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The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition?

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Animals often increase their apparent willingness to incur risk when foraging in groups, presumably because group membership reduces an individual's risk of predation. As group size increases, however, competition for resources may also increase, resulting in a decrease in the quantity of resources available to each member of the group. When resources are scarce, individuals might be expected to increase their foraging effort in an attempt to increase their share. Such increases in effort will often appear to increase an individual's risk of predation. Thus, increased competition may contribute to the frequently observed relationship between risk-taking behaviour and group size. To date, no experimental assessment of the relative importance of these two mechanisms exists. We argue that to differentiate between the hypotheses of 'risk reduction' and 'increased competition', it is necessary to quantify the effect of predation risk on the form of the relationship between group size and risk-taking behaviour, and thus, to manipulate both group size and predation risk. We conducted an experiment to determine the relative importance of risk reduction and increased competition to the foraging decisions of juvenile coho salmon, *Oncorhynchus kisutch*. We recorded the foraging behaviour of 18 focal individuals in the presence and absence of a predator, and in the company of zero, one and three conspecifics. As group size increased from one to four, focal fish captured more prey items, ventured closer to the feeder (and predator) to intercept them, and decreased their use of cover. Furthermore, although focal individuals captured fewer prey items and intercepted them further from the feeder in the presence of the predator than in its absence, the form of the relationship between risk-taking behaviour and group size was not affected by the level of predation risk. The results of our experiment are consistent with the interpretation that increases in risk-taking behaviour with group size occurred primarily as a consequence of increased competition for scarce resources.

It is generally accepted that animals can reduce their risk of predation by associating with conspecifics (for reviews see Pulliam & Caraco 1984; Lima & Dill 1990). A number of mechanisms may render group membership safer than solitary existence, including earlier detection of approaching predators (i.e. 'many eyes': Pulliam 1973; Powell 1974; Lazarus 1979), 'confusion' of attacking predators (Neill & Cullen 1974; Milinski & Heller 1978) and, when predators are limited in their ability to capture more than a single prey item per attack, simple numerical 'dilution' of risk (Foster & Treherne 1981; Morgan & Godin 1985). When the presence of predators results in lost opportunities for prey (e.g. feeding, searching for a mate, provisioning young), reducing risk by associating with conspecifics may allow individuals to behave in a less cautious manner, engaging in what might appear to be increasingly risky behaviour as group size increases. Such apparent changes in risk-taking behaviour with group size (hereafter referred to as the 'group size effect') have been frequently demonstrated. For example, animals are often observed to decrease their level of vigilance as group size increases (for reviews see Elgar 1989; Lima 1990; Roberts 1996), despite evidence that nonvigilant individuals are more likely to be captured by predators (Fitzgibbon 1989). Similarly, animals have been observed to make fewer visits to protective cover (Magurran & Pitcher 1983), inspect predators more closely (Magurran 1986), remain longer in the presence of a predator before fleeing (Dill & Ydenberg 1987), and resume feeding more quickly after exposure to a predator (Morgan 1988) when in the presence of conspecifics.

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As group size increases, however, competition for resources may also increase, particularly when those resources are scarce and essential for survival (Lima 1990). As a consequence of increased competition, individuals may be forced to exert greater effort to obtain their share of the available resource (Clark & Mangel 1986; Mitchell et al. 1990; Shaw et al. 1995), and hence, may appear more willing to engage in apparently high-risk behaviours than when alone (e.g. Barnard et al. 1983; Dill & Fraser 1984). Thus, increased competition may represent an additional explanation for the frequently observed positive relationship between risk-taking behaviour and group size (see Elgar 1989; Lima 1990; Roberts 1996; Beauchamp & Livoreil 1997; Beauchamp 1998). These two mechanisms need not be mutually exclusive: both risk reduction and increased competition may contribute to the group size effect. However, no experimental assessment of the relative importance of the two mechanisms exists (Lima 1990), in part because most authors have been content to accept the risk reduction hypothesis (see Lima 1990; Roberts 1996), but also because it is unclear how to separate their effects.

Although there exist examples for which risk reduction is clearly the most parsimonious explanation (e.g. Elgar 1986; Cresswell 1994), most studies that claim to provide support for the risk reduction hypothesis have consisted of a comparison of the vigilance behaviour of individuals in small and large groups (see Roberts 1996). Rarely is predation risk manipulated and its effect on the relationship between risk-taking behaviour and group size reported (but see Morgan 1988). However, a comparison of the form of the relationship between group size and risk-taking behaviour at different overall levels of predation risk may provide information about the relative importance of risk reduction and increased competition. For example, consider the behaviour of a small bird, foraging within a flock which varies in size over time. For any given level of predation risk, we might expect the bird's distance from protective cover to increase with increasing group size. Now imagine that a predatory hawk has recently been sighted in the area. As a consequence of an increase in the perceived overall level of predation risk, we might expect the bird to decrease its distance from cover. However, as we shall show, the magnitude of this decrease for any given flock size will depend on whether increasing group size reduces predation risk, increases resource competition, or both.

