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The benefit of large broods in barnacle geese: a study using natural and experimental manipulations

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Summary

1. In precocial birds, where the young feed themselves, the costs and benefits of brood size are still poorly understood. An experimental manipulation of brood size was employed to examine the effects of brood size on both parents and young in a wild population of barnacle geese [*Branta leucopsis* (Bechstein)] during brood-rearing on Svalbard.

2. Social dominance of the family unit, the amount of vigilance behaviour of the parents, the growth of the goslings in the family unit and an index of body condition for female parents during moult were all positively correlated with brood size.

3. When brood size changed as a result of natural events (i.e. predation or adoption) or experimental manipulation, rates of dominance, parental vigilance, gosling growth and female parent condition changed in a similar direction to the observed relation between the variable and brood size in unchanged broods.

4. After fledging, the fast-growing goslings in large broods survived better during autumn migration, while there was no apparent net cost in survival or next-year breeding for the parents.

5. Via a direct effect of brood size on dominance of the family unit, large broods were beneficial for both parent and young in a situation where there was strong intraspecific competition for the available food resources.

6. This study provides a clear demonstration of a causal relationship between brood size and various components of both gosling and adult fitness and is of direct relevance to the phenomenon of adoption and the evolution of brood size in this species.

Key-words: adoption, *Branta leucopsis*, brood size manipulation, fitness, social dominance.

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Introduction

Evolution favours those individuals able to raise the largest number of successfully reproducing offspring. A large brood size seems, at first sight, favourable, but there are usually costs, which increase with brood size, for both young and parents. The young might suffer from competition for food (Lack 1947), while the parents might suffer from costs of parental care,

which reduce their future reproduction (Williams 1966; Charnov & Krebs 1974).

Costs associated with large broods have been well explored in altricial birds where parents feed their young. A larger brood requires more work by the parents, or growth and survival of the offspring will be reduced. For example, de Kogel (1997) studying zebra finches *Taeniopygia guttata* (Vieillot) showed that individuals reared in large broods suffered in terms of reduced body size, condition and survival compared to those reared in smaller broods. In precocial birds, like geese, the young feed themselves, and parental costs are mainly related to antipredator behaviour, intraspecific interactions and leading young to food (Boyd 1953; Black & Owen 1989a,b; Sedinger & Raveling 1990). Several behaviours, which

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can be interpreted as parental investment, show a positive correlation with brood size in geese. A relation between dominance and brood size has been demonstrated in barnacle geese (*Branta leucopsis* Bechstein: Black & Owen 1989a), white-fronted geese (*Anser albifrons* Scopoli: Boyd 1953), Canada geese (*Branta canadensis* L. Hanson 1953; Raveling 1970), bar-headed geese (*Anser indicus* Latham: Lamprecht 1986) and lesser snow geese (*Anser caerulescens caerulescens* L. Gregoire & Ankney 1990; although not confirmed by Mulder, Williams & Cooke 1995). Also a relation between vigilance and brood size has been found in barnacle geese (Forslund 1993), bar-headed geese (Schindler & Lamprecht 1987), Canada geese (Sedinger & Raveling 1990), lesser snow geese (Williams, Loonen & Cooke 1994) and black brant (*Branta bernicla nigricans* L.: Sedinger, Eichholz & Flint 1995a). Dominance and vigilance are potentially costly. Vigilance is negatively correlated with time for feeding (Black & Owen 1989b). Negative relationships with brood size have been reported for body mass and timing of wing moult in female Canada geese (Lessells 1986) and rate of wing moult in female lesser snow geese (Williams *et al.* 1994). Lessells (1986) found no negative effect on growth of Canada goose goslings with increasing brood size, while a positive relationship between brood size and growth of goslings was shown for lesser snow geese (Cooch *et al.* 1991) and greater snow geese (*Anser caerulescens atlanticus* L.: Lepage, Gauthier & Desrochers 1998).

The optimal brood size can vary among individuals because parents differ in abilities and resources (Drent & Daan 1980). Brood size manipulations have been used to study individual optimization. While there is a long list of such experiments in altricial birds (see, e.g. Dijkstra *et al.* 1990; Stearns 1992), only five studies employed brood size manipulations to study the cost of reproduction in precocial birds (Safriel 1975; Rohwer 1985a; Lessells 1986; Arnold 1992; Székely, Karsai & Williams 1994).

Parental quality could potentially affect brood size. Parents which do not guard their offspring are likely to lose young. Positive correlations between dominance and vigilance with brood size would result from this differential mortality. Alternatively brood size could directly affect dominance and vigilance, independent of differences in parental quality. When the brood size at hatch is randomly manipulated, the effect of brood size can be studied irrespective of parental ability. Moreover care should be taken to ensure that the range within which brood sizes are manipulated corresponds to the range actually experienced in the population (Lessells 1993).

In this study we explore the costs and benefits of brood size on three levels: in the natural situation with constant brood sizes; when brood size changes by natural causes; and in a manipulation experiment. We will show that brood size affects dominance in barnacle geese and that both the female parent and

the young benefit from this increase in dominance during brood rearing. When individual goslings were traced to their wintering grounds, survival was positively related to growth rate and not negatively influenced by brood size.

Methods

All data were collected from a population of wild barnacle geese in Ny-Ålesund, Svalbard (78°E55'N, 11°E56'E). This breeding population was established in 1980 and had increased in size to over 200 nesting pairs in 1993. Since 1987, geese were caught and ringed with individually coded plastic leg rings. The data reported in this paper were collected from 1992 and 1993. In these years, 70% of the local population was individually recognizable from afar by coded leg rings and the majority of the breeding pairs had at least one ringed parent.

We consider the effect of brood size on agonistic and vigilance behaviour of adults, gosling growth, adult body mass and adult moult. Initially, we examined the relationship of each factor with brood size in unmanipulated families. We also examined the effects of changes in brood size in two ways. First, the effect of natural changes as a result of predation or adoption in brood size was evaluated using unmanipulated families. Secondly, brood size at hatch was manipulated to study the effect of brood size experimentally.

BROOD SIZE MANIPULATION EXPERIMENT

In the hatching period, nests were checked on a daily basis for hatching eggs or goslings. All hatching eggs and goslings were marked using web tags (Alliston 1975). If two nests in the same hatching stage (pipped eggs, wet or dry goslings) were found, two goslings from one nest were moved to the other nest creating a reduced and an enlarged family. Almost all of these families were recognizable because the parents had individually coded rings. Families without marked parents during the nesting phase were identified via the rings of their web-tagged goslings; both parents and young were ringed individually during a catch in the moulting period.

