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ORIGINAL ARTICLE

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Do changes in risk-taking affect habitat shifts of sticklebacks?

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Abstract The distribution of individuals is often the outcome of conflicting demands, such as between predator avoidance and reproduction. A factor that has seldom been considered in studies on habitat choice is time-dependent changes in risk-taking. We investigated the distribution of threespine sticklebacks, *Gasterosteus aculeatus*, over two breeding seasons and found it to change with time towards shallower areas with a more open habitat structure. Shallow and structurally less complex habitats were probably favorable due to a higher reproductive rate, but costly due to an increased risk of predation. Contrary to expectation, changing predation pressure was not a predictor of the shift in habitat use and, thus, not the proximate cue. Instead date was the main predictor. This suggests that increased risk-taking in relation to predation contributed to the habitat shift. The possibility was supported by a laboratory experiment that showed sticklebacks to take larger risks and prefer more predator-exposed areas at the end of the season than at the start of the season. These results demonstrate that temporal changes in risk-taking occur and can influence habitat choice, which points to the importance of considering risk-taking, in addition to predation pressure, when studying the effect of predators on distribution.

Keywords Habitat complexity · Predation risk · Predator-prey interaction · Refuge use · Reproduction

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Introduction

The distribution of individuals within a habitat is often the outcome of conflicting demands, such as between feeding and predator avoidance or between reproduction and predator avoidance (Sih 1997; Alonzo 2002; Lima 2002). Several studies have found predation risk to be one of the main factors that determine the distribution of individuals (Kerfoot and Sih 1987; Lima and Dill 1990; Norrdahl and Korpimäki 1998; Rochette and Dill 2000; Forsman et al. 2001). To reduce predation risk, prey often stay in structurally complex habitats where the movement or vision of the predator is restricted and the risk of predation reduced (Savino and Stein 1989). These habitats may be costly in terms of lower foraging rate, increased energy loss due to increased competition and activity, or less favorable environmental conditions for reproduction. Thus, whether an individual should stay in a low risk or move to a high-risk habitat depends on the costs and benefits of the use of each habitat (Gilliam and Fraser 1987; Mangel and Clark 1988; Houston and McNamara 1999).

Several studies have investigated how habitat use, and especially refuge use, depends on different factors such as the size and predation susceptibility of individuals (Krause et al. 1998; Persson and Crowder 1998), food availability and hunger (Koivula et al. 1995; Dill and Fraser 1997), and predation intensity (Scarratt and Godin 1992; Sih 1992; Persson and Eklöv 1995; Johansson and Englund 1995). A factor that has received less attention, but which might have a profound influence on habitat use, is the extent of changes in the risk of predation that an individual is prepared to take. According to life-history theory, risk taking and investment into reproduction may increase towards the end of the lifetime when the pay-off from investment into survival decreases (Charlesworth 1980; Roff 1992). The use of predator-exposed habitats could therefore increase when the prospect of survival and future reproductive opportunities decreases.

In the threespine stickleback, *Gasterosteus aculeatus*, large variations have been found both within and among populations in the choice of nest site, ranging from open sand to concealed sites in dense vegetation (Whoriskey and FitzGerald 1994). The underlying cause of this variation is largely unknown, but differences in predation risk have been suggested to be one of the influencing factors (e.g., Moodie 1972). We investigated the distribution of threespine sticklebacks over two breeding seasons, and related changes in distribution, to changes in environmental conditions and decreasing future reproductive opportunities. We especially investigated changes in predation pressure and possible changes in risk-taking in relation to predation, as predators are known to induce a preference for vegetated nest sites where predation risk is lower (Candolin and Voigt 1998). Earlier studies have found sticklebacks with a low probability of future reproduction to increase their risk-taking by adjusting their courtship activity with less regard to predators and by increasing their investment in a costly sexual signal, red nuptial coloration (Candolin 1999, 2000). It is possible that sticklebacks also increase their risk-taking in their choice of a habitat towards the end of the season. Sticklebacks in the present area have only one breeding season, at the age of 2 years, during which they breed repeatedly. During this time, they can complete up to at least three breeding cycles in the field (Candolin, personal observation) and up to six breeding cycles in the laboratory (Candolin 2000). We carried out both a correlative field study, in which we investigated the distribution of sticklebacks during two breeding seasons in a bay with a high predation pressure, and an experimental laboratory study where we allowed males breeding at different times of the season to choose a breeding site and court females in the presence or absence of predators.

