



Are there physiological correlates of dominance in natural trout populations?

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Competition over limited resources can lead to serious injury and may be minimized by the formation of social hierarchies. However, there are often physiological consequences associated with social status which can affect both dominant and subordinate animals. In salmonid fish, at least under laboratory conditions, physiological costs are mainly associated with subordination. The structure of hierarchies formed among salmonids in the laboratory is likely to be different from those formed in complex natural environments, and yet little is known about the physiological consequences of dominance in the field. We tested the hypothesis that there are specific physiological correlates associated with specific social behaviours among natural populations of juvenile salmonid fish by observing brown trout, *Salmo trutta*, in small streams. Fish were tagged and their behaviour observed by video recording over several weeks at three sites along Devonport Leat (Devon, U.K.). Although diet and tissue metal concentrations differed between sites, the behaviour of the fish at the three sites was very similar. At the end of the observation period, we sampled fish for parameters including specific growth rate, plasma cortisol and osmolality, brain monoamines and gut contents. There was no relationship between social status and growth rates but, contrary to laboratory predictions, dominant fish had higher plasma cortisol. We conclude that physiological correlates of dominance do exist among these natural fish populations but they may differ to those found in the laboratory. Further research is now required to test a wider range of physiologies in the field.

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The production of a large number of offspring in a resource-limited environment exerts a selective force over developing salmonid fish, with only those able to compete efficiently being able to survive the first few months of life. Among salmonid populations, competition for food, shelter and mates can result in the formation of dominance hierarchies, usually through successive dyadic encounters within a social group network (Chase et al.

2003). Hierarchies formed within populations of stream-dwelling salmonid fish may remain stable for long periods of time (Bachman 1984; Abbott et al. 1985) suggesting potential benefits for population survival. The stability associated with dominance hierarchy formation is likely to benefit both dominant and subordinate animals through a reduction in costly fighting compared to unstable systems (Gurney & Nisbet 1979; Bachman 1984). Stable hierarchies may also reduce predation risk by increasing vigilance (Griffiths et al. 2004).

Dangerous fighting may be minimized by social hierarchies but physiological costs are often associated with the resulting social status (Sloman & Armstrong 2002). Under laboratory conditions, physiological costs of social status can affect both dominant and subordinate fish but have mainly been associated with subordination. Interactions between dyads of fish elicit chronic changes in subordinates, including elevation of the stress hormone cortisol

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in the blood plasma (Fox et al. 1997; Øverli et al. 1999; Sloman et al. 2001a), increased susceptibility to disease (Peters et al. 1988; Pottinger & Pickering 1992), increased brain serotonergic activity (Øverli et al. 1998, 1999; Winberg & Lepage 1998), increased sodium turnover (Sloman et al. 2004) and decreased growth rates (Abbott & Dill 1989; Sloman et al. 2000). Additionally, subordinate fish may be more susceptible to certain waterborne aquatic toxicants (Sloman 2007); subordinate rainbow trout, *Oncorhynchus mykiss*, accumulate more copper and silver during waterborne exposure (Sloman et al. 2002, 2003). Among groups of fish in the laboratory environment, subordination is also associated with higher plasma cortisol, higher adrenocortical activity and lower hepatic glycogen content (Boddingius 1976; Ejike & Schreck 1980; Scott & Curie 1980). In dominant fish, physiological costs include an initial transitory elevation of plasma cortisol during paired encounters, although this normally declines subsequently in contrast to subordinate fish (Øverli et al. 1999), and increased susceptibility to dietary contaminants (Campbell et al. 2005).

