Behav Ecol Sociobiol (2002) 52:102–108
DOI 10.1007/s00265-002-0493-z

ORIGINAL ARTICLE

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Can laboratory studies on dominance predict fitness of young brown trout in the wild?

Received: 15 June 2001 / Revised: 5 April 2002 / Accepted: 8 April 2002 / Published online: 9 May 2002

Abstract Laboratory studies suggest that dominance and aggression increase fitness, but this hypothesis has rarely been tested under natural conditions. We therefore designed a combined laboratory–field experiment to detect how social status and aggression relate to growth rate, movement and habitat choice in a natural stream. In 1998 and 1999, juvenile brown trout were caught in the wild and paired in staged dyadic contests in the laboratory where relative dominance rank was determined. Three categories of fish could be distinguished: dominants, subordinates and non-aggressive individuals of indeterminate status. All tested fish were released back into the stream and recaptured after 3 and 8 weeks. Dominant fish grew faster than subordinates, but non-aggressive fish grew as fast as dominants. Social status had no significant effect on recapture rates. Movement was not significantly related to status, but smaller individuals were more mobile and preferred faster-flowing habitats closer to the shore than larger fish. The utilisation of pool and riffle habitats varied among status categories, but this relationship was not consistent between years. These results support the hypothesis that dominance increases fitness in the wild. However, our findings also indicate that less aggressive individuals can be successful in heterogeneous natural habitats. Thus, studies performed under laboratory conditions may overestimate the fitness advantage of aggressive behaviour.

Keywords Growth rate · Habitat choice · Movement · *Salmo trutta* · Social status

Communicated by M. Abrahams

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Introduction

In organisms competing by interference, socially dominant individuals are often more successful than subordinates in defending resources such as food, profitable or protected feeding areas and mates (Andersson 1984; Caraco et al. 1989; Ekman 1987; Fausch 1984; Johnsson and Björnsson 1994). Dominance has therefore often been regarded as a reliable indicator of fitness (Huntingford and Turner 1987). In fish, this view is supported by laboratory experiments showing that dominant individuals grow faster than subordinates (Li and Brocksen 1977; Metcalfe 1989, 1991; Metcalfe et al. 1989). However, natural environments are often more heterogeneous and spatially less restricted than laboratory environments, which may allow for more diverse behavioural strategies (Metcalfe et al. 1995; Milinski and Parker 1991). For example, aggressive behaviour may increase the risk of predation in nature (Jakobsson et al. 1995) but not in the laboratory. Further, excessive aggression may incur metabolic costs (Pucket and Dill 1985), which may be higher in the wild than in the laboratory where food is often abundant and maintenance costs lower. Moreover, losers of conflicts in nature are often able to retreat to refuges to avoid injury and stress, whereas such opportunities are restricted in most laboratory studies. Because such mechanisms may reduce fitness differences between dominant and subordinate individuals in the wild, laboratory studies may generally overestimate the fitness advantages of dominance and aggressiveness.

Richer habitats are expected to attract the more competitive individuals and to support a higher population density than poorer areas, with a higher average benefit in the richer habitat. Several studies, mainly on birds, support this prediction (reviewed by Sutherland 1995). Social status may thus affect movements, if dominants force subordinates to move to less optimal areas (Clarke and Ekman 1995). This hypothesis was supported by Nakano (1994), who showed that dominant red-spotted masu salmon (*Oncorhynchus masou ishikawai*) were more sedentary than subordinates (see also Chapman and

Bjornn 1969). However, dominant individuals should also be more able to displace territory owners (Jenkins 1969; Johnsson et al. 1999a), so dominance could be associated with a mobile exploratory behaviour in environments where resources are temporally variable, whereas subordinates in such populations may face higher costs of leaving their territory. Studies by Armstrong et al. (1997, 1999) suggest that Atlantic salmon (*Salmo salar*) have a high level of space-sharing rather than fixed territories and that dominant individuals use space freely and force subordinates to adjust their positions accordingly.

Most dominance studies have been performed either in artificial streams or in laboratory environments. In this study, we investigated to what extent standard laboratory estimates of social status can predict fitness in a natural stream. We predicted that dominant, more aggressive fish grow faster than subordinates in the wild, because: (H1) dominants are more able to protect and utilise profitable feeding habitats. Alternatively, there are no differences in growth rate between subordinate and dominant fish because: (H0) the relative benefit of dominance is limited in the wild. Without any exclusive predictions, we also checked whether social status affects movement and habitat choice.