Methods

Field study

We studied the distribution of sticklebacks in a shallow bay in the archipelago near Tvärminne Zoological Station in southern Finland over two breeding seasons, from 1 May to 18 July 1994 and from 1 May to 13 July 1996. The fish are anadromous and arrive in the bays at the beginning of May, the adults disappearing in July while the juveniles stay until autumn (Candolin and Voigt 2003). The bay is about 30 m long and up to 15 m wide with a maximum depth of about 1.5 m. Habitat structure varies from open sand bottom to dense algae growth (mainly *Fucus vesiculosus* and *Cladophora glomerata*). The predation pressure from terns (*Sterna hirundo* and *S. paradisaea*) is high with terns circling over the bay for most of the days. Fish predators have never been observed in the bay, due to a narrow connection with the sea. We caught sticklebacks with transparent Plexiglass traps every second to fourth day, depending on weather conditions, at two different water depths and in habitats of two different structures. The placement of the traps was randomized within the depth and habitat zones to avoid repeatedly catching the same territorial males. Both territorial and non-territorial individuals were caught with the traps (Candolin and Voigt 2003). The traps were 20×20×40 cm and had wings, 20×60 cm, that directed fish towards the opening of the trap, 1.5×20 cm. We had four sampling areas, two with a low structural complexity (about 25% of the sampled area covered by large stones and larger algae, mainly *F. vesiculosus*) and two with a high structural complexity (about 75% coverage). Structural complexity did not change markedly over the season, as *F. Vesiculosus* is a slow growing algae. In each sampling area we caught sticklebacks from two locations with different water depths, 30 cm and 80 cm, 30 cm being closer to the shore. We placed two traps at each water depth (16 traps in total). The shortest distance between the four sampling areas was about 10 m and the distance between the two water depths within the areas was 1–3 m. The traps were put out in the afternoon and taken up the following day at noon. Sticklebacks and terns were active most of this time as the dark period is short at this time of the year in the study area. The sex of the fish was determined when possible, i.e. when the fish were in breeding condition and nuptially colored or gravid. Only adult fish over 40 mm were counted. The fish were released back at the site of capture after measurements.

In 1994, temporal variation in predation pressure from terns was recorded by noting the number of attacks by terns in the bay during 1–2 h/day over the season. Attack rate is given both as absolute attack rate and as relative attack rate by dividing attack rate by the number of fish caught on that day. The observations were carried out in the mornings of the same days as the traps were emptied of fish, throughout the breeding season. The temperature of the water was measured at depths of 30 and 80 cm at noon on each sampling day. Predation pressure, water temperature and number of fish caught were averaged over two consecutive sampling dates to reduce variation in the data that could have arisen due to random factors, such as weather conditions.

The distribution of sticklebacks between the two water depths and the two habitat structures was related to date, predation pressure, water temperature and density of sticklebacks (total number of adult sticklebacks caught in the traps) through multiple logistic regressions, as each individual could choose its preferred water depth and habitat structure, because of the short distances between the sampling points. This assumes that each individual can be considered an independent observation. Because individuals were grouped by the traps, we also carried out analyses of covariance on number of fish caught per trap, with habitat depth and structure as main factors and date and the other variables as covariates. The number of fish per trap was Poisson distributed, which confirms the expectation that the occurrence of one fish in a trap is independent of the occurrence of other fish. We therefore applied a square root +0.5 transformation to the numbers per trap. Covariates that did not influence the dependent variable directly or through an interaction with the main factors were excluded from the analyses, when this did not influence the significance of the main factors. The results were qualitatively similar to the results gained with logistic regression (the same significant effects were found), and we therefore only present the results from the logistic regression. When data from both years were analyzed, we included year as a covariate in the models, but excluded non-significant interaction terms.

Some degree of pseudoreplication is possible if the same fish were caught repeatedly in the traps. However, this is likely to be a rare event as the density of fish is high in the bay. Moreover, pseudoreplication should reduce, and not increase, the probability of finding significant differences in the distribution of fish, making the test more conservative.