If we assume that the bird experiences only a reduction in predation risk as a consequence of increasing group size, the relative reduction in perceived risk with the addition of another flockmate will be greater when the overall level of predation risk is high, for example

$$\left(\frac{2p}{n}-\frac{2p}{n+1}\right)>\left(\frac{p}{n}-\frac{p}{n+1}\right)$$

where n is the number of birds in the flock and p is the probability of a capture being made by the predator. Thus, we might expect the bird to increase its distance from cover more rapidly with increasing group size when the overall risk of predation is relatively high (Fig. 1c). However, if increased competition is the only consequence of an increase in flock size, the increase in distance from cover with group size should be independent of the overall level of predation risk (Fig. 1b). When increasing group size both reduces predation risk and increases resource competition, the strength of competition experienced within a flock of a given size will be independent of the overall level of risk. However, the reduced cost of high risk behaviour, and thus the net benefit of increasing foraging effort with increasing flock size, will be greater when the overall level of predation risk is relatively low. Therefore, we might expect the bird to increase its distance from cover more rapidly with increasing group size when risk is low (Fig. 1d). Note that in generating these predictions we have assumed that (1) all individuals, regardless of group size, experience a higher risk of predation in the presence of a predator than in its absence (see Fig. 1a), (2) groups of different sizes are attacked by the predator with equal probability, (3) the strength of competition is inversely proportional to group size, and (4) resources are in short supply and provide the same fitness benefit to all individuals.

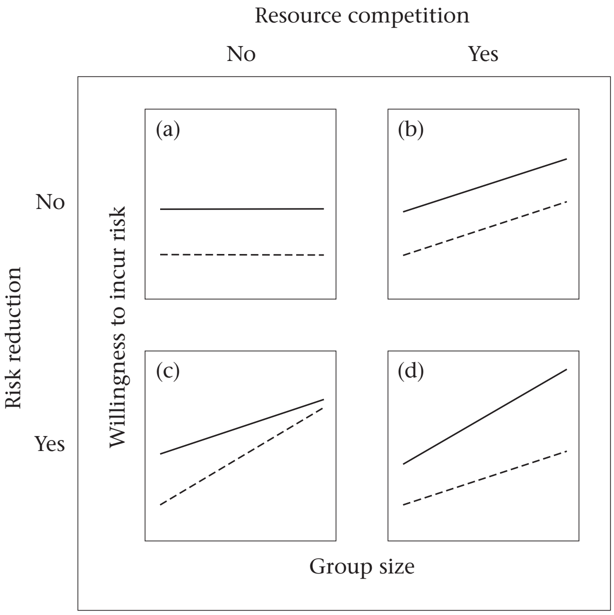

Figure 1. Hypothesized form of the relationship between group size and risk-taking behaviour under high (– – –) and low (——) levels of overall predation risk when (a) the risk of predation and the strength of competition are independent of group size, (b) the strength of competition increases with increasing group size, (c) predation risk decreases with increasing group size, and (d) predation risk decreases and the strength of competition increases with increasing group size.

We conducted an experiment to assess the relative importance of risk reduction and increased competition to the foraging decisions of juvenile coho salmon, *Oncorhynchus kisutch*. Although previous work has indicated that the foraging behaviour of these fish is sensitive to both predation risk and the presence of conspecifics (e.g. Dill & Fraser 1984; Grand & Dill 1997), it is unclear whether individuals experience a reduction in risk or an increase in the strength of competition (or both) with increasing group size. As a consequence of the flexibility of their social system (ranging from territoriality to 'fright huddling' or shoaling; see Sandercock 1991 and references therein), both explanations are equally plausible. In the experiment described here, both predation risk and group size were manipulated, permitting examination of the effect of predation risk on the form of the relationship between group size and risk-taking behaviour, and thus, differentiation between the risk reduction and increased competition hypotheses. Because previous experiments suggest that coho can reduce their perceived risk of predation by decreasing their foraging activity (e.g. Dill & Fraser 1984; Martel & Dill 1995) and increasing their use of cover (Grand & Dill 1997; Reinhardt & Healey 1997), we assumed that an individual's willingness to incur risk was inversely correlated with the amount of time it spent under cover, its hesitancy to attack prey, and the distance from the predator at which it captured prey. In order to hold overall resource availability constant across group size treatments, focal individuals were separated from other group members by a clear, Plexiglas barrier, thus preventing actual, but not perceived competition for resources (see below).

