

Correlation between male size and territory quality: consequence of male competition or predation susceptibility?

Ulrika Candolin and Heinz-Rudolf Voigt

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Territory characteristics correlate with male characteristics in several species. This can result from male competition for the best territories, or from males varying in their ability to pay other costs of territoriality, such as predation risk costs. In a population of threespine sticklebacks, *Gasterosteus aculeatus*, we found the biggest males to defend the biggest territories with a low structural complexity and a high female encounter rate. By experimentally manipulating competition intensity and habitat structure, we show that both male competition and predation exposure influenced the distribution of territories among males. Males increased the size of their territory when a neighbouring male was removed, whereas they reduced their territory when habitat complexity and cover from predators were reduced, with large males reducing their territory size less than smaller males. This suggests that large males occupy large, open territories both because of their superior competitive ability and because of their either lower predation susceptibility or higher risk-taking. Large, open territories were beneficial in mate attraction and male competition and predation exposure therefore biased mating opportunities towards large males. This suggests that cost of territoriality to males may reduce mate choice costs to females by securing that large males are encountered more often than small males, and by providing an additional cue, territory quality, which indicates which males are worth inspecting.

U. Candolin, Dept of Biology, FIN-20014 University of Turku, Finland (present address: Dept of Zoology, Univ. of Bern, Wohlenstr. 50a, CH-3032 Hinterkappelen, Switzerland [ulrika.candolin@esh.unibe.ch]). – H.-R. Voigt, Dept of Limnology and Environmental Protection, FIN-00014 University of Helsinki, Finland.

In species where males establish breeding territories a correlation is often found between male traits and territory characteristics, such as between body size and territory size or location (e.g. Price 1984, Balmford et al. 1992, Roithmair 1994, Bart and Earnst 1999). This can be due to either male competition for the best territories, or to males differing in their ability to pay other costs of territory maintenance, such as predation risk costs or energetic costs (Andersson 1994). Several studies have demonstrated an effect of competition and dominance status or condition on territory characteristics, such as on territory size, tenure or quality (e.g. Cutts et al. 1999, Alcock 2000, Heg et al. 2000). Less

attention has, however, been given to the other factors that could also influence individual variation in territory quality. Especially predation susceptibility and risk taking could influence territory characteristics if predation exposure depends on the size and location of the territory. The optimal territory could then differ among individuals, depending on their predation susceptibility and preparedness to take risks.

If the ability to pay social and predation risk costs of establishing and maintaining a territory depends on male quality, then the cost of territoriality could secure that the best male occupies the best territory. This could increase the benefits of female choice by securing

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that the choice of the best male also results in the choice of the best territory that provides the most direct benefits to the female, or vice versa, that the choice of the best territory secures the choice of the best male. Alternatively, a correlation between male characteristics and territory characteristics may increase the number of cues that can be used in mate choice, which may facilitate female choice by decreasing mate choice costs and errors (Johnstone 1996, Candolin and Reynolds 2001).

In the threespine stickleback, *Gasterosteus aculeatus*, males establish territories during the breeding season to which they attract females to spawn (Wootton 1976). Most studies have, however, concentrated on the importance of male traits in determining mating success whereas less attention has been given to territory characteristics (see review in Rowland 1994). Male traits, such as red nuptial coloration and courtship behaviour, are highly flexible and are influenced by both male competition and predation risk (Candolin 1998, 1999a). Especially male competition influences red colour expression by increasing the difference among males in colour expression and by increasing the honesty of the colour as a signal of male parental ability (Candolin 2000). It is possible that male competition and predation exposure also influence territory characteristics (Rowland 1994, Whoriskey and FitzGerald 1994, Candolin and Voigt 1998). Male competition and predation risk could then influence mating success by influencing both male traits and territory characteristics. Breeding sticklebacks are highly susceptible to predators due to their bright red coloration and their conspicuous courtship behaviour (Moodie 1972, Whoriskey and FitzGerald 1985a).

We investigated whether a relationship between male size and territory quality exists in the field and if this is influenced by male competition or predation exposure, or both. Although larger males are better competitors for territories and females (Rowland 1989, Bakker 1994, Baube 1997), male size might also determine the susceptibility to predation, or alternatively, the amount of risk a male is willing to take. The distribution of males could then as well be due to size-dependent risk-taking or predation susceptibility as to competitive ability.

