Short-term dominance: stability and consequences for subsequent growth

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Dominance status was determined among groups of four fish by using individuals from eight brown trout *Salmo trutta* populations. Subsequent growth of the fish was later recorded in larger groups. Seven months after the first set of trials, an additional set of dominance trials was performed by using the same fish. Social status affected subsequent growth; individuals having the lowest ranks grew less when compared to the higher ranking fish. Furthermore, the short term dominance hierarchy was rather stable between the two trials. This was especially the case with the lowest ranking fish, which tended to remain in the lowest position also in the second trial. The results suggest that the short term dominance trials done among few conspecifics reflect relatively well not only the subordinates' relative but also absolute social status.
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INTRODUCTION

For an individual living in a dominance hierarchy, social status is likely to have far reaching consequences on further performance. Individuals with high social status usually gain more food and higher reproductive success compared to individuals with low status (Huntingford & Turner, 1987; Metcalfe *et al.*, 1989; Pusey *et al.*, 1997). Fishes are ideal model species for investigating the effects of long-term interactions, as the indeterminate nature of growth makes it possible to correlate individual competitive ability with further performance (Ward *et al.*, 2006). Dominant salmonids are generally larger than subordinates (Johnsson *et al.*, 1999), however, this can be both a cause or a consequence of high status. Large body size is an advantage in dominance hierarchy formation, but the large size of a dominant individual may

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also be a consequence of the benefits related to high status, such as better access to resources (Huntingford *et al*., 1990).

In salmonids, high metabolic rate, high aggressiveness and boldness towards predation threat are traits often connected to dominance, while the subordinates are often characterized with low metabolic rate and low aggressiveness (Metcalfe *et al*., 1995; Cutts *et al*., 2001; Sundström *et al*., 2004). The dominant fish may have the advantage of fast growth *via* high metabolic rate; in addition, high aggression level helps in acquiring and maintaining profitable food territory. Subordinates, on the other hand, have increased glucocorticoid secretion (although the opposite was found by Creel, 2001), which is generally interpreted as stress response (Eijke & Schreck, 1980; Winberg & Lepage, 1998). Prolonged stress is known to cause general behavioural inhibition, in other words, suppression in feeding, aggression and activity (Øverli *et al*., 1998, 2004). Dominance hierarchies may also be influenced by intra-individual genetic variation with dominant fishes having higher heterozygosity (Tiira *et al*., 2003, 2005). All these factors suggest that dominant individuals should have higher growth rate.

Several studies have measured the growth of individual salmonids differing in social status, and although some studies have found higher growth in dominant individuals (Metcalfe *et al*., 1989; Metcalfe *et al*., 1992; Johnsson & Björnsson, 1994; Nakano, 1995), many studies have found no, or in some cases negative (Huntingford & García de Leániz, 1997), effects of dominance on subsequent growth rate (Adams & Huntingford, 1996; Cutts *et al*., 2001; Martin-Smith & Armstrong, 2002; Vøllestad & Quinn, 2003). The main explanation for these negative results has been that although high status has benefits, it also carries costs. Costly aggressive behaviour is needed to obtain and defend resources (Neat *et al*., 1998). In addition, although the fast metabolic pathway may be advantageous to fishes (prior residence and possibility for high growth rate), it can also be a major energetic cost (Cutts *et al*., 2002).

Short-term dominance assessments are frequently used in determining the social status of an animal. Conclusions are often derived from status determined among few individuals during a short time period in setups only rarely resembling natural situations. Individuals with high relative competitive ability are assumed to have also higher fitness. This short-term assessment of competitive ability, however, is a relative measure, depending on the number of competitors in the local environment, and an individual's own competitive ability compared with these particular conspecifics. As most dominance trials with fishes are conducted in small groups in a short period of time (Bailey *et al*., 2000; Lahti *et al*., 2001; Vøllestad & Quinn, 2003; Sundström *et al*., 2004), it is important to know if the relative status of an individual is stable. Another question of importance is if dominance status measured in small groups during a short period of time is reflected on later performance of the fishes? These are the basic assumptions which most studies investigating the effect of dominance rely on, yet the knowledge of the stability and generality of the dominance hierarchy is largely missing. Cutts *et al*. (2001), however, found in Arctic charr *Salvelinus alpinus* (L.) that a measure of competitive ability and aggression was stable over 6 months.