METHODS

Experimental Subjects

We captured a total of 90 wild, young-of-the-year coho salmon by pole seine from the Salmon River, Langley, British Columbia, Canada, on 22 July and 13 August 1996. Individuals were chosen such that they ranged in mass from 1.4 to 2.0 g ($\bar{X} \pm SD=1.68 \pm 0.16$ g, $N=90$) and in fork length from 50 to 60 mm ($\bar{X} \pm SD=54.8 \pm 1.7$ mm, $N=90$). Fish were returned to the laboratory and placed in a 170-litre flow-through aquarium where they were maintained at 12–15°C on a 14:10 h light:dark cycle until they were to be used in the experiment. Fish were fed live, adult brine shrimp (*Artemia* sp.) ad libitum while in the flow-through aquarium.

Three days before each experiment began, five fish of similar mass (coefficient of variation, CV: $\bar{X} \pm SD=2.14 \pm 1.11$, $N=18$ groups of five fish) and fork length (CV: $\bar{X} \pm SD=1.27 \pm 0.517$, $N=18$) were chosen from the stock tank. Individuals were randomly designated as either the focal individual, a solitary 'companion', or one of a group of three companion fish. Fish were then transferred to one of two 'glide' sections of the stream channel in which experiments were to be conducted (see below). The focal individual was released into the 'foraging arena', while solitary and grouped companions were placed upstream of the foraging arena, in two flow-through enclosures (see below). Experiments were conducted over 1 month, beginning 3 August and ending 5 September 1996.

Apparatus and General Methods

We conducted experiments in an artificial stream channel (Fig. 2) in the woods of the Burnaby Mountain campus of Simon Fraser University. The concrete channel (described more completely elsewhere; Grand 1997) consisted of two shallow, rectangular glides (water depth=18 cm) separated from one another by a width of concrete and two deep pools. An additional concrete wall divided one of the pools in two, providing a barrier over which water was pumped to create a continuous, circular flow. Pools were covered with plywood to reduce algal growth and prevent extraneous food (i.e. winged insects) from entering the system. A plastic tent, with walls of fine mesh, was erected over the entire channel to prevent further the entry of both extraneous food and leaf litter. Opaque plastic blinds attached to the mesh prevented disturbance of the fish during foraging trials; we made observations of fish behaviour through small slits cut in these blinds.

Each glide was further divided into two sections: a downstream foraging arena (120 × 115 cm; L × W) and an upstream holding area (110 × 115 cm; L × W) which contained both the predator and the two flow-through, companion group enclosures (Fig. 2). Upstream and downstream sections of each glide were separated from one another, and the pools at each end, by mesh dividers (mesh opening=5 mm), thus restricting the movement of the focal fish to the foraging arena within a single glide (see Fig. 2). The predator, a single 1-year-old coho salmon measuring 15 cm in fork length, was housed in a small, glass aquarium (41 × 21 × 24 cm; L × W × D; water depth=18 cm), which was placed lengthwise against the mesh barrier separating the upstream holding area from the foraging arena. Because coho of this size are capable of preying on smaller members of other salmonid species (Parker 1971), and small coho are often preyed upon by both coho smolts (McMahon & Holtby 1992) and other salmonids (Sandercock 1991), we believe that focal individuals perceived the larger fish as a predator rather than merely as a very large competitor. The predator aquarium was surrounded on three sides by opaque, white Plexiglas, thus preventing the companion fish from directly observing the predator between trials. The side of the predator aquarium closest to the foraging arena was fitted with two removable opaque Plexiglas blinds, which prevented the focal fish, and any companion fish present, from seeing the predator both between trials and during 'no predator' trials.

Companion groups were housed in two clear Plexiglas enclosures (42 × 31 × 31 cm; L × W × D), the narrow ends of which were covered with 5-mm mesh screen, permitting continuous circulation of water through them. An identical, empty companion group enclosure was placed in the foraging arena, immediately adjacent to the point from which prey were delivered (see Fig. 2). A single, cover structure (34-cm long piece of PVC pipe cut lengthwise; diameter=11 cm) was suspended above the surface of the water along the opposite wall of the foraging arena. To reduce differences between light levels below the structure and those elsewhere in the channel, we drilled eight holes (diameter=1 cm) at regular intervals along the length of the pipe.

