

ARTICLE

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Postfledging crèche behavior in the European shag

Received: October 19, 2000 / Accepted: February 28, 2001

Abstract Formation of a postfledging crèche in the European shag *Phalacrocorax aristotelis* on the Cíes Islands (northwest Spain) was studied. There was no relationship between the number of birds in a crèche and environmental temperature. Moreover, the number of juveniles in the crèche was not correlated with adult peck rate per juvenile. Also, predation was not reported on the studied population. Therefore, their postfledging crèche did not serve as protection from thermal stress, aggressiveness of adults, or predators. In the crèche studied, fledglings are faithful to their perch, which serves as a functional unit where they form a group consisting of stable members. I postulate that there may be advantages in the formation of crèches, which allow adults to be able to locate their young and continue their postfledging parental care and also enable chicks to exercise and develop fishing skills. Adults remained in the crèche during the entire period, but their number depended on the hour and tide, which would be associated with the effectiveness of fishing according to these factors. Moreover, crèches may facilitate finding mates and forming feeding groups.

Key words European shag · Creching · Parental care · Postfledging · Juvenile independence

Introduction

Crèches (formation of groups of chicks belonging to two or more broods in breeding areas) are common among seabirds such as penguins, pelicans, gulls, and terns (reviews in Davis 1982; Evans 1984). The behavior has also been reported in some species of cormorants (European shag, *Phalacrocorax aristotelis*: Snow 1963; Velando 2000;

crowned cormorant, *P. coronatus*: Willams and Cooper 1983; Brandt's cormorant, *P. penicillatus*: Carter and Hobson 1988). The functions of crèche formation are hypothesized to be thermal regulation and protection against aggressive behavior from conspecific adults and predators (Knopf 1979; Davis 1982; Evans 1984). It has also been suggested that they may improve, in part, parental care (Evans 1984).

Parental care in birds includes all types of investment contributing to the support and survival of chicks. Studies on parental care previously considered only the period from hatching to fledging. However, many species of seabirds continue caring for the young after they leave the nests (Burger 1980). In seabirds, the improvement of foraging efficiency with age suggested that a period of apprenticeship is needed to develop foraging skills (Wunderle 1991) and, therefore, that parental investment during this apprenticeship should be adaptive (Burger 1980). In the shag family, adults feed chicks for a long period after fledging (20–50 days: Palmer 1962; Snow 1963; Potts 1969; Cramp and Simmons 1977). In this family, adults are more efficient than immatures at fishing (Morrison et al. 1978). Thus, the prolonged care after fledging may be attributed to the necessity to develop specific skills for the difficult activity of catching fish by shags (Burger 1980).

The function of creching behavior can be different according to breeding cycle. In the Brandt's cormorant, two phases in crèche formation were reported (Carter and Hobson 1988). The first phase consists of formation of crèches at the nesting sites, which occurs primarily at night and serves as thermal regulation. In the second phase, crèches are formed in nearby places outside the nesting site. In these crèches, chicks are fed by their parents. Carter and Hobson (1988) suggested that crèche formation facilitates the apprenticeship of chicks.

In this article, I analyze postfledging crèche formation in the European shag from Cíes Islands (Galicia, northwest Iberian Peninsula). I examined the following hypotheses on crèche functionality: (1) thermal regulation, suggesting that low environmental temperature facilitates juveniles being in the crèche; and (2) protection from adult aggressiveness,

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suggesting that juveniles form a crèche when adult attack rate is high. The predation avoidance hypothesis, suggesting that they form a crèche when predation risk is high, cannot be tested because there was no predation on juveniles during the study and there are no documented cases for the studied population (Velando 1997). Moreover, I report the fidelity of juveniles to the crèche, the temporal and spatial use of crèches, and the feeding behavior of adults to juveniles.

Materials and methods

A breeding population of the European shag consisting of about 1000 pairs nests in cavities formed by fallen granite rocks on Cíes Islands (Velando et al. 1999a). Nests (89 in 1994, 93 in 1995, and 80 in 1996) were visited every 10 days during the chick rearing period from 1994 to 1996 in four adjacent areas (Campana, Portelo, Faro, and Popa Fragata). I marked the bill of the chicks with indelible color marker while they were breaking the shell or immediately after hatching. Each chick was tagged with a strip of colored Velcro across the tarsus. These strips were adjusted to tarsus size during growth. The chicks were tagged with metallic rings and with a plastic ring with an individual two-digit combination when 15 days old to facilitate identification from a distance.