An earlier study investigated the population level association between aggressiveness and growth rate among 10 Finnish brown trout *Salmo trutta* L. populations. In that study, a positive correlation between aggressiveness and growth was found among populations (Lahti *et al*., 2001). In this study a closer look at dominance and

growth at the individual level was taken by using individual data from eight of the populations included in the previous study. The following questions were addressed: (1) do fish with different status differ in growth rate and (2) is the dominance hierarchy measured in small groups in a short period of time repeatable after several months?

MATERIALS AND METHODS

STUDY FISH

Juveniles from eight *S. trutta* populations originating from different parts of Finland (Lahti *et al.*, 2001) were used. All the study fish originated from hatchery strains; however the number of generations bred artificially in the hatchery varied among the populations (Lahti *et al.*, 2001). The populations were brought to the facilities of the Saimaa Fisheries Research and Aquaculture in Enonkoski, eastern Finland, (62° N; 28° E) from other hatcheries as eyed-stage eggs, and thereafter the fish were raised under similar conditions. Detailed information on the populations and hatchery conditions is given in Lahti *et al.* (2001).

BEHAVIOURAL OBSERVATIONS

The first dominance rank trials were conducted between 14 September and 29 October 1998. Three sides and the top of 10 aquaria (400 mm × 250 mm, water depth 300 mm) were covered with opaque plastic to avoid disturbance and to prevent fish from jumping out. Water turnover in the aquaria was adjusted to $4 \, l \, min^{-1}$ and the photoperiod was kept constant at 14L:10D. Water temperature during the experiment varied between 5·9 and 9·3° C (mean 7·6° C). From each population, 32 individuals were used in the trials. The mean size of tested fish differed between populations, the mean ± fish total length (L_T, mm) varying from $8·2 \pm 0·2$ mm (population Luutajoki) to $9·6 \pm 0·2$ mm (populations Iijoki, Kemijoki) being on average $9·1 \pm 0·2$ mm.

Four similar-sized (within 0·5 g) fish originating from the same population were selected for each trial. The fish density (40 fish m^{-2}) was relatively high compared to the situation in the wild, but was chosen to ensure a competitive environment (high interaction environment; Ruzzante & Doyle, 1993). It was well below the usual hatchery densities. The fish were anaesthetized with MS-222 (tricaine methanesulphonate), L_T (to the nearest mm) and mass (M, to the nearest 0·1 g) were measured, and each fish was individually marked. To enable recognition of individuals, the fish were marked with two methods: with trial-specific cold-brands (Bourgeois *et al.*, 1987) and with individual tail clips within trials (Lahti *et al.*, 2001). Tail clipping had no influence on the dominance rank of the fish (χ^2 test: d.f. = 9, $P > 0.05$, $n = 316$). Thereafter, the fish were transferred to the trial aquarium, and left to acclimatize until the following day when the observations were started.

During 14–25 April 1999, *c*. 8 months after the first dominance rank trials, the experiment was repeated by using the same groups of four fish as in the first rank determination. Due to mortality and the difficulty in identifying some of the fish again, however, only 124 (31 trials) of the original 256 fish could be included in the second set of trials. Hence, a failure in finding even one of the original fish prevented the trial from being repeated. All experimental procedures were conducted as in the first set of trials, however, the fish were not marked again. Water temperature during the experiment varied between 3·1 and 4·5° C (mean 3·9° C).

During both sets of trials, behavioural observations were made twice a day (0800 and 1600 hours) on sequential days. One observation period lasted for 30 min. As food stimulates aggressive behaviour (Newman, 1956) the fish were fed at the beginning of each observation period (the same food pellets as in the holding tanks). Food was provided in excess, and the fish were not fed outside the observation period. The pellets were provided in a circular floating plastic frame (diameter 80 mm), which prevented the pellets from running through the outlet and ensured that the food was always provided at the same spot. The number

of aggressive behaviours (nip, charge, chase, lateral display, frontal display and approach; Keenleyside & Yamamoto, 1962) and food items eaten by each individual fish were recorded. Most frequently observed behaviours were approach, charge, nip and chase. Approach is a mild threat with slow swimming towards another fish. The approaching fish does not go too close to the other fish, whereas charge is more rapid and more serious threat, including fast swimming towards another fish and can end in a nip (bite). Chase is a repeated charge. Approach and charge, which were the least costly and risky behaviours, were classified as mild aggressions. Nip, chase, frontal display and lateral display were more costly behaviours (chase), required physical contact (nip) or took place in actual fighting, where both fish were motivated to fight (lateral and frontal displays). An observer sitting still at a distance of 1 m from the aquarium recorded the behaviour. Mean number of aggressions and foraging (number of food items eaten) per 30 min observation period was calculated for each fish and used later in the analysis.

