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Sex differences in resource utilization by the peacock blenny

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This paper presents data on the seasonal variation of gonadosomatic, hepatosomatic and feeding indices in nesting males, females and female-like males of the blenniid fish *Salaria pavo*. Eviscerated condition factors, female fecundity and feeding rates are also presented. The results are consistent with the hypothesis that females maximize their feeding rates during reproduction, converting food into eggs through repeated spawning. Nesting males feed at a very low rate during the breeding season. It is argued that one major component of the reproductive costs in these males is the reduction of feeding opportunities. Female-like males present lower reproductive costs, which probably reflects the compromise between fertilizing some eggs and growing.

Key words: *Salaria pavo*; Blenniidae; reproductive costs; parental care; body condition; alternative reproductive tactics.

INTRODUCTION

The costs of parental care in teleost fishes, and the ways in which males and females invest resources in reproduction have been studied in several fish species (e.g. Miller, 1984; Sargent & Gross, 1986; Almada, 1990). At low to moderate latitudes, which allow a long breeding season, it is found that females spawn repeatedly and, in some cases, produce a total weight of eggs that may exceed their own weight (Wootton, 1973; Barlow, 1984; Miller, 1984). In these situations, it is expected that, for females, the breeding season is a period of maximal feeding, in which food is steadily converted into eggs. This ability of females to increase fecundity, combined with male territoriality and the ability of males to care for an increasing number of eggs with little additional cost, has been considered by several authors as one of the factors that has contributed to the repeated evolution of male parental care in bony fishes (Blumer, 1979; Baylis, 1981; Gitleman, 1981; Barlow, 1984; Almada, 1990). For males that care and guard the eggs, one of the likely features of male reproductive investment is a reduction of feeding opportunities during the breeding season (e.g. Qasim, 1957; Miller, 1984; Sargent & Gross, 1986; Santos & Almada, 1988; Chellappa *et al.*, 1989; Almada *et al.*, 1992; Santos, 1992; Almada & Santos, 1995; Smith & Wootton, 1995; Santos *et al.*, 1996).

Salaria pavo (Risso, 1810) is ideal to test this hypothesis. Like all other blenniids, the male guards and cares for the eggs, and there is no defined parental cycle. The male may guard the nest for many weeks, and a succession of females may spawn in the same nest, increasing significantly the duration of continuous parental care. In addition, in the population studied here, the nests were densely aggregated and the nesting males minimized their excursions from the nest and

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occupied breeding territories that were virtually limited to the nest hole, therefore with no food resources. There was an excess of mature males that could not establish nests and nesting males were significantly larger than non-nesting males. The smaller non-nesting males were almost identical to females both in morphology and behaviour and acted as sneakers (female-like males), while the larger ones acted as floaters and tried to take over the nests of parental males. Several aspects of the biology and behaviour of this population have been described in previous papers (Almada *et al*., 1994, 1995; Gonçalves *et al*., 1996). In this paper, data is presented on the patterns of resource utilization by male and female *S. pavo*.

MATERIALS AND METHODS

The population studied was found in a lagoon environment at Ria Formosa, southern Portugal (36°59′ N, 7°51′ W), where the only available cavities were bricks used by clam culturists to delimit their fields. The boundaries of adjacent clam cultures were delimited by several kinds of hard debris (bricks, tiles, stones) that formed ridges 10–20 cm high. All the nests found occurred intertidally along these ridges. When the tide ebbed, nesting males stayed inside the bricks, while most females and non-nesting males moved to the channels and adjacent eelgrass beds.

Fish samples were collected during the breeding season of 1988 (August), 1990 (May), 1991 (July), 1993 (April, September) and 1994 (January). Fish were caught with the help of a hand-net and killed with an overdose of quinaldine. The following measurements were taken: body weight (W), eviscerated weight (W_e), gonad weight (W_g), liver weight (W_l), gut weight (W_a), and standard length (L). The guts were inspected for the amount of food present and were classified as: empty or with few items, and partially or completely full. The presence of blenniid eggs was also recorded. All samples were kept to a minimum and were collected during several years, since this species has been listed as vulnerable in Portugal (ICN, 1993), and this is the only stable population known in the country. Indeed, the biological material used in this study was not specifically collected for this purpose and was available as a by-product of a broader study on the biology of *S. pavo*, aimed to acquire information needed for the conservation of this species. Additional measurements were taken from live fish that were returned immediately to their habitat. The following indices were calculated:

gonadosomatic index, $I_G = 100\ W_g/W$;
hepatosomatic index, $I_H = 100\ W_l/W$;
feeding index, $I_F = 100\ W_a/W$;
eviscerated condition factor, $K_e = 1000\ W_e/L^3$.

