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VARIATION IN PARENTAL CARE WITH OFFSPRING AGE IN THE GREATER FLAMINGO¹

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Key words: Age; Greater Flamingo; parental care; *Phoenicopterus ruber roseus*.

Several studies have predicted how parental investment should change in relation to the age of offspring (Williams 1966, Winkler 1987). The Reproductive Value Hypothesis (RVH) states that parents should be prepared to invest more in older juveniles because they have a higher probability of surviving to breeding age. This may occur because older juveniles are closer to maturation and because the instantaneous rate of juvenile mortality generally decreases with increasing age (Clutton-Brock 1991). Increase in feeding effort with chick age has been documented for some species of colonial waterbirds. In Pigeon Guillemots (*Cepphus columba*) provisioning rates increased with chick age, only during the first part of the nestling period (Emms and Verbeek 1991). Feeding rates were not observed to vary with chick age in the closely related Black Guillemot (*Cepphus grylle*), but size of fish delivered to the nest increased with chick age (Cairns 1987). As chicks grow older they also have greater food requirements, and increased parental care might simply correspond to the higher energetics and nutritional demands of the offspring. Further evidence for increased parental care with increasing age of offspring comes from studies of brood defense. Brood defense has been reported to increase with nestling age in several passerine species (Andersson et al. 1980, Redondo and Carranza 1989, but see Knight and Temple 1986, Westmoreland 1989).

However, the observed increase in parental care with

offspring age can also be influenced by confounding variables such as parental age and or quality. Breeding success is known to increase with parental age in several bird species (Saether 1990) and this can be the result of increased experience with age. In addition, as parents grow older, their potential for future reproduction decreases. Thus the cost of reduced future reproductive success should decline with age and older parents should be selected to invest more in offspring compared to younger parents (Pugesek 1981). Therefore, it is important to control for parental age when considering variation in parental care with offspring age.

Here, we analyze data from two years on the duration of feeding bouts by Greater Flamingo (*Phoenicopterus ruber roseus*) parents of known age and sex to their offspring. We show that only male parental care increases with offspring age. We discuss our results in relation to lifetime reproductive success and costs of reproduction.

METHODS

The Greater Flamingo is a filter-feeder that breeds in dense colonies often numbering several thousands of pairs. Females lay a single egg and both parents share incubation. Flamingos have bred intermittently in the saline lagoons of the Camargue in southern France for centuries (Johnson 1983). In every year since 1972, they have bred in the Etang du Fangassier, part of the large complex of commercial salt pans of Salin de Giraud. On average, since 1977, 12% of the chicks have been banded each year with darvic rings engraved with alphanumeric codes (Johnson 1989).

Birds start to gather at the breeding site in March. Egg laying usually begins in April and continues for four to six weeks. At about 10 days of age the chicks

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TABLE 1. Comparison of the variation in feeding bout length in relation to offspring age between year 1985 and year 1989.

Year	<i>r</i>	<i>n</i>	<i>P</i>
Males			
1985	0.638	20	0.002
1989	0.609	9	0.082
Difference between means: $F_{1,27} = 3.01$ ns			
Difference between slopes: $F_{1,27} = 0.188$ ns			
Difference between intercepts: $F_{1,27} = 0.888$ ns			
Females			
1985	-0.116	17	0.656
1989	0.284	11	0.398
Difference between means: $F_{1,26} = 3.56$ ns			
Difference between slopes: $F_{1,26} = 0.841$ ns			
Difference between intercepts: $F_{1,26} = 3.243$ ns			

form small crèches on the breeding island, before leaving the nesting island to join a single large crèche, which can hold several thousand chicks (Johnson 1983). The young fly 70–90 days after hatching when they are independent. Until 70 days of age the young are unable to feed by themselves as the filter apparatus of the bill is not fully developed (Jenkin 1957). During this time, parents do not regurgitate food for their offspring (Studer-Thiersch 1975) but feed them with a secretion formed by glands lying in the upper digestive tract (Lang 1963). This secretion consists of fat, protein carbohydrate and blood. At the time crèches form, feeding chicks is the only component of parental expenses.

