

Effect of environmental enrichment upon resource holding power in fish in prior residence situations

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Abstract

Resource holding power (RHP), as expressed by gaining dominance, can be affected by extrinsic and intrinsic factors. Extrinsic factors that increase the RHP include e.g. prior exposure to the contest area. The pay-off asymmetry hypothesis was tested according to which there is an asymmetry in the value the resident's territory has for the resident and intruders, i.e. the resident loses more than intruder opponents when losing the contest over a territory in which it has invested much energy during the exploration of food and shelter resources, during the settlement of conflicts with territorial neighbours, etc. This asymmetry will increase the resident's chance to win the fight over intruders. If the resident-intruder asymmetry is enhanced by presenting resource-rich territories to e.g. fish (structurally diverse or 'rich' aquariums), the hypothesis predicts that the resident's dominance chance (probability to win the fight) will be higher than in structurally 'poor' aquariums. It was found that residents were proportionately more often dominant (fight winners) than intruders in the rich compared to the poor aquariums in all seven tested fish species. This demonstrates that a high territory resource value (aquarium enrichment) significantly facilitates the expression of the resident's dominance advantage (prior residence effect). In contrast to dominance, aggressive behaviour before the dominance settlement did not generally differ between residents and intruders when compared in rich and poor aquariums. This suggests that dominance in itself and aggression prior to dominance settlement are at least partially guided by different motivational systems. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Body size has often been found as one of the most reliable predictors of contest outcome in

intraspecific fights between animals (Braddock, 1949; Heuts, 1979; Jacobsson et al., 1979; O'Neill, 1983; Beaugrand and Zayan, 1985; Turner and Huntingford, 1986; Englund and Otte, 1991; Jackson and Cooper, 1991; Olsson, 1992; Ribowski and Franck, 1993; Heuts and Nijman, 1998). Resource holding power (RHP; also named resource

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holding potential), i.e. the capacity of standing ones ground (dominating) on the site of the contest so as to enjoy a particular resource on the site while compelling the (subordinate) contest loser to leave the site, is thought to depend in part on body size relative to the size of the opponent (e.g. Parker, 1974). Besides size and other intrinsic factors (such as sex and age, often confounding with size, or the energy reserves available as measured by the fat content (Marden and Waage, 1990)), RHP is also believed to depend on transitory changes in motivation or physiological state (e.g. Clutton-Brock and Albon, 1979; Robertson, 1986; Balmford et al., 1992). Thus, during the reciprocal-assessment phase of the contest the fighting animals have to take into account their own motivational state and the state of their opponent, in addition to their own body size relative to the size of their opponent. The resistance offered by any adversary (resistance expressed in ritualized and/or damage-inflicting aggression) is, by definition, the adversary's actual RHP in a given situation.

This situation comprises two types of factors that will determine the offered resistance and the fight outcome, i.e. (1) The perception of factors inherent in the actual fight situation. This can be related to cognizance of the opponent (e.g. Zayan, 1974), perception of relative body size, and perception of the motivational or physiological part of the RHP, expressed in the aggression level or fight willingness of the opponent. (2) Experiential factors that precede the fight situation, such as previous exposure to versus non-exposure to the environment in which the fight takes place (i.e. a pure prior-residency experiment: Braddock, 1949; de Boer and Heuts, 1973; Zayan, 1974; Heuts, 1979; Ribowski and Franck, 1993; Beaugrand et al., 1996; Heuts and Nijman, 1998), familiarity with some of the cues present in the contest area (de Boer and Heuts, 1973; Heuts, 1979), prior dominance and prior subordination experience (e.g. Thines and Heuts, 1968; Beaugrand et al., 1991, 1996), etc. These experiential factors can be associated with the environment of the actual fight. Together, the actual-fight-situation component and the experience component of the RHP may result in RHP differences between two contestants.