Methods

Experimental procedures

The experiment was performed on 1-year-old (1+) anadromous brown trout in Lerån, a small coastal stream in S.W. Sweden, 50 km north of Göteborg. The fish were caught using standardised electrofishing in a section of the stream, 3–4 m wide and located 20 km from the sea. By using a rope, marked every 2 m and running parallel with the stream, the position at capture was estimated for each individual. We also roughly estimated: (1) the distance to the shore (close to shore or in the middle of the stream) and (2) stream speed: fast [with turbulent water surface (riffles)] or slow [with smooth water surface (pools)]. We continued fishing in an upstream direction until 56 trout were caught (in 150 m). These were individually transferred to perforated tanks in the stream, where they were anaesthetised using 2-phenoxyethanol (0.5 ml/l), marked with passive integrated transponder (PIT) tags and measured for wet weight and fork length. The fish were then transported to the Department of Zoology, Göteborg University.

In the laboratory, pairs of fish were size-matched on the basis of weight (to control for size effects on dominance; see Huntingford et al. 1990) and transferred to aerated plastic aquaria (25×20 cm) containing river water (maintained at 15 °C) and a transparent glass divider to keep individuals separated. The fish were left for 2 days in order to acclimatise. In 1999, each fish was fed three live caddis larvae (*Rhyacophila* sp.) and the opercular (gill cover) beat rate (Metcalfe et al. 1987) was recorded on days 1 and 3 (at 9.00 a.m.) to estimate the acclimatisation/stress status of each fish. On day 3, we removed the dividers in all aquaria and monitored behaviour for 5 min (6 min in 1999). For each fish, we recorded its vertical position (upper or lower half of the aquarium), freezing (resting motionless at the bottom), body colour (bright or dull) and feeding. In addition, we observed the following agonistic interactions: (1) display, either lateral or frontal, where one or both fish erect all fins, (2) circling, where two fish circle round each other, (3) attack, where one fish charges at the other, (4) bite and (5) hunt, where one fish pursues the escaping combatant (see also Fernö et al. 1976; Noakes 1980). This procedure was repeated on the following day, but with two 2-min observation periods (three periods in 1999), separated by 3 h. The procedure was designed to minimise stress sustained from the contests. All fish were protected from injuries by the transparent glass divider, which was put back as soon as a clear social hierarchy was established and between observations. Huntingford et al. (1993) found that subordinate parr of Atlantic salmon resumed feeding 2 days after receiving a direct attack, with the previously dominant companion still visible. Thus, we did not expect any long-term effects of the dyads on feeding behaviour.

On the following day, the fish were transferred back to the stream and released from the shoreline at the same metre section as they were caught. This procedure was repeated four times; twice during 10–18 May 1998 and twice during 3–11 May 1999, resulting in a total number of 224 juvenile sea trout being studied. In each year, the fish were caught in two adjacent stream sections. The size of the fish at capture was 5.0±0.17 g and 77.4±0.8 mm. There were no differences in initial size, either between years or due to the ascribed social status.

Fish were recaptured twice, on 2 June and 11 August 1998 and on 2 June and 10 August 1999. Fishing started 100 m downstream and continued to 100 m upstream of the section of release; and thus about 350 m of the stream was fished. At the first recapture, the position and habitat utilisation of each fish was determined as before. The fish were then anaesthetised, wet weight and fork length were measured and the fish were released at the place of capture. This procedure was repeated at the final recapture.

Treatment of data and statistical analysis

Performance in the wild

Individuals that were recaptured twice (seven individuals in 1998, five individuals in 1999) were excluded from the analysis of the first recapture. The specific growth rate [SGR (equivalent to the percentage increase in size per day)] in weight (w) and length (l) was calculated as $\mathrm{SGR}_w=100(\log w_f - \log w_i)$ g day^{-1} and $\mathrm{SGR}_l=100(\log l_f - \log l_i)$ mm day^{-1}, where i is the initial weight or length and f is the final weight or length (Ricker 1979). The residuals obtained from the linear regression (log w vs log l) were used as a measure of condition index, from which the change in condition index during the test period (from capture to recapture) was calculated and used as one of the measures of performance.

