



The importance of hatching date for dominance in young shags

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In birds, conditions and experience in the nest may influence the social rank of juveniles after they become independent. Three main factors may be involved: (1) mass at fledging, larger birds being better able to compete; (2) brood hierarchy, dominance in the brood continuing after the birds leave the nest; and (3) hatching date, birds hatching earlier having more experience and a greater ability to compete. I studied the effect of these factors on the agonistic behaviour of juvenile European shags, *Phalacrocorax aristotelis*, in crèches. Of all the factors, only hatching date had a significant influence on the dominance rank of juveniles. Birds that hatched earlier had a higher rank. Additionally, males were somewhat more aggressive than females. The importance of an individual's hatching date for its social rank may have consequences for its future reproductive value.

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Agonistic behaviour, which is common in species living in groups, results in individuals forming a social hierarchy (Huntingford & Turner 1987). Thus, dominant animals are better able to compete and take advantage of resources (e.g. Ekman & Askenmo 1984; Arcese & Smith 1985; Westman 1990). In many birds, the period of independence after fledging leads to their introduction into a social group and the determination of a new hierarchy among the juveniles (Garnett 1981). In this way, factors existing prior to fledging may affect social rank during independence (Boag & Alway 1980).

In many birds, after fledging, juveniles gather on perches that serve as crèches (e.g. Davis 1982; Evans 1984; Carter & Hobson 1988), where parental care is continued (Burger 1980). In the European shag, *Phalacrocorax aristotelis*, the crèches are stable social units: only 8% of juveniles move away from the perches where they normally reside (unpublished data). In the crèches, fledglings are often aggressive, especially while being fed by the adults (Snow 1963). Since crèches are stable social units, an individual's dominance rank may affect its ability to compete for resources. Hatching date, brood hierarchy and size of chicks at fledging may influence the social hierarchy and their recruitment into the population (Watts & Stokes 1971; Boag & Alway 1980; Spear & Nur 1994). I tested the following three hypotheses in juvenile European shags.

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(1) Mass at fledging. The relative mass of juveniles at fledging can determine the direction of dominance. In stable groups, the largest birds are usually dominant (e.g. Ketterson 1979; Richner et al. 1989). In great tits, *Parus major*, for example, the weight of the fledgling has the largest long-term effect on its social rank (Garnett 1981).

(2) Brood hierarchy. A size hierarchy within a brood caused by asynchronous hatching may determine the dominance rank of individuals during independence (Boag & Alway 1980). In the blue-footed booby, *Sula nebouxii*, early social experience also influences the brood hierarchy, the older chick dominating its sibling: in an experiment in which unrelated chicks were paired, senior chicks dominated junior ones, even though the latter were, on average, 32% heavier (Drummond & Osorno 1992; see also Drummond & Canales 1998). European shag chicks hatch over a 2-day interval, which leads to a hierarchy determined by size at a very early age (Stockland & Amundsen 1988). This hierarchy could affect agonistic behaviour during independence.

(3) Hatching date. Hatching date, and consequently early social experience in the group, can influence the social rank of juveniles. In the genus *Parus*, for example, the first fledglings that settle in an area dominate birds that fledge later (review in Matthysen 1990). This suggests that juveniles need social experience to develop competitive skills. Individuals must compete for dominance and they learn from their first encounters with opponents (Huntingford & Turner 1987; Clutton-Brock &

Parker 1995). These hypotheses are not mutually exclusive, however, and some species of birds show positive correlations between mass at fledging, hatching date and brood rank (O'Connor 1984).

METHODS

Study Area and Nestling Data

I studied shags on the Islas Cíes (Ría de Vigo, Galicia, northwest Spain) between March and June 1996. The Islas Cíes holds a nesting population of ca. 1000 pairs of shags, which nest in hollows underneath rocks (Velando et al. 1999). During the hatching period, I visited 56 nests daily. I recorded the order, date and time of hatching of each chick in the brood either directly or estimating them from the prehatching stages of each egg (cracked, surface broken, distinct hole cut by chick; see Stokland & Amundsen 1988). Brood size was two or, usually, three chicks.

