J. mar. biol. Ass. U.K. (1996), 76, 529–538
Printed in Great Britain

FEMALE MIMICRY AS A MATING TACTIC IN MALES OF THE BLENNIID FISH *SALARIA PAVO*

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In this paper we present evidence for female mimicry in a population of *Salaria pavo* (Pisces: Blenniidae). Parental males differ markedly from females by the presence of a large crest on the head and anal glands on the two spiny rays of the anal fin. We found a proportion of smaller and younger males that are almost identical to females both in morphology and behaviour. These 'female-like' males lack secondary sexual characters and actively court parental males, displaying the female's colour pattern and courting behaviour. These males are sexually mature and their gonadosomatic indices are higher than those of parental males. Female mimicry is considered to be a functional way to achieve sneak fertilizations.

INTRODUCTION

In many teleost species in which males compete aggressively for females, some males (typically small ones) adopt behaviours and colour patterns that mimic those of the receptive females as a means of approaching spawning fish and sneaking fertilizations (for a recent review on the occurrence of these alternative reproductive tactics see Taborsky, 1994).

In blenniids, spawning takes place in cavities defended by males which guard the eggs until hatching (e.g. Gibson, 1969, 1982; Thresher, 1984; Almada & Santos, 1995). In this family, although the reproductive behaviour of several species has been studied in detail (for a review see Almada & Santos, 1995), alternative mating tactics have only been found in *Parablennius sanguinolentus* (Pallas, 1811) (Santos, 1985; Santos & Almada, 1988; Santos, 1992; Santos et al., 1995). In this species, small mature males lacking secondary sexual characters, act as sneakers, seeking opportunities to intrude into the nests of parental males during spawning, whereas somewhat larger males behave as satellites (*sensu* Wirtz, 1982) of specific nests. Both types of parasitic males are younger and smaller than parental males. In other blennioids, nest intrusions and sneaking by smaller and younger males were described for several tripterigiid species (Wirtz, 1978; Thresher, 1984; de Jonge & Videler, 1989).

Although in the previously-mentioned cases parasitic males differ from territorial males presenting colour patterns and/or morphological characteristics similar to females, no female mimicry was found. Sneakers get access to spawning females by quick intrusions into the nests.

In this paper, we present evidence for female mimicry in sneaking males of the blenniid *Salaria pavo* (Risso, 1810). Although large males and females differ markedly in morphology and colour patterns (Fishelson, 1963; Patzner et al., 1986), we found small 'female-like' males that display the female's spawning colour pattern and courtship behaviour to sneak fertilizations. The large males with fully developed crests and anal glands were either parentals (defending a nest) or floaters (that move around the nests and often behave aggressively to the nesting males). The breeding ecology and behaviour of this population have been described by Almada et al. (1994) and Almada et al. (1995). Parental males form dense nest aggregations and females are the courting sex, actively displaying to males and competing intensely for access to nests, which are very scarce in the study area.

MATERIAL AND METHODS

Behavioural observations were conducted by snorkelling on 97 nests in the breeding seasons of 1988 and 1994 (total observation time was 24 h 54 min). In each observation we recorded: (a) the number of nests in each aggregation; (b) the number of visits and identity of the visitor (floater, large males with developed secondary sexual characters i.e. a large crest on the head and glands on the two spiny rays of the anal fin; sneaker, small males without secondary sexual characters; or female); (c) the number of agonistic interactions and the identity of the participants; and (d) the number of courtship episodes and the identity of the initiator. In the field, sneakers were distinguished from females by the lack of a swollen abdomen and less marked courtship colour patterns. When courting, females and sneakers display a pattern of dark stripes on a light background on the head and anterior part of the body. This pattern is less marked in sneakers and is almost restricted to the head. It is likely that the observed number of courtship episodes by these males may have been underestimated since all fish that upon collection were classified as female-like males, proved to be males after gonad inspection, and some fish classified as females proved to be males.