I located perches used by the shags on the Isle of Faro (Cíes Islands; Fig. 1) after the chicks fledged during the breeding seasons of 1994, 1995, and 1996. This island was divided into isolated areas (see Fig. 1). I defined perches as locations used by a group of shags and crèches as a group of young shags alone or with adults located in a perch. To study the fidelity and the use of perches weekly, censuses were made in all the perches on the same day from June to July of 1994 and 1995. Numbers of adults, juveniles, and individuals were identified with tag digits using a 45× telescope. The census followed the same order every time, starting at perch A and ending at perch Z (see Fig. 1).

In 1995 and 1996, perch R was the object of a combination of studies: an “instantaneous” hourly study and an “ad libitum” study for an entire day every week during July. The instantaneous study consisted of recording and identifying the number of adults and juveniles. Atmospheric temperature was recorded during each census using a digital thermometer placed at the observation point. Tide levels were also recorded and treated as a dichotomous variable (high and low tide), as well as hour of day and week of observation (from July, ranging between 1st and 4th week).

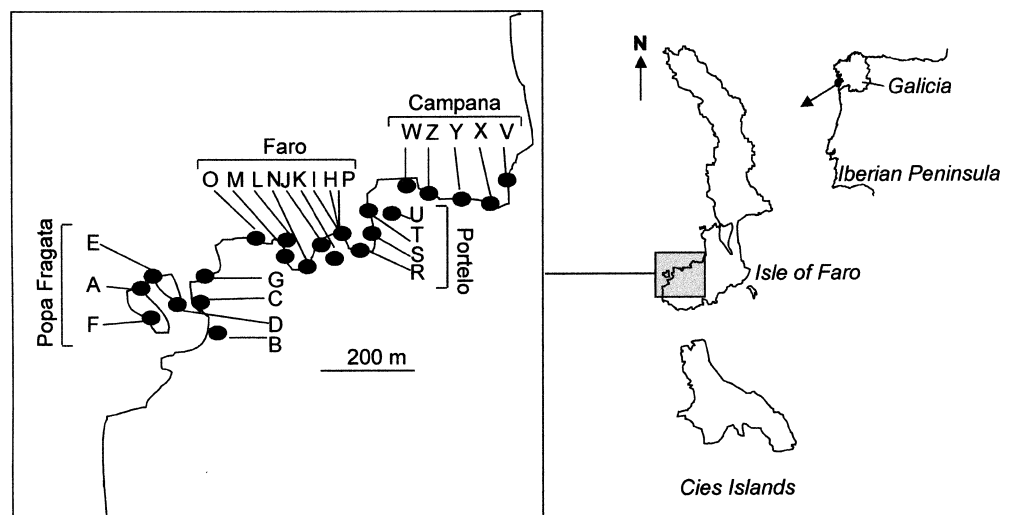
The general linear model (GLM) by specification of Poisson errors and log link (McCullagh and Nelder 1989) was fit to determine the variables affecting the presence of juveniles and adults in the perch. Correlation coefficients of GLMs were calculated by $r = \text{SSXY} / (\text{square root } \text{SSX} \cdot \text{SST})$, where SSXY stands for the sum of the products x times y , SSX is the sum of squares for x , and SST is the total sum of the squares (Crawley 1993). Adults in the crèche fed the juveniles. I recorded feeding behavior, attempts to steal food, and arrivals at the crèche in the ad libitum sampling. In 1996, I observed 40 juveniles continuously in 1-h blocks, for a total of 70 h of observation from June 28 to July 17 (for details, see Velando 2000); all chicks studied fledged between June 1 and June 25. The attack rate of adults per juvenile was analyzed in relation to the presence of adults in the crèche. Data are expressed as means \pm SE.

