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SOME FEATURES OF THE TERRITORIES IN THE BREEDING MALES OF THE INTERTIDAL BLENNY *LIPOPHRYS PHOLIS* (PISCES: BLENNIIDAE)

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In this paper we present data on the organization of the territories in males of *Lipophrys pholis* during the breeding season. Data were collected during high tides by skin- and scuba-diving and during low tides by direct inspection of nests. Our study area was located at Arrábida, Portugal. The main results are: (i) The territories of the breeding males of this species are temporary, being established each breeding season. (ii) The guarding males stay in the nest holes with the egg masses while the tide is low and are subjected to several hours of emersion in each tidal cycle. (iii) Even when the nests are submerged the fishes stay inside the nest for an average of 92% of the time. All the activities performed outside the nest correspond to an average of 27 minutes per day. (iv) There was a low frequency of territorial intrusions. Conspecific intruders released a significantly higher frequency of agonistic responses than did *Coryphoblennius galerita*. (v) Removal experiments showed that vacated territories are not occupied by other males during the same breeding season. (vi) Without the presence of the guarding male the eggs are slowly destroyed by predation and infection, but some eggs can still survive and hatch up to five days after the removal of the parental male. The results are discussed in terms of the probable costs and benefits of breeding intertidally.

INTRODUCTION

In contrast to the rich literature on the ethology of tropical and Mediterranean blenniids (for references see Wirtz, 1978 and Thresher, 1984), data on the behaviour of the intertidal species of the north-eastern Atlantic are still scarce (Qasim, 1956; Gibson, 1967, 1968; Fives, 1980; Almada *et al.*, 1983; Santos, 1985a,b).

Direct field observations of the social behaviour of these intertidal fishes are important for a better understanding of the behavioural peculiarities associated with the colonization of intertidal biotopes.

In several tropical and subtropical blenniids both males and females defend permanent individual territories (Fishelson, 1975; Losey, 1976; Nursall, 1977). In other species the males defend permanent territories while the females tend to have home ranges that broadly overlap (Phillips, 1977).

The data available for temperate species suggest that in many cases only the males are territorial and that territoriality is restricted to the breeding season (Gibson, 1967; Almada *et al.*, 1983; Louisy, 1983).

In this report we present preliminary data on the territoriality of the parental males of *Lipophrys pholis* (Linnaeus, 1758). This is an intertidal species found in the north-eastern Atlantic and North Sea, from Morocco to Norway (Zander, 1986). It occurs in tide pools and rocky walls often subjected to strong wave action. Its reproductive behaviour in captivity was described by Qasim (1956). Gibson (1967), based on a capture/recapture method, showed that the fishes have a home range that may include several pools, although they tend to visit some pools more often than others. Gibson (1968) studied the social behaviour of the juveniles in captivity. Almada *et al.* (1990b) provided an ethogram of the breeding males of this species in natural waters.

In this paper we addressed the following questions: (i) To what extent are the territories seasonal or permanent? (ii) In what way is the time budget of the parental males affected by the tidal cycle? (iii) How important are the actions of the parental males for the survival of the eggs? (iv) Are there any non-territorial fishes that can occupy vacated territories?

MATERIAL AND METHODS

Study Area

Data were collected at Arrábida coast Portugal (38°28'N 8°59'W) between the beaches of Alpertuche and Pilotos.

On the western Portuguese coast the predominant direction of the waves is north-west; as the Arrábida coast faces south-east it is subjected to low wave action, except when south winds blow. This coast consists of a Jurassic calcareous cliff. At low tide, between the cliff and the sea, an area of sand, boulders and large rocks becomes uncovered. These rocks present crevices, holes and small caves, that the males of *Lipophrys pholis* use as nests during a long breeding season that begins at least as early as December and is virtually ended in June (Almada *et al.*, 1990a). The observations were made on the vertical walls of these rocks.

Apart from *L. pholis* we found only two other fish species on the rock walls: the blenniids *Coryphoblennius galerita* (Linnaeus, 1758) and *Lipophrys canevae* (Vinciguerra, 1880).

Behavioural Observations

Data were collected by skin- and scuba-diving. The total amount of observation time was about 54 hours.

From a sample of identified nests (30) we selected 12 for focal-animal observations (Altmann, 1974). Each observation lasted from 12 to 20 minutes. The amount of focal observation time was 13h 38m. The distribution of the observations during the day ranged from 10h 15m to 18h 15m. They were made in March and April 1986 and April 1987.

The area around each nest was arbitrarily divided as follows: (i) taking the nest as centre, a series of concentric circles was drawn. The difference of radius between consecutive circles was 10 cm; (ii) this diagram was divided into four quadrants (up, down, left and right).

