Behav Ecol Sociobiol (1991) 29:255–261

Behavioral Ecology and Sociobiology

Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger

Vytenis Gotceitas* and Jean-Guy J. Godin

Department of Biology, Mount Allison University, Sackville, New Brunswick, Canada E0A 3C0

Received October 10, 1990 / Accepted June 6, 1991

Summary. Following exposure to a predator, socially dominant individuals may reduce their risk of predation by waiting until subordinates have resumed foraging before doing so themselves. Although such status-related ordering in the resumption of foraging activity has been observed in several bird species, the underlying mechanism(s) facilitating such a delay remains unknown. Social status per se and status-related foraging benefits prior to a threat of predation (i.e., individual hunger level) have both been suggested as possible mechanisms. We tested between these two alternative suggestions using pairs of stream-dwelling juvenile Atlantic salmon, for which the dominant-subordinate relationship was known. Fish were tested at equal and unequal hunger levels. Fish were presented with drifting prey, followed by a predation threat in the form of an aerial predator model. Which fish (i.e., dominant or subordinate) initially resumed foraging activity after exposure to the predator model was recorded. When both fish were at an equal hunger level, the dominant fish was more likely to resume foraging first. When the dominant and subordinate fish differed in their hunger level, the hungrier fish was the first to resume foraging regardless of social status. These results support the conclusion that hunger level, rather than social status per se, determines the order in which juvenile Atlantic salmon resume foraging after exposure to a predator.

Introduction

Dominant-subordinate relationships represent a common type of social structure found in a variety of different taxa, where socially dominant individuals typically get priority access to any number of contested resources (e.g., Krebs and Davies 1984) resulting in increased feeding and growth rates relative to subordinates. For example, numerous bird species spend varying amounts of time living in groups (=flocks). Flocking behavior confers certain benefits to individuals, including reduced risk of predation (Powell 1974; Ekman 1987) and increased probability of locating food (Krebs et al. 1972; Baker et al. 1981). However, due to the social structure of many such flocks not all flock members necessarily benefit equally. Dominant individuals can displace subordinates to less rewarding foraging sites (Peters and Grubb 1983; Ekman and Askenmo 1984) and/or sites further away from shelter, which increases the subordinates' risk of predation (Ekman 1987; Hogstad 1988; Desrochers 1989).

Recently, several studies have shown that, after exposure to a predator, subordinate birds in a flock are often the first to emerge from cover and resume feeding (De Laet 1985; Hegner 1985; Hogstad 1988). Although in doing so subordinates may benefit by gaining access to preferred foraging sites, they nevertheless incur the risk that the predation threat may still be present. By waiting until subordinates have resumed feeding before starting themselves, dominant individuals may incur a cost in terms of lost foraging opportunity and prey depletion in preferred sites. However, a dominant individual could benefit by waiting, in that subordinate activity might provide a means by which to assess habitat safety without the dominant having to expose itself to any potential predation hazard. Once judged safe, the dominant could then resume foraging, supposedly being able to compensate for any initial foraging costs by displacing subordinate individuals from preferred feeding sites.

Although dominant individuals have been shown to wait longer than subordinates before resuming to forage after exposure to predation hazard, the mechanism(s) underlying this delay is not known. It has been suggested (De Laet 1985; Hegner 1985; Waite and Grubb 1987) that the dominant individual's social status per se may allow it to delay and then make up any costs through its inherent ability to displace subordinates from preferred feeding sites once the threat of predation is gone.

---

* *Present address:* Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1C 5S7

Offprint requests to: V. Gotceitas at the present address

Alternatively, it may be that dominant individuals can delay longer because they are less hungry than subordinates, due to status-related foraging benefits gained prior to the threat of predation. In the latter case, a delay may not represent any significant cost to the dominant with respect to lost foraging opportunity.

Among fishes, salmon, trout, and charr (Salmonidae) characteristically show a social structure commonly described as a dominance hierarchy (Jenkins 1969; Metcalfe 1986), where dominant fish occupy and defend preferred (i.e., shelter, current, food) locations in any given section of the stream (Cunjak and Green 1984; Fausch 1984). Foraging by stream-dwelling salmonids typically involves movement by fish up into the water column to intercept food drifting downstream. However, as foraging activity may increase the probability of detection by predators, fish temporarily reduce such activity following a predation threat (Dill and Fraser 1984; Metcalfe et al. 1987; Huntingford et al. 1988). Therefore, one might predict that, after exposure to a predator, dominant fish may wait until subordinates have resumed foraging before resuming themselves, thereby using subordinate activity as a cue to the current level of predation hazard present. However, nothing is known about the order in which salmonids resume foraging after exposure to predation threat with respect to social status.

In this study, we used pairs of juvenile Atlantic salmon (*Salmo salar* L.) to test the hypothesis that subordinate fish are more likely to resume foraging sooner than dominant individuals after exposure to a predation threat. We also addressed the more general question of whether an animal's social status per se or its hunger level, as related to its social rank, is responsible for any observed status-specific ordering in resumption of foraging activity following a threat of predation.