Experimental study

To investigate whether preferences for structured habitats and the amount of risk males are willing to take change over the breeding season, we allowed males collected at the start and at the end of the season (6 May and 4 July in 1995) to breed in the absence and presence of predators, according to a 2×2 factorial design. The predators used in the experiment (fish) differed from the predators occurring in the investigated bay (birds), but both fish and bird predators induce a preference for more structured habitats where sticklebacks are more difficult to detect and catch (Candolin and Voigt 1998; Krause et al. 1998). Stickleback males were collected

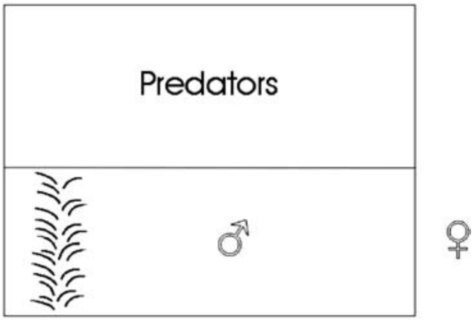

Fig. 1 Experimental aquarium with a predator and a male section with a row of vegetation

from the same bay where the field study had been carried out, from an area with medium habitat complexity (about 50% open) at a depth of 50 cm. They were housed in holding aquaria at 18°C under a natural light cycle for 2–8 days, at a density of ten fish per 125-l aquarium, and then transferred to individual aquaria (60×80 cm). The sticklebacks were fed once a day ad libitum with frozen chironomid larvae. Perch were caught from the sea with a seine just before experimentation and kept in the experimental aquaria for 3–6 days. They were not fed during this time and were all healthy at the end of the trials.

Each experimental aquarium had been divided into a predator and a male section by transparent Plexglass dividers (Fig. 1). Both sections were 30×80 cm. Along one of the short ends of the male section was a row of artificial vegetation (see Candolin and Voigt 1998). The end with the row of vegetation was alternated between replicates. Sand and tufts of algae (*Cladophora*) covered the bottom of the male section and served as nesting material. The males were allowed to breed in either the presence or absence of predators, two perch, *Perca fluviatilis*, 22–30 cm long. Several different predators (12) were used, randomized among replicates. To stimulate nest building and breeding behavior, we showed a model of a gravid female to the male for 10 min twice a day. A dummy female was used to prevent differences in female behavior from influencing male behavior. The dummy female was held outside the aquarium and always at the open short end of the male section, thus creating a trade-off between courtship and perceived predation risk. When the male had built a complete nest, we recorded the location of the nest and the time that the male spent courting the dummy female (see Candolin 1997). Distance of the nest to the row of vegetation was log +1 transformed. The condition factor of the males was calculated as wet weight/(standard body length)^3. For each of the treatments, we tested 15 different males. All fish, both sticklebacks and perch, were released back in the sea after the experiments.

Results

Field study

Table 1 Multiple logistic regression for the determinants of the distribution of threespine sticklebacks, *Gasterosteus aculeatus*, in 1994 and 1996

	Water depth		Habitat structure	
	Wald	*P*	Wald	*P*
All sticklebacks, n=1,793				
Date	255.91	<0.001	35.94	<0.001
Year	3.83	0.051	7.43	0.006
Date×year			12.14	<0.001
Whole model	χ^2=309, df=2, P<0.001		χ^2=131, df=3, P<0.001	
Breeding males, n=549				
Date	55.68	<0.001	16.84	<0.001
Year	0.11	0.739	6.12	0.013
Date×year			12.00	0.001
Whole model	χ^2=63, df=2, P<0.001		χ^2=34, df=3, P<0.001	
Gravid females, n=340				
Date	30.13	<0.001	45.81	<0.001
Year	16.82	<0.001	<0.001	0.964
Date×year	12.35	<0.001		
Whole model	χ^2=90, df=3 P<0.001		χ^2=57, df=2, P<0.001	

The habitat use of sticklebacks changed with time towards shallower water and to habitats with lower structural complexity, with the shift to more open areas occurring earlier in 1994 than in 1996 (Table 1, Figs. 2, 3). The same habitat shifts are found for each sex when analyzed separately (Table 1, Figs. 2, 3). However, females showed more pronounced shifts than males (interaction between date and sex: water depth: Wald=6.06, P=0.014, habitat structure: Wald=15.34, P<0.001). No significant difference was detected between the sexes in the choice of habitat structure (Wald=0.22, P=0.64), or water depth (Wald=3.65, P=0.056).