Fish samples for gonadal inspection and age determination were collected during the breeding seasons of 1990, 1991 and 1993. Fish were caught with a hand net and killed with an overdose of quinaldine. The following measurements were taken: body weight; gonad weight; standard length (SL); head height (HH) (maximal height of the head); body height (BH) (at the level of the pectoral fin); and development of anal fin glands coded as: 0, not visible; 1, intermediate (the typical folds and circumvolutions of a fully developed gland were not visible); 2, fully developed. The otoliths were removed for subsequent reading. Additional samples were taken (August 1988, April–September 1993, and January 1994) to determine the timing of annual ring formation in the otoliths. All samples were kept to a minimum and were collected during several years, since this species is vulnerable in Portugal (ICN, 1993). Additional morphometric measurements were taken from live fish that were immediately returned to their habitat. The development of the testicular gland in relation to the testis was assessed using the testicular gland index: TGI, $\sqrt{ab} \, / \, \sqrt{cd}$; where *a* is the length of the testicular gland; *b*, the width of the testicular gland; *c*, the length of the testis and *d*, the width of the testis. Gonads were fixed in Bouin's fluid and afterwards processed for histological sections. Testes sections were dehydrated, embedded in paraffin and stained with haematoxylin-eosin.

Statistical analysis was performed using the PC computer programmes STATISTICA for Windows 4·0 (Copyright Statsoft 1993) and BIOM (Copyright F. James Rohlf, 1984).

RESULTS

Morphological variation among males

Males attain larger size than females (SL: mean=10·0 cm, SD=1·90, range=5·3–13·4 cm, N=89, for males; and mean=7·2 cm, SD=1·48, range=4·5-10·2, N=73, for females; Mann-Whitney test: Z=4·313, $P<0{\cdot}001$). The contrast between females and males with fully developed secondary sexual characters is very striking (Fishelson, 1963; Zander, 1975; Papaconstantinou, 1979; Patzner et al., 1986) and there is a large variation with size in the expression of these characters in males (Almada et al., 1994). The males in which these traits are less developed are hardly distinguishable from females, except on close inspection of the genital papilla. These female-like males are specially interesting, since histology of their gonads and gonadosomatic index values revealed that a large proportion of them are fully mature fish (see below).

One way to express the relative development of the crest is the ratio head height (HH):body height (BH). Since males attain larger sizes than females, the observed difference in profile could merely reflect the effects of a common allometric pattern of growth. To answer this question an analysis of covariance (ANCOVA) was done, using the regressions between log SL and log HH and between log SL and log BH for males and females (Table 1). For HH, the regression equations for males and females differ both in slope and intercept, while for BH only the intercepts are significantly different. In small males the ratio HH:BH is similar to that of females, but it increases progressively as males attain larger sizes. Thus there is a wide spectrum of variation from female-like to fully crested males. The development of the anal glands also increases with size, and is strongly associated with crest development, when the effect of size is removed (partial correlation $r=0{\cdot}677$, $P<0{\cdot}01$, N=31). The larger males also display a very distinct and conspicuous colour pattern (Fishelson, 1963; Patzner et al., 1986).

Table 1. *ANCOVA based on fish measured in May 1990 using the regressions between log SL/log HH and between log SL/log BH for males and females.*

	Regression equations		ANCOVA			
	Males (N=31)	Females (N=28)	Intercepts		Slopes	
			$F_{1,56}$	*P*	$F_{1,55}$	*P*
logSL/logHH	y=-1.07+1.47x	y=-0.95+1.24x	55.470	<0.001	4.802	<0.05
logSL/logBH	y=-0.91+1.25x	y=-0.82+1.12x	4.868	<0.05	3.458	n.s.

Development of male reproductive system

It could be argued that small female-like males without crest and anal fin glands are immature juveniles. However, this is not true for at least a substantial proportion of these males. In Figure 1 we present histological testicular sections of female-like males, compared with those of parental males.