Methods

Fish and holding conditions. Juvenile Atlantic salmon (4.2–5.7 cm SL) were collected by electrofishing from the Northwest Miramichi River, New Brunswick, Canada. Fish were transported to the laboratory at Mount Allison University, where they were housed in a communal stream tank at 10° C, under a 12 h L:12 h D light regime. Fish were fed freeze-dried euphausiid crustaceans (*Euphausia pacifica*) once a day. Food was introduced on the water surface at the upstream end of the tank and allowed to drift downstream.

Prior to testing, fish of equal weight (mg) and length (cm) were paired, and these pairs were housed in separate flow-through aquaria ($40.5 \times 20 \times 26$ cm) for a minimum of 7 days under the same temperature and light regime as above. This procedure facilitated the development of a dominant-subordinate relationship between the fish. Fish were observed daily during this 7-day period, and the dominant fish in each pair was identified as that individual initiating and subsequently displacing the other in the majority of social interactions (e.g., chasing, and frontal and lateral displays, *sensu* Keenleyside and Yamamoto 1962). A period of 7 days appears to be sufficient for such a relationship to stabilize (Keenleyside and Yamamoto 1962). Fish were fed once a day while in these aquaria. Sufficient food was introduced to insure that both fish fed. There was no significant difference in weight between individual fish in each pair ($n = 40$ pairs) following their use in the experiment (paired t-test; $t = 1.00$, $df = 39$, $P > 0.32$).

Experimental apparatus and procedure. Experiments were conducted in one channel ("experimental channel") of a double-channeled, flow-through, recirculating stream tank ($240 \times 117 \times 53$ cm), maintained under a 12 h L:12 h D light regime and a water temperature of 10° C (Fig. 1). Water depth was maintained at 21 cm and mean ($\pm$SE) water current velocity across the width of the channel was 8.24 (± 0.09) cm/s. This is within the range of current velocities naturally selected by juvenile Atlantic salmon (e.g., Morantz et al. 1987). The experimental channel (150×55 cm) was screened off at both its upstream and downstream ends to prevent fish from exiting. The floor of the channel was marked at 10-cm intervals along its length with black marker lines to facilitate measurement of the distance fish traveled to capture prey. A gravel pad (55×50 cm) was situated at the downstream end of the channel and two pieces of opaque Plexiglas (30×12 cm), positioned equidistant from the front, back, and middle of the gravel pad, were suspended 7 cm above the gravel to provide overhead cover for the fish. Two flat stones (11.5×7 cm) were placed on the gravel equidistant from the front, back, and middle of the gravel pad, as well as the inside edge of the overhead cover, to provide potential holding stations for the fish (i.e., where the fish sits while inactive). An automatic food dispenser was located at the upstream end of the channel, above the water, and behind a blind which obscured it from the fish's view. Another blind, with a viewing slit, was attached to the glass side of the experimental channel to eliminate external disturbances and allow direct observation into the channel.

Each experimental trial was preceded by a period of acclimatization to the experimental channel. The pair of fish to be tested, previously starved for 24 h, was introduced into the experimental channel between 1300 and 1400 hours the day before testing. At 1600 hours food was provided in such a manner that both fish ingested approximately the same number of prey (5 ± 2 euphausiid

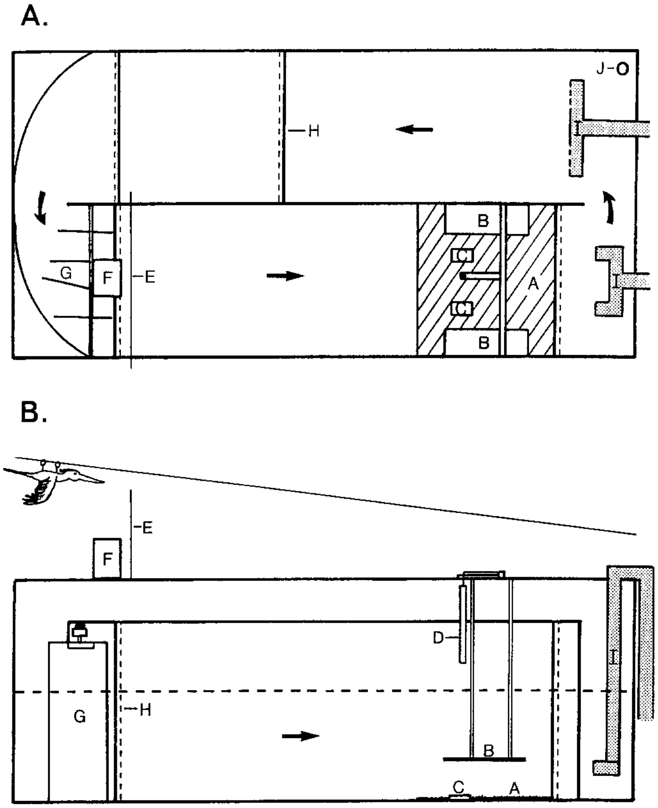

Fig. 1. A Top view of experimental stream tank. **B** Side view of experimental channel in stream tank. *A*: gravel pad; *B*: overhead cover; *C*: flat stone; *D*: clear Plexiglas rod (simulates dive by aerial predator); *E*: blind; *F*: automatic feeder; *G*: flow control baffles; *H*: screen; *I*: inflow and outflow pipes leading to a pump and refrigeration unit; *J*: overflow standpipe. *Arrows* indicate direction of current

crustaceans). This feeding was to insure that both fish would forage in the experimental channel.