In 1994, several environmental factors were recorded and two were found to vary over time: the temperature at 30 cm depth increased with time (linear regression: r^2=0.73, b=0.13, $F_{1,10}$=26.50, P<0.001, Fig. 4) and predator attack rate per fish showed a bimodal curvilinear relationship with time, with peaks at the start and end of the season (cubic regression: r^2=0.71, $F_{1,8}$=6.58, P=0.015, Fig. 5). Though nonsignificant, a few other factors showed patterns of potential interest: the density of sticklebacks (total number of fish caught in the traps) showed a peak one month after the start of the breeding season, (quadratic regression: r^2=0.46, $F_{1,9}$=3.90, P=0.060, Fig. 2a), whereas the largest differences in temperature between 30 cm and 80 cm water depth occurred at the end of the season (r^2=0.29, b=0.02, $F_{1,10}$=4.05, P=0.072, Fig. 4). When the environmental factors are included in the logistic regression model, date remained as the main predictor of the distribution of all fish (Table 2). Increased difference in temperature between shallow and deeper water was related to the shift towards shallower water, as was the reduction in fish density later in the season. Predation pressure (as per capita risk) did not predict the changes in habitat use. Correlation between the independent variables, collinearity, which can decrease the reliability of the individual regression coefficients, did not pose a problem as the tolerance of all variables were >0.20 (VIF<5) (Kleinbaum et al. 1988)

When the analysis is restricted to males in breeding condition and to gravid females, date remained as the main predictor of the changes in distribution (Table 2). For gravid females, the shift towards shallower water coincided with increased difference in temperature between 30 and 80 cm water depth, and weakly so with increased temperature of shallow water. Thus, time of the