AGONISTIC INTERACTIONS

Each day at various times throughout the 24-h daylight period, we tried to locate all goose flocks close to the village. The geese were observed with telescopes from tents and houses to minimize disturbance. Whenever an interaction was observed between two families, the ring codes and number of goslings of both the aggressor and the opponent, and the final result of the interaction, were recorded. Interactions were classified according to whether the focal family won or lost the fight or whether there was a draw. Sometimes a contest between two families involved a series of interactions

before the final result was clear. Therefore only the final interaction between two individually marked families on a given day was used in the analysis. In the analysis of natural trends, all sampled interactions were used except those involving manipulated families. Per family, a 'win score' was calculated as the number of fights won divided by the total number of interactions in which at least one family member was involved. This 'win score' was calculated over all the interactions of a family, together with the average brood size in these interactions. We have used only 'win scores' of families based on at least five interactions, except for the comparison between 'win score' before and after predation, because otherwise sample size would become too low.

PARENTAL VIGILANCE

Systematic behavioural observations of time devoted by parents to scanning the environment were made of paired adults with at least one colour-ringed adult. The total time head up of one of the parents during a period of 1 minute was recorded. Only observation periods without preening or sleeping were used. Where possible, this was carried out for five subsequent minutes and the average percentage of time vigilant per individual per day was used in the analysis. These values were arcsine transformed and analysed using hierarchical linear modelling (see Appendix).

GOSLING GROWTH

Hatch dates of families with at least one ringed parent could be established during daily nest checks or by 'backdating' using the estimate of gosling age at first sighting, based on plumage and body proportions derived by Larsson & Forslund (1991). Hatch dates determined using the back-dating method were calibrated with sightings of marked families of which hatching was observed during the daily nest checks. The back-dating method proved to be reliable to within ± 2 days. Many goslings, including all goslings from experimentally manipulated families, were marked at hatch with numbered web tags. In the period before fledging, goslings were caught, individually ringed, sexed, measured and weighed. Family relations were established from resightings after ringing. Only data from the first capture of a gosling were used, to exclude artefacts caused by effects of catching on growth. The age of the goslings at the catch ranged from 15 to 44 days and was 35 days on average.

Body mass was measured with an electronic balance (accuracy ± 5 g) at least 2 hours after capture, to ensure that the digestive tract was empty. Body mass was corrected for time in captivity, assuming a linear decrease in body mass because of evaporative water loss. This loss was about 9 g h^{-1} for both goslings and adults as derived from repeated weighing at 3 and

4 hours after the catch of a sample of 61 adults and 29 goslings. Total tarsus length was measured to the nearest 0.1 mm with dial callipers as the distance between the extreme bending points when the foot was bent at the intertarsal joint and the 'ankle' (Dzubin & Cooch 1992). Mid-wing was measured to the nearest 1 mm on the outside of the natural-folded wing, from the elbow joint to the outside bend of the carpal joint with a plastic ruler. Head length was measured to the nearest 0.1 mm as the longest distance from the back of the head to the distal tip of the bill using dial callipers (Dzubin & Cooch 1992). A principal component analysis (PCA) was used to combine body mass, total tarsus, mid-wing and head length to obtain one single derived variable for gosling size, the first principal component (PC1). This variable explained 91.3% of the variation in the original data and indicates overall size. Gosling mass was included in the PC1 because it is unlikely that mass of goslings at age of capture contained nutrient reserves (Sedinger, Flint & Lindberg 1995b).

Gosling size (PC1) was analysed using hierarchical linear modelling (Bryk & Raudenbush 1992) with the computer program ML3 (Prosser, Rasbash & Goldstein 1991). This method allows analyses of variances and covariances, while taking into account the nested relationship of several goslings belonging to the same family and controls simultaneously for multiple independent variables (see Appendix). For each model, a growth curve was fitted with age and age² as possible independent variables. Year and sex were entered as factors and hatch date as a covariate. The effect of brood size was analysed using the number of goslings in the family at the time of the catch. In an alternative model, two variables described brood size: the number of goslings at hatch and the number of goslings that disappeared in the time interval between hatching and catching. The number of goslings at hatch, at the catch and the hatch date were transformed to deviations from the average values for that year. All interactions between the independent variables were also tested and only variables which contributed significantly to the model were retained. The parameter estimates are given as the estimate \pm standard error and significance is based on a two-tailed *t*-test.

ADULT BODY CONDITION

Adult geese were caught during wing moult. In this period body masses of breeding birds are at a constant level for about 4 weeks (Owen & Ogilvie 1979). Only measurements of the first catch were used when the same bird was caught more than once during the flightless period. Body mass, total tarsus, mid-wing and head length were measured for adults in a similar way as for the goslings. In addition to these measures, three other size measurements were taken using dial callipers to the nearest 0.1 mm. Mid-toe was measured

as the distance from the base of the nail to the outside of the bent 'ankle'. Bill length and bill height were both measured from the bottom of the V-point on the upper mandible, where the integument meets the horny portion of the mandible (Dzubin & Cooch 1992). Bill length was the distance from this point to the tip of the bill, while bill height was the distance perpendicular to the long axis of the bill. Body mass was corrected for structural size using a PCA of six measurements (total tarsus, midtoe, mid-wing, head length, culmen and bill height). The residuals from the regression line of body mass on the first principal axis (PC1) were used as an estimate for body condition. Data were pooled over 1992 and 1993 and males and females were analysed separately.

ADULT MOULT

Moult stage was recorded as the length of the ninth primary (second outermost primary) as measured from the insertion of the remige calamus at the skin surface to the distal end of the feather with a thin, flexible ruler placed between the 9th and 10th primaries (Dzubin & Cooch 1992). Only adults that successfully hatched goslings and of which the hatch date was known either by direct observation or by back-dating were included in the analysis.

SURVIVAL TO THE WINTERING GROUNDS

In autumn and winter, the Svalbard barnacle geese concentrate at the nature reserve Caerlaverock in Scotland on the Solway Firth, where rings are read regularly. The average number of sightings per individual on the wintering grounds was 8.7. If a ringed goose was seen more than once at Caerlaverock or in the subsequent summer in Ny-Ålesund, it was regarded as a survivor. Single observations were discarded as possible misreadings. When adult geese were accompanied by goslings, the brood size was noted.

For a direct comparison of survival between the experimental categories, we made trios of enlarged, control and reduced broods, which differed by not more than two goslings in brood size before manipulation and 2 days in date of hatching, in order to ensure a control group similar to the experimental groups at the beginning of the experiment. There were 16 trios which were recognizable by at least one ringed parent. In these 48 families, survival of the goslings, based on changes in brood size, and the survival of the ringed parents, based on resightings, were compared from hatching (after manipulation) to the wintering grounds.