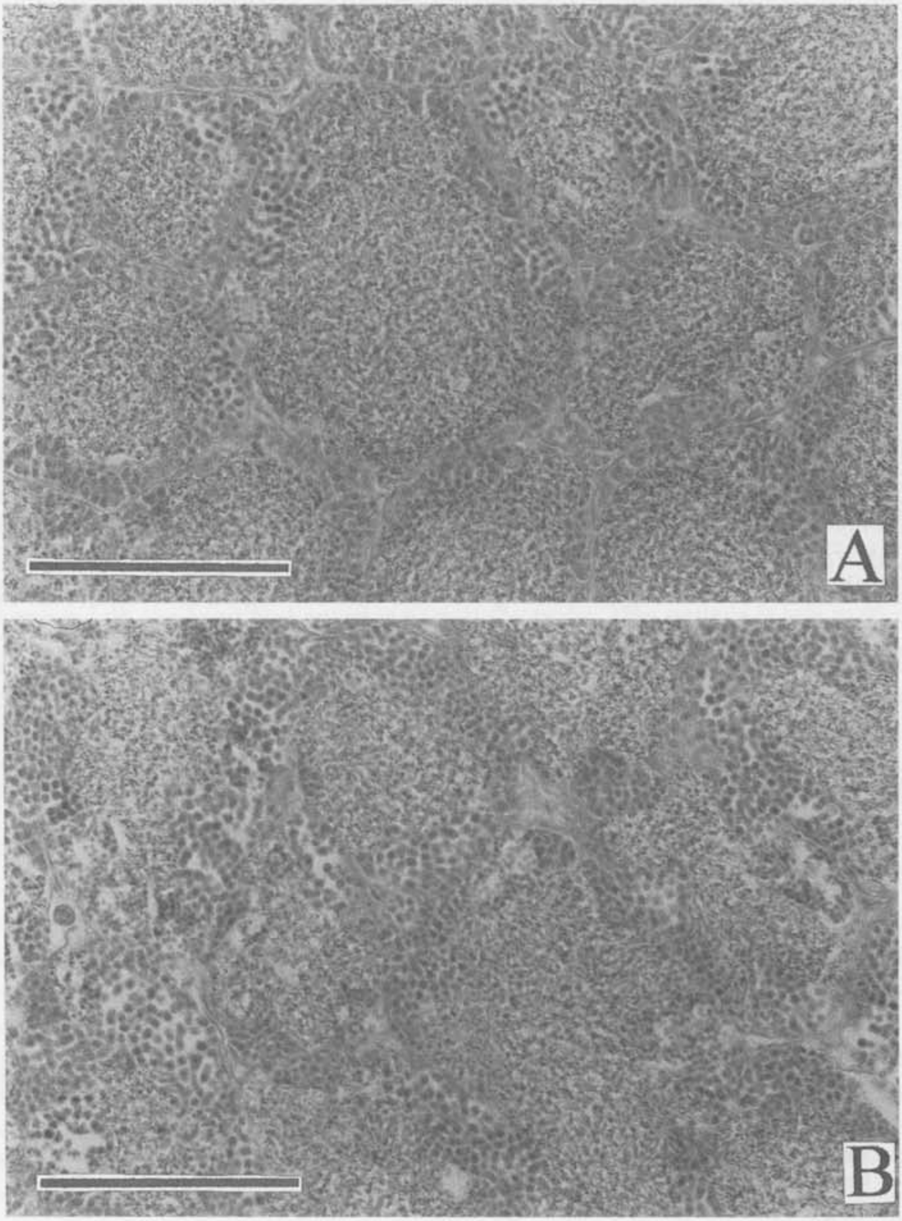

Figure 1. Histological testicular sections of (A) female-like male and (B) parental male. Note the testicular tubules full of spermatids in both cases. Scale bar: 100 µm.

In both cases the testicular tubules were full of spermatids with no apparent difference in structure between them. Histochemical investigations of both types of males confirmed these results as they failed to reveal any differences in enzymatic activity related to steroid production in their gonads (R.A. Patzner et al., unpublished data). Moreover, sperm could be collected from the vas deferens of female-like males, and its mobility was confirmed by observation of the seminal fluid under the microscope (x1000).

The gonadosomatic index (gonad weight x 100 / body weight) of parental and female-like males and its variation with standard length during the breeding season is presented in Figure 2. The most striking pattern is the clear bimodality in the gonadosomatic index values (GSIs) of female-like males. While 54·2% have GSIs equal or lower than those of parental males, the remaining 45·8% have GSIs well above those of parental males, and there is a gap between 0·975 and 2·392 GSI values. Patzner & Seiwald (1987) studied the testicular cycle of this species in the Mediterranean and showed that the GSI of males ranges from 2·26 ±0·26 at the onset of the breeding season, to ~0·4 near its end. Our results lie within this range of variation for parental fish, while some female-like males have much higher values (the maximum value was 4·528).