DETERMINING THE DOMINANCE RANK

Dominance rank of the four fish (ranks 1 to 4) was determined exclusively on the basis of their aggressiveness. Aggressiveness has been used as an indicator of dominance in several studies (Holtby *et al*., 1993; Nakano, 1995) and is considered as a reliable measure of dominance in salmonids (Metcalfe *et al*., 1989; Bailey *et al*., 2000).

At the end of each observation day, the dominant individual in each trial was determined based on the number of performed aggressions. An individual was regarded as dominant, if it (1) performed most aggressions towards other fish, and also responded aggressively in encounters where aggressions were directed towards itself, or (2) if it could perform aggressions towards others without receiving any. In the rare cases where the fish classified dominant under (1) and (2) was not the same individual, the one that performed most aggressions towards the other fish was classified as dominant. The dominant fish was removed from the trial and the procedure was repeated during the following days until only one fish was left, thereby ranking fish from dominance rank 1 (dominant) to 4 (subordinate). In cases where dominance remained uncertain for some fish, however, the maximum duration of each trial was set to 6 days and, consequently, the observation period per trial varied from 3 to 6 days. Those ($n = 33$) fish that showed no aggressive behaviour during the first behavioural trial were excluded from the later analyses. This was done, as the ranking of these fish is difficult and non-aggressive fish are not always subordinate. Höjesjö *et al*. (2002) showed that non-aggressive *S. trutta* could grow as fast as dominants, and faster than subordinates, which grew at slower rate.

GROWTH

Individual growth rates were monitored for all populations from the date they entered the behavioural trials (between 14 September and 29 October 1998) until April 1999. The first size measurement (L_T and M) for each fish was done just before it entered the behavioural trials. In between the measurements, the fish were kept in population-specific standard hatchery tanks (200 fish per tank). The specific growth rate (G, % day^{-1}) for individually known fish was calculated according to Jobling (1994): $G = 100[(\ln M_2 - \ln M_1)T^{-1}]$, where M_1 is the body mass at the start of the behavioural trial and M_2 is the body mass either in January 1999 (growth 1) or in April 1999 (growth 2), and T is the length of the growing period in days, calculated individually for each fish. The tail clips (and also cold brands) healed quite quickly: in January 1999 only 71·5% of the study fish were recognizable for the re-measurements. To be able to recognize the fish in the following spring the fish were re-marked in January 1999 with passive integrated transporter tags (PIT; length 12 mm, diameter 2 mm). Tags were placed inside the body cavity of anaesthetized fish.

ETHICAL NOTE

Aggression among individuals did not result in physical damage, and in general, escalated (fierce) fights were very rare in the experiment. Fish were properly anaesthetized before being marked with cold-branding and tail clipping, and unnecessary stress was avoided. Marking with two methods was done because the cold-brand mark, which was necessary for recognizing the fish in later measurements, was not visible enough in the aquarium to allow individual recognition. Cold branding is a commonly used marking method in fish hatcheries (Bourgeois *et al.*, 1987), and it is a good way for individual marking when the fishes are too small to be, for example, marked with PIT-tags. The fish are marked with a small mark to the skin using liquid nitrogen. The equipment includes a tank with liquid nitrogen that is used to make a small (2×2 mm) stick of iron cold. The cold stick is pressed lightly to the skin of the fish for *c.* 2 s leaving a tiny mark in the skin. The procedure is very quick, and does not stress the fish for long. No infection or diseases were found in any of the fish in the marked area. Irritation in the marked area was not observed, nor was there any mortality in the experiment due to marking. The fish recovered from the anaesthetic within $1-3$ min of the marking and were left to recover from the anaesthetic in smaller containers approximately for an hour before placing them in the experimental aquaria. The fish were observed eating in the following day of the marking, indicating that they had recovered from the anaesthetic. In the dominance trials two fish died when they jumped out of the experimental aquarium.