Methods

We carried out the study in a shallow bay in the Baltic Sea in southern Finland (60°N, 23°E). The density of breeding sticklebacks is high in the bay and habitat structure varies from stony bottoms with dense algae growth (mainly *Fucus vesiculosus* and *Cladophora glomerata*) to sandy patches with sparse

vegetation. The predation pressure is high with terns (*Sterna hirundo* and *S. paradisaea*) circling over the bay for most of the day during the breeding season. Fish predators are scarce as fish that prey on sticklebacks seldom enter the bay through the narrow connection with the sea. The bay has steep rocky shores and a big stone in the middle from which the sticklebacks can easily be observed.

We did the investigation at the height of the breeding season, 2–22 June 1994, between 08:00 and 17:00. We determined the relationship between male size and territory quality for 48 randomly chosen males and then investigated the influence of male competition and cover from predators on territory characteristics. We first observed each territorial male for 30 min and marked the position of his nest and his territory on a map. Territory size was determined by observing the behaviour of the male and was measured as length \times width. This was due to most territories being rectangularly formed with the territory stretching along large stones under which the nest was built. The habitat structure of the territory was determined by estimating the percentage of the territory that was open and not covered by large stones or high algae that obstructed the view. The activity level of the male was determined as the percentage of the time that he could be seen in his territory, i.e. when he was not at the nest or hiding among the stones and algae. The number of females that visited the territory was noted. Immediately after the 30 min of male observations, the male was randomly subjected to one of three treatments described below.

Male competition

We investigated the effect of male competition on territory and male characteristics for 12 males by removing a neighbouring male with a hand net and 2 h later observing the focal male for another 30 min. All males resumed normal behaviour within a few minutes after the neighbouring male had been removed.

Predation exposure

We investigated the influence of habitat structure and exposure to predators on territory and male characteristics by manipulating habitat structure and 2 h later observing the male for 30 min. For 12 males, the structural complexity of the territory was reduced by removing about 20% of the stones and algae, and for 12 males the structural complexity was increased by adding stones and algae by about 20%. All males resumed normal behaviour within 30 min after the territory had been manipulated.

Control

We left the territories unmanipulated for 12 males but disturbed the water so that the males would experience the same disturbance as the males whose territories were manipulated. Two hours later we observed the males for 30 min.

After experimentation, we caught each male with a hand net or a Plexiglas trap and determined his standard body length to the nearest mm. We cut the tip of his posterior dorsal spine so that he could be recognised and would not be observed twice, and released him back into the sea. We were unable to inspect the nests for eggs for most males, as the nests were under or between stones that were too heavy to move. Male size varied between 46 and 58 mm (mean \pm SE = 52.8 mm \pm 0.4).

To estimate the relationship between habitat complexity and predation pressure, we compared the attack rate of terns in two 2 \times 2-m large areas with different habitat structure, about 25% open and 75% open, during 4 d, for 2 h in the mornings of each day. We then changed the structure of the two areas by adding or removing algae so that the proportions were reversed, i.e. to 75% and 25% open, respectively. The following 4 d, we observed the attack rate of terns in the areas. Since habitat manipulation can change the number and activity of sticklebacks, we recorded the mean number of sticklebacks that could be sighted within 1 m² of each area both when the habitat was unmanipulated and when it was manipulated. This was done by observing the areas once every 5 min for 30 min once a day during the 8 d of tern observations.

Results

Male size correlated positively with territory size, the openness of the territory, and female encounter rate, but not with the activity level of the male (Table 1). Thus, large males occupied the largest territories that had a low structural complexity and a high female encounter rate.

The removal of a competing male resulted in an increase in territory size and in female encounter rate (Table 2). This occurred despite the fact that the vacated territory was occupied by a new male in at least 5 cases.

The increase in structural complexity had no significant influence on male territory size or on female encounter rate (Table 2). The reduction in structural complexity led to a reduction in territory size and an increase in female encounter rate (Table 2). The reduction in territory size depended on male size with large males reducing their territory size less than smaller males (interaction term in repeated measures ANCOVA with male size as covariate, $F_{1,10} = 8.67$, $p = 0.015$). The responses to increased structural complexity and competitor removal did not significantly depend on male size ($p > 0.1$).