All prey items presented to any one pair of fish during both the acclimatization and experimental trial periods were of equal size. However, a range of prey sizes (i.e., 2–4 mm long, 1 mm in diameter, and weighing 0.9–1.6 mg) was used to compensate for the range in size of fish among the different pairs tested (i.e., 4.2–5.7 cm SL). Based on preliminary observations, three food items represents approximately 10% of the satiation level (i.e., 25 ± 2.3 prey items) in fish of the size used in this study. Therefore, when determining hunger level of individual fish during the course of an experimental trial, if the difference in the total number of prey ingested by each fish in the pair being tested was ≤ 3 food items, fish were assumed to be at an equal hunger level.

Each pair of fish was observed both during the acclimatization period, before and after feeding, and prior to beginning an experimental trial. This was to verify whether the particular dominant-subordinate relationship established in the holding aquaria remained after fish had been moved to the experimental channel. The same criteria as in the aquaria was used to identify dominant and subordinate individuals.

The experiment was designed so that each experimental trial (Fig. 2) tested both whether (1) an individual's social status per se (i.e., fish at an equal hunger level) or (2) an individual's hunger level affects which fish of a pair initially resumes foraging after exposure to a predator. Our experiment was also designed to simulate the progression in foraging activity and changes in hunger level experienced by juvenile salmon on a daily basis in nature (Godin, Classon, and Randall, unpublished data).

Each experimental trial ($n = 40$) began between 0900 and 0930 hours the morning following the period of acclimatization, with the presentation of three prey items to initiate feeding activity in the fish (Fig. 2, test block 1). Throughout the experimental trial, prey were presented such that each item was introduced only after the previous prey had either been captured or had been caught in the screen at the downstream end of the experimental channel. Prey were presented at random time intervals. Presentation of the third prey item was followed by the presentation of a predation threat in the form of a stuffed belted kingfisher (*Ceryle alcyon*). The model simulated a kingfisher in flight (i.e., wings extended laterally). A kingfisher model was used because kingfishers are known predators of juvenile Atlantic salmon (White 1937, 1938). The bird was released from an upstream position, where it was concealed from the fish by a blind, so that if "flew" downstream along a clear monofilament line over the center of the experimental channel. As the model passed over the gravel pad, a clear Plexiglas rod ($21.5 \times 1.5 \times 1.5$ cm), suspended over the center of the pad (Fig. 1D), was dropped down into the water to just above the gravel and then immediately raised back to its original position above the water. This was to simulate a diving capture attempt by the kingfisher.

Immediately after presentation of the predator model, another prey item was introduced at the upstream end of the channel. This was followed with the presentation of other prey, one at a time, until a total of three had been captured. Because the difference in the number of prey captured by the dominant and subordinate fish prior to presentation of the predator model in test block 1 was ≤ 3, fish were assumed to be at an equal hunger level (D = S1; D = dominant fish, S = subordinate fish, 1 = test block 1) at the time of presentation of the predation threat. Therefore, test block 1 tested whether social status per se has any effect on the order in which individuals resume foraging following exposure to a predation threat.

Following test block 1, fish were presented with a total of 15 prey items over the course of three successive feeding sessions (i.e., 5 items per feeding session) spaced randomly every 30–60 min (Fig. 2, feeding sessions 1 to 3). The third feeding session was followed (i.e., 30 to 60 min later) by a second test block (test block 2). This was identical in protocol to test block 1 (Fig. 2), except that at the time of presentation of the predation threat in test block 2, the fish were at one of three different "hunger levels" as a result of their feeding history in the preceding three feeding sessions. Therefore, test block 2 tested whether an individual's hunger level had any effect on the order in which individuals resume foraging following exposure to a predation threat.

