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A FIELD EXPERIMENT TO TEST NEST CHOICE IN THE PEACOCK BLENNY, *LIPOPHRYS PAVO* (TELEOSTEI, BLENNIIDAE)

F. RUCHON, T. LAUGIER, J.P. QUIGNARD

Laboratoire d'Ichthyologie, Université Montpellier II, et Techniques du Languedoc,
place Eugène-Bataillon, cc 102, 34095 Montpellier cedex 5, France

PISCES
BLENNIIDAE
BEHAVIOUR
NEST-CHOICE
MATE-CHOICE

ABSTRACT. – Male and female nest choice in the peacock blenny, *Lipophrys pavo* Risso, was studied by monitoring artificial nests during the spawning season. Nests differed by entrance and internal size and were designed to capture male and to estimate size and development stage of brood without damages. Globally, observations of males and broods were much more frequent in nests with smallest entrance size. For a given entrance size, males were more present and broods occurred sooner in the smallest nests. Criteria of male nest choice could not be clearly determined. Females preferred to spawn in nests with small entrance and in smallest nests. Presence of eggs in the nest considerably increased the nest attractiveness. In nests with eggs, the guarding-male can change without brood destruction suggesting the occurrence of allopaternal care in this species.

PISCES
BLENNIIDAE
LIPOPHRYS
NIDIFICATION
COMPORTEMENT

RÉSUMÉ. – Les critères de choix du nid par les mâles et les femelles de la Blennie paon, *Lipophrys pavo* Risso, ont été étudiés à l'aide de nids artificiels placés dans le milieu naturel. Ces nids diffèrent les uns des autres par la taille de leur ouverture et par leur volume intérieur. Ils ont été visités régulièrement durant la saison de reproduction. Lors de chaque visite, les mâles ont été capturés, marqués ou identifiés. La taille des pontes et leur état de développement ont été estimés. L'observation de mâles et de pontes est plus fréquente dans les nids à petite entrée. Pour une même taille d'entrée, plus le nid est petit plus la présence de mâles et de ponte est fréquente. Les critères de choix du nid par les mâles n'ont pu être clairement mis en évidence. Les femelles préfèrent pondre dans les nids à petite entrée et dans les petits nids. La présence de ponte accroît l'attractivité du nid. Les mâles gardant les nids sont parfois remplacés par un autre mâle sans qu'il y ait de destruction des pontes, ce qui suggère l'existence de soins allopaternels.

INTRODUCTION

Among nesting fish with male parental care (76 % of teleost fish with parental care, Blumer 1982, Gross & Sargent 1985), a distinction can be made between species that use pre-existent nesting structures (e.g., many Gobiidae, Blenniidae, Cottidae, Pomacentridae, Tripterygiidae), more or less fitted out, and those that construct their nests (e.g. Labridae, Gasterosteidae). Within these latter, males seem to build nests as close as possible to the ideal nest, according to the availability of resources. In species using pre-existent nesting structures (natural cavities, mollusk shells, ...), one can imagine that males seek for an "ideal nest" in their environment, and this optimum nest has to make multiple functions possible which are

not necessarily compatible. Indeed, the nest should be attractive for females and provide a good shelter for male and eggs against predators and/or conspecifics. Furthermore, the size of the nest may be important in controlling potential paternity of males.

Studies have scarcely dealt with the choice of nests by males. They generally show that males prefer the largest nests as they may statistically contain more eggs (Lindström 1988, Nellbring 1993) or they may provide the best shelter against predators (DeWitt 1993). Some multi-species studies have demonstrated that male nest choice criteria are species specific, even within kin species (Crabtree & Middaugh 1982, Koppel 1988). For instance, in blenniids, some species use nests that closely fit their bodies (e.g., most *Lipophrys*, *Aidablennius sphinx*), but many others

prefer nests with entrances much larger than their body width (e.g., most *Parablennius*, *Lipophrys pholis* and *L. trigloides*) (Kotrschal 1988). On the other hand, female mate choice has been extensively studied, specifically with regards to male traits as size (e.g. Downhower & Brown 1980, Brown 1981, Thompson 1986, Hastings 1988a, Bisazza & Marconatto 1988, Côté & Hunte 1989), courtship (Cole 1982, Knapp & Warner 1991), age (Côté & Hunte 1993) or color pattern (Unger & Sargent 1988), but more rarely to nest characteristics (Thompson 1986, Hastings 1988a, Bisazza *et al.* 1989, Côté & Hunte 1989, DeWitt 1993). Likewise, the presence of eggs in the nest, as well as brood size and maturity, was reported to positively affect female mate choice in several species (Marconatto & Bisazza 1986, Sikkel 1989, Knapp & Sargent 1989, Kraak & Videler 1991, Kraak & Groothuis 1994, Knapp *et al.* 1995).