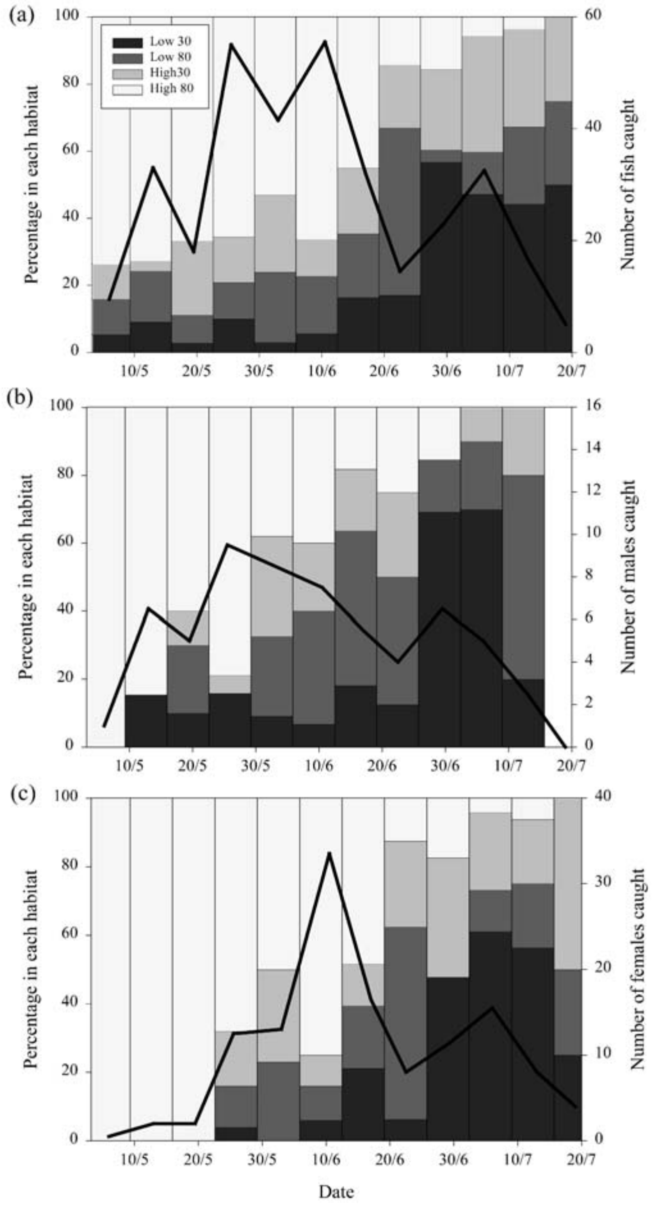

Fig. 2 Number of threespine sticklebacks, *Gasterosteus aculeatus*, caught over the breeding season in 1994 (*line*) and percentage of these that were caught in the four habitats with low or high structural complexity and 30 or 80 cm water depth (*bars*); **a** all fish, **b** breeding males, **c** gravid females

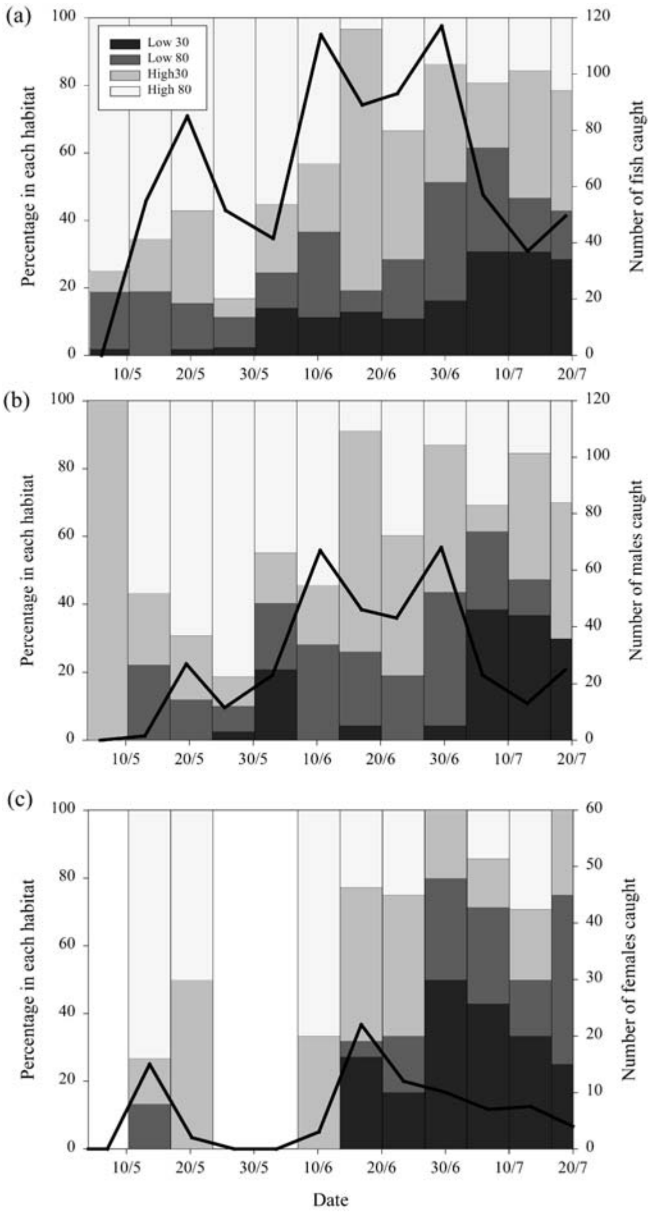

Fig. 3 Number of fish caught over the breeding season in 1996 (*line*) and percentage of these that were caught in the four habitats with low or high structural complexity and 30 or 80 cm water depth (*bars*); **a** all fish, **b** breeding males, **c** gravid females

season, water temperature and density of fish predicted the distribution of sticklebacks, whereas predation pressure was not a direct cause of the shift in distribution.

A relationship occurred between the density of fish and predation pressure in 1994. The density of fish was highest at the end of May and beginning of June when the absolute attack rate by predators was low (i.e. attack rate not corrected for the density of fish) (linear regression, r^2=0.22, $F_{1,21}$=6.07, P=0.022). This occurred at the time when the terns were incubating their eggs (personal observation) and attack rate temporarily decreased (Fig. 5).

