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ARTICLE

Hierarchical status and colour preference in Nile tilapia (*Oreochromis niloticus*)

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Abstract We studied the colour preference of isolated Nile tilapia (*Oreochromis niloticus*) and whether previous residence or body size can affect environmental colour choice. In the first phase, a cylindrical tank was divided into five differently coloured compartments (yellow, blue, green, white and red), a single fish was introduced into the tank and the frequency at which this fish visited each compartment was recorded over a 2-day study period. An increasingly larger fish (approx +2 cm in length each time) was then added into the tank on each of days 3, 5 and 7 (=four fish in the tank by day 7), and the frequency at which each fish visited the different compartments of the tank was observed twice a day to obtain visit frequency data on the differently sized fishes. This experiment was replicated six times. In the first phase, the solitary fish established residence inside the yellow compartment on the first and second days. Following theintroduction of a larger fish, the smaller fish was displaced from the occupied compartment. Nile tilapia possibly shows this preference for yellow as a function of its visual spectral sensitivity and/or the spectral characteristics of its natural environment. Moreover, body size is an important factor in determining hierarchical dominance and territorial defence, and dominant fish chose the preferred environmental colour compartment as their territory.

Keywords Body size · Environmental colour · Hierarchy · Fish · Previous residence

Introduction

An adaptive characteristic of territorial fish species is the manifestation of social organization in a dominance hierarchy (Noble 1939). Some physiological and morphological factors have been recognized to affect dominance status, including hormonal condition, usually associated with reproduction (Pankhurst and Barnett 1993; Pankhurst 1995), gender (Brillet 1981), body size (Chellappa et al. 1999), body colour (Suter and Huntingford 2002; Volpato et al. 2003) and previous residence (Huntingford and Garcia de Leaniz 1997). Body size is one of the most important factors affecting dominance: the larger the fish, the higher its social rank (Turner and Huntingford 1986; Chellappa et al. 1999). Thus, the higher growth rate shown by dominant fish (Fernandes and Volpato 1993) has been considered to be a stabilizing factor on the social hierarchy of the group (Gilmour et al. 2005). However, prior residency has also been shown to be an advantage for the resident when fighting off an intruder (Deverill

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et al. 1999). For instance, the owner of a territory has priority for dominance on any intruder – the prior-residence effect (Huntingford and Garcia de Leaniz 1997 – and previously dominant and subordinate fish are expected to be the winner and loser, respectively, in future combats – the prior social-hierarchy effect (Hsu and Wolf2001). Although these factors have been well described and accepted for social hierarchy in fish (Sloman and Armstrong 2002), the interactions among them and with other environmental features are still unknown.

One environmental characteristic that affects fish physiology is the background or light colour. Some environmental colour effects on fish have been shown to modulate several physiological and behavioural responses, such as feeding (Duray et al. 1996), growth (Dowing and Litvak 2000), reproduction (Volpato et al. 2004), aggression (Hoglund et al. 2002) and stress response (Volpato and Barreto 2001). While spectral characteristics of the light environment can affect fish physiology and behaviour, exactly how the wavelength of light modulates fish response is still unclear. One way to identify physical parameters that may improve fish fitness can be achieved by preference tests. One example of such tests are the food-preference tests that have been used to improve the palatability of the diet (Fraser 1993). Preference tests have been used quite extensively in animal studies because the preferred condition can provide some clues as how to improve animal welfare (Gonyou 1994). Therefore, light wavelength-preference tests can be the first step to gaining an understanding of how fish recognize these environments and which ones are most favourable. Moreover, for diurnal species able to discriminate a wide range of colours, such as Nile tilapia (*Oreochromis niloticus*), a suitable ambient wavelength can help the animal discriminate details in the environment, thereby providing that animal with various advantages, including feeding, defence or mating (Levine 1980; Wheeler 1982; Yokoyama 2000).

Any factor affecting physiological and behavioural responses can also interfere with the dominance status, decreasing or increasing aggressiveness and social stress (Fanta 1995). Social stabilization and the decrease in aggression is crucial for individuals competing for survival. On the other hand, the preference of a particular fish population for a specific colour in the environment could increase acquired territory defence and agonistic behaviour.

