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Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*)

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Summary. During their first 1–2 years of life, juvenile coho salmon (*Oncorhynchus kisutch*) are stream-dwelling, and feed upon drifting invertebrates. They move upstream from a holding position to intercept individual prey items; the distance moved (attack distance) is an increasing, but decelerating, function of prey size. Since the fish are presumably more visible to predators during such feeding excursions, prey size and risk are associated variables.

The effect on attack distance of the presentation of a model predator (a photograph of a rainbow trout) was examined in the laboratory. Attack distances are shortened following presentation of a predator; this is particularly true when the prey are large (Fig. 1). The extent of the reduction of attack distance is directly related to predator presentation frequency, although there appears to be a minimum level to which it will decline (Fig. 2). Hungry fish and fish in the presence of a competitor (simulated by a mirror) are less responsive to the predator, suggesting a trade-off of energetic requirements and risk (Fig. 3 and Table 3). The effect of predation risk should be to reduce the relative proportion of large prey in a juvenile coho's diet, and its net rate of energy intake.

Introduction

An optimal foraging strategy is generally considered to be one which maximizes an animal's average rate of energy intake (Pyke et al. 1977). One reason for expecting an animal to maximize the temporal efficiency of its foraging is that the performance of feeding behaviour may increase the likelihood of the animal being detected by its own predators. Thus, in one sense, optimal foraging theory considers risk of predation when predicting a forager's behaviour. However, the theory implicitly assumes that risk of predation is a function only of foraging time, and is independent of the type of resource utilized. When predation risk varies between patches or prey types, an animal would be expected to take the degree of risk into account when deciding where to feed or what items to include in its diet, i.e. to trade off mortality risk and energy gain so as to maximize fitness.

When the best habitat patches are also the most risky, several species have been shown to make such trade-offs (Milinski and Heller 1978; Mittlebach 1981; Sih 1982; Grubb and Greenwald 1982; Cerri and Fraser 1983; Edwards 1983; Werner et al. 1983; Power 1984). No study has examined the effect of predation risk on diet choice within a patch, although Iwasa et al. (1984) have modelled an analogous situation for host preference of parasitoids.

If a foraging animal is to balance predation risk and energetic value in reaching foraging decisions, it must first be able to estimate the degree of risk involved. One potentially useful risk measure is the frequency with which potential predators are seen in the habitat, since this measure combines information on predator density and activity. Although several studies have shown that foragers alter their behaviour after being presented with a real or simulated predator, either of themselves (Milinski and Heller 1978; Krebs 1980; Caraco et al. 1980) or of their young (Freed 1981; Martindale 1982), in none of these studies was predator presentation frequency varied to determine whether the animals were sensitive to the degree of risk. The main purpose of the present study was to ex-

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amine this question in juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum).

Juveniles of this species live in streams, feeding primarily on drifting prey. Individuals are characteristically territorial, returning to a central station after each feeding foray or aggressive interaction. Territory size varies inversely with food availability (Dill et al. 1981), suggesting that the fish are energy maximizers, and individual survival and population size may be food limited (Mason 1976). Coho salmon colour and patterning (bars and spots) render the fish cryptic against the gravel substrate of the stream, and the fish possess numerous behavioural and physiological mechanisms to enhance background matching (Donnelly and Dill 1984).

To a human observer, the fish are far more visible when moving than when stationary. We assume that they are also more visible to fish and bird predators when moving, and that risk increases with distance travelled. In this study we take advantage of the fact that the fish travel greater distances to obtain larger prey (Dunbrack and Dill 1983), and that prey size and predation risk are therefore correlated. We test the hypotheses that juvenile coho will not travel as far to obtain prey of a given size when potential risk is increased, and that the extent of this reduction of travel distance will be correlated directly with degree of risk but inversely with hunger and competitor pressure. We varied risk by altering the frequency of appearance of a model predator adjacent to a feeding coho.

Materials and methods

General

All experiments were conducted in a small artificial stream channel (185 cm long × 19 cm wide) housed within an environmental chamber (described more fully by Dunbrack and Dill 1983). Water depth was 14 cm, and 2160 lux illumination was provided by fluorescent lights on a natural photoperiod. Water velocity and temperature were controlled within each experiment, but varied between experiments.

