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Influence of Movement by Coho Salmon (*Oncorhynchus kisutch*) Parr on Their Detection by Common Mergansers (*Mergus merganser*)

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Abstract

A common reaction in juvenile salmonids that detect predators is to decrease activity. To test whether there is a survival advantage to reduced movement under such circumstances, juvenile coho salmon (*Oncorhynchus kisutch*) were placed with common mergansers (*Mergus merganser*) under laboratory conditions that precluded crypsis. Mergansers were more likely to attack fish that moved than fish that remained stationary, and the relation between the lag time for detection by the birds and fish movement rate is best described as inversely exponential. The lag time for detection was not correlated with fish size. The risk of detection of prey by visual predators should be determined by both predator and prey behaviour, but our results suggest that in this case prey behaviour is more important. In the field, territorial coho juveniles do feed more and grow faster than other, non-territorial fish. They also spend a smaller proportion of their time moving. The present experiment suggests that territorial coho may also suffer less mortality than non-territorial fish, which would lower their ratio of mortality risk to growth rate.

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Introduction

Coho salmon (*Oncorhynchus kisutch*) typically spend the first and sometimes the second year of their lives in streams (CHAPMAN 1962). Some fish hold feeding territories while others stay on the periphery of these territories or are non-territorial (DILL et al. 1981; PUCKETT & DILL 1985). All juvenile coho eventually migrate to sea, where they spend 2–3 yr before coming back to fresh water to spawn. Since larger smolts have higher survival at sea (MATTHEWS & BUCKLEY

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1976; BILTON 1978; OLSON 1978; BILTON et al. 1982; but see HOLTBY et al. 1990), juvenile coho should maximize their growth rate in fresh water. Rapid growth requires high food intake, and individuals could be exposed to predation as a result of increased feeding activity (DILL 1983). Prey activity influences the likelihood of attack by many vertebrate predators (e.g. rainbow trout, WARE 1973; yellow-bellied racers, HERZOG & BURGHARDT 1974; barn and screech owls, KAUFMAN 1974; white crappie, WRIGHT & O'BRIEN 1982; garter snakes, MOREY 1990). Although many studies on prey movement concern fish (as predators), none of them have focused on the interactions between fish and piscivorous birds.

Potential prey decrease their activity level when they detect predators (LIMA & DILL 1990), suggesting that prey reduce their risk of detection by visual predators by moving less. This is especially likely to be true for cryptic prey. Coho parr are cryptic over natural substrate (DONNELLY & DILL 1984) and it is therefore probable that they gain a survival advantage from immobility in the presence of visual predators. Indeed, juvenile coho significantly reduce their activity in the presence of common mergansers, both in the field and in the laboratory (MARTEL & DILL 1993). Other juvenile salmonids respond similarly to predation risk: they may curtail the distance they will travel to attack prey items (DILL & FRASER 1984; GOTCEITAS & GODIN 1991) and reduce their overall movement (METCALFE et al. 1987; HUNTINGFORD et al. 1988).

One of the most important predators of juvenile coho is the common merganser (*Mergus merganser*); in some instances these birds have been estimated to be responsible for 24–65 % of the fish mortality in a given stream (WOOD 1987). A merganser typically dips its head underwater while searching for prey (LINDROTH & BERGSTRÖM 1959). The probability of a merganser detecting a fish will be a function both of the bird's sensory (we assume primarily visual) capabilities and the rate and duration of its scanning bouts while foraging; detection will also depend on the amount of time the fish spends moving. This can be expressed as either movement rate (moves per unit of time) or the percentage of the fish's time budget spent moving. These two measures are expected to be correlated and an increase in either should translate into a higher probability of a fish moving when a foraging bird happens to be looking in its direction. The average duration of a movement bout should also influence the probability of detection.

