

THE ACTIVITY BUDGET AND BEHAVIOR PATTERNS OF FEMALE THREESPINE STICKLEBACKS, *GASTEROSTEUS ACULEATUS* (L.), IN A QUÉBEC TIDAL SALT MARSH¹

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Résumé

Le comportement et la répartition du temps d'activité chez les épinoches femelles à trois épines (*Gasterosteus aculeatus* L.) vivant dans les marelles d'un marais salant ont été étudiés en 1983. Les femelles étaient actives le jour, mais en repos le soir. Elles se sont adaptées aux concentrations basses en oxygène dissous en allant respirer à la surface de l'eau et aux températures élevées en cherchant dans leurs marelles des abris contre la chaleur. D'autres corrélations significatives entre le comportement des poissons et certaines variables environnementales sont décrites. Ces modèles de comportement aident les poissons à exploiter, pour des fins de reproduction, un habitat particulièrement instable.

Abstract

The behavior and time budget of female threespine sticklebacks (*Gasterosteus aculeatus* L.) in salt marsh tide pools were studied during 1983. Females were diurnal, being quiescent at night. They responded to low levels of dissolved oxygen by performing aquatic surface respiration and to high temperatures by seeking refuge in slightly cooler parts of the pools. Other significant correlations between environmental variables and female activity are also reported. These behavior patterns presumably facilitate the exploitation of this highly variable habitat for stickleback reproduction.

Introduction

The first reactions of most organisms to shifting environmental conditions are changes in behavior (Manning, 1979). Fish provide good examples of behavioral adaptations: laboratory studies show that most species adjust their activities to variations in water temperature, dissolved oxygen concentration and light levels (e.g. Thorpe, 1978). But as fish are difficult to observe in nature, field studies of their behavioral ecology are relatively rare.

Despite the popularity of the threespine stickleback, *Gasterosteus aculeatus* L., in ethological research, few field studies have examined its behaviour (Wootton, 1976). At Isle-Verte (Québec), this species breeds in tide pools subjected to large fluctuations in water temperature and dissolved oxygen concentration (Ward & FitzGerald,

1983). Recently, Reeb *et al.* (1984) observed that territorial male *G. aculeatus* at this site adjusted their behavior in response to fluctuations in these two environmental variables. However, there are no field investigations of the activity patterns of female *G. aculeatus* nor of their behavioral adaptations to large environmental changes. The specific objectives of this field study were to measure the activity budget of female *G. aculeatus*, and to describe their behavioral adaptations to changes in their environment.

Materials and methods

THE SITE

The study was done in a salt marsh along the south shore of the St. Lawrence Estuary near Isle-Verte, Québec. This area contains an extensive series of tide pools ranging in surface area from 1 to 1000 m². Further details on the study site are provided in Reed & Moisan (1971), Worgan & FitzGerald (1981a) and Ward & FitzGerald (1983). Three species of sticklebacks, the three-

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spine (*Gasterosteus aculeatus*), the blackspotted (*G. wheatlandi*), and the ninespine (*Pungitius pungitius*) migrate from the St. Lawrence Estuary to the tide pools to spawn during May and June. With the exception of rare occurrences of fourspine sticklebacks (*Apeltes quadracus*) and mummichogs (*Fundulus* sp.) no other fish are present.

BEHAVIOR

Observations of female *G. aculeatus* were conducted from 19-22 June, 1983 toward the end of their breeding period. At this time diel fluctuations in water temperature and dissolved oxygen are most pronounced (Ward & FitzGerald, 1983). Nineteen females from 11 pools were captured with a dip net, and individually marked with a small segment of colored electrical wire insulation slipped over a dorsal fin spine. The females were then returned to their original pools and given 24 h to recover from the tagging procedure before observations started. No adverse effects of tagging were noted. We observed only *G. aculeatus* because most *G. wheatlandi* had returned to the St. Lawrence Estuary at this time, while *P. pungitius* spent most of its time hidden in the algae and was difficult to observe.

We took care not to disturb the fish when approaching the pools. If they fled upon our arrival, we waited until they had resumed normal activity before starting our observations.

