ORIGINAL ARTICLE

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Effects of territory quality, food availability and sibling competition on the fledging success of oystercatchers (*Haematopus ostralegus*)

Abstract We investigated the fledging probability of oystercatcher, *Haematopus ostralegus*, chicks as a function of hatching order, brood size, territory quality and food availability. Sibling dominance was related to the hatching order in both low- ('leapfrogs') and high-quality ('residents') territories. Differences in hatchling mass might have aided the establishment of a dominance hierarchy, since breeders produced small late eggs and hatchlings. These mass differences were most pronounced in leapfrogs, and in large broods in years with lower food availability ('poor' years). Late hatchlings fledged less often and with lower body masses compared to early hatchlings in all situations. Leapfrogs produced smaller broods and hatched their broods more asynchronously in poor years than leapfrogs breeding in years with more available food ('good' years) and residents breeding in both poor and good years. Large brood sizes resulted in lower survival of hatchlings in poor years. These results favour the 'brood reduction' hypothesis. However, contrary to the expectations of this hypothesis, hatching order also affected fledging success in residents. Moreover, large brood size resulted in higher survival of hatchlings in good years, particularly in residents. Thus, although large broods experienced losses due to sibling competition in some years, they nevertheless consistently produced more fledglings per brood in all years, both as leapfrogs and residents. We believe this effect is due to parental quality correlating with initial brood size. Most leapfrogs, at best, fledged one chick successfully each year, losing chicks due to starvation. Nevertheless, leapfrog broods were reduced in size after hatching significantly less quickly than resident broods. These results suggest that breeders lay and hatch insurance eggs to compensate for unpredictable losses due to the high predation rates on both nests (ca 50%) and chicks (ca 90%), in accordance with the 'nest failure' hypothesis.

Keywords Territory quality · Hatching asynchrony · Egg mass · Sibling competition · Fledging success

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Introduction

Hatching asynchrony (HA) in birds is the timespan between the hatching of the first and the last egg. In many bird species, first hatchlings become dominant over later hatchlings due to HA. Typically, the smaller chicks at the bottom of the hierarchy have lower fledging probabilities than larger chicks at the top of the hierarchy due to differences in starvation and predation rates (reviewed by Ricklefs 1993; Mock and Parker 1997). Parental investment in these late hatchlings seems a waste of effort. At face value, parents should benefit by interfering in the sibling competition and feeding all hatchlings equally. Or they might produce fewer hatchlings, hence ensuring that no chicks are lost to starvation. So why do parents produce 'large' broods which hatch 'asynchronously'? Why do parents allocate food to their nestlings differentially?

Many hypotheses have been proposed to explain this phenomenon, following the paradigm that HA evolved from the parents' and siblings' behavioural decisions to maximize their fitness (see reviews by Magrath 1990; Mock and Forbes 1995; Stenning 1996; Mock and Parker 1997). Some of these hypotheses relate to the parents adapting to predictable environments, using HA as a tool to ensure, for example, favourable chick feeding conditions by reducing the maximum peak load of the parents

('peak load reduction' hypothesis; Hussell 1972) or by reducing sibling competition within a brood by creating a stable dominance hierarchy ('sibling rivalry reduction' hypothesis; cf. Lack 1947). Hypotheses based on predictable fitness effects on nest predation ('nest failure' hypothesis; Clark and Wilson 1981) and predation on the incubating parent ('predation on parent' hypothesis; Hussell 1972; Ricklefs 1993) also fall into this category. The resultant adaptive timing of incubation might in these cases lead to HA as a side-effect. Other hypotheses relate to situations where parents are unable to predict the breeding environment, for example when chick feeding conditions are unpredictable at the time of laying (e.g. Pijanowski 1992; Lamey and Lamey 1994). In these cases, parents might use HA to induce brood reduction in the unfavourable feeding conditions (Lack 1947), and thereby maximize their overall success ('brood reduction' hypothesis or 'resource tracking' hypothesis; Temme and Charnov 1987). A final possibility is that parents are facing constraints and that their behaviour to cope with these constraints leads to HA (e.g. Mead and Morton 1985). An example includes laying dates which are constrained to later than optimal values ('hurry up' hypothesis; Clark and Wilson 1981). Since earlier laying is impossible, parents might start incubation on the first egg, trying to hatch the majority of eggs closest to the optimal date, leading to HA. Another example of a constraint occurs when egg viabilities decrease if eggs have not been incubated from laying onwards ('egg viability' hypothesis; Cannon et al. 1986; Veiga and Viñuela 1993). Again, this might favour incubation starting immediately after the first egg is laid and would as a side-effect lead to HA. These seven hypotheses are not mutually exclusive.

Theoretical work (Winkler and Wallin 1987; Parker et al. 1989; Godfray and Parker 1992; Forbes 1993; Rodriguez-Girones 1996) has linked the outcome of parent-offspring conflict and sibling rivalry over the amount of parental investment received by each sibling to the experimental and theoretical work on the optimization of brood size (see review by Mock and Parker 1997). Not surprisingly, the problem of brood size optimization cannot be decoupled from the optimization of investment per offspring, and vice versa, and thus the new models provide the crucial step to understand both.

In this paper, we want to analyse the fledging probability of oystercatcher, *Haematopus ostralegus*, chicks as a function of territory quality, food availability, hatching order and brood size. Our study population on the island of Schiermonnikoog shows marked differences in territory quality and large differences in year-to-year food supply. Breeders establish nesting territories on the saltmarsh and feed on mudflat territories. Pairs on the edge of the saltmarsh occupy high-quality territories ('residents') because they have an adjacent feeding territory with low transport costs of food to their chicks. Pairs breeding further inland occupy low-quality territories and are termed 'leapfrogs', because they have to transport every food item to the chicks from a separate feeding ter-

ritory on the mudflat (Ens et al. 1992). Many leapfrog chicks starve to death, and as a consequence, leapfrogs raise about one-third as many chicks as residents (Ens et al. 1992, 1995; Heg 1999; Heg et al. 2000). By experimentally supplying surplus food to the leapfrogs, Ens et al. (1992) established that due to these transport costs, leapfrogs are more strongly food limited and face stronger sibling competition than residents. Further, Ens et al. (1995) and Heg (1999) showed that the territory quality differences are highly persistent. As Ens et al. (1995) have shown, leapfrogs and residents are unlikely to differ in average parental quality, so we attribute all differences between leapfrogs and residents to differences in territory quality.

Although we did not perform experiments, we use this natural variation in territory quality and annual variation in food availability to explore the oystercatchers' breeding behaviour. We predict that breeders in low-quality territories, the leapfrogs, produce smaller broods and/or adaptively reduce their brood size (e.g. by sibling competition), particularly in years with low food supply. In contrast, breeders in high-quality territories, the residents, are expected to produce broods hatching more synchronously, particularly in years with a good food supply. First, we analyse how within-family dominance relationships are established and which chicks become dominant, in relation to hatching order and hatchling mass. Second, we present the effects of within-family differences in hatching order on fledging probability and fledging mass. Finally, we investigate the effects of brood size and sibling competition on the fledgling production of the parents.