Based on previously observed changes in behaviour of salmon in the presence of predators (MARTEL & DILL 1993), we predicted that, in an environment where crypsis is ineffective, salmon that were moving when a merganser was looking would be more likely to be attacked than salmon that were stationary, and that the risk of detection of salmon by mergansers would be related to fish movement. Such an environment is not uncommon in nature: although territorial coho parr are usually cryptic while on their territories (DONNELLY & DILL 1984), they are occasionally displaced by other fish over other types of substrates (e.g. sand patches) against which they are not cryptic. Non-territorial fish are also regularly forced to move over less-desirable substrates.

Most previous studies on prey activity relate movement to risk of detection

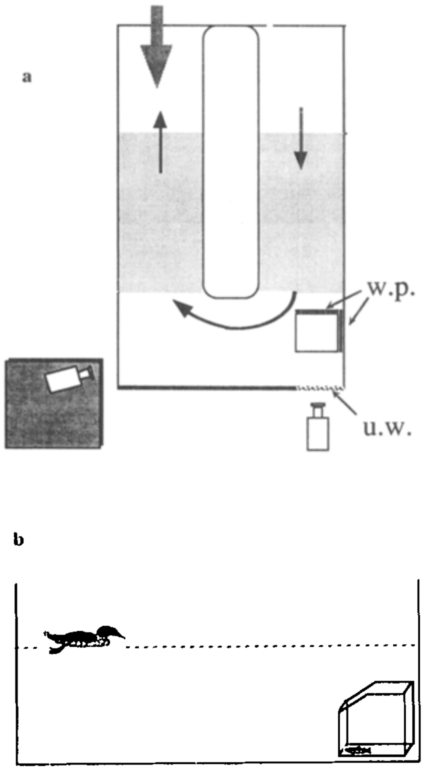

Fig. 1: a. Stream channel viewed from above, showing relative positions of the two cameras. Grey arrow indicates birds' entrance point, black arrows the direction of water flow. Stippled areas are shallow sections (<0.2 m depth), white areas are pool sections; w.p., white panels; u.w., underwater window. b. View of pool area and fish enclosure from the side. Animals not to scale

by predators in semi-quantitative terms (moving prey are usually compared with immobile prey and are reported to elicit *more* strikes from predators). In this paper, we attempted to quantify the shape of the function relating risk of detection of prey movement. To our knowledge, ours is the first study to determine the shape of this function.

Methods

Trials were conducted outdoors at the Animal Care Facility at S.F.U. in Aug. 1990, and Mar. and May 1991 in the pool section (1.2 × 2.4 × 1.2 m) of a U-shaped flow-through stream channel (Fig. 1). Water was pumped through the system at a rate of approximately 2.3 l/s (details, DONNELLY 1985). This channel usually housed three adult common mergansers, which were fed commercial dog food ad libitum and live salmon parr occasionally. These birds had been captured as approximately 10-day-old chicks (in 1986), and since merganser chicks are precocious they would have had the experience of capturing live prey in the wild (WHITE 1957). Coho salmon juveniles were obtained from the Chilliwack Hatchery, Chilliwack, British Columbia. They were housed in indoor tanks at S.F.U. (16:8 photoperiod) and transferred to outdoor tanks at least 1 week prior to experiments.

An hour before the beginning of trials, the birds were transferred to another holding pen. All birds were fed 1.5 h before the trial. At the beginning of each trial, a salmon parr ($\bar{x} = 9.5$ cm TL, SD = 1.7, n = 33) was released into an open-top transparent plexiglass enclosure (0.5 × 0.5 × 0.7 m) situated in the pool section of the channel (Fig. 1) and left to acclimate for at least 5 min. The enclosure was set on a white background and had white panels along two of its sides to make the fish more visible. We used a white background to eliminate crypsis: the goal of the experiment was to isolate the effects of prey movement on predator detection time. Like many other cryptic animals (e.g. HEINEN 1985; MOREY 1990), juvenile coho are more likely to move when over non-cryptic backgrounds. Moreover, individual juvenile salmonids can vary in terms of crypsis over natural substrate (DONNELLY 1985). The use of a uniform, non-cryptic substrate thus minimized any variability in the results due to natural differences in crypsis among individuals.