The effect of status on performance in the wild (the response variable y) was analysed using the following general additive model: y = status + initial size + year + time of recapture + (year × status) + (time of recapture × status) + (initial weight × status), where status is a class variable with three levels (see below), initial size is a continuous variable, year is a class variable with two levels (1998, 1999) and time of recapture is a class variable with two levels (first recapture, second recapture). The response variable y was either continuous (specific growth rate, change in condition index, movement) or categorical [recapture (two levels: recaptured or not), habitat utilisation, stream position (two levels), flow speed (two levels)]. For continuous response variables, we used a general linear model; and for categorical variables, we used a logistic model. When testing effects on change in condition index we did not include the independent variable initial size from the model. In addition, we also analysed the difference in initial weight between years and due to status, using the following general linear model: initial weight = year + status + (year × status). Movement (the distance between initial and subsequent capture positions) was analysed both as relative movement (upstream/downstream movement included) and absolute movement (direction of movement ignored). Habitat utilisation was measured as the position in the stream at the first capture (two classes: along bank or in mid-stream) and as habitat type (two classes: riffle or pool). The interaction terms were excluded from final tests when no significant interaction effect was found.

In addition we used a two-sample t-test to check for differences in condition index between experimental fish and non-experimental fish (non-PIT-tagged fish) caught in the stream at the first recapture in 1999.

Table 1 Significance values from: (1) the general linear model, using growth rate, movement and change in condition index as response variables, and (2) the logistic model, using recapture, stream position and flow speed as the response variables. Recapture (recaptured or not), flow speed (riffle or pool) and stream position (near bank or in mid-stream) are dichotomous variables, whereas all others are continuous variables. *Subscript values* denote degrees of freedom (main effect first, followed by error term), * $P \leq 0.05$, – variables not included in the model

Response variable	Status	Initial size (weight/length)	Year	Time of recapture	Status × year	Status × time of recapture	Status × initial size (weight/length)
Growth rate (weight)	$F_{2,76}=5.0$; $P=0.009^*$	$F_{1,76}=22.6$; $P<0.001^*$	$F_{1,76}=0.74$; $P=0.40$	$F_{1,76}= 443.6$; $P<0.001^*$	$F_{2,70}=1.04$; $P=0.36^*$	$F_{2,70}=0.36$; $P=0.70$	$F_{2,70}=0.19$; $P=0.82$
Growth rate (length)	$F_{2,76}=3.6$; $P=0.031^*$	$F_{1,76}=29.3$; $P<0.001^*$	$F_{1,76}= 1.2$; $P=0.28$	$F_{1,76}=8681.9$; $P<0.001^*$	$F_{2,70}=2.3$; $P=0.11$	$F_{2,70}=1.35$; $P=0.26$	$F_{2,70}=0.31$; $P=0.74$
Movement (relative)	$F_{2,74}=2.2$; $P=0.12$	$F_{1,74}=0.78$; $P=0.38$	$F_{1,74}=1.5$; $P=0.23$	$F_{1,74}=0.71$; $P=0.40$	$F_{2,70}=2.2$; $P=0.12$	$F_{2,70}=1.20$; $P=0.31$	$F_{2,70}=0.67$; $P=0.51$
Movement (absolute)	$F_{2,76}=0.48$; $P=0.62$	$F_{1,76}=4.3$; $P=0.042^*$	$F_{1,76}=0.92$; $P=0.34$	$F_{1,76}=4.0$; $P=0.05^*$	$F_{2,70}=0.83$; $P=0.44$	$F_{2,70}=0.02$; $P=0.98$	$F_{2,70}=0.036$; $P=0.96$
Condition index	$F_{2,77}=0.066$; $P=0.94$	–	$F_{1,77}=0.01$; $P=0.92$	$F_{1,77}=4.6$; $P=0.035^*$	$F_{2,73}=0.26$; $P=0.77$	$F_{2,73}=1.00$; $P=0.37$	–
Recapture	$\chi^2_{2,144}=1.8$; $P=0.41$	$\chi^2_{1,144}=2.5$; $P=0.11$	$\chi^2_{1,144}=9.3$; $P=0.0023^*$	–	$\chi^2_{2,144}=0.61$; $P=0.74$	–	–
Stream position	$\chi^2_{2,148}=0.53$; $P=0.77$	$\chi^2_{1,148}=3.5$; $P=0.061$	$\chi^2_{1,148}=6.3$; $P=0.012^*$	–	$\chi^2_{2,148}=2.7$; $P=0.26$	–	–
Flow speed	$\chi^2_{1,148}=4.0$; $P=0.13$	$\chi^2_{1,148}=3.8$; $P=0.052$	$\chi^2_{1,148}=16.0$; $P<0.001^*$	–	$\chi^2_{2,148}=10.9$; $P=0.0044^*$	–	–
Flow speed (1998)	$\chi^2_{2,74}=7.2$; $P=0.028^*$	$\chi^2_{1,74}=4.6$: $P=0.033^*$	–	–	–	–	–
Flow speed (1999)	$\chi^2_{2,73}=6.4$; $P=0.040^*$	$\chi^2_{1,73}=0.33$; $P=0.56$	–	–	–	–	–