STATISTICAL ANALYSES

The effect of the dominance rank on subsequent growth was analysed with linear mixed model, using G as the dependent variable. Dominance rank was used as a fixed factor and L_T (in the beginning of the experiment) as covariate. The population term was fitted in the model as a random factor by using restricted maximum likelihood (REML) estimation. Hatchery background and the migration form (lake-run, sea-run or resident) were included also in the initial analyses in the model as fixed factors, however they did not have any significant effects on G and were not included in the final models. Separate analyses were run for ranks determined in September 1998 (first dominance trial) and in April 1999 (second dominance trial). All linear modelling was done with Proc Mixed in SAS (version 8·02; www.sas.com). The stability of the dominance ranks measured was tested with a χ^2 test of independence.

RESULTS

The fish differing in their dominance status in first trial differed in their subsequent G after 7 months in April 1999 [Fig. 1(b) and Table I(b)]. In January 1999, however, there were no significant differences among the ranks [G_1; Fig. 1(a) and Table I(a)]. Specifically, the fish ranked as number one (dominants) (Tukey $P < 0·05$) and number two (Tukey, $P < 0·01$) had higher G_2 compared with the fish ranked as number four [Fig. 1(b)]. The result of second dominance trial was reflected already in G measured in January [G_1; Table I(a)], where ranks one (Tukey, $P < 0·05$) and two (Tukey, $P < 0·05$) and three (Tukey, $P < 0·05$) had significantly higher growth compared with rank four [Fig. 1(c)]. Similarly, the result of second dominance trial was clearly influenced by the G measured in April 1999 (G_2); ranks one (Tukey, $P < 0·05$), two (Tukey, $P < 0·01$) and three (Tukey, $P < 0·05$) had significantly higher growth compared with rank four [Fig. 1(d)].

The second dominance rank determined in April 1999 was not independent from the rank determined 9 months earlier (χ^2, d.f. $= 9$, $P < 0·01$; Table II). Fish ranked
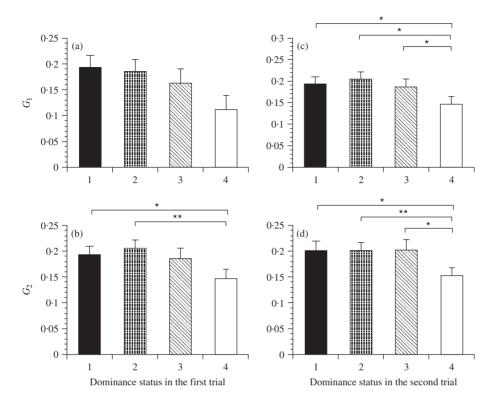
FIG. 1. Least-squares mean ± S.E. growth rates (G) (a) measured in January 1999 (G_1) and (b) in April 1999 (G_2) of *Salmo trutta* of different ranks (1 to 4) in the first dominance trial done in the autumn, and (c) measured in January 1999 (G_1) and (d) in April 1999 (G_2) of the fish of different ranks (1 to 4) in the second dominance trial, done in April 1999. Significance of the pair-wise differences between the ranks is marked as follows: *, $P < 0.05$, **, $P < 0.01$.

as subordinates (rank four) performed rather similarly in the second set of trials as in the first trials: the fish ranked as number four in the first trials, which were more often than expected found to be ranked number four also in the second trials, obtained the highest χ^2 values (Table II and Fig. 2). More fish than expected ranked as second in the first trials were ranked as third (Table II and Fig. 2) in the second round. Fewer four rank fish than expected entered the third rank in the second set of trials. In general, fish ranked as first tended to stay in the two highest ranks in the second set of trials, fewer number ones than expected were observed as ranked subordinates (Table II and Fig. 2). In the first dominance trials the fish were all size matched, but even in the second trial no difference was observed in M or L_T of the fish (M ANOVA, $F_{3,79}$, $P > 0.05$; L_T $F_{3,79}$, $P > 0.05$; Fig. 3).

