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ABSTRACT

Changes in environmental conditions affect social interactions and thus may modify an individual's competitive ability within a social group. We subjected three-spined sticklebacks, Gasterosteus aculeatus, housed in groups of four individuals, to environmental perturbations to assess the impact on dominance hierarchy stability. Hierarchy stability decreased during increased turbulence or lowered water levels ('simulated drought') whereas control hierarchies became more stable in a constant environment. The dominant individual either became more aggressive and remained dominant during the environmental manipulation or was usurped by a lower rank member. Only simulated drought affected rates of aggression where levels of aggression were higher after the water level was dropped which may be the result of an increased encounter rate in these conditions. When there were large size differences between the group members, the dominant individual performed the greatest amount of aggression and ate the largest proportion of food and there was little aggressive behaviour from the lower ranks. In groups of similar-sized individuals, aggression was much higher. The benefit of being dominant was to gain weight over the experimental period whereas ranks 2 and 3 lost weight. The lowest rank, 4, actually gained weight over the experimental period. This study suggests that it would benefit an individual to be dominant, highly aggressive and gain weight or be submissive, avoid aggressive interactions and, by sneakily obtaining access to food, also gain weight. Altering environmental conditions has a profound effect on social behaviour in this study.

Introduction

The prevalence of dominant–subordinate relationships in animal societies suggests that there is an adaptive significance to achieving a high rank when in a group (Huntingford & Turner 1987). Functional explanations have focused on access to resources such as food or mates (e.g. Postin 1997; Basquill & Grant 1998). Competition by overt aggression may be extremely costly, possibly causing fatal injury, enhanced predation risk, greater energy expenditure or stress leading to increased susceptibility to pathogens (Huntingford & Turner 1987). Rather than costly fighting, contests tend to involve ritualized displays allowing assessment of competitor's ability. A classic example of an assessment display is the roaring and parallel walk of rutting red deer stags (Cervus elaphus; Payne 1998). The ability to form or establish stable dominance hierarchies is an evolutionary 'solution' to competition for resources among conspecifics. 'Knowing your place' in a pecking order allows individuals to avoid both costly fights and the use of costly assessment signals (Barnard & Burk 1979; Sirot 2000). Individuals should be aggressive if they do not know a conspecific's rank position (unfamiliar or unsettled rank position) until the ranks have been settled (Tindo & Dejean 2000; Utne-Palm & Hart 2000). Once an individual recognizes a conspecific's rank (e.g. when foraging with familiar fish, Gasterosteus aculeatus, Utne-Palm & Hart 2000) or when the ranks are settled (Tindo & Dejean 2000) overt aggression may not be necessary.

The investigation of dominance hierarchies can be useful in studies of social behaviour as this allows the prediction of a variety of social outcomes including the distribution of resources such as food, shelter and access to mates (Richards 1974). In general, the distribution of agonistic behaviour between individuals has been accepted as the most useful criterion for measuring dominance as dominance is a property of all interactions between individuals in a group. A dominant animal may be thought of as one whose behaviour is not limited by others, while a subordinate is limited by the action of others and this has wide implications on the behavioural strategies adopted by animals of different social status (Deag 1977).

Recent research has suggested that hierarchies are not stable when environmental conditions are altered. There has been a focus on interspecific dominance and ecological change. However, intraspecific competition will by its very nature be more intense as generally animals within one population congregate in preferred habitats and compete for the same resources (Mayer & Berger 1992). The resulting dominance hierarchies within species should be affected by differing environmental conditions. Habitat quality has been shown to affect the nature of dominance hierarchies in several species (Pruetz & Isbell 2000). When food patches were widely dispersed, aggression levels were low and dominance hierarchy structure was unstable, which is in contrast to the highly aggressive and stable hierarchies when food patches were few and clumped (Pruetz & Isbell 2000). Relatively few studies have examined the impact of environmental change on intraspecific dominance hierarchies. Sloman et al. (2000) reported that rainbow trout hierarchies, *Oncorhynchus mykiss*, became unstable when water levels were decreased but did not provide information about each individual's response. In brook trout, *Salvelinus fontinalis*, aggressive behaviour and territory size of individuals decreased when water velocity increased (McNicol & Noakes 1984).

Environmental perturbations (or disturbance) are an integral and ubiquitous part of ecological systems (Holling 1973; Neubert & Caswell 1997); therefore, it is vital that these are taken into account when analysing the social behaviour of any species. Most studies on behaviour have been conducted under precise, controlled conditions, which is necessary when addressing functional questions; however, the natural environment is rarely constant. Individuals that may do well in one particular set of environmental conditions may not do so well when conditions change and this affects their probability of survival and possibly overall fitness. Empirical studies have shown that dominant individuals of this species secure more matings, and have offspring with better parasite resistance (Kraak et al. 1999; Barber et al. 2001). This raises the question of how we define the fittest individual within a hierarchy as we would normally identify the dominant as the fittest. However, if the dominant cannot maintain its dominant position when the environment changes, this challenges our assumption that we can use dominance as a fitness correlate. Therefore, it is crucial to understand how altering the environment influences the structure of hierarchies but also what impacts this has on individual behaviour. The present study aims to unravel the effects of ecological changes on the structure, stability and benefits of rank position within a dominance hierarchy using three-spined sticklebacks, *G. aculeatus*, and examine each individual's response to abiotic disturbance. This will provide more detailed information about how each individual is affected by an environmental challenge and what impact this has on the dominance hierarchy. Aquatic species encounter a wide variety of environmental perturbations in the wild and these are easily reproducible in the laboratory aquarium. Outside the breeding season, sticklebacks live in mixed sex shoals and juvenile aggression becomes visible, in laboratory conditions, at 4 wk from hatching (Bakker 1986). Juveniles within groups display agonistic behaviour that is commonly comprised of unilateral attacks or displacements (Wright & Huntingford 1993). This potential for the formation of a dominance hierarchy and the fact that sticklebacks can colonize various habitats, such as ponds, rivers and estuaries, and are subject to a wide variety of environmental disturbances make it a good species for the examination of the impact of ecological change on the stability of the hierarchy and the pay off to individual rank members.