Results

Use of perches

There was no crèche formation before the chicks left the colonies. Chicks stayed at the nest sites until they were 40 days old. When they were over 40 days old, they were often found in other places in the colony, but not associated with chicks from other nests. Nests in Faro Island were located

Fig. 1. Distribution of perches ($n = 25$) on the Isle of Faro, Cíes Islands, Galicia, Northwest Spain, Iberian Peninsula) grouped by areas: Popa Fragata, Faro, Portelo, and Campana. Each area was defined as a zone where the shags can visualize all the perches in this area and visually isolated from other areas



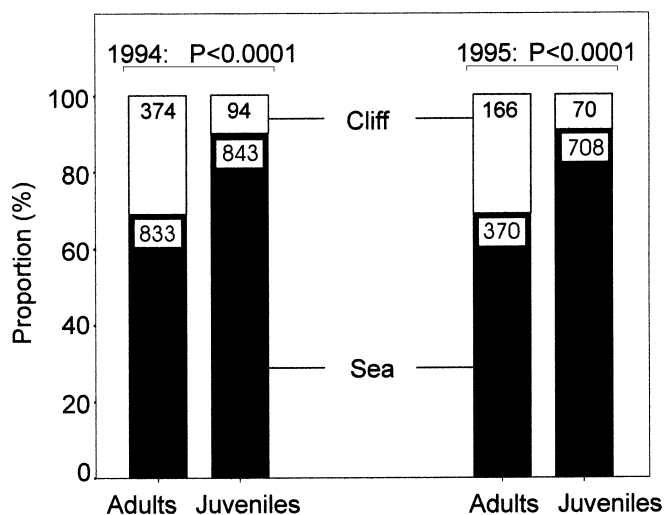


Fig. 2. Proportion of accumulated birds on perches (numbers on bars) on the Isle of Faro, Cíes Islands, located at sea level or at the cliff level in 1994 (14 daily counts) and 1995 (5 daily counts), depending on age. Probabilities are given for each year's distribution between ages and type of perch using Fisher's exact test (two-tailed)

in high cliffs (>100m high); chicks leave the colony flying toward the sea. After leaving the colony, they gather on rocks over the sea and located beneath the cliffs, where they form crèches. Crèche juveniles were observed swimming, diving, and flying to follow adults.

I compared the accumulated number of shags on each perch according to whether they were located at sea level or on a cliff. I found that most adults used the sea-level perches in both 1994 and 1995 ($\chi^2 = 174.55$ and $\chi^2 = 80.72$, respectively; $df = 1$ and $P < 0.0001$ in both cases) as the juveniles did in the 2 years ($\chi^2 = 586.00$ and $\chi^2 = 513.40$, respectively; $df = 1$ and $P < 0.0001$ in both cases). Although cliff perches were less commonly used, in these perches there were more adults than juveniles (Fig. 2). The perches at sea level were used as crèches whereas those on the cliff were used by roosting birds. In this way, there were differences in access to sea-level perches; 66% of adults ($n = 142$) reach the crèche by flying, whereas 94% of juveniles ($n = 222$) reach the crèche by swimming from the sea ($\chi^2 = 143.80$, $df = 1$, $P < 0.0001$).

Presence of birds in the crèche

A GLM analysis showed that there were more juveniles in the crèche in 1994 than in 1995 (Fig. 3; $F_{1,90} = 51.23$, $P < 0.0001$). The week had a significant effect on the number of juveniles in the crèche in both years (Fig. 3; 1994: $F_{1,43} = 3.85$, $P < 0.05$; 1995: $F_{1,45} = 20.85$, $P < 0.0001$). The presence of juveniles in the crèche was related to their age (Fig. 4a). Thus, 70% of juveniles in the crèche were between 60 and 80 days old. The average age when each chick entered the crèche did not differ between years (Mann-Whitney test: $Z = 0.20$, $n = 39$ chicks, $P > 0.1$). The hour and tide level did not significantly influence the number of juveniles in the crèche ($P > 0.05$, in all cases).

The number of adults in the crèche was lower in 1994 than in 1995 (Fig. 3; $F_{1,90} = 13.48$, $P < 0.001$), and it was significantly affected by tidal level in both years (1994: $F_{1,43} = 5.56$, $P = 0.02$; 1995: $F_{1,45} = 13.51$, $P < 0.001$). The number of adults was higher at high tide than at low tide (Fig. 3). There was a significant relationship between the number of adults in the crèche and hour of the day in 1995 ($F_{1,45} = 22.66$, $P < 0.0001$) but not in 1994 ($F_{1,43} = 0.97$, $P > 0.05$). Moreover, week did not affect the presence of adults (Fig. 3; $P > 0.05$, in both years).

