Nestling size rank in the little egret (Egretta garzetta) influences subsequent breeding success of offspring

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Abstract Few studies have investigated the long-term fitness consequences of nestling size hierarchies in altricial birds. In this study, we investigated whether or not the size rank order of siblings influences subsequent breeding success in the little egret, *Egretta garzetta*. From a marking program allowing individual recognition of wild birds, we obtained data on the breeding success of 56 pairs comprising individuals for which the size rank order was known. The breeding success in these pairs was positively influenced by the age of the marked bird but negatively affected by the laying date of the pair and the size rank order of the marked individual. There was also a significant difference between breeding colonies. We suggest two main hypotheses for a link between size rank order of individuals and their breeding success and we discuss our results in relation to current hypotheses on the adaptive value of hatching asynchrony.

Key words Breeding success · *Egretta garzetta* · Hatching asynchrony · Nestling size rank

Introduction

In many altricial birds, size hierarchies of nestlings within broods are the result of hatching asynchrony (Magrath 1990; Clark and Wilson 1991; Stenning 1996) or egg size differences within clutches (Parsons 1970; Schifferli 1973). When a size rank hierarchy is established within the brood, competitive asymmetries exist among siblings and the smallest are often reported to suffer from food shortage (Lebedeva 1994; Horak 1995; Slagsvold et al. 1995). A high mortality rate and a reduced fledging body mass are frequent consequences of this food shortage (Lemel 1989; Tinbergen and Boerlijst 1990; Stenning 1996). Although considerable attention has been devoted to understanding the adaptive value of size hierarchies within broods, current hypotheses remain the subject of much debate (see Stenning 1996 for a recent review).

Interest has been growing in understanding not only the short-term effects of brood reduction but also the long-term fitness consequences for the nestlings which survive it (e.g. Spear and Nur 1994; Horak 1995; Slagsvold et al. 1995; Mock and Parker 1997). Such information is essential to understand for instance the costs and benefits of hatching asynchrony in an evolutionary perspective. Several recent studies have demonstrated reduced post-fledging survival of individuals according to their hatching rank order (Husby 1986; Spear and Nur 1994; Horak 1995; Slagsvold et al. 1995; but see Hafner et al. 1998). However, whether or not the rank order of siblings affects their later breeding success is poorly documented. Assuming that food shortage during growth may subsequently lead to various disorders (e.g. McRoberts 1965; Morse and Vohra 1971; Ricklefs 1983; Haywood and Perrins 1992; Lesage and Gauthier 1998), we would expect chicks that enjoyed size advantages during their nestling lives to become more robust and successful breeders when they mature. Despite theoretical expectations for a role of the rank order on subsequent breeding performance, there is no empirical evidence from natural populations.

As in other heron species (e.g. Fujioka 1985; Inoue 1985; Mock and Parker 1986), little egret eggs hatch asynchronously (1- or 2-day intervals; Inoue 1985). Because of their size superiority (and sometimes sibling aggression; e.g. Inoue 1985), senior siblings obtain more than their proportionate share of the total food and, consequently, the development of chicks within broods shows substantial variation (Inoue 1985). Nevertheless,

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after fledging, there is no significant effect of rank on survival or the age at first breeding (Hafner et al. 1998). The aim of this study was to evaluate evidence for an influence of the size rank order of nestlings upon subsequent breeding success.

Methods

A marking program of little egret chicks, allowing individual recognition in the field of individual birds after fledging, was initiated in 1981 (for details see Hafner et al. 1998). To avoid excessive disturbance at the colonies, we did not mark chicks as soon as they hatched. Consequently, we cannot be sure which chick really hatched first, second and so on. Because the magnitude of the correlation between size rank and hatching rank is not precisely known, we only considered in this study nestling size ranks from measurements of tarsus length, a reliable estimator of the age in little egret chicks (McClure et al. 1959; Inoue 1985). To mark chicks and determine their size rank, we attempted to catch whole broods when the largest chick was 20–25 days of age with the largest chick (i.e. longest tarsus) assigned rank a, the second largest rank b and so on. In a brood of four chicks there may be up to 8 days difference between the first- and last-hatched chick (H. Hafner, unpublished observations). Different types of bands were used during this study. Initially, from 1981 to 1987, the birds were marked using combinations of colour rings. Since colour rings offered only a limited number of combinations, the marking scheme was changed using only striped darvic rings in 1987, and from 1988 on, wing tags. The tags were made of light, flexible, vinyl-coated polyester and were clipped on to the patagium (Pineau et al. 1992). Alphanumeric codes (legible in the field at a distance of 100 m) were written on the tags. Tagging had no apparent influence on the breeding performance of the adults (Pineau et al. 1992).