The fish's behaviour was filmed through a 75 × 95 cm underwater window, using a video camera. After the 5 min acclimation period, one of three common mergansers (two females and a male) was selected randomly and released at the downstream end of the stream channel (Fig. 1 a). Its actions were filmed using a second camera installed above the channel. The cameras were synchronized so that fish movement could subsequently be correlated to bird behaviour. Observers concealed behind a blind could watch the bird's behaviour via a mirror set at an angle above the pool area and the fish's behaviour via a TV monitor. Birds were tested only once a day (except on one occasion when the two females were tested twice in the same day), with at least a 1-hr separation between trials. Since testing could only be carried out when weather conditions were not inclement, time between trial days varied. To minimize the likelihood of birds diving without looking, in the expectation that a fish was present, 'blank' trials, in which no fish was present in the enclosure, were randomly interspersed in the trial sequence. The birds were also regularly fed fish in the area around the enclosure, so they could not be certain that only the enclosure needed to be searched.

Variables measured for birds were number of head dips (head submerged beyond eye level), timing and duration of each dip, and lag time (latency time), or time elapsed from the first look (head dip) in the direction of the prey to the onset of attack (the first dive). We assumed that birds had to look in the direction of the fish in order to see it. Given that mergansers probably can see fish without pointing towards them, lag time as defined here is an underestimate of the time required (necessary) to detect the salmon. This measure also makes the simplifying assumption that whenever a merganser detects a fish, it will attack regardless of its internal state (satiation level) or the cost of attack. While this is probably not true in field situations, the assumption is reasonable under laboratory conditions where the satiation level of the birds can be controlled and where there is no variance in the physical surroundings of the prey.

The variables measured for fish were the number of moves per min (a fish was considered to have moved if it moved at least 0.25 body length, or approximately 2 cm, in any direction), duration of moves and stationary bouts, and % of the observation period spent moving. The variables were measured both 'before bird' (from 1 min after introduction of the fish to introduction of the bird) and 'after bird'. It was possible, using the synchronized cameras, to determine for each bird dip whether the fish was moving or motionless at that moment.

The untransformed data did not meet the various parametric tests' assumptions, and distribution-free tests were used for most analyses. When non-parametric tests were used, SE were shown in the results to indicate the magnitude of the variation. Parametric tests were used only when transformation of data showed that the assumptions of normality (Lilliefors's test) and homoscedasticity (Bartlett's test) were met. Although observations were made repeatedly on the same three birds, lag time and duration of head dips were not correlated for any bird with date of trial (Spearman rank correlations) and the assumption of independence was therefore respected. No fish was used in more than one trial.

Results

Fish that moved when a merganser was looking in their direction were significantly more likely to elicit dives than fish that stayed motionless (Table 1). Fish moving when birds dipped their heads were attacked on 15.2 % of these occasions, whereas stationary fish were attacked on only 1.4 % of these occasions.

Table 1: Contingency table analysis of bird behaviour (dive or not) in relation to whether the fish was moving when the bird dipped its head in that direction. $\chi_1^2 = 7.623$, $p < 0.01$, G test

Fish behaviour	Bird dives	Bird does not dive	Total
Moving	22	123	145
Stationary	11	757	768

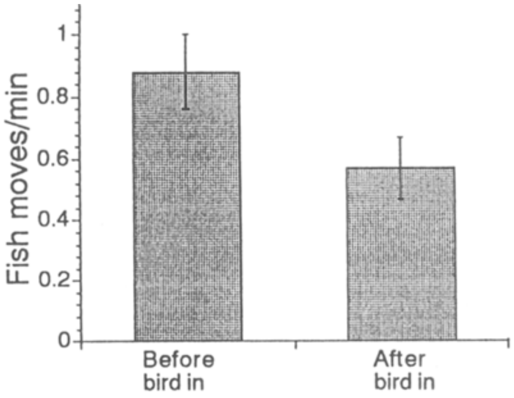

Fig. 2: Average fish movement rates (±SE) in the 2 min before and 2 min after introduction of a merganser to the stream channel. Z corrected for ties = −1.852, p = 0.03, one-tailed test; Wilcoxon signed-rank test, n = 33, $p < 0.05$