The successive locations that a fish visited during each observation period were recorded on a plastic sheet. We also recorded the different behavioural categories performed by the fish in each location with a predetermined code.

In these observations we used one minute as the time unit. During each observation the following data were recorded: (i) frequency of visits to the nest, their duration and the postures adopted by the fish; (ii) frequency of excursions out of the nest, their duration, locations visited and the activities performed by the fish during each excursion; (iii) appearance of intruders, their species, the location of their closest approach to the nest and whether they withdrew without apparent reaction by the resident male or left after agonistic action of the territorial fish.

The activities performed out of the nest were recorded as follows: feeding - a single act or a bout of them were treated as one unit; agonistic interactions - a fish oriented to, threatened, attacked or chased an intruder (no reciprocal fights were observed); patrolling - if during an excursion a fish visited its territory without feeding and no intruder was present when the fish went out of the nest, the excursion was classified as patrolling; courtship was too rarely observed to be quantified.

The Use of Time

To find the duration of emersion of each nest, we have determined, during low tide, the height of eleven nests to the hydrographic zero. Data were then fed into a computer programme ('Ábaco' developed by the authors) which calculates for any set of given points the submersion and emersion times, and the fraction of submersion time that falls within daylight hours. The data needed are: tidal amplitude, the time of day at which high and low tide occur, and the time of sunrise and sunset.

The formulae used for computations of tidal waves assume that they are sinusoidal and are based on the tide tables provided by the Hydrographic Institute (Portugal).

The programme was run with the tidal cycles from 1 February to 30 April 1986. It is within this period of time that the peak of the breeding season occurs. The intervals between sunrise and sunset were based on monthly means.

Removal Experiments

In order to determine to what extent the presence of the parental male is important to the survival of the eggs, we removed six males from their nests during low tide.

After removal of the parental males, the egg masses inside the nests were observed during low tide. This was done with the help of a flashlight and natural light reflected by a mirror. The relative positions of distinct egg masses and the approximate area that they occupied were drawn on sketches. These sketches were used in subsequent visits as a reference from which the effects of infection, predation and hatching on the different egg masses were qualitatively estimated. The nests were also visited during high tide to check the possible occurrence of new occupants.

All the statistical methods used in this work followed Conover (1980) and Sokal & Rohlf (1981).

RESULTS

Occupation of Holes

Holes that were used at any time by males as nests were subsequently inspected during low tides at frequent intervals.

At each visit the following data were recorded: presence of eggs, presence of a black male, presence of a non-parental fish, presence of a crab and absence of any occupant.

Table 1. *Relative frequencies of the presence of eggs, black males, non-parental fish, crabs and absence of any occupant, in holes at various intervals*

		Occupation by *Lipophrys pholis*					
Date	N	Eggs	Black males	Non-parental fish	Total	Crabs	Empty
23.12.87	19	0.158	0.211	0.158	0.369	0.158	0.474
02.02.87	19	0.158	0.158	0.368	0.526	0.105	0.368
15.02.87	19	0.421	0.421	0.158	0.579	0.053	0.368
05.03.87	19	0.263	0.316	0.053	0.369	0.105	0.526
14.03.87	19	0.895	0.895	0.000	0.895	0.105	0.000
30.03.86	12	1.000	0.917	0.000	0.917	0.000	0.083
23.04.87	19	0.789	0.737	0.000	0.737	0.053	0.210
26.04.86	12	0.500	0.500	0.083	0.583	0.000	0.417
17.05.86	12	0.250	0.250	0.167	0.417	0.167	0.416
11.06.87	19	0.000	0.105	0.053	0.158	0.474	0.368
27.09.88	19	0.000	0.000	0.158	0.158	0.105	0.737
29.11.88	19	0.000	0.000	0.157	0.157	0.211	0.632

Data are listed by months independently of the year, starting at the beginning of the breeding season. In each sample only holes that had been used as nests on previous dates were included.

The results are presented in Table 1 and show that:

(i) The presence of *Lipophrys pholis* in holes is higher in the breeding season than at other times of the year (Fisher Exact Probability Test: P(one tailed)<0·01; number of nests=19; means of occupation pooled for breeding and non-breeding dates in 1987 and 1988; non-occupation includes holes that were empty and holes that were occupied by crabs). The rate of occupation reached a maximum of 0·917 at the peak of the breeding season (March) and declined sharply after the breeding season, reaching a minimum of 0·157 in November. For each year the occupation rate rose again as the breeding season began. This trend is also confirmed by a significant correlation between the number of holes containing eggs and the number of holes occupied by fishes, parental or non-parental (Spearman Rank Correlation: r_s=0·951, P<0·01, number of visits=12). These results indicate that only a low proportion of fishes used the nests as shelter out of the breeding season and a high proportion of new territories was established in the nesting area each year. Thus we conclude that the territories of the males of *L. pholis* are restricted to the breeding season and are not the preferred shelter sites of females and non-breeding males.