Low tide field inspections were made during the 1988 breeding season. A total of 40 m of ridges was selected for regular inspection. All nesting males found were captured with the help of a hand-net, measured to the nearest mm, weighed and marked. Marking was performed by fin clipping. In each monthly visit, all caught individuals were inspected and if they were already marked, their identity was recorded.

Focal behavioural observations were conducted by snorkelling on 65 nesting males and 16 females in the breeding season of 1994 (total observation time = 35 h 21 min). In each observation, the number of feeding acts performed by the fish, and the net distance moved (the linear distance from the starting point to the finishing position) were recorded.

One group of fishes (four nesting males, one floater male and five females) was kept in a 78 × 40 × 35-cm aquarium with gravel and boulders to provide shelter. Photoperiod was kept constant (LD 16 : 8) by a fluorescent light (18 W), and temperature varied from 27 to 28° C. They were fed with common cockles (*Cerastoderma* spp.) and live marine

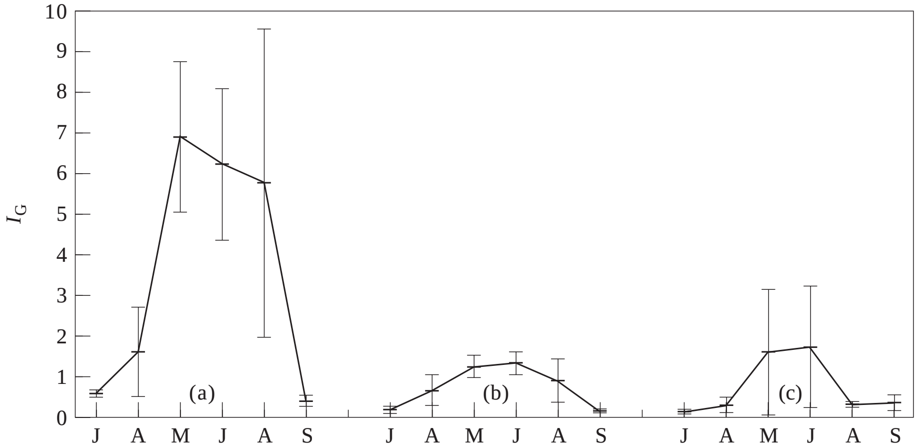

FIG. 1. Variation of mean (± S.D.) gonadosomatic indices (I_G) in (a) females, (b) nesting males, and (c) female-like males throughout the year.

invertebrates. Glass parallelepiped nests (3 × 3 × 15 cm) with narrow apertures were constructed. Each nest was wrapped with a black plastic sheet. The total area covered by the egg layer was measured by removing the black plastic sheet and applying a 1-cm^2 grid, counting the number of squares occupied by the spawn. Also, the density of eggs was determined to estimate the total number of eggs present in each nest. The egg masses were followed during 30 days.

Statistical analysis of the data was performed using Statistica for Windows 4.5 and the simulation statistical program Actus (Estabrook & Estabrook, 1989) designed for the analysis of contingency tables. This program uses random numbers to simulate 1000 tables, each with the same row and column total of the original table. Each simulated table is compared with the original data table. Values smaller than 50 are one-tailed significant ($P<0{\cdot}05$). The significance of χ^2 is assessed by the number of times out of 1000 that the value of χ^2 for the simulated tables is equal to or greater than that for the original table (Estabrook & Estabrook, 1989).

Data transformations were applied to comply with the assumptions of ANOVA (Sokal & Rohlf, 1981), and non-parametric tests were used when those assumptions could not be satisfied.