We examined the influence of environmental perturbations, water levels (simulated drought) and turbulence (increased flow within the tank) on the structure and stability of a dominance hierarchy when comparing these with undisturbed hierarchies. Individual response to the ecological variation was assessed to determine the changes in levels of aggression and also foraging rate. These ecological factors may impose different energetic demands upon the individual fish and so individuals may do better or worse in the altered environment and potentially increase or decrease in rank position. The stability of the hierarchy may be disrupted because of changes in performance of each individual. We also determined the benefit of each rank position within the hierarchy in terms of weight change over the experimental period.

Methods

Collection and Maintenance of Animals

Three-spined sticklebacks (*G. aculeatus*, length 31.8–53.7 mm; weight 0.42–2.29 g) were collected twice from Inverleith pond, Edinburgh, between Nov. 1999 and Mar. 2000 using mesh fish traps. This involved using two cohorts within each population and, therefore, there was two size classes used which explains the wide range of sizes used. The fish were transferred to aquaria, chosen at random and put into groups of four and were housed in tanks that were 45 x 30 x 30 cm in size. Each tank (n = 24), had a gravel substratum, was filled with aerated freshwater kept at $12 \pm 1°C$ and had an adjustable internal filter (Interpet, Surrey, UK). We kept the fish on a light–dark cycle of 8:16 h (L:D). This was necessary to maintain the non-breeding condition. Individual fish was identified through marking them with a coloured plastic ring placed over a dorsal spine (blue, yellow, pink, green) which was not related to their rank position (Kruskal–Wallis Test of colour and rank, H = 2.37, df = 3 p = 0.499, n = 96).

We chose the small group size of four to allow more accessible data analysis, although this may not be the most natural group size. We fished different populations using hand nets and minnow traps and found that group size can range from a few individuals to over 20 per catch (pers. obs.). Fish were weighed to the nearest 0.1 g and length measured by standard measurements (excluding caudal fin) to the nearest 0.1 mm before beginning the experiment. These measurements allowed us to calculate size differences for each social group. Group size difference was determined as the weight of the smallest fish divided by the weight of the largest fish in each group (length and weight were highly correlated r = 0.852, p = 0.007 so only weight was used as this was used as a measure of growth during the experiment). Fish were weighed at the end of the completed experiment to investigate any weight change over time, a factor that was also investigated in analysis. Fish were not sexed primarily as it had been observed that the pre-breeding aggressive behavior of male and female sticklebacks is indistinguishable (Huntingford 1979).

Behavioural Observations

A pilot trial was undertaken to ascertain the time taken for a group of four sticklebacks to develop a stable dominance hierarchy. Four tanks of four fish were allowed to settle over a week then observed over 7 d, during two observation periods of 20 min a day. This demonstrated that each experimental group became stable after 4 d. Therefore, in the subsequent experiments described below, the experimental groups were left for 7 d after being transferred to the aquarium, to allow the formation of a hierarchy and then the observations began for a further 14 d.

We made observations twice daily, AM and PM, for 20 min per tank during the light period and the number of agonistic interactions performed during that period was recorded as well as food intake during the PM observations. Agonistic behaviour recorded consisted of attacks and retreats. An attack or chase was defined as an approach by one fish from more than one body length away that could involve physical

contact if the receiver did not retreat before contact was made. A retreat was the direct movement of one fish away from an attacking fish. In some cases the receiver of an attack would not retreat but would attack the attacking fish. This would be recorded as attacks made by both fish. These definitions were similar to those recorded in other studies of different fish species (e.g. Bailey et al. 2000).

In the PM observation, we introduced prey into the middle of the tank at the start of the 20-min trial and the number of prey items eaten by each individual recorded, as well as the agonistic behaviour. The prey were red mosquito larvae, and these were presented in a plastic microtitre plate with one larva in each of the holes on the plate, held in place with vaseline. This method was chosen to make the food clumped and, therefore, defensible as this arrangement of resource patterning contributes to hierarchy formation (Ryer & Olla 1996; Goldberg et al. 2001). This method also enabled the feeding rate to be more accurately noted as the fish were only feeding in one region of the tank. We filled plates with a total of 48 worms available, thereby allowing 12 worms per fish per day.

The order of observations was randomly allocated between the tanks so as to remove any bias or order effect that may have occurred. The data were recorded from each trial by speaking into a dictaphone. The tapes were played back after the observations so that each fish could be scored for the number of attacks, number of retreats and number of prey items eaten. We calculated the dominance score by deducting the number of retreats performed from the number of attacks. This meant an individual making a high number of attacks but receiving few attacks would be scored highly whereas an individual making a low number of attacks and receiving a high number of attacks would have a low score. This method, used in other studies (Hughes 1992; Bailey et al. 2000; Sloman et al. 2000, 2001), gave a score for each individual within a group. The individual with the highest score was the dominant and ranked 1 whereas the individual with the lowest score was ranked 4. Thus a hierarchy could be calculated for each group under the different environmental conditions.