Juvenile coho salmon (*Oncorhynchus kisutch*) were collected from the Salmon River, Langley, B.C., by seining riffles and shallow pools. Prior to and between experiments they were housed in visual isolation in small (12 × 26 cm) tanks. One day before testing, individual fish were acclimated in a screened-off section of the channel, from which they could not view the experimental fish or its treatment. The acclimated fish was moved to the experimental section when the trial of the previous fish had been completed.

Dead adult dipterans were used as prey items in all experiments. *Drosophila melanogaster* (ebony strain), *D. gibberosa*, and female onion flies *Hylemya antigua* were chosen to provide three distinct fly sizes. Fly size is expressed as body area (length × width); the three species averaged 0.021 ± 0.001, 0.060 ± 0.002 and 0.136 ± 0.004 cm^2, respectively (mean ± standard error, $n = 20$ of each species). Dipterans of similar sizes are regularly eaten by coho in the field. All fish were maintained between trials on a mixed diet of flies.

Prey items were dropped onto the flowing channel surface at intervals of 3–5 min, and only when the experimental fish held a constant position at the downstream end of the channel over a small piece of black plexiglass, simulating the rocks used in the field as holding stations. A meter stick running the length of the channel and visible in an angled overhead mirror allowed the experimenter to collect data on fish position without being in direct view of the fish.

Surface water velocity was determined by dropping flies onto the water surface and timing their passage to a number of points along the channel. The relationship derived was satisfactorily linear, despite slight variation due to pulsing wave action caused by the paddlewheel, and did not vary with fly size.

Three measurements were obtained for each prey item eaten by each experimental fish: reaction distance (RD), attack distance (AD), and attack time (TA). Reaction distance is defined as the distance from which the fish began its attack on the fly. Attack distance is the distance travelled by the fish from its holding position to the capture point, in the horizontal plane. A digital stopwatch (accurate to 0.01 s) was used to measure attack time from when the fish left the holding position to the time of prey capture.

Concentration on the fish's behaviour prevents the experimenter from following the fly and hence determining reaction distance directly. However, since the fly floats from its initial position to the capture point in the same period of time it takes the fish to swim there, reaction distance can be determined from water velocity (V_w) and the relationship $RD = AD + V_w(TA)$, since AD and TA are known. Although the fish's speed undoubtedly influences its detectability to predators, this parameter could not be determined in the present experiments owing to the fact that the coho frequently accelerated, slowed down, or even stopped during an attack. Thus, attack velocity is not simply AD/TA.

The predator stimulus was provided by a 20 cm laminated photograph of a rainbow trout (*Salmo gairdneri*), a natural predator in the Salmon River, produced by enlarging a colour plate from Carl et al. (1959). The photo was suspended on fine monofilament line and moved with a pulley system, a 6V DC motor, and a switching device with a logic circuit. Between presentations the predator was not visible to the experimental fish since it was positioned behind an opaque partition at the downstream end of the channel to the fish's right. At each presentation the model "swam" forward 1 m, into the fish's view, and then "drifted" backward behind the screen. The model was presented at pre-determined intervals during the light phase of the photoperiod, except during the feeding trials themselves.

The effect of predator exposure on attack behavior

Each of twelve fish (mean fork length 72.3 ± 1.7 mm) was observed in the stream channel on two occasions (trials) lasting two days each. During control trials fish were fed and observed on both days (C-1 and C-2) without any intervening model presentation. During experimental trials, the fish were presented with the model predator at 22.5 min intervals for the entire period (less the dark phase) between the two sets of observations (E-1 and E-2). Whether a particular fish received the control or experimental trial first was determined at random; 7 received the control trial first. Control and experimental trials were separated by 12–26 days. The experiment tests the hypothesis that exposure to the predator will cause a reduction in reaction and attack distance and attack time, i.e. that E-2 values for these parameters will be significantly less than C-2 values. Since each fish served as its own control, paired t-tests were used for statistical analysis.