While social rank based on some pre-determined cues (e.g. previous residence and body size) is important, the establishment of residence in a better place – for example, under the preferred environmental colour – is also necessary for a better adjustment of the fish in the territory. Since environmental colours can affect fish physiology and behaviour, we designed an experiment to test the colour preference of isolated Nile tilapia and whether previous residence or body size can affect environmental colour choice. We used the Nile tilapia (Order Perciformes, Family Cichlidae, Subfamily Pseudocrenilabrinae) for the tests because it is an aggressive, territorial and diurnal species in which social hierarchy is evident (Corrêa et al. 2003) and colour vision has been described (Levine and MacNichol 1982; Fanta 1995).

Materials and methods

Nile tilapia used in the present study were housed for approximately 7 months in a 1500-l indoor tank at a density of one fish/m^3. Water was continuously re-circulated and aerated, and the water temperature averaged 23.7°C. The photoperiod consisted of 12 light to12 dark. Commercial dry pellets (Purina, Campinas, Brazil) were offered once per day in excess (over 5% of the fish biomass). The total length of each ranged from 5 to 15 cm (weight range: 3.57–81.2 g); all fish used in the experiments were randomly chosen from the stock tank.

The experimental tank consisted of a 50-cm-diameter cylindrical tank with five radial compartments around a central compartment (Fig. 1). The surface area of each compartment (central or radial) was identical (327 cm^2), and each compartment was equally illuminated with white fluorescent light (500 lx). Different colours (blue, green, red, white, yellow) were randomly chosen for each compartment and were achieved by covering the compartment with coloured

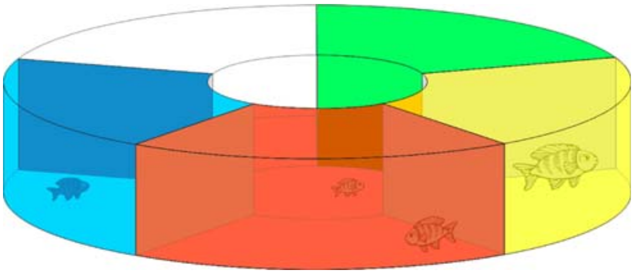

Fig. 1 Diagram of the experimental tank used to test colour preference of Nile tilapia of different body sizes (mean total length: 5–11 cm). The tank was 50 cm in diameter, divided into five radial compartments around a central area. The colour of each compartment was obtained by covering that compartment with coloured cellophane (blue, white, green, yellow and red); the central area was not covered. The tank was illuminated with white fluorescent light which provided the radial compartments with 120 lx and the central area with 500 lx

cellophane; the central area was not covered. Light intensity in the coloured compartments was then adjusted to 120 lx (as used by Volpato et al. 2004) by adding layers of the same coloured cellophane. This light intensity was also used because it allows the passage of clear colour light, since colour vision is dependent on light, and it is not high enough to cause eye damage. The uncovered central compartment into which the fish were introduced received the higher illumination (500 lx) to discourage fish from remaining there.

A small fish, (average total length: 5 cm; fish A) was taken from the stock tank and isolated in the experimental aquarium for 1 day for acclimatization, following which the visit frequency in each compartment was observed and recorded for 2 experiment days. Data were collected on each experimental day from 0800 to 0820 hours and from 1400 to 1420 hours. During both 20-min periods we observed which compartment the fish was occupying at 2-min intervals. Thus, for each period we had ten observations (20 observations per day).

After 2 days, a 2-cm longer fish (average total length: 7 cm; fish B) was introduced into the experimental aquarium, and the visit frequencies of both fishes inside each compartment were observed as described above. After 2 more days, a third, yet larger, fish was introduced into the tank (fish C; mean total length: 9 cm) and, after a further 2 days, we introduced the last and longest fish (fish D; mean total length: 11 cm) into the tank. The same observation procedure with respect to the visit frequencies of all fishes in the compartments was repeated each day until the eighth day. Fish (experimental and stock) were not fed during the experimental period, but this fasting period was not long enough to induce energy loses based on lipid levels (Miglavs and Jobling 1989). This experiment was independently replicated six times.

