. Harrington of Cornell University disproves this traditional idea with respect to yellow-fever mosquitoes, demonstrating instead the existence of a complex and fascinating pattern of nonrandom mating with respect to acoustic signals.

It is no news to any of us that mosquitoes produce a noise in flight. These annoying buzzes consist of a fundamental tone plus harmonics. In yellow-fever mosquitoes the fundamental of the female's buzz is lower than that of the male's buzz. Recently it has been shown that courting pairs of this species converge in their flight tones. The two fundamentals do not converge; rather, the second harmonic of the male's tone converges with the third harmonic of the female's at approximately 1200 Hz, or the male's fundamental converges with the female's second harmonic at about 800 Hz. Both sexes are able to hear the other's tone and converge on it. What Cator and Harrington demonstrate in this issue is that harmonic convergence affects mating.

Figure 2. A male yellow-fever mosquito mates with a tethered female. Photo: Charles Walcott.

The authors allowed mating between a tethered female and free-flying males in the laboratory (Fig. 2). Pairs that converged at harmonics were more likely to mate successfully than pairs that did not converge. Females were able to reject males by kicking them or holding them off with their legs, and such rejections were more likely in pairs that did not show harmonic convergence. This pattern of rejection by females argues that female choice is responsible, at least in part, for the pattern of nonrandom mating.

Cator and Harrington went on to investigate the fitness consequences of nonrandom mating by harmonic convergence. They found that females from converging pairs did not have higher survival, fecundity or net reproductive rate than females from pairs that did not converge. Thus harmonic convergence does not seem to have any direct fitness benefit to females, although the authors caution that effects are still possible under other environmental circumstances. A different story was found for indirect benefits. Sons of pairs that showed harmonic convergence were themselves more likely to show harmonic convergence when they mated. As would then be expected, sons of converging pairs had higher mating success than sons of pairs that did not converge. This result supports the classic benefit of female choice evolved through the runaway mechanism, that is, sons inherit the mating advantage of their attractive fathers, but the interpretation is complicated by the possibility that females as well as males contribute to harmonic convergence in mating pairs.

Cator and Harrington's study has an importance beyond what it tells us about the possibilities for sexual selection in insect mating swarms. Yellow-fever mosquitoes are carriers not only of the disease they are named after but of dengue fever as well. Both dengue and yellow fever are major human health problems in tropical countries, together causing millions of cases of infection and tens of thousands of deaths per year. Basic knowledge of the mating behaviour of the mosquito vector, such as is provided by the Cator and Harrington study, may eventually contribute to the control of the vector and thus of these diseases.

William A. Searcy
Executive Editor

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NEWS

Salmon can sniff out predators

12 September 2011, by Felicity Perry

Salmon know when their most common predator is around, because they can tell that it's eaten salmon before, new research shows. Young fish can do this too, even if they've never encountered that particular predator before.

European otter.

Researchers from the University of Swansea put young Atlantic salmon in tanks of water, some sections of which were scented with diluted otter faeces. They found the fish tended to avoid the scented water – provided the otter in question had previously eaten salmon.

'It's the predator's diet – not just its own smell – that's alerting the salmon,' explains Dr Laura Roberts from the University of Swansea, co-author of the report published in *Animal Behaviour*.

Otters are common predators of salmon so it's clearly useful to the fish to be able to sniff them out.

The smell acts as an early-warning system for the fish, even when they can't see the predator. It lets them work out the potential risk of being eaten and balance predator avoidance with other vital activities like foraging and reproducing.

Previous studies have shown that some fish can detect the presence of other predatory fish, but this is the first research to show the mechanism works for mammal predators too.

'We wanted to test whether the salmon were able to recognise the otter as a threat using just chemical cues, and also to see whether they were detecting the smell of the predator's itself or of its diet,' says Roberts.

The researchers tested individual fish in a 'Y-maze chamber' – essentially a trough with two arms and a holding tank at one end. This arrangement meant different scents could be released into the arms of the tank and kept separate, while allowing the salmon to swim into whichever arm it chose.

In each test, differently scented water was introduced to each arm of the tank: either unscented, scented with the faeces of an otter that hadn't eaten salmon, or scented with faeces of an otter that had eaten salmon.

The researchers measured the salmons' avoidance behaviour by seeing how much time they spent in different parts of the tank. The fish seemed unperturbed by water scented with faeces from the non-salmon eating otter. But when the water was scented by the salmon eater's faeces the fish steered clear, avoiding that arm of the tank around 85 per cent of the time.

The researchers monitored other behaviours associated with predator avoidance, and these also varied depending on the scent. For example, more of the fish rested motionless on the bottom of the tank (known as 'freezing') in the presence of the salmon-diet scent. Fish exposed to this scent also breathed more quickly – a stress response which can be a reaction to the presence of a predator.

This suggests the fish aren't reacting simply to the otter's presence; they are reacting to the smell of an otter that has proved to be a predator by eating other salmon. And this ability gives them a head start in a world where many different creatures are out to eat them.

'The salmon's ability to sense these chemicals helps them react to a wide range of predators without the need to learn about each individual species,' says Roberts.

Laura Jayne Roberts & Carlos Garcia de Leaniz. Something smells fishy: predator-naive salmon use diet cues, not kairomones, to recognize a sympatric mammalian predator. *Animal Behaviour*, 2011, doi: 10.1016/j.anbehav.2011.06.019

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BBC NEWS
SOUTH WEST WALES

19 September 2011 Last updated at 12:08

Salmon can 'sniff out' predators - Swansea uni research

Salmon can sense mammal predators because they can tell whether they have eaten salmon before, according to new research.

Swansea University scientists found the fish can "sniff out" otters and other common predators.

Smell acts as an early warning system for the fish.

"It's the predator's diet - not just its own smell - that's alerting the salmon," said Dr Laura Roberts, co-author of the scientific report.

Although previous studies have shown that some fish can detect the presence of other predatory fish, this is the first research to show that fish can also sense mammal attackers.

Y-maze chamber

The researchers tested individual Atlantic salmon in a "Y-maze chamber" - a trough with two arms linked to a holding tank at one end.

Different scents were released into each arm of the tank - one scented by otters which had eaten salmon and the other with the scent of non-salmon-eating otters.

The salmon's avoidance behaviour was measured by recording how much time they spent in different parts of the tank.

They found the fish tended to avoid the water which had been scented by otters which had eaten salmon - around 85% of the time - but did not avoid water scented by non-salmon-eating otters.

"We wanted to test whether the salmon were able to recognise the otter as a threat using just chemical cues, and also to see whether they were detecting the smell of the predator's itself or of its diet," said Dr Roberts, whose research was published in the Animal Behaviour Journal.

"The salmon's ability to sense these chemicals helps them react to a wide range of predators without the need to learn about each individual species."