The peacock blenny, *Lipophrys pavo* (Risso, 1810), has been the subject of several descriptive articles relating to its reproductive behaviour (Fishelson 1963, Westerhagen 1983, Patzner *et al.* 1986, Uiblein 1989, 1993, Almada *et al.* 1994, 1995, Gonçalves *et al.* 1996, Gonçalves & Almada 1997) and its nesting sites (Kotrschal 1988, Almada *et al.* 1994, Ruchon 1995, Oliveira *et al.* 1999). Although none of these studies has directly dealt with the issue of nest choice, this species appears to be opportunist and able to use various kinds of nests. In this study, we attempted to determine the nest choice criteria of males and females of this species in a Mediterranean coastal lagoon (Maugio, south of France). With that aim, artificial nests differing in internal volume and entrance size were placed in the field and were monitored for two months during the breeding season of this species. Results are discussed with regards to male nest choice and female mate choice (male and nest) and their consequences on sexual selection within the population.

MATERIAL AND METHODS

Study species: *Lipophrys pavo* is a small benthic fish usually living in shallow rocky shores (Fishelson 1963, Zander 1972, Kotrschal 1988). This species differs from other Blenniidae species by its ability to colonize biotopes where hard substrates are scarce (Moosleitner 1980, Almada *et al.* 1994), and by its great euryhaline and eurythermal tolerance limits (Marion 1890, Paris & Quignard 1971, Zander 1972, Müller *et al.* 1973, Moosleitner 1988, Patzner & Seiwald 1988). It exhibits a resource defense mating system with paternal egg care (Fishelson 1963, Westerhagen 1983, Patzner *et al.* 1986, Almada *et al.* 1994). There are no stable social groups and females can breed with several males. Females are batch spawners and lay a single layer of eggs inside a cavity guarded by the male. The male's care extends to aerating the eggs by fanning and defending

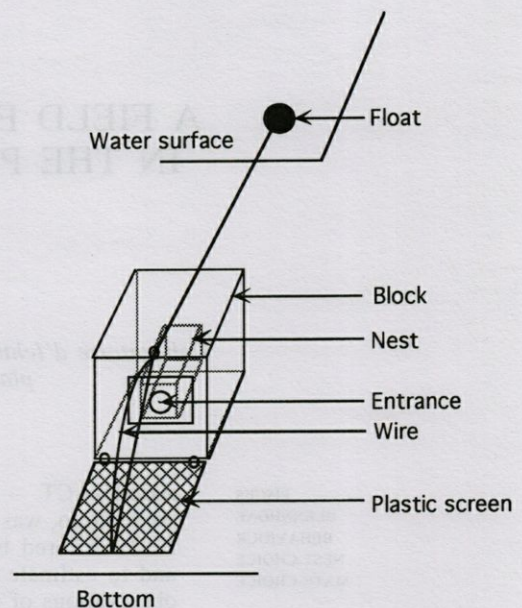


Fig. 1. – Artificial nest inside its block as set in the field.

the nest against predators and conspecifics. Most of the time the male lies in the nest with its head outside.

The studied population lives in a coastal Mediterranean lagoon, Mauguio Lagoon, France (Ruchon *et al.* 1995). It exhibits a highly variable demographic structure (age and size) owing to stressful environmental conditions (Ruchon *et al.* 1998). During the study, the population density was high, and most of the fishes were two years old and their size ranged from 50 to 128 mm (total length) and from 53 to 99 mm in males and females respectively. The breeding season extends from April to the beginning of September (Ruchon *et al.* 1993). During this period, batch fecundity increases with the decrease of egg size. Egg size is positively related to female size (Ruchon *et al.* 1993). During the breeding season, there are some kleptogamic males (sneakers) exhibiting female mimicry (Ruchon *et al.* 1995).

In this soft-bottom lagoon, potential nest sites are scarce and patchy and consisted of some artificial stonebeds and reefs of *Ficopomatus enigmaticus* (a calcareous polychaete). Natural nests of *L. pavo* are of various forms. All hard and cleaned substrates are used (rocks, holes in *F. enigmaticus*'s reef, wood, shells, beer cans, etc.). Hence, nest form could vary from deep cavity to open surface. Nest size was also variable and nests contained from 174 to 13,600 eggs (Ruchon 1995).