(ii) There is a significant correlation between the presence of eggs in holes and the black coloration of occupants (r_s=0·993, P<0·01, N=12). There were almost no black fishes out of the breeding season; thus our results confirm that black coloration is 'typical' of breeding males. In November (1988) two to four weeks before the beginning of the breeding season, we found occupying holes four fishes that exhibited an intermediate colour pattern, uniformly brown but not as dark as during the breeding season. This finding, and the fact that during the breeding season some males are black although their holes contain no egg masses, indicates that black coloration must depend on the social status of the fish or on its maturational condition, or both. Since dominant males in aquaria do not show the black coloration except during the breeding season (personal observations) we conclude that this depends on physiological factors associated with sexual maturation.

(iii) Some holes that served as nests may be used by crabs (*i.e. Pachygrapsus marmoratus* (Fabricius, 1787) and *Eriphia verrucosa* (Forskall, 1775)). There is a significant negative correlation between the presence of fishes and crabs (r_s=0·769, P<0·05, N=12). This suggests the possible existence of competition between *L. pholis* and crabs for the occupation of holes.

Table 2. *Mean emersion time and mean daylight submersion time of 11 nests between two consecutive high tides*

Nest	Height to the Hydrographic zero (m)	Mean emersion time	Standard deviation	Mean daylight submersion time	Standard deviation
1	1.39	3h 19m	1h 33m	4h 35m	2h 34m
2	1.69	4h 56m	38m	3h 43m	1h 43m
3	1.93	6h 00m	16m	3h 09m	1h 16m
4	2.02	6h 23m	18m	2h 57m	1h 08m
5	2.06	6h 34m	21m	2h 52m	1h 05m
6	2.07	6h 36m	21m	2h 50m	1h 04m
7	2.10	6h 44m	24m	2h 46m	1h 02m
8	2.15	6h 58m	29m	2h 39m	59m
9	2.17	7h 03m	32m	2h 36m	57m
10	2.24	7h 22m	41m	2h 26m	54m
11	2.74	9h 54m	1h 39m	1h 07m	49m
Overall means		6h 32m		2h 53m	

Data based on 172 tidal cycles, 1 February to 30 April 1986.

The Use of Time

In Table 2, we present data on the mean emersion time and the mean submersion time occurring during daylight hours, between two consecutive high tides, for 11 nests.

In Table 3, we present the percentage of time spent in the nest by individual males when they are immersed. Although there is a considerable variation among males, all of them spend most of the time inside the nest.

Inspection of Table 2 shows that, on average, between two consecutive high tides, the nests stay out of water about 6h 32m and that the mean diurnal submersion time is about 2h 53m. For one day, we have on average for the eleven nests 12h 38m of emersion time

Table 3. *Percentage of time spent outside and inside the nests and the number of excursions of parental males during high tide observations*

Nest	Total observation time (min)	Time in (min)*	Time out (min)*	Time in (%)	Time out (%)
A	115	114.5	0.5	99.6	0.4
B	115	101.0	14.0	87.8	12.2
C	108	98.5	9.5	91.2	8.8
D	120	94.5	25.5	78.8	21.2
E	55	55.0	0.0	100	0.0
F	60	60.0	0.0	100	0.0
G	120	119.5	0.5	99.6	0.4
H	55	51.5	3.5	93.6	6.4
I	13	13.0	0.0	100	0.0
J	20	18.0	2.0	90.0	10.0
K	20	14.0	6.0	70.0	30.0
L	17	17.0	0.0	100	0.0
Total	818	756.5	61.5	92.5†	7.5†

*Total amount of time spent inside/outside the nest. †Mean percentage.

and 5h 34m of diurnal submersion time. This is the mean amount of time for which the nests are submerged during day time. Since blenniids tend to be diurnal fishes (Wirtz, 1978), this is probably the maximum amount of time in which feeding and all other activities performed outside the nest are possible. Since, on average, 92% of this time is spent inside the nest (Table 3), we can conclude that all activities performed out of the nest, including feeding, are restricted to about 27 minutes per day (10 minutes for the highest nest and 43 minutes for the lowest nest). These values will vary with the location of the nest, tidal amplitude and sea conditions. During neap tides some nests may even stay unsubmerged for 72 hours while others remain submerged for more than 96 hours.