Behavioural studies

Social status in each pair was determined on the basis of aggressive interactions, body colour and position of the fish. Dominant fish were more often positioned in the middle of the aquarium and had a brighter coloration than subordinates (Keenleyside and Yamamoto 1962; O'Connor et al. 1999). A fish was assumed to be dominant if it won most of the interactions and if accompanying differences in colour and position could be observed during all three observation periods. However, in most of the ranked pairs (where aggressive acts were observed), there were several aggressive interactions during the first observation period and sometimes also during the second. During the last period, the rank was often clear with an obvious difference in colour and/or position.

Opercular beat rate and number of caddis larvae eaten were analysed with the Kruskal Wallis one-way analysis of variance. The difference in opercular beat rate between the first and last recording was analysed with a paired *t*-test. The overall difference in size between categories was analysed with a general linear model ANOVA.

Results

Social status

Of the total 112 pairs of fish studied, a clear dominance rank was set in 79 pairs (33 pairs in 1998, 46 pairs in 1999). Dominance could not be determined in the remaining 33 pairs (23 pairs in 1998, 10 pairs in 1999). In most of these pairs, we could not detect any aggression at all and these fish are therefore referred to as non-aggressive. Both of the paired fish in this category were often brightly coloured and did not show any signs of being subordinate. Hence, three categories of fish were distinguished: dominant, subordinate and non-aggressive. Overall, there were no significant differences in initial size between these categories.

Opercular beat rate (beats per minute) during the first and last reading were: 27.6±1.6 beats min^{-1} (n=32) and 24.8±1.2 beats min^{-1} (n=31) for dominants, 26.5±1.1 beats min^{-1} (n=29) and 23.8±0.7 beats min^{-1} (n=33) for subordinates and 28.8±1.2 beats min^{-1} (n=17) and 24.3±1.3 beats min^{-1} (n=18) for non-aggressive fish, respectively. No significant difference in beat rate between the first and last reading was found for any category. Further, opercular beat rate did not differ between status categories, indicating that all categories of fish acclimatised at a similar rate. Categories did not differ in the number of caddis larvae consumed. All fish ate at least one caddis larva and 88.3% of the dominant fish, 91.2% of the subordinates and 86.6% of the non-aggressive fish ate all three larvae.

Relation between field performance and social status

Recapture rate

Recapture rate did not differ between the three status categories (Table 1). On average, 34.2% of the subordinate, 36.7% of the dominant and 40.9% of the non-aggressive individuals were recaptured. In total, 54 fish (48%) were