Experimental Manipulations

The experiments consisted of two different treatments that manipulated water level and turbulence. There was also an undisturbed control treatment. Each of the three treatments was applied to eight tanks (n = 24). To control for the effect of the time course of the experiment, four tanks were left in pre-manipulation state for 4 d before the conditions changed for 7 d. The remaining four tanks were left for 7 d prior to changing the conditions for 7 d. This experimental design ensured that any changes in dominance behavior were because of the change in environmental conditions and not simply because of the time course of the experiments (one-way anova comparison of dominance scores obtained before environmental change between tanks held for 4 d and tanks held for 7 d in control conditions, $F_{1,23} = 0.17$, p = 0.684; Table 1). In the water level treatment, the water level was lowered by siphoning off the water via the internal pump so that the outflow ran out of the tank with minimal disturbance to the fish. The depth was reduced from 23.4 to 13 cm over a period of a few minutes. In natural conditions, drought significantly reduces water levels in rivers and ponds (Taniguchi et al. 2004). In the turbulence treatment, we increased turbulence by increasing the filter power to double (from 180 to 360 l/h). This simulated spate which is a result of increased inflow of water into natural water bodies which has been shown to affect the behaviour of fish (e.g. Carlsen et al. 2004). The control groups were not manipulated during the time course of the experiment.

At the end of the experiment each fish was removed from the tank and weighed to determine any weight changes that may have occurred during the experimental procedure. After this the fish were humanely killed by overdose in MS222 (100 mg/l) (MS222, Sigma, Dorset, UK).

Statistical Analyses

To obtain a stability value, we used Kendall's Coefficient of Concordance to test how concordant the dominance score was for each rank within a hierarchy and this gave a coefficient value between 0 and 1 with 0 meaning no stability and 1 meaning totally stable. This was performed using daily dominance score against the average rank of each of the four fish per tank in week 1 and comparing this with week 2. We deducted the coefficient value obtained before the manipulation (first 4 or 7 d) from the value obtained during the manipulation (second 7 d). Therefore, a negative value indicated a reduction in stability and a positive value indicated an increase in stability. For example, one group had a coefficient value of 0.68 before water levels were lowered but afterwards the dominant was deposed and the third rank also lost position (ranks 1, 2, 3, 4 became 2, 1, 4, 3 respectively) giving a much lower coefficient of 0.38. In contrast, in the control, one group had a coefficient of 0.69 and the rank positions did not change over the experimental period (ranks 1, 2, 3, 4 maintained their status) and the coefficient was similar, 0.72, for the second time period. A two-factor anova was used to assess if the coefficient values were significantly different before and after the manipulation and also between treatments.

Table 1: Number of days that the two sets of tanks (1–4 and 5–8) were subject to the experimental manipulations over the course of the experiment

	Water Level		Turbulence		Control	
	High	Low	High	Low	No Change	No Change
Tanks 1-4	4	7	4	7	4	7
Tanks 5-8	7	7	7	7	7	7

A pair of two-factor anovas with one repeated measure (a 'one within and one between' model) were used to determine the effects of disturbance ('before' or 'after' – repeated measure) and the treatment type ('control', 'turbulence' or 'drought') on the rate of food intake and the rate of aggression. The data for these analyses were transformed to give a normal distribution (ln +1). To assess whether there was a relationship between size ratio and level of aggression within each tank we used Spearman rank correlation. This test was also used to assess if there was a relationship between food intake and size ratio.

Each rank member was compared to assess whether absolute size, performance of aggression and food intake was related to dominance position using Kruskal–Wallis tests. The weight change of each rank over the experimental period was compared using a Kruskal–Wallis test.

Results

What Were the Characteristics of Each Rank Position?

The dominant individual was neither the longest (Kruskal–Wallis, $H = 0.28$, df = 3, $p = 0.96$, n = 96) nor the heaviest fish ($H = 0.76$, df = 3, $p = 0.86$, n = 96) within a group. The dominant individual ate the greatest proportion of food (Fig. 1; $H = 97.06$, df = 3, $p < 0.001$, n = 96) and performed the most aggressive acts (Fig. 2; $H = 404.34$, df = 3, $p < 0.001$, n = 96). When comparing the rate of aggression minus defensive (retreats) acts, the second rank performs more aggression than retreats whereas the third and fourth ranks perform more defensive acts than aggressive attacks (Fig. 2).

The dominant individual gained weight over the experimental period, fish ranked 2 and 3 lost weight whereas fish ranked 4, the lowest rank, gained weight (Fig. 3; Kruskal–Wallis, H = 15.21, df = 3, p = 0.002, n = 96).