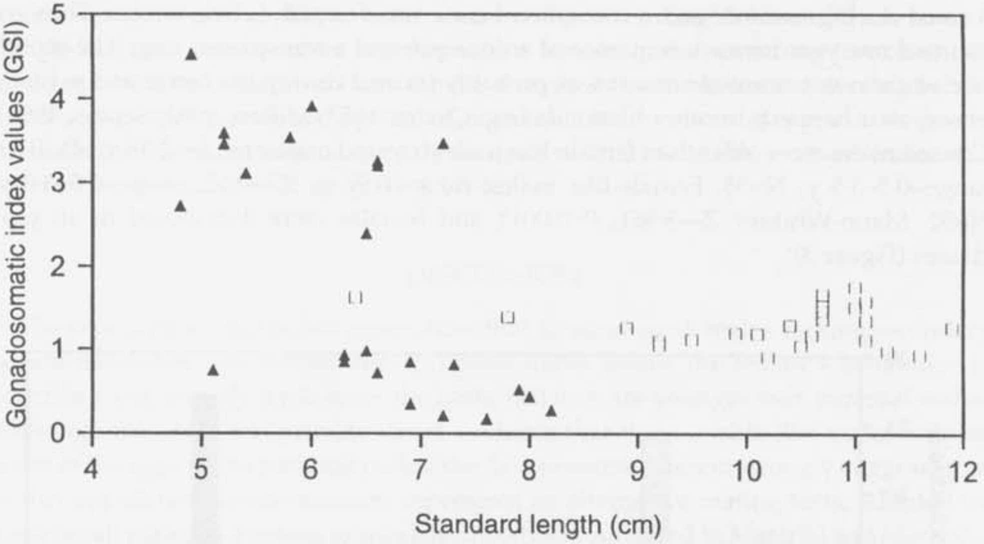

Figure 2. Gonadosomatic index values (GSI) of □, parental males (N=24); ▲, female-like males (N=24) and its variation with standard length for samples taken in May 1990, July 1991 and July 1993.

Based on the results presented in Figure 2, we classified the female-like males in two groups according to their GSI values: <1·0 (group 1–54%), and >2·3 (group 2–46%). They differ both in SL (group 1: mean=6·98 cm, SD=0·85, range=5·1–8·2 cm, N=13; group 2: mean=5·84 cm, SD=0·80, range=4·8–7·2 cm, N=11. Mann-Whitney Z=-2·670, *P*<0·01), and in the HH:BH ratio (group 1: mean=0·996 cm, SD=0·092, range=0·83–1·15 cm, N=13; group 2: mean=0·909 cm, SD=0·046, range=0·83–1·00, N=11. Mann-Whitney Z=-2·216, *P*<0·05). Thus, the latter group contains fish of smaller sizes, less developed crests and bigger testes. The fact that group 1 fishes are larger, show a more developed crest, and have low GSI values, raises the possibility that they may be in the transition to the large male's phenotype.

A comparison of the testicular gland index (TGI) between parental males and group 1 and group 2 of female-like males revealed that there is a significant difference among groups (parental males: mean=0·430 cm, SD=0·052, range=0·323–0·540 cm, N=14. Group 1: mean=0·530 cm, SD=0·069, range=0·419–0·648 cm, N=9 and group 2: mean=0·367 cm, SD=0·020, range=0·339–0·393 cm, N=7. ANCOVA: $F_{2,27}=19{\cdot}81$, $P<0{\cdot}001$). Group 2 female-like males (those with the highest GSIs) have significantly lower TGIs than either group 1 fishes or parental males (Tukey HSD test: group 2-parental males, $P<0{\cdot}05$ and group 2–group 1, $P<0{\cdot}001$). Parental males and group 1 fishes also have significantly different TGI values (Tukey HSD test, $P<0{\cdot}001$), being higher in group 1. Since the group 1 female-like males have the lowest GSI values and are possibly in the transition to the large male's phenotype, their higher TGIs suggests that the testicular gland may develop at a faster rate than the testes during the differentiation process.

Age determination

Observations of otoliths in seasonal samples revealed that an opaque zone was formed during summer and a transparent zone was formed during winter. Thus we counted one year for each sequence of an opaque and a transparent ring. The otolith nucleus was not counted since it was probably formed during the larval and juvenile phase, as it happens in other blenniids (e.g. Qasim, 1957; Milton, 1983; Santos, 1992). Crested males were older than female-like males (crested males: mean=2·78 y, SD=0·51, range=0·5–3·5 y, N=53. Female-like males: mean=0·97 y, SD=0·42, range=0·5–2·0 y, N=52. Mann-Whitney Z=-5·581, $P<0{\cdot}001$), and females were distributed in all year classes (Figure 3).