Because of the density and movements of birds within the crèche it is usually difficult to record the frequency and duration of adult–young interactions. However in 1985 and 1989 the duration of several complete feeding bouts was recorded. Age of chicks was either known accurately or determined from plumage characteristics (Johnson et al. 1993), and sex of their ringed parents was known from previous observations at the nest in the same or preceding breeding seasons.

RESULTS

In 1985 and 1989, the Camargue crèche consisted of 7,800 and 7,100 chicks, respectively. Data for 37 complete feeding bouts from parents of known age and sex were obtained in 1985 and 20 in 1989. The age of chicks varied between 14 and 95 days in 1985 and between 20 and 93 days in 1989. Mean feeding bout duration was 14 and 11 min in 1985 and 1989, respectively.

There was no difference between the two years in variation in parental care with chick age for either males or females (Table 1). Therefore, we pooled data from the two years for each sex. There was a significant difference between sexes in variation in parental care with age. Male but not female parents increased the duration of feeding bouts with chick age (Fig. 1, Analysis of covariance [ANCOVA] $F_{1,55} = 5.547$, $P = 0.021$). There was no difference in intercept between the two regressions ($F_{1,55} = 0.01$, ns) for males and females. We

performed a stepwise multiple regression (Sokal and Rohlf 1981) to test for the relative contribution of chick age and male age on feeding bout duration. Only chick age was retained as significant ($F_{1,27} = 20.65$, $P = 0.0002$).

DISCUSSION

Several researchers have suggested that parents should not rely on the amount of past investment but on prospective value of their offspring when making decisions about allocation of parental effort (Clutton-Brock 1991). As chicks grow older they might be of higher reproductive value because of their increasing chance of surviving to breeding age. In the Camargue, older chicks are less susceptible to predation than younger ones (Salathé 1983, this study). This would favor increased parental effort with offspring age.

The present study shows that in the Greater Flamingo, only male parental effort increases with increasing offspring age. Although older flamingos tend to nest earlier (Cézilly et al., unpubl. results), variation in parental age had no effect on variation in feeding bout length in this study. However, the older parents considered here were only 12 years old. Flamingos live up to 34 years in the wild and over 50 years in captivity. Thus, the absence of covariation between parental age and feeding bout duration within this study may be affected by the age structure of the present ringed population. Future research should help in assessing the potential effect of parental age on feeding bout duration.

Because of fundamental sex differences in initial parental investment (Trivers 1972) and risk of extra-pair copulation resulting in uncertain paternity, male parental effort has previously been expected to be less than female parental effort in monogamous species (Alexander 1974). However, this view has been challenged by Burger (1981), who suggested that males in monogamous species invest heavily in territorial defense, mate guarding, and mate provisioning and would therefore be as prone as females to invest in parental care. In flamingos, males invest little energy in territorial defense since the pair occupies the nest site only a few days prior to egg laying, and males provide no food to their mate. However, mate guarding lasts several weeks before egg laying (pers. obs.).

Why do males not provision at higher rates when chick demand is low, since they seem capable of working harder? In several species, moderate investment by males in parental effort has been explained by a higher investment in attempted extra-matings (Westneat 1988, Carey 1990, Creelman and Storey 1991). However, this explanation is not appropriate for flamingos in this study. Once the crèche is formed there is no opportunity for successful reproduction through extra-pair copulation since the breeding island has by then been deserted by adults, and no female would attempt to breed in isolation from conspecifics. Alternatively, females may be physiologically limited in their ability to face increasing demands from older chicks. First, the inability of females to increase feeding bouts might be due to a lower ability than males to produce sufficient amounts of secretion, as females are slightly smaller than males. Females may also suffer higher