Experimental study

Analyses of variance showed a significant interaction between predator treatment and time of the season on the location of the nest and on courtship activity: males breeding at the end of the season reacted less to predators than males breeding at the start of the season. Generally, males built their nest closer to vegetation and performed less courtship in the presence of predators. The significant effect of date on nest location indicates that males breeding at the end of the season generally chose more exposed nest sites than males breeding at the start of the

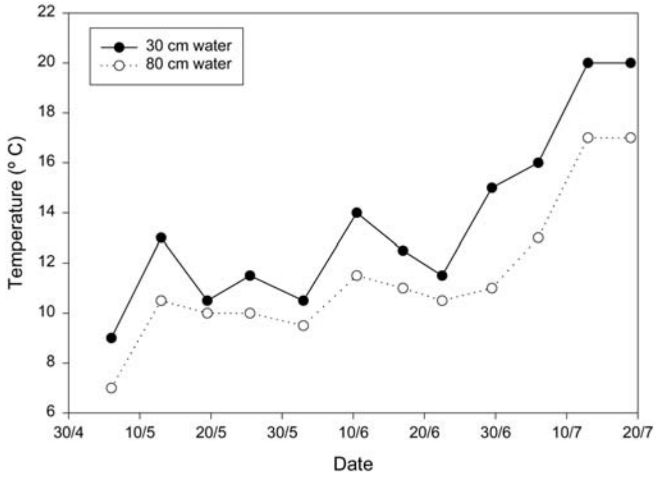

Fig. 4 Water temperature at 30 and 80 cm water depth, averaged over two consecutive sampling dates

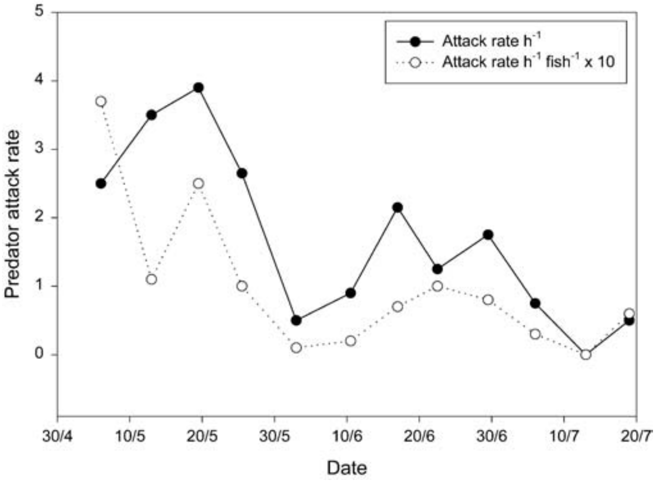

Fig. 5 Absolute attack rate by terns and attack rate per fish (×10), averaged over two consecutive sampling dates

Table 2 Multiple logistic regression for the determinants of the distribution of sticklebacks in 1994

	Water depth		Habitat structure	
	Wald	*P*	Wald	*P*
All sticklebacks, *n*=667				
Date	12.14	<0.001	22.44	<0.001
Predator attack rate (h^{-1} $fish^{-1}$)	1.12	0.291	2.04	0.154
Temperature at 30 cm	2.01	0.156	0.35	0.555
Temperature difference 30–80 cm	11.43	0.001	0.02	0.894
Density of sticklebacks	8.97	0.003	0.08	0.774
Whole model	χ^2=137.61, *df*=5, *P*<0.001		χ^2=90.51, *df*=5, *P*<0.001	
Breeding males, *n*=123				
Date	6.34	0.012	4.76	0.029
Predator attack rate (h^{-1} $fish^{-1}$)	0.01	0.978	0.01	0.917
Temperature at 30 cm	2.00	0.157	0.04	0.840
Temperature difference 30–80 cm	0.99	0.319	0.93	0.336
Density of sticklebacks	0.01	0.975	0.31	0.575
Whole model	χ^2=22.58, *df*=5, *P*<0.001		χ^2=30.79, *df*=5, *P*<0.001	
Gravid females, *n*=250				
Date	5.02	0.025	8.74	0.003
Predator attack rate (h^{-1} $fish^{-1}$)	0.22	0.638	0.01	0.940
Temperature at 30 cm	3.33	0.068	1.84	0.175
Temperature difference 30–80 cm	3.96	0.047	0.94	0.333
Density of sticklebacks	0.36	0.550	0.112	0.737
Whole model	χ^2=76.04, *df*=5, *P*<0.001		χ^2=57.66, *df*=5, *P*<0.001	