The notion that it is the apparent asymmetry in the value of a territory for the resident and the intruder — residents have more to lose than intruders — that causes residents to win more often than intruders, has been termed the pay-off asymmetry hypothesis (Alcock, 1998; see also Bradbury and Vahrenkamp, 1998). A resident has invested more than the intruder in exploring its environment and, when present, in getting acquainted with its neighbours (Eason and Hannon, 1994). Additionally, the resident generally has more knowledge about its environment and can use this to its advantage in dyadic conflicts with intruders. The pay-off asymmetry hypothesis predicts that residents with a more valuable territory (e.g. due to a higher tenure length) will have a higher chance to dominate intruders than residents with a less valuable territory. This has indeed been found in birds and fish (e.g. Zayan, 1974, 1975; Heuts, 1979; Krebs, 1982; Beletski and Orians, 1989; BAH, unpublished data). The pay-off asymmetry hypothesis, further, predicts that intruders that manage to build up a certain tenure length of the territory while the resident is temporarily absent or not aware of the presence of the intruder, will be more aggressive and have a higher chance of winning the fight against the resident if the tenure length of the intruders becomes longer (Bradbury and Vahrenkamp, 1998). Thus, all other factors being neutralized, the residency effect (fight winning probability of the residents) should be greater in structurally diverse and resource-rich environment than in structurally poor environments without resources. This prediction was tested in seven species of fish by conducting a pure prior-residency experiment in two experimental situations, i.e. in aquariums with sand, plants, stones, pots, etc. and aquariums devoid of these structures.

Moreover, a number of studies have found that the duration of fights won by intruders was generally greater than fights won by residents (e.g. Zayan, 1974; Riechert, 1978; Smith and Arcese, 1989; Leimar et al., 1991). Hence, it was expected that the difference in duration between resident-won and intruder-won contests would be greater in the rich than in the poor aquarium environment, i.e. extra long dominance settlement latency times

were expected if intruders won the fight in the rich aquarium environment, as opposed to shorter latency times if intruders won in the poor environment.

2. Material and methods

2.1. Subjects and material

Seven species of three fish orders, i.e. Characiformes, Cyprinodontiformes, and Perciformes, were tested (see Table 1). All fish came from the laboratory stock at the Department of Animal Behaviour, University of Amsterdam and were originally obtained from Mollienisia fish retailer, Amsterdam. They were normally maintained in a number of large (200 l) community tanks. For the experiments the fish were isolated in identical plexiglass aquariums (25 × 16 × 18 cm) or all-glass aquariums (30 × 20 × 20 cm). Water was maintained at ca. 22°C and was charcoal-filtered. The fish received Tetramin flake food daily, always after the experiments. The enrichment consisted of sand and small pebbles on the aquarium bottom, black tape on the outer aquarium wall, pots and naturally shaped pits in the sand bottom. Plants, pots, and pits may be valu-

able resources during reproduction, as they can be used e.g. to deposit eggs. Black tape on the outer aquarium wall and other visual cues have been demonstrated to increase the RHP (dominance probability) of the resident (de Boer and Heuts, 1973). The poor environment consisted of aquariums without any sand on the bottom, nor any other garniture. Both members of any resident-intruder pair had been isolated before during exactly the same time period, either both in an enriched aquarium, or both in a bare ('poor') aquarium. The isolation period differed between species based on experience gained in previous experiments (Heuts, 1979) and varied from a few hours to 7 days. The test period (observation time) of the resident-intruder pairs after their assemblage was 30 min. Table 1 gives details on the enrichment and isolation periods for each of the seven species.

2.2. Procedures

The applied prior residence schedule followed the procedure described by de Boer and Heuts (1973). A resident-intruder pair was constituted by introducing an intruder into the aquarium of a resident fish. Both resident and intruder were netted out of their aquariums and introduced into

Table 1
Study species and potentially valuable enrichment of the aquarium

Order	Sex (m/f)	Maximum difference in body length	No. pairs	Isolation period (days)	Potentially valuable enrichment
<i>Species</i>					
Characiformes					
<i>Hyphessobrycon eques</i>	m + f	<5%	13	1–4	Sand, pebbles, small snails, plants, tape on wall
Cyprinodontiformes					
<i>Xiphophorus helleri</i>	m	<10%	62	1–7	Sand, pebbles, small snails, plants, tape on wall
<i>Xiphophorus maculatus</i>	m	<10%	28	1–4	Sand, pebbles, small snails, plants, tape on wall
<i>Aphyosemion gardneri</i>	m	<5%	23	1–4	Sand, pebbles, small snails, plants, tape on wall
Perciformes					
<i>Pseudocrenilabrus multicolor</i>	m + f	<10%	120	1/8–2	Naturally shaped pit in sand
<i>Haplochromis burtoni</i>	m	<5%	60	1–2	Naturally shaped pit in sand
<i>Pelvicachromis taeniatus</i>	m + f	<3%	66	1–6	Pit on sand with lateral opening