The attack rate of terns was higher in the habitat with lower structural complexity both before and after habitat manipulation; before manipulation: 0.62 (\pm 0.25 SD) attacks/h compared to 0.25 (\pm 0.29) attacks/h in the more complex habitat (Wilcoxon matched-pairs signed ranks test on values per hour; $N = 8$, $T^- = 0$, $p < 0.05$), after manipulation: 0.75 (\pm 0.29) attacks/h compared to 0.25 (\pm 0.29) attacks/h in the more complex habitat ($T^- = 0$, $p < 0.05$). The attack rate is still higher in the open area when adjusting for the mean number of sticklebacks observed in the areas at a given time (due to more fish being observed in the more complex habitat); before manipulation: 1.03 (\pm 1.37) attacks h⁻¹ fish⁻¹ compared to 0.20 (\pm 0.39) attacks h⁻¹ fish⁻¹ in the more complex habitat ($T^- = 0$, $p < 0.05$), after manipulation: 0.94 (\pm 0.68) attacks h⁻¹ fish⁻¹ compared to 0.25 (\pm 0.47) attacks h⁻¹ fish⁻¹ in the more complex habitat ($T^- = 0$, $p < 0.05$). Thus, the attack rate per fish in a given area increased when the structural complexity of the habitat was reduced (Mann-Whitney U -test; $N = 8$, $U = 10.5$, $p = 0.016$) and tended to decrease when structural complexity was increased ($U = 16.0$, $p = 0.064$).

Discussion

Big males defended the biggest territories with a low structural complexity and a high female encounter rate. This could be due to big males being competitively superior in the competition for the best territories, or to big males either experiencing lower viability costs of large, open territories, or receiving larger mating benefits and therefore investing more in territorial maintenance and risk taking. The experimental manip-

Table 1. Spearman's rank order correlation coefficients between different male and territory characteristics.

	Male size	Territory size	Territory structure	Female encounters	Male activity
Male size	1				
Territory size	0.80*	1			
Territory structure	0.78*	0.64*	1		
Female encounters	0.66*	0.72*	0.53*	1	
Male activity	0.11	0.15	0.20	0.12	1

$N = 48$. * $p < 0.001$.

Table 2. Male and territory characteristics (mean \pm SE) before and after territory manipulation.

	Before	After	<i>t</i> or * <i>T</i> –	<i>p</i>
A. Removal of competitor				
Territory size (dm ²)	29.2 \pm 4.9	31.9 \pm 4.6	3.22	0.008
Territory structure (% open)	51.1 \pm 6.1	53.8 \pm 5.4	1.41	0.19
Female encounters/30 min	1.17 \pm 0.37	1.75 \pm 0.41	*0	0.001
Male activity (%)	37.5 \pm 2.4	34.2 \pm 1.4	1.50	0.16
B. Increased habitat complexity				
Territory size (dm ²)	24.7 \pm 4.5	25.3 \pm 4.4	0.95	0.36
Territory structure (% open)	61.3 \pm 5.2	41.7 \pm 4.8	47.00	0.000
Female encounters/30 min	1.00 \pm 0.30	0.83 \pm 0.21	*46	0.60
Male activity (%)	33.9 \pm 2.0	33.5 \pm 1.3	0.23	0.82
C. Reduced habitat complexity				
Territory size (dm ²)	21.8 \pm 2.9	16.8 \pm 3.2	4.69	0.001
Territory structure (% open)	58.8 \pm 4.6	78.8 \pm 4.6	8 \times 10 ¹⁶	0.000
Female encounters/30 min	1.17 \pm 0.27	1.58 \pm 0.26	*0	0.001
Male activity (%)	32.3 \pm 2.0	31.8 \pm 1.78	0.23	0.82
D. Control				
Territory size (dm ²)	27.6 \pm 3.7	27.8 \pm 3.7	0.26	0.80
Territory structure (% open)	60.0 \pm 4.1	60.8 \pm 4.1	1.00	0.34
Female encounters/30 min	0.92 \pm 0.26	1.00 \pm 0.21	*28	0.46
Male activity (%)	35.3 \pm 2.5	34.5 \pm 1.8	0.54	0.60

Paired *t*-test and * Wilcoxon matched-pairs signed ranks test were used. *N* = 12.

ulation of competition intensity and habitat structure suggests that both male competition and cost of territory maintenance in terms of predation exposure influenced the distribution of territories among males. Male competition influenced territory size as males increased the size of their territory when a neighbouring territorial male was removed. Predation exposure, on the other hand, appeared to influence territory size as males reduced their territory when the complexity of the territory was reduced. That habitat complexity does influence predation pressure is demonstrated by the change in the attack rate of terns with the change in habitat complexity. It is possible, however, that the reduction in territory size was also due to changes in other factors than predation exposure that changed with a change in habitat complexity. Nevertheless, increased predation pressure was most likely one of the main factors that induced the change in territory size, as predation pressure is high in the present bay and an important mortality source.