Nest design: For this study we constructed 48 nest blocks. Square section nests were built watertight with transparent Plexiglas plates sealed with silicon glue (Fig. 1). Nests were lodged into concrete blocks (150 × 200 × 200 mm, c.a. 5 kg) from which they were easily removable. A circular nest entrance was drilled out of a removable black PVC plate which was fixed to the block (Fig. 1). A float was attached to each block. When the block was removed, the nest entrance was automatically closed by a screen made of plastic mesh; and when it was replaced this screen was kept

away from the entrance by a stainless wire. Two diameters of nest entrance were used: 19 (s) and 22 mm (l). These diameters allow all the males to get inside the nest as demonstrated in a preliminary study (Ruchon 1995). Nests were 105 mm long and 3 square sections were used: 30 × 30 mm (S), 50 × 50 mm (M), 70 × 70 mm (L). By combining nest and entrance size, 6 types of nest were built in 8 replicates (Ss, Sl, Ms, Ml, Ls, Ll).

Methodology: On April 17, 1992, nest blocks were placed in Manguio lagoon on bare and flat soft-bottom at a mean depth of 0.5 m in an area where natural nests of *L. pavo* had never been observed. The 6 nest types were alternately settled along two lines parallel to the edge. Nests were separated from each other by 2 m in order to limit potential interactions. These 48 artificial nests were visited 8 times from May 4 to June 10 always around noon. At each visiting date, nests were removed one by one. Males and females captured inside the nest were carefully transferred into an anesthetizing bath of phenoxy 2-ethanol (0.1‰ in seawater) and measured (total length, ± 1 mm). When males were encountered for the first time, they were tagged by subcutaneous injection of blue alcyan between two rays of the dorsal fin. *L. pavo* has a skin without scales, thus limiting the risks of infection due to manipulations and dye injection. Fish were then placed in a bath of antibiotic (furaltadone, 0.1‰ in seawater). This tagging technique has been previously tested in aquaria with males of different size. Fish exhibited neither cutaneous necrosis nor abnormal behaviour, and during the aquaria or the present field experiments, neither morbidity nor mortality was observed.

Broods kept in water were mapped by applying a previously squared acetate sheet on nest sides and average density of eggs in a grid cell was estimated. Total number of eggs was estimated by number of grid cells occupied by eggs. Developmental stage of broods were also noted. Then nests with eggs and male were replaced in the field at the same place. Nests with no eggs were cleansed from fouling and deposits.

To characterize the utilization of nests by males and females, 6 situations were defined according to the situation observed on the previous visiting date. On the first visit, and subsequently if there were no eggs in the nest on the preceding visit, 3 events might have occurred: POS (possession): the presence of a male without eggs, NES (nesting): the presence of a male and eggs, VAC (vacancy): the absence of male and eggs.

If there was a male (identified by tagging) with eggs in the nest at the preceding visiting date, the events that might have occurred were: CON (continuation): the observation of the same male with eggs, ROB (robbery): change of male with persisting brood, DES (desertion): the observation of an empty nest (no male, no eggs).

RESULTS

On the first visit, *i.e.* two weeks after the nests were installed, 30 out of the 48 available nests were occupied by a male and 9 nests already

contained eggs and male (Fig. 2). Over the studied period (384 nest inspections), the presence of a male in the nests was observed in 77% of the cases (294 observations), accounting for 124 different males. Presence of brood in the nests occurred in 58% of the cases (224 observations). The presence of broods without a male was never encountered. Likewise, other fish species or potential predators were never observed inside the nests.

Brood structure inside the nest

In most cases, the first eggs in the nest were always laid in a spot-like cluster. Subsequent broods were laid besides and round the initial "spot" that they enlarged progressively. Rapidly, broods in the nest became a mosaic of eggs exhibiting different developmental stages within which different egg batches were hardly distinguishable. Batches were laid upon all sides of the nest. Broods in the nests were always healthy showing that water renewal, oxygenation and nest cleaning were satisfactory.

Some egg surveys showed that the development time of eggs was about 10 days at the beginning of the experimentation with a mean daily water temperature of 18 °C and less than 5 days at the end with a mean water temperature of 25 °C (daily amplitude of 10 °C).

Mean egg density among nests was $X \pm sd = 54 \pm 8$ eggs cm^{-2} , $N = 224$. With this average egg density considered, a small nest could contain up to 7,290 eggs, a medium nest 12,690 eggs, and a large nest 18,522 eggs, if all nest surfaces were covered. And if a female of an average size (80 mm) had a mean batch fecundity of 900 eggs (Ruchon *et al.* 1993), a small nest could very well house up to 8 female batches, a medium nest 14 batches, and a large nest 20 batches.

Temporal changes of brood mean surface area

Brood mean surface area was globally higher in nests with small entrance size than in nests with large entrance size (Fig. 3). This difference came from the greater variability exhibited by nests with large entrance size (Fig. 2). Some nests among the latter remained empty of eggs throughout the study while others were almost full. The same observation was to be made with Ls nests.