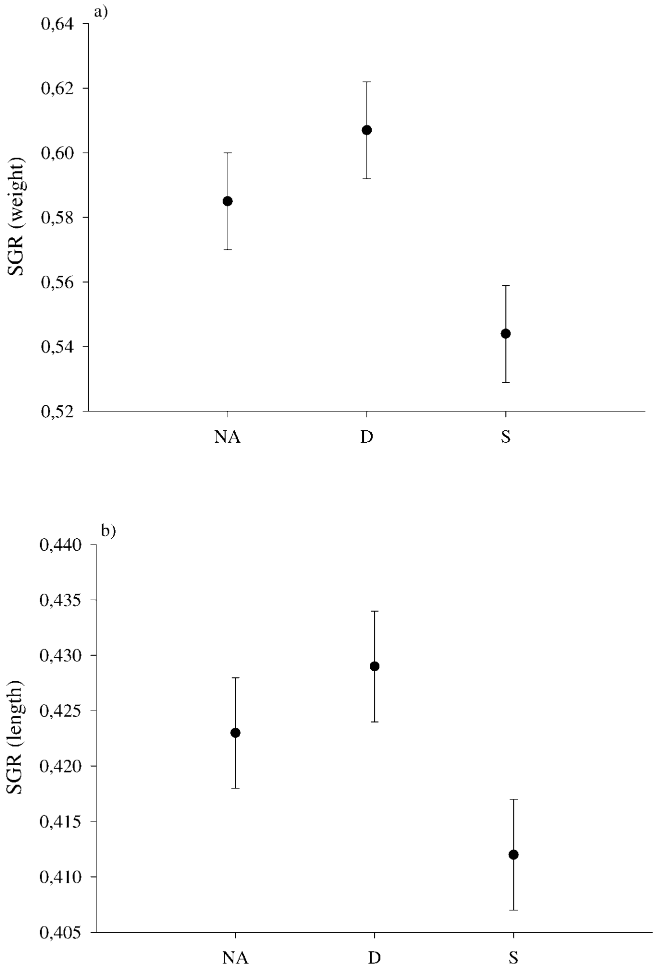

Fig. 1 Specific growth rate (*SGR*; least mean square), based on the general linear model in weight (**a**) and length (**b**) for non-aggressive (*NA*), dominant (*D*) and subordinate (*S*) brown trout. *Each standard error bar* denotes one standard error of group mean

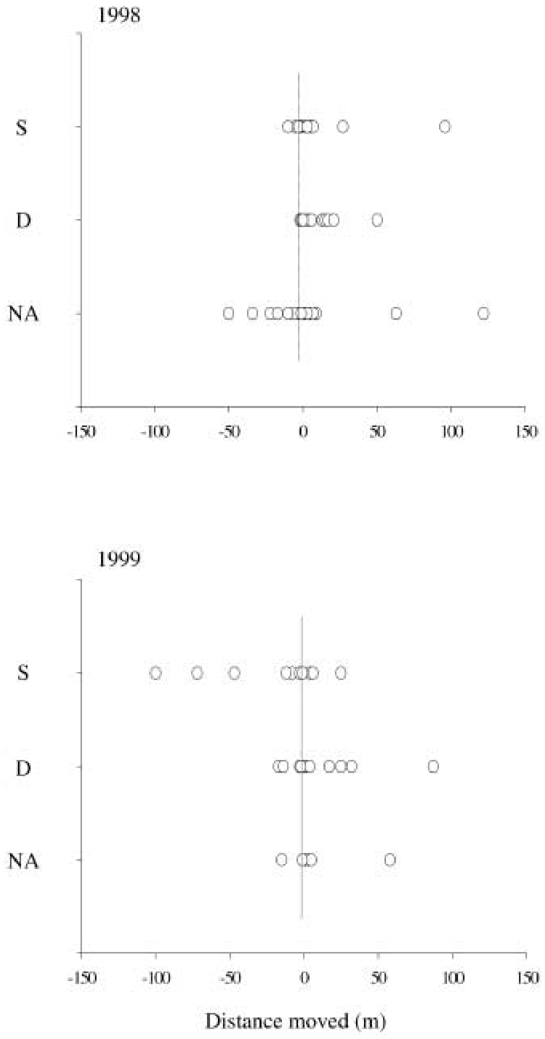

Fig. 2 Movement (distance between initial capture and recapture positions) for non-aggressive (*NA*), dominant (*D*) and subordinate (*S*) brown trout in 1998 and 1999. *Negative numbers* denote downstream movement and *positive numbers* upstream movement

recaptured in 1998 (15, 39, respectively, for the two recaptures) and 29 fish (26%) in 1999 (9, 20, respectively, for the two recaptures).

Growth and change in condition

Specific growth rate was affected by status, both in weight and length (Table 1). A Tukey multiple comparisons test (Wilkinson 2000) revealed that subordinate individuals grew slower in weight than dominant fish (P=0.007), whereas no significant difference could be detected between subordinate and non-aggressive fish (P=0.121), or between dominant and non-aggressive fish (P=0.538; Fig. 1a). Subordinate individuals also grew slower in length than dominants (P=0.025), while there were no differences between dominant and non-aggressive fish (P=0.597), or between subordinate and non-aggressive fish (P=0.230; Fig. 1b). Smaller fish had a higher growth rate both in weight and length. Generally, fish caught during the spring recapture had a higher growth rate, both in weight (0.77±0014 g) and length (0.69±0.005 mm), compared with fish caught during the summer recapture (0.38±0.012 g, 0.15±0.004 mm; Table 1). No other significant effects on growth rate were found. Change in condition was affected by time of recapture (Table 1), with a higher condition index at the second recapture, but no other significant differences were found. Moreover, the experimental fish (n=9) did not differ in condition index (two-sample t-test) from non-experimental fish (n=22) caught in the stream at the first recapture in 1999, suggesting that the experiment had no long-term effects on condition (t_{29}=–1.40, P=0.173).

