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THE RELATIVE GROWTH OF DOMINANT AND SUBORDINATE JUVENILE STEELHEAD TROUT (*SALMO GAIRDNERI*) FED EQUAL RATIIONS

by

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(With 1 Figure)
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Introduction

Growth depensation (the increase in variance of a size-frequency distribution with time due to differences in growth rates (MAGNUSON, 1962)) occurs in a variety of species of animals (shrimp, RA'ANAN & COHEN (1984); amphibia, RICHARDS (1958), ROSE (1959); birds, NELSON (1978)). It is a particularly common feature of fish populations, especially in captivity (MAGNUSON, 1962; YAMAGISHI, 1962; GUNNES, 1976), where dominant fish exhibit superior growth rates relative to subordinates (BROWN, 1946; YAMAGISHI, 1962; CARLINE & HALL, 1973; LI & BROCKSEN, 1977). A significant portion of this variation can be attributed to differential access to food: dominants defend point sources of food or areas of high prey encounter rate (YAMAGISHI, 1962; WANKOWSKI & THORPE, 1979; RUBENSTEIN, 1981), thus interfering with the feeding of subordinates. Increased rations reduce growth depensation (MAGNUSON, 1962; KOEBELE, 1985), but high variation still persists. These studies have found that increasing the spatial dispersion of food, making it more difficult or costly to defend and equalizing access, leads to decreased variation.

An alternative cause of growth depensation is that subordinates may convert food to dry biomass (gross growth efficiency of WEBB (1978)) less efficiently than dominants. NEWMAN (1956) and KALLEBERG (1958) sug-

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gested that reduced growth efficiency could be due to higher subordinate activity levels. CARLINE & HALL (1973) suggested that subordinates experienced higher metabolic rates, and JOBLING & WANDSVIK (1983) postulated an "undefined psychological stress" as a cause of growth depensation.

The complex of physiological conditions that occur in fish challenged by sub-optimal environments is generally referred to as the "stress syndrome" (MAZEAUD *et al.*, 1977). Some of these physiological parameters, including elevated corticosteroid production, blood glucose and lactate levels, have been correlated with position in a dominance hierarchy (ERICKSON, 1967; NOAKES & LEATHERLAND, 1977; EJIKE & SCHRECK, 1980). Steelhead trout (*Salmo gairdneri*) induced to struggle for 2 min showed higher plasma cortisol concentrations and oxygen consumption than undisturbed fish (BARTON & SCHRECK, 1987). The energetic costs of relatively "stressed" subordinate fish should therefore be higher than those of the dominant. These added costs should result in reduced growth relative to the dominant even if access to and consumption of food is equalized; as a result, subordinates should show a lower growth efficiency.

The present experiment was designed to test the hypothesis that relative dominance status dictates the relative growth of juvenile steelhead trout consuming equal rations. Access to food was controlled in size- and age-matched pairs of juvenile steelhead trout by separating fish briefly at feeding times, enabling them to consume equal rations. This ensured that the dominant had no advantage in obtaining food. It was predicted that dominants should grow faster than subordinates; this growth difference should be a measure of the metabolic cost of subordination.

Steelhead (anadromous rainbow trout) rear in freshwater for one to four years before emigrating to the ocean. During this freshwater residence, steelhead compete aggressively for territories and/or access to food (HARTMAN, 1965). Success in aggressive interactions has been shown to influence growth rate in juvenile steelhead (ABBOTT *et al.*, 1985), and size at downstream emigration in turn affects saltwater survival (SLANEY & HARROWER, 1981) and, therefore, fitness.

Materials and methods

Groups of 300-400 juvenile Englishman River winter-run steelhead trout were obtained from the Fraser Valley Trout Hatchery, Abbotsford, B.C., during the summers of 1981 and 1982. All fish were F1 progeny of wild parents. Fish for the present experiment were

selected concurrently with the weighing of large numbers of fish for a separate growth study.