Throughout the experiment, fish were fed live, adult brine shrimp obtained weekly from a local aquarium

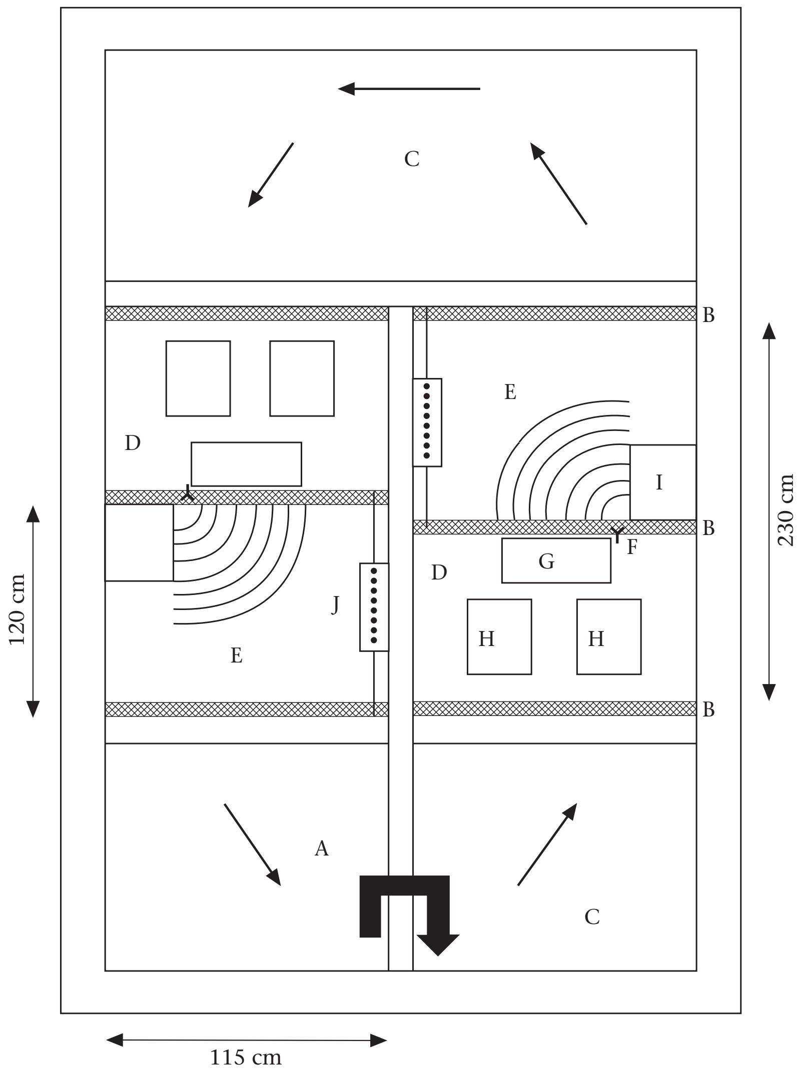

Figure 2. Schematic top view of the experimental stream channel. Water was pumped over a concrete barrier (A) and travelled downstream through a series of six mesh barriers (B) which separated the pools (C) from the glides containing the holding areas (D) and foraging arenas (E). A Y-shaped feeding tube (F) was attached to the mesh barrier at the upstream end of each foraging arena, directly adjacent to the predator aquarium (G). Companion groups were transferred between clear Plexiglas enclosures in the upstream holding area (H) and the foraging arena (I). A single cover structure (J) was placed along the opposite wall of the foraging arena. Arrows in the pools indicate the direction of water flow, and solid arcs, the lines used to delineate 10-cm intervals to the observer.

store. Prey were sieved and only those unable to pass through a 1350-μm mesh screen were used. Brine shrimp (∼60 per day) were placed in a 4-litre Erlenmeyer flask filled with water collected from the channel. Prey and water drained from the flask through a 70-cm length of tygon tubing (diameter=5 mm) fastened to a glass spout attached to the bottom of the flask (after Abrahams 1989). The feeding tube emptied into a Y-shaped plastic tube attached to the back side of the mesh barrier at the upstream end of each glide (see Fig. 2). Prey in the feeder were kept in suspension by means of a stir bar constantly rotated by a magnetic stir plate. The flask was sealed with a rubber stopper penetrated by a glass tube which extended to the bottom of the flask. A length of tygon tubing was attached to the top of this tube and sealed at the other end with a 23.5-gauge syringe. The feeder could be operated remotely by simply removing the plunger from the syringe, and allowing air to enter the apparatus.

A series of seven arcs, drawn at 10-cm intervals along the bottom of each glide, radiated outward from the point at which prey were delivered (see Fig. 2), thereby delineating prey capture zones for the observer. Hereafter, we refer to the interval nearest the feeder as zone 1 and the interval furthest from the feeder as zone 7. Because prey items were carried directly downstream by water currents and most prey captures occurred immediately adjacent to the companion enclosure (see Fig. 2), we believe that an individual's willingness to expose itself to predation is reflected in part by the foraging zone in which it chooses to capture prey. All trials were videotaped from above, using a High-8 Sony video camera suspended 120 cm above the surface of the water.