**Fig. 1:** Mean number (±SD) of food items per minute eaten by each of the four ranks within the dominance hierarchies (n = 24 for each rank)
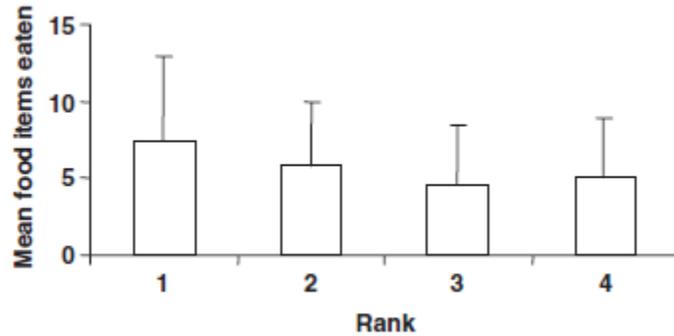
Fig. 2: Mean number (±SD) of aggressive minus defensive acts per minute performed by each rank member within dominance hierarchies (n = 24 for each rank)
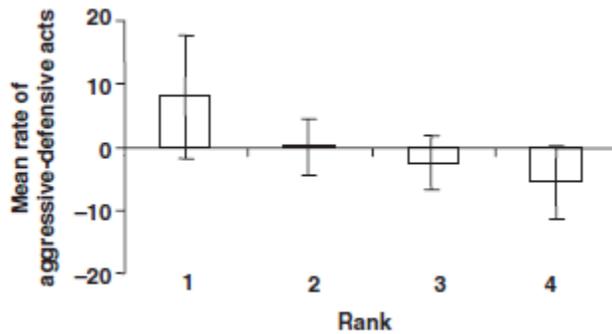
Fig. 3: Mean weight (±SD) change of each rank member over the experimental period (n = 24 for each rank)
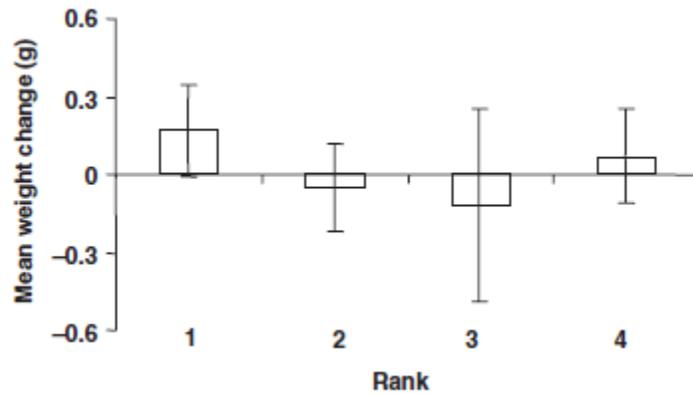
Stability of the Dominance Hierarchy Subject to Environmental Variation

There were changes in the stability of the dominance hierarchies in the three treatment groups when the environmental conditions were manipulated. Kendall coefficients of concordance were calculated before and after treatment and signify stability (Table 2). There was a reduction in stability in the water level and turbulence treatments but hierarchies became more stable in the control treatment (Fig. 4; Two-way anova; before and after effects, $F_{1,18} = 12.11$; $P = 0.001$). However, there was no significant effect between treatments ($F_{2,18} = 2.93$; $P = 0.065$) but there was an interaction between treatment and before and after effects ($F_{2,18} = 5.97$; $P = 0.005$). The dominant individual at the beginning of the experiment was ranked first throughout the experiment in 17 of the 24 tanks (Table 3). In the other seven tanks (four in turbulence, three in water level) the dominant was deposed when the environmental conditions were manipulated (e.g. dominance coefficient in water level went from 0.68 to 0.38 and in turbulence from 0.60 to 0.41 demonstrating a decrease in stability) and this tended to happen when the fish within the group were of a similar size (<10% size difference). Rank changes occurred between ranks 2 and 3 with rank 3 becoming rank 2 after manipulation in seven tanks (three in turbulence, three in water level and one in control treatments). Rank changes occurred between ranks 3 and 4 with rank 4 increasing its rank to 3 in six tanks (two in turbulence, two in water level and two in control treatments). In two tanks, rank 4 became rank 2 and the previous rank 2 dropped to ranks 3 or 4.

Table 2: Kendalls Coefficient of Concordance values for the turbulence, drought and control treatment groups before and after manipulation for each hierarchy within the 24 tanks

Tank	Turbulence		Drought		Control	
	Before	After	Before	After	Before	After
1	0.68	0.38	0.56	0.42	0.50	0.50
2	0.45	0.35	0.66	0.44	0.60	0.71
3	0.69	0.47	0.64	0.40	0.63	0.58
4	0.49	0.29	0.67	0.50	0.53	0.68
5	0.46	0.28	0.58	0.35	0.56	0.70
6	0.58	0.32	0.71	0.53	0.64	0.66
7	0.48	0.34	0.65	0.44	0.69	0.72
8	0.74	0.49	0.60	0.41	0.62	0.69

*Are Aggression Levels and Foraging Affected by the Environmental Changes?*

Aggression levels significantly increased after water levels were lowered to simulate drought ($F_{2,12} = 4.87$, $p = 0.041$). There was no difference in levels of aggression when comparing pre- and post-manipulation aggression in the turbulence ($F_{2,12} = 0.37$, $p = 0.545$) and control treatments ($F_{2,12} = 1.71$, $p = 0.192$). More aggression was performed in the water level treatment when compared with the other two treatments after the environmental conditions were altered (Fig. 5; $F_{2,18} = 4.97$, $p = 0.007$). Mean aggression levels within each group was correlated to the weight ratio between the smallest and largest individuals (Spearman rank, $rS = 0.567$, $p < 0.01$, $n = 24$). When the individuals within a group had a large size

difference, the dominant individual performed the majority of aggressive acts whereas when the groups were of similar size all the ranks performed a more equal proportion of the aggression (Fig. 6). Aggressive acts were performed more in the observations without food present (repeated measures anova, $F_{2,42} = 27.01$, $p < 0.001$).