Protection from thermal stress

In my sampling study, temperature oscillated between 17.5°C and 35°C ($\bar{x} = 27.0 \pm 0.4$). I did not find significant relationships between temperature and the number of juveniles in the crèche (see Fig. 4; $r = 0.07$, $F_{1,90} = 0.4$, $P > 0.1$). This relationship also was not significant after controlling the effect of year and week by introducing these variables in the GLM ($r = 0.07$, $F_{1,88} = 0.49$, $P > 0.1$). Moreover, temperature did not affect the number of adults in the crèche ($r = 0.01$, $F_{1,90} = 0.04$, $P > 0.1$) or also when the effect of year, tide, and hour was controlled ($r = 0.01$, $F_{1,87} = 0.04$, $P > 0.1$).

Protection from conspecific aggressiveness

The number of juveniles in the crèche was not related to the presence of adults in 1994 ($r_s = 0.11$, $n = 47$, $P > 0.05$) and in 1995 ($r_s = 0.08$, $n = 47$, $P > 0.05$). Attack rate of adults per juvenile was very low (mean = 0.04 ± 0.01 pecks per individual per hour; $n = 35$). The number of juveniles in the crèche was not correlated with the adult peck rate per juvenile ($r_s = 0.03$, $n = 70$, $P > 0.05$). Juvenile peck rate was not related to the number of juveniles ($r_s = 0.04$, $n = 70$, $P > 0.05$).

Fidelity to crèche

A total of 26 counts were taken to study the movements of juveniles between crèches on the 25 perches on the Isle of Faro after fledging. I observed a total of 89 and 147 tagged juveniles in 1994 and 1995, respectively. The spatial distribution of the juveniles in the crèches was related to the nests where they hatched in both years (see Fig. 4b; ANCOVA, year effect: $F_{1,8} = 0.001$, $P > 0.1$). In fact, 70% of birds were observed less than 100m from the natal nest. Juveniles exhibited great fidelity to perch; thus, of 160 juveniles that were seen more than once, 84% were from the same perch, 12% belonged to a different perch but to the same area, and 4% were from different perches and different areas (see Fig. 4c). There were no differences between years on perch fidelity (Fig. 4c; $\chi^2 = 1.85$, $df = 1$, $P > 0.1$). The proportion of juveniles that were seen on the same perch as in the prior count was not related to juvenile age, grouped each 10 days (1994: $r_s = -0.16$, $n = 5$, $P > 0.1$; 1995: $r_s = 0.00$, $n = 5$, $P > 0.1$).