Experimental Procedures

Each focal fish ($N=18$) experienced all six combinations of ‘predator’/’no-predator’ and companion group size (0, 1 and 3) treatments. To reduce the possibility of carry-over effects between trials, we varied the order of treatment combinations among individuals. Companion group size treatments were blocked within predator/no predator treatments, such that each focal fish experienced a block of three predator trials and a block of three no-predator trials. We randomized the order of predator/no-predator treatment blocks between focal individuals, such that half of the fish experienced the three predator treatments first, while the other half experienced the three no-predator treatments first. Within predator/no-predator treatment blocks, companion group size treatments were randomized, such that focal individuals experienced the three companion group sizes in different orders.

Each focal fish experienced all six treatment combinations within a single day, at 0930, 1100, 1230, 1400, 1530 and 1700 hours. Experiments in the two glides were conducted on alternate days. At 0800 hours on the morning of each experiment, the feeder was filled and set on the stir plate, and the companion group for the first trial was dip-netted and gently transferred to the Plexiglas enclosure in the foraging arena. Fish were then left undisturbed for the next 90 min. Immediately preceding each trial, we removed either one or both opaque Plexiglas blinds from the front of the predator aquarium, allowing the focal fish and any companion fish present to view either the second piece of Plexiglas or the predator (in no-predator and predator trials, respectively). After waiting an additional 10 min, we activated the video camera remotely and began the foraging trial. During each 15-min trial, a single brine shrimp was introduced to the focal fish approximately every 3 min by simply removing the plunger from the syringe and reinserting it as soon as a prey item was visible in the feeding tube. Because similar-sized coho salmon are capable of consuming 30–40 brine shrimp over the same period of time (see Grand 1997; Grand & Dill 1997), we believe that focal fish perceived prey to be limiting in this experiment. For each of the five prey items introduced during each trial, we recorded whether the prey was captured and if so, the foraging zone (1–7; i.e. within 10, 20, 30, 40, 50, 60 or 70 cm of the feeder) in which it was intercepted. Because distances beyond foraging zone 7 could not be accurately quantified (either visually or on video), prey interceptions occurring there were arbitrarily and conservatively given a value of 8 (i.e. scored as 80 cm). During the 3 min following the introduction of each prey item, the location of the focal fish (i.e. foraging zone 1–7, under cover or elsewhere) was recorded at 30-s intervals. At the end of each trial, the camera was turned off and the Plexiglas blind(s) returned to the front of the predator aquarium. The companion group was returned to the upstream enclosure and replaced with the group (if any) to be used in the next trial. After the final trial of the day, all fish were captured, removed from the stream channel, and replaced with the next focal individual to be tested and its companions. Companion fish were never used with more than a single focal individual.

Data Analyses

For each focal individual, we recorded (1) the total number of prey captured per trial (max=5), (2) the average distance at which prey were intercepted (foraging zone 1–7 or beyond), (3) the proportion of time spent under cover, and (4) the proportion of time spent in foraging zones 1–7. Data were collected from the videotape and used to confirm and clarify observations made visually at the time of the trials.

Mean prey capture distance, time under cover, and time spent in foraging zones 1–7 were analysed using standard two-factor repeated measures analysis of variance (ANOVAR), with predator presence/absence and companion group size as factors, and each individual’s response to the six treatment combinations as repeated measures. Because the number of prey captured by each individual during each trial was scored as a single, discrete response (i.e. 0, 1, 2, 3, 4, or 5 prey items), we performed repeated measures analysis of variance on this variable using generalized estimating equations (GEE; Diggle et al. 1994), again using predator presence/absence and companion group size as factors. Unlike standard analysis of variance, the GEE procedure transforms the variable onto an appropriate scale and models the response using a Poisson distribution, thus, generating a Z statistic in place of the familiar F statistic. Initially, all data were coded according to (1) whether the focal individual experienced the predator block of treatments first or second and (2) the order in which the focal individual experienced companion group sizes within each block. However, because all such order effects and their interactions with the two main effects were nonsignificant (all $P>0.25$), both coding variables were subsequently dropped from the model. Thus, P values reported represent those from the two-way ANOVARs and are two tailed unless stated otherwise.