For a given entrance size (s or l), variation of mean surface area between nests of different sizes (S, M or L) was less pronounced and varied in the course of the season (Fig. 3). Concerning the nests with small entrance, at the beginning of the experiment, the smaller they were, the higher was the mean brood surface area. When available inner surface area of the smallest nests became progres-

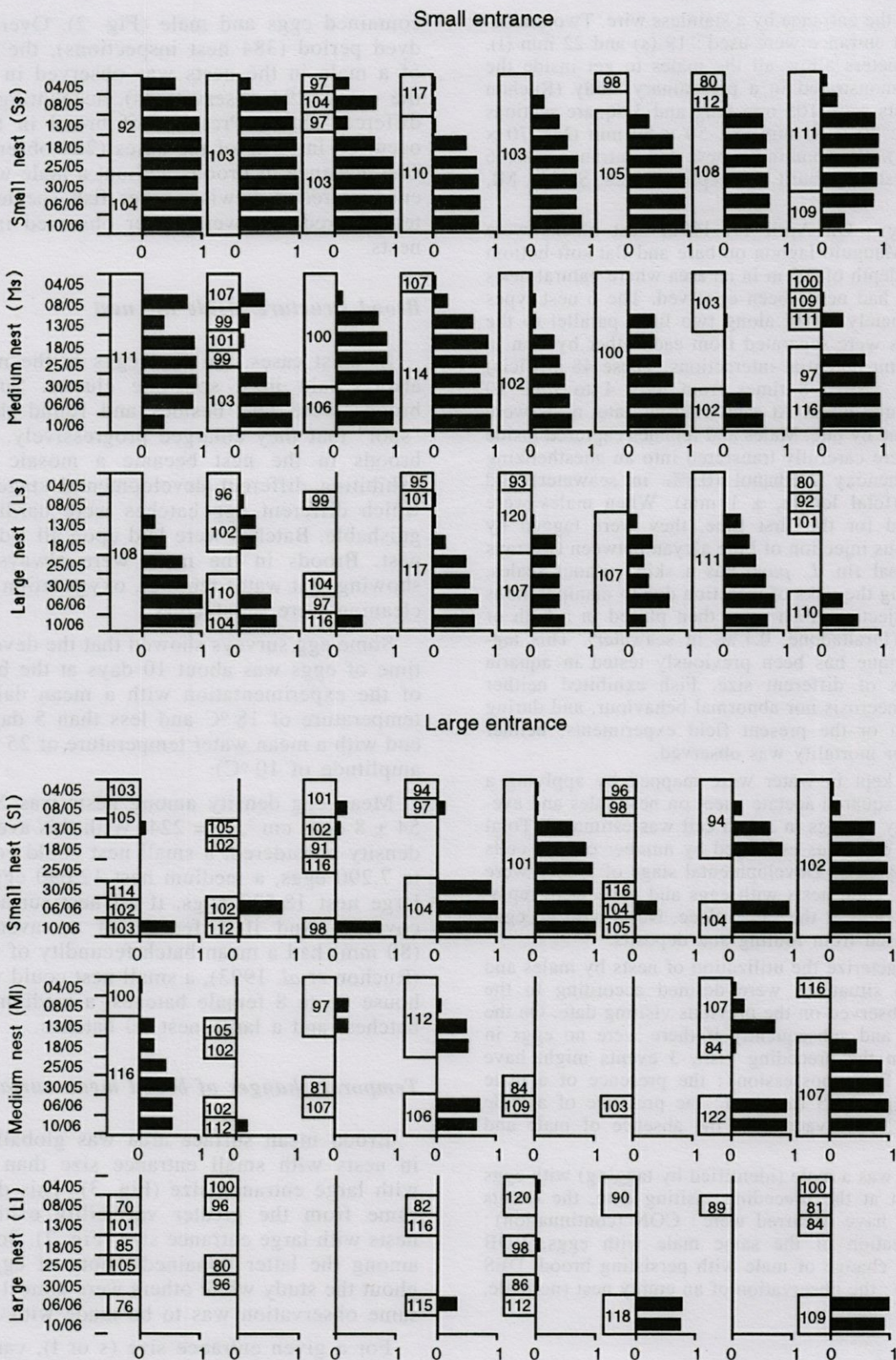


Fig. 2. – Males presence and size (white vertical bars) and percentage of internal surface area occupied by eggs (black horizontal bars) for the 48 artificial nests at each visiting dates. As an example, for the first small nest with small entrance a male of 92 mm was seen from May 5 to May 25, and a second male of 104 mm from May 30 to June 10.