For all goslings, which were ringed and measured, with known hatch date, and which survived at least until 10 August, the survival during autumn migration was tested as a function of brood size, hatch date, experimental manipulation, year and gosling size. To minimize the effect of predation before fledging,

10 August was chosen as a date close to fledging when most goslings were resighted. We assume that all goslings seen on that date survived until the start of autumn migration (late September). Brood size at hatch before manipulation, after manipulation and on 10 August were tested. As a measure of gosling size independent of age we used a residual on the growth curve of gosling size (PC1, calculated as under gosling growth) against age. This growth curve was calculated using hierarchical linear models with age, age² and sex as explanatory variables (see Appendix and Table 2).

NEXT-YEAR BREEDING PERFORMANCE OF MANIPULATED PARENTS

In the year following the manipulation, the date of arrival to the breeding ground, the clutch size and the laying date of parent geese were monitored. Only pairs for which all these data were available have been used in the analysis.

Results

PREDATION IN RELATION TO BROOD SIZE MANIPULATION

As a result of experimental manipulation, a total of 40 broods in 1992, and six broods in 1993 changed in brood size. Consequently, 131 web-tagged goslings were part of an enlarged family and 41 goslings belonged to reduced families. Almost the same distribution was found in catches in Ny-Ålesund later in the season: 32 web-tagged goslings from enlarged families and 11 goslings from reduced families were caught in this period ($\chi^2_1 = 0.02$, $P = 0.888$). This implies that there was no significant difference in survival between the two categories, although most families decreased in size as a result of predation by glaucous gulls (*Larus hyperboreus* Gunnerus) and arctic fox (*Alopex lagopus* L.). The experimental categories initiated at the nest were still present during moult.

AGONISTIC INTERACTIONS

Unmanipulated families

There was a positive correlation between the 'win score' and the average brood size (Fig. 1). If the number of goslings is the direct cause, there should have been a change in 'win score' after a change in brood size. First, we checked if there was a decreasing trend in 'win score' over the season. When the 'win score' of 29 families with constant brood size was compared in the 2 weeks before and 2 weeks after 21 July, there was no significant difference ($Z = -0.3484$, $P = 0.728$). For all families where a change in brood size was observed, the 'win score' was calculated before and after the change. 'Win score' decreased from 0.58 ± 0.04 (average \pm SE) to 0.32 ± 0.04 with

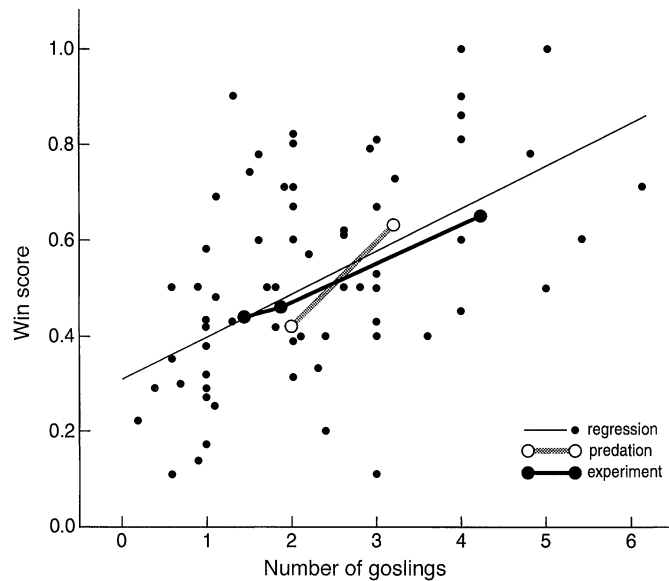


Fig. 1. The proportion of all interactions won ('win score') is positively correlated with brood size. The positive trend for unmanipulated broods is similar to the observed change when individual families lost goslings as a result of natural predation and to the average values for the different experimental categories, in which brood size was manipulated at hatch. The small dots are 'win scores' of individual families based on at least 10 interactions, as function of the average brood size over all interactions in that given year and the regression line is fitted through these points ['win score' = $0.309 + 0.089 \times$ (no. of goslings), $r^2 = 0.25$, $n = 85$, $P < 0.001$]. The 'predation' line represents the decrease in 'win score' when brood size is partially predated, the 'experiment' line represents the average 'win score' for the different experimental categories.

families changing on average from 2.7 ± 0.2 to 1.3 ± 0.2 goslings. This decrease in 'win score' was significant (Wilcoxon matched-pairs signed-rank test: $Z = -3.99$, $n = 64$, $P < 0.001$). This decrease was not merely a change in behaviour following total brood loss. Even after exclusion of families which lost all offspring, 'win score' decreased from 0.63 ± 0.05 to 0.42 ± 0.05 ($Z = -2.87$, $n = 41$, $P = 0.004$). In this sample the number of goslings changed from 3.2 ± 0.2 to 2.0 ± 0.2 (Fig. 1). Brood size was thus a major determinant for the proportion of interactions won by a family.

Manipulated families

The difference between the experimental categories was consistent with results from the observations on the natural broods (Fig. 1). Enlarged broods had a 'win score' of 0.65 ± 0.08 ($n = 9$), reduced broods 0.44 ± 0.10 ($n = 8$) while control broods had a 'win score' of 0.46 ± 0.14 ($n = 85$). These differences were significant using a one-tailed test (Kruskal-Wallis ANOVA: $\chi^2 = 4.65$, $P = 0.049$ one-sided). A multiple comparison indicated a significant difference between the control and the enlarged group and the reduced and enlarged group.

The average number of goslings for all 'win scores' for the experimental categories (reduced, control and enlarged) were 1.44, 1.86 and 4.22, respectively. If we estimate the expected 'win score' for the three experimental categories from the relationship for unmanipulated broods (Fig. 1), the predicted values of 0.43, 0.47 and 0.68 for reduced, control and enlarged

broods, respectively, are almost identical to the observed values (0.44, 0.46 and 0.65, respectively).

PARENTAL VIGILANCE

Unmanipulated families

In 1992, 219 protocols were collected of 53 adults of unmanipulated broods. In unmanipulated broods, parental vigilance decreased with increasing hatch date (estimate \pm SE: -0.020 ± 0.004 , $P < 0.001$). Parental vigilance decreased with a linear (-0.033 ± 0.006 , $P < 0.001$) and a quadratic term (0.00066 ± 0.00014 , $P < 0.001$) of the number of days since hatch, resulting in a rapid decrease in the first 15 days after hatch. There was also a significant difference between the sexes (0.0618 ± 0.0307 , $P = 0.044$), with males typically being more vigilant. There was no interaction between the three variables. The effect of brood size, when added to this model was not significant (0.015 ± 0.011 , $P = 0.171$). If manipulated broods were included, which increased the number of protocols to 403 and the number of adults to 95, vigilance was significant positively correlated to brood size (Table 1).