Table 3: Dominance rank from rank 1 to rank 4 in each tank (n = 8 per treatment) in the days before manipulations occurred (B) and the days following the manipulation (A) for the turbulence, drought and control treatments

Tank	Turbulence			Drought			Control		
	Ratio	B	A	Ratio	B	A	Ratio	B	A
1	0.98	1	2	0.99	1	2	0.95	1	1
		2	4		2	1		2	2
		3	3		3	4		3	4
		4	1		4	3		4	3
2	0.90	1	3	0.91	1	2	0.90	1	1
		2	1		2	1		2	3
		3	2		3	4		3	2
		4	4		4	3		4	4
3	0.93	1	3	0.88	1	2	0.86	1	1
		2	4		2	1		2	2
		3	1		3	3		3	4
		4	2		4	4		4	3
4	0.89	1	3	0.82	1	1	0.75	1	1
		2	1		2	3		2	2
		3	2		3	2		3	3
		4	4		4	4		4	4
5	0.86	1	1	0.77	1	1	0.64	1	1
		2	3		2	3		2	2
		3	2		3	4		3	3
		4	4		4	2		4	4
6	0.77	1	1	0.72	1	1	0.60	1	1
		2	2		2	3		2	2
		3	4		3	2		3	3
		4	3		4	4		4	4
7	0.62	1	1	0.68	1	1	0.58	1	1
		2	2		2	3		2	2
		3	4		3	2		3	3
		4	3		4	4		4	4
8	0.53	1	1	0.60	1	1	0.55	1	1
		2	2		2	2		2	2
		3	3		3	3		3	3
		4	4		4	4		4	4

Fig. 5: Mean rate per minute (_SD) of aggressive acts performed in dominance hierarchies subject to lowered water levels (Water), increased turbulence and for the control groups (n ¼ 8 for each treatment)
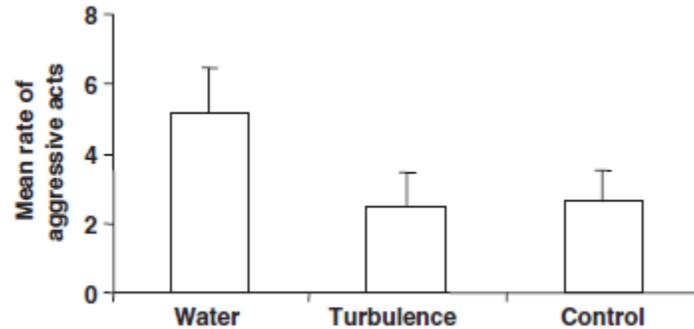
Fig. 6: Mean rates of aggression within each tank showing the relationship between rate of aggression and size ratio
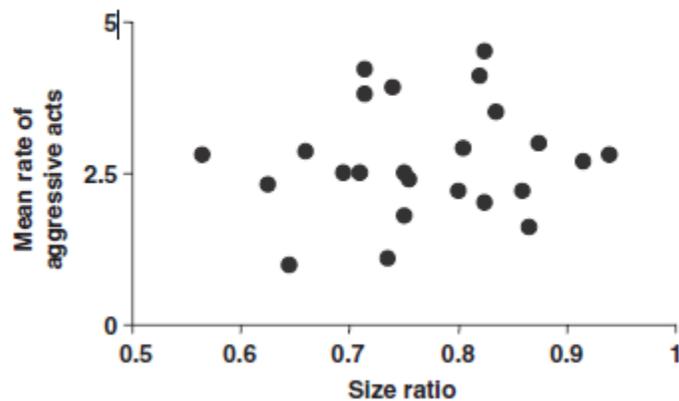
Food intake (mean number of prey items per minute) was similar over the three different treatments ($F_{2,18}$ = 2.25, p = 0.130) and there was no difference between pre- and post-manipulation feeding rates ($F_{2,42}$ = 2.71, p = 0.095). Feeding rate was correlated with the size difference within groups (rS = 0.352, p = 0.050, n = 24); each individual within a similar-sized group obtained a more equal proportion of the available food, whereas in the groups with large size differences the dominant monopolized the food and ate the greatest proportion.

Discussion

The stability and structure of the dominance hierarchies of the three-spined stickleback, *G. aculeatus*, were influenced when the fish were subject to an environmental perturbation. The hierarchies became less stable when drought and increased turbulence were simulated but stability increased when the hierarchies were undisturbed. This may reflect the demands of the environmental manipulation to which the fish were subjected. Lowering water levels, which will increase density and encounter rates, and increasing turbulence may place extra energy demands upon the fish and so constrain their behaviour. Perhaps the dominant individuals could not cope as well in this new environment and were deposed or became more aggressive because of the increased energy demands thus increasing hunger levels or the value of the food resource. Similar evidence has been demonstrated in studies where increasing water velocity reduced aggression levels in brook charr (McNicol & Noakes 1984) and dominant brown trout lost

their physiological advantage over subordinates (Sloman et al. 2002) whereas simulated drought disrupted the hierarchies of this species (Sloman et al. 2001). It was expected that hierarchies in stable conditions should increase in stability over time as is the case in other species where constant conditions in acute experiments result in stable hierarchies once they have formed (e.g. Forkman & Haskell 2004). However, these dominance relationships in undisturbed conditions may be a result of being held in confinement within laboratory conditions. Disturbing the conditions caused many hierarchies to become unstable and this may reflect a more natural situation rather than the stable hierarchies we generally see under constant conditions that may be an artefact.