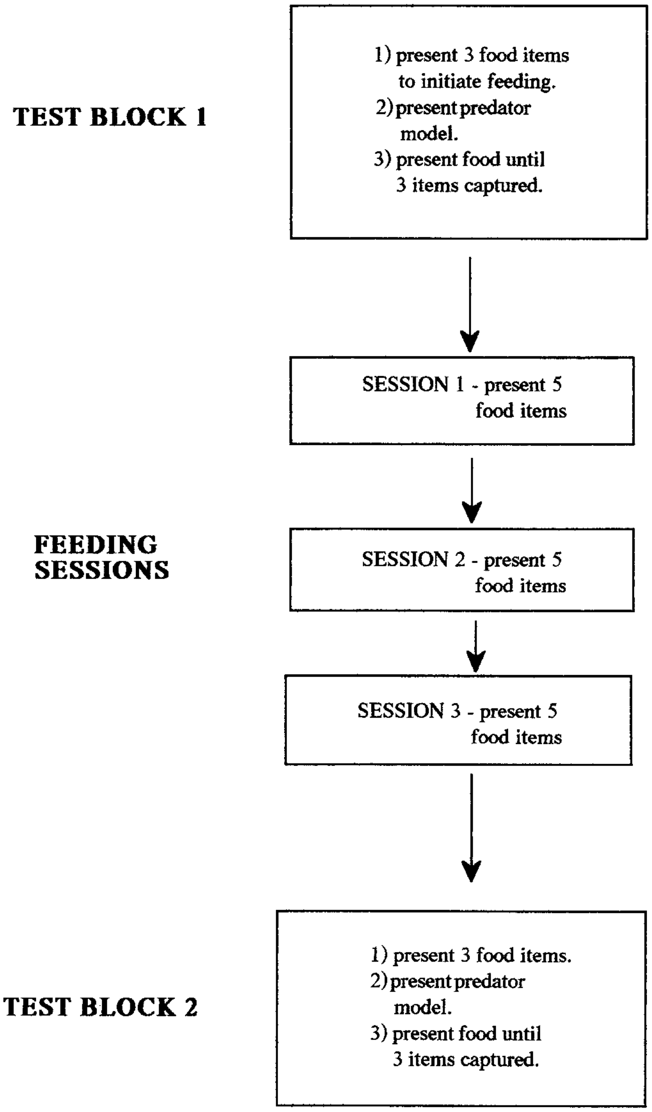

Fig. 2. Flow chart illustrating chronological order of events within each experimental trial. *Arrows* denote a random time interval of 30 to 60 min

Hunger level of individual fish was determined by recording the number of prey captured by the dominant and subordinate fish during the three feeding sessions and up to presentation of the predator in test block 2 (maximum = 18 prey/fish, approximately 72% of satiation level). If the difference in prey captured between fish was ≤ 3 items, the fish were again assumed to be at an equal hunger level (D = S2; D and S as before, 2 = test block 2), but one significantly lower than that in test block 1 (i.e., D = S1, fish previously starved for 17 h vs D = S2, minimum number of prey captured = 7/fish). One fish was assumed to be hungrier than the other if the difference in the number of prey captured between fish was ≥ 4 ($D > S$: more prey captured by dominant than subordinate; $S > D$: more prey captured by subordinate than dominant).

Due to a limited number of naive fish available, we did not run controls for possible sequence effects (i.e., habituation to the predator model between presentations in test blocks 1 and 2). However, we feel such effects are unlikely, given our experimental design. First, Metcalfe et al. (1987) found that the effects of exposure to a fish predator on foraging behavior of juvenile Atlantic salmon was no longer evident within 2 h of exposure. Second, as predation from natural aerial predators represents an unpredictably occurring event, it would seem maladaptive for salmon to habituate to an overhead stimulus after only one presentation (i.e., test block 1). In our study, presentations of the kingfisher model were separated by at least 2 h.

Forty pairs of fish were tested, one pair at a time, and no fish was used more than once. The following data were recorded for each pair of fish tested:

1. The number of prey captured by the dominant and subordinate fish before exposure to the predator was compared to determine the effect of social status on foraging rewards (*G*-test).
2. The location of each fish in the experimental channel (i.e., under overhead cover, upstream, or on the gravel pad), immediately before and after presentation of the predator was recorded. Fish distribution was compared to determine any preference of location before and after exposure to the predator by the dominant and subordinate fish (*G*-test).
3. Following presentation of the predator model in both test blocks 1 and 2, we recorded which fish was the first to move from where it had sought cover, and which was the first to capture a prey item. Movement from cover is here defined as either an aborted attack towards a prey item (i.e., movement up into the water column towards a prey without capturing it), movement out from under the overhead cover, or movement for a distance of at least three body lengths (i.e., minimum of 12.6 cm) from where the fish came to rest after exposure to the predator. Which fish was the first to move and which was the first to capture prey after exposure to the predator was determined for each hunger level category; D = S1, D = S2, D > S, and S > D (*G*-test).
4. The time (seconds) elapsed until fish resumed foraging after exposure to a predator was compared among hunger level categories (ANOVA).
5. All trials were recorded on video tape using an overhead camera. Recordings were analyzed to determine the distance (cm) fish traveled to capture individual prey items. The distance traveled to capture prey before exposure to a predator was compared to that traveled to capture the first, second, and third prey item captured after exposure to the predator for both dominant and subordinate fish (paired *t*-test).

In all statistical analyses, the level of significance was set at $P<0.05$.