To get more insight in to the dominance relations of the *S. trutta* the three first ranks from the first experiment were combined and tested for the independency of only two ranks (*i.e.* ranks one to three and four). Ranks determined in the second trial were found to be highly dependent on the ranks in the first trial (χ^2, d.f. = 1, $P < 0.001$) indicating that the stability of the dominance ranks primarily depended on the low likelihood of the subordinate fish entering any of three higher ranks, and *vice versa* (Fig. 2).

TABLE I. The *F*-statistics for the linear mixed effects models where the response variables specific growth rate (G) (a) G_1 and (b) G_2 were tested for the fixed effects first trial (dominance rank of the first trial), second trial (dominance rank of the second trial) and total length (L_T) of the fish in the beginning of an experiment, while population was used as random factor

(a)

G_1				
Fixed effects	Numerator d.f.	Denominator d.f.	F	P
Rank in first trial	3	72·9	2·48	> 0.05
L_T	1	61	33·24	$< \mathbf{0.001}$
Random effects		Z		P
Population		0·90		>0.05
Fixed effects	Numerator d.f.	Denominator d.f.	F	P
Rank in second trial	3	71·9	3·46	$< \mathbf{0.05}$
L_T	1	49·3	33·63	$< \mathbf{0.001}$
Random effects		Z		P
Population		0·63		>0.05

(b)

G_2				
Fixed effects	Numerator d.f.	Denominator d.f.	F	P
Rank in first trial	3	72·7	2·84	$< \mathbf{0.05}$
L_T	1	68·6	20·19	$< \mathbf{0.001}$
Random effects		Z		P
Population		1·12		>0.05
Fixed effects	Numerator d.f.	Denominator d.f.	F	P
Rank in second trial	3	71·6	3·44	$< \mathbf{0.05}$
L_T	1	67·6	19·40	$< \mathbf{0.001}$
Random effects		Z		P
Population		1·07		>0.05

Z, Wald Z-test.

DISCUSSION

The dominance hierarchy of *S. trutta* was shown to affect their subsequent growth rate at least 8 months following the initial dominance trial. The fish in the lowest position in the dominance hierarchy (rank four) grew less compared to fish of the higher ranks. In January 1999, G of different dominance ranks did not differ, however, by April 1999, G of both higher ranks (one and two) differed significantly from rank four. Thus the difference between G of ranks one and four appeared during the growth period from January 1999 to April 1999. Spring is usually a period of rapid growth, and this probably accelerated the growth differences between dominants and subordinates. The second dominance hierarchy clearly reflected the G of the individuals; fish reaching higher status grew more than lowest ranked fish.

Dominance status in the present study was determined among four fish per aquarium; however, during the growth period the fish were kept in large tanks with large group size, *i.e.* in an environment differing from the setting where the relative competitive ability was determined. In addition, the amount food was

TABLE II. Observed (O) and expected (E) frequencies and cell χ^2 values of different dominance ranks 1, 2, 3 and 4 ($n = 83$) in the repeated experiment 2 compared to experiment 1

	1 (experiment 2)	2 (experiment 2)	3 (experiment 2)	4 (experiment 2)
1 (experiment 1) O	8	11	3	4
E	5·33	7·83	4·39	8·46
χ^2	1·34	1·28	0·44	2·35
2 (experiment 1) O	3	6	8	7
E	4·92	7·23	4·05	7·81
χ^2	0·75	0·21	3·86	0·08
3 (experiment 1) O	4	5	3	4
E	3·28	4·82	2·70	5·20
χ^2	0·16	0·01	0·03	0·28
4 (experiment 1) O	2	3	0	12
E	3·48	5·12	2·87	
χ^2	0·63	0·88	2·87	7·57

unlimited, which may even out any stronger effects of individual competitive ability and decrease the advantage of dominance. Despite these factors, this short-term estimation of dominance had significant effect on subsequent growth. The results suggest that the short-term dominance determinations done among few conspecifics can also reflect the individual's overall competitive ability even within the context of a larger social group.