Table I. – Frequencies (%) of POS-NES-VAC events and CON-ROB-DES events according to nest type.

Nest type	POS	NES	VAC	number of cases	CON	ROB	DES	number of cases
Ss	40.0	53.4	6.6	15	87.7	12.3	0	49
Ms	42.9	47.6	9.5	21	82.5	10.0	7.5	40
Ls	47.1	23.5	29.4	34	86.2	10.3	3.5	29
S1	34.2	31.6	34.2	38	76.0	4.0	20.0	25
M1	21.4	21.4	57.2	42	76.2	4.8	19.0	21
L1	30.4	10.7	58.9	56	33.4	0	66.6	6

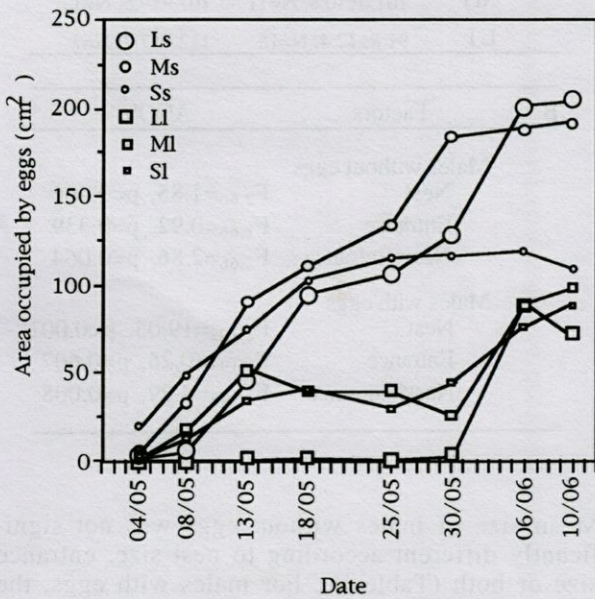


Fig. 3. – Evolution of mean surface area (cm²) occupied by eggs in each nest type during the experiment.

sively overlaid with eggs, this trend was inverted. Hence, from May 13 to May 30, medium nests (Ms) exhibited the greatest mean brood surface area, and after June 6, the large nests (Ls) were those with the highest mean brood surface area. For nests with large entrances, brood mean surface areas were similar to those of small and medium nests (S1 and M1 respectively) and increased irregularly until June 10. Large nests (L1) were almost empty during the 3 first weeks, and from the fourth week onwards (May 30), mean surface area covered by eggs quickly increased and reached the level close to those of smaller nests with large entrance size. It must be pointed out that this effect is only due to two nests (Fig. 2).

Nest utilization

Globally, observations of males and broods were much more frequent in nests with small entrance size (Chi-square test; for male : $\chi^2 =$

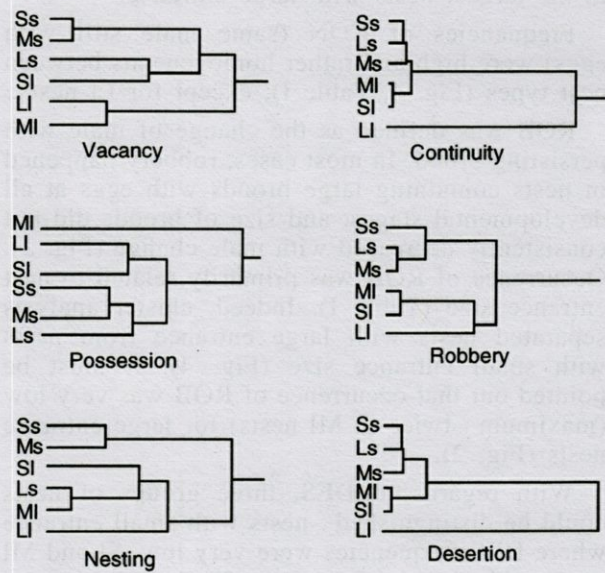


Fig. 4. – Cluster analysis (euclidian distance and single linkage method, Systat package) of nest type for each event of nest utilization.

57.6, df = 2, p < 0.001; for broods : $\chi^2 = 67.2$, df = 2, p < 0.001). And for each entrance size, the presence of males and eggs was all the more frequent and the first broods to be found as the nest were smaller (Fig. 2). Similarly, variability of nest success within a nest type increased with nest size and entrance size (Fig. 2).

The frequency distributions of VAC-POS-NES were significantly heterogeneous within nest types (Chi-square test : $\chi^2 = 36.9$, df = 12, p < 0.001).