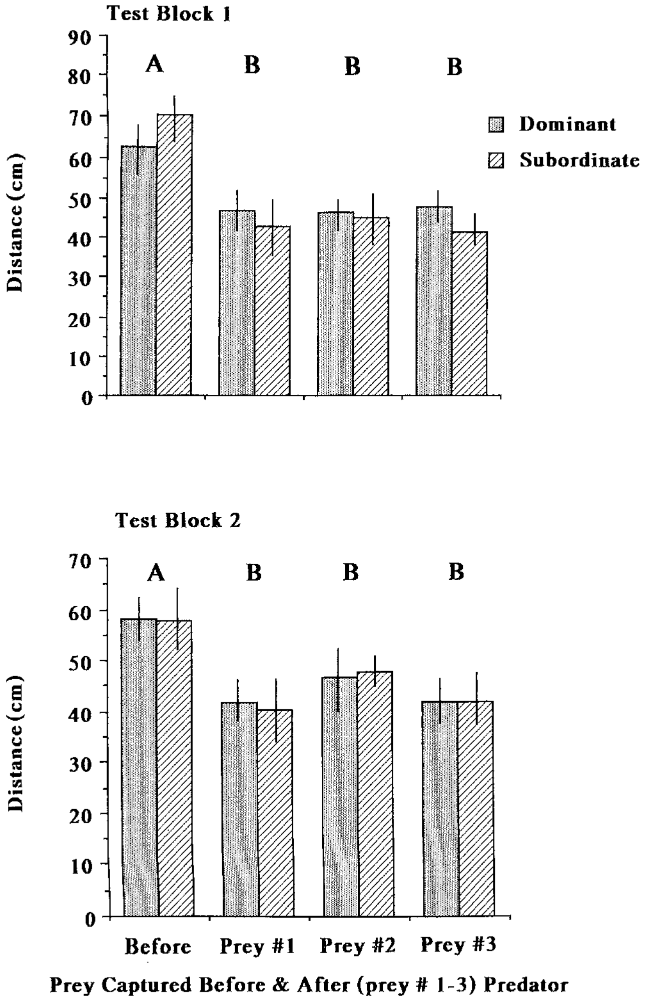

Fig. 3. Mean (±SE) distance (cm) dominant and subordinate fish traveled to intercept a prey item immediately before and for the first three prey items (Prey 1, 2, and 3) captured following exposure to the predator model, when fish were at an equal (test block 1) and unequal (test block 2) hunger level. Within each test block, means with the same letter are not significantly different. * denotes a significant difference between the dominant and subordinate fish

Results

Prior to presentation of the predator model in both test blocks 1 ($G=14.21$, $df=1$, $P<0.005$) and 2 (i.e., feeding sessions 1 to 3, and beginning of test block 2; $G=5.94$, $df=1$, $P<0.025$), the dominant fish captured significantly more prey than the subordinate. Therefore, social status appears to confer a foraging advantage to dominant individuals in the absence of predation threat.

Prior to exposure to a predation threat, regardless of social status or hunger level, significantly more fish were found on the gravel pad (D = S1: $G=72.8$, D > S: $G=52.8$, S > D: $G=16.4$, D = S2: $G=19.5$; $df=2$, $P<0.005$). In comparison, only 4 (3 dominant and 1 subordinate) out of 80 fish occupied a position under the overhead cover. Exposure to the kingfisher model produced a typical overhead fright response (cf. Suboski and Templeton 1989) in all fish, in both test blocks 1 and 2. Following exposure to the model, regardless of social status or hunger level, significantly more of the fish that were on the gravel pad prior to the predation threat sought shelter under the overhead cover (D = S1: $G=62.7$, D > S: $G=50.8$, S > D: $G=11.4$, D = S2: $G=11.4$; $df=2$, $P<0.005$). Each of the 4 fish that were under the overhead cover prior to exposure to the predator model remained there following exposure. In contrast, among those fish occupying positions upstream of the gravel pad prior to a predation threat, half sought shelter under the overhead cover while the others remained in an upstream position (D = S1: $G=0.02$, D > S: $G=0.01$, S > D: $G=0.11$, D = S2: $G=1.39$; $df=1$, since 0 fish chose the gravel pad, $P>0.05$). In the latter case, fish typically moved further upstream from their original position and then remained there, motionless, on or near the bottom.

The distance fish traveled to capture a prey item decreased significantly after exposure to the predator model (Fig. 3). This was true for the first (test block 1: $t=4.47$, $df=39$, $P<0.002$; test block 2: $t=3.28$, $df=39$, $P<0.003$), second (test block 1: $t=3.93$, $df=39$, $P<$