Groups of fish were initially held in 136.2-l flow-through aquaria until it was ascertained that they would feed, and then deprived of food for two days prior to weighing and sorting. Water temperature ranged from 8 to 11°C, and a 14-h photoperiod (95 lx at the water surface) was maintained. Fish were anesthetized with MS 222, and weighed to the nearest 0.1 mg on an electronic balance after excess water had been removed with absorbant paper. Fork length was measured to the nearest 0.5 mm. After weighing, each fish was allowed to recover in an isolated vessel. During the sorting process pairs most similar in size and length were set aside for use in the experiment. Twelve pairs that differed by no more than 0.2 mg (< .1%) and 1 mm (usually within 0.5 mm), or about 1.5%, were established over the 2 year period. The size of the pairs of fish varied between 163.5 and 298.3 mg in weight, and 28.1 and 36.0 mm in length.

Each pair of fish was placed in a 45.5-l aquarium equipped with a central opaque, removable divider. Dechlorinated water entered and drained from opposite ends of the tank and flowed through the tanks sequentially. Fish were randomly placed on the inlet or outlet side of the divider. Identifying characteristics of fish, such as fin and parr markings, were recorded during a 24-h acclimatization period. The barrier was then removed and the fish allowed to interact. Dominance was assessed by the ability to deliver unreciprocated nips, unrestricted use of both sides of the tank and typical rank coloration (ABBOTT *et al.*, 1985); fish that met all three of these criteria were considered dominant. Fish were fed equal rations of live *Tubifex* during a short separation period until dominance was determined, usually within two days.

The experimental feeding regime ensured that there was no possibility of the dominant receiving a larger ration than the subordinate. Food organisms (various sizes of brine shrimp *Artemia salina*, fruit fly *Drosophila melanogaster*, and onion fly *Hylemya* (= *Delia*) *antigua*) were placed in size-matched pairs. Fish were separated by lowering the central divider and the subordinate was fed one prey item. If that prey was eaten then the dominant was presented with the matching prey. This was continued until either the subordinate or the dominant refused a prey item. Thus, the only possible disparity in ration level was that the dominant could refuse one prey item after the subordinate had fed. This occurred in 12 instances of a total of 798 feedings, with brine shrimp as the prey in each case. Fish were separated for less than 5 min per feeding period.

Fish were usually fed twice per day, at 10.00 and 14.00 h. Behavioural observations were made for two, 10 min observation periods before and after separation. When several pairs were run concurrently one tank was observed per feeding. Nips, charges, chases, displays, and crosses of the tank centerline were recorded using a Datamyte 800 event recorder. Rate of crossing the centerline was assumed to be a measure of ability to use space and search for food; it is also a crude index of activity level. Holding position and presence or absence of typical salmonid subordinate coloration were noted, and fin damage was recorded. Experiments were ended when three of three observers independently identified the same fish as larger.

Fish were then separated, deprived of food for two days to allow elimination of gut contents, and their weight and length measured. Fish were dried at 40 C for 3 d and then re-weighed. For the calculation of dry weight increases paired fish were assumed to have equal percent dry matter at the beginning of the experiment (the mean of their final percent dry weights).

Results

Ten of twelve dominant fish grew faster than their paired subordinate whether growth was measured as wet or dry weight increase (Table 1),

TABLE 1. Growth increments (mg) of paired juvenile steelhead

Pair #	Wet weight increase		Dry weight increase		Days of growth
	Dom.	Sub.	Dom.	Sub.	
1	238.7	182.4	41.5	30.6	40
2	291.4	210.4	53.6	37.7	46
3	219.6	165.6	38.2	30.9	29
4	215.7	206.3	41.3	36.8	29
5	200.5	199.5	37.0	37.5*	29
6	162.9	168.9*	27.5	30.3*	29
7	218.0	199.2	38.4	36.1	29
8	339.1	326.1	64.5	59.3	37
9	356.5	371.7*	68.7	66.4	37
10	346.5	297.0	62.1	52.8	37
11	139.0	116.9	24.0	19.4	37
12	82.6	76.2	13.3	11.3	27
\bar{X}	234.2	210.0	43.5	37.4	33.8

* Indicates pairs in which the subordinate's weight increased faster than the dominant's weight.

although the 10 fish with greater wet weight increases were not the same 10 fish with greater dry weight increases. The average daily growth of dominants was 0.51% initial dry wt/day greater than the average daily growth of subordinates (4.21 cf. 3.70% dry wt./day). The magnitude of differences within pairs was significant (Wilcoxon matched-pairs signed-rank test, $p < .05$). The growth rates of dominant pair members were 12.3% (range -9.9 to 46%) greater on average than the growth rates of their subordinate tank-mates.