Lower growth rate for subordinates has also been found in other studies. In studies conducted with Atlantic salmon *Salmo salar* L. and rainbow trout *Oncorhynchus mykiss* (Walbaum), subordinates were found to grow slower than dominants (Metcalfe, 1986, Metcalfe *et al.*, 1989, 1992). Similarly to the present study, dominance in these experiments was screened in simplified arenas and growth rate was measured after a period spent in larger holding tanks. Also subordinate *S. trutta*, tested for dominance in the laboratory, had lower subsequent growth performance in natural stream (Höjesjö *et al.*, 2002). On the other hand, *S. alpinus* (L.) juveniles, which were subordinates in behavioural experiments done in small tanks, did not have lower growth rate when housed in larger tanks (Adams & Huntingford, 1996). In another study with *S. alpinus*, however, the fish with the lowest ranks (7 to 10) had lower growth rate as compared to higher ranks (Cutts *et al.*, 2001).

Why do subordinates have poorer growth performance in an environment where food is not a limiting factor? Subordinate individuals are known to suppress feeding, aggression and activity; this general behavioural inhibition is often a result of chronic stress in unpredictable and potentially dangerous situations (Øverli *et al.*, 1998; Höglund *et al.*, 2001). Behavioural effects of social defeat have shown also to decrease reproductive behaviour (D'Amato, 1988) and increase submissive and defensive behaviours towards other individuals (Blanchard *et al.*, 1993; Hsu *et al.*, 2006). Social stress for subordinates is probably prolonged in captivity as the escaping possibilities are limited (Øverli *et al.*, 1999). It is difficult, however, to determine if a physiological response is cause or a consequence of the observed behaviour.
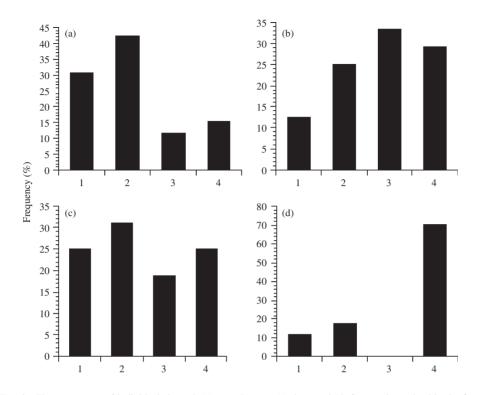
FIG. 2. The percentage of individuals in rank (a) one, (b) two, (c) three and (d) four as determined in the first dominance trials in relation to their rank in the second set of trials.
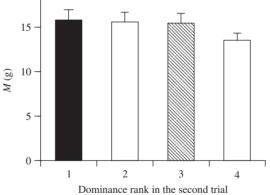

FIG. 3. The mean + S.E. body mass (M) of the fish of different dominance ranks (1 to 4) in the second dominance trial.

The dominance hierarchy among the four fish in the repeated trials was found to be rather stable. Among the fish with the extreme ranks, the dominants tended to hold their high rank while the ones lowest in the hierarchy were more likely to be losers also in the second set of trials. This result is reflected also in their growth performance, which was significantly lower for subordinates compared with other

ranks. Stable dominance over longer time periods has also been found in *S. alpinus* (Cutts *et al*., 2001) and in blackbirds *Turdus merula*, where competitive ability was measured over 2–4 years (Cresswell, 2001).

There are at least two possible explanations for a dominance hierarchy to persist in two repeated experiments separated by a period of up to 8 months spent in a different social environment. Firstly, fish may recognize each other again when reunited in the second round, and remember either the good or bad success in that particular situation, which then affects their subsequent behaviour (Griffiths & Ward, 2006). Secondly, and most likely, the status reached among the four fish actually reflects an individual's stable competitive ability. This hypothesis is strengthened by the fact that the most probable reason for the two hierarchies to be correlated is that in the second trial the subordinate fish were smaller in size due to the difference in *G* between the ranks. As size in an important determinant of dominance, the small low-ranking fish were more likely to end up as subordinates. Even though the effect of earlier memory cannot be ruled out, as the fish of different status differed in their later growth performance, it can be concluded that the short-term relative status reflects individual's stable competitive ability.

To conclude, the dominance hierarchy determined in aquariums among four fish seems to reflect not only relative but also the absolute status of the fish. This was supported by the different growth performance, measured in another environment, by fish differing in their short-term social status, and was also reflected in the stability of the dominance hierarchy between two dominance trials separated by 8 months.