On each of the four observation days, the subject fish was presented with three flies of each prey type in random order, and the attack parameters determined. Onion fly females possess light colored abdomens in comparison with the dark bodies of the two *Drosophila* species. To minimize this difference all flies used were dyed in a Sudan Black – alcohol solution and dried prior to presentation. The fish readily accepted the flies and showed no ill effects. Sometimes flies were attacked only after they had drifted past the fish's holding position, producing negative attack distances (32.6, 1.4 and 0.7% of the attack distances for small, medium and large flies, respectively). This occasionally resulted in the calculation of negative RD values as well (3.5% of the reaction distances for small flies only), but absolute values of reaction and attack distances were used in all statistical analyses. Each fish contributed only one datum per fly size per day (the mean value) to these analyses.

Water temperature in the channel was 12–13° C, and surface water velocity was 8.8 cm/s.

The effect of frequency of exposure, hunger, and disturbance

This experiment tests the hypotheses: [i] that any effect noticed in the first experiment was not due simply to disturbance; [ii] that the extent of reduction of attack parameters is directly related to the frequency of model presentation; and [iii] that hungry fish alter their behaviour less than satiated ones in response to exposure to the predator model.

Five fish (56.2 ± 1.2 mm) were each run under six different treatment conditions. Models were presented in four of these treatments every 5.5, 11, 22.5 or 45 min. In a fifth treatment the model was presented at 45 min intervals, but was covered with a black, rectangular shroud. The sixth treatment was a control (no predator presentation). The experimental protocol was as in the previous experiment, i.e. one day of observation both pre- and post-treatment. Each fish was given a randomly chosen treatment and then returned to its holding tank until all five fish had completed one treatment. The cycle then began again with the first fish and continued until all five fish had received each of the six treatments. This required 56–70 days per fish.

The prey were *D. gibberosa*. Each observation day, the experimental fish received eight flies, the approximate satiation ration based on feeding experiments, allowing determination of the effect of hunger. Water temperature was 13–14.5° C, and surface velocity 11.1 cm/s (the increase from the previous experiment resulted from installation of a new paddlewheel). Paired t-tests were used to compare treatment means.

The effects of competitor presence

The purpose of this experiment was to test the hypothesis that fish are less sensitive to risk in the presence of a potential competitor. A mirror on the wall of the channel, adjacent to the holding position and opposite the partition from behind which the predator appeared, served as a simulated competitor. A juvenile coho will react aggressively towards its mirror image, and such behaviour was occasionally observed in this experiment. Ten fish (59.7 ± 2.7 mm) were run with the mirror in place, and ten (60.3 ± 3.0 mm) without it.

The behaviour of each fish in this experiment was observed on only one day, following a day of model presentation at 5.5 min intervals. This experiment therefore differs from the others in that pre-treatment data were not collected.

Onion flies were used as prey, but were not dyed. Each fish received 8 prey. Water temperature was 14–16° C and velocity 11.1 cm/s.

Results

The effect of predator exposure on attack behavior

Coho reaction distance, attack distance, and attack time are all increasing functions of prey size (Fig. 1 and Table 1). Only the data for the second day of each trial are graphed (C-2 and E-2); data for the first days show the same asymptotic relationships.

There were no significant differences in the attack parameters for any prey size between the two trials on day 1 (prior to predator exposure). However, both reaction and attack distances increased between day 1 and day 2 in the control trial, probably as the result of increased familiarity with the testing apparatus. These increases were significant for large flies. It is because of this acclimation ef-

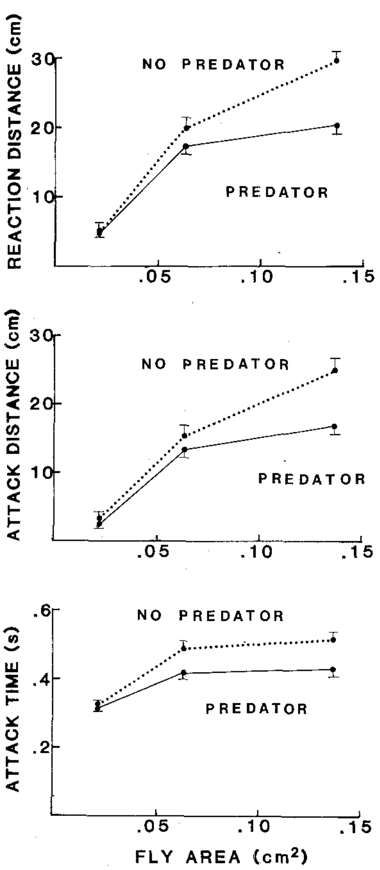

Fig. 1. Attack parameters of juvenile coho on three sizes of fly, with or without preceding exposure to the predator model. Day 2 (post-treatment) data only. Standard errors and statistical comparisons are in Table 1 (trials C-2 and E-2)