Nine of twelve dominants contained a greater proportion of dry matter at the end of the experiment than did their paired subordinates, but the magnitude of differences within pairs was not significant (Wilcoxon test, $p > .05$). Average % dry weight at the end of the experiment was 17.7%.

Dominants made greater use of the tank area by crossing the center of the tank more frequently (133.3 times on average) than subordinates (an average of 29.5 times) during pre- and post-feeding observation periods (Wilcoxon tests, $p < .05$). Dominants also committed more aggressive acts before and after feeding (Wilcoxon tests, $p < .05$): dominants committed an average of 214.8 aggressive acts before and after feeding compared to 45.3 committed by subordinates. There were no significant differences between pre- and post-feeding activity levels within either dominants or subordinates (Wilcoxon tests, $p > .05$).

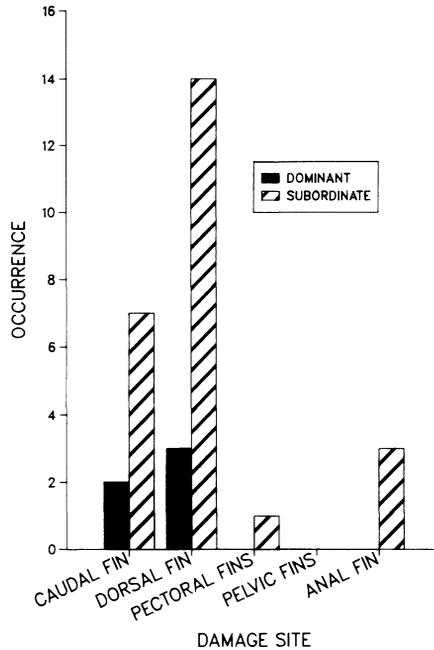


Fig. 1. Occurrence of fin damage (observed instances of fresh damage) in juvenile steelhead trout judged to be dominant and subordinate.

Subordinates received more fin damage than dominants (Fig. 1) and most damage was inflicted on the dorsal fins.

Discussion

As predicted, growth in juvenile steelhead was dominance-related. Paired fish of virtually equal size fed equal rations grew at different rates; dominants grew faster by 0.51% dry body weight/day, on average, representing a 12.3% advantage over the subordinate in gross growth efficiency.

KOEBELE (1985) found that growth depensation in fish that were removed from social interaction while feeding was less than that of interacting fish. Trios of juvenile *Tilapia zilli* were fed equal rations while briefly separated. The growth variance of these trios was the same as that of permanently isolated fish, but significantly less than that of grouped fish that were competing for food. However, no predictions regarding relative growth and behavioural status were tested and behavioural observations were not reported.

The similarity of size and age of the fish at the start of our experiments minimised any difference in growth potential due to heredity or early developmental conditions, since both members of a pair had achieved the same growth under the same rearing conditions. As both members of a pair were of similar age (within 7 d) this also suggests similar initial metabolic efficiencies. Previous social experience may strongly affect future competitive performance (FREY & MILLER, 1972; FRANCIS, 1983; ABBOTT *et al.*, 1985), but in the original hatchery populations, each member of a pair should have had equal access to a variety of different sized competitors, and the chance of individual experience prior to the experiments and subsequent recognition between pair members, should have been minimal. Differential foraging ability or direct interference competition were not permitted to play a role in feeding due to the method of food presentation.

It is unlikely that increased activity accounted for the low growth rates of subordinate steelhead. Behavioural observations of this study and others (KALLEBERG, 1958; MASON & CHAPMAN, 1965) indicate that increased movements associated with aggression and feeding are not generally correlated with subordination. In fact, unless forced to swim in faster currents, subordinates generally are less active than dominants. LI & BROCKSEN (1977), CARLINE & HALL (1973) and EJIKE & SCHRECK (1980) found that high levels of activity and aggression were correlated with high food intake and growth efficiency. JOBLING & WANDSVIK (1983) hypothesized that "psychological stress" might cause starvation or reduced appetite. Highly "stressed" fish have been observed to cease feeding (ABBOTT, 1986) and subordinate fish have been shown to voluntarily reduce food intake (ABBOTT *et al.*, 1985). In the present study subordinates always maintained an appetite and consumed increasing amounts of food over the course of the experiment; it could not be determined if voluntary intake of subordinates was less than that of the dominants, however.