Table 2

Dominance frequencies of residents ('R') and intruders ('N') in structurally diverse and resource-rich ('Rich') and structurally poor ('Poor') aquariums^a

Species	Rich R:N	Poor R:N	Trend
<i>Hyphessobrycon eques</i>	6:4	4:5	+
<i>Xiphophorus helleri</i>	16:5*	10:7	+
<i>Xiphophorus maculatus</i>	7:4	2:4	+
<i>Aphyosemion gardneri</i>	5:6	5:7	+
<i>Pseudocrenilabrus multicolor</i>	15:3*	18:15	+
<i>Haplochromis burtoni</i>	9:2	11:3	+
<i>Pelvicachromis taeniatus</i>	15:2*	9:7	+

^a 'Trend' (plus sign) indicates that residents compared to intruders more often gained dominance in the rich than in the poor aquariums.

* Significant difference between the dominance frequency of residents and intruders ($P < 0.05$; binomial test).

the aquarium of the resident fish. A resident-intruder pair usually comprised fish slightly differing in size (see Table 1; standard length not including the tail fin). The number of larger residents did not diverge more than 10% from the number of larger intruders in any of the seven tested species.

Immediately after the introduction continuous behavioural recording started (Martin and Bateson, 1993). The following behavioural patterns are considered in this paper:

1. A *dominance sign* is a suddenly accelerated approach towards the opponent which is associated with, or immediately followed by, rapidly swimming away or slowly swimming away with depressed back fin of the approached fish.
2. A *dominance decision* is a succession of six identical dominance signs by one of the two opponents. That individual is subsequently referred to as the dominant partner (cf. de Boer and Heuts, 1973; Ribowski and Franck, 1993).
3. An *attack* is a suddenly accelerated approach without regard of the behaviour of the approached fish. An attack can include a bite or a bite attempt.
4. A *tail beat* is a sudden, heavy and short, often repeated undulating movement through the whole body in the horizontal plane with maxi-

mally spread fins, mostly performed during lateral display.

For statistical analysis Siegel (1956) was used. Yates correction for continuity was applied where appropriate.

3. Results

Size clearly favoured winning probability, as the larger partner predominantly gained dominance in all species (binomial test, $P < 0.05$ in each species). When rich and poor environments were combined the prior residency effect was apparent in four species as the residents became significantly more often the dominant partner than the intruders (Table 2: *Xiphophorus helleri*, binomial test, 26 vs. 12, $P < 0.05$; *Pseudocrenilabris multicolor*, 33 vs. 18, $P < 0.05$; *Haplochromis burtoni*, 20 vs. 5, $P < 0.05$; *Pelvicachromis taeniatus*, 24 vs. 9, $P < 0.01$). However, a significant prior residency effect was not apparent in the first attack or number of attacks prior to the first dominance sign in any of the separate or combined species.

In none of the individual species did we find a significant difference in the residency effect between the rich and the poor environment. However, *P. taeniatus* showed a clear trend in this direction (resident/intruder dominance frequency 15/2 in rich vs. 9/7 in poor environment, Fisher exact probability test, $P < 0.10$). In each species residents were proportionately much (or slightly) more often dominant than intruders in the rich compared to the poor environment (Sign test, $N = 7$, $x = 0$, $P < 0.02$; Table 2). This means that the rich environment favoured resident dominance significantly more than the poor environment did for the seven species as a whole. If each of the individual species receives the same weight while reducing the sample size of each species to the sample size of the least frequently tested species (*X. maculatus* with 17 test pairs) the contrast between relative resident-dominance in the rich versus the poor test environments for the combined reduced numbers of the seven species is only marginally significant in a two-by-two table, i.e. the ratio of resident- to intruder-won fights

was marginally significantly larger in the rich than in the poor environment ($\chi^2 = 2.79$, $df = 1$; $P < 0.10$).

Individuals which scored the first dominance sign were most likely to end up as the dominant partner, i.e. the first to score six successive dominance signs in each of the seven species under study (binomial test, always $P < 0.05$). Latency times of the first dominance sign in dyads won by residents did not significantly differ from latency times in dyads won by intruders in any of the seven species, nor in the pooled data of the species (Mann–Whitney U test, all $P > 0.05$). Furthermore, first-dominance-latency times in rich and poor aquarium environments did not significantly differ from each other in the individual or combined species (Mann–Whitney U test, all $P > 0.05$).