Methods

We have been studying an oystercatcher population on the island of Schiermonnikoog (see Ens et al. 1992; Heg 1999; Heg et al. 2000), where 70–149 breeding pairs were individually colour-marked in the breeding seasons 1983–2000. The analyses in this article are restricted to the breeding seasons 1986–1995. The breeding territories were searched every other day for new nests and existing nests were visited for new eggs. Oystercatchers lay one to four eggs, and eggs are laid at about 28-h intervals. Occasionally, females lay a fifth egg to compensate for losses during egg laying. Since these clutches are very rare (n=4, ca 0.5% of the clutches) they have been omitted from most of the analyses. The eggs were individually marked with a waterproof marker, measured (length, width to the nearest 0.1 mm) and weighed (to the nearest 0.1 g). Egg loss to predators (mostly gulls) is high, thus clutch size is underestimated in the many cases when eggs had been depredated before being found (Ens 1991). In some nesting territories, no eggs were found at all, although all pairs produced nest scrapes. If two or more new eggs were found in a nest, the laying order was assigned according to remnants of uric acid and blood of the female on the eggshell of the last-laid egg. Sometimes a nest was found containing a complete clutch, and the laying order was assigned according to the relative mass loss of the eggs. If eggs are depredated during egg laying, the female usually lays the remainder of the clutch in another nest cup. If the first clutch is lost early in the season, females produce a replacement clutch within 8–12 days, usually in another nest cup. Pairs produced up to three replacement clutches. Second (n=15) and third (n=1) replacement clutches were, however, very rare.

Nests were visited once or twice a day around the time of clutch hatching. By colour marking the eggtooth of chicks in eggs that had begun to hatch, the newly hatched chicks found on subsequent visits could be assigned to an egg and their hatching order determined. In the early years 1986–1991 and on days with continuous bad weather in 1992–1995, some nests were less intensively visited, resulting in missing values for HA, hatching order and chick mass. Many nests hatched almost simultaneously. These chicks were given the same hatching order unless hatching order could be determined on the basis of one or more chicks found (1) with their eggshell attached or partly attached and still wet, (2) completely or partly wet and brooded, (3) with an intact eggtooth which their sibs had lost. Newly hatched chicks were individually marked with a colour dye and measured within 1 day of hatching (mass to the nearest 0.1 g; head length, bill length and tarsus length to the nearest 0.1 mm). Hatchling mass was corrected for the degree of dryness of the down (wet or dry). HA was analysed in days, where the zero value indicates that all chicks hatched on the same day.

Oystercatcher chicks are precocial, i.e. they leave the nest cup and wander around in the territory within 1 day of hatching. Thus, to establish whether they have survived, undisturbed observations from hides are necessary. Usually several times a week, but at least weekly, each hide was visited and all leapfrog and resident territories in the neighbourhood were observed for parents caring for chicks and noting which chicks were still alive (recognizable from the colour dyes on their belly). If physical interactions between sibs for food items were seen (e.g. fights, pulling and pushing, stealing food), the chick which eventually won and ate the food was recorded.

The frequency of visits to and observations of the territories was increased just before fledging, to determine fledging success and to catch the fledglings for final measurements and banding. Fledging age was 33.7±0.2 (SE) days (range 22–53 days, n=365), defined as the day at which wing length reached 180 mm and chicks are able to fly within a few days, and body measurements were taken: mass (to the nearest 1 g), wing length (to the nearest 1 mm), head length, bill length and tarsus length (all to the nearest 0.1 mm; see Kersten and Brenninkmeijer 1995). Most fledglings were measured just before 30 days of age (mean deviation in days: –1.3±0.2, range –17 to +17 days, n=365). However, to derive comparable body masses of all chicks with known fledging age, we derived a formula to scale their mass to 30 days of age. This was done as follows. (1) Fledging age (in days) was determined for all fledglings caught and measured. In some cases, fledging age was not known exactly. However, in both slow- and fast-growing chicks, wing growth rate is about 5.5 mm per day between day 15 and fledging (Kersten and Brenninkmeijer 1995), so from the wing length at capture, fledging age could be estimated by extrapolation. (2) From chicks caught twice between day 15 and fledging, we calculated the daily growth rate (g/day). This rate correlated negatively with fledging age (in parentheses SE of the coefficient): daily growth rate=19.73 (±2.07)–0.30 (±0.06)×fledging age, R^2=0.15, P<0.0001, n=142). So chicks fledging at an early age grow fast. (3) We used this formula to calculate the body mass of all chicks at day 30 of age. Parents raise only one brood successfully to fledging each year, with zero to two (rarely three) fledglings per brood.

The breeding population experiences large fluctuations in available prey species. Large fluctuations are reported from other parts of the Wadden Sea as well (e.g. Beukema 1974; Beukema et al. 1993; Zwarts and Wanink 1993; Camphuysen et al. 1996; Zwarts et al. 1996). However, these publications reveal that *within* a single breeding season, both prey numbers and biomass are generally predictable. Large numbers of prey in April are followed by large numbers through the whole breeding season. Bivalve and worm prey species burrow closer to the surface of the mudflats during April, May and June (oystercatcher broods hatch from 28 May onwards; peak hatching is in mid-June), and thus food is more accessible then than later in the season. Prey accessibility is also roughly predictable, albeit worms vary in burying depth with the tide and temperature (Evans 1987) and do not surface during

excessive rain or drying of the top layer (Dankers et al. 1981). Adult breeders feed on several bivalves, of which *Macoma balthica* is the most important in the breeding season. During the breeding season, in particular, they also eat worms, mainly *Nereis diversicolor* and to a lesser extent the lugworm *Arenicola maritima* (Bunskoeke et al. 1996; de Vlas et al. 1996).

Resident pairs feed chicks with relatively small prey species like *Nereis* and to a lesser extent *Macoma*. Although the numbers of *Macoma* have steadily declined, *Nereis* numbers have remained relatively high, except in 1990, 1991 and 1993 (Fig. 1a). The year 1990 was excluded from the analysis, since virtually all chicks drowned due to an exceptionally high flood on 6 July (Ens et al. 1995), and relaying did not occur. Hence, we defined the years 1986–1989, 1992, 1994 and 1995 as years with high food availability for the residents ('good' years) and the years 1991 and 1993 with relatively low numbers of both *Nereis* and *Macoma* as 'poor' years. The estimated gram ash-free dry mass/m² (±SE; see Zwarts 1991; Bunskoeke et al. 1996) of the major prey species for residents comparing good (n=7) and poor years (n=2) was 5.4±1.3 versus 1.9±0.7 for *Macoma* and 6.4±0.5 versus 4.5±0.3 for *Nereis*.

Leapfrogs have to transport every food item singly over large distances to their chicks (Ens et al. 1992; Heg 1999), so *Macoma* and *Nereis* are less profitable for them. Accordingly, they rely on large bivalves like mussels *Mytilus edulis* from a small musselbed 350 m downshore (Ens and Alting 1996), cockles, *Cerastoderma edule*, and two clam species, *Mya arenaria* and *Scrobicularia plana*. Similarly, Safriel et al. (1996) have shown that leapfrogging oystercatchers on the island of Skokholm preferably transport larger food items to their chicks. However, the musselbed in our study area decreased to an insignificant size during the early 1990s, and has not re-established (Fig. 1B; in other areas of the Wadden Sea some recovery has been reported, see Camphuysen et al. 1996). Samples from transported shellfish to leapfrog chicks indicate that before the decline of the musselbed, mussels were an important prey species fed to chicks (Fig. 1C). Afterwards, other large prey items like cockles and clams were transported, instead of mussels. But these larger species are not available in many leapfrog territories, since their distribution appears to be either limited (cockles) or the large profitable clams bury too deep for most individuals to locate and catch them (Zwarts and Wanink 1989; D. Heg, personal observation). Moreover, the catching rate of large clams compared with mussels is very low, since mussels lie exposed on the mudflats, whereas the clams are buried in the mud and first have to be detected (D. Heg, personal observation). Thus, leapfrogs experienced progressively worse feeding conditions for food transports to chicks in the 1990s, and relied more heavily on less profitable prey species like *Nereis* and *Macoma* (D. Heg, personal observation; note that large-sized specimens of these species provide relatively small amounts of food compared to medium-sized clams and mussels). So, for the leapfrogs, we defined the breeding seasons 1986–1989 as good years and those of of 1991–1995 as poor years as regards food availability.