These calculations assume that wave action is negligible, which is unrealistic. However, except when south winds blow, changes of water level caused by wave action near the rock walls hardly exceed 0·5 m. Wave action will thus shorten the total emersion and submersion time and create a period of intermittent submersion. Our observations suggest that males become more and more inactive as the tide ebbs and cease to leave the nest when it starts to be exposed to air.

Activities Outside the Nest

In Figure 1 we present the relative frequencies of the main activities performed outside the nest, namely feeding, agonistic interactions and patrolling.

Inspection of Figure 1 indicates that for the parental males of this species the defended area around the nest corresponds broadly to the area where feeding occurs. Thus, for the parental males, territory and home range have the same area. Due to the scarcity of data, estimates of territory size must be taken with caution. Our observations suggest that an area having the nest as focal point and extending as far as 60 cm, entails the space where most activities are performed (feeding, 88·9%; patrolling, 88·1%; agonistic interactions, 91·7%). This does not mean that territories are circles with a 60-cm radius. In several

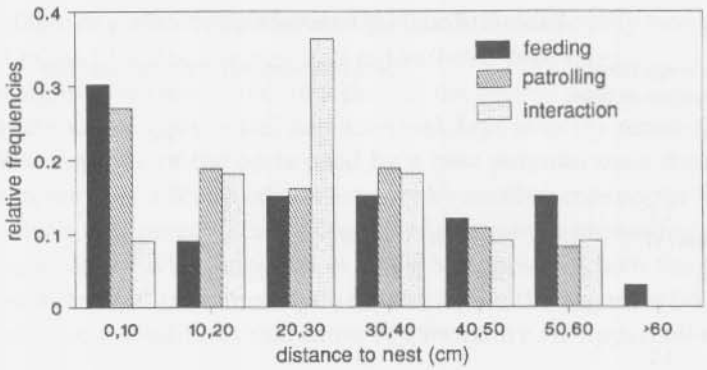

Figure 1. Spatial distribution of the main activities performed by the parental males outside the nest. Data were collected from eight nests. The total number of activities recorded was 81.

instances we found inter-nest distances smaller than 60 cm (N=9; mean=40·3 cm; SD=14·97 cm; range 13-59 cm) with no apparent inter-male aggression. Rather, the territories probably have an irregular shape being more spread in the directions where the nearest neighbour is further away. Thus, the nest is the focal point of the territory but in many cases will not be its geometric centre.

Territorial Intrusions and Agonistic Behaviour

Taking the arbitrary distance of 60 cm from the nest as the territorial limit we observed 22 intrusions by conspecifics and 12 by *Coryphoblennius galerita*, yielding on average 2·49 intrusions per hour (13h 38m of focal observation time).

In Table 4, we present data on the minimum distance to the nest to which intruders were able to get.

It seems that, for many intruders, the presence of the resident fish is in itself sufficient to induce them to retreat. It is also probable that the dark coloration of the fish and the 'part out' posture may have signal value in themselves. It can be seen that conspecifics elicited a higher proportion of agonistic responses than did *C. galerita* (respectively 54·5% and 8·3%; G-test: G=5·738, df=1, P<0·01). The effective exclusion of all conspecifics from the territory indicates that the females do not reside inside the territories of the males.

Table 4. *Behavioural responses of parental males to territorial intrusions by conspecifics and* Coryphoblennius galerita

Intruder	Behavioural response	Distance to the nest (cm) *							
		0	10	20	30	40	50	60	Total
L. pholis	Agonistic response	1	1	2	3	2	1	2	12
	No reaction	0	1	3	2	1	0	3	10
C. galerita	Agonistic response	0	0	1	0	0	0	0	1
	No reaction	2	0	0	6	0	2	1	11

*Each value of distance represents the nearest point to the nest that an intruder could reach before retreating.

Table 5. *Results of removal experiments*

Nest	Changes in egg masses and occupation of holes		Days after removal of the parental fish 1	2	3	4	5	6
1	Predation		-	-	-	+	+	
	Infection		-	-	-	+	+	ALL
	Hatching		-	-	-	+	-	
		LT	-	-	-	-	-	-
	Occupation	HT	BM	BM	-	-	-	-
2	Predation		+	-	-			
	Infection		-	+	+	ALL		
	Hatching		-	-	-			
		LT	-	-	-	-	-	-
	Occupation	HT	-	-	-	-	-	-
3	Predation		-					
	Infection		-					
	Hatching		+	ALL				
		LT	-	-	-	-	-	-
	Occupation	HT	-	-	-	-	-	-
4	Predation		+	-				
	Infection		-	+	ALL			
	Hatching		-	-				
		LT	-	-	-	-	-	-
	Occupation	HT	GAL	-	-	-	-	-
5	Predation		-	+				
	Infection		-	-				
	Hatching		+	+	ALL			
		LT	-	-	-	-	-	-
	Occupation	HT	NPL	-	-	-	-	-
6	Predation		-	-	-	-	-	
	Infection		-	-	-	-	+	ALL
	Hatching		-	-	-	+	-	
		LT	-	-	-	-	-	-
	Occupation	HT	GAL	-	-	-	-	-