Influence of Birds on Fish Movement

There was no difference in fish movement rate (moves/min) when fish were grouped by individual bird (Kruskal–Wallis H corrected for ties = 0.03, df = 2, p = 0.98, n = 33), so the results were pooled for all birds. The presence of birds appeared to influence fish movement: fish decreased their rate of movement in the first 2 min after the introduction of a bird into the channel (Fig. 2). Average duration of fish movement was also shorter when birds were present (12.9 s vs. 28.8 s, Z = − 2.73, $p < 0.01$, Wilcoxon's signed-rank test, n = 33). There was no significant difference in the percentage of time the fish spent moving before and after introduction of a bird (t = 0.786, df = 32, p = 0.44, paired t-test on arcsine-transformed data).

Influence of Fish Movement on Head Dipping by Birds

Birds varied significantly with regard to duration of head dips (Kruskal–Wallis H corrected for ties = 99.408, df = 2, $p < 0.001$, n = 824), and results are consequently presented separately for each bird. The average duration of the birds' head dips was not significantly different when fish were moving or stationary (Table 2). Birds also varied significantly in terms of dip rate (Kruskal–Wallis H corrected for ties = 9.506, $p < 0.01$, df = 2, n = 327). However, bird dip rate

Table 2: Average duration (s) of head dips for the three mergansers tested. U' = Mann–Whitney U. SEs are in parentheses. Durations of dips immediately preceding a dive are not included

Bird	n (trials)	Dips while fish moving duration	n	Dips while fish stationary duration	n	U'	p
Female 1	14	0.62 (0.02)	36	0.70 (0.02)	226	4 736.5	0.11
Female 2	13	0.56 (0.02)	101	0.53 (0.01)	446	24 486.5	0.16
Male	6	1.05 (0.05)	2	0.59 (0.08)	13	24	0.10

(dips/30-s interval) and fish movement rate (moves/30-s interval) were not significantly correlated for any of the three birds ($r_s = 0.1$, $n = 201$; $r_s = -0.06$, $n = 116$; $r_s = 0.71$, $n = 8$).

Influence of Fish Size and Movement on Lag Time for Detection by Birds

Fish size was not correlated with fish movement rate ($r_s = 0.128$, $p = 0.47$, $n = 33$), so the effect of size and movement on detection lag time may be examined independently. Birds differed significantly in the duration of their lag times ($F_{2,30} = 8.98$, $p < 0.001$, ANOVA on transformed data to respect the test's assumptions [Box–Cox–Bartlett $\lambda = 0.22168$]). The male's lag times were shorter than those of either female ($p < 0.03$, Tukey HSD tests) and were dropped from subsequent analyses, except where noted. The two females' lag times were not different, and were pooled. Bird lag time and fish size were not correlated, either for the female mergansers ($r_s = 0.054$, $p = 0.79$, $n = 27$) or the male ($r_s = 0.029$, $p = 0.94$, $n = 6$). Also, bird lag time and fish size were not significantly correlated, for either those fish that were moving before the bird dived ($r_s = -0.44$, $p = 0.66$, $n = 19$) or those that were stationary ($r_s = 0.57$, $p = 0.13$, $n = 8$).

The correlations between the various fish movement characteristics, lag time duration and number of dips are shown in Table 3. Bird lag time was positively correlated with total number of head dips and duration of fish stationary bouts, and negatively correlated with fish moves per minute; the latter relationship was best described as an inverse exponential (Fig. 3).