Data selection and analysis

We used all clutches and replacement clutches in the analyses, hence excluding in most analyses pairs with no nest found (about 10% of pairs). Fledging probability analyses were carried out on all the hatchlings, hence excluding 48.7% of the clutches (n=1,136) where no egg hatched, mainly due to the high predation pressure on eggs. The results were analysed with SPSS/PC+ 5.01 (Norusis 1990) and GLIM (Crawley 1993). Data on fledging probability were analysed with logistic regressions, where the main effects were entered as categorical variables (SPSS converts each variable with n categories into a group of n–1 dummy variables) using a stepwise maximum-likelihood method to decide whether an effect should be deleted from the model, starting with the full model (the full model contains all the effects, including all the interactions; Norusis 1990). Significant results are depicted with their effect on the log-likelihood ratio when removed from the final model. Data concerning HA (0–3 days) were analysed with

Fig. 1A–C Numbers of available prey species. **A** typical resident prey species. **B** typical leapfrog prey species. **C** Shellfish transported to leapfrog chicks
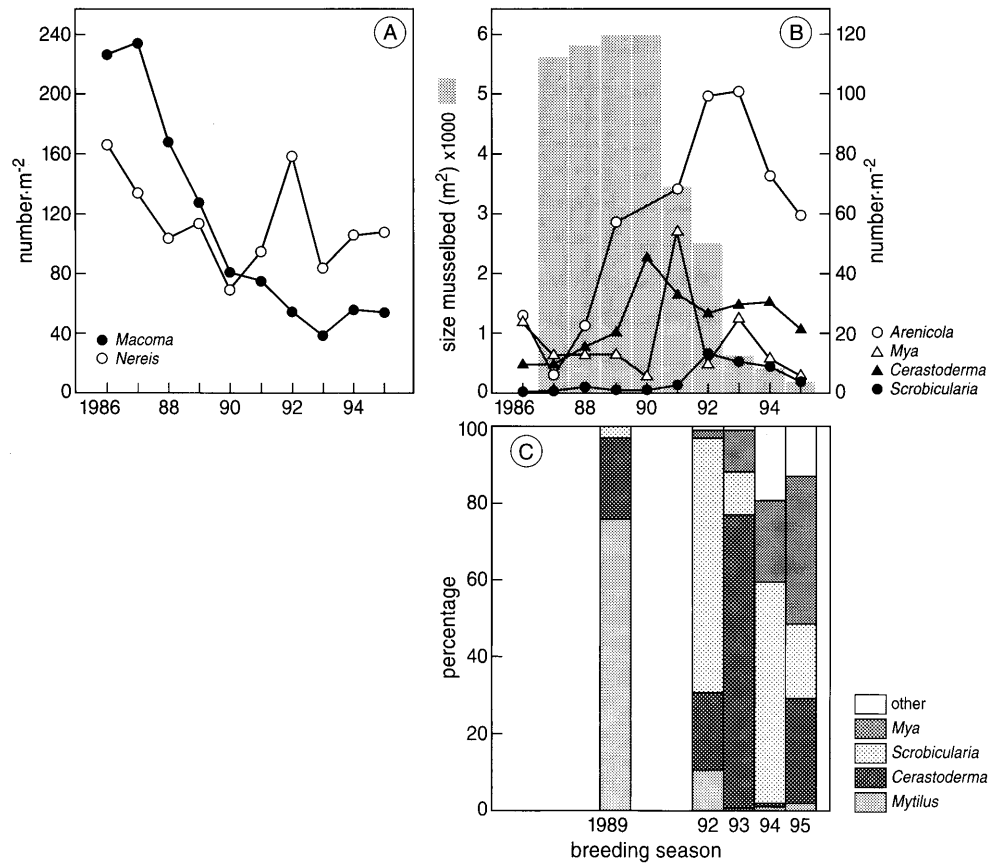
Poisson regressions using GLIM. GLIM uses a logarithmic link function to ensure positive counts (negative counts have no meaning) and a maximum-likelihood method to estimate the parameters (Crawley 1993). Non-significant interactions and main effects were deleted from the model until the final model was reached containing only significant effects. Significant effects are indicated with their effect on the deviance when removed from the final model.

Results

We analysed three methods by which parents might influence sibling competition at hatching: (1) by adjusting clutch or brood size; (2) by adjusting the order of hatching by the degree of HA, or (3) by adjusting the size of the hatchlings by varying egg size. Both hatching order and hatching size might influence the within-brood dominance hierarchy and subsequent hatchling survival.

Brood size at hatching

The first method to vary the degree of sibling competition at hatching is to adjust brood size. As we had originally hypothesized, leapfrogs laid smaller clutches and hatched fewer chicks than residents, particularly in poor years. These differences in brood size at hatching are largely explained by the differences in the initial clutch size (Table 1). Since oystercatcher chicks are semi-pre-

cocial, parents might use an additional method for reducing the brood size at hatching: abandon the nest with the first hatchling(s), leaving unhatched offspring to die. In 27 cases, parents abandoned the nest leaving one pipped egg in the nest cup; in 4 cases, two eggs; in 2 cases, three eggs and in 1 case, four eggs. All chicks within these abandoned eggs died, so the brood size was reduced. We observed this behaviour in 4.5% of the nests with hatchlings (*n*=701). Although the mean number of deserted pipped eggs per brood is rather low (mean±SE, residents: 0.06±0.02, *n*=294; leapfrogs: 0.06±0.02, *n*=407), in some clutch sizes and territories it contributed significantly to the reduction in brood size. However, the results did not support the hypothesis that leapfrogs abandoned pipped eggs more often than residents to reduce brood size (Table 2). In fact, the percentage of abandoned pipped eggs varied significantly with breeding status, food availability and clutch size in concert.

Order and size of hatchlings

The second method to vary the degree of sibling competition at hatching is to adjust the level of HA. Oystercatchers start incubating before the last egg in the clutch is laid (D. Heg, personal observation), so it is not surprising that many broods hatched asynchronously. Contrary to expectation, leapfrogs did not hatch their broods more asynchronously than residents (Table 1). But, as

Table 1 Reproductive parameters of residents and leapfrogs in years with *poor* and *good* food availability. Given are means±SE and in parentheses the sample sizes (number of clutches, except fledgling production: number of breeding pairs). Significant differences comparing poor to good years within each territory quality class are indicated(df=1 in each case). Results of the ANOVAs are indicated in the lowest rows by the *F*- and *P*-values (*terr* territory quality, df=1; *food* food availability, df=1; *inter* interaction, df=1). For clutch size: *first* first clutch, *replacement* first replacement clutch (due to low sample sizes, clutch and brood size for the second and third replacement clutches are not presented)