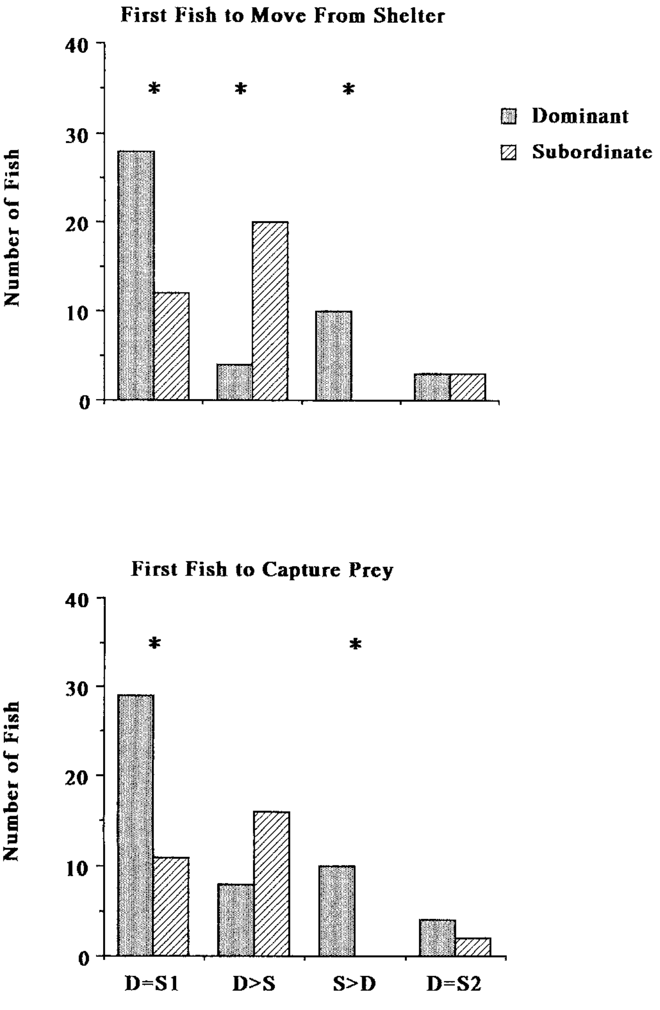

Fig. 4. Total number of dominant and subordinate fish to initially move from shelter and to initially capture a prey item, following exposure to a predator model, in relation to their feeding history prior to the predation threat. Feeding history; test block 1, D = S1: fish at an equal hunger level; test block 2, D > S: dominant fish captured more prey items than subordinate, S > D: subordinate fish captured more prey than the dominant, D = S2: dominant and subordinate fish captured an equal number of prey (but overall hunger level of both fish lower than in D = S1). * denotes a significant difference between the number of dominant and subordinate fish

0.006; test block 2: $t = 2.74$, $df = 39$, $P < 0.011$), and third (test block 1: $t = 3.44$, $df = 39$, $P < 0.002$; test block 2: $t = 5.38$, $df = 39$, $P < 0.001$) prey item captured after exposure to the predator. There was no significant difference in this pattern between the dominant and subordinate fish (Fig. 3). Therefore, the predator-mediated reduction in distance traveled to capture a prey item persisted for some time after exposure to the predator model.

There was no significant difference in the response of fish to presentation of the kingfisher model between test blocks 1 (D = S1) and 2 (D = S2, D > S, S > D) with respect to (1) shifts in location within the experimental channel and (2) a reduction in distance traveled to capture the next three prey items following exposure to the predator. Therefore, habituation to the predator model over the course of an experimental trial was not apparent.

In test block 1, with both fish at an equal hunger level (D = S1), the dominant fish was more likely to be both the first to move out from cover in response to ($G = 10.02$, $df = 1$, $P < 0.005$), and the first to capture ($G = 8.23$, $df = 1$, $P < 0.005$), a prey item after exposure to the predator (Fig. 4, D = S1). In test block 2, hunger level had a significant effect on which fish was the first to resume foraging after exposure to the predator. In those trials where the dominant fish had captured more prey and, therefore, was presumably less hungry than the subordinate (D > S), the subordinate was more likely to be the first to respond to a prey item following exposure to the predator ($G = 15.19$, $df = 1$, $P < 0.005$), but was not necessarily the first to capture one ($G = 2.72$ $df = 1$, $0.1 > P > 0.05$; Fig. 4, D > S). However, in this latter case, the subordinate fish did capture the first prey item in twice as many trials as the dominant. Moreover, in half of the trials in which the dominant fish was the first to capture a prey item, the subordinate had been the first to respond to a prey item by moving out from cover. When the subordinate captured more prey than the dominant (S > D) prior to the predation threat, the dominant fish was both the first to respond to ($G = 13.86$, $df = 1$, $P < 0.005$) and capture ($G = 13.87$, $df = 1$, $P < 0.005$) a prey item following exposure to the predation threat (Fig. 4, S > D). Finally, when both fish had previously captured the same number of prey (D = S2) and were at an equal, but lower, hunger level than that in test block 1 (i.e., fish had captured 7 to 11 prey/fish), dominant and subordinate fish were equally likely to be the first to respond to ($G = 0.01$, $df = 1$, $P > 0.1$) or capture ($G = 0.68$, $df = 1$, $P > 0.1$) a prey item after exposure to a predator (Fig. 4, D = S2).

Finally, exposure to the kingfisher resulted in a delay in the resumption of foraging. The duration of this delay was significantly affected by hunger level for both dominant ($F = 10.67$, $df = 3{,}55$, $P < 0.0001$) and subordinate fish ($F = 2.8$, $df = 3{,}29$, $P < 0.05$). Fish waited significantly longer before resuming to forage when they had eaten an equivalent (i.e., D = S2, $\bar{x} = 270 \pm 96$ s) or greater (i.e., D > S, $\bar{x} = 207 \pm 34.8$ s or S > D, $\bar{x} = 180 \pm 41.4$ s) number of prey than their counterpart, prior to presentation of the predator. The minimal delay after exposure to a predation threat occurred when both fish were at an equal and high hunger level (i.e., D = S1, $\bar{x} = 51 \pm 11.4$ s).