RESULTS

GONADOSOMATIC INDEX

The mean (± S.D.) female gonadosomatic indices (I_G) reached a peak in May (6·93 ± 1·84, range = 5·16–9·30, $n=6$), while the nesting males and female-like males reached the highest I_G values in July (1·36 ± 0·29, range = 0·90–1·75, $n=10$; and 1·73 ± 1·49, range = 0·17–3·59, $n=9$, respectively) (Fig. 1). The I_G values were in accordance with the breeding season previously described for this population: end of April to September (Almada *et al.*, 1994). In female-like males I_G values were high for a shorter period (May–July).

HEPATOSOMATIC INDEX

The highest values of the hepatosomatic index (I_H) were reached prior to reproduction (females: 3·88 ± 1·07, range = 2·28–5·92, $n=8$, in April; nesting males: 3·44 ± 1·09, range = 1·06–4·45, $n=8$, in April; female-like males: 3·32 ± 0·64, range = 2·30–4·30, $n=8$, in January) (Fig. 2). There was a highly

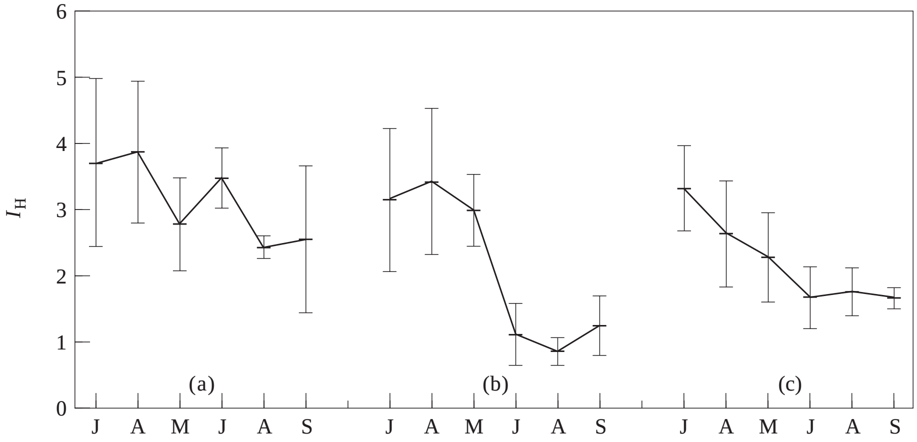

FIG. 2. Variation of mean (±S.D.) hepatosomatic indices (I_H) in (a) females, (b) nesting males, and (c) female-like males throughout the year.

significant difference both between months (Kruskal–Wallis test: H (5, $n=135$) $=51{\cdot}36$, $P<0{\cdot}001$) and sexual categories (Kruskal–Wallis test: H (2, $n=135$) $=25{\cdot}99$, $P<0{\cdot}001$). I_H values in July, August and September were significantly lower ($P<0{\cdot}001$) than January and April (Dunn's test: Jan/Jul, $Q=4{\cdot}37$; Jan/Aug, $Q=4{\cdot}49$; Jan/Sep, $Q=5{\cdot}16$; and Apr/Jul, $Q=4{\cdot}02$; Apr/Aug, $Q=4{\cdot}20$; Apr/Sep, $Q=4{\cdot}78$). In females overall I_H values were significantly higher ($P<0{\cdot}001$) than in both types of males (Dunn's test: females/nesting males, $Q=4{\cdot}89$; females/female-like males, $Q=3{\cdot}65$).

In nesting males I_H declined sharply from May to July and recovered only after the breeding season (between October and January). Females showed some variation in I_H, but the values remained high during the breeding season. Female-like males showed an intermediate pattern with a smoother decline as breeding progressed.

EVISCERATED CONDITION FACTOR AND WEIGHTS

The highest values of the eviscerated condition factor (K_e) were reached prior to reproduction (April) by females (13·00 ± 0·98, range = 11·73–14·17, $n=8$) and nesting males (15·69 ± 1·37, range = 13·78–15·06, $n=8$). Female-like males reached their highest K_e values in September (13·06 ± 0·91, range = 12·37–14·97, $n=8$) (Fig. 3). There was a highly significant difference both between months and sexual categories (Table I). In females, K_e dropped significantly from April to July (Tukey HSD test: $P<0{\cdot}01$) and recovered from July to September (Tukey HSD test: $P<0{\cdot}05$). In July, K_e of females was significantly lower than that of nesting males (Tukey HSD test: $P<0{\cdot}05$). Nesting males had K_e values in April that were significantly higher than those of females (Tukey HSD test: $P<0{\cdot}01$) and female-like males (Tukey HSD test: $P<0{\cdot}01$). Their K_e values then decreased significantly to July (Tukey HSD test: $P<0{\cdot}001$), August (Tukey HSD test: $P<0{\cdot}01$) and September (Tukey HSD test: $P<0{\cdot}001$). K_e variation in female-like males was not significant.