One 10 min observation per fish was collected during each of the following time periods: 1) 04h00-06h00, 2) 08h00-10h00, 3) 12h00-14h00, 4) 16h00-18h00 and 5) 20h00-22h00. We also used a Javelin model 226 night vision scope on 21 June to make two hours of casual observations of female behavior at night. The apparatus permitted direct, non-intrusive, observations of fish by magnifying ambient moonlight levels. We abandoned our original plan to make regular nocturnal observations of tagged females because we were unable to locate them rapidly in the narrow field of the Javelin scope. Consequently our night observations were made on untagged fish. Behavioral events were recorded with a Datamyte model 800 event recorder (Electrogeneral Corporation), or with a tape recorder. We registered the frequency of and time spent (duration data) in the following activities: 1) movements (swimming) from one part of a pool to another, 2) feeding, 3) resting, 4) performing aggression, 5) receiving aggression, 6) nest raiding, 7) hiding, 8) courtship and 9) disrupting other females' courtship rituals. Movements consisted of slow swimming from one part of a pool to another. When feeding, the fish fed mostly upon the benthos. They took bits of mud into their mouth and spat them into the water

column, separating potential prey from the non-edible fraction. Suitable items were then captured. Occasionally the fish rose and struck at prey, probably copepods, in the water column. In resting behavior, the fish were motionless, floating above the pool's bottom. Performing aggression involved the female charging at another fish. In receiving aggression, females were either attacked by other females, or charged by territorial males. Nest raiding involved a female trying to force its way into a nest to eat the eggs within. Since this behavior does not seem to be related to food availability (Whoriskey, unpubl. data), we did not classify it as feeding. When hiding, females were concealed in algal patches or under a pool's bank. We defined as courtship the activities from a male's initial approach to the point where the female was chased from the nest following spawning. Wootton (1976) provides an excellent description of the courtship ritual of these fish. Disruption of courtship occurred when a female or a group of females entered a male's territory as he was courting another female. No aggression was shown by the intruder(s) at this time, but a male broke off courtship behavior to chase the invader(s) out of his territory. With the exceptions of hiding, courtship, disrupting courtship, and aggression we also determined whether these behaviors were performed either in groups or alone. A group was defined as 2 or more individuals within 1 m of each other showing synchronous behavior. This gave us a total of 13 behavior patterns.

Concomitant with these observations of behavior, we measured water temperatures and dissolved oxygen levels (Yellow Springs Instruments, model 57 oxygen meter) about 5 cm below a pool's surface. Mean pool depths, and the percentage of surface area covered with algae were also determined.

STATISTICAL ANALYSIS

Behavior data were non-normal, not transformable to a normal distribution, and heteroscedastic, so we used non-parametric statistics. Comparisons of female behavior between daily periods were made with a Friedman ANOVA by ranks followed by STP tests (Sokal & Rohlf, 1969). Correlation coefficients (Kendall's τ) were calculated between behavior and selected environmental variables using Statistical Analysis Systems programs (Helwig & Council, 1979).

Results

Females spent most of their time resting in groups (19%), hidden (31%) or swimming in groups (14%) (Table I). Excluding the time spent

TABLE I

Percent of time spent by female *G. aculeatus* at different activities

Behavior	% total time
Movements alone	8.59
Movements in group	13.71
Feeding alone	6.69
Feeding in groups	6.46
Resting alone	11.20
Resting in groups	19.29
Nest raiding alone	0.23
Nest raiding in groups	0.13
Performing aggression	0.03
Receiving aggression	0.07
Courtship	2.16
Interrupting courtship of other females	0.00
Hidden	31.44
Total	100.00

Data are from pooled samples from 5 daily observation periods (see text). Total observation time 945.38 min. $n = 19$ in each period.

hidden, females were in groups 58% of the time. The only statistically significant differences in behavior among time periods were that females spent more time swimming in groups at 04h00-06h00 than at 20h00-22h00 (duration data, Friedman's ANOVA and STP tests: Fig. 1), and they hid less often between 04h00-06h00 than later in the day (frequency data, Friedman's ANOVA and STP tests; not illustrated). Our two hours of night observations between 23h30 and 01h30 showed that, after dark, females dispersed throughout the pools and rested alone.