Discussion

Movement may be the cue mergansers used to recognize prey: they attacked moving prey disproportionately more often than stationary ones. Similar results have been found for at least two other avian orders (KAUFMAN 1974; GOSS-CUSTARD 1977) and for other vertebrate classes (see literature cited in Introduction). Our interpretation assumes that all dives within the enclosure were attacks, and not searches for as-yet-undetected prey. The latter interpretation is unlikely: in all trials, the birds dived directly towards the fish without altering the course

Table 3: Spearman rank correlations between fish movement characteristics while bird was present and bird detection indices. n = 27

	Duration of average fish movement bout (s)	Duration of average fish stationary bout (s)	Fish moves/min	% Time fish moving	No. of head dips
Duration of average fish stationary bout (s)	0.11				
Fish moves/min	−0.18	−0.88**			
% Time fish moving	0.48*	−0.74**	0.67**		
No. of head dips	0.30	0.53*	−0.54*	−0.24	
Bird lag time	0.30	0.50*	−0.49*	−0.22	0.93***

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.0001$

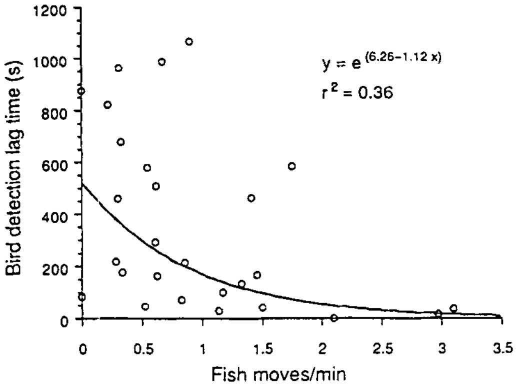

Fig. 3: Bird detection lag time as a function of fish moves/min. The regression equation was calculated from transformed data (ln Y vs. X) to respect the model's assumptions. $p < 0.002$. When the two outermost data points on the X axis (>2.5) are removed, the equation of best fit becomes $Y = 6.39 - 1.33X$, $r^2 = 0.26$, $p < 0.01$

of their swimming. Although we did not record bird behaviour during the blank trials (when no salmon was present), and cannot thus present a formal analysis, these trials usually lasted more than 20 min before the birds dived (long lag time), and the dives were often 'erratic', with the birds zigzagging in the water column, and probing with their bills on the substrate once on the bottom. These behaviour patterns are more indicative of underwater searches than were the behaviour patterns observed during trials with fish.

Juvenile salmonids tend to reduce their activity in the presence of predators: Atlantic salmon parr (*Salmo salar*) curtailed their activities (METCALFE et al. 1987; HUNTINGFORD et al. 1988) and coho and Atlantic salmon parr significantly reduced their attack distance on food items (DILL & FRASER 1984; GOTCEITAS & GODIN 1991) when in the presence of piscine or avian predator models. Overall, the activity budgets of the fish in this experiment were the same whether birds were present or not. However, when a bird entered the stream channel, fish significantly reduced their average movement duration. Typically, fish froze when the bird first appeared and this is reflected in their change in movement rate in the first 2 min of the birds' presence (Fig. 2). However, there was no control and the possibility of acclimation cannot therefore be excluded. Although fish with different experience may have behaved differently, it is unlikely that the hatchery fish used in the experiment had previously experienced merganser attacks. HOWARD (1983), however, does suggest that avian predation occurs at some BC salmon hatcheries.

Fish movement did not influence the amount of time birds spent looking underwater. This was not due to the birds all looking for the maximum allowable time, since mergansers routinely stay underwater for more than 3 s per dive (DEWAR 1924; WOOD & HAND 1985; G. MARTEL unpubl. data), and physiological limitations on the part of the birds can be ruled out. Because the birds often made the transition from the last dip to a dive without raising their heads above the water level, it was difficult to assess the exact duration of the last head dips, and they were not included in the data set. But even when they were estimated and compared with the rest of the dips, the head dips immediately preceding a dive were only of significantly longer duration for female 2 (1.1 ± 0.15 vs. 0.69 ± 0.01 s, $U'_{262,14} = 2653$, $p < 0.01$) and there was no difference related to fish movement. There was also no correlation between fish movement rate and bird dip rate. This suggests that mergansers do not change their scanning behaviour some time prior to attacking the fish; rather, scanning rate is constant and risk of detection is influenced only by fish movement rate.