Discussion

Social status had a significant effect on the number of prey captured by juvenile Atlantic salmon when there was no apparent risk of predation. Dominant individuals typically captured more prey than subordinates. These results are consistent with those previously reported for salmonid fishes (Cunjak and Green 1984; Fausch 1984; Metcalfe 1986) and a variety of other organisms (Hodapp and Fry 1982; Ekman and Askenmo

1984; Stamps 1984; De Laet 1985; Waite 1987; Waite and Grubb 1987).

Following an aerial predation threat, regardless of social status, most fish sought shelter under overhead cover and waited, on average for 236 s, before resuming to forage. Fish also significantly reduced the distance they were willing to travel to capture, at least, the next three prey items. Since aerial predators cannot be directly monitored while under overhead cover, a delay before resuming normal activity would seem advantageous with respect to avoiding predation. Further, given that prey movement is important in prey detection by visual predators (Ware 1971; Convey 1988; Gotceitas and Colgan 1988), a reduction in attack distance once foraging had resumed can also be interpreted as an anti-predator response. Similar changes in foraging tactics in response to predation hazard have previously been reported for juvenile Atlantic salmon (Metcalfe et al. 1987; Huntingford et al. 1988) and other salmonids (Dill and Fraser 1984; Grant and Noakes 1987).

In this study, the subordinate fish was not necessarily the first to resume foraging following exposure to a predation threat. This is opposite to that reported for various bird species (De Laet 1985; Hegner 1985; Hogstad 1988), and is inconsistent with the hypothesis that social status per se is the primary factor regulating status-specific ordering in the resumption of foraging activity following a predation threat (i.e., dominant expected to wait for subordinate). Instead, which fish was the first to resume foraging was dependent on hunger level. When fish were at an equal and relatively high hunger level, the dominant fish was most likely to initially resume foraging. In contrast, when fish were at unequal hunger levels, it was the hungrier fish, regardless of social status, that was the first to resume foraging. Therefore, at least in juvenile Atlantic salmon, it appears that an individual's hunger level, and not its social status per se, is the primary factor regulating any delay in the resumption of foraging activity after exposure to a predator. However, it remains to be seen whether status-related hunger level, rather than social status per se, is also the primary factor mediating such status-specific ordering in birds and other animals.

Preliminary analysis of field data (Godin, Classon and Randall; unpublished data) indicates that juvenile Atlantic salmon collected just after dawn generally had less food in their stomachs, and showed little inter-individual variation in this regard, compared with samples collected later in the day. Results from the present study suggest that dominant fish would be at least as likely as subordinates to resume foraging after exposure to a predator, and, therefore, would be expected to be equally as vulnerable to predation during the early part of each day. However, given that the probability of attacking a prey item after exposure to a predator decreases with a reduction in hunger level, and that a status-related foraging advantage exists (Fausch 1984; Metcalfe 1986; present study), vulnerability to predation should decrease during the course of the day much more rapidly for dominant than for subordinate individuals. Further, having reached a hunger level at which they delay longer than subordinates before resuming foraging, dominants may gain an additional advantage in that subordinate activity may serve as an indicator of habitat safety. If status-related hunger level proves to play a similar role in the status-specific order in which other animals resume foraging after exposure to predation, a similar diel cycle in vulnerability among individuals could be expected. De Laet's (1985) observations that dominant great tits (*Parus major*) were the first to arrive at feeding sites in the morning is consistent with such a prediction.

In their study on escape behavior and use of cover by juvenile brook trout (*Salvelinus fontinalis*), Grant and Noakes (1987) reported a positive relationship between increased latency to resume foraging and overall wariness towards predators with increasing body size of the trout. Similar relationships have also been noted for a number of other salmonids (see Grant and Noakes 1987). These authors suggested three possible explanations for such observations. First, if smaller fish derive a greater benefit from rapid growth than larger ones, they should, therefore, be more willing to accept a greater risk to forage. Second, if conspicuousness and vulnerability to visual predators increases with body size in juvenile salmonids, then increased wariness with increasing body size should be favored. Third, smaller fish may resume foraging sooner than larger, dominant individuals in order to take advantage of reduced competition following a predation threat. Our results do not support this third explanation, but do provide yet a fourth possibility. Dominance status is positively correlated with body size in stream salmonids (Grant and Noakes 1987), and dominant individuals tend to occupy the most rewarding foraging sites (Fausch 1984; Metcalfe 1986). Therefore, dominant fish might generally be expected to have lower hunger levels than subordinates. This being the case, the positive relationship between body size and increased wariness towards predators might be related to the negative effect of reduced hunger level on the tendency for fish to accept risk in order to forage, as demonstrated in our study.