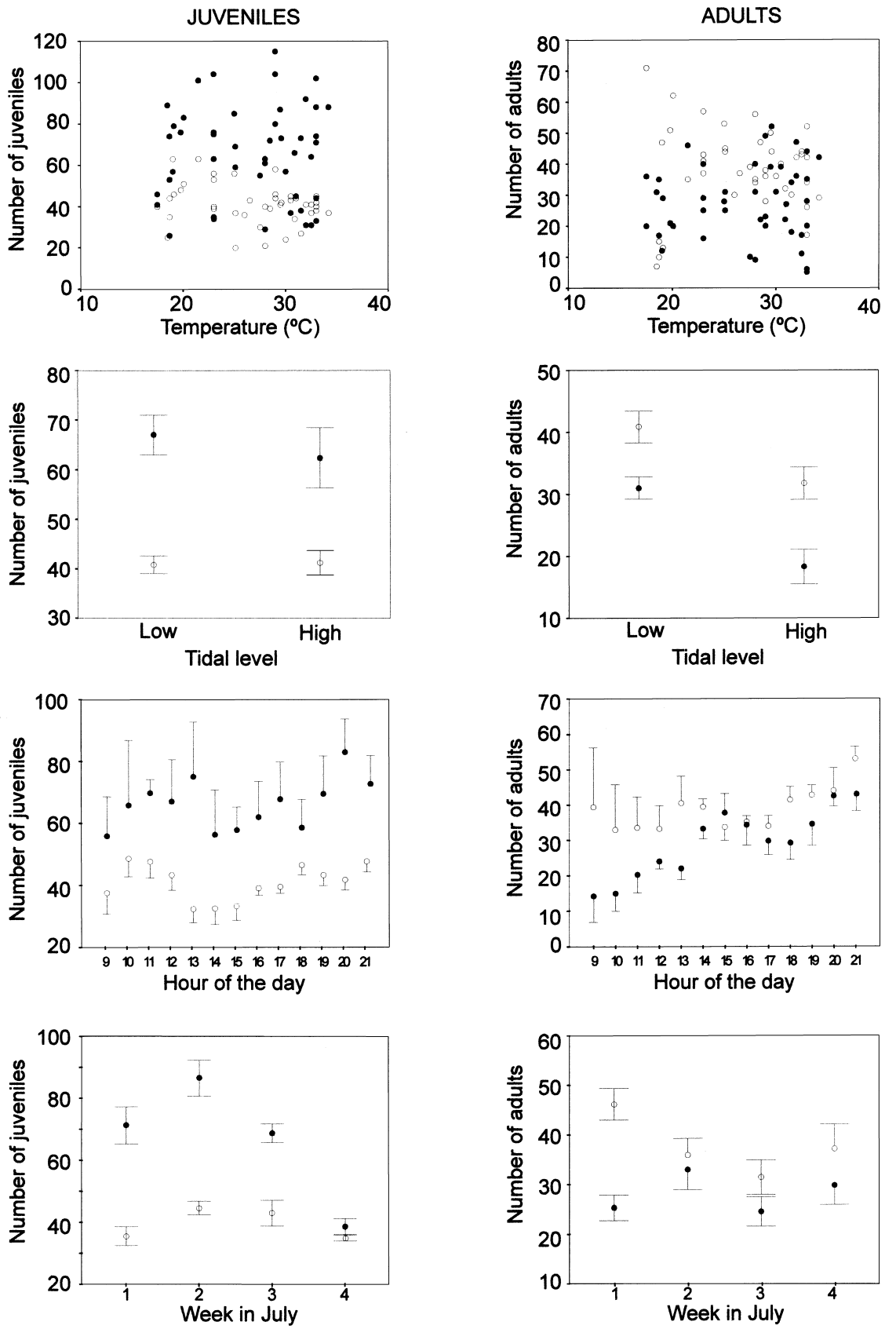


Fig. 3. Mean number (\pm SE) of juveniles (*left*) and adults (*right*) on perch R in Portelo, I. Faro, Cies Islands, in relation to environmental temperature, tide level, hour, and week in July in 1994 (*open circles*) and 1995 (*solid circles*)