From the marking/recapture procedure, we were able to follow individual nesting males from March to September. These data revealed that nesting males

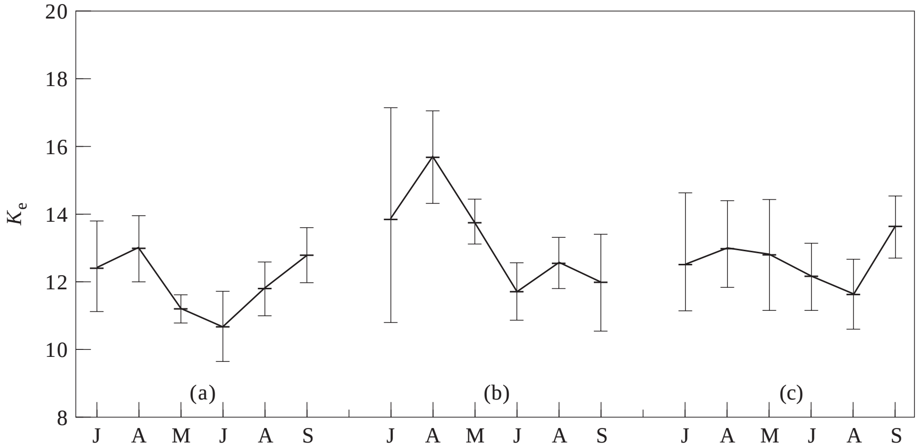

FIG. 3. Variation of mean (±S.D.) eviscerated condition factors (K_e) in (a) females, (b) nesting males, and (c) female-like males throughout the year.

TABLE I. Two-way ANOVA results for the effects of month and sexual categories on the eviscerated condition factor (K_e)

Effects	d.f.	MS	*F*	*P*
Month	5	0·302	12·13	0·000001
Sexual categories	2	0·346	13·91	0·000004
Interaction	10	0·116	4·66	0·000014

lost weight significantly from June to July (Wilcoxon signed ranks test: $Z=2{\cdot}67$, $P<0{\cdot}01$, $n=10$) and July to September (Wilcoxon signed ranks test: $Z=2{\cdot}20$, $P<0{\cdot}05$, $n=6$). This method failed in following females and female-like males since they were highly mobile (Almada *et al*., 1994).

FEEDING

The highest values of the feeding index (I_F) were reached prior to reproduction by nesting males (4·55 ± 1·22, range=3·35–6·65, $n=7$, in January) and by female-like males (5·06 ± 1·50, range=3·40–7·61, $n=7$, in April), and in the beginning of the breeding season by females (4·54 ± 1·74, range=2·92–7·15, $n=6$, in May) (Fig. 4). There was a highly significant difference both between months and sexual categories (Table II). The females showed a slight increase in I_F from January to May and the values stayed high during the breeding season. In nesting males, I_F values decreased from January to August. Their I_F was significantly lower than that of female-like males in April (Tukey HSD test: $P<0{\cdot}05$) and of females (Tukey HSD test: $P<0{\cdot}05$) and female-like males (Tukey HSD test: $P<0{\cdot}05$) in July. The I_F of nesting males decreased significantly from January to May (Tukey HSD test: $P<0{\cdot}05$), July (Tukey HSD test: $P<0{\cdot}001$) and August (Tukey HSD test: $P<0{\cdot}01$). I_F variation in females and female-like males was not significant.