Factors other than level of satiation, such as overall condition, energetic demands or deficit (e.g., Godin and Sproul 1988; Abbott and Dill 1989), and previous experience with predators (e.g., Dill and Fraser 1984) may also affect the likelihood of an individual being the first to resume foraging following exposure to a predator. Further work is needed to investigate the effects of such factors, as well as to determine the primary factor(s) affecting the order in which individuals resume foraging activity following a predation threat in other species.

Acknowledgements. We thank G. Brown, P. Colgan, T. Ehlinger, J. Grant, I. Jamieson, J. Kieffer, B. Lavery, S. Reebs, and two anonymous reviewers for their helpful comments on the manuscript. We also thank R. Randall for his assistance with fish collection, G. Hansen for preparing the kingfisher model, and W. Settle for construction of the feeder. This research was supported by a postdoctoral fellowship and operating grant from the Natural Sciences and Engineering Research Council of Canada to V. Gotceitas and J.-G. J. Godin, respectively, and a Fisheries and Oceans Canada/NSERC subvention grant to J.-G. J. Godin.

References

Abbott JC, Dill LM (1989) The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. Behaviour 108:104–113

Baker MC, Belcher CS, Deutsch LC, Sherman GL, Thompson DB (1981) Foraging success in junco flocks and the effects of social hierarchy. Anim Behav 29:137–142

Convey P (1988) Competition for perches between larval damselflies: the influence of perch use on feeding efficiency, growth rate and predator avoidance. Freshwater Biol 19:15–28

Cunjak RA, Green JM (1984) Species dominance by brook trout and rainbow trout in a simulated stream environment. Trans Am Fish Soc 113:737–743

Desrochers A (1989) Sex, dominance, and microhabitat use in wintering black-capped chickadees: a field study. Ecology 70:636–645

Dill LM, Fraser AHG (1984) Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behav Ecol Sociobiol 16:65–71

Ekman J (1987) Exposure and time use in willow tit flocks: the cost of subordination. Anim Behav 35:445–452

Ekman JB, Askenmo EH (1984) Social rank and habitat use in willow tit groups. Anim Behav 32:508–514

Fausch KD (1984) Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can J Zool 62:441–451

Godin J-GJ, Sproul CD (1988) Risk taking in parasitized sticklebacks under threat of predation: effects of energetic need and food availability. Can J Zool 66:2360–2367

Gotceitas V, Colgan P (1988) Individual variation in learning by foraging juvenile bluegill sunfish (*Lepomis macrochirus*). J Comp Psychol 102:294–299

Grant JWA, Noakes DLG (1987) Escape behaviour and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. Can J Fish Aquat Sci 44:1390–1396

Hegner RE (1985) Dominance and anti-predator behaviour in blue tits (*Parus caeruleus*). Anim Behav 33:762–768

Hodapp A, Frey D (1982) Optimal foraging by firemouth cichlids, *Cichlasoma meeki*, in a social context. Anim Behav 30:983–989

Hogstad O (1988) Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. Ibis 130:45–56

Huntingford FA, Metcalfe NB, Thorpe JE (1988) Feeding motivation and response to predation risk Atlantic salmon parr adopting different life history strategies. J Fish Biol 32:777–782

Jenkins TM (1969) Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim Behav Monogr 2:57–123

Keenleyside MHA, Yamamoto FT (1962) Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour 19:139–169

Krebs JR, Davies NB (1984) Behavioural ecology: an evolutionary approach, 2nd edn. Sinauer, Sunderland, MA

Krebs JR, MacRoberts MH, Cullen JM (1972) Flocking and feeding in the great tit *Parus major*: an experimental study. Ibis 114:507–530

Laet JF de (1985) Dominance and anti-predator behaviour of great tits *Parus major*: a field study. Ibis 127:372–377

Metcalfe NB (1986) Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. J Fish Biol 28:525–531

Metcalfe NB, Huntingford FA, Thorpe JE (1987) The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. Anim Behav 35:901–911

Morantz DL, Sweeney CS, Shirvell CS, Longard DA (1987) Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 44:120–129

Peters WmD, Grubb TC (1983) An experimental analysis of sex-specific foraging in the downy woodpecker, *Picoides pubescens*. Ecology 64:1437–1443

Powell GVN (1974) Experimental analysis of the social value of flocking in starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim Behav 22:501–505

Stamps JA (1984) Rand-dependent compromises between growth and predator protection in lizard dominance hierarchies. Anim Behav 32:1101–1107

Suboski MD, Templeton JJ (1989) Life skills training for hatchery fish: social learning and survival. Fish Res 7:343–352

Waite TA (1987) Dominance-specific vigilance in the tufted titmouse: effects of social context. Condor 89:932–935

Waite TA, Grubb TC (1987) Dominance, foraging and predation risk in the tufted titmouse. Condor 89:936–940

Ware DM (1971) Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. J Fish Res Board Can 28:1847–1852

White HC (1937) Local feeding of kingfishers and mergansers. J Biol Board Can 3:323–338

White HC (1938) The feeding of kingfishers: food of nestlings and effect of water height. J Fish Res Board Can 4:48–52