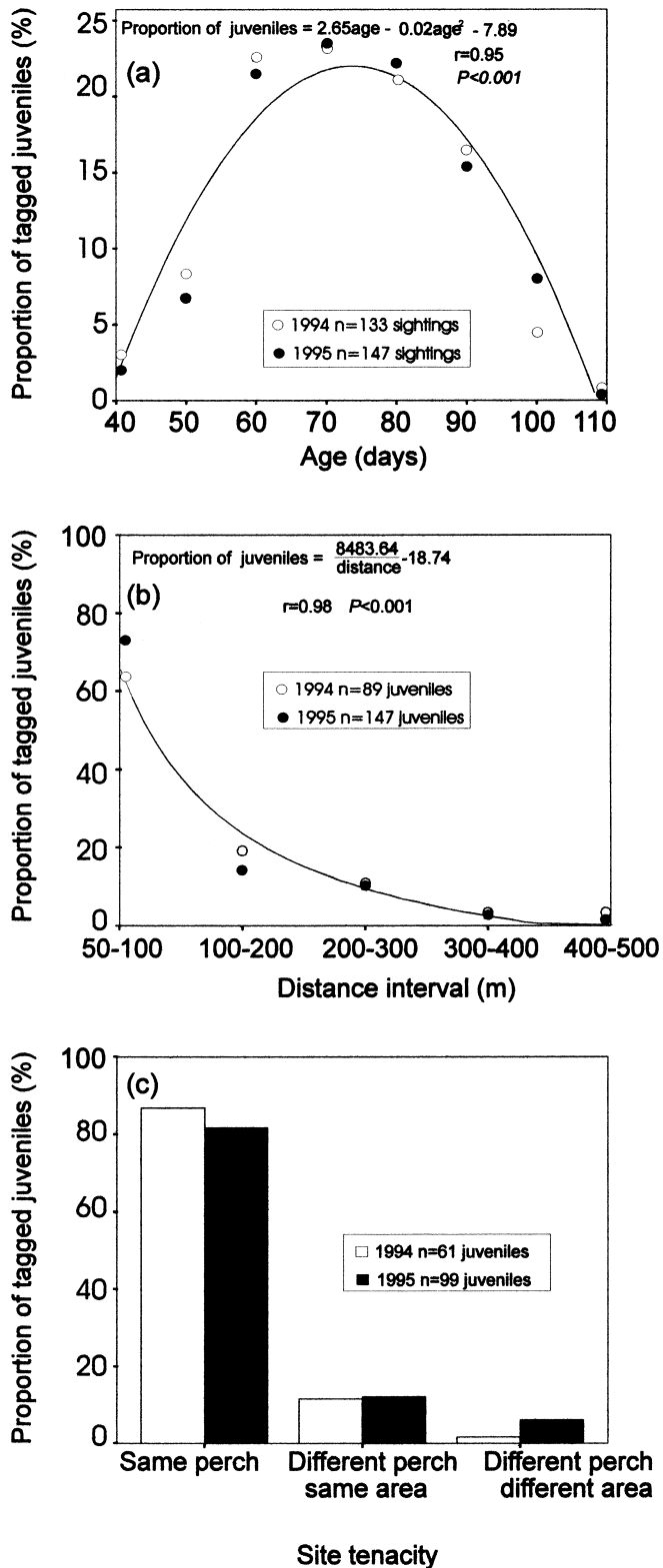


Fig. 4a–c. Proportion of tagged juveniles on perches on the Isle of Faro, Cíes Islands, in relation to (a) their age, grouped each 10 days; (b) the distance to the natal nest, grouped each 100 m; and (c) their fidelity to the perches of juveniles that were seen more than once (see Fig. 1 for area definition)

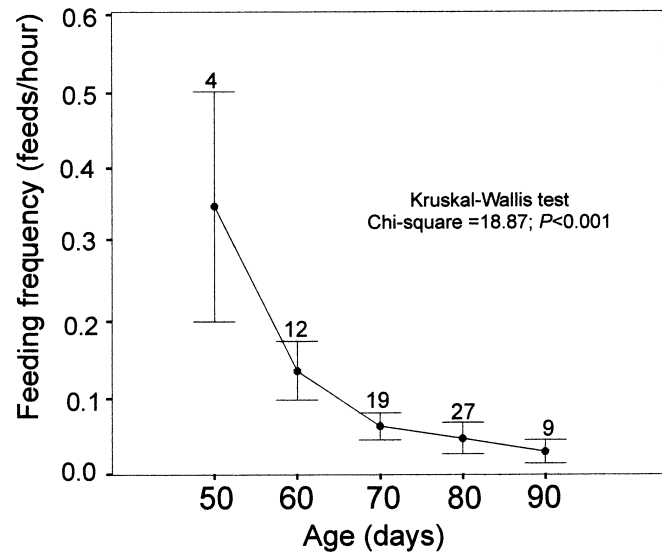


Fig. 5. Mean number of feeds per hour (\pm SE) received per juvenile by age (days) on perches R in Portelo, I. Faro, Cíes Islands. Juvenile age was grouped for each 10 days

Feeding behavior

In the crèche, each juvenile was fed by adults in a mean frequency of 0.17 ± 0.02 feeds per hour ($n = 35$ individuals). The frequency of feeds decreased with juvenile age (Fig. 5). No juvenile older than 100 days was fed by adults. Some juveniles attempted to reach the adult mouth when other juveniles were feeding from its parent's throat. Of the 314 feeds recorded, 78 (24%) occurred with an attempt to steal food and in 23 (7%) food was successfully stolen. All attempts made by the tagged juveniles ($n = 18$) to steal food were carried out by birds that were not siblings. Of the 20 feedings in which we successfully identified adults and chicks, all cases consisted of adults feeding their offspring.

Discussion

This study shows that parental care in European shags continues for more than a month after fledglings leave the nest. Postfledgling parental care is carried out on rocks near the sea, where crèches are formed. The crèches are not formed before leaving the colony. The number of juveniles was fewer in 1995 than in 1994 in postfledgling crèches. This difference was a result of the smaller number of chicks fledged in 1994, which was related to food limitations during adverse weather events that occurred during this year (Velando et al. 1999b).

The first classical explanation for crèche formation posited that the crèche has a dilution effect on predation (Munro and Bedard 1977; Knopf 1979; Davis 1982; Evans 1984). Thus, for example, in the rockhopper penguin *Eudyptes crestatus*, chicks were frequently prey to skuas if solitary but were never taken in crèches (Pettingill 1960). However, this hypothesis cannot be tested in the Cíes

Islands because there was no observed pressure from predators during my long-term study (6-year study: Velando 1997; Velando et al. 2001). There is no evidence that crèches reduce predation risk in the order Pelecaniformes (Nelson 1978; Johnsgard 1993).