Dissolved oxygen concentration and water temperature were at minimal values (0.04 mg/L and 16°C) between 04h00-06h00 (Table II). The maximal dissolved oxygen concentration (18.6 mg/L) was recorded between 16h00 and 18h00, while the peak temperature of 29°C was registered in both the 12h00-14h00 and 16h00-18h00 time periods.

Fish responded differently to low oxygen stress than to high temperatures. In the former case females grouped together and performed aquatic surface respiration (Lewis, 1970), obtaining oxygen from the water layer at the pool's surface where pO_2 is maximal due to diffusion of atmospheric oxygen. In the latter case, as water temperatures rose above 28°C, all females took cover under a pool's bank or in algal clumps where water temperatures were 0.2-1.0°C lower than in the rest of the pool.

Females fed significantly more often and spent less time moving in groups as dissolved oxygen

concentrations increased (Table III). They hid more, and were attacked more often and for longer periods by territorial males as the temperature rose. By contrast, in pools with greater algal cover we noted a decrease in the duration and frequency of the attacks the females received, and a decrease in the number of attacks they directed to other fish. Finally, fish in deeper pools were more likely to rest alone than fish in shallower pools.

Discussion

Jones (1952) reported that threespine sticklebacks showed strong respiratory stress at dissolved oxygen concentrations of <0.3 mg/L, while Jordan & Garside (1972) estimated 28.8°C as the

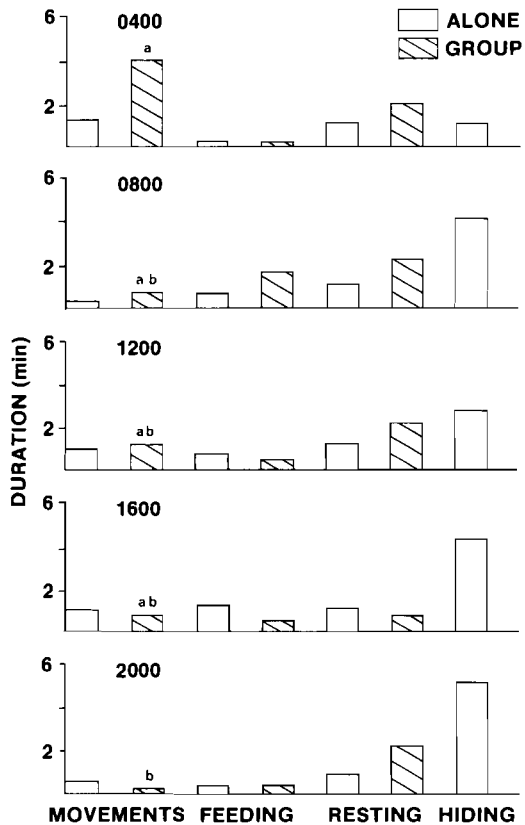


Figure 1. Daily patterns of the most frequently occurring female behavior. Values are the mean number of minutes a behavior was performed, per 10 min observation period. Significant differences (Friedman ANOVA followed by a STP test) between time periods are indicated by letters above the histograms. Histograms with a letter in common are not significantly different from each other. If no letters are present, no significant differences occurred. Nineteen 10 min observations were made during each time period.

TABLE II
Daily patterns in dissolved oxygen concentration and water temperature

Period	Dissolved oxygen concentration (mg/L)		Temperature (°C)		n
	Mean	Range	Mean	Range	
04:00-06:00	1.83	0.04-3.00	17	16-20	19
08:00-10:00	6.64	2.40-15.00	18	17-24	19
12:00-14:00	14.11	12.00-17.80	26	20-29	19
16:00-18:00	14.20	8.80-18.60	27	24-29	17
20:00-22:00	8.40	4.40-12.20	21	20-23	19

Data were collected from 11 tide pools between 19 and 22 June, 1983.