	Clutch size		Brood size		Number of clutches	Hatching asynchrony all clutches (days)	Annual fledgling production	
	First	Replacement	First	Replacement			All pairs[a]	≥One hatchling[b]
Residents								
Poor	2.93±0.08 (92)	2.42±0.19 (19)	1.53±0.15 (92)	1.20±0.28 (20)	1.16±0.05 (96)	0.42±0.07 (65)	0.18±0.04 (96)***	0.26±0.05 (65)***
Good	2.91±0.05 (294)	2.47±0.11 (59)	1.53±0.08 (294)	0.86±0.15 (58)	1.17±0.03 (309)	0.34±0.04 (223)	0.45±0.04 (309)	0.64±0.05 (225)
Leapfrogs								
Poor	2.46±0.05*** (354)	2.28±0.10 (72)	1.01±0.07*** (354)	0.59±0.12* (73)	1.04±0.03 (414)	0.38±0.03** (256)	0.10±0.02 (414)*	0.23±0.03 (258)*
Good	2.76±0.06 (201)	2.57±0.15 (30)	1.41±0.09 (202)	1.10±0.24 (30)	1.06±0.03 (220)	0.11±0.03 (141)	0.23±0.03 (220)	0.35±0.05 (142)
F, P_{terr}	18.0****	0.004, 0.94	7.7**	0.5, 0.47	8.3**	ns[c]	14.6[a], ****	14.6[b], ***
F, P_{food}	7.9**	1.9, 0.17	7.2**	0.7, 0.39	0.3, 0.59	ns[c]	16.5[a], ****	16.5[b], ***
F, P_{inter}	5.7*	0.7, 0.41	4.1*	4.9*	0.008, 0.93	29.3[c], ***	6.4[a], 0.055	6.4[b], *

* P<0.05; ** P<0.01; *** P<0.001; **** P<0.0001; *ns* not significant
[a] Including breeders with no nest found or no eggs hatched
[b] Excluding breeders with no nest found or no eggs hatched
[c] All clutches lumped. Poisson regression, total deviance χ^2=566.9, df=684. Full-model deviance χ^2=537.7, df=681; interaction deviance χ^2=29.3, df=3

Table 2 Percentage of abandoned pipped eggs within the clutches of residents and leapfrogs in years with poor and good food availability. Given are means±SE with the sample size (number of clutches) in parentheses. Logistic regression indicated a significant interaction of all three main effects (territory quality×food availability×clutch size), deviance=9.4, df=3, P=0.02, n=699 (all main effects and other interactions were not significant)

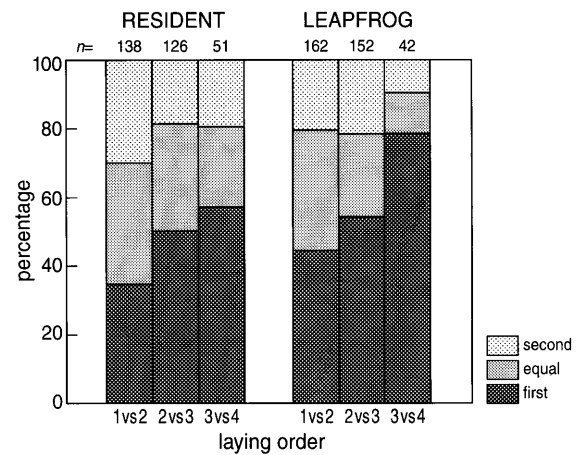|	Clutch size		
	2	3	4
Residents			
Poor years	0.0±0.0 (11)	0.0±0.0 (37)	6.3±0.1 (16)
Good years	8.1±6.0 (37)	9.9±3.6 (121)	4.5±2.5 (67)
Leapfrogs			
Poor years	2.0±2.0 (49)	10.2±3.1 (156)	0.0±0.0 (52)
Good years	0.0±0.0 (27)	3.6±2.0 (83)	16.7±11.6 (36)

Fig. 2 Hatching order in relation to egg-laying order (*1* first egg, *2* second egg, *3* third egg, *4* fourth egg) for residents and leapfrogs. *First* first-laid egg hatched first, *equal* both eggs hatched at the same time, *second* last-laid egg hatched first. Statistics: earlier laid eggs hatched first (residents and leapfrogs combined) – binomial tests (ignoring synchronous hatching), 1 vs 2 P=0.003 (n=204), 2 vs 3 P<0.00001 (n=215), 3 vs 4 P<0.00001 (n=77)

expected, leapfrogs hatched their broods more synchronously in good years than in poor years (Table 1). Asynchronous hatching should result in the first-laid eggs hatching first and this is what we observed: laying order correlated with hatching order (Fig. 2). A hierarchical loglinear analysis (n=671),with backward elimination of the terms territory quality (resident or leapfrog; df=1), laying order (1 vs 2, 2 vs 3 or 3 vs 4; df=2), result (first, equal or second; df=2) and their interactions produced a significant interaction between order×territory quality (G=75.4, df=2, P<0.0001; due to differences in sample sizes) and order×result (G=11.5, df=4, P =0.02; the outcome depended on order; model G=6.9, df=6, P=0.33). Since there were no significant differences between residents and leapfrogs, the data were lumped in the statistical analyses accompanying Fig. 2. In many cases, the first- and the second-laid eggs hatched almost simulta-

Fig. 3 Egg mass and hatchling mass of residents and leapfrogs in relation to clutch size and laying order. Hatchling mass correlated with egg mass (R^2=0.71, P<0.00001, n=574). For statistics see Table 2. Reduction in egg size from penultimate egg to last egg, clutch size 2: residents –2%, leapfrogs –2.2%; clutch size 3: residents –3%, leapfrogs –4.5%; clutch size 4: residents –3.4%, leapfrogs –3.7%. In clutch size 4, the size was also reduced from egg 2 to 3: residents –1.1%, leapfrogs –3.9%
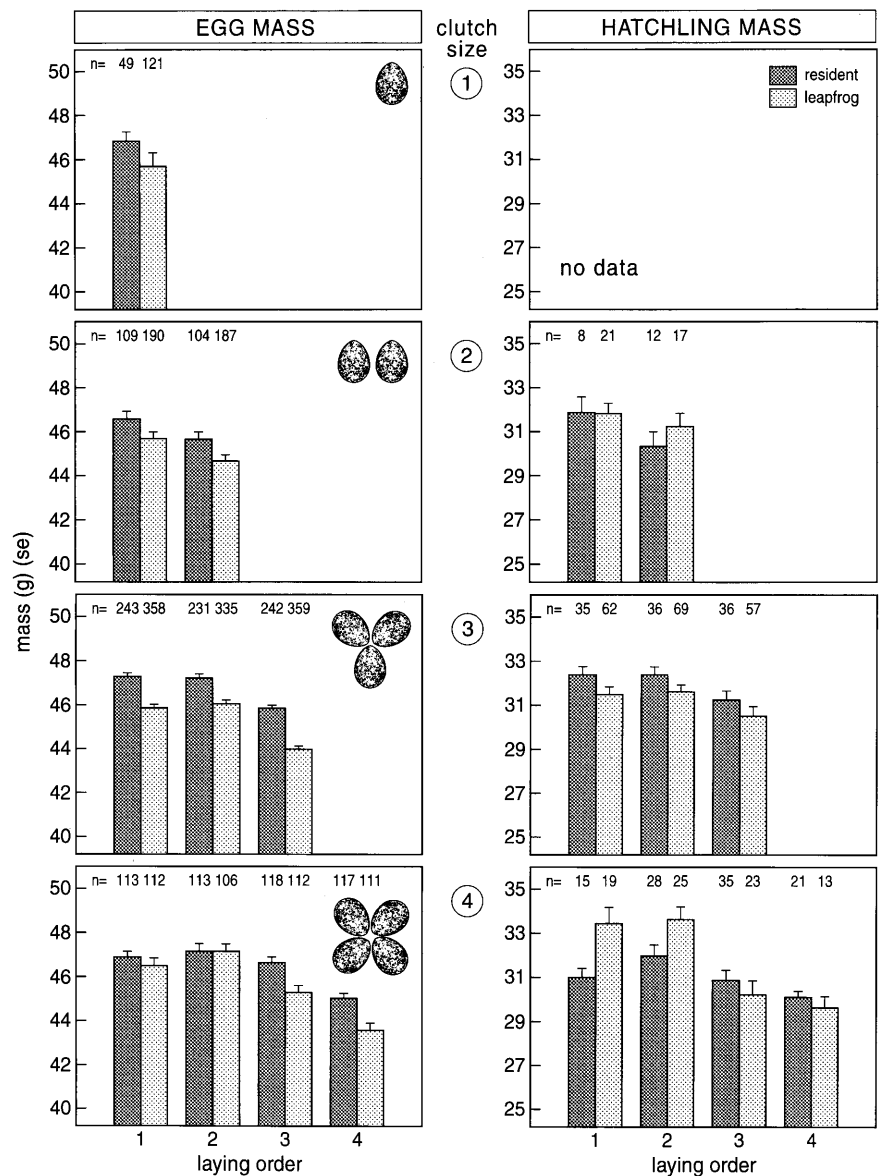
neously, suggesting that most parents started incubation after the second egg had been laid.