Movement

Most individuals (79%) moved less than 20 m (Fig. 2). Movement ranged from 122 m upstream to 100 m down-

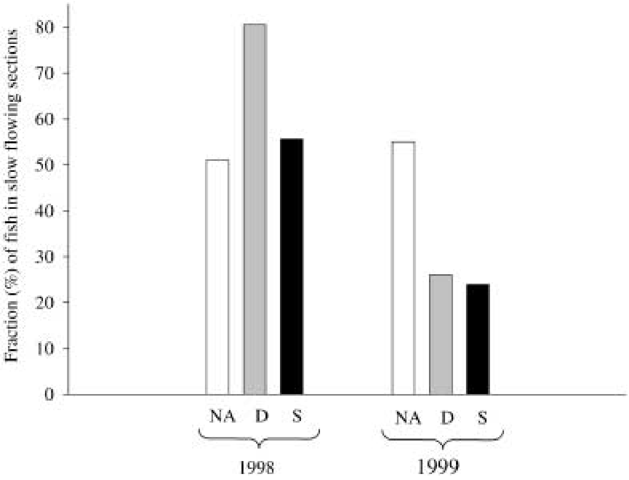

Fig. 3 Utilisation of slow-flowing sections in the stream for non-aggressive (*NA*), dominant (*D*) and subordinate (*S*) fish in 1998 and 1999

stream. Smaller individuals moved more than larger fish and movement was also affected by the time of recapture (Table 1). We found no effect of status on movement.

Stream position

More fish were captured close to the shore than in mid-stream [n=213; df=1; χ^2=14.90; P=0.0001 (intercept)]; and this was more pronounced in smaller individuals (Table 1). No significant effect of status was found. However, there was a significant variation between years (Table 1) with fish being captured closer to the shore in 1998. No significant interaction between year and status was found.

Flow speed

There was no significant relation between status and utilisation of pool and riffle habitats. However, there was an effect of year, with more fish captured in pools in 1998 than in 1999 (Table 1). There was also an interaction between year and status, indicating that dominant individuals utilised pools more in 1998 than in 1999, whereas dominant and subordinate fish were captured in riffles to a larger extent than non-aggressive fish in 1999 (Table 1, Fig. 3). Smaller individuals were more often found in faster-flowing riffles (Table 1).

Discussion

Our results support hypothesis H1 that dominant individuals grow faster than subordinates in the wild, which is consistent with the findings of Nakano (1994). Dominance was assessed simply on the basis of dyadic contests between size-matched opponents, which could lead to a conservative assessment of the effects of status (Huntingford et al. 1990). But, social status in the laboratory experiment was reflected in differential growth in the wild. However, fish that were non-aggressive in the laboratory dyads grew as fast as dominant fish. Recapture rate and change in condition were also independent of status, which suggests that the fitness of dominant and non-aggressive fish was similar.

These results raise questions both about the fitness relevance of aggressive behaviour and about the mechanisms tending to preserve diversity in behavioural traits. Habitat complexity, both in space and time, may allow less aggressive individuals to coexist with more dominant and/or aggressive individuals (Wilson et al. 1994). When population size is low and the number of available feeding sites is high, it might pay to avoid costly aggressive interactions. However, when the opposite is true, individuals might be forced into costly interactions in order to stand a chance of obtaining one of the few feeding sites.