Forslund (1993) found a correlation between changes in intensity of vigilance and changes in brood size in barnacle geese. When brood size decreased, vigilance also decreased. The decrease was most pronounced for females. We also compared the amount of vigilance of parents before and after predation of goslings. The average amount of vigilance was calculated for each parent before and after predation,

Table 1. A hierarchical linear model of the percentage vigilance of parent geese, which was arcsine transformed before the analysis. The data set included both manipulated and unmanipulated families and consisted of 403 protocols of 95 individuals. For details on hierarchical linear modelling see Appendix

		Estimate	SE	P
<i>Null model</i>				
Fixed	Constant	0.530	0.014	< 0.001
Random	Variance family level τ^2	0.009	0.003	
	Variance individual level σ^2	0.031	0.002	
Deviance		-188.4		
<i>Final model</i>				
Fixed	Constant	0.757	0.064	< 0.001
	Sex (female = 0, male = 1)	0.066	0.022	0.002
	Hatch date (days since 1 July)	-0.012	0.004	0.002
	Days since hatch	-0.026	0.004	< 0.001
	(Days since hatch) ²	0.00054	0.00011	< 0.001
	Goslings leaving nest	0.026	0.007	< 0.001
Random	Variance family level τ^2	0.004	0.002	
	Variance individual level σ^2	0.027	0.002	
Deviance		-264.6		

after correcting for sex, hatch date and days since hatch, using a multiple regression model. There was no significant difference in the amount of vigilance before and after predation (Wilcoxon matched-pairs test: $Z = -1.48$, $n = 29$, $P = 0.139$, average decrease of 1.5 ± 0.12 goslings).

Manipulated families

After correcting for sex, hatch date and days since hatch, the average level of vigilance per individual was calculated. The three experimental groups differed significantly (Fig. 2; Kruskal-Wallis ANOVA, $\chi^2 = 17.10$, $P < 0.001$). Parents with an experimentally reduced brood size were less vigilant than those in the other two categories. There was no significant difference between the control and the enlarged group. The aver-

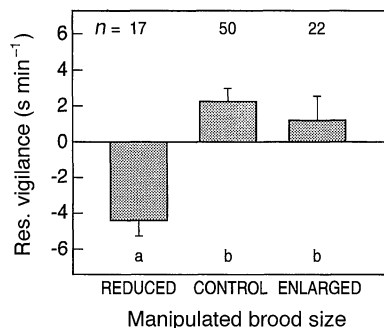


Fig. 2. Mean residual vigilance time for the three manipulation categories. Sample sizes (numbers) and significant differences (different characters) are also shown. Parents of experimentally reduced families are less vigilant compared to parents of experimentally enlarged or control families.

age number of goslings was 1.4, 2.8 and 3.2 for reduced, control and enlarged families, respectively.

GOSLING GROWTH

Unmanipulated families

In 1992 and 1993, a total of 142 goslings from 64 families of known age were caught. Of these 91 goslings belonged to 46 unmanipulated families. There was a significant positive effect of brood size at ringing on body size (PC1) of goslings. Over the range of analysed ages, from 14 to 44 days, the size of all goslings in a family increased by 0.14 ± 0.05 ($P = 0.004$) for each extra gosling in the family at the catch (Table 2). The effect of a natural change in brood size as a result of predation or adoption can be assessed by replacing the number of goslings at the catch in the model by two different but related variables: the number of goslings at hatch and the number of goslings lost since hatch (which has negative values when goslings are adopted). Both variables contributed significantly to variation in body size. When the brood was one gosling larger at hatch, the size of all goslings in the brood increased with 0.16 ± 0.06 units ($P = 0.008$). However, gosling size decreased by almost the same amount when this gosling was subsequently lost (-0.12 ± 0.06 , $P = 0.049$). This supports the hypothesis that growth of a gosling is directly influenced by the actual number of goslings in a family.

Manipulated families

The effect of the experiment was also studied using a hierarchical linear model. The data set included all

Table 2. A hierarchical linear model describing gosling size (PC1) in the data set without any experimentally manipulated families (91 goslings in 46 families). For details on hierarchical linear modelling see Appendix

		Estimate	SE	<i>P</i>
<i>Null model</i>				
Fixed	Constant	-0.09	0.14	0.519
Random	Variance family level τ^2	0.876	0.198	
	Variance individual level σ^2	0.110	0.023	
Deviance		183.0		
<i>Basic model</i>				
Fixed	Constant	-5.97	0.78	0.000
	Age (range 14–44 days)	0.31	0.06	0.000
	Age ²	-0.0034	0.0010	0.001
Random	Variance family level τ^2	0.126	0.038	
	Variance individual level σ^2	0.085	0.018	
Deviance		94.7		
<i>Final model</i>				
Fixed	Constant	-5.57	0.61	0.000
	Age (range 14–44 days)	0.26	0.05	0.000
	Age ²	-0.0025	0.0008	0.003
	Sex (female = 0, male = 1)	0.24	0.07	0.000
	Year 92	0.13	0.10	0.170
	Hatch date (range -5 to +5)	-0.12	0.03	0.000
	Year 92*hatch date	0.14	0.05	0.003
	Brood size at catch (range -2 to +2)	0.14	0.05	0.004
Random	Variance family level τ^2	0.047	0.020	
	Variance individual level σ^2	0.079	0.016	
Deviance		61.5		

The null model represents the total variation in the sample. The basic model represents the general growth curve with age and age² as explanatory variables. The final model contains all variables which gave a significant contribution to the model.

control families used for analysing the natural trend and all manipulated families. Brood size at catching was described using three variables: the number of goslings at hatch before manipulation, the number of goslings lost since hatch, and a variable describing the experiment (EXP). The values of EXP were -2, 0 and 2, representing the change in number of goslings during the experimental manipulation. In this way, the manipulation could be analysed as a covariate and the sum of all three variables was the number of goslings at the catch.

All three variables, which together described brood size, contributed significantly to the final model (Table 3). The manipulation had a significant effect on gosling growth in the model (coefficient for EXP: 0.09 ± 0.036 , $P = 0.013$). When the brood size was experimentally increased at hatch, growth rate increased for all goslings in the family; when the brood was reduced, the growth rate was reduced. Because there was a significant interaction between the number of hatchlings before manipulation and the age of the goslings, the strength of the effect depended on age. A positive effect of brood size at hatch before manipulation is only apparent in our data beyond the age of 3 weeks. Without the interaction term, the regression coefficient for the number of hatchlings would be

0.10 ± 0.036 ($P = 0.012$). The effect of the loss of a gosling on body size as a result of predation was -0.11 ± 0.026 units ($P < 0.001$). This value was close to the values of the other two parameters which represent a difference in brood size. Adding one extra gosling at hatch to a family was similar in effect to a natural difference in brood size of one gosling, resulting from initial brood size differences or subsequent predation or adoption.