I marked the bill of the chicks with indelible colour markers while they were breaking the shell or immediately after hatching. Each chick was differentiated in the nest by the coloured marks. When the chicks were 5 days old, I also tagged each one with a strip of coloured velcro across the tarsus. These strips were adapted to tarsus size during growth. At 15 days old, the chicks were tagged with a plastic ring with an individual two-digit combination to facilitate identification from a distance. When the chicks were 50 days old, I weighed them with a spring balance to the nearest 10 g. I measured the culmen, head, tarsus and wing of each chick about seven times during the first 15 days of life and subsequently every 4 days until they first flew. These morphometric measurements allowed us to sex the chicks by means of a discriminant analysis (A. Velando, J. Graves & J. Freire, unpublished data).

Observations and Data Analysis

After fledging, the juveniles gathered on rocks near the sea beneath the colonies, where they formed crèches. I observed a single crèche, located over a flat rock above sea level in the Isla do Faro, continuously in 1-h blocks. I carried out 70 h of observations from 28 June to 17 July (all the chicks studied fledged between 1 and 25 June). I studied the agonistic behaviour of 37 tagged juveniles. The following categories were recorded: give peck, receive peck, vertical threat gape and horizontal threat gape. In a horizontal threat gape the chick extended its neck horizontally towards another bird that was not close by, with the bill open or closed (Snow 1963; van Tets 1965). I converted behavioural categories into frequencies by dividing the number of actions of each behaviour by the number of hours that the bird was in the crèche. All statistical tests were two tailed. Data are expressed as means \pm SE.

Ethical Note

In the Islas Cíes, the main source of variability in breeding performance of shags was due to one or more

eggs failing to hatch in 38% of the nests. Thus, to avoid disturbing the birds, I studied colonies that had not been visited during the incubation period. In these colonies, the main cause of yearly chick mortality was the adverse weather (Velando et al. 1999) and for this reason I did not visit them on rainy and windy days. During the hatching period, the colonies were visited daily. During this period each visit lasted less than 1 h to avoid the chicks cooling when they were dependent on parental warmth (Østnes & Bech 1997). In Islas Cíes, there was no predation on eggs or chicks in 6 years of study. During the study there were no desertions and reproductive success in the colonies was similar to that in the nonvisited control areas (visited areas: 1.83 chicks/nest; controls: 1.79; Mann-Whitney test: $Z=0.06$, $N_1=56$, $N_2=26$, $P=0.95$). When I measured a brood, I removed and returned all the chicks at the same time. The shags fledged at 55–62 days and my visits did not appear to cause premature fledging (in the U.K. the chicks fledge at 48–58 days, Snow 1960). The study was carried out in Parque Natural Islas Cíes, with permission from the Dirección General de Conservación de la Naturaleza (Ministerio de Medio Ambiente) and Servicio de Medio Ambiente Natural (Xunta de Galicia).

RESULTS

Weight at Fledging

I carried out a GLM analysis to identify the effect of hatching date, hatching order and sex on weight of chicks at fledging. Before leaving the nest, male chicks weighed significantly more than females (males: 1722 ± 14 g, $N=51$; females: 1473 ± 16 g, $N=47$; $F_{1,88}=10.51$, $P=0.002$). Chick weight decreased with hatching date ($F_{1,88}=4.99$, $P=0.028$), but within sexes this was significant only for females (Fig. 1). The hatching order had no effect on the weight of fledglings ($F_{2,88}=0.37$, $P=0.69$; Fig. 1), and all interaction terms were nonsignificant (sex*hatching date: $F_{1,88}=0.51$, $P=0.48$; sex*hatching order: $F_{2,88}=2.31$, $P=0.10$; hatching date*hatching order: $F_{2,88}=0.89$, $P=0.41$).

Dominance Rank of Juveniles

To determine the dominance hierarchy, I carried out a principal component analysis on the correlation matrix of frequencies of the aggressive categories recorded. The first principal component (PC1) accounted for 56% of the variance, with an eigenvalue of 2.23 and Pearson correlation coefficients of 0.868 ($P<0.001$), 0.816 ($P<0.001$), 0.732 ($P<0.001$) and -0.522 ($P<0.01$) for frequency of give peck, vertical threat gape, horizontal threat gape and receive peck, respectively ($df=35$ in all cases). The resulting PC1 was a synoptic descriptor of dominance rank of juveniles in the crèche.