The dominant individual responded to the environmental variation either by becoming more aggressive and significantly increasing its dominance over the second rank or being unable to continue as dominant and being deposed. The loss of dominance tended to happen when the fish within a group were of a similar size. The size difference between the smallest and largest individual correlated with the level of aggression performed by all four individuals. When there was little size disparity within a group, the lower ranks challenged the dominant whereas when there was a large size difference the much smaller fish did not engage the dominant as much. This agrees with Game Theory models that predict that when there is a large size difference between animals, it does not pay the smaller individual to engage a larger individual in a fight it is unlikely to win (Parker 1974). When animals are more size matched, each animal has a more even chance of winning and in these experiments the dominant was more likely to be deposed and aggression levels were higher when the individuals within the hierarchy were of a similar size.

Aggression levels were higher after drought was simulated than in the other two treatments. This was probably because of the reduction of individual space in the drought treatment, which forced the fish to come into closer contact with one another and resulted in more aggressive encounters. Aggression level also increases in medaka, Oryzias latipes, when the population density increases and individual space is reduced (Ruzzante & Doyle 1990) and high densities also increase the rate of aggression in ruffe, Gymnocephalus cernuus (Savino & Kostich 2000).

Food intake was the same in all three treatments as the same amount of food was available to each group. The dominant individual monopolized the food resource by performing the most aggression within the groups. This was most pronounced when the size disparity within the groups was large. Similar results were demonstrated in groups of individuals of differing sizes of Atlantic salmon, Salmo salar, (Adams et al. 2000). The dominant individual in hierarchies of other species obtain the greatest proportion of food and also perform the most aggression (e.g. zebra fish, Danio rerio, Basquill & Grant 1998; white sea bream, Diplodus sargus, Castro & Caballero 1998; bonobo, Pan paniscus, Vervaecke et al. 1999). Rank 2 did engage the dominant in aggression as it performed more aggression than defensive acts and continued to do so throughout the experiments and this is possibly because the benefits of being dominant are sufficiently advantageous to the second rank for it to continue trying to become dominant. Ranks 3 and 4 performed more defensive acts than aggression as not only were they attacked by the dominant they also had to contend with the second rank. These results agree with other studies on dominance hierarchies (e.g. sparrows, Junco hyemalis, Barta & Giraldeau 1998; crayfish, Procambarus clarkii, Issa et al. 1999; Atlantic salmon, S. salar, McLean & Metcalfe 2001; brown trout, Salmo trutta, Sloman et al. 2001) and provide evidence for the hypothesis that the dominant's behavior is not limited by the other rank members but the behaviour of lower rank members (e.g. access to food) is limited by the dominant (Deag 1977).

One of the benefits of being dominant was a gain in weight over the experimental period, which can be explained by the dominant obtaining the greatest proportion of food. Ranks 2 and 3 lost weight and this

agrees with current research on stress physiology whereby ranks 2 and 3 are the most stressed in a hierarchy (Winberg et al. 1991; Sapolsky 1992; Fernandes & Volpato 1993; Sloman et al. 2000). Even though they obtain food, they use energy to engage the dominant and one another in fights that they do not win and it has been suggested that this is stressful (Sloman et al. 2000). In salmonids, stress results in a reduction of food conversion efficiency (Metcalfe 1986) so this may also account for why ranks 2 and 3 lost weight. Surprisingly rank 4 gained weight over the experimental period. The strategy rank 4 adopts is to avoid aggressive interactions and 'sneakily' obtain access to food whilst the dominant is fighting (Pers. obs.). Therefore, rank 4 was not wasting energy engaging in aggression as seen in the greater amount of defensive acts performed by rank 4 and this may result in weight gain. Conversely rank 3 also performs more defence than aggression yet it actually loses weight as it still engages the higher ranks. In this study, it would pay for a fish to be highly aggressive and monopolize the food resource or avoid aggressive encounters and obtain food in a 'sneaky manner'. This 'sneaky' strategy has also been observed in Atlantic salmon (S. salar) when they are dominated by brown trout (S. trutta; Ho¨ jesjo¨ et al. 2005). Differences in the foraging strategy utilized by individuals within a hierarchy according to their social position have been demonstrated in sparrows, J. hyemalis (Barta & Giraldeau 1998), oystercatchers, Haematopus ostralegus (Caldow & Goss-Custard 1996) and great tits, Parus major (Verbeek et al. 1999).

These results may also provide evidence for the mechanisms of growth compensation in fish. Growth compensation is a phenomenon whereby a fish deprived of food for a period of time compensates by eating more when food is available and actually catches up to the weight of a similar fish which has not been deprived (Nicieza & Metcalfe 1997; Ali & Wootton 2000; McLean & Metcalfe 2001). This has been demonstrated in the three-spined stickleback (Zhu et al. 2001). These sticklebacks are often found shoaling and shoals are generally comprised of similar-sized individuals (Peuhkuri 1999; Hoare et al. 2000a,b; Krause et al. 2000). If a stickleback of smaller size is placed into a shoal of larger individuals, it compensates by increasing its foraging rate so as to increase its size (Peuhkuri 1998). Conversely, a larger stickleback placed into a smaller sized shoal reduces its foraging rate (Peuhkuri 1997). It has been shown that these 'odd' individuals are at a greater risk of predation (Peuhkuri 1998). It is possible that in these experiments, as the dominant individual is not the largest fish, it is compensating by being aggressive and obtaining most food to catch up in size to the larger individuals within the group The rank 4 fish, which were usually the smallest individuals within the groups, may be adopting their non-aggression strategy to catch up in size to the other fish within the group. Thus there may be an external influence on growth rate dependent upon group size as well as an internal influence demonstrated in other studies (Nicieza & Metcalfe 1997; Ali & Wootton 2000; McLean & Metcalfe 2001). Social interactions are important determinants of growth in Arctic charr, S. alpinus (Jobling 1985) and in gilthead sea bream, Sparus aurata (Karplus et al. 2000). Further experiments need to be carried out to test this growth compensation hypothesis.