Figure 3 shows the average growth curve for goslings. Also displayed is the mean growth experienced when families deviated by one gosling from the average brood size for whatever reason. The average increase in size for a gosling between an age of 35 and 36 days was 0.07 units (PC1, calculated from the model in Table 3). At this age, experimentally adding one gosling to the family at hatch had a positive effect on the size of all other family goslings, the effect equating to an age difference of 1.3 days.

ADULT BODY CONDITION

Unmanipulated families

We first analysed families with a constant number of goslings from the first observation until the first catch

Table 3. A hierarchical linear model describing gosling size (PC1) as a result of brood size in a data set with both experimentally manipulated and natural brood sizes (142 goslings in 64 families). Brood size at catch is split into three different variables. The number of goslings before the experiment, the change in brood size resulting from experimental manipulation (EXP) and the number of goslings lost since leaving the nest

	Estimate	SE	<i>P</i>	
<i>Null model</i>				
Fixed	Constant	0.005	0.112	0.964
Random	Variance family level τ^2	0.701	0.143	
	Variance individual level σ^2	0.172	0.027	
Deviance		293.3		
<i>Basic model</i>				
Fixed	Constant	-5.96	0.57	0.000
	Age (range 14–44 days)	0.31	0.04	0.000
	Age ²	-0.0035	0.0007	0.000
Random	Variance family level τ^2	0.112	0.028	
	Variance individual level σ^2	0.080	0.013	
Deviance		129.0		
<i>Final model</i>				
Fixed	Constant	-5.89	0.40	0.000
	Age	0.30	0.03	0.000
	Age ²	-0.0032	0.0005	0.000
	Sex	0.28	0.05	0.000
	Hatch date	-0.12	0.02	0.000
	Year 1992	0.12	0.07	0.088
	Year 1992*hatch date	0.10	0.03	0.003
	Brood size before exp.	-0.66	0.15	0.000
	Brood size before exp.*age	0.03	0.00	0.000
	Exp. change in brood size (EXP)	0.09	0.04	0.009
	Natural decline in brood size	-0.11	0.03	0.000
Random	Variance family level τ^2	0.026		
	Variance individual level σ^2	0.070		
Deviance		62.4		

The null model represents the total variation in the sample. The basic model represents the general growth curve with age and age² as explanatory variables. The final model contains all variables which gave a significant contribution to the model.

in the flightless period. Adult female body mass was positively related to the number of goslings ($F_{1,27} = 4.88$, $P = 0.036$) with a slope of 33 g per gosling. There was no correlation between size of the female parent (PC1) and the number of goslings ($F_{1,26} = 0.01$, $P = 0.910$). Body condition, indexed as body mass corrected (linearly) for body size, was positively correlated with the number of goslings (Fig. 4; $F_{1,25} = 10.98$, $P = 0.003$), and differed between years ($F_{1,25} = 5.46$, $P = 0.028$). For adult males, no significant relation was found between body mass, body size or residual mass and number of goslings.

When females that experienced a change in brood size over the period between hatch and catch were included in the data set, there was still a positive correlation between residual body mass and number of goslings at the catch ($F_{1,60} = 6.74$, $P = 0.012$) after controlling for yearly variation ($F_{1,60} = 4.99$, $P = 0.029$). When the number of goslings at the catch was expressed as the number of goslings at hatch and the number of goslings lost since that moment, both

variables were significant (Table 4). The body condition of a female was directly correlated with brood size. In this data set there was no relation with the number of goslings and body mass, in contrast to the data set above which included only females with constant family size. For males there was no trend found with the number of goslings in any of the analyses above.

Manipulated families

Manipulated families showed a trend similar to those described above for unmanipulated families. The values for residual body mass for the three experimental categories were -33 ± 29 g ($n = 9$), -4 ± 13 g ($n = 63$) and 53 ± 23 g ($n = 9$) for females with reduced, control and enlarged broods, respectively (Fig. 4). The difference in condition between categories approached significance (Kruskal–Wallis ANOVA: $\chi^2 = 5.56$, $P = 0.06$). A direct comparison between enlarged and reduced broods was significant

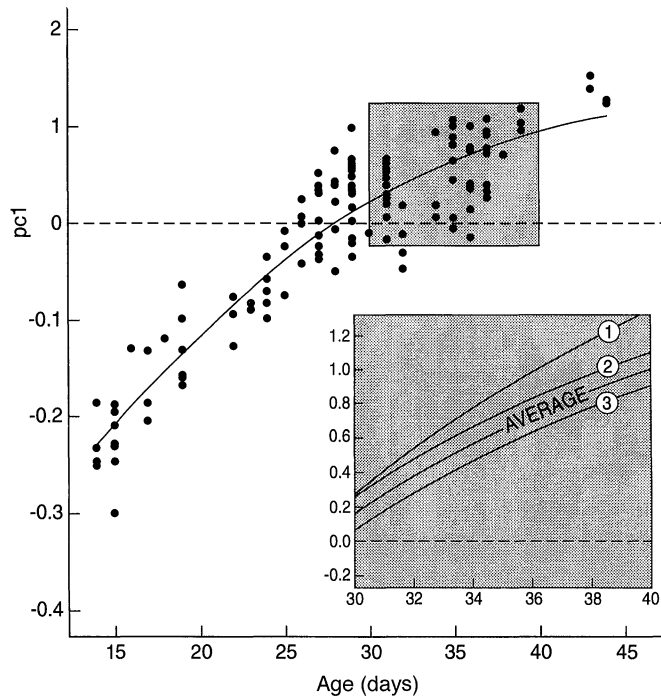


Fig. 3. (a) The growth of goslings [first principal component (PC1)] calculated from body mass, total tarsus, mid-wing and head] as a function of age. (b) Detail from (a) showing calculated trends for the average brood size (average), when the brood size is one gosling larger than the average brood size at hatch (line 1) or after the experimental manipulation (line 2). Line 3 shows the effect on size when brood size decreases with one gosling due to predation. Brood size has a direct effect on gosling size.