The third method to vary the degree of sibling competition at hatching is to adjust hatchling mass. Hatchling mass was strongly dependent on the mass of the egg, which was strongly dependent on the laying order (Fig. 3, Table 3). Moreover, the difference in mass between the first and the latest egg was larger in poor years, particularly in leapfrogs (Table 4). Hence, chicks from first-laid eggs might have a twofold benefit: (1) they hatched first and (2) they were heavier at hatching compared to their sibs. The masses of both resident and leapfrog hatchlings, and thus the intraclutch differences in hatchling mass, were almost entirely explained by the differences in egg masses (Fig. 3). On top of that, leapfrogs chicks from the first two eggs in the largest clutch size (four) tended to hatch relatively heavy (Fig. 3, Table 4), contributing to the intraclutch differences in hatchling mass in the largest broods.

In summary, we conclude that leapfrogs produced smaller broods with larger intraclutch variations in hatchling mass compared to residents, particularly in poor years. HA occurs in both leapfrog and resident broods. The first-laid eggs produced the first and hatched the heaviest hatchlings. Hence, we expected stronger effects of hatching order on sibling competition and fledging success in leapfrogs compared to residents. However, we first analysed the effects of these differences in hatching order and mass on the subsequent within-family dominance.

Dominance of hatchlings and hatching order

To establish whether early hatchlings were dominant over later hatchlings, all within-brood aggressive interactions over food between chicks were analysed. Comparing winners to the closest loser sibling (sometimes more than

Table 3 Egg mass and hatchling mass in relationship to territory quality (resident or leapfrog), clutch size (*2–4*) and laying order (*1–4*). Results of ANOVAs are given for each clutch size separately, with egg mass as a covariate for hatchling mass. Two-way interactions were all non-significant, except for egg mass in clutch size 4 where the interaction was almost significant (territory quality×laying order, $F_{3,894}=2.54$, $P=0.055$). $df=1$ for all variables, except laying order, where $df=$(clutch size–1)

Clutch size	n	Territory quality		Laying order		Egg mass	
		F	P	F	P	F	P
Egg mass							
2	590	10.5	0.001	11.7	0.001		
3	1,768	86.8	<0.0001	56.6	<0.0001		
4	902	13.8	<0.0001	33.2	<0.0001		
Hatchling mass							
2	64	0.47	0.63	0.03	0.88	60.02	<0.0001
3	295	3.76	0.053	1.26	0.29	855.3	<0.0001
4	179	15.7	<0.0001	1.08	0.36	537.2	<0.0001

Table 4 Mass difference (g) between largest and smallest egg within the clutches of residents and leapfrogs in years with poor and good food availability. Given are means±SE and sample sizes (number of clutches) in parentheses. Three-way ANOVA ($n=2,539$): territory quality, $df=1$, $F=14.4$, $P<0.0001$; food availability, $df=1$, $F=60.0$, $P<0.0001$; clutch size, $df=2$, $F=78.2$, $P<0.0001$; interactions: territory quality×food, $df=1$, $F=24.2$, $P<0.0001$; territory quality×clutch size, $df=2$, $F=3.2$, $P=0.04$; food×clutch size, $df=2$, $F=5.8$, $P=0.003$; territory quality×food×clutch size, $df=2$, $F=2.9$, $P=0.06$)

	Clutch size		
	2	3	4
Residents			
Poor years	1.84±0.24 (45)	2.91±0.20 (109)	3.65±0.29 (48)
Good years	1.82±0.14 (164)	2.86±0.12 (356)	3.66±0.20 (185)
Leapfrogs			
Poor years	2.09±0.11 (340)	3.20±0.08 (591)	4.12±0.14 (173)
Good years	1.93±0.24 (93)	1.97±0.17 (310)	2.48±0.20 (125)

Table 5 Characteristics (mean±SE) of sibs winning or losing a physical fight for food ($n=41$ interactions). Also given are the mean±SE differences between the two values (winner value minus loser value), its significance and the two-tailed a posteriori power of the tests, given the observed outcome

Sib	Laying order	Hatching order	Hatchling mass (g)
Winner	1.6±0.1	1.2±0.1	31.1±0.3
Looser	2.2±0.1	2.0±0.1	30.6±0.3
Difference	–0.6±0.2	–0.8±0.2	0.5±0.3
Statistic	Binomial test[a]	Binomial test[b]	Paired t-test $t=1.7$
P	0.12	0.001	0.10
Power	0.40	0.99	0.61

[a] In 26 cases, the chick hatched from an earlier-laid egg won the interaction, in 15 cases the chick hatched from a later laid egg won
[b] $n=28$, excluding sibs with the same hatching order (hatched at approximately the same moment). In 23 cases, the earlier-hatched chick was dominant, in 5 cases, the later-hatched chick won the interaction

two sibs were involved in the fight), winners had hatched earlier (Table 5). In addition, laying order and hatchling mass tended to correlate with winning in the predicted direction, although not significantly (Table 5). Thus parents might influence sibling competition by hatching the broods asynchronously, so that some sibs hatch earlier than others. This might in turn affect the fledging probability of individual chicks, which is analysed below.

Hatching order and fledging probability

Hatching order had strong effects on the chicks' prospects to survive until fledging. For both residents and leapfrogs, both in years with low and high food availability, chicks hatching first survived better (Fig. 4). Contrary to our expectation, this effect was most pronounced in good years. Nevertheless, in good years most chicks from most brood sizes and hatching orders survived better than in poor years. In good years, chicks from large broods survived better than chicks from small broods, and the difference in fledging probability between early and late hatchlings increased. In contrast, in poor years, chicks from small broods survived better. In the situation where we expected the severest sibling competition (large leapfrog broods in poor years), the later hatchlings survived less well. However, resident pairs with large broods in poor years also had difficulties raising young, but with no indication of survival probability depending on hatching order (Fig. 4). Thus hatching order had effects on relative fledging probability, its absolute value depending on brood size, territory quality and food availability as well.