To compare data from each fish, we used the number of times daily each fish was in each of the differently coloured compartments. For example, on day 1 fish A was inside the white compartment six times, inside the green compartment four times and inside the yellow compartment ten times (20 observations).

We applied two procedures for the statistical analysis. For the data of the first 2 days, when fish A was alone in the tank, we used the Friedman ANOVA to compare visit frequency in the different compartments. In the analysis of the whole visit frequency data, we applied linear mixed modelling with related significance tests. The visit frequencies in each compartment (blue, green, red, white, yellow and centre) were analysed separately. Our primary goal was to test if the visit frequency in each compartment was dependent on whether the fish was the biggest in the tank (on the current day) or not. Thus, we specified a linear mixed model with the visit frequency as the response and the fish being the biggest (yes/no) as a two-valued explanatory fixed factor. We also put the daily number of fishes (one, two, three or four) in the tank and the replication (1, 2,..., 6) into the model as additional fixed factors to control for their effect. Since we have repeated measures on each individual fish in our data, we used the fish individual as a random factor to account for the possible autocorrelation. The significance of each fixed effect was tested by the appropriate F test.

When a new fish was introduced to the tank, the social hierarchy in the fish group was suppressed, to be re-established on the following day. Therefore we decided to use in the analysis only those days (2, 4, 6 and 8) on which the hierarchy was established.

The mixed model analysis was carried out with the MIXED procedure of the SAS statistical package.

Results

On the first observation day, the solitary fish (fish A) spent most of its time inside the yellow and centre compartments (Friedman ANOVA; df=5, χ^2=13.3, p=0.02; Fig. 2 day 1). During the second day, this fish showed a preference for the yellow compartment (Friedman ANOVA; df=5, χ^2=14.8, p=0.01; Fig. 2 day 2).

When a new fish is introduced to a group, recognition of the other fish by body colour and size and social status occurs (Volpato et al. 2003), and interactions take place in order to re-establish social scale. Since this takes some time, there was no clear establishment of hierarchy on the first day when a bigger fish was introduced to our experimental tank. The social status seemed to become defined on the following day (see Fig. 2).

On days 2, 4, 6 and 8, when the hierarchical status was established, the largest of the fish showed significantly higher visit frequency than its smaller counterparts to the yellow compartment (F=56.7, df = 1, 32, p<0.001). Correspondingly, on these same days the visit frequencies of the smaller fish to the green and white compartments were significantly higher . Visit frequency in the other compartments (red, blue and centre) did not differ significantly. In all of the significance tests carried out, the variation due to the replications and varying number of fishes in the tank was