A GLM analysis showed that males had a slightly and significantly higher dominance rank than females ($F_{1,26}=6.10$, $P=0.021$); however, neither hatching order nor weight of juveniles had a significant effect on the dominance rank (PC1) in the crèche (hatching order:

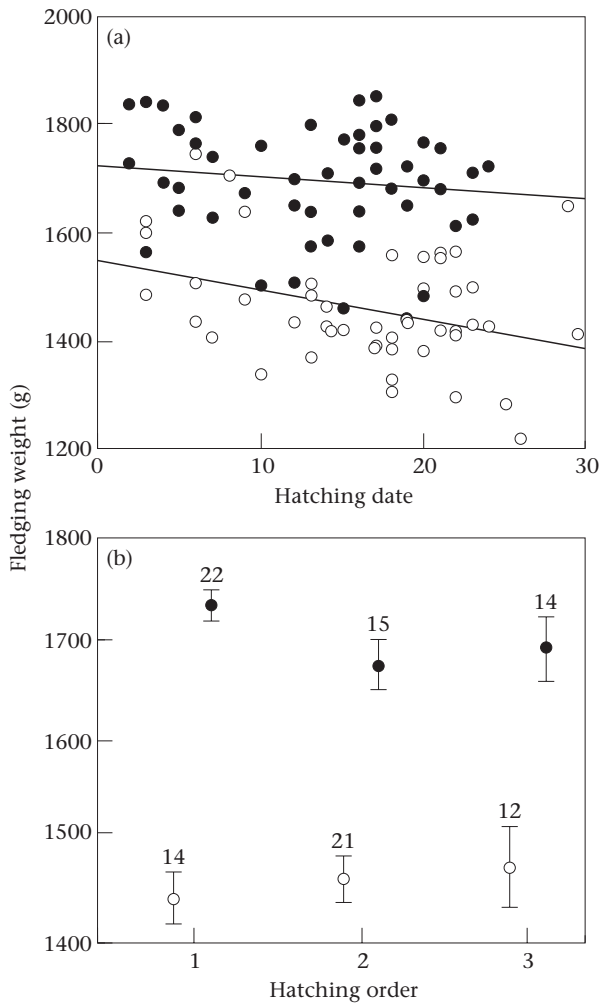


Figure 1. Relationship between fledging weight (measured at 50 days old) of males (●) and females (○) and (a) hatching date (day 1=1 April; linear trend of both sexes is shown: males: $R^2=0.02$, $N=51$, NS; females: $R^2=0.13$, $N=47$, $P<0.05$) and (b) the hatching order ($\bar{X}\pm SE$, N).

$F_{2,26}=0.45$, $P=0.64$; fledging weight: $F_{1,26}=0.25$, $P=0.62$; Fig. 2). The effect of hatching date was significant, birds that hatched earlier having a higher dominance rank ($F_{1,26}=26.15$; $P<0.001$; Fig. 2). The interaction terms were all nonsignificant (hatching order*fledging weight: $F_{2,26}=0.03$, $P=0.97$; hatching order*hatching date: $F_{2,26}=0.36$, $P=0.70$; hatching date*fledging weight: $F_{1,26}=0.05$, $P=0.83$).

DISCUSSION

I found a clear relationship between hatching date and agonistic behaviour of juvenile European shags during independence. Birds that hatched earlier had a higher dominance rank than those that hatched later. However, brood hierarchy and fledging weight did not affect dominance rank. The year of study, 1996, was a good year for breeding shags in Islas Cíes, with low chick mortality (Velando et al. 1999) and apparently abundant sandeels (Ammodytidae),