Table 1. Mean (±S.E.) attack parameters of juvenile coho in control (C) and experimental (E) trials, in response to three sizes of flies on days 1 (pre-treatment) and 2. $N=12$ in all cases. Bracketed values are significantly different (* signifies $P<0.05$; ** $P<0.01$)

Fly size (Type)	Fish group	Reaction distance (cm)	Attack distance (cm)	Attack time(s)
Small	C-1	4.1±0.7	2.9±0.6	0.34±0.01
(*Drosophila melanogaster*)	C-2	5.3±1.0	3.6±0.8	0.33±0.01
	E-2	4.9±0.7	2.6±0.6	0.32±0.01 >*
	E-1	5.6±0.7	3.3±0.5	0.36±0.01
Medium	C-1	16.0±1.5	11.8±1.5	0.46±0.03
(*D. gibberosa*)	C-2	19.9±1.4	15.5±1.4	0.49±0.02
	E-2	17.4±1.1	13.6±1.1	0.42±0.02 >**
	E-1	19.5±1.5	14.8±1.5	0.54±0.02
Large	C-1	22.6±1.6 >**	17.3±1.6 >**	0.56±0.03
(♀ *Hylemya antigua*)	C-2	30.0±1.4 >**	25.1±1.4 >**	0.52±0.02 >*
	E-2	20.6±1.2 >**	16.9±1.2 >*	0.42±0.02 >**
	E-1	26.5±1.3	21.1±1.4	0.60±0.05

fect that the statistical comparisons testing for the effect of predator exposure were carried out between the control and experimental trial values for day 2 (Fig. 1).

Exposure to the predator model caused a similar overall lowering of the curves for each of the attack parameters. Percentage reduction was always greatest for the largest prey, and all decreases for the largest prey were statistically significant ($P<0.01$). There were no significant effects of predator exposure on the attack parameters for the two smaller prey types.

Despite the previously noted increases in the attack parameters during the control trials, all attack parameters for all prey sizes declined between day 1 and day 2 in the experimental trials, i.e. the negative effect of predator exposure exceeds the positive effect of acclimation.

These results support the hypothesis that juvenile coho salmon are less willing to travel long distances, or to spend long periods of time moving, to obtain prey when risk of predation is increased. The effects are most marked when the prey are large, and the foraging trips of greater length and, presumably, greater risk.

The effects of frequency of exposure, hunger and disturbance

Both attack distance (Fig. 2) and reaction distance (not shown) were dependent on risk level, as measured by frequency of model presentation. While presentation of a predator at a frequency of 1.33 h^{-1} significantly reduced both reaction and attack distances, more frequent presentation produced a greater decrease in both parameters (Table 2). However, the fish appeared indifferent to frequencies higher than 2.67 h^{-1} (22.5 min intervals). Attack time did not vary with predator presentation frequency.

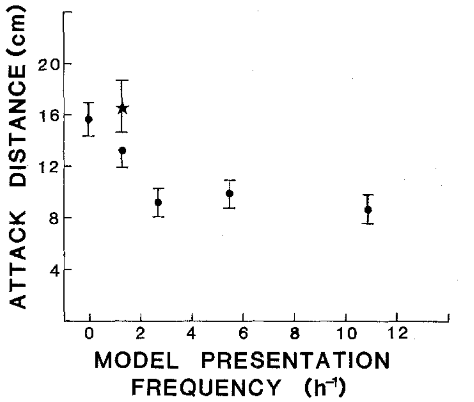

Fig. 2. Mean attack distance (±SE) to medium-sized flies by coho salmon, as a function of the frequency of presentation of a model predator (day 2 data only). Star denotes presentation of the covered model

The fact that the covered model did not cause changes relative to the control in any attack parameter shows that the fish are not responding simply to large moving objects or to disturbance per se. Rather, the coho appear sensitive to some specific visual feature of the predatory fish model.