In addition, the pay-off for alternative behavioural strategies may be dependent on their associated metabolic requirements. Metcalfe et al. (1995) found that dominant fish had higher standard metabolic rates (SMR) than subordinates. A high SMR has previously been interpreted as a disadvantage, since more energy would be needed to maintain this level of metabolism (Bryant and Newton 1994; Hogstad 1987; Rösskaft et al. 1986). However, Metcalfe et al. (1995) suggested that a high metabolic rate in salmon (*S. salar*) may be beneficial, since it would allow a greater metabolic scope and thereby potential for rapid growth (e.g. Priede 1985). If high metabolic rate and aggressive behaviour were always the best strategy, one would expect a continuous evolution towards more aggressive individuals with increasingly higher metabolic rate. However, there are certain counter-selective forces: if the relative metabolic rate of an individual is inflexible, a subordinate fish with lower metabolic rate would carry a lower cost of existence during periods with limited food supply (Metcalfe et al. 1995). However, O’Connor et al. (2000) showed that the SMR in salmon is flexible. Fish with a higher metabolic rate reduced their SMR more during periods of food shortage, relative to individuals with a lower metabolic rate. Similar mechanisms may select against increased growth hormone secretion in the wild, despite its growth-promoting effects under a range of environmental conditions (Johnsson et al. 1999b, 2000). Further, Hofmann and Fernald (2000) found that changes in somatic growth rate were induced by changes in social status. They detected that neurons containing somatostatin, a known inhibitor of growth hormone, increase in dominant and socially descending animals. Such physiological plasticity can allow animals to reallocate resources from reproduction to growth or vice versa, depending on their status. Dominance can also be costly, due to aggressive interactions (Grant 1997; Jakobsson et. al. 1995) that might incur metabolic costs (Pucket and Dill 1985), increase the risk of predation (Jakobsson et al. 1995), or decrease the available time to forage (Elliot 1994). In accordance with this, Metcalfe (1986) found that subordinates more willing to compete did worse in terms of growth, compared with fish that appeared to adopt a less competitive strategy. Clearly, there can be situations where the cost of aggressiveness may be higher than the potential benefit of an occupied territory.

In the present study, there were no clear differences in movement due to status, although subordinates seemed to move more downstream than dominant and non-aggressive fish (Fig. 2). Regardless of social status, however, most fish moved less than 20 m. This is consistent with most previous studies, which have shown that stream-living salmonids are mainly stationary, even though a fraction of the population may move over quite long distances (Armstrong and Herbert 1997; Heggenes et al. 1991; Hesthagen 1988; but see Gowan et al. 1994 for a different view).

In 1998, dominant fish were more often positioned in pools than subordinates and non-aggressive fish, whereas, in 1999, dominant and subordinate individuals were more frequent in riffles, compared with non-aggressive fish. Hence, dominant individuals showed the largest variation in flow-speed position, which might suggest that they are more able to utilise the more profitable feeding areas, which may change between years (Dolmen 1988; Nakano 1994). Non-aggressive fish showed no variation in flow-speed position, which may suggest that they are habitat generalists adopting a floater strategy (Jenkins 1969; Rosenzweig 1991). Generally, the food supply increases with the speed of flowing water (Hynes 1970; Wankowski and Thorpe 1979). However, at a certain point, the energetic cost of holding a position becomes higher than the potential benefit from feeding (Fausch 1984). This might explain why the preference for flow speed varied between the years.

In agreement with Bremset and Berg(1999) and Dolmen (1988), we found that smaller individuals were positioned closer to the shoreline and in sections with fast-flowing water. Several studies have demonstrated that larger individuals are superior in contests with smaller conspecifics (Jenkins 1969; Newman 1956). The smaller fish in our study might therefore have been forced to the shoreline and to faster-flowing sections by competition from dominant individuals.

In summary, we have shown that dominants grow faster than subordinates in a natural river. However, we also found that less-aggressive individuals of indeterminate social status grew as fast as dominants. Our results suggest that dominance increases growth rate in the wild. However, the findings also indicate that less-aggressive individuals can perform well in heterogeneous natural habitats. Previous laboratory studies performed in homogenous and/or spatially restricted environments may therefore have overestimated the fitness advantages of aggressive behaviour.

Acknowledgements J.H. was supported by grants from the Hvidtfeldtska Överskottsstiftelsen and the Royal Swedish Society of Science. J.J. was financed by the Swedish Council for Forestry and Agricultural Research. The study was approved by the Ethical Committee for Animal Research in Göteborg (license 136/96). This study would have been impossible to perform without valuable help in the field from Ulrika Bothin, Göran Höjesjö, Rickard Johansson, Ove Mauritzson, Lars-Erik Sundström, Fredrik Sundström and Uno Unger.

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