To investigate whether the observed effects were unduly influenced by small sample size, and thus whether statistically nonsignificant effects might be safely interpreted as such, we simulated Z score distributions (for prey capture number) and F distributions (for the remaining three variables) using randomization techniques (see Thomas & Juanes 1996). For each variable, we randomly reassigned the 108 observed responses (i.e. six responses by each of 18 fish) to the six treatment combinations and analysed the newly generated data set (as described above). Randomization and reanalysis were performed 5000 times per variable, resulting in a distribution of Z scores and F statistics to which the original test statistics could be compared. The proportion of randomizations producing test statistics larger than the original test statistic are indicative of the true probability of observing any particular effect. Agreement between the P values generated by the original analysis and those inferred from the randomization procedure (P_{rand}) suggests that observed effects were not unduly influenced by sample size. For all nonsignificant effects, we report

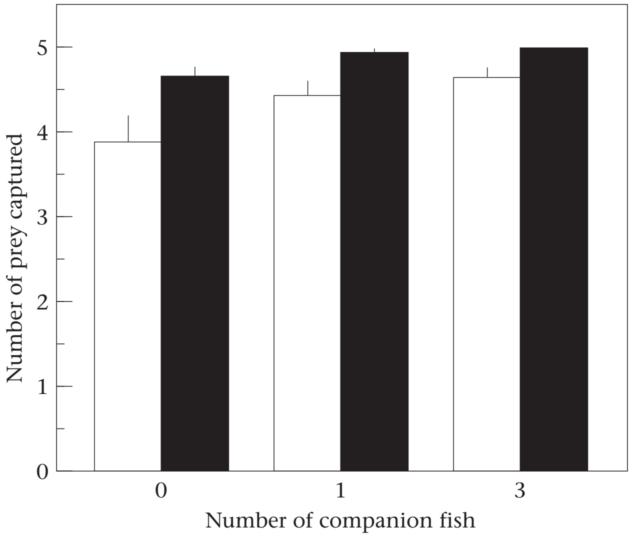

Figure 3. Mean+SE number of prey items captured by focal individuals in the presence of zero, one and three companion fish, in the predator (☐) and no-predator (■) trials. *N*=18.

both the original *P* values and those generated by the randomization procedure.

RESULTS

General Behaviour of the Fish

Foraging behaviour and patterns of space use varied widely among focal fish. Some individuals treated the cover structure as a central place, venturing out from it only to intercept prey. Others ignored the structure entirely, instead remaining upstream, displaying to their competitors and scanning the water surface for prey. Companion fish usually remained at the upstream end of their Plexiglas enclosure, darting towards prey items as they entered the adjacent foraging arena. In some cases, it appeared that focal individuals were alerted to the arrival of prey by the behaviour of companion fish.

Prey Capture

The total number of prey items captured by focal individuals was influenced by both the presence of the predator and the number of companion fish present (Fig. 3). Focal fish captured fewer prey items in the presence of the predator than in its absence (Z_1=2.687, *P*=0.007), and the number of prey captured increased with increasing companion group size (Z_1=2.396, *P*=0.017).

Mean prey capture distance was also influenced by the presence of the predator and the number of companion fish present (Fig. 4). Focal fish captured prey closer to the feeder (i.e. closer to the predator) in the predator's absence than in its presence ($F_{1,17}$=18.104, *P*=0.001), and prey capture distance decreased with increasing companion group size ($F_{2,34}$=12.728, *P*<0.001). Interactions between predator presence and the number of companion fish were not significant for either prey capture number or mean prey capture distance (Z_1=1.401, *P*=0.159, P_{rand}=0.195; $F_{2,34}$=1.230, *P*=0.305, P_{rand}=0.359, respectively), suggesting that the observed change in foraging behaviour with increasing group size was primarily a consequence of increased resource competition (see Fig. 1b).

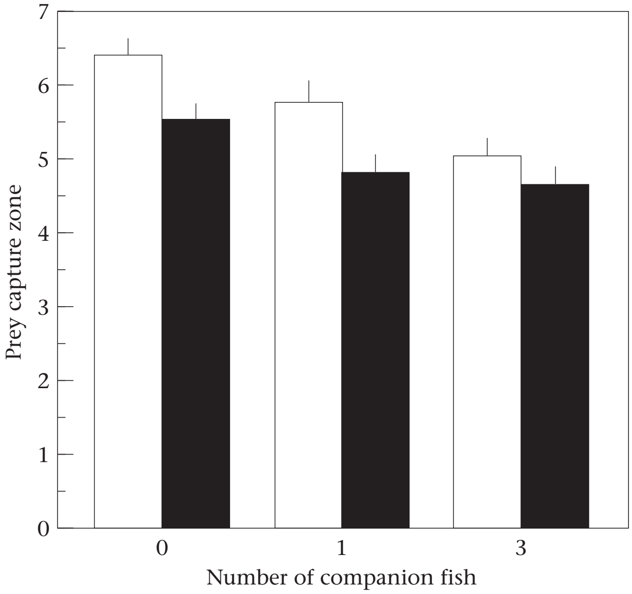

Figure 4. Mean+SE zone of prey capture by focal individuals in the presence of zero, one and three companion fish, in the predator (☐) and no-predator (■) trials. *N*=18.