Other classical hypotheses postulated that crèches serve as a thermal regulator for chicks (Davis 1982; Schreiber and Chovan 1986). In postfledging shag crèches, there were no significant relationships between the number of juveniles and environment temperature. In our sampling study, the temperature oscillated among high values (mean 27°C). Thus, influence of crèche formation on thermal regulation could be not important in temperate regions such as Cíes Islands.

Moreover, it has been proposed that adult aggressiveness is an important proximate factor underlying the dynamics of crèche formation (Tourenq et al. 1995). Crèche formation to avoid harassment by conspecifics has been reported, for example, in the chinstrap penguin *Pygoscelis antarctica* (Young 1994; Moreno et al. 1997) and the Adélie penguin *Pygoscelis adeliae* (Penney 1968). Thus, fledglings have a high level of adult harassment in some seabird species (e.g., in penguins: Penney 1968; Young 1994; Côté 2000). Nevertheless, in my study the number of juveniles on a crèche did not influence the probability of being attacked by adults. Adult shags were not aggressive with young. Each juvenile received fewer than a mean of 0.5 attacks per day. Adult aggressiveness seems not to be an outstanding force in crèche formation in this species.

Carter and Hobson (1988) raised the question of functional differences of crèche formation during pre- and postfledging in Brandt's cormorant. According to the authors, juveniles used crèches while they were carrying out flight and swim exercises near the sea in the second phase. During the course of my research, I found that juveniles occupied perches easily accessible from the sea. The most important contribution of parents at this time was offspring feeding. Adults feed their young even though other fledglings attempt to steal the food.

Juveniles were observed swimming, diving, and flying following adults. These behaviors could be related to the development of juvenile skills. Although juveniles were fed by their parents during the creching period, as juveniles became older, they were fed less by parents (Fig. 5), and they paid less and less attention to the perch (see Fig. 4a); these changes may reflect better fishing skills acquired by juveniles. In the red-footed booby *Sula sula*, juveniles spend longer and longer periods on exploratory flights, returning each day until one day they cease to return (Nelson 1968). Thus, birds that acquire more practice while they are still under parental care will be better able to survive the winter, with more efficient prey-catching skills (Lack 1967; Wunderle 1991).

Juvenile European shags could follow adults to feeding zones and return to the place to which they know their parents will return (Carter and Hobson 1988). The juveniles had high perch tenacity, which indicates that crèches are social stable units. A stable group membership facilitates personal recognition among individuals and development

of a dominance hierarchy (Ekman and Askenmo 1984; Matthysen 1990). In European shag crèches, there was a stable hierarchy between juveniles; this hierarchy was determined by social experience in the group (Velando 2000). Stable dominance relationships lower the frequency and intensity of overt hostility (Guhl 1968; Matthysen 1990). The creching period leads to juvenile introduction into a social group where they develop social skills (see Velando 2000).

The largest number of adults on perches was seen at the end of the day and during low tides, which indicates a preference in the time of feeding. There was no apparent relationship between date and number of adults on the perch. In 1994, when the number of fledged chicks was low, the number of adults in the crèche was higher (see Fig. 3). Moreover, six tagged unsuccessful breeders were observed in crèches. These facts could indicate that perches could have a socially oriented purpose for adults. In her review on parental care, Burger (1980) reported that most adult seabirds return to their breeding places after the period of independence and, in some cases, such as the red-footed booby *Sula sula*, they carry out sexual activity. In crèches of the European shag, there is a high frequency of mountings and behaviors related to mate selection (Velando 1997; see also Graves and Ortega-Ruano 1994; Ortega-Ruano and Graves 1991). Thus, the crèche could be a place where adults reinforce the bond with their current mate or choose a future mate and, at the same time, feed their young. Moreover, this species forms feeding groups when fishing for sand eels (Ammodytidae), the most important prey in the Cíes Islands (Velando and Freire 1999; Velando et al. 1999b). It may also be advantageous to form relatively stable groups that are better able to exploit ecological variations in the environment.

Acknowledgments I thank J. Freire and J.E. Ortega-Ruano for their advice during the study, and thank Jorge Domínguez, Carlos Alonso-Alvarez, and two anonymous referees for their valuable comments on the manuscript. I am grateful to Xunta's Wildlife Service (Servicio de Medio Ambiente Natural, MAN) for help in this study.

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