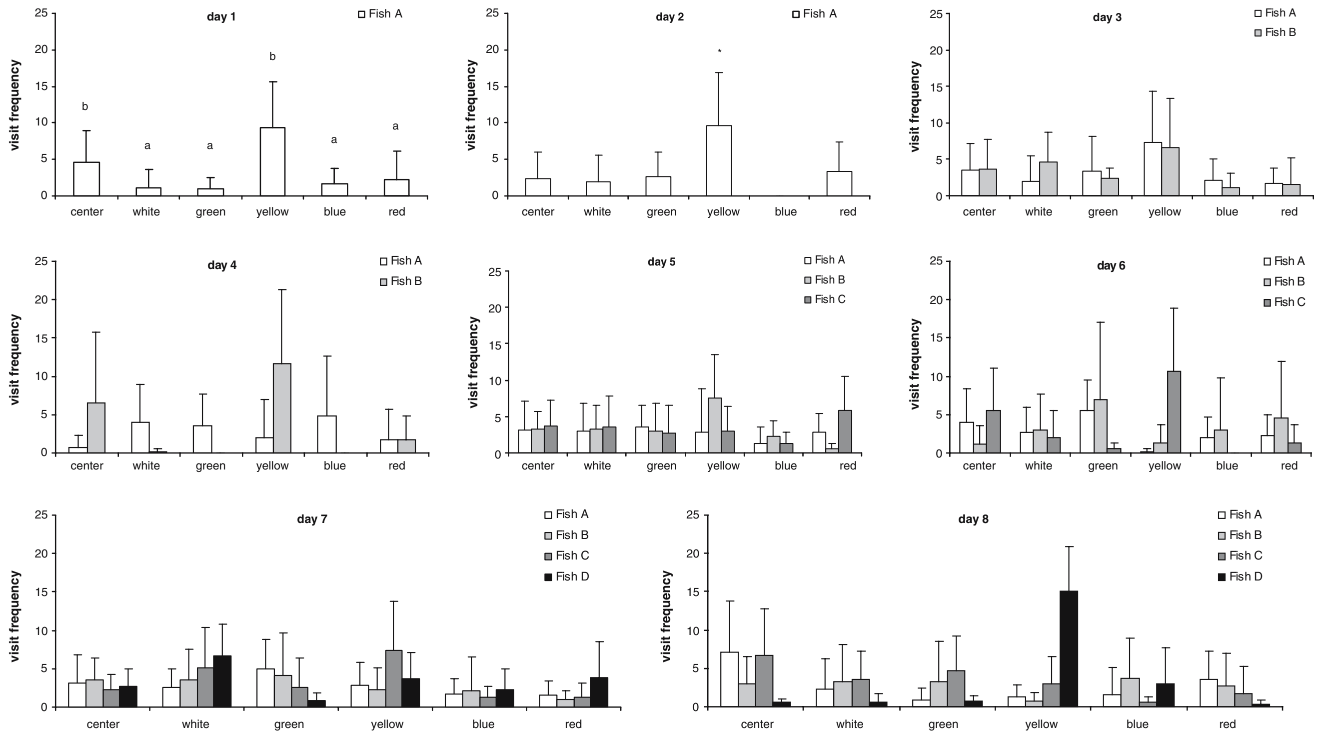

Fig. 2 Average visit frequency in each of the coloured compartment. *Bar values* are the means of two observation periods (0800 and 1400 hours) for each day. *Vertical bars* represent standard deviation. Fish were introduced into the aquarium every 2 days in an ascending length order (fish A = approx. 5 cm, B = approx. 7 cm, C = approx. 9 cm and D = approx.11 cm length). *Different letters* and *asterisks* indicate statistical differences ($p<0.05$, Friedman Anova) for the isolated fish (days 1 and 2). The experiment was replicated six times

Table 1 Estimated mean visit frequency of all Nile tilapia to each of the coloured compartment on days when hierarchical status was well established (days 2, 4, 6 and 8) ± standard error (n=6)

Fish size[a]	Colours of compartments					
	Blue	Green	Red	White	Yellow	Centre
Biggest	0.8±0.9	1.0±0.1	1.0±0.9	1.2±0.7	12.4±1.0	3.7±1.1
Others	2.5±1.1	4.9±1.0	2.7±0.8	3.5±0.8	1.2±1.1	3.2±1.1
F test (df=1, 32)	F=1.9, p=0.18	F=9.0, $p < 0.01$	F=2.1, p=0.16	F=4.5, p=0.04	F=56.7, p<0.001	F=0.1, p=0.73

[a] Fish size was measured in terms of total length. The estimates and F tests are based on the mixed model analysis

controlled. The mean visit frequencies, estimated from the model, of fish in each compartment on days 2, 4, 6 and 8 are shown in Table 1. Figure 2 shows the mean values of visit frequency in each compartment for fishes A, B, C and D.

Discussion

In this study we based the preference of a fish for a particular colour on the frequency at which that fish occupied the correspondingly coloured compartment of the test tank. A single isolated Nile tilapia increased its visit frequency to the yellow compartment from the first to the second day of observation. Although some studies of fish environmental preferences have been published (Sekine et al. 1997; Johnsson et al. 2000; Hofmann and Fischer 2002), even between white and black backgrounds (Serra et al. 1999), this is the first study in which a fish has been shown to have a colour preference.

The Nile tilapia of our study showed a clear preference for a yellow environment. The natural habitat of *O. niloticus* is primarily a green background colour (Fanta 1995), which means that the light that reaches this environment comprises wavelengths between 500 and 570 nm (Kageyama 1999), which encompasses the green and yellow part of the visible spectrum. According to Munz (1958), the spectral location of the pigments of fish that evolved in this kind of environment may be correlated with the colours of the light available to them, which could have influenced the choice of our tilapia for the yellow environment.