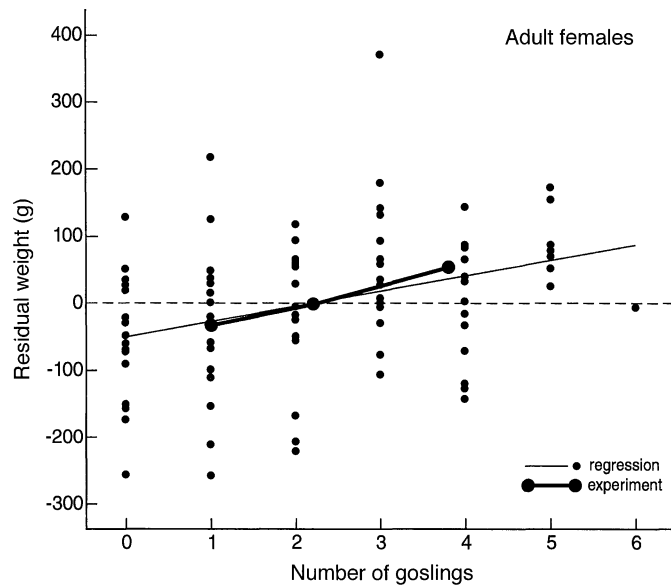


Fig. 4. Body condition of females, expressed as the residual body mass after correction for size [first principal component (PC1)], is positively correlated with brood size. The small dots represent unmanipulated females. The dotted line is the regression line through these points (residual body mass = $-49.1 + 22.3 * (\text{no. of goslings})$, $r^2 = 0.12$, $n = 95$, $P < 0.001$). The 'experiment' line is the average residual mass for the three experimental categories where brood size is manipulated at hatch.

(Mann–Whitney U-test: $Z = -2.20$, $P = 0.028$). The average brood size at the catch for reduced, control and enlarged broods was 1.0, 2.2 and 3.8, respectively. For males, there were no differences in body condition among the three categories.

ADULT MOULT

Unmanipulated families

A total of 126 moulting adult geese with known hatch date were caught in 1992 and 1993. Ninth primary

Table 4. Change in body condition [body mass corrected for first principal component (PC1)] for adult females. Body condition is positively correlated with the number of goslings at hatch but declines when goslings are predated

	Estimate	F	d.f.	P
Constant	-67.2	4.06	1	0.048
Goslings at hatch	34.4	7.01	1	0.010
Goslings lost	-21.5	4.34	1	0.042
Year (1992 = 0, 1993 = 1)	56.0	4.58	1	0.036
Residual			59	

length at ringing was significantly related to the lapsed time since hatching, and differed significantly between the two years. No effect of sex was found. No relation was found among the unmanipulated adults between the length of the largest primary and the number of goslings at the catch ($F_{1,122} = 0.06$, $P = 0.809$) or with the number of goslings at hatch ($F_{1,122} = 0.10$, $P = 0.752$). Brood size did not affect the growth of the primaries.

Manipulated families

Data were corrected for time since hatching and year using the model of unmanipulated families. Average residual length of the ninth primary for reduced, control and enlarged broods were -0.66, 0.00 and 0.47 cm, respectively, but these values were not significantly different (Kruskal-Wallis ANOVA: $\chi^2 = 0.09$, $P = 0.955$). There was also no significant difference in residual length of the ninth primary between the experimentally reduced and enlarged families (Mann-Whitney U-test: $Z = -0.23$, $P = 0.820$). This did not change when data for both sexes were analysed separately. In this study no effect of brood size on wing moult was found.

SURVIVAL OF GOSLINGS TO THE WINTERING GROUNDS

Based on brood sizes of the selected enlarged-control-decreased trios of recognizable families, 11% of the goslings survived from hatching to the wintering grounds (enlarged 11/94 = 12%, control 6/54 = 10%, reduced 3/25 = 11%). Survival rates of goslings to the wintering ground did not differ among the experimental categories ($\chi^2_2 = 0.11$, $P = 0.95$), which demonstrates that goslings in large broods did not suffer an increased mortality during migration.

Of all 94 ringed goslings that were seen after 10 August, 34% were never seen on the wintering grounds or in the following summer and presumably died during autumn migration. In a sample of 52 ringed goslings from unmanipulated families, there was no relation between survival during autumn migration and brood size at hatch ($\chi^2_1 = 0.03$, $P = 0.87$) or brood size at the end of the rearing period ($\chi^2_1 = 2.36$, $P = 0.12$). When the entire sample was

considered, including the manipulated broods, the analysis yielded conflicting results, depending on how the manipulated broods were classified. Whereas gosling survival (between 10 August and arrival on the wintering grounds) was positively related to overall brood size, there was a negative effect with regard to the manipulation experiment, suggesting that enlarged broods survived less well (Table 5). To further explore this relationship, we examined the data in more detail. The negative experimental relationship was found to be a result of the inclusion of eight goslings originally categorized as stemming from enlarged broods. By 10 August however, these broods had been reduced to what we classified as a small brood size, i.e. less than three goslings. The growth model already predicted that the loss of a gosling in the family reduced the body size of the remaining goslings. These enlarged broods lost several goslings and, as a consequence, the remaining goslings grew slower. Gosling size corrected for age for these enlarged broods which had less than three goslings on 10 August (residual PC1 \pm SE: -0.33 ± 0.12 , $n = 8$) was significantly smaller than the gosling size for the enlarged broods which kept more than three goslings in the brood at that date (residual PC1: 0.29 ± 0.07 , $n = 26$; t -test: $t = -4.30$, $P < 0.001$). When the logistic regression model included the size of the gosling corrected for age (residual PC1), this variable was highly significant and there was no residual effect of brood size or experimental manipulation (Table 6, Fig. 5). Therefore, we conclude that gosling size influenced survival, and that goslings that grew quickly survived best. Brood size affected gosling growth, but a simple relation between brood size on a sample date and survival was not found because changes in brood size resulting from predation or adoption influenced gosling size. Note that there was no significant effect of hatch date in both models analysing survival of goslings (Tables 5 and 6).

SURVIVAL OF PARENTS TO THE WINTERING GROUNDS AND FUTURE REPRODUCTIVE SUCCESS

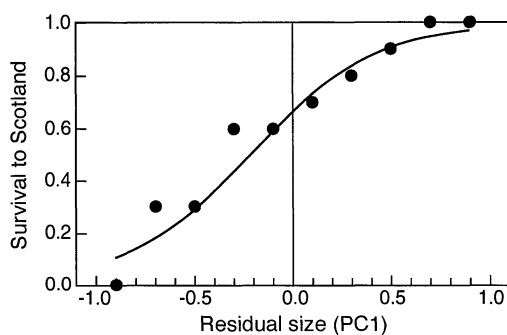
Survival of parents was very high. Only 2 out of 81 geese (= 2%) were not seen after the autumn migration. All parents of enlarged broods survived

Table 5. Logistic regression of the effect of brood size on the survival of goslings to the wintering grounds. The variable 'experiment' denotes the change in gosling number as a result of experimental manipulation: -2, 0, 2. There were no significant interactions between variables

	(Change in) deviance	d.f.	<i>P</i>	Parameter estimate
Null model	120.57	93		
Final model	109.31	91		
Constant		1		-0.78
Brood size 10 August	7.03	1	0.008	0.59
Experiment	4.23	1	0.040	-0.45
<i>Rejected terms</i>				
Brood size before manipulation	1.42	1	0.233	-0.32
Brood size after manipulation	0.72	1	0.395	-0.19
Hatch date	0.68	1	0.410	-0.12
Year	0.60	1	0.439	0.40