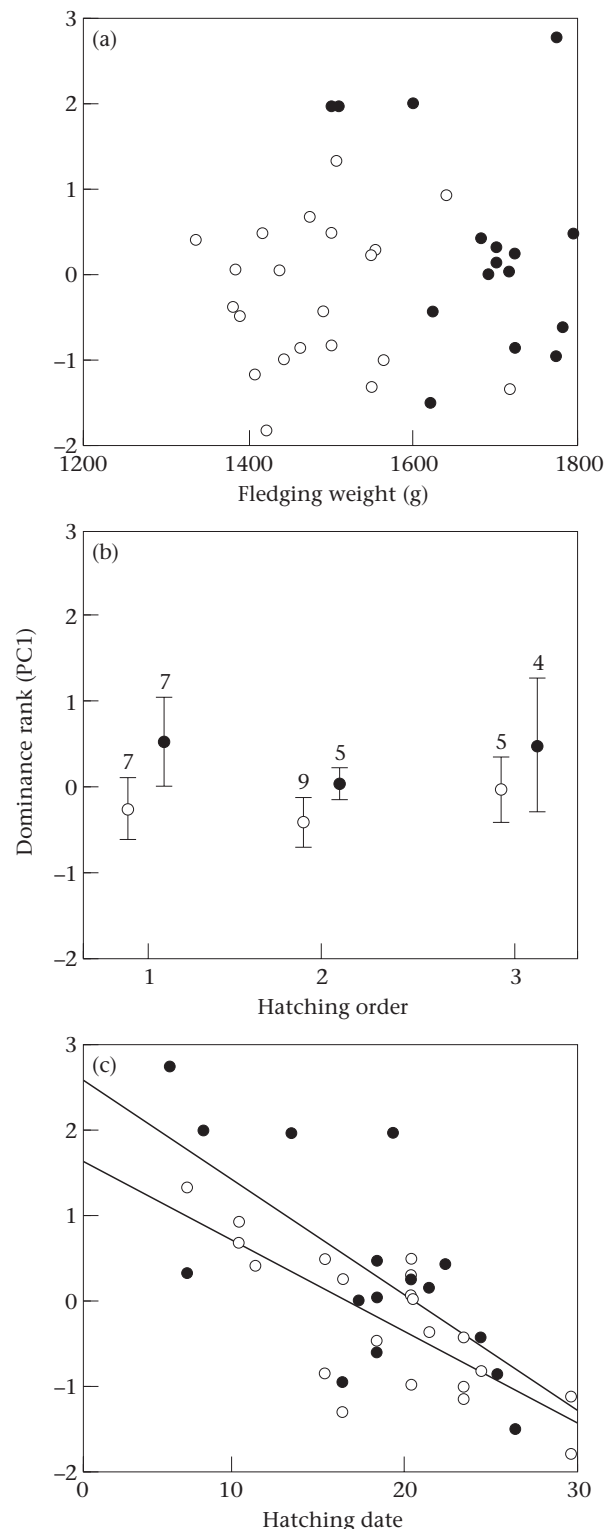


Figure 2. Relationship between the dominance rank (PC1 from a principal components analysis) of male (●) and female (○) juveniles in the crèche and (a) fledging weight (no linear trend was observed in either sex), (b) hatching order ($\bar{X}\pm SE$, N) and (c) hatching date (day 1=1 April; linear trend of both sexes is shown: males: $R^2=0.47$, $N=16$, $P<0.01$; females: $R^2=0.61$, $N=21$, $P<0.05$).

the most important prey in the breeding season (Velando & Freire 1999). Thus, in this year, there was not much variation in weight between individuals, especially males. In carrion crows, *Corvus corone*, experimentally underfed chicks achieved lower social status in the flock (Richner et al. 1989). In the European shag, fledging weight and brood hierarchy may thus influence juvenile dominance only in years when food is scarce.

In a study of great tits, hatching date affected the dominance rank of juveniles in the first week after fledging, but size was more important in the second week (Garnett 1981; but see Matthysen 1990). In my study, however, although the hatching date had a slight effect on weight at fledging, the weight of juveniles did not significantly influence their social rank. Sex also had an effect on rank, with males being slightly more dominant than females. During the period of independence, shags acquire secondary sex traits such as calls (males make an 'ark' sound, while females are silent; Snow 1963) which may cause the intensity of male threats to escalate. In several species, males in groups are more aggressive than females (e.g. Ketterson 1979; Piper & Wiley 1989).

The effect of hatching date on dominance of juvenile shags suggests that social experience in the group may determine the dominance hierarchy, which is established during the first few encounters between individuals, as happens in other animals (Huntingford & Turner 1987). In flocks of many species, the birds that start the group dominate those arriving later (e.g. Holberton et al. 1990). In shags, when late chicks fly from the nest to the crèche, they presumably lose their first fights and have a low social rank. Learning submissive behaviour, as shown by subordinates, has been described as an imposed weakness (Drummond & Osorno 1992). Moreover, aggressive tendencies and dominance status are correlated with slight differences in adrenal gland activity and brain chemistry (Brown 1975). In crèches of the European shag subordinate juveniles are less skilled in warding off other juveniles during feeding and the birds whose food is successfully stolen are those with a lower social rank (unpublished data). Dominant birds, therefore, are at an advantage when competing for resources. Thus, the hatching date may have long-term fitness consequences causing the future reproductive value of chicks to decline throughout the season. In addition to the advantages of early breeding discussed elsewhere (e.g. territory quality, mate quality and mating success, see Møller 1994), the chicks of early breeders may thus attain a higher social status and have better chances of survival (Perrins 1966; Nisbet & Drury 1972; Harris et al. 1992, 1994; Spear & Nur 1994).

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