The environmental conditions had a significant effect on the structure and stability of the dominance hierarchies in this study. Different environmental variables may have distinctive effects upon hierarchy stability and upon individuals with differing ranks. Therefore, our study suggests that ecological variability has a major impact on individuals and their position within dominance hierarchies. Future experimentation should assess the impact of other ecological variations that may have a major impact on behaviour and ecology.

Literature Cited

Adams, C. E., Huntingford, F. A., Turnbull, J., Arnott, S. & Bell, A. 2000: Size heterogeneity can reduce aggression or promote growth in Atlantic salmon parr. Aquac. Int. 8, 543—549.

Ali, M. & Wootton, R. J. 2000: Variation in rates of food consumption and evidence for compensatory responses in the 3-spined stickleback Gasterosteus aculeatus in relation to growth and reproduction. Ecol. Freshw. Fish 9, 103—108.

Bailey, J., Alanärä , A. & Brännäs, E. 2000: Methods for assessing social status in Arctic charr. J. Fish Biol. 57, 258—261.

Bakker, T. C. M. 1986: Aggresiveness in sticklebacks. Behavior 98, 1—144.

Barber, I., Arnott, S. A., Braithwaite, V. A., Andrew, J. & Huntingford, F. A. 2001: Indirect fitness consequences of mate choice in sticklebacks: offspring of brighter males grow slowly but resist parasitic infections. Proc. R. Soc. Lond. B 268, 71—76.

Barnard, C. J. & Burk, T. 1979: Dominance hierarchies and the evolution of "individual recognition". J. Theor. Biol. 81, 65—73.

Barta, Z. & Giraldeau, L. A. 1998: The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing scrounging game. Behav. Ecol. Sociobiol. 42, 217—223.

Basquill, S. P. & Grant, J. W. A. 1998: An increase in habitat complexity reduces aggression and monopolization of food by zebra fish (Danio rerio). Can. J. Zool. 76, 770—772.

Caldow, R. W. G. & Goss-Custard, J. D. 1996: Temporal variation in the social rank of adult oystercatchers Haematopus ostralegus. Ardea 84A, 389—400.

Carlsen, K. T., Berg, O. K., Finstad, B. & Heggberget, T. G. 2004: Diel periodicity and environmental influence on the smolt migration of Arctic charr, Salvelinus alpinus, Atlantic salmon, Salmo salar, and brown trout, Salmo trutta, in northern Norway. Environ. Biol. Fishes 70, 403—413.

Castro, J. J. & Caballero, C. 1998: Dominance structure in small groups of juvenile white-seabream (Diplodus sargus). Aggress. Behav. 24, 197—204.

Deag, J. M. 1977: Aggression and submission in monkey societies. Anim. Behav. 25, 465—477.

Fernandes, M. D. & Volpato, G. L. 1993: Heterogeneous growth in the Nile tilapia – social stress and carbohydate-metabolism. Physiol. Behav. 54, 319—323.

Forkman, B. & Haskell, M. J. 2004: The maintenance of stable dominance hierarchies and the pattern of aggression: support for the suppression hypothesis. Ethology 110, 737—744.

Goldberg, J. L., Grant, J. W. A. & Lefebvre, L. 2001: Effect of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. Behav. Ecol. 12, 490—495.

Hoare, D. J., Krause, J., Peuhkuri, N. & Godin, J. G. J. 2000a: Body size and shoaling in fish. J. Fish Biol. 57, 1351—1366.

Hoare, D. J., Ruxton, G. D., Godin, J. G. J. & Krause, J. 2000b: The social organization of free-ranging fish shoals. Oikos 89, 546—554.

Höjesjö , J., Armstrong, J. D. & Griffiths, S. W. 2005: Sneaky feeding by salmon in sympatry with dominant brown trout. Anim. Behav. 69, 1037—1041.

Holling, C. S. 1973: Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4, 1—24.

Hughes, N. F. 1992: Ranking of feeding positions by drift feeding Arctic grayling (Thymallus arcticus) in dominance hierarchies. Can. J. Fish. Aquat. Sci. 49, 1994—1998.

Huntingford, F. A. 1979: Pre-breeding aggression in male and female three-spined sticklebacks (Gasterosteus aculeatus). Aggress. Behav. 5, 51—58.

Huntingford, F. A. & Turner, A. K. 1987: Animal Conflict. Chapman and Hall, London.

Issa, F. A., Adamson, D. J. & Edwards, D. H. 1999: Dominance hierarchy formation in juvenile crayfish Procambarus clarkii. J. Exp. Biol. 202, 3497—3506.

Jobling, M. 1985: Physiological and social constraints on growth of fish with special reference to Arctic charr, Salvelinus alpinus. Aquaculture 44, 83—90.

Karplus, I., Popper, D. & Goldan, O. 2000: The effect of food competition and relative size of group members on growth of juvenile gilthead sea bream, Sparus aurata. Fish Physiol. Biochem. 22, 119—123.

Kraak, S. B. M., Bakker, T. C. M. & Mundwiler, B. 1999: Sexual selection in sticklebacks in the field: correlates of reproductive, mating, and paternal success. Behav. Ecol. 10, 696—706.

Krause, J., Butlin, R. K., Peuhkuri, N. & Pritchard, V. L. 2000: The social organisation of fish shoals: a test of the predictive power of laboratory experiments for the field. Biol. Rev. 75, 477—501.