Table 6. Analysis of the effect of gosling size corrected for age on the survival of goslings to the wintering grounds using logistic regression. The variable 'experiment' denotes the change in gosling number as a result of the experimental manipulation: -2, 0, 2. There were no significant interactions between variables

	(Change in) deviance	d.f.	<i>P</i>	Parameter estimate
Null model	120.57	93		
Final model	100.27	92		
Constant		1		0.56
Gosling size	20.29	1	<0.001	2.89
<i>Rejected terms</i>				
Brood size before manipulation	1.72	1	0.190	-0.33
Brood size after manipulation	1.36	1	0.244	-0.14
Brood size 10 August	0.80	1	0.370	0.16
Hatch date	0.14	1	0.706	-0.06
Year	0.05	1	0.829	0.12
Experiment	0.90	1	0.344	-0.20

**Fig. 5.** Barnacle goose gosling survival during autumn migration in relation to gosling size corrected for age [residual of growth curve of first principal component (PC1) against age]. Data points indicate mean survival within classes of size.

following experimental manipulation did not show any significant effect of the manipulation (Table 7). There was thus no indication for a fitness cost to the parents of raising extra goslings.

Table 7. Change in clutch size and hatch date of individual pairs and arrival date on the breeding grounds in the year following experimental manipulation of the brood size. There are no significant differences between the experimental categories (arrival: $F_{2,25} = 1.69$, $P = 0.204$; clutch size: $F_{2,25} = 0.47$, $P = 0.631$; hatch date: $F_{2,25} = 0.13$, $P = 0.882$)

	<i>n</i>	Arrival (1 = 1 June)	Change in clutch size	Change in hatch date
Enlarged	7	2.6 ± 1.2	0.0 ± 0.4	-0.4 ± 0.6
Control	11	6.5 ± 1.9	-0.3 ± 0.5	-0.5 ± 1.0
Reduced	10	6.1 ± 1.0	-0.6 ± 0.3	-1.0 ± 0.6

and the two parents which died had already lost their goslings before fledging. A comparison of the first sighting on the breeding grounds and the changes in individual clutch size and hatch date in the year

Discussion

This study is the first to show a benefit of enlarged brood size in a precocial bird species for both parents and offspring in the period from hatching to fledging. The goslings in enlarged broods grow faster, while the female parent also has a better body condition during moult. Even after fledging, no negative effects of enlarged brood sizes were found in our study.

The effect of brood size on social dominance of the family is, in our view, the proximate mechanism underlying these results. Geese engage regularly in social interactions during foraging to secure undisturbed feeding and monopolize the best food (Lazarus & Inglis 1978; Black & Owen 1989a). We observed that large families used more feeding space than small families (D. Heg, observations in 1990) as did Lessells (1987) for the lesser snow goose. Prop, van Eerden & Drent (1984) showed some evidence that a large brood with a high dominance status had also better access to the best feeding spots during the flightless period. In their study, large brood size could result from a high dominance, because the better feeding conditions for dominant broods affected survival of goslings and thus brood size. We have taken this point further by showing that dominance is a consequence of brood size. An experimental change in brood size affects the 'win score' exactly according to the observed positive relationship between brood size and 'win score' in unmanipulated families.

How does brood size affect 'win score'? Black & Owen (1989b) suggested for wintering barnacle geese that goslings 4–11 months of age might contribute to vigilance and repelling neighbours. When goslings actively help during interactions, large brood sizes would have high 'win scores', but overt aggression by goslings towards other families in the pre-fledging period is very rare (Lessells 1987). In only seven out of 2122 observed fights in our study did goslings participate in threat behaviour. Although goslings rarely help actively during aggressive encounters, it may well be that during an encounter with another family unit, the presence of the goslings has a direct effect on the outcome.

Brood size might also change the motivation of the parents and the opponents to engage in social interactions (Lamprecht 1986; Black & Owen 1989a). A change in motivation of the parents is indicated by an increase in the attack frequency and the intensity of attack (Boyd 1953; Black & Owen 1989a). In our study 'win score' was strongly correlated with 'aggressiveness'; of 2122 observed fights, 1881 were won by the initiator of the fight, 43 ended in a draw while in 198 fights the attacked family displaced the attacker at the end of the fight.

Additionally, the motivation of the opponent might change. Most interactions involve threatening and displacement without actual fights (Boyd 1953). As actual strength or fighting ability is not tested during

such interactions, the attacked goose might rely on a signal to assess the strength of the attacker. In small passerines, experimental manipulation of plumage variation has shown that plumage acts as a signal for social status (Fugle *et al.* 1984; Järvi & Bakken 1984; Rohwer 1985b; Møller 1987). Brood size might act as an honest signal for competitive ability, because brood size is a result of the competitive ability (see also Lamprecht 1986; Black & Owen 1989a,b).

Some goose studies did not find a relation between dominance and brood size. In a recent study, Mulder *et al.* (1995) could not confirm a dominance hierarchy among families of wild lesser snow geese in relation to brood size. Although in their study large families won, on average, more interactions than small families, the sample size was low and the effect of brood size not significant. Furthermore, their data refer to geese which had discovered an extremely rich area (a former enclosure) and the rate of interactions was at least 24 times higher than in the surrounding areas. In such a situation, the motivation to engage in a fight might increase for all geese, but the gains might be smaller for large families, because it becomes very difficult to keep the family unit together. Scott (1980) also found in Bewick's swans *Cygnus columbianus bewickii* Yarr. that stable dominance relationships do not occur in high density feeding situations. In studies with small populations of (semi-) captive geese also, no clear relation between dominance and brood size has been discovered (Lamprecht 1986; Cloutier & Bédard 1992). It may be relevant to note that in these captive studies food was not in short supply as inferred in the snow goose and Bewick's swan studies mentioned.

The competitive advantage of an increased dominance as a function of brood size, will only result in growth or condition differences when there is strong competition between families for good feeding spots in a patchy environment. In our study population, this competition exists, as shown by an overall decline in gosling growth and adult size as the population has increased over the past decade (Loonen, Oosterbeek & Drent 1997). Cooch *et al.* (1991) also found a positive effect of brood size on gosling growth. In their study area there is a well-documented decline in food availability (Williams *et al.* 1993). In a study with experimentally manipulated brood sizes, Lessells (1986) did not find an effect of brood size on gosling growth, but she was studying a newly established Canada goose population, which was rapidly increasing. It would be enlightening to investigate this relationship in a saturated population, where food competition would be more intense.