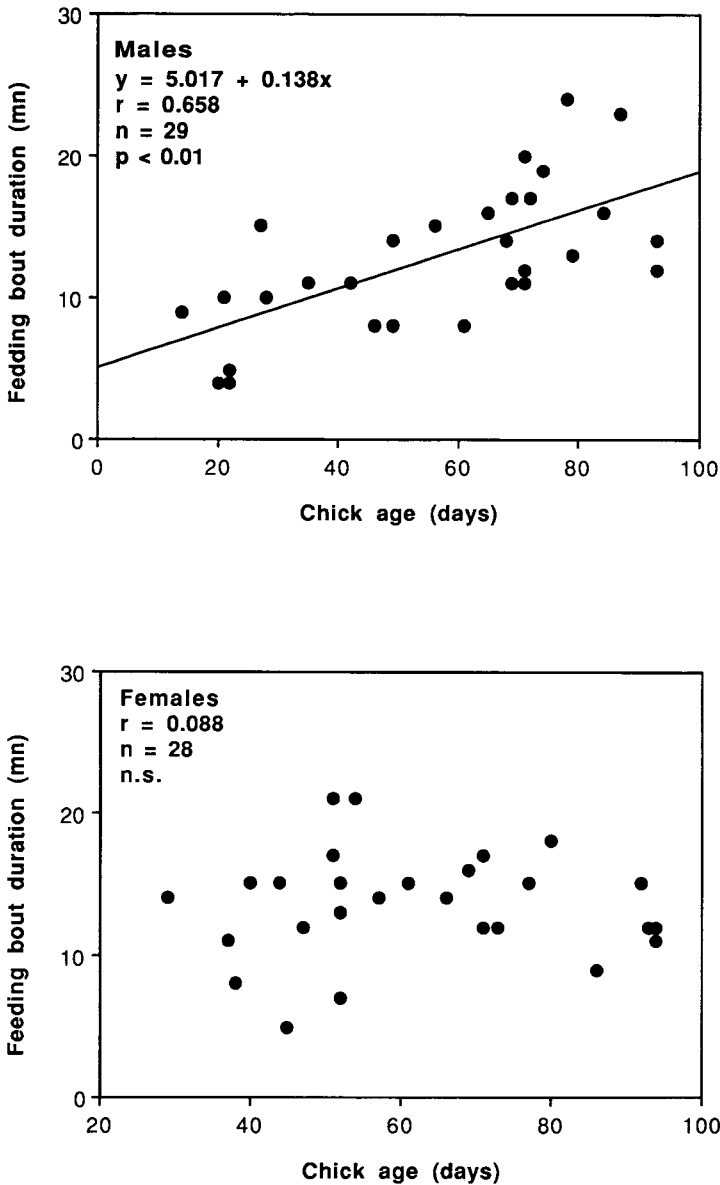


FIGURE 1. Feeding bout duration in relation to chick age in the Greater Flamingo. Data from 1985 and 1989 are pooled.

costs than males in earlier stages of reproduction as suggested by patterns of nest desertion (Cézilly 1993). They may therefore remain physiologically stressed and unable to adjust to the greater requirements of older chicks. Captive flamingos have been observed increasing feeding bouts with offspring age (Studer-Thiersch 1975), but no sex-related differences were reported. However, captive females may have had considerably better feeding conditions than in the wild.

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EFFECTS OF HEIGHT OF NEIGHBORING NESTS ON NEST PREDATION IN THE RUFIOUS TURTLE-DOVE (*STREPTOPELIA ORIENTALIS*)

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Key words: Rufous Turtle-Dove; nest predation; area-restricted searching; breeding density; nest height.

In many bird species, nest predation is one of the most significant causes of breeding failure (Ricklefs 1969).

Breeding density is often considered to affect nest predation. Higher breeding density often results in lower predation pressure for species which will mob nest predators (Berg et al. 1992, Westneat 1992). Alternatively, in species which build cryptic nests and do not attack nest predators, nest predation tends to be higher when nesting density is high (Murton 1958, Krebs 1970, Fretwell 1972, Dunn 1977, Weller 1979, Page et al. 1983, Hill 1984). In some experimental studies using

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