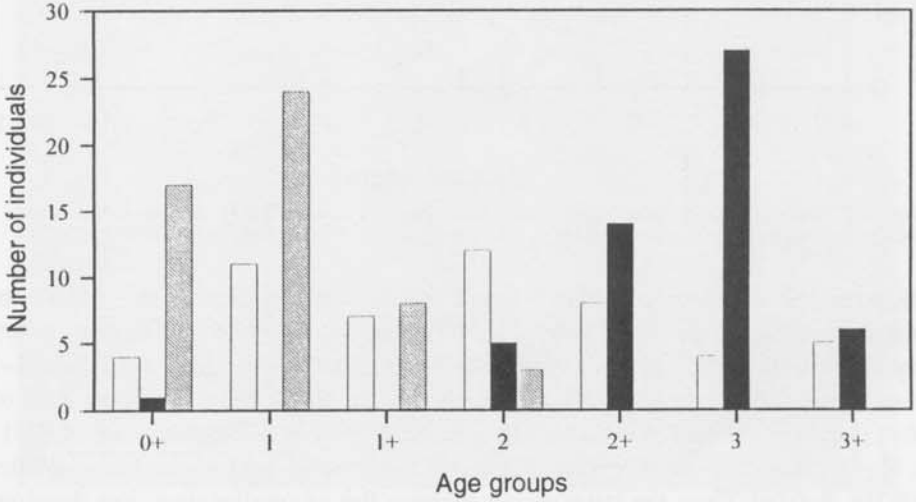

Figure 3. Age group distribution of females (hollow bars, N=51); female-like males (striped bars, N=52) and crested males (black bars, N=53) for samples taken in August 1988, May 1990, July 1991, April, July and September 1993 and January 1994.

Most female-like males were fish born in the previous year and most crested males were ~3 y-old. The only crested male from the year class 0+ was found in a very small isolated nest, far from the nest aggregations. For both sexes, age and size were well correlated (Spearman rank correlation: $r_s=0{\cdot}824$, $P<0{\cdot}001$, N=105 for males and $r_s=0{\cdot}872$, $P<0{\cdot}001$, N=51 for females). Group 1 and group 2 of female-like males did not differ in age (group 1: mean=0·92 y, SD=0·40, range=0·5–2·0 y, N=13 and group 2: mean=0·91 y, SD=0·20, range=0·5–1·0 y, N=11. Mann-Whitney: Z=0·292, $P>0{\cdot}05$).

Behavioural observations

In this population, the females are the courting sex (Almada et al., 1995). When a receptive female approaches a nest, it assumes a specific conspicuous colour pattern while performing exaggerated pectoral fin and opercular movements (Fishelson, 1963; Patzner et al., 1986). Some female-like males were observed approaching and courting parental males, with the female's characteristic colour patterns and movements. We observed 29 courtship episodes of female-like males, with three of them being performed when a female was already inside the nest, and four occurring simultaneously with a display of a courting female. Additionally, on six different occasions female-like males were observed trying to enter a nest without courting. In one of these cases a female-like male tried to enter together with a female. In the remaining five cases, we could not be sure if there was any female already in the nest, since spawning in this species may last for several tenths of minutes. One or more of these males were consistently found in the proximity of the nests in 31% of the observations (mean=0·5 female-like males, SD=0·8, range=0–4, N=42).

DISCUSSION

The results presented in this paper show that: (i) some small males, lacking secondary sexual characters, are mature fish; (ii) these males mimic the female's behaviour in courtship and actively try to enter the nests; (iii) they are younger than parental males. Although we could not provide direct evidence that these female-like males fertilize some of the eggs of the parental males, the data presented herein strongly suggests that in this population female mimicry represents an alternative mating tactic adopted by some small males as a means to sneak fertilizations. As stated in Material and Methods, the frequency of courtship by female-like males is probably underestimated since some of them could not be distinguished from females in the field. The presence of females in the nests when female-like males tried to enter them is probably also underestimated, since they could be already inside the nest when the observation started. In addition, Patzner (1984) showed that the micropile of the eggs of *Salaria pavo* is in the centre of the attachment disk, suggesting that sperm must be released before spawning. Thus, it is possible that female-like males gain access to fertilizations even if they enter a nest and release sperm when a female is absent. Since it is not known how fertilization actually occurs this issue deserves further attention. The intrusions of small males into the nests could also represent attempts at egg predation. Although the behavioural data presented does not exclude this possibility, it would not explain why these small males have large mature testes. Moreover, eggs were absent from the gut contents of females and female-like males and were found only in small numbers in the parental males (E.J. Gonçalves & V.C. Almada, unpublished data).