From 1982 to 1997, marked adult breeding birds were searched for weekly, from 20 May to 30 July in each colony. Observations were made by scanning as many nests as possible throughout the whole colony. The activities of marked birds such as nest-building, incubating, defending nest territories and feeding chicks were recorded. Once classified as a breeding bird, we attempted to determine how many chicks the individual was able to raise together with its partner. The following limitations of this study should be noted: (1) finding both partners of a pair marked in a population of 4000 adults is unlikely; (2) there are no apparent external differences between the sexes; (3) only exceptionally could a nest belonging to a marked bird be visited because of the difficulties in climbing to it. Therefore, our measure of brood size (see below) can be related to only one of two partners of a pair of unknown sex, and information on other breeding parameters, e.g. clutch size and growth rate of chicks are lacking. Brood size was measured in nests where the chicks were about 20–25 days of age. The number of chicks begging for food was counted when a parent attended the nest to feed the brood. These data were collected just before the oldest chick in a brood was able to fly, thus providing a reasonable estimate of the number of chicks fledging. To avoid bias, all these data were collected by observers who had no knowledge of the rank order of the marked parent. Chick mortality after the age of 20 days is negligible (1.6%, $n = 387$ chicks in 103 nests; H. Hafner unpublished data) so that the number of fledglings per brood at 40 days is identical to the number of chicks at 20 days.

The contribution of different variables to the brood size of marked individuals was derived by a multiple-regression procedure with all independent variables kept in the final model (Draper and Smith 1981). We studied the following independent variables: age and size rank of the marked bird and brood size in the nest of origin, year and time of laying by the pair (day of year) and colony site. Statistical analyses were performed using Systat 5 version 5.2.1. for the Macintosh (Wilkinson 1990). All tests were two tailed. Results were considered significant at the 5% level.

Results

From the 3788 chicks of known rank marked in the brood between 1983 and 1997, we were able to collect information on the breeding success (brood size) of 56 pairs in 11 colonies: rank a ($n_1 = 25$), b ($n_2 = 15$), c ($n_3 = 13$) and d ($n_4 = 3$); individuals were between 1 and 9 years old (mean ± SD: 3.55 ± 1.96 years). The mean age of marked individuals was not significantly different between ranks (ANOVA, $F_{3,52} = 1.44$, $P = 0.24$). There was no significant difference in the proportion of birds of different ranks in the 11 colonies studied [Fisher exact test on $r \times k$ contingency table (Raymond and Rousset 1995): $P = 0.28$]. The mean laying date (±SD) was 133 ± 8 days and the mean brood size (±SD) was 2.93 ± 0.78.

The size of the brood raised was significantly influenced by the colony site (Table 1). In addition, both the size rank order of the marked individual (Fig. 1) and the laying date of the pair negatively explained the size of the brood raised (Table 1). While the age of the marked individual positively explained the size of broods produced by marked pairs (Table 1), neither brood size in the marked parent's nest of origin, nor season of nesting had a significant effect (Table 1). The final model was highly significant ($R^2 = 0.64$, $N = 56$, $P < 0.0001$).

Discussion

Relationships between laying date, age of individuals and brood size have been widely documented in birds (Lack 1954; Perrins 1970; Järvinen 1989; Perrins and McCleery 1989). As in other studies, we found that

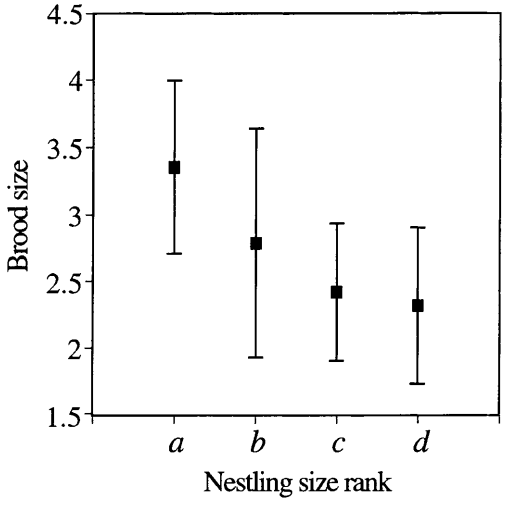

Fig. 1 Mean brood size of pairs according to the size rank order of the marked member of the pair [ANOVA for unbalanced sample sizes, $F_{3,53} = 6.89$, $P < 0.001$; multiple comparisons (Student-Newman Keuls procedure) show significant differences for the comparison *a* vs *b* and *a* vs *c*]. *Vertical bars* indicate standard deviation

Table 1 Summary statistics of multiple regression analysis (size of brood raised as dependent variable). Interaction terms were not significant

Variable	Sum of squares	*df*	Standardized regression coefficient	*P*
Colony	7.34	9		0.01
Year	0.231	1	−0.13	0.38
ln(age)	2.29	1	0.35	0.008
Rank	6.12	1	−0.52	0.0005
Brood size	0.42	1	−0.14	0.24
Laying date	1.38	1	−0.23	0.04

earlier laying within a season results in larger brood size. Whether this correlation reveals causation or only an association cannot be determined from these data. Mean brood size also increases with age of parents (at least the marked member of the pair). Older individuals may be more successful in acquiring nest sites of good quality and have more experience in parental care (Yasukawa 1981; Thomas et al. 1995). Our study also indicates that colony site has a significant effect on brood size. This phenomenon could be the result of variation in the quality of breeding sites. In addition, individuals in poor condition, and less able to breed successfully, could be more often restricted to breeding sites of poor quality. More information is needed to improve understanding of brood size variation between colonies.