Fledging mass

As expected, both territory quality and food availability affected the fledging mass of the chicks. Residents produced heavier fledglings than leapfrogs, particularly in years with high food availability (Fig. 5). Hatching order correlated only marginally with fledgling mass. This was because parents raising many chicks also produced
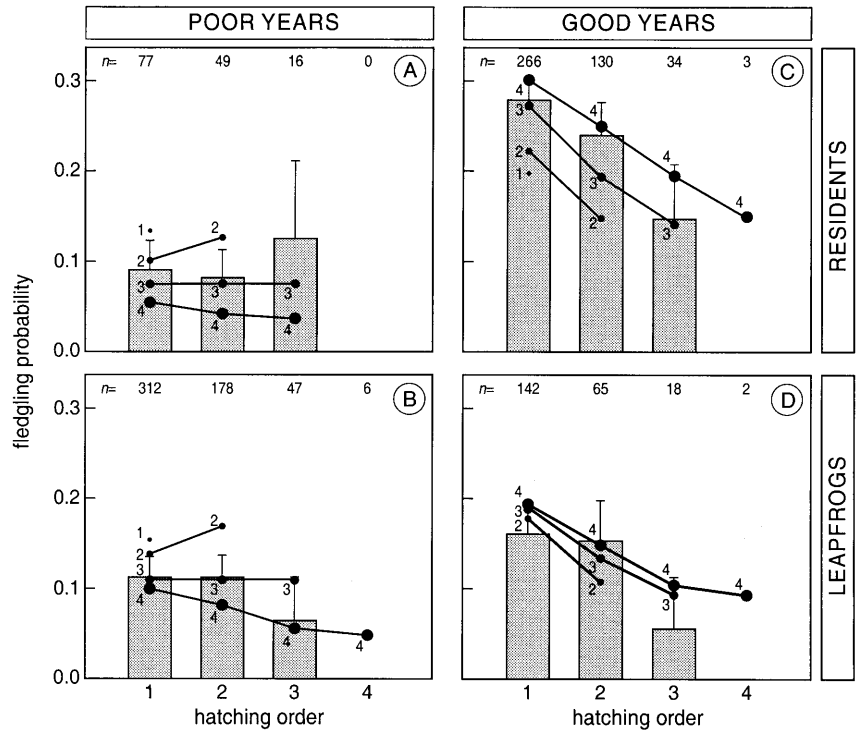
164

Fig. 4 Fledging probability
(±SE) in relation to territory
quality (residents **A,C**, leap-
frogs **B,D**), food availability
(poor **A,B**, good **C,D**), hatch-
ing order (*1–4*) and clutch size
(*1–4*). Logistic regression
showed significant effects of
several of these factors and
their interactions on the fledging
probability (χ^2-statistic,
P-value): food availability
(12.6, <0.001), interactions
clutch size×hatching order (4.6,
0.03), food availability×hatch-
ing order (5.7, 0.02), food
availability×clutch size×hatch-
ing order (5.0, 0.03) and terri-
tory quality×food availabili-
ty×clutch size (9.1, 0.003); full
model χ^2=1,182, *df*=14; final
model χ^2=1,130.2, *df*=5,
P<0.0001. The calculated
model values for the different
clutch sizes (1, 2, 3 and 4) are
indicated with the *filled circles*
and are connected by *lines*

Fig. 5 Fledging mass (±SE) in
relation to territory quality
(residents **A,C**, leapfrogs **B,D**),
food availability (poor **A,B**,
good **C,D**) and hatching order
(*1–3*). ANOVA (*n*=191): terri-
tory quality *F*=6.7, *df*=1,
P=0.011; food *F*=4.4, *df*=1,
P=0.04; hatching order *F*=2.8,
df=2, *P*=0.06; interactions terri-
tory quality×food *F*=7.8, *df*=1,
P=0.006; territory quality×
hatching order *F*=0.44, *df*=2,
P>0.1; food×hatching order
F=1.5, *df*=2, *P*>0.1; territory
quality and food and hatching
order *F*=0.02, *df*=1, *P*>0.1
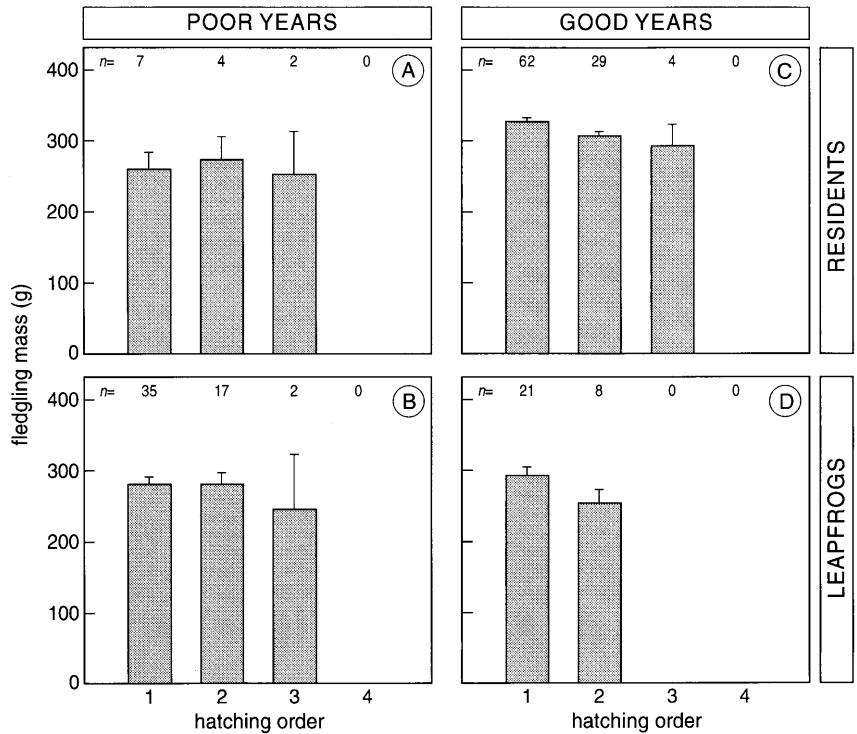
heavy chicks thus counteracting the potential effect of hatching order. We analysed this effect by lumping parents fledging two or three chicks, and we obtained the following four-way ANOVA of fledging mass (*n*=191): territory quality *F*=6.1, *df*=1, *P*<0.0001; food *F*=7.4, *df*=1, *P*=0.007; hatching order *F*=3.7, *df*=2, *P*=0.03; brood size at fledging *F*=3.2, *df*=2, *P*=0.04 (interactions were suppressed due to the small sample size).

Reproduction and sibling competition

Fledgling production of the breeders was not related to the level of HA, but was related to territory quality, food availability (Fig. 6) and brood size (Fig. 4). As expected, the brood size effect on the production was most pronounced in good years (values derived from the logistic regression): in residents the production increased from
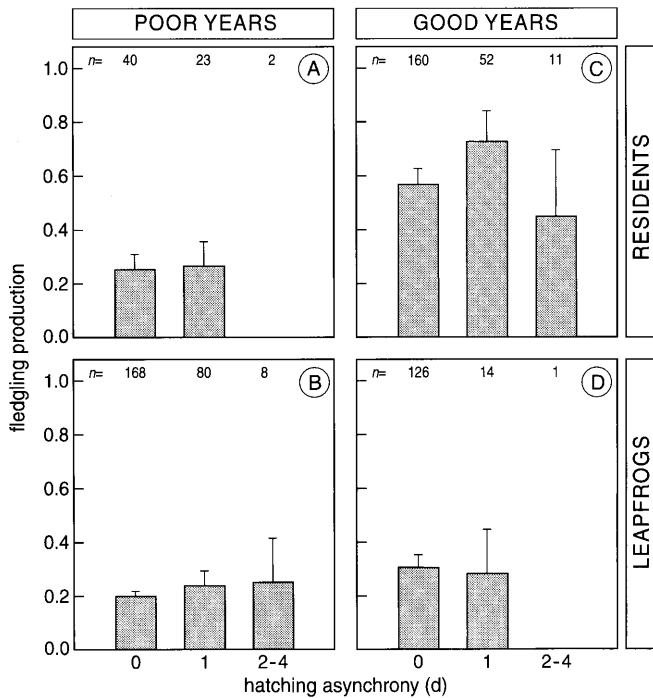
Fig. 6 Fledgling production (±SE) of a breeding pair in relation to territory quality (residents **A,C**, leapfrogs **B,D**), food availability (poor **A,B**, good **C,D**) and hatching asynchrony (*1–4* days). Poisson regression including these factors and brood size at hatching on fledgling production showed significant effects of brood size and the interaction territory quality×food availability only: full model deviance χ^2=544.1, *df*=669; final model deviance χ^2=548.9, *df*=680 (coefficient±SE, *df*, *P*-value): brood size deviance χ^2=19.4 (0.31±0.07, 1, <0.0001), interactions territory quality×food availability deviance χ^2=50.0 (high-poor –2.24±0.32, high-good 0.93± 0.26, low-poor –0.07±0.28, low-good 0.26±0.29, 3, <0.0001)

0.37 (brood size 1) to 0.94 chicks (brood size 4) and in leapfrogs from 0.19 to 0.49 chicks, compared to poor years from 0.15 to 0.37 chicks and from 0.13 to 0.34 chicks, respectively. Hence, although both residents and leapfrogs lost relatively more hatchlings in large broods in good years, the net effect of brood size still remained positive in all combinations of territory quality and food availability. Residents and leapfrogs did not differ much in fledgling production in poor years.