Table 3 Breeding characteristics of males breeding at the start and at the end of the season in the absence or presence of predators. Means ±SE are given except for distance to vegetation for which untransformed means are given together with back calculated confidence intervals

	Start of season		End of season		$F_{1,56}$ values		
	No predators	Predators	No predators	Predators	Predator	Date	P× D
Distance to vegetation (cm)	11.1 (3.2–12.2)	1.5 (0.4–1.9)	19.1 (7.9–20.4)	12.9 (6.0–14.5)	13.0**	26.7***	5.91*
Courtship activity (s)	405±35	207±29	401±41	363±28	12.6**	5.13*	5.79*
Body length (mm)	53.7±0.6	54.1±0.6	53.5±0.8	54.8±0.7	1.55	0.17	0.37
Condition factor	12.3±0.2	12.1±0.2	11.2±0.2	11.0±0.2	0.80	26.8***	0.04

* *P*<0.05 ** *P*<0.01 *** *P*<0.001.

season, irrespective of predator presence. Males subjected to the different treatments did not differ in body length, but males tested at the end of the season had a lower condition factor (Table 3). The behavior of the predators did not differ between the two time periods (number of attacks on the sticklebacks per hour: t_{58}=0.76, *P*=0.45).

Discussion

The distribution of threespine sticklebacks changed over the breeding seasons towards shallower water and structurally less complex areas. This could be due to changes in habitat preferences of sticklebacks when environmental conditions or intrinsic properties of the fish change, or to sticklebacks being prevented from aggregating in shallow open areas at the start of the season, because of predation removing individuals or competition with other species excluding sticklebacks. Of these possibilities, changes in direct predation and interspecific competition intensity are unlikely to be the main causes of the shift. Predation pressure by terns, the main predators, was not a predictor of the shift in distribution, and the only other fish species that co-occurs at higher densities with the threespine stickleback is the ninespine stickleback, *Pungitius pungitius*, which is competitively inferior (Ketele and Verheyen 1985) and prefers more vegetated, concealed areas (Wootton 1976). Thus, the temporal shift in distribution is most likely due to changes in habitat preferences.

Why would the habitat preference of sticklebacks change over the breeding season? The choice of a habitat should reflect the costs and benefits of staying in a particular habitat. Shallow water can be advantageous compared to deeper water because of a higher mean temperature that results in faster development time of eggs and juveniles and faster egg production rate in females (Wootton 1976). This increases the rate of reproduction, presuming that enough food is available, and decreases the time that offspring are most vulnerable to predation. Structurally less complex habitats are favorable because of a higher female encounter rate than in structurally highly complex areas (Candolin and Voigt 2001). However, both shallow water and open habitats are costly due to increased risk of predation from terns, which are the major predators on sticklebacks in the present area during the breeding season. Terns frequently catch sticklebacks in shallow water, but are unable to reach sticklebacks at deeper water. Increased structural complexity in turn reduces the risk of predation (Candolin and Voigt 2001) and allows more courtship (Candolin and Voigt 1998). Thus, sticklebacks have to trade between safety and reproductive rate in their choice of a breeding site.