Since results of the control and covered model treatments did not differ from one another, they were pooled for subsequent analysis of the influence of hunger. Similarly, the data for the three highest presentation frequencies were pooled to provide the best data set for examining hunger effects when risk is high. These pooled data were regressed against fly number (1 through 8). In the no-predator treatments, neither reaction distance

Table 2. Mean (±standard error) attack parameters of coho salmon feeding on medium-sized flies following presentation of predator models at various frequencies. Means bracketed together do not differ at $P=0.05$; other differences are significant ($n=40$ in all cases)

Treatment	Predator frequency (h^{-1})	Reaction distance (cm)	Attack distance (cm)	Attack time(s)
No model	–	20.1±1.5	15.7±1.3	0.42±0.02
Covered model	–	20.9±2.0	16.7±2.0	0.50±0.04
45.0 min interval	1.33	18.4±1.5	13.3±1.4	0.49±0.03
22.5 min interval	2.67	14.5±1.2	9.2±1.1	0.51±0.05
11.0 min interval	5.45	15.5±1.1	9.9±1.1	0.54±0.05
5.5 min interval	10.91	14.1±1.1	8.7+1.1	0.49±0.04

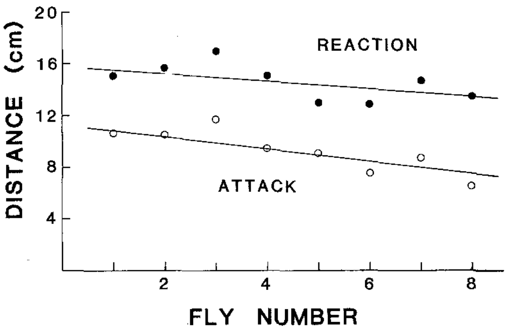

Fig. 3. The influence of satiation (fly number) on mean reaction and attack distances of coho salmon in high risk situations. Data are pooled from the three highest presentation frequencies ($n=15$). Standard error bars have been omitted for clarity, but only the regression for attack distance is significant. The comparable lines for low risk situations have greater y-intercepts and insignificant slopes

Table 3. Mean (±S. E.) attack parameters of juvenile coho in the presence or absence of a simulated competitor (a mirror). Probability values calculated from F tests ($n=80$ in all cases)

	Reaction distance (cm)	Attack distance (cm)	Attack time(s)
Mirror	13.7±1.0	9.5±0.9	0.42±0.01
No mirror	10.7±0.7	6.5±0.5	0.45±0.02
P	<0.01	<0.01	N.S.

nor attack distance varied with fly number. However, attack distance (Fig. 3) declined with increasing satiation in the high risk treatments [$F=3.21$, P (one-tailed) <0.05]. Reaction distance was not significantly affected. Attack time data were not examined in this way since this parameter did not vary significantly with model frequency.

The attack distance data suggest a trade-off between hunger and predation risk in determining foraging behaviour: the coho are willing to take greater risks (i.e. travel greater distances to food items) when hungry than when satiated. As satiation proceeds the fish become increasingly predation risk sensitive. Since reaction distance is not a function of satiation, the fish's ability to detect the prey does not appear to be affected by hunger. Rather, the fish appear to make a behavioural "decision" as to the distance they are willing to travel to obtain the prey item.

The effect of competitor presence

All attack parameters were altered by the presence of the simulated competitor (Table 3). Reaction and attack distances were significantly greater when the mirror was present than when it was absent, and attack time was reduced, although not significantly so. Assuming that the presentation of the predator model reduces reaction and/or attack distances (as in the preceding experiments), these data indicate that juvenile coho are less sensitive to predation risk in the presence of a competitor. This suggests another type of trade-off in their decision-making process.

There was no consistent effect of fly number on any attack parameter, in contrast to the results of the previous experiment. This may be the result of a counteracting acclimation effect operating in the present experiment. The data were collected on each fish's first day of feeding experience in the experimental channel, and reaction and attack distances tended to increase over the first few prey items. When data for the first two flies are eliminated, slopes of the regressions of reaction and attack distances against fly number are both negative, in both the mirror's presence and absence. However, these declines are nonsignificant ($P>0.05$).