Frequencies of VAC (no male, no eggs) were generally greater in nests with large entrance size (Table I). Three groups of nests could be differentiated (Fig. 4) : Ss-Ms with VAC frequencies lower than 10 %, Ls-S1 with frequencies about 30 %, and Lm-L1 with frequencies higher than 50 %.

Frequencies of POS (a male, no eggs) ranged from 21.4 to 47.5 % (Table I) and were not related to nest type (Chi-square test : $\chi^2 = 6.8$, df = 5, p = 0.232). Nests with small entrance (Ss, MS

and Ls) with highest frequencies could be distinguished from S1 and L1 nests (Fig. 4), and M1 nests which exhibited the lowest POS frequency. Males seen on two consecutive dates in a nest without eggs were observed 11 times (Fig. 2). This may reflect either a strong disturbance during manipulations or that these males did not succeed in breeding, or both.

With regards to NES (male, first eggs), cluster analysis separated Ss and Ms nests from other nest types (Fig. 4, Table I). It must be pointed out that S1 nests exhibited higher NES frequency than Ls nests. The lowest NES frequency occurred in the largest nests with large entrance.

Frequencies of CON (same male still with eggs) were high and rather homogeneous between nest types (Fig. 4, Table I), except for L1 nests.

ROB was defined as the change of male with persisting brood. In most cases, robbery happened in nests containing large broods with eggs at all developmental stages, and size of broods did not consistently decrease with male change (Fig. 2). Occurrence of ROB was primarily related to nest entrance size (Table I). Indeed, cluster analysis separated nests with large entrance from nests with small entrance size (Fig. 4). It must be pointed out that occurrence of ROB was very low (maximum : twice in M1 nests) for large entrance nests (Fig. 2).

With regards to DES, three groups of nests could be distinguished : nests with small entrance where DES frequencies were very low, S1 and M1 nests with frequencies about 20 % and L1 nests (Table I) the highest frequency.

Male and female characteristics

All males captured in artificial nests exhibited strong secondary sexual characteristics (large crest, well-developed anal glands) and corresponded to the "nest-breeder" male type described by Ruchon *et al.* (1995).

The mean size of males seen in nests was $X \pm sd = 104.2 \pm 8.2$ mm, $N = 124$ (70-122 mm). This mean size was higher than that of males in the population during this period. According to Ruchon *et al.* (1998) they were large two year-old males.

Among all nests, size of males without eggs ($X \pm sd = 99.7 \pm 10.9$ mm, $N = 72$) was smaller than that of males with eggs ($X \pm sd = 105.2 \pm 6.2$ mm, $N = 199$; ANOVA : $F_{1,269} = 32.3$, $p < 0.001$). Within a nest type, mean size of males with eggs was always higher than that of males without eggs except for S1 nests (Table II). However, the difference was only significant for Ls (Mann-Whitney U-test : $U = 184$, $N_1 = 17$, $N_2 = 37$, $p = 0.015$) and L1 nest (Mann-Whitney U-test : $U = 11$, $N_1 = 18$, $N_2 = 7$, $p = 0.002$).

Table II. – A, Size ($X \pm sd$ in mm, N) of males without eggs and with eggs according to nest type. B, Two-way ANOVA for the effect of nest size (S, M, L) and entrance size (s, l) on male size for males without eggs and males with eggs separately.

A	Nest type	Males without eggs	Males with eggs
	Ss	99.5±15.3, N=4	104.9±5.6, N=60
	Ms	102.9±3.8, N=9	105.5±5.8, N=50
	Ls	102.5±10.1, N=4	109.7±5.2, N=37
	S1	103.5±7.6, N=13	101.5±3.4, N=33
	M1	101.6±10.8, N=11	107.9±9.5, N=12
	L1	91.8±12.4, N=18	112.4±7.7, N=7

B	Factors	ANOVA
	Males without eggs	
	Nest	$F_{2,66}=1.85$, $p=0.166$
	Entrance	$F_{1,66}=0.92$, $p=0.339$
	Nest*Entrance	$F_{2,66}=2.86$, $p=0.064$
	Males with eggs	
	Nest	$F_{2,193}=19.05$, $p<0.001$
	Entrance	$F_{1,193}=0.26$, $p=0.607$
	Nest*Entrance	$F_{2,193}=4.99$, $p=0.008$

Mean size of males without eggs was not significantly different according to nest size, entrance size or both (Table II). For males with eggs, the effect of entrance size on males size was not significant while that of nest size was. Males size increased with nest size. Interaction of the two factors was also significant (Table II). Among all nest types, no size difference was noted between males in cases of ROB (Paired t-test : $t = 0.763$, $n = 14$ $p = 0.458$).