Data were collected during the six consecutive days after the removal of the parental fish.
LT, low tide. HT, high tide. BM, occupation by *Lipophrys pholis* showing black coloration. NPL, occupation by a non-parental *Liophrys pholis*. GAL, occupation by *Coryphoblennius galerita*. ALL, all eggs of the nest suffered the indicate change.

Removal Experiments

In six nests the parental male was removed during low tide and the egg masses were described as mentioned in Material and Methods. These nests were visited on subsequent days. The disappearance of eggs was taken as indicating predation. The occurrence of a white milky appearance was taken as indicating that the eggs were infected or dead. If advanced embryos (with pigmented eyes) disappeared leaving empty egg capsules, we assumed that hatching had probably taken place. The results of this experiment are summarized in Table 5 and suggest the following conclusions:

(i) Predation does not occur immediately after the removal of the parental male and some egg masses can survive for some days without being harmed. From a sample of six nests observed one day after the removal of the guarding male only two showed signs of predation. On the fifth day one nest had not suffered predation.

(ii) The first signs of infection were detected on the second day.

(iii) Apparently some eggs can still hatch several days after the removal of the male.

(iv) In no case was one of the nests used by a new parental male during the same breeding season nor was it occupied consistently by another conspecific as shelter.

We can conclude that parental care plays a definite role in promoting egg survival. However, in contrast to what happens in other biotopes in which the removal of a parental fish leads to an almost immediate destruction of the egg mass (Wirtz, 1978), in the case of *L. pholis* the conditions that cause egg mortality are apparently less severe.

DISCUSSION

The active defence of the area around the nest by the males of *Lipophrys pholis* probably serves at least two functions: (i) to keep potential egg predators and other intruders away from the nest; (ii) to minimize feeding activities of conspecifics in the area surrounding it.

Qasim (1956) notes that in the males of this species little feeding occurs during the breeding season. Such a feeding restriction associated with parental care has been documented for the males of some gobiids (Miller, 1984; Magnhagen, 1986). Miller (1984) and Santos & Almada (1988) also refer to a decrease in the condition factor of the parental males in several gobiids and *Parablennius sanguinolentus* (Pallas, 1811), respectively, which is probably due to reduced feeding and/or high energetic demands. Zander (1990a,b) showed that the breeding males of the gobiid *Pomatoschistus minutus* (Pallas, 1770) nest in areas that are not the most favourable for feeding while females exploit the most productive zones. This finding also indicates that the needs related to parental care (namely the need for adequate nest sites) may force the guarding males to restrict their feeding opportunities.

The defence of food resources may be essential for the survival and breeding success of the parental males of *L. pholis* in a period when parental care restricts their movements to a very small area. It is interesting to note that intrusions by conspecifics elicited a higher proportion of agonistic responses than the intrusions by *Coryphoblennius galerita*, whose adults have distinct feeding habits (Gibson, 1972).

In the case of the parental males of *Lipophrys pholis* the location of the nests in the intertidal zone must further restrict feeding opportunities since the nests remain out of water for a substantial proportion of the time.

From the present study it was estimated that all activities performed outside the nest, including feeding, took on average 27 minutes per day.

The fact that in our population the egg masses were not quickly preyed upon after the removal of the parental males and the absence of any predation attempt during the behavioural observations suggest that breeding in the intertidal zone, although costly in terms of time available for feeding, may effectively reduce both predation pressure upon the eggs and the energetic demands required to chase egg predators away.

In contrast, blenniids and tripterygiids nesting on lower levels of the shore face frequent attempts at egg predation (Wirtz, 1978; Almada *et al*., 1987).

Finally, Laming *et al*. (1982) demonstrated that, when out of water, *L. pholis* shows a reduced metabolic rate. This means that the low tide time must be a period of reduced energy expenditure by the fish, which probably also helps to compensate for reduced feeding opportunities.

More detailed comparative work on the bioenergetics of the breeding male blenniids nesting in different habitats may prove to be a fruitful ground for a better understanding of the behavioural ecology of benthic fishes of rocky shores.

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