The most important intrinsic factor associated with colour perception is the absorbance of eye pigments. Spady et al. (2006) demonstrated the presence of seven cone opsin genes code for seven photosensitive pigments in Nile tilapia. These authors observed that tilapia has photosensitive pigments (λ_{max}) at 360 nm (SWS1), 425 nm (SWS2B), 456 nm (SWS2A), 472 nm (Rh2B), 518 nm (Rh2Aβ), 528 nm (Rh2Aα) and 561 nm (LWS) along the visible spectrum. Other fish with pigment absorbances similar to those of Nile tilapia are also considered to have cones sensitive to longer wavelengths, and these may also prefer a yellow light environment. According to Cohen and Forward (2002), visual sensitivity is enhanced in environments where the visual pigments are able to maximize photon capture. Thus, Nile tilapia visual pigments possibly better match the wavelengths present in the yellow environment, which could have driven the choice of the yellow environment.

In this study we also observed that the fish seemed to avoid a red environment, as the visit frequency to the red compartment was very low. For Nile tilapia, the longest pigment wavelength absorbance is 561 nm (Spady et al. 2006), so the red environment in which light wavelength is around 610 nm may restrict vision, as photons are not well captured by the cones. As an herbivorous species, Nile tilapia feeds on plants, algae, weeds and macrophytes (Lowe-McConnell 1975; Tengjaroenkul et al. 2000) and may not need specialized visual sensitivity for foraging on animals. Hence, medium to longer wavelength pigments may improve visibility in its natural environment. Also, the better vision may favour territorial defence displays.

Muntz (1973) showed an association between the environmental light spectrum where a population lives and the retinal pigment absorbance. For cichlids, Muntz (1973) and Partridge et al. (1989) reported the presence of yellow cornea and retina that may work as a filter for light under 500 nm. This kind of intra-eye filter is characteristic of diurnal teleosts and can minimize light incidence on the eye, thereby improving vision (Muntz 1973). Based on these facts and our results, we can conclude that environmental characteristics and eye and retina pigments are determinants of colour perception and preference in Nile tilapia. However, the effects of colour preference on growth, feeding and well being in this species still need to be investigated.

The yellow colour preference of Nile tilapia was affected by a determinant hierarchical factor: body size. Despite some reports that previous residence is a strong stimulus when social interactions take place (Brännäs 1995; Huntingford and Garcia de Leaniz 1997), this factor was not strong enough to allow a smaller resident fish to keep its preferred colour compartment. In fact, in our study the bigger fish always chased the smaller resident fish out of its preferred compartment (yellow) and then subsequently always took over occupancy of it. This benefit of size was also found by Beaugrand et al. (1996) and Schuett (1997), who proposed that body size is an important factor determining dominance and priority of access to resources. Moreover, it is well established that body size gives advantages in the ability to win fights and that winners often have priority access to mates and critical resources (Huck et al. 1986; Chase et al. 1994). Indeed, a functional consequence of body size relates to competition ability to access shelter sites. This conclusion is supported by the relation between body size and visit frequency to the yellow compartment by our Nile tilapia groups. Other compartment colours did not present the same pattern of occupation as the yellow compartment; smaller fish made significantly higher visit frequencies to the green and white compartments than to the red, while visits to the blue and centre compartment were more randomized. Although the green and white environment was significantly visited by the subordinate fish, there was not a single hierarchical class that occupied these compartments for most of the experimental time.

The preference of the introduced fish for the yellow compartment may have been because yellow is the preferred colour of this species, as seen in this study, or because the intruder became dominant and tried to occupy the exact place of the resident. Faria et al. (1998) have shown a relation among dominance rank, time spent in shelters and habitat preference in juvenile *Lipophrys pholis* and *Coryphoblennius galerita*. These authors suggested that dominant animals became more aggressive and that this agonistic behaviour allows them to have access to preferred habitats and shelters. Gibson (1968), studying groups of *L. pholis*, also concluded that one consequence of dominance is the definition of some sort of order of priority of access to shelter, with the subordinate fish retreating quickly from a shelter site when dominant individuals approach.