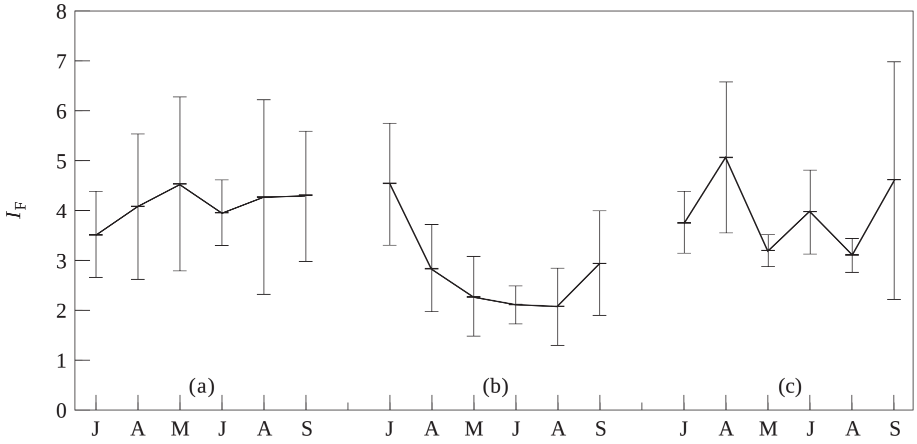

FIG. 4. Variation of mean (±S.D.) feeding indices (I_F) in (a) females, (b) nesting males, and (c) female-like males throughout the year.

TABLE II. Two-way ANOVA results for the effects of month and sexual categories on the feeding index (I_F)

Effects	d.f.	MS	*F*	*P*
Month	5	2859	3·33	0·007686
Sexual categories	2	19 449	22·66	0·000001
Interaction	10	3206	3·73	0·000242

Females also had significantly fewer empty guts while nesting males had more empty guts than expected by chance (Table III). Another interesting feature was that 65% of the nesting males had blenniid eggs in their guts ($n=26$), while only one female did ($n=27$). In addition, females performed significantly more feeding acts per min (females, mean = 0·319, S.D. = 0·283, range = 0–0·846, $n=16$; nesting males, mean = 0·017, S.D. = 0·077, range = 0–0·533, $n=65$; Mann–Whitney *U*-test: $Z=-6{\cdot}28$, $P<0{\cdot}001$), and significantly higher maximal displacements (females: mean = 564·3 cm, S.D. = 503·6, range = 50–2000 cm, $n=14$; males: mean = 12·9 cm, S.D. = 37·2, range = 0–200 cm, $n=65$; Mann–Whitney *U*-test: $Z=6{\cdot}23$, $P<0{\cdot}001$) than nesting males.

FEMALE FECUNDITY

The developmental time of 15 days given by Patzner & Brandstätter (1988) was used to estimate the number of hatched eggs. This number was added to the total number of eggs in that inspection, resulting in the cumulative number of eggs laid in the interval considered (Table IV). It was assumed that most eggs were fertilized and that mortality prior to hatching could be ignored. The rate of eggs laid per female was calculated by subtracting the number of eggs from the first count from the total number of eggs laid and dividing by the number of days (30) and by the number of females (five). A mean daily rate of 162 eggs laid per

TABLE III. Occurrence of empty guts on the different sexual categories on samples taken during the breeding season (May, July and August) and statistical analysis using ACTUS

	Nesting males	Female-like males	Females
Empty guts	18	6	2
Partially or completely full guts	8	25	25
Statistical analysis			
Simulated values < observed values:			
Empty guts	996	165	11*
Partially or completely full guts	3*	843	962
Observed values < simulated values:			
Empty guts	4*	906	998
Partially or completely full guts	999	212	68

$^{*}P<0{\cdot}05$ (one-tailed).

$\chi^2=26{\cdot}78$, d.f. $=2$, $P<0{\cdot}001$. For details of ACTUS see Estabrook & Estabrook (1989).

TABLE IV. Cumulative numbers of eggs present in each nest from the aquarium group: four nesting males, one floater male and five females

Day	Male 1	Male 2	Male 3		Male 4	Total
			Nest A	Nest B		
1	2118	219	?			2337
2	2426	490	?			2916
7	3966	2541	?			6507
12	5236	3773	4543			13 552
17	7431	4225	1155			12 811
23	9587	7123	*	130	693	17 533
30	13 861	9345	*	616	2888	26 710

?, Presence of eggs could not be determined.

*Eggs were destroyed by the floater male.

female was obtained. The mean weight of each egg was 0·75 mg ($n=20$). Using the mean daily rate of 162 eggs and multiplying by 4 months (the duration of the breeding season), each female would lay an average of 14·6 g of eggs in each breeding season. The mean weight of the females in the low tide inspections in June and July (the peak of the breeding season) was 8·8 g ($n=20$). If these calculations are realistic, total ovarian expenditure over the 4-month breeding season could be higher than somatic weight.