Mayer, M. & Berger, A. 1992: Territoriality and microhabitat selection in two intertidal New Zealand fish. J. Fish Biol. 40, 243—256.

McLean, A. & Metcalfe, N. B. 2001: Social status, access to food and compensatory growth in juvenile Atlantic salmon. J. Fish Biol. 58, 1331—1346.

McNicol, R. E. & Noakes, D. L. G. 1984: Environmental influences on the territorialty of juvenile brook charr, Salvelinus fontinalis, in a stream environment. Environ. Biol. Fishes 10, 29—42.

Metcalfe, N. B. 1986: Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. J. Fish Biol. 28, 525—531.

Neubert, M. G. & Caswell, H. 1997: Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology 78, 653—665.

Nicieza, A. G. & Metcalfe, N. B. 1997: Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. Ecology 78, 2385—2400.

Parker, G. A. 1974: Assessment strategy and the evolution of fighting behaviour. J. Theor. Biol. 47, 223—243.

Payne, R. J. H. 1998: Gradually escalating fights and displays: the cumulative assessment model. Anim. Behav. 56, 651—662.

Peuhkuri, N. 1997: Size assortative shoaling in fish: the effect of oddity on foraging behaviour. Anim. Behav. 54, 271—278.

Peuhkuri, N. 1998: Shoal composition and foraging in sticklebacks. Behav. Ecol. Sociobiol. 43, 333—337.

Peuhkuri, N. 1999: Size-assorted fish shoals and the majority's choice. Behav. Ecol. Sociobiol. 46, 307—312.

Postin, J. P. 1997: Dominance, access to colonies, and queues for mating opportunities by male boat-tailed grackles. Behav. Ecol. Sociobiol. 41, 89—98.

Pruetz, J. D. & Isbell, L. A. 2000: Correlations of food distribution and patch size with agonistic interactions in female vervets (Chlorocebus aethiops) and patas monkeys (Erythrocebus patas) living in simple habitats. Behav. Ecol. Sociobiol. 49, 38—47.

Richards, S. M. 1974: The concept of dominance and measures of assessment. Anim. Behav. 22, 914—930.

Ruzzante, D. E. & Doyle, R. W. 1990: Behavioural and growth responses to the intensity of intraspecific social interaction among medaka, Oryzias latipes. J. Fish Biol. 37, 663—673.

Ryer, C. H. & Olla, B. L. 1996: Social behaviour of juvenile chum salmon, Oncorhynchus keta, under the risk of predation: the influence of food distribution. Environ. Biol. Fishes 45, 75—83.

Sapolsky, R. M. 1992: Cortisol concentrations and the social significance of rank instability among wild baboons. Psychoneuroendocrinology 17, 701—709.

Savino, J. F. & Kostich, M. J. 2000: Aggressive and foraging behavioural interactions among ruffe. Environ. Biol. Fishes 57, 337—345.

Sirot, E. 2000: An evolutionary stable strategy for aggressiveness in feeding groups. Behav. Ecol. 11, 351—356.

Sloman, K. A., Gilmour, K. M., Taylor, A. C. & Metcalfe, N. B. 2000: Physiological effects of dominance hierarchies within groups of brown trout, Salmo trutta, held under simulated natural conditions. Fish Physiol. Biochem. 22, 11—20.

Sloman, K. A., Taylor, A. C., Metcalfe, N. B. & Gilmour, K. M. 2001: Effects of an environmental perturbation on the social behaviour and physiological function of brown trout. Anim. Behav. 61, 325—333.

Sloman, K. A., Wilson, L., Freel, J. A., Taylor, A. C., Metcalfe, N. B. & Gilmour, K. M. 2002: The effects of increased flow rates on linear dominance hierarchies and physiological function in brown trout, Salmo trutta. Can. J. Zool. 80, 1221—1227.

Taniguchi, G. A., Bicudo, D. D. & Sennab, P. A. C. 2004: Abiotic variables in littoral-limnetic gradient of an Oxbow lake of Mogi-Guacu river floodplain, southeastern Brazil. Braz. Arch. Biol. Technol. 47, 961—971.

Tindo, M. & Dejean, A. 2000: Dominance hierarchy in colonies of Belonogaster juncea juncea. Insectes Soc. 47, 158—163.

Utne-Palm, A. C. & Hart, P. J. B. 2000: The effects of familiarity on competitive interactions between threespined sticklebacks. Oikos 91, 225—232.

Verbeek, M. E. M., DeGoede, P., Drent, P. J. & Wiepkema, P. R. 1999: Individual behavioural characteristics and dominance in aviary groups of great tits. Behavior 136, 23—48.

Vervaecke, H., DeVries, H. & Van Elsacker, L. 1999: An experimental evaluation of the consistency of competitive ability and agonistic dominance in different social contexts in captive bonobos. Behavior 136, 423—442.

Winberg, S., Nilsson, G. E. & Olsen, K. H. 1991: Social rank and brain levels of monoamines and monoamine metabolites in Arctic charr, Salvelinus alpinus. J. Comp. Physiol. A 168, 241—246.

Wright, P. J. & Huntingford, F. A. 1993: Agonistic interactions in juvenile sticklebacks (Gasterosteus aculeatus) in relation to local predation risk. Ethology 94, 248—256.

Zhu, X., Cui, Y., Ali, M. & Wootton, R. J. 2001: Comparison of compensatory growth responses of juvenile 3-spined stickleback and minnow following similar food deprivation protocols. J. Fish Biol. 58, 1149—1165.