The most striking result of this study remains, however, the influence of the size rank order of a parent (the marked member of a pair) on breeding performance, suggesting that size hierarchy within broods has long-term fitness consequences on individuals by influencing their breeding success. Although we cannot determine precisely from our data why the breeding success of individuals is influenced by their size rank order, two main hypotheses may be suggested.

First, the 'damage hypothesis' suggests that lack of food experienced during growth would impair some physiological functions or some traits more or less involved in the reproductive processes. Growth rate depression can for instance affect neural and organ development (Richner et al. 1989; Lesage and Gauthier 1998) or adult body size (McGillivray 1984; Boag 1987; Cooch et al. 1991; Larsson and Forslund 1991; Sedinger and Flint 1991; Haywood and Perrins 1992; Sedinger et al. 1995), an important reproductive fitness component. Since stored nutrient is necessary to produce eggs (Martin 1987; Monaghan and Nager 1997) and larger individuals are usually able to store larger reserves than smaller individuals (Sedinger et al. 1995), smaller females may be less fecund. Stress resulting from food shortage during growth could also affect the developmental stability of individuals and then fitness-correlated parameters. Higher developmental instability could itself decrease the reproductive potential of individuals depending on the structure concerned (e.g. Møller 1997).

Alternatively, density-dependent processes, such as competition, could act to emphasize condition differences among individuals after fledging. The 'competition hypothesis' thus stipulates that the smallest individuals within a brood could later have, from a physiological point of view, the same reproductive potential as other individuals, but they would remain in poor condition due to a constant disadvantage in competition with conspecifics. This phenomenon could well explain their lower breeding success since, for numerous reasons, body condition and breeding success in birds are closely related. For instance, body condition influences social rank (Searcy 1979; Arcese and Smith 1985; Lamprecht 1986; Richner et al. 1989), fecundity and laying date (Monaghan and Nager 1997), probabilities of obtaining mates or breeding sites of high value (Møller 1991a), parental abilities (Andersson 1994) and susceptibility to parasitic infections (Møller 1991b, 1996). Further research is needed to determine the proximate link between nestling size rank and breeding success in the little egret.

Finally, it is possible that chicks in nests where food is insufficient move more often than other chicks to adjacent nests to be parented by adoptive adults (e.g. Mock 1984; Morris et al. 1991; Avital et al. 1998). If smallest individuals within a brood later have low parental abilities, this would lead to an apparent higher brood size in other nests. We cannot exclude this hypothesis since the breeding success in our study was based on the number of chicks begging for food at an age when they are able to leave the nest.

Whatever the exact cause of the lower brood size in the nest of low-ranking individuals, this study supports the idea that size hierarchies within broods have long-term fitness consequences on individuals by influencing their breeding potential. Since little egret post-fledging survival does not differ between early and late-hatched individuals (Hafner et al. 1998), these results suggest that a full understanding of the fitness consequences of size hierarchies within broods also requires information on the subsequent breeding success of offspring. The brood reduction hypothesis suggests that hatching asynchrony establishes a size rank hierarchy within a brood that may facilitate efficient elimination of excess offspring if food becomes scarce, thereby ensuring the survival of at least some offspring (Lack 1947; Magrath 1989; Martins and Wright 1993). The offspring quality assurance hypothesis stipulates that size hierarchy within a brood ensures that at least some offspring will have adequate growth and will reach a high quality when leaving the nest (Slagsvold 1986; Amundsen and Slagsvold 1991). This last hypothesis thus primarily focuses on offspring quality rather than on offspring number. Given the decreasing breeding success with

decreasing size rank order of individuals, our results give some support to the offspring quality assurance hypothesis with, however, a clear advantage in being the largest chick within a brood. If senior siblings are of much greater value to the parents, and distinction between seniors and juniors is a behavioural option exercised by the parents (e.g. commencing incubation early), the parental 'decision' could be interpreted as true parental manipulation of offspring. Further information is needed to understand the quantity/quality trade-off implicit here, since parents invest in laying third and fourth eggs while the apparent highest pay-off comes from producing one or two highly competitive offspring.

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