Use of Space

The proportion of time spent by focal individuals under cover and within 70 cm of the feeder (i.e. within foraging zones 1–7) was influenced by companion group size, but not by the presence of the predator (Fig. 5). Focal individuals spent less time under cover (Fig. 5a; $F_{2,34}$=11.528, *P*<0.001) and more time within 70 cm of the feeder (Fig. 5b; $F_{2,34}$=6.559, *P*=0.012) as companion group size increased from zero to three, although the greatest change in space use occurred between the solitary and single companion fish treatments. However, focal individuals did not alter the relative amounts of time spent under cover (Fig. 5a; $F_{1,17}$=0.849, *P*=0.370, P_{rand}=0.366) or their proximity to the feeder (Fig. 5b; $F_{1,17}$=0.041, *P*=0.842, P_{rand}=0.841) in response to the presence of the predator.

Interactions between predator presence and the number of companion fish did not significantly affect the proportion of time spent either under cover or within 70 cm of the feeder ($F_{2,34}$=1.649, *P*=0.207, P_{rand}=0.209; $F_{2,34}$=0.043, *P*=0.958, P_{rand}=0.841, respectively). Again, these results suggest that the observed effect of group size on space use occurred primarily as a consequence of increased resource competition, rather than being due to a reduction in perceived risk of predation with increasing group size.

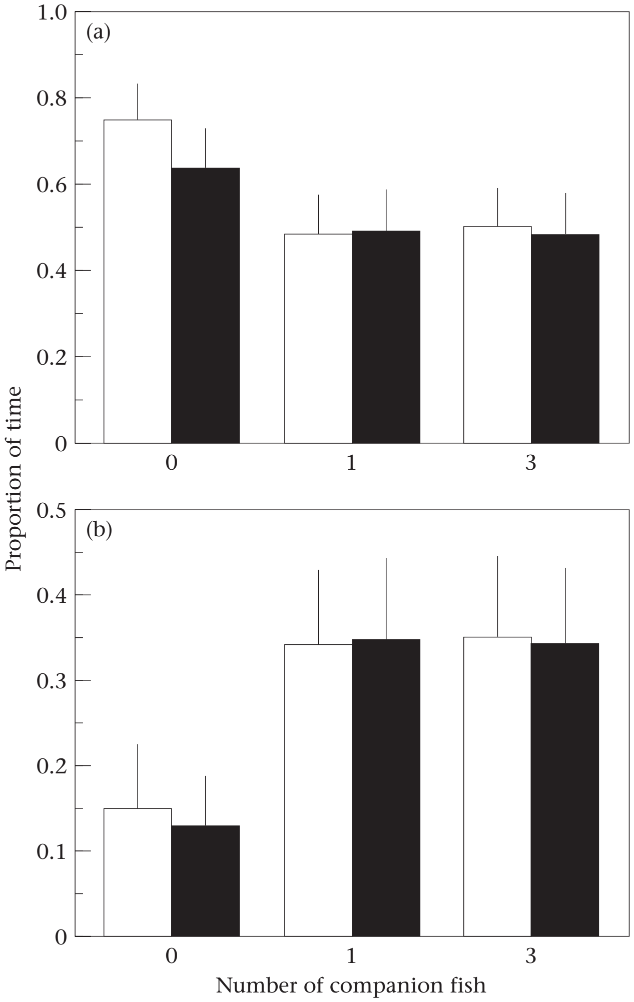

Figure 5. Mean+SE proportion of time spent by focal individuals (a) under cover and (b) within 70 cm of the feeder, in the presence of zero, one and three companion fish, in the predator (□) and no-predator (■) trials. *N*=18.

DISCUSSION

Juvenile coho salmon varied their foraging behaviour in response to both group size and predation risk. Focal individuals captured fewer prey items and intercepted them further from the feeder in the presence of the predator than in its absence, regardless of the number of conspecifics present, as expected if increased activity and proximity to the feeder (and predator) increase an individual's perceived risk of predation (Dill & Fraser 1984). As companion group size increased from zero to three fish, focal individuals captured a greater number of the available prey, ventured closer to the feeder to intercept prey, and decreased their use of cover, as expected if associating with conspecifics either decreases predation risk (Lima 1990; Roberts 1996) and/or increases the strength of competition (Shaw et al. 1995). However, the form of the relationship between risk-taking behaviour and group size was not affected by the presence of the predator, as indicated by the lack of any statistical interaction between group size and predation risk effects. Thus, the results of this experiment are consistent with the conjecture that changes in risk-taking behaviour with group size by juvenile coho salmon occurred primarily as a consequence of increased competition for scarce resources (see Fig. 1b).