The observation of a female being spawning in the nest occurred 22 times, with comparable occurrence frequencies between nest types (Chi-square test : $\chi^2 = 1.7$, $df = 2$, $p = 0.42$). Synchronous multiple spawning with two or three females in the same nest was observed three times. Females size ranged from 64 to 94 mm and showed no relationship with males size (Pearson correlation : $r = 0.26$, $n = 26$, $p = 0.228$). Likewise, there was no effect of nest size and entrance size on size of females (two-way ANOVA : $p > 0.05$).

DISCUSSION

In our experiment one may consider that artificial nests were successfully utilized by *L. pavo* in spite of their location in a sand-silty area which

was not the usual habitat of this species in Manguio lagoon. This success can be explained by the behavioural plasticity and mobility of this species. Indeed, *L. pavo* was reported to live either in rocky, sandy or muddy zones (Zander 1972, Moosleitner 1980, Santos *et al.* 1989, Almada *et al.* 1994), and to undertake large scale displacements (Moosleitner 1980, Santos *et al.* 1989). Furthermore, the scarcity of potential nest sites in the lagoon (Ruchon 1995, Ruchon *et al.* 1995) might strengthen the exploratory behaviour of fishes and reduce their selectivity for nests. Compared to natural nests of the lagoon (mostly opened surfaces), artificial nests looked like dark, closed cavities which were likely to be highly attractive to this species. Our results showed that all the nests could be successfully used by fishes. All the fishes, even the largest, could get inside the nests. So one can consider that it was really the preference of *L. pavo* that we have tested.

We initially attempted to test the choice of nest by males, hypothesizing that entrance size would determine the protection of male and eggs against predators and undesirable conspecifics while nest size would determine maximal number of eggs expected from males. Unfortunately, the results did not allow to answer the question clearly. Size of males did not affect the type of nest they might occupy (a male with no egg), and no significant differences in possession frequency could be detected between nest types. However, males seemed to prefer nests with small entrances. We lack behavioural information for a better interpretation. For instance, male have been rarely observed twice in the same nest without eggs, suggesting that male territoriality was linked to the presence of eggs and was weak before the first eggs were laid. Furthermore, it is likely that during this period of low territoriality, the stress of manipulation disturbed males and scared them away. In fact, most of the results dealt with the female choice according to the characteristics of male and those of nest.

Lipophrys pavo females preferred to spawn with the largest males, or at least, they discarded the smallest since nesting males (with eggs) were generally larger than occupying males (with no eggs). However, the size range of males guarding eggs was rather large (84-120 mm) and suggested that male size was not the only criterion of female mate choice, and that other male traits were taken into account by females. Indeed vigor of courtship, age, condition and/or secondary sexual characteristics may also condition the choice of females (Kodric-Brown 1990).

As before the first batch, size distribution of males was very large and almost homogeneous among nest types, the effect of nest characteristics (entrance and internal nest size) on female mate choice could be examined regardless of the size

of males holding the nests. The first factor influencing the females choice was the entrance size, the size of the nest (or internal volume) appeared as a factor of lesser importance. Indeed, females preferred first to spawn in nests with narrow entrance. Nests with narrow entrance always exhibited the highest frequencies of nesting (first eggs in the nest) and average number of eggs throughout the experiment. Of course, one can wonder if it was only the entrance size or the association entrance-male size that was selected by females. If so the larger the male for a given entrance, the most attractive would be the nest for the females. Likewise, the poor success of nests with large entrance could be explained by the scarcity of males large enough to fill the entrance hole. The preference of females for nests with small entrance probably concerns egg protection. With regard to nest size, females appeared to preferably spawn in the smallest nests. The increase of size in successful male with nest size suggests that the choice of nest size was not independent of the size of male.

In the course of the experiment, the presence of eggs in nests appeared to be a determining factor in female mate choice and was more important than factors of male size or nest and entrance size. Indeed, frequencies of continuity were high whatever the nest type or the male size, and the presence of eggs could compensate for the initial bad quality of nests. For instance, nests with large entrance which seemed *a priori* not attractive to females, performed as well as those with smaller entrance since they contained some eggs. The presence of eggs as a factor of female mate choice has been reported in several nesting fish species with male parental care (Ridley & Rechten 1981, Marconato & Bisazza 1986, Kraak & Videler 1991). This strategy would allow females to limit the risks of egg predation by dilution effect (Rohwer 1978, Constantz 1985, Unger & Sargent 1988). This assumption is strengthened by the fact that females of *L. pavo* laid their eggs as close as possible to other eggs present in the nest. In addition to this, the presence of eggs in the nest which indicated former male success, would be perceived by the female as the guarantee that a male is a good genitor and a good guardian (Ridley & Rechten 1981, Hastings 1988b). This preference of females for nests with eggs tended to strengthen the initial choice operated on characteristics of nest, and might lead, in the field, to a concentration of broods in a reduced number of nest.