We were interested to see whether parents, particularly leapfrogs, in poor years lost doomed chicks more quickly (either due to starvation or predation) than parents in better circumstances. By feeding or protecting some chicks less, they might reduce the brood size to a chick number that they are able to feed to fledging, given the low food availability. Most chicks were lost early in life, both by residents and leapfrogs (Fig. 7A). The chicks of interest, however, are those which did not survive. As expected, these chicks were lost more quickly in poor years than in good years, both in residents and leapfrogs (Fig. 7B). However, leapfrogs cared for non-surviving chicks longer than did residents, in both poor and good years (Fig. 7B).

Discussion

Hatching order and sibling competition

We found a correlation between egg mass and laying order, which is typical for many bird species (e.g. Parsons 1972; Nisbet 1978; Nol et al. 1984; Slagsvold et al. 1984). Egg mass decreased with laying order, and as ex-
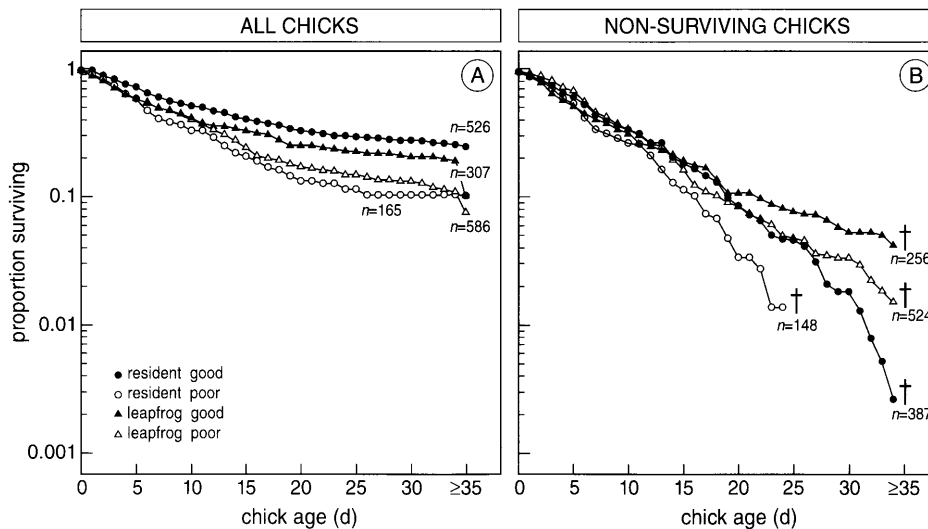

Fig. 7 Cumulative survival of all chicks (**A**) and non-surviving chicks only (**B**, excluding fledged chicks) for leapfrogs (*triangles*) and residents (*circles*) in good (*filled symbols*) and poor (*open symbols*) years. **A** The survival curves were significantly different (Lee-Desu procedure: Wilcoxon's Z=27.6, *df*=3, *P*<0.0001); median survival time in days: leapfrogs poor years 8.77, *n*=586, leapfrogs good years 8.25, *n*=307 (Z=0.7, *df*=1, *P*=0.40), residents poor years 6.75, *n*=165, residents good years 11.78 *n*=526 (Z=21.0, *df*=1, *P* <0.0001); all other pairwise comparisons were significant (*df*=1, *P*<0.002), except residents poor years vs leapfrogs good years (Z=1.9, *df*=1, *P*=0.16). **B** The survival curves were significantly different (Lee-Desu procedure: Wilcoxon's Z=14.9, *df*=3, *P*=0.002); median survival time in days: leapfrogs poor years 7.85, *n*=524, leapfrogs good years 6.29, *n*=256 (Z=8.5, *df*=1, *P*=0.004); residents poor years 6.28 *n*=148, residents good years 7.36 *n*=387 (Z=3.9, *df*=1, *P*=0.047); all pairwise comparisons were non-significant (*df*=1), except residents poor years vs leapfrogs poor years (Z=11.1, *df*=1, *P*=0.001)

pected, decreased more strongly in low-quality territories and in large clutches. Smaller eggs usually take less time to hatch (Landauer 1967; Parsons 1972; Drent 1975; Bollinger 1994), but despite this mass difference, the first-laid eggs still hatched earlier than later-laid eggs. We found a significant effect of hatching order on within-family dominance: early hatched chicks won competition over food items from later-hatched chicks, similar to Safriel's (1981) and Groves' (1984) findings in earlier studies on European and American oyster-catchers. Older hatchlings probably have the first experience with accepting and handling food and thus gain dominance over younger hatchlings. Hatching order translating into dominance hierarchies and differential feeding of chicks has been demonstrated in numerous studies (see Mock and Parker 1997). Moreover, in poor years, leapfrogs produced eggs with larger within-clutch mass differences and hatched their brood more asynchronously than residents and leapfrogs in good years. This might help to establish a dominance hierarchy and lead to rapid brood reduction in those years (e.g. Magrath 1989; Slagsvold et al. 1995). In poor years, hatchling mass differences in leapfrogs were even more pronounced than the egg mass differences. This might indicate that the first hatchlings of leapfrogs in poor years (1) accepted food from their parents immediately after hatching, while later hatchlings and all hatchlings in good years took more time before they accepted food, or (2) the resources in early laid eggs in poor years are somehow more efficiently converted into the growth of the embryos compared to both later-laid eggs in poor years and all eggs in good years.

Our results indicate that the advantage of hatching first is much more important than the advantage of hatching with a large body mass. These results agree well with results from experiments designed to test egg mass effects on fledging success independent of other variables. The experiments indicate that natural variation in egg mass plays a minor role in explaining the variation in fledging success, since the variation in chick growth rate supercedes any mass difference at hatching (Nisbet 1978; Reid and Boersma 1990; Salzer and Larkin 1990; Simmons 1994; but see Bollinger 1994).