Many other studies have demonstrated similar effects of group size on risk-taking behaviour (for reviews see Lima 1990; Roberts 1996). Although risk reduction is clearly the most parsimonious explanation when resources are superabundant (e.g. Elgar 1986; Cresswell 1994), it need not be the only explanation for changes in risk-taking behaviour with group size when resources are more limited in their availability. Despite acknowledging that their results might be explained in part by increased competition for resources, most authors have been content to attribute the effect to risk reduction (e.g. Beauchamp & Livoreil 1997). Indeed, much of the literature on the group size effect has focused on elucidating the specific mechanism by which increasing group size might reduce predation risk (e.g. 'confusion', 'vigilance', or 'dilution'; Roberts 1996), to the exclusion of nonrisk related alternatives (i.e. the 'confounding variables' of Elgar 1989). However, many of these experiments did not manipulate predation risk (e.g. Bertram 1980; Magurran & Pitcher 1983; Magurran et al. 1985), and hence, cannot rule out increased competition as a contributing factor. Similarly, experiments that attribute group size effects in the absence of a predator entirely to increased competition (e.g. Barnard et al. 1983) cannot rule out the possibility that risk reduction contributed to the observed effect. While animals presumably perceive a nonzero risk of predation in the presence of a predator, they may not perceive zero risk in its absence (Lima & Dill 1990). Thus, to evaluate the relative importance of risk reduction and increased competition to any observed group size effect, it is necessary to compare the form of the relationship between group size and risk-taking behaviour at various levels of predation risk: both risk of predation and group size must be manipulated.

We are aware of only one other study in which both group size and predation risk were varied. Morgan (1988) examined the roles of hunger, group size and predator presence on the foraging behaviour of bluntnose minnows, *Pimephales notatus*. She observed that latency to forage was greater in the presence of the predator than in its absence, and decreased as group size increased from three to 20. Similarly, foraging rates were lower in the presence of the predator and increased with increasing group size. From these results, Morgan (1988) concluded that the observed decrease in foraging activity with decreasing group size was primarily a response to an increased need to be vigilant for predators (i.e. the risk reduction hypothesis). However, all interactions between group size and predation risk effects were nonsignificant, suggesting that the form of the relationship between group size and risk-taking behaviour was the same, both in the presence and absence of the predator. Thus, Morgan's (1988) results are consistent with the interpretation that the increases in risk-taking behaviour with group size which she observed were primarily a consequence of increased competition for resources.

The idea that increases in group size might lead to increased competition for resources and thus to greater risk taking, is not new. Barnard et al. (1983) and Dill & Fraser (1984) sought experimental evidence for such an effect over a decade ago. Dill & Fraser (1984) observed that juvenile coho salmon increased their foraging activity in the presence of an apparent companion (the focal individual's mirror image). Their conclusion that increases in risk-taking behaviour with increasing group size were primarily due to competition seems appropriate, given that the mirror was placed such that focal individuals saw themselves leaving the safety of their companion when attempting to capture prey. However, because the relationship between risk-taking behaviour and group size was only quantified at a single level of predation risk (i.e. in the presence of a model predator), the possibility that focal individuals perceived their risk of predation to be lower in the presence of the companion than in its absence cannot be ruled out. Similarly, Barnard et al. (1983) observed that common shrews, *Sorex araneus* L., increase their allotment of time to foraging activity when in the presence of a conspecific. They attributed these results solely to increased resource competition, presumably because no predator was present during the experiment. However, if shrews perceive a nonzero risk of predation, even in the absence of any immediate threat, they may have perceived their risk of predation to be even lower in the presence of the conspecific and adjusted their behaviour accordingly.

In generating predictions about the effect of predation risk on the form of the relationship between group size and risk-taking behaviour, a number of simplifying assumptions were made. Relaxation of these assumptions may lead to predictions other than those illustrated in Fig. 1. For example, we assumed that predator attack rate was independent of group size (as was certainly the case in our experiment, where the small size of the predator enclosure effectively prevented the predator from accelerating in the direction of the prey), which may not be true if large groups are more visible and more easily detected by predators than small groups (see Krause & Godin 1995). In this case, risk-taking behaviour might be expected to increase less quickly with increases in group size, making it difficult to distinguish between the scenarios depicted in Fig. 1b, c. However, the simple verbal models developed here can easily be altered to include the relevant biological features of any animal's foraging ecology. The specific predictions generated here are less important than the general approach advocated.

Despite the considerable research effort into understanding the relationship between group size and risk-taking behaviour (see reviews in Elgar 1989; Lima 1990; Roberts 1996), it is still unclear whether animals adjust their behaviour in response to a reduction in predation risk or an increase in the strength of resource competition with increasing group size. Most research has focused on the risk reduction hypothesis and the various mechanisms by which it might arise (Roberts 1996). Relatively little attention has been paid to nonrisk related hypotheses, although much of the evidence used in support of risk reduction can also be attributed to increased resource competition. Future research should be directed towards explicit consideration of the two effects and empirical tests to determine their relative importance.

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