upper lethal temperature for the same species adapted to our salinities. Between 04h00-06h00, 12h00-14h00 and 16h00-18h00 respectively, the dissolved oxygen concentrations or water temperatures approached or exceeded these thresholds, and the fish performed special behaviors to counter these stresses. During periods of low dissolved oxygen levels they banded into schools and performed aquatic surface respiration (Lewis, 1970), a common response to hypoxia (Kramer, 1983). But even with the use of the surface oxygenated layer the fish became sluggish and failed to show the antipredator flight behaviors necessary to avoid bird predation at the site (Whoriskey & FitzGerald, 1985). The schools they used for performing aquatic surface respiration may serve as an antipredator tactic, as individuals in a school are less likely to be captured than isolated fish (Keenleyside, 1979). At high temperatures (>28°C), the fish took cover in refuges slightly cooler (0.2-1.0°C) than the surrounding water. We recorded a maximum water temperature of 29°C, so the small differences in the refuges may determine whether a fish survived as it labored near its thermal maximum.

Contrary to Worgan & FitzGerald (1981b), but in accordance with Walsh & FitzGerald (1984) we found no early morning feeding peak (Fig. 1). Walsh & FitzGerald (1984) attributed the difference between their results and those of Worgan & FitzGerald (1981b) to different weather patterns in the different years in which the respective studies were done. The former was conducted on a cloudy day at a minimum air temperature of 2°C, while the latter occurred on a sunny day at a minimum air temperature of 7°C. Our work, similar to Worgan & FitzGerald's (1981b), was conducted on sunny days at high temperatures (Table II), but we still found no feeding periodicity. Other factors, possibly differences in prey availability, may explain why our results differ from those of Worgan & FitzGerald

(1981b). The three feeding studies, taken together, demonstrate clearly how prevailing field conditions can alter daily cycles.

Most fish which have been studied alter their behavior in response to the often regular cycles of environmental variation which occur in nature (Spieler & Kendall, 1984; Thorpe, 1978). We have presented limited data showing that these females are diurnally active, in response to predictable day/night changes in light intensity. Evening activity is uncommon in some fish (Helfman, 1981), but others are specialized for nocturnal life (McFarland *et al.*, 1979). Sticklebacks depend heavily on their visual senses for information about the environment (Wootton, 1976), and they are probably limited in their night activities by low light levels.

Two other important environmental variables, water temperature and dissolved oxygen concentration, also influenced female behavior at this site (Table III). However, these variables may or may not show regular diel cycles (Table II; Ward & FitzGerald, 1983). For example, the pools are shallow (usually 30 cm or less in depth) and are easily agitated by the wind. This agitation mixes atmospheric oxygen into the water and prevents the expected occurrence of oxygen depletion by evening algal respiration. Also, oxygen production by algae kept the dissolved oxygen concentration of the water high during the periods of high temperature (Table II) when oxygen solubility was lowest. Thus the behavior of the females should be quite variable, and care must be taken to account for the effects of these environmental influences when collecting data on fish behavior at this site.

These results illustrate some of the behaviors of female threespine stickleback which enable them to breed in the tide pools despite the rapid environmental fluctuations which occur there.

TABLE III

Kendall's correlation coefficients between the duration and frequency of behavior, and environmental variables

	<i>Duration</i>					<i>Frequency</i>				
	<i>Movements in group</i>	<i>Feeding alone</i>	<i>Giving aggression</i>	<i>Receiving aggression</i>	<i>Hidden</i>	<i>Resting alone</i>	<i>Feeding alone</i>	<i>Giving aggression</i>	<i>Receiving aggression</i>	<i>Hidden</i>
Dissolved oxygen concentration ¹	-0.2313**	0.2076**	NS	NS	0.2372**	NS	0.2043*	NS	NS	0.2825**
Water temperature ²	NS	NS	NS	0.2120*	0.2494**	NS	NS	NS	0.2344**	0.3132**
Percent algal cover ³	NS	NS	-0.2001*	-0.2399**	NS	NS	NS	-0.1998*	-0.2773**	NS
Depth ³	NS	NS	NS	NS	—	0.1853*	NS	NS	NS	NS

Outside of the values presented in the table, no other significant correlations were found.

¹ $n = 91$

² $n = 93$

³ $n = 95$

* $P < 0.05$

** $P < 0.01$

NS = not significant

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