Contrary to expectation, predation pressure was not a predictor of the distribution of sticklebacks and, thus, not the proximate cause of the habitat shift. Instead, date turned out to be the main predictor. Although this does not exclude the possibility that lower predation pressure at the end of the season has favored the evolution of a shift in habitat preferences, the high level of predation at the time the shift occurred suggests that increased risk-taking later in the season could have contributed to the habitat shift. This possibility was supported by the experimental study that found males nesting at the end of the season to react less to fish predators and to prefer more exposed nest sites than males nesting at the start of the season. A possible caveat is that the predators used differed from the main predators occurring in the bay. However, both fish and bird predators induce a preference for structurally more complex habitats where sticklebacks are more difficult to detect and catch (Candolin and Voigt 1998; Krause et al. 1998). Thus, the laboratory experiment demonstrated that changes in risk-taking does occur and can induce a shift in habitat use. The shifts found in the field and in the laboratory are unlikely to be due to a higher proportion of risk-reckless individuals occurring later in the season, as risk-reckless individual are likely to die sooner rather than be the ones to survive to the end of the season. Moreover, earlier studies have demonstrated that time-dependent changes in risk-taking occur, with males becoming more brightly colored (more conspicuous to predators) and adjusting their coloration and courtship activity with less regard to predators when future reproductive opportunities decrease (Candolin 1999, 2000). Time-dependent changes in risk-taking and reproductive investment have also been demonstrated in other fish species with parental care (Magnhagen and Vestergaard 1991; Magnhagen 1992)

The shift in habitat choice could be induced by increasing water temperature and changing daylight hours, as both factors have been found to regulate the reproductive cycle of males and females (Baggerman 1980; Guderley 1994). Interestingly, the major shift in distribution occurred after midsummer, which suggests that decreasing daylight hours induced an increase in risk taking and a shift of habitat. Alternatively, increased risk taking could be a direct response to impaired body condition. The shift towards shallower water coincided with a decline in fish numbers, which supports the possibility that sticklebacks shifted to more predator-exposed area when survival probability decreased and the fish started to die off (sticklebacks of the present population do not survive until a second breeding season). Individuals are expected to invest less in survival and take larger risks when future reproductive opportunities decrease (Charlesworth 1980; Roff 1992).

For gravid females, increased difference in temperature between shallow and deeper water predicted, together with date, the change towards shallower water. This suggests that increased benefits of shallow water, in terms of faster reproductive rate, favored the change in the distribution of females. Females also showed a more pronounced habitat shift than males. This could be due to females being able to quickly adjust their habitat choice to present environmental conditions and decreasing future reproductive opportunities, whereas breeding males are bound to a nest for 2–3 weeks, while attracting females and caring for offspring, and therefore less free to shift habitat.

The importance of factors other than risk-taking, predation risk and water temperature in inducing a shift towards more predator-exposed areas is unknown, but cannot be excluded. For example, increased predation rate on eggs in vegetated areas towards the end of the season, or fewer cannibalistic groups that visually search for nests to raid, could favor a shift of nesting males towards more open areas (Foster 1994; Huntingford et al. 1994). Food availability is unlikely to have had a direct impact on the distribution of breeding males, as males usually do not feed while caring for their offspring (Wootton 1976), but could have affected the distribution of gravid females and non-breeding individuals. More studies are needed to determine the importance of these and possible other factors.

A significant relationship occurred between predation pressure and the density of sticklebacks. Most breeding activity took place while terns were incubating their eggs (personal observation) and predation pressure was low. The concentration of breeding activity to this short time period further reduced the risk of predation to individual fish. Thus, temporal changes in predation pressure seem to influence the timing of the height of breeding activity, but have less impact on temporal changes in the distribution of fish. Several other studies carried out in aquatic environments, and especially marine environments, have found strong effects of predators on prey populations (Sih 1985; Kerfoot and Sih 1987; Chambers and Trippel 1997). Predation is often one of the main factors that regulate the abundance and distribution of prey populations, both directly by removing prey and indirectly through the behavioral responses of prey. However, the effect of temporal changes in risk-taking on the distribution of prey has received less attention, although life-history theory predicts that temporal changes in risk-taking should occur over the lifetime (Charlesworth 1980; Roff 1992).

In conclusion, this study shows that the distribution of sticklebacks changes over the breeding season towards more predator-exposed areas. This coincides with increased risk-taking when future reproductive opportunities decrease, and with increased temperature of shallow water. Predation pressure, on the other hand, is not a predictor of the habitat shift. These results imply that attention should be paid not only to changes in predation pressure, but also to changes in risk-taking, when investigating temporal changes in the distribution of individuals.

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