The fact that the female-like males with larger testes have smaller testicular glands than parental males agrees with the available data for other blennioids in which parasitic male tactics are known (de Jonge et al., 1989 for *Tripterygion tripteronotus* (Risso, 1810) and *T. delaisi* (Cadenát & Blache, 1970); Santos, 1992 for *Parablennius sanguinolentus*). Apart from a probable role in sperm maturation (Lahnsteiner & Patzner, 1990; Lahnsteiner et al., 1990), Reinboth & Becker (1986) found that in the males of *S. pavo* the testes and testicular gland differ in their enzymatic activity, in what concerns steroid metabolism. They conclude that testosterone is mainly synthesized in the testes, while the testicular gland is the main source of 11-oxygenated steroids. Brantley et al. (1993) reviewing the available data on the levels of testosterone and 11-ketotestosterone in territorial and parasitic teleost fish males, found that testosterone did not show a consistent pattern of variation between the two types of males across species. In contrast, levels of 11-ketotestosterone were consistently higher in territorial males. One of the known functions of 11-ketotestosterone is related with the expression of male secondary sexual characters (Liley & Stacey, 1983). This evidence raises the possibility that the physiological basis for the difference in the expression of secondary sexual characters between female-like and parental males, may be a low level of production of 11-ketotestosterone by the reduced testicular gland of female-like fish.

The data presented for *S. pavo* are consistent with an ontogenetic sequence in male reproductive tactics, as found in *P. sanguinolentus* (Santos, 1992; Santos et al., 1995). The breeding season of this population extends from April to September (Almada et al., 1994). Thus fish born in the previous year may differ in age by many months so it may happen that only males born at the beginning of the breeding season became fully mature during the following year. Nevertheless, both high and low GSI female-like males may later became parentals. Circumstantial evidence points in this direction. A female-like fish kept for two years in captivity was observed to repeatedly court nesting males in the aquarium, develop a crest in the second year, and genital inspection showed that it was a male (E.J. Gonçalves & V.C. Almada, unpublished data). Examination of histological sections of male testes in this population failed to reveal any trace of sex change (L. Fishelson, personal communication).

In discussing the occurrence of multiple male reproductive tactics in fish, Taborsky (1994) argued that, when there is great variation in resource-holding potential among males, parasitic reproductive behaviour is more likely to represent tactics in which males are making 'the best of a bad job', rather than strategies with equal payoffs. In this population, nest sites are scarce, leading to strong competition between females for access to the available nests. Thus, only the largest males can secure territories, with floater crested males ready to take over vacated nests (Almada et al., 1994; Almada et al., 1995). We suggest that, for small males, female mimicry represents a compromise that enables some small fish to sneak fertilizations at a size in which they could not establish and defend a nest. The intense competition between females leads to the frequent occurrence of several females displaying simultaneously to the same male, frequent aggressive interactions between females, and attempts by females to follow other females as they enter the nests. Parental males are very selective and reject most courtship attempts (Almada et al., 1995). In these conditions (intense courtship by females and high rates of rejection by males), a small male whose behaviour and colour pattern mimics those of the females and tries to follow them into the nests, is much more likely to achieve sneaking than a male that lacks the female display and courtship colour patterns.

The authors would like to express their gratitude to the staff of Parque Natural da Ria Formosa for their valuable help during the field work, and especially to its Director Arq^{to} Nuno Lecoq. We would also like to thank Professor Lev Fishelson for valuable help in the histological procedures, Elsa Rodrigues who reviewed the English, and two anonymous referees. This study is part of a project supported financially by Junta Nacional de Investigação Científica e Tecnológica (JNICT-PBIC/1313/MAR/92).

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Submitted 27 March 1995. Accepted 2 July 1995.