In only two species residents in the rich environment showed significantly more attacks than intruders (*P. multicolor*, $\chi^2 = 3.90$, $df = 1$, $P < 0.05$; *X. helleri*, $\chi^2 = 3.85$, $df = 1$, $P > 0.05$). Generally, a relation between dominance and the number of attacks was not found prior to the first dominance sign in data of separate or combined species.

In contrast to dominance, the resident-intruder difference in aggressive behaviour in the rich environment did not significantly differ from the poor environment if the results of all species were pooled. A significant rich–poor difference pertaining to the aggression of single species was only found in *A. gardneri*, in which residents surpassed intruders in their tail beat frequency significantly more often in the rich-environment test pairs than in the poor-environment test pairs (surpassing/not-surpassing = 7/2 and 2/10 in the rich and poor environment respectively: Fisher exact probability test, $P < 0.05$).

4. Discussion

The present study confirms the general conclusion drawn by Bradbury and Vahrenkamp (1998) that both game models and empirical studies demonstrate that previous exposure to (familiarity with) a contest area ('territory') increases the chance of winning the contest.

It was demonstrated that, at least in fish, exposure to a rich environment with a potentially high reproductive value, leads to an increase of the owner's RHP, as the owner significantly more often won fights in it than in a poor environment when meeting intruders. This is a clear demonstration of the apparent asymmetry in the valuation of a territory by residents compared to intruders, and hence, it supports the pay-off asymmetry hypothesis. In contrast, aggression, as defined by attacks, did not show such a clear relationship.

In the present study, factors which might be responsible for the increased valuation of the aquarium environment include: (i) a potential increase in mate acquisition; (ii) investment in an all-purpose territory which also might attract mates; (iii) increased knowledge of the food and hiding places; (iv) negotiation of territory boundaries, although the nearest neighbours were in adjacent aquariums with whom only visual contact was possible.

Similar to the experiments of Zayan with *X. helleri* (1975: p. 478, Table 16) a significant relationship was not found between rate of aggression before the first dominance sign and dominance. This suggests that dominance and aggression are at least partially guided by different motivational systems (cf. Zayan, 1974; Heuts, 1979). As reviewed by Zayan (1975) there seems to be a clear relation between aggression and dominance once a stable dominance hierarchy has become established, but prior to dominance settlement this relationship seems to be absent.

Several studies have found that take-over (intruder-won) contests are longer than owner-won contests (Zayan, 1974; Riechert, 1978; Smith and Arcese, 1989; Leimar et al., 1991). Such differences were not found when latency times of first dominance sign in take-over contests were contrasted to owner-won contests. The latency times of first dominance sign were neither a reliable predictor of contest outcome (resident or intruder dominance), nor a reliable predictor for contest duration. Likewise, significant differences were not found between rich and poor environments with respect to the latency time of the first dominance sign.

Finally, the authors wish to make two cautious comments on the methodology of prior residence experiments employed so far, that may preclude drawing straightforward inference about the exact role of prior residency. Firstly, the intruders gain experience with one additional new environment compared to the resident at the moment the observations start. Thus, in the usual prior residence experiments the intruders get the opportunity to know two new environments after their removal from the community tanks, whereas the residents get to know only one new environment outside the community tank. The experiment could also be carried out with residents that have been exposed to e.g. three new environments and intruders that have been exposed to only two new environments. Secondly, residents and intruders are not tested with identical opponents, i.e. residents meet an intruder opponent, whereas intruders meet a resident opponent. Hence, the residents' dominance advantage could be explained by this opponent-difference instead of being explained by the difference in familiarity with the test area. Ideally, identical opponents (third parties) should be presented to the residents and intruders, such as conspecifics that are intermediate between residents and intruders with respect to familiarity with (prior exposure to) the test aquarium (intermediate because they e.g. have experience with only a part of the visual cues of the resident's aquarium). Another type of experiment is e.g. to use 'intermediate resident opponents' that have been exposed to the test aquarium during a shorter time than the residents (while using residents that were exposed several times in succession to an aquarium that may only be equivalent to the prospective test aquarium).

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