References

Adams, C. E. & Huntingford, F. A. (1996). What is a successful fish? Determinants of competitive success in Artic charr (*Salvelinus alpinus*) in different social contexts. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 2446–2450.

Bailey, J., Alanärä, A. & Brännäs, E. (2000). Methods for assessing social status in Arctic charr. *Journal of Fish Biology* **57**, 258–261. doi:10.1006/jfbi.2000.1303

Blanchard, D. C., Sakai, R. R., Mc Ewen, B. & Weiss, S. M. (1993). Subordination stress: behavioral, brain and neuroendocrine correlates. *Behavioral Brain Research* **58**, 113–121.

Bourgeois, C. E., O'Connell, M. F. & Scott, D. C. (1987). Cold-branding and fin-clipping Atlantic salmon smolts on the Exploits River, Newfoundland. *North American Journal of Fisheries Management* **7**, 154–156.

Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology and Evolution* **16**, 491–497.

Cresswell, W. (2001). Relative competitive ability does not change over time in blackbirds. *Journal of Animal Ecology* **70**, 218–227.

Cutts, C. J., Adams, C. E. & Cambell, A. (2001). Stability of physiological and behavioural determinants of performance in Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 961–968.

Cutts, C. J., Metcalfe, N. B. & Taylor, C. (2002). Juvenile Atlantic salmon (*Salmo salar*) with relatively high standard metabolic rates have small metabolic scopes. *Functional Ecology* **16,** 73–78.

D'Amato, F. R. (1988). Effects of male social status on reproductive success and on behaviour in mice (*Mus musculus*). *Journal of Comparative Psychology* **102,** 146–151.

Eijke, C. & Schreck, C. (1980). Stress and social hierarchy rank in coho salmons. *Transactions of the American Fisheries Society* **109,** 423–426.

Griffiths, S. W. & Ward, A. (2006). Learned recognition of conspecifics. In *Fish Cognition and Behaviour* (Brown, C., Laland, K. & Krause, J. ed), pp. 139–157. Cambridge: Blackwell Publishing.

Höjesjö, J., Johnsson, J. I. & Bohlin, T. (2002). Can laboratory studies on dominance predict fitness of young brown trout in the wild? *Behavioral Ecology and Sociobiology* **52,** 102–108.

Holtby, L. B., Swain, D. P. & Allan, G. M. (1993). Mirror-elicited agonistic behaviour and body morphology as predictors of dominance status in juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 676–684.

Hsu, Y., Earley, R. L. & Wolf, L. L. (2006). Modulating aggression through experience. In *Fish Cognition and Behaviour* (Brown, C., Laland, K. & Krause, J., eds), pp. 96–113. Cambridge: Blackwell Publishing.

Huntingford, F. A. & Turner, A. K. (1987). *Animal Conflict.* London: Chapman & Hall.

Huntingford, F. A. & García de Leániz, C. (1997). Social dominance, prior, residence and the acquisition of profitable feeding sites in juvenile salmon. *Journal of Fish Biology* **51,** 1009–1014. doi:10.1111/j.1095-8649.1997.tb01539.x

Huntingford, F. A, Metcalfe, N. B., Thorpe, J. E., Graham, W. D. & Adams, C. E. (1990). Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology* **36,** 877–881.

Höglund, E., Kolm, N. & Winberg, S. (2001). Stress induced changes in brain serotogenic activity, plasma cortisol and aggressive behaviour in Arctic charr (*Salvelinus alpinus*) in counteracted by L-Dopa. *Physiology and Behaviour* **74,** 381–389.

Jobling, M. (1994). *Fish Bioenergetics.* London: Chapman & Hall.

Johnsson, J. I. & Björnsson, B. Th. (1994). Growth hormone increases growth rate, appetite and dominance in juvenile rainbow trout, *Onchorhynchus mykiss*. *Animal Behaviour* **48,** 177–186.

Johnsson, J. I., Nöbbelin, F. & Bohlin, T. (1999). Territorial competition among wild brown trout fry: effects of ownership and body size. *Journal of Fish Biology* **54,** 469–472. doi:10.1111/j.1095-8649.1999.tb00846.x

Keenleyside, M. H. & Yamamoto, F. T. (1962). Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour* **19,** 139–169.