Interestingly, the increase in structural complexity did not significantly influence territory size. This suggests that male competition sets an upper limit to the size of a territory and that a male cannot further increase his territory when the predation cost of the maintenance of a large territory is reduced. Competition for territories appears to be high in the present bay, as experimentally vacated territories were quickly occupied by new males. This contrasts with some other stickleback populations where nest sites appear not to be limited (Whoriskey and FitzGerald 1985b).

Whether large males took larger risks or experienced lower risk than small males by maintaining large territories with a low structural complexity is not known. It

is possible that they were at lower risk because of their larger size or because of better escape tactics. Small fish usually experience higher predation pressure than larger fish (Sogard 1997) and an indication of this has been found in the stickleback with bird predators (Krause et al. 1998). However, large males might take larger risks than small males if they have fewer future reproductive opportunities and therefore invest in breeding as a terminal effort (Candolin 1999b). This might be the case if the largest males are the oldest males that will soon die.

Large males probably competed for and maintained large, sparsely vegetated territories because of their benefit in mate attraction. The rate of female encounters correlated with the size and openness of the territory, and an increase in the size or openness of a territory resulted in an increased female encounter rate. It is notable that the reduction in habitat complexity increased female encounter rate despite reducing the size of the territory. Thus, the openness of the territory was more important than the size of the territory in determining female encounter rate. This could be due to increased visibility of males in open habitats, or to a female preference for open habitats. There might, however, be a limit to how open a habitat may be and still be beneficial. In the present bay some vegetation is always present and hiding places are always found. Open sand bottoms do not occur. It is likely that both males and females would have avoided areas without vegetation and hiding places, as have been found in earlier correlative and experimental studies (reviewed by Whoriskey and FitzGerald 1994).

Habitats with a low structural complexity may, however, be costly not only to males but also to females by

increasing the risk of predation. This makes the finding of higher female encounter rate in open territories intriguing. It is possible, however, that the increased predation risk cost is offset by reduced search time, due to increased visibility of males, or to an increased encounter rate with high quality males. Large males that maintain large, open territories under intense male competition and high predation pressure may be of high genetic and/or phenotypic quality. Moreover, it is possible that only males of high phenotypic quality court females in predator exposed areas as habitat complexity is known to influence courtship activity under the risk of predation (Candolin and Voigt 1998). Thus, costs of establishing and maintaining a territory could ensure that the best males occupy the best territories, as proposed by the handicap theory (Zahavi 1975). Territory quality would then signal male quality. Laboratory experiments have found that large males are preferred by females (Rowland 1989) and have a higher mating success than small males in the field (Kraak et al. 1999). However, as far as we know, this is the first demonstration that environmental conditions, such as the presence of competitors and predators, can bias mating opportunities towards large stickleback males.

The assumption that predation risk ensures that high quality males occupy the best territories with a high female encounter rate rests on the assumption that large males are high quality males that are less susceptible to predators. If it turns out that large males defend more open territories than small males because they take larger risks, then the choice of a large male with a predator exposed habitat may not necessarily result in the choice of a good father or of a male of high genetic quality. The only benefit a female might then receive by mating with the most visible male may be reduced search time. The costs of maintaining a territory with a high female encounter rate could then even result in a bias in mating opportunities towards poor quality males, which could increase the costs or errors of female mate choice. However, large males have been found to have a higher reproductive success than smaller males in another stickleback population (Kraak et al. 1999) and in some other species (e.g. Bisazza and Marconato 1988, Wiegman and Baylis 1995). It is therefore likely that large males are good fathers. Moreover, male size may correlate with viability and indirect genetic benefits as has been found for other species (e.g. Simmons 1987, Reynolds and Gross 1992).

To conclude, this study shows that male size correlates with territory quality and females encounter rate in a stickleback population. This is due to both male competition and predation exposure determining the distribution of territories among males. Thus, environmental conditions and costs of territoriality bias mating opportunities towards large males, which might facilitate female choice.

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