Hatching asynchrony hypotheses

Because first hatchlings were dominant over later hatchlings, we expected these differences to translate in the fledging probability and the fledging mass of the chicks. Indeed, later hatchlings had poorer survival and lower fledging masses than early hatchlings, particularly in leapfrog territories in poor years. Moreover, leapfrogs reduced their clutch and brood size in poor years compared to leapfrogs in good years and residents in all years. Finally, non-surviving chicks were lost more quickly in years with poor compared to years with good food availability, both in leapfrogs and residents. Similar results have been obtained in other bird species (e.g. Boland

Table 6 Principal findings of this study and their agreement with the major hypotheses adressing the occurrence of hatching asynchrony and its effects: + supports the hypothesis, – disproves the hypothesis, *blank* neither supports nor disproves the hypothesis (hypotheses: *BR* brood reduction, *NF* nest failure, *PL* peak load reduction, *SR* sibling rivalry reduction, *PP* predation on parent, *HU* hurry up, *EV* egg viability)

	BR	NF	PL	SR	PP[a]	HU	EV
Hatching asynchrony[b]	+	−	+	+	+		+
Dominance hierarchy	+			+			
Survival depends on hatching order[b]	+/−						
Clutch size[b]	+	+	+	+			
Rate of chick loss[b]	−	+	−	−			
Rate of brood reduction[b]	−	+	−	−			

[a] This hypothesis is unlikely due to the low parental predation rate
[b] Whether this factor varied with territory quality and food availability in the predicted direction according to the specific hypothesis

et al. 1997; Wiehn et al. 2000). These facts all fit the 'brood reduction' hypothesis, and this hypothesis is supported by many of our findings (Table 6). An alternative explanation is that the leapfrogs produced fewer and smaller eggs in poor years compared to the residents because they had difficulties finding food in poor years. Residents might be less affected by these poor feeding conditions. However, this explanation seems unlikely, since leapfrogs actually have higher intake rates than residents in all years, because they have better feeding territories than the residents (Ens et al. 1992). It is the high food transport costs from these feeding territories to their nesting territories which make leapfrog nesting territories less profitable for raising chicks (Ens et al. 1992).

The 'brood reduction' hypothesis assumes that the critical resource(s) during chick rearing are unpredictable, and most authours do not validate or critically discuss this assumption. In oystercatchers, this unpredictability might reside in the number of rainy days, sea water temperature and amount of sunshine during chick feeding, since the burying depth and activity of worms is related to these environmental characteristics (Evans 1987; Pienkowski 1983; Zwarts and Wanink 1993). However, how this short-term unpredictability might affect the foraging opportunities for oystercatchers on the long run, e.g. over a whole chick rearing period of circa 30 days, and thus influence fledging success, is not yet established. Particularly prolonged rain and chilling seems to affect chick survival (D. Heg, unpublished data); this effect is probably exacerbated by the fact that during rain, parents stop feeding altogether. Many of these findings can be explained by the other hypotheses as well. For example, the rapid elimination of the majority of chicks, particularly in years with poor food availability, agrees well with both the 'brood reduction' and the 'nest failure' hypotheses. Hence, we have to turn to negative evidence for each of the hypotheses.

We found only limited evidence for or against the 'predation on parent', 'hurry up' or 'egg viability' hy-

potheses (Table 6). Nevertheless, the 'predation on parent' hypothesis seems unlikely, since breeding oyster-catchers have a very low breeding season mortality (April–September). The principal predator, the peregrine (*Falco peregrinus*), is absent during this season, and other carnivores are absent from the island year round. From the colour-banded males and females, residents plus leapfrogs, exposed to summer predators (*n*=4,826 bird years, 1984–1997) only one male and one female from a leapfrog pair were depredated during incubation on the nest by a feral cat (0.04%, or about 4% of the total summer mortality). These three hypotheses will not be discussed any further.

For the other four hypotheses, two facts about chick elimination favour the 'nest failure' hypothesis and speak against the other three hypotheses, including the 'brood reduction' hypothesis. First, most chicks disappear when very young, when predation is the most likely cause of their disappearance, since the food demands of these chicks are very low. Predation rate is probably variable, due to differences in activity and prey choice of the chick's principal predators, the herring gull *Larus argentatus* and mew gull *L. canus*, depending on the fluctuations in alternative prey available to these gulls (e.g. fish stocks). Oystercatchers are not able to deter predators completely from eating their chicks, although they make detection of their chicks more difficult by attacking the gulls and warning the young vocally (the chicks conceal themselves at alarm calls; from ca 14 days of age they are usually not predated, particularly because they can run fast). These arguments fit the 'nest failure' hypothesis. Second, breeders in low-quality territories (leapfrogs) cared longer for non-surviving chicks than breeders in high-quality territories (residents), even though leapfrogs must gain most from quickly reducing their brood size from hatching onwards. Many of the leapfrog chicks eventually died at a relatively old age due to starvation (see also Ens et al. 1992). Only in leapfrogs have we observed whole broods dying of starvation at an old age, instead of parents fledging one chick and eliminating the rest. This result shows that the parents which have to work the hardest (leapfrogs) wasted their care in non-surviving chicks the longest. This fact can only be accounted for by the 'nest failure' hypothesis: leapfrogs raise 'marginal offspring' in case 'core offspring' are predated (see Mock and Forbes 1995; Forbes et al. 1997).

Additional negative evidence was found for the 'brood reduction' hypothesis. First, although fledgling survival, as expected, was related to hatching order in *poor* years, this pattern was even more pronounced in *good* years, contrary to expectation (hence the +/– sign in Table 6). This is a surprising finding, in particular because in good years, late-hatched chicks in large broods nevertheless survived better than late-hatched chicks in smaller broods. The most likely explanation is that parents are not in complete control of sibling competition: although they manage to bring more food in good years, nevertheless some of this food is monopolized by the first hatchlings which grow bigger at the expense of the survival prospects of their later-hatched siblings. The data on the within-brood dominance hierarchy support this explanation. An additional finding in agreement with this interpretation is the fact that surviving resident chicks grew bigger in good years, compared to resident chicks in poor years. Second, brood reduction by parents leaving pipped eggs unhatched did not follow the predicted patterns: (1) pipped eggs were not abandoned more frequently in poor than in good years and (2) leapfrog parents did not abandon pipped eggs more often than resident parents did. However, we have difficulties interpreting these two observations. We think it is unwarranted to assume that parents invariably leave pipped eggs with fit chicks. That parents leave unfit chicks might provide an alternative explanation for the variation in the percentage of abandoned pipped eggs described. Many of these chicks were not able to crack the eggshell within 2 days, and parents left these chicks after this period. The percentage of unfit chicks might vary with the circumstances, e.g. food availability and/or territory quality.

If these facts are to agree with the 'nest failure' hypothesis, leapfrogs have to lose more chicks than residents to predators or the predation rate on leapfrog chicks must be more unpredictable than that on resident chicks. We think these arguments apply, because leapfrog chicks seem more restless and less reactive to predator alarm calls by their parents, probably because they are on average more hungry than resident chicks (similarly, we have seen restless resident chicks when they were not fed properly). Likewise, Swennen (1989) has shown experimentally that eider ducklings *Somateria mollissima* in poor body condition reacted slower to their parents' alarm calls and were predated more often than ducklings in good health.

Conclusions

The present results provide support for the 'brood reduction' and the 'nest failure' hypotheses. Support for the 'brood reduction' hypothesis is generated by the effect of hatching order on survival, and the adjustment of clutch size by leapfrogs combined with the quick elimination of chicks in years with poor food availability. However, some facts did not support the brood reduction hypothesis, notably the slower rate of chick loss in leapfrogs compared to residents. We invoke the 'nest failure' hypothesis to explain this fact. These two hypotheses interact: if brood reduction is operating, early hatchlings can grow fast and thereby escape predation. Unpredictability in egg predation might add to the benefits of producing large clutches, even though most parents appear capable of fledging only one chick (sensu the 'nest failure' hypothesis). These ideas await further experimental testing.

From a parental perspective, an increase in brood size reduced the fledging probabilities of late hatchlings and the average fledging probabilities of all hatchlings in

poor years. Nevertheless, total fledgling production from a brood remained positively correlated with brood size in all situations. Furthermore, although parents with larger broods raised more chicks, fledging mass correlated positively with brood size. We do not believe that this effect is explained, or at least entirely explained, by siblings facilitating each other's survival, e.g. in large broods chicks are able to huddle and thereby reduce mortality due to chilling. This effect is more likely due to parental quality, since Heg (1999) has shown that some individual females are able to lay early, produce large broods and fledge many chicks every breeding season. Experimental brood size manipulation in oystercatchers might resolve the issue.

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