In addition to this clear preference for the yellow compartment, visit frequencies inside the other compartments were also high, mainly during the first day when the bigger fish had been introduced. According to Faria et al. (1998), instead of defending well-defined areas, each fish may visit and defend several hiding places, and more dominant individuals tend to have priority of access to these places, forcing the subordinates to leave them. However, the fact that fish A mainly occupied the yellow compartment, without any sort of pressure from social interactions when isolated, indicates its basic preference for the yellow environment and suggests that the yellow environment was chosen by the intruders because of the colour, which was preferred by fish of any social rank but acquired only by the dominant and bigger fish. Thus, it is likely that the priority of access to shelter sites may be one reason for agonistic behaviour in fishes.

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References

Beaugrand JP, Payette D, Goulet C (1996) Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience, and prior residency. Behaviour 133:303–319

Brännäs E (1995) First access to territorial space and exposure to strong predation pressure: a conflict in early emerging Atlantic salmon (*Salmo salar* L.). Evol Ecol 9:411–420

Brillet C (1981) Agonistic behaviour of the amphibious fish *Periophthalmus sobrinus* Eggert. Quantitative analysis. 2. Influence of size and sex on the establishment of dominance/subordination relationships and the use of the agonistic repertoire. Biol Behav 6:35–57

Chase ID, Bartolomeu C, Dugatkin LA (1994) Aggressive interactions and inter-contest interval: how long do winner keep winning? Anim Behav 48:393–400

Chellappa S, Yamamoto ME, Cacho MS, Huntingford FA (1999) Prior residence, body size and the dynamics of territorial disputes between male freshwater angelfish. J Fish Biol 55:1163–1170

Cohen JH, Forward Jr RB (2002) Spectral sensitivity of vertically migrating marine copepods. Biol Bull 203:307–314

Corrêa AS, Fernandes MO, Iseki KK, Negrão JA (2003) Effect of the establishment of dominance relationships on cortisol and other metabolic parameters in Nile tilapia (*Oreochromis niloticus*). Braz J Med Biol Res 36:1725–1731

Deverill JI, Adams CE, Bean CW (1999) Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout. J Fish Biol 55:868–875

Dowing G, Litvak MK (2000) The effect of photoperiod, tank colour and light intensity on growth of larval haddock. Aquacult Int 7:369–382

Duray MN, Estudillo CB, Alpasan LG (1996) The effect of background color and rotifer density on rotifer intake, growth and survival of the grouper (*Epinephelus suillus*) larvae. Aquaculture 146:217–224

Fanta E (1995) Influence of background color on the behaviour of the *Oreochromis niloticus* (Cichlidae). Braz Arch Biol Technnol 38:1304–1316

Faria C, Almada V, Nunes MdoC (1998) Patterns of agonistic behaviour, shelter occupation and habitat preference in juvenile *Lipophrys pholis*, *Coryphoblennius galerita* and *Gobius cobitis*. J Fish Biol 53:1263–1273

Fernandes MO, Volpato GL (1993) Heterogeneous growth in the Nile tilapia: Social stress and carbohydrate metabolism. Physiol Behav 54:319–323

Fraser D (1993) Assessing animal well-being: common sense, uncommon science. In:Food animal well-being. Purdue University Office of Agricultural Research Programs, West Lafayette, pp 37–54

Gibson RN (1968) The agonistic behaviour of juvenile *Blennius pholis* L. (Teleostei). Behaviour 30:192–217

Gilmour KM, DiBattista JD, Thomas JB (2005) Physiological causes and consequences of social status in salmonid fish. Integr Comp Biol 45:263–273

Gonyou HW (1994) Why the study of animal behavior is associated with the animal welfare issue. J Anim Sci 72:2171–2177

Hofmann N, Fischer P (2002) Temperature preferences and critical thermal limits of burbot: Implications for habitat selection and ontogenetic habitat shift. Trans Am Fish Soc 131:1164–1172

Hoglund E, Balm PHM, Winberg S (2002) Behavioural and neuroendocrine effects of environmental background colour and social interaction in Arctic charr (*Salvelinus alpinus*). J Exp Biol 205:2535–2543

Hsu Y, Wolf LL (2001) The winner and loser effect: what fighting behaviours are influenced? Anim Behav 61:777–786