Lahti, K., Laurila, A., Enberg, K. & Piironen, J. (2001). Variation in aggressive behaviour among populations and migration forms in brown trout (*Salmo trutta*). *Animal Behaviour* **62,** 935–944.

Martin-Smith, K. M. & Armstrong, J. D. (2002). Growth rates of wild stream-dwelling Atlantic salmon correlate with activity and sex but not dominance. *Journal of Animal Ecology* **71,** 413–423.

Metcalfe, N. B. (1986). Intraspecific competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *Journal of Fish Biology* **28,** 525–531.

Metcalfe, N. B., Huntingford, F. A., Graham, W. D. & Thorpe, J. E. (1989). Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society B* **236,** 7–19.

Metcalfe, N. B., Wright, P. J. & Thorpe, J. E. (1992). Relationships between social status, otolith size at first feeding and subsequent growth in Atlantic salmon (*Salmo salar*). *Journal of Animal Ecology* **61,** 585–589.

Metcalfe, N. B., Taylor, A. C. & Thorpe, J. E. (1995). Metabolic rate, social status and life-history strategies in Atlantic salmon. *Animal Behaviour* **49,** 431–436.

Nakano, S. (1995). Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *Journal of Animal Ecology* **64,** 75–84.

Neat, F. C., Taylor, A. C. & Huntingford, F. A. (1998). Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. *Animal Behaviour* **55,** 875–882.

Newman, M. A. (1956). Social behaviour and interspecific competition in two trout species. *Physiological Zoology* **29,** 64–81.

Øverli, Ø., Winberg, S., Damsgård, B. & Jobling, M. (1998). Food intake and spontaneous swimming activity in Arctic charr (*Salvelinus alpinus*): role of brain serotonergic activity and social interactions. *Canadian Journal of Zoology* **76,** 1366–1370.

Øverli, Ø., Harris, C. A. & Winberg, S. (1999). Short-term effects of fights for social dominance and the establishment of dominant-subordinate relationships on brain monoamines and cortisol in rainbow trout. *Brain, Behaviour and Evolution* **54,** 263–275.

Øverli, Ø., Korzan, W. J., Höglund, E., Winberg, S., Bolling, H., Watt, M., Forster, G. L., Barton, B. A., Øverli, E., Renner, K. J. & Summers, C. H. (2004). Stress coping style predicts aggression and social dominance in rainbow trout. *Hormones and Behaviour* **45,** 235–241.

Pusey, A., Williams, J. & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science* **277,** 828–831.

Ruzzante, D. E. & Doyle, R. W. (1993). Evolution of social behaviour in a resource-rich, structured environment: selection experiments with medaka (*Oryzias latipes*). *Evolution* **47,** 456–470.

Sundström, L. F., Petersson, E., Höjesjö, J., Johnsson, J. I. & Järvi, T. (2004). Hatchery selection promotes boldness in brown trout (*Salmo trutta*): implications for dominance. *Behavioural Ecology* **15,** 192–198.

Tiira, K., Laurila, A., Peuhkuri, N., Piironen, J., Ranta, E. & Primmer, C. R. (2003). Aggressiveness is associated with genetic diversity in landlocked salmon (*Salmo salar*). *Molecular Ecology* **12,** 2399–2407. doi:10.1046/j.1365-294X.2003.01925.x

Tiira, K., Laurila, A., Enberg, K., Piironen, J., Aikio, S., Ranta, E. & Primmer, C. R. (2005). Do dominants have higher heterozygosity? Social dominance and genetic variation in brown trout, *Salmo trutta*. *Behavioural Ecology and Sociobiology* **59,** 657–665.

Vøllestad, L. A. & Quinn, T. P. (2003). Trade-off between growth rate and aggression in juvenile coho salmon, *Oncorhynchus kisutch*. *Animal Behaviour* **66,** 561–568.

Ward, A. J., Webster, M. M. & Hart, P. J. B. (2006). Intraspecific food competition in fishes. *Fish and Fisheries* **7,** 231–261. doi: 10.1111/j.1467-2979.2006.00224.x

Winberg, S. & Lepage, O. (1998). Elevation of brain 5-HT activity, POMC expression, and plasma cortisol in socially subordinate rainbow trout. *American Journal of Physiology* **43,** R645–R654.