Lag time was significantly correlated with total number of dips (Table 3), and using the latter as our index of detection would have led to similar results. We feel that lag time is a more realistic index of salmon detection by mergansers. Lag time takes into account the influence on merganser foraging behaviour of factors such as vigilance for their own predators. The trials were conducted outside, and the birds frequently scanned the sky. The overflight of birds, such as hawks, or distant noises sometimes briefly startled the mergansers, and this may have led to an increase in their lag time.

The fact that fish size was not correlated with detection time suggests that mergansers may not rely on visual acuity alone for the detection of their prey. The foraging success of the mink (*Mustela vison*), a piscivorous predator operating in an environment similar to that of mergansers, is more readily explained in terms of detection of directional movement (DUNSTONE & CLEMENTS 1979) than in terms of visual acuity (SINCLAIR et al. 1974). Mergansers have been observed both in the field and under laboratory conditions to probe with their bills under rocks and into fissures (WHITE 1957; LINDROTH & BERGSTRÖM 1959; MARTEL unpubl. obs.), and fish thus flushed are quickly snatched, a tactic that emphasizes motion perception. It is more important for birds foraging under these conditions to assess where a potential prey is going rather than its nature. Mergansers were often observed to lunge at quickly moving objects (MARTEL unpubl. obs.).

The lack of correlation between fish size and detection time suggests that even the smallest fish we used subtended a supra-threshold visual angle in the experimental environment. A bird on the surface at the farthest end of the pool would be approximately 2.7 m from a fish at the bottom of the enclosure. The angular size of the smallest fish (TL = 6.2 cm), when normal to the birds' line of sight, would thus be 39 min, well within the spatial resolution capability of birds (KIRSCHFELD 1976), even when the effect on angular size of the angle from which the fish was viewed is taken into account.

The use of a white background to eliminate crypsis enabled us to isolate the effect of prey movement on predator detection time and to describe the shape of this function (Fig. 3). Even small increases in parr movements per min can translate into great increases in probability of detection by mergansers, or reduced detection lag time. Activity levels while an avian predator is detected nearby are therefore expected to drop, which they did in the first 2 min after bird introduction in this study, as well as in a field study (MARTEL 1992). Conversely, the average duration of stationary bouts by fish should have an effect on the likelihood of fish being detected. In extreme cases, fish that did not move were detected later (the birds had longer lag times) than those that moved. But the exact relationship between stationary bout duration and lag time is unclear: the correlation is reduced to 0.23 (cf. 0.50 in Table 3) when the effect of fish moves per min is partialled out.

This experiment clearly establishes that risk of detection by avian predators is directly related to coho parr movement. Movement can thus be used as an index of risk of predation, although the exact shape of the relation between detection and mortality is not known. Territorial coho parr spend a smaller proportion of their time engaged in swimming activities than either 'floaters' or non-territorial fish (PUCKETT & DILL 1985). Territorial fish also enjoy an advantage in net energy intake over fish adopting the other two tactics (PUCKETT & DILL 1985), and territory size is inversely related to benthic food density (DILL et al. 1981). Thus, although non-territorial fish may use antipredator tactics such as schooling, territoriality in coho may not only result in energetic advantages but may also reduce predation risk. Since the energy intake advantage will translate into higher growth rates, territoriality could lower the ratio of mortality risk to growth rate (WERNER & GILLIAM 1984; GILLIAM & FRASER 1987) and be strongly selected for in areas where avian predation is important.

Our finding that the amount of coho parr movement influences their detectability by birds has some broader implications. First, it suggests that coho mortality rate is affected by their behaviour and can thus be viewed as being at least partially under their control (LIMA & DILL 1990). Secondly, the precise shape of the function relating risk of detection to prey movement should be of considerable use in models of prey selection where encounter probabilities have to be estimated (cf. STEPHENS & KREBS 1986).

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