Huck UW, Lisk RD, Allison JC, van Donegen CG (1986) Determinants of mating success in the golden hamster (*Mesocricetus auratus*): social dominance and mating tactics under seminatural conditions. Anim Behav 34:971–989

Huntingford FA, Garcia de Leaniz C (1997) Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. J Fish Biol 51:1009–1014

Johnsson JI, Carlsson M, Sundstroem LF (2000) Habitat preference increases territorial defence in brown trout (*Salmo trutta*). Behav Ecol Sociobiol 48:373–377

Kageyama CJ (1999) What fish see. Frank Amato Publ, New York

Levine JS (1980) Vision underwater. Oceanus 23:19–26

Levine JS, MacNichol EJ Jr (1982) Color vision in fishes. Sci Am 216:108–117

Lowe-McConnell RH (1975) Fish communities in tropical freshwater. Longman, New York

Miglavs I, Jobling M (1989) The effect of feeding regime on proximate body composition and patterns of energy deposition in juvenile Arctic charr, *Salvelinus alpinus*. J Fish Biol 35:1–11

Muntz WRA (1973) Yellow filters and the absorption of light by the visual pigments of some Amazonian fishes. Vision Res 13:2235–2254

Munz FW (1958) The photosensitive retinal pigments of fishes from relatively turbid coastal waters. J Gen Physiol 42:445–459

Noble GK (1939) The experimental animal from the naturalist's point of view. Am Nat 73:113–126

Pankhurst NW (1995) Hormones and reproductive behavior in male damselfish. Bull Mar Sci 57:569–581

Pankhurst NW, Barnett CW (1993) Relationship of population density, territorial interaction and plasma levels of gonadal steroids in spawning male demoiselles *Chromis dispilus* (Pisces: Pomacentridae). Gen Comp Endocrinol 90:168–176

Partridge JC, Shand J, Archer SN, Lythgoe JN, Van Groningen-Luyben WAHM (1989) Interspecific variation in the visual pigments of deep-sea fishes. J Comp Physiol 164:513–529

Schuett GW (1997) Body size and agonistic experience affect dominance and mating success in male copperheads. Anim Behav 54:213–224

Sekine M, Imai T, Ukita MA (1997) Model of fish distribution in rivers according to their preference for environmental factors. Ecol Model 104:215–230

Serra EL, Medalha CC, Mattioli R (1999) Natural preference of zebrafish (*Danio rerio*) for a dark environment. Braz J Med Biol Res 32:1551–1553

Sloman KA, Armstrong JD (2002) Physiological effects of dominance hierarchies: laboratory artefacts or natural phenomena? J Fish Biol 61:1–23

Spady TC, Parry JWL, Robinson PR, Hunt DM, Bowmaker JK, Carleton KL (2006) Evolution of the cichlid visual palette through ontogenetic subfunctionalization of the opsin gene arrays. Mol Biol Evol 23:1–10

Suter HC, Huntingford FA (2002) Eye colour in juvenile Atlantic salmon: effects of social status, aggression and foraging success. J Fish Biol 61:606–614

Tengjaroenkul B, Smith BJ, Caceci T, Smith SA (2000) Distribution of intestinal enzyme activity along the intestinal tract of cultured Nile tilapia, *Oreochromis niloticus* L. Aquaculture 182:317–327

Turner GF, Huntingford FA (1986) A problem for game theory analysis: assessment and intention in male mouthbrooder contests. Anim Behav 34:961–970

Volpato GL, Barreto RE (2001) Environmental blue light prevents stress in the fish Nile tilapia. Braz J Med Biol Res 34:1041–1045

Volpato GL, Luchiari AC, Duarte CRA, Barreto RE, Ramanzini GC (2003) Eye color as indicator of social rank in the fish Nile tilapia. Braz J Med Biol Res 36:1659–1663

Volpato GL, Duarte CRA, Luchiari AC (2004) Environmental color affect Nile tilapia reproduction. Braz J Med Biol Res 37:479–483

Wheeler TG (1982) Color vision and retinal chromatic information processing in teleost: a review. Brain Res Rev 4:177–235

Yokoyama S (2000) Molecular evolution of vertebrate visual pigments. Progr Retin Eye Res 19:385–419