Patzner (1985), based on the frequency distribution of oocyte stages, determined that, in an Adriatic population of this species, fecundity (F) showed a rectilinear relationship with body length expressed by the equation: $F=125L-5125$ (where L was the standard length in mm). Applying this formula to our data, the daily rate of eggs laid per female would be 82. This value is half that determined with direct egg counts. Our method may have overestimated the number of eggs if the females are overfed, or the method used by Patzner (1985) could have underestimated the number of eggs laid, if stage I and stage II oocytes would both develop in that breeding season. A third hypothesis is that female fecundity was much higher in our population. Either way, the weight in eggs laid by a female during the breeding season would be equal to or greater than her own body weight.

DISCUSSION

This paper shows that one major component of the costs of reproduction in nesting males is a reduction of feeding opportunities. Indeed, during the breeding season, nesting males showed a lower feeding index and feeding rate and, a higher proportion of empty stomachs than females. Nesting males also lost weight, their I_H declined, and their K_e decreased significantly during the breeding season. In addition, they did not grow during this period. Such a deterioration in the condition of parental males had previously been reported in *Lipophrys pholis* (Linnaeus, 1758) (Qasim, 1957), *Parablennius sanguinolentus* (Valenciennes, 1836) (Santos & Almada, 1988; Santos, 1992; Santos *et al*., 1996), and other fish taxa with male parental care (e.g. Miller, 1984; Crivelli & Britton, 1987). For *S. pavo*, this reduced feeding is not a consequence of a suppression of the feeding motivation. Indeed, nesting males kept in aquaria will take food readily if it passes near the nest entrance (pers. obs.).

It seems likely that the nesting males engage in filial cannibalism as a means of diminishing their energy intake deficit. This behaviour has been described for several fish species with male parental care [e.g. *Oxylebius pictus* Gill by DeMartini (1987); *Gasterosteus aculeatus* L. by FitzGerald (1991); *Hypsypops rubicundus* (Girard) by Sikkel (1994); see also FitzGerald (1992)]. Although the eggs found in the guts of nesting males might represent dead embryos removed as part of the male's parental activities, we noted that some embryos showed no sign of damage.

It is suggested that this reduced feeding is caused or enhanced by the dense nest aggregations found in this population, and by the constant pressure exerted by non-nesting males, both floaters and sneakers (Almada *et al*., 1994, 1995; Gonçalves *et al*., 1996). In fact, nesting males do not defend food reserves, and leave their nests infrequently (Gonçalves & Almada, 1997) and for short distances (as shown by the small maximal displacements). This behaviour makes sense if one considers that the nests are cavities with narrow entrances that are much easier to defend for a male that is inside. With the high pressure of floaters and sneakers, a male that leaves the nest frequently, would face the risk of having to dislodge an intruder, that would have the advantage of being inside the nest.

The presence of dense nest aggregations and the excess of males without nests may also explain the differences between our results and those of Podroschko *et al*. (1985). These authors found that I_H did not deteriorate during the breeding season in males of an Adriatic population of *S. pavo*, who defended small territories around the nest (Patzner *et al*., 1986). However, such a comparison is made more difficult by the fact that these authors collected their fishes with baited traps, which could have biased the samples in favour of males that were feeding actively.

It is also important to note that this reduction of feeding by the nesting males was not a mere consequence of a shortage of food in the area. Non-nesting males and especially females kept feeding actively during the breeding season, and the available evidence suggests that this high level of feeding was responsible for the large number of eggs produced by the females throughout the season. Despite their high level of egg production, the I_H of females was not reduced during the breeding season, and their K_e, although depressed in the peak of the breeding season, was quicker to recover than that of males.

Finally, the data suggest that the female-like males incurred lower reproductive costs, at least in terms of energy. The I_G values also suggest that, for these males, the breeding season may have been shorter, but more data are needed to test this hypothesis. These males were smaller and younger than the nesting males (Gonçalves *et al*., 1996) and it is likely that their reproductive biology reflects a compromise between the need to try to fertilize some eggs, and the need to grow, becoming able to secure nests and act as parental males.

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