Criteria of female mate choice tend to optimize their global reproductive success through egg survival and the genetic quality of offspring (fitness) (Kodric-Brown 1990). But, factors allowing females to appreciate the expected genetic quality and the protection of eggs are the same.

Indeed, a large male is, generally, *a priori* a good guardian and a good genitor; many eggs guarantee both a lower risk of predation and the recognition of the genetic quality and the caring capacity of males; and a small entrance limits the risk of predator intrusion and parasitic fertilizations. The convergent effects of this factor makes difficult their distinction or their ordination.

The existence of precise criteria in female mate choice, and notably the fact that females select preferentially nests with eggs, led to concentrate broods in a small number of nests, and therefore to concentrate reproduction on few males. This tendency was especially true at the beginning of the breeding season, a crucial period for the renewal of the population (Ruchon *et al.* 1998), and therefore led to a strong sexual selection upon males. To avoid such an intrasexual selection, males may adopt an alternative reproductive strategy (kleptogamia) as described in this population (Ruchon *et al.* 1995). The change of guarding-male (defined as robbery) is another alternative to better distribute paternities and egg care between males. Robbery was defined as the change of male with persisting brood. Male change could result from a desertion followed by the possession by a new male. This situation probably occurred when nests contained few eggs close to hatching (*e.g.*, 7th Ss nest between May 8 and 13, males : 112-108). In most of the robbed nests, there were large broods with eggs at different developmental stages, and it is unlikely that these nests had been abandoned. Even though robbery was more frequent in nests with narrow entrance, the small number of cases and the lack of reliable behavioural information did not allow to further interpret this result. However, the absence of size difference between the 'robbed' male and the 'robber' male suggests that other factors, as male condition or motivation, should intervene in the process of nest robbery. Nest robbery was rarely followed by an important decrease of brood size inside the nest, there was therefore no or little destruction of broods by the new male, and this constitutes an evidence of allopaternal care. This phenomenon is rarely encountered in fishes, but it has been reported in some species as *Ophioblennius atlanticus* (Santos 1995), *Pimphales promelas* (Unger & Sargent 1988), *Etheostoma olmstedi* (Constantz 1985), or in *Padogobius martensi* (Bisazza *et al.* 1989). The male that seizes a nest already full would take energy to care for offspring of the former male; moreover, it will not be able to fertilize many eggs until the eggs formerly present in the nest are hatched. This cost is probably compensated by the attractiveness such a full nest exerts on females, and therefore by the benefits that the new male will get from. It is probably this positive balance that allows the existence of allopaternal care in this population.

In this population of *L. pavo*, we have already described the effect of low nest sites availability on male sexual selection, favoring the existence of an alternative reproductive male strategy (kleptogamic males) or discarding a fraction of the male population from the reproduction (non-functional males, Ruchon *et al.* 1995). To this effect, it is necessary to add the combined effect of the mode of nest choice and the range of available nests (entrance size, internal surface) which may also affect the intensity of male sexual selection. As females prefer nests already containing eggs, the distribution of broods among nests should depend on nest size, quite independently of their abundance. For example, assuming a population with a 1 : 1 sex-ratio and mean nest capacity of ten female batches, only a male out of ten will fertilize and keep eggs. Conversely, if available nests have a reduced internal surface (only one batch capacity), females will have to distribute their egg batches on a larger number of nests and males, *i.e.* one batch for a male (assuming a sex-ratio of 1 : 1). In this case, the sexual selection exerted on males will be weaker. These cases are obviously extreme ones but one can find some equivalents in nature. For instance, the latter case was observed in some sympatric blenny species, including *L. pavo*, that nest in holes of small endolithic bivalves (Kotrschal 1988). No male alternative strategy could be detected in these populations. On the other hand, Almada *et al.* (1994) described a population of *L. pavo* where nests were very scarce and large but also easy to defend: "only the bricks having one of the end obstructed and the other opening narrowed". In this population, there existed some kleptogamic males (Gonçalves *et al.* 1996). Therefore, the intrasexual male selection which probably accounts for alternative male reproductive strategy in these populations, may be mostly affected by the size of nests rather than their ability to be defended. In the lagoon of Mauguio, and in nature more generally, nest size is linked to the size of its opening, large cavities with narrow entrance are quite scarce. Hence, the preference of females for nests with small entrances would tend to better distribute broods between males and indirectly to reduce the selection upon them.

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