Hierarchies formed under laboratory conditions may, however, be very different to those formed in more complex environments which allow more diverse behavioural strategies (Milinski & Parker 1991). While correlates of social status have been found among groups of fish held in seminatural environments (Li & Brocksen 1977; Noakes & Leatherland 1977; Sloman et al. 2000), the physiological consequences of social status in the natural environment are largely unknown. Within seminatural environments, linear relationships between physiological correlates and behaviour may break down; Sloman et al. (2000) found that second-ranking fish within groups of four brown trout had significantly lower growth rates than all the other ranks of fish. Growth is one of the few parameters that has been measured in the field but to date studies have yielded conflicting results. Dominant red-spotted masu salmon, *Oncorhynchus masou ishikawai*, living within mountain stream pools have higher growth rates (Nakano 1995), but growth does not correlate with social status in Atlantic salmon, *Salmo salar*, living in riffle areas of natural streams (Martin-Smith & Armstrong 2002). Additionally, Harwood et al. (2003) found no evidence for a relationship between growth and dominance rank in Atlantic salmon living in a natural stream but this is in contradiction with the results obtained by Höjesjö et al. (2002) in young stream-dwelling brown trout, *Salmo trutta*.

It is likely that when food sources are predictable, for example in mountain stream pools, the costs associated with monopolization of resources are small and the growth benefits of dominance become apparent (Harwood et al. 2003). However, if food becomes spatially and temporally variable, for example in stream riffles, then the cost of monopolization may increase. Elevated energy expenditure associated with dominance has been documented in the laboratory (Metcalfe 1986; Cutts et al. 2001) and may explain why under less predictable conditions no growth benefits of dominance are seen (Höjesjö et al. 2004). Additional complexities associated with the natural environment include the presence of predators and interspecific competition both of which can influence

the functioning of dominance hierarchies (Martel & Dill 1993; Harwood et al. 2002). In addition, physical structure may affect the relative payoff from dominant/subordinate strategies (Höjesjö et al. 2004). Therefore, to further our understanding of how social behaviour interacts with physiology, more studies are required in the natural environment (Johnsson et al. 2006) using other physiological correlates which may be more indicative than growth of immediate costs of social status.

Within the Dartmoor National Park, Devon, U.K., natural brown trout populations inhabit a series of man-made watercourses, known as leats, some of which date back to the 16th century. These leats are now akin to natural streams and are relatively shallow in places making it possible to record fish behaviour from above with video cameras. One of the primary reasons for the construction of Dartmoor leats was to provide power for mining activities, which persisted on Dartmoor until the 20th century, and so there is also the potential for fish inhabiting these leats to be exposed to elevated trace metal concentrations, some of which are known to correlate well with social rank under laboratory conditions (Sloman et al. 2002, 2003). To determine whether there are physiological correlates of dominance in natural brown trout populations, we chose three sites along Devonport Leat with the aim of observing existing dominance hierarchies. The hypotheses being tested were that there would be measurable physiological correlates of social behaviour and that position in a social hierarchy may affect uptake of waterborne trace metals.

METHODS

We studied the behaviour of wild brown trout at three sites on the Devonport Leat within the Dartmoor National Park, Devon, between 12 May and 21 August 2006. Devonport Leat receives its water from the three Dartmoor river systems, the West Dart River, Cowsic River and Blackbrook River. Site 1 was an 11 m stretch of leat (width $\bar{X} \pm \text{SE} = 1.45 \pm 0.03$ m; depth: 20 ± 1.0 cm) located within a coniferous plantation, with sparse vegetation along the banks. At this point the leat consisted of a gravel bottom with some large rocks (range 5–12 cm in diameter, occupying <20% of the riverbed area in total) throughout its length, and very little vegetation. Sites 2 (length: 11 m; width: 1.53 ± 0.04 m; depth: 25.0 ± 1.4 cm) and 3 (length: 11 m; width: 1.53 ± 0.05 m; depth: 21.2 ± 1.2 cm) were sequentially downstream of site 1 but situated in open farmland. The distance between sites 1 and 3 was approximately 1 km, with site 2 situated in between. Preliminary studies showed that the juvenile brown trout inhabiting this leat generally remained within a 10 m range. The vegetation along the banks of sites 2 and 3 was more plentiful than at site 1 and consisted of grasses, reeds and thistles, with some vegetation overhanging the water. As at site 1, the leat at sites 2 and 3 consisted of an approximately flat gravel bottom but additionally had a patchy distribution of vegetation within the leat itself.

At each site, we removed all brown trout by electric fishing using a pulsed DC unit (Safari Research Surveyor,

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