The most likely explanation for the results is that dominant status is associated with reduced costs, or, conversely that subordinate status is associated with increased costs. ROWELL (1974) argues that a dominant is in a normal unstressed condition and that subordinate behaviour represents the measurable result of dominance interactions. Although large shrimp (*Macrobrachium rosenbergii*) actually show enhanced growth in the presence of smaller conspecifics (RA'ANAN & COHEN, 1984), the growth of small fish is usually depressed relative to larger fish (JOBLING, 1985). Additional evidence that social interaction may affect metabolic

rates is provided by WIRTZ (1975) and WIRTZ & DAVENPORT (1976). Blennies (*Blennius pholis*) exposed to conspecifics, or to their own reflection, exhibited decreased food conversion efficiency and increased oxygen consumption, respectively. Since dominant growth rates in this study were not exceptionally high (ABBOTT, 1986), depression of subordinate growth rates appears to be the likely explanation of the observed growth depression.

Several behavioural and physiological indicators of "stress" are likely to be associated with higher energetic costs in subordinates. Higher gill ventilation and fin beat rates suggest a higher rate of energy utilization or reduced energetic efficiency (EJIKE & SCHRECK, 1980). Efficiency of gill and renal osmotic functions is impaired as a result of increased corticosteroid production (MAZEAUD *et al.*, 1977), suggesting that more energy must be expended to maintain homeostasis. The increased blood glucose levels resulting from mobilization of liver glycogen indicate that more energy is being used (MAZEAUD *et al.*, 1977), and high lactate levels indicate that glucose is being metabolised by relatively inefficient anaerobic pathways (BEGGS *et al.*, 1980). Aggressive activity of dominants is apparently reflected in the greater amount of damage sustained by the subordinates. Repair of tissue should also entail an added cost for subordinates.

An attempt to indirectly monitor "stress" parameters in this study was to measure percent dry weight. Due to decreased osmotic efficiency, stressed freshwater fish may have a higher water content than unstressed ones, and EJIKE & SCHRECK (1980) and FAGERLUND *et al.* (1981) have shown that dominants have higher percent dry matter content than subordinates. Most dominants in the present study had higher percent dry weights, as expected, but the overall average difference was not significant.

How closely the "stress" levels of the experimental fish correspond to those of fish in natural conditions is not known. The fish did not appear to be stressed as severely as fish in hierarchies of eight fish competing for food, where some subordinates were observed to stop feeding and die (ABBOTT, 1985). The subordinates did not suffer great physical damage, and were not held at high densities. Several studies of wild stream dwelling salmonids and fish in stream channels suggest that wild fish may be under similar levels of stress. Subordinate or floater (non-territorial) juvenile coho salmon (*Oncorhynchus kisutch*) have less access to food, may be forced to hold in disadvantageous positions, and are continually at risk of attack (PUCKETT & DILL, 1985). Such situations and high density con-

ditions resulting from low stream flows and/or hierarchy formation in pools (*e.g.* HARTMAN, 1965) may produce comparable levels of stress in the wild.

Both territory ownership and primary hierarchy position are examples of dominance in salmonids. The present results indicate that models based on time or calories transacted in feeding and defense of territories (DILL, 1978; HIXON, 1980; SCHOENER, 1983) underestimate the advantage of territory ownership, since they do not take into account the metabolic advantage of dominance *per se*. This could alter optimal territory size or even the decision whether or not to hold territory. The importance of initial success in competitive interactions (MASON & CHAPMAN, 1965; ABBOTT *et al.*, 1985) may insert a further bias towards territoriality. These results offer some explanation of why animals will spend apparently inordinate amounts of time and energy to achieve and maintain dominance, as reported in salmonids by KALLEBERG (1958) and MASON & CHAPMAN (1965).

Summary

The hypothesis that behavioural dominants experience growth advantages relative to subordinates was tested in size-matched pairs of juvenile steelhead trout (*Salmo gairdneri*). Even though access to food was equalized, dominants grew 12.3% faster on average than paired subordinates. As subordinates were less active than dominants this growth difference is attributed to the physiological costs of "stress".

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