Discussion

When juvenile coho salmon have been exposed to a predator, and thus are assumed to perceive that the risk of predation is high, they travel less far to obtain food items than when they have not had such experience. This is an example of what Maiorana (1976) called submergent behavior, "a reduction in the foraging activity of an individual in order to make it less susceptible to predation". The extent of the reduction in attack distance is greater at higher frequencies of predator presentation, suggesting that coho are able to judge the level of risk and adjust their behaviour accordingly. The fish appeared indifferent to predator presentation frequency above a certain level, but this may have been partly the result of habituation at high frequencies counteracting the main effect.

The coho also appear to make trade-offs between risk of predation and food intake. When the fish are hungry, and each prey item consumed has a high marginal benefit, they do not appear to weight risk as heavily as they do when more satiated. Thus, with increasing satiation, their attack distance is progressively reduced, but only when predation risk is high (i.e. when predators are frequently sighted). The possibility remains that the apparent satiation effect was the result of some other cumulative change in the fish in the experiment, but it is difficult to imagine another factor whose effect is expressed only when predation risk is high.

The coho's food is presented to it on what is essentially a conveyor belt, and it therefore may seem that any movement toward the prey is unnecessary, since the prey will eventually drift to the fish (or close beside it) in any event. However, at the high fish densities present in field situations, a coho which does not move toward its prey is likely to lose it to a nearby territory holder or to a roaming nonterritorial fish. When apparent density is increased in the laboratory (using a mirror), the coho again reduce the weighting given to risk and travel further to prey than when they are tested in visual isolation. Once again, they appear to trade-off predation risk against the cost of lost foraging opportunity. Similar sorts of trade-offs have previously been demonstrated when risk is greatest in the most profitable patches (references in Introduction), and when risk and feeding efficiency vary in opposite ways with distance to cover (Lima et al. 1984).

We have no way of predicting the quantitative form of the trade-off at this time, since the risk in this study was apparent rather than real, and probabilities of mortality cannot be assigned to the different model presentation frequencies. In addition, the precise relationships between food intake and survival and eventual reproductive output cannot be defined, although there is evidence that high feeding and growth rates are directly correlated with fitness in coho salmon (Dill et al. 1981). Thus the costs (predation) and benefits (energy intake) cannot presently be expressed in a common metric, although Gilliam's (1982) model points the way to an eventual solution to this dilemna.

Changes in attack distance are consistent with hypotheses based on risk reducing behaviour, while changes in attack time are not always so. This suggests that the distance moved by the fish may be the more important of these parameters in attracting the attention of potential aerial or aquatic predators. Swimming velocity was not uniform and could not be measured, although it is probably also important in attracting a visual predator's attention. The relationship between these three movement parameters and detection probability is likely to be complex. For a given path length, a faster fish may be more visible than a slower one, but for a shorter period of time, suggesting that there may be an intermediate velocity at which detection is most probable.

Since encounter rate with prey is strongly dependent on reaction distance (Dunbrack and Dill 1983), the overall lowering of reaction distance observed in these experiments will have the effect of reducing a fish's encounter rate with all sizes of prey. The results of the first experiment suggest that this reduction should be most marked for large prey. Thus, in the presence of predators, coho should capture fewer and smaller prey items than in their absence. A preliminary attempt to test this hypothesis under semi-natural conditions in the field proved unsuccessful, however, probably because of habituation to the predator – a rainbow trout in a plexiglass compartment adjoining a mesh pen containing the coho.

Changes in diet (rather than patch use) caused by predation risk to an individual have not previously been documented, although they should occur whenever risk varies with prey type. Such can be considered the case in the present system since the coho travel further (and presumably expose themselves to greater risks) to obtain larger prey. Similar effects should occur for any ambush predator whose attack distance varies with prey type, or for any animal that is vulnerable while handling prey and whose handling time or level of activity while handling is prey-type dependent. For example, Thompson (1983) has suggested that foraging plovers do not always select the most profitable prey available, since the long handling times of these large prey may increase the risk of attack by predators and kleptoparasites. Such studies indicate the subtle effects predators may have on the foraging behaviour of their prey, and eventually, through second order effects, upon the organization of entire communities.

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