What are the fitness consequences associated with enlarged broods? Lessells (1986) found negative effects of brood size on body mass and timing of moult in female Canada geese. She also found that females of experimentally enlarged broods laid their eggs later in the following year, although there was no effect on

survival and clutch size in the following year. In our study, where competition for food played an important role, the burden of increased parental care seems to be compensated by the improved access to the best feeding spots and both the goslings and the parents benefit. For the parents, we found that females in enlarged broods had a better body condition, while there was no effect on body condition for males. The male takes a larger share in social interactions and vigilance than the female, and both behaviours increase in frequency with brood size (Lazarus & Inglis 1978; Lamprecht 1986; Sedingler & Raveling 1990; this study). For the female, the costs of parental behaviour are more than compensated by the better feeding opportunities, while for the male costs and benefits associated with large broods seem to be in balance. For both parents we found a very high survival rate during autumn migration and no indication of negative effects of brood enlargement in the following breeding season. However, additional benefits of larger brood sizes were not apparent in the following breeding season; we found no difference in subsequent timing of nesting or clutch size.

Other descriptive studies, evaluating the costs of parental care in relation to brood size reported that those geese which had produced large families did better in terms of survival (Petersen 1992), clutch size in the following year (Williams *et al.* 1994) and number of young brought to the wintering grounds in the next year (Black & Owen 1989b). This relationship might be because of the individual quality of parents. However, our work suggests that this improved performance might be mediated by the presence of goslings.

The goslings in large broods might be heavier at fledging, but is their future reproductive success enhanced? As the first step towards future reproductive success, survival to the next year was analysed in this study. Owen & Black (1989) found that body mass affected survival of goslings during autumn migration, although both age and growth rate could have affected the result. They corrected for some of the variation due to age by using plumage characteristics of the gosling. In our study the ages of the goslings were known and the body sizes of the goslings were corrected for their age. We found that the survival of goslings during the autumn migration is clearly related to their growth and the brood size of their family. Prop *et al.* (1984) had shown already that larger broods of barnacle geese suffer proportionately less mortality during autumn migration, but in their study a causal relation was not yet clear because they did not undertake experiments. Sedingler *et al.* (1995b) showed in Brent Geese that several life-history traits, like the age of first breeding, and clutch size, were positively related with the size of the gosling. Choudhury, Black & Owen (1996) showed that large-sized barnacle geese in our population had a higher probability of breeding successfully in any particular year

and produced more goslings than did smaller birds. Via the effect on growth rate of the gosling, brood size thus plays an important role in determining the future fitness of the gosling.

Optimal brood size is usually explained as a trade-off between costs and benefits for parents and young (for review see Stearns 1992). In our study, we have identified benefits for both parents and young in enlarged broods. But clutch size may be limited by body reserves prior to laying (Ankney, Afton & Alisauskas 1991) or by a trade-off between postponing incubation to produce an extra egg or start incubation and hatch earlier (Pettifor, Perrins & McCleery 1988; Dalhaug, Tombre & Erikstad 1996). In our model of gosling growth, the negative effect of postponing hatch by one day is about equal to the positive effect of having an extra gosling in the family (Table 2).

Nest parasitism and adoption of young have been documented in geese (Black, Choudhury & Owen 1996) and are alternative mechanisms by which brood size could be increased. These phenomena are also observed in our study population (I. Tombre, personal communication and own observation) and have been confirmed by DNA analyses (Choudhury *et al.* 1993). Our study suggests that increasing brood size can be advantageous for the goslings in the family, and can even have a positive effect on the condition of the female parent, during the moult.

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Appendix

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HIERARCHICAL LINEAR MODELS

A hierarchical linear model (HLM) is a special type of regression model that is designed for data with a hierarchical structure. In our barnacle goose data, goslings, the primary measurement units, are nested or clustered within families, the secondary units. The HLM takes into account the nested data structure by incorporating a random error term for each level in the data. Level 1 units are then correlated via the common level 2 error term. This amounts to assuming a different regression model for every level 2 unit with explanatory variables and an error term at the first level. All regression coefficients and error terms are assumed to be related to each other. This leads to the formulation of regression models for the regression coefficients in which explanatory variables at the second level may be used. Also, a joint distribution for the level 1 error terms is assumed. Similar models are also known as mixed or random effects models, or covariance component models.

A GENERAL HLM FORMULATION

We shall demonstrate the hierarchical linear modelling approach by formulating a general two-level model and applying it to our gosling data, with, for now, one explanatory variable at the first level (denoted by x_{ij} , e.g. gosling sex) and one at the second level (denoted by z_j , e.g. family size). The regression equation at the first level is:

$$Y_{ij} = \beta_{0j} + \beta_{1j}x_{ij} + R_{ij}$$

where Y_{ij} is the dependent variable, PCI as an index

for body size, for gosling i in family j , and β_{0j} and β_{1j} are regression coefficients that vary over the goose families. The parameter β_{0j} is often called the random intercept, β_{1j} the random slope. The use of random intercepts and random slopes implies that the intercepts and regression slopes differ over the higher-order units. R_{ij} is the level 1 error term, with expected value 0 and variance σ^2 . Note that this model can be viewed as a regression model per family (level 2 unit): leaving out all subscripts j leads to a familiar regression equation formulation.

The HLM continues with modelling the regression coefficients. The most general level 2 regression equations for this model are:

$$\beta_{0j} = \gamma_{00} + \gamma_{01}z_j + U_{0j},$$

and

$$\beta_{1j} = \gamma_{10} + \gamma_{11}z_j + U_{1j}.$$

The regression coefficients γ_{pq} ($p = 0, 1; q = 0, 1$) are the so-called fixed effects. They do not vary over the goose families and can be seen as the average over the whole population of families. In this formulation, the random intercept and random slope are partly explained by a level 2 variable. The random error terms U_{0j} and U_{1j} (also called the random effects, as is R_{ij}) represent the differences that remain between the level 2 units. For these terms a bivariate normal distribution is assumed with expectation 0 and a covariance matrix with elements $\text{var}(U_{0j}) = \tau_0^2$, $\text{var}(U_{1j}) = \tau_1^2$ and $\text{cov}(U_{0j}, U_{1j}) = \tau_{01}$.

The complete HLM, given the above formulation, is then:

$$Y_{ij} = \gamma_{00} + \gamma_{01}z_j + \gamma_{10}x_{ij} + \gamma_{11}z_jx_{ij} + U_{0j} + U_{1j}x_{ij} + R_{ij}.$$

It shows all fixed regression coefficients, with accompanying explanatory variables. The new explanatory variable z_jx_{ij} is the product of the level 1 and level 2 variables, a so-called cross-level interaction term. All random error terms are also present; note the 'interaction' between U_{1j} and x_{ij} . This shows that the variance of Y_{ij} depends on the value of x_{ij} and thus variance heterogeneity can be modelled. The general model can easily be expanded with more explanatory variables. Note that it is not necessary to assume random regression coefficients (slopes) for all first-level explanatory variables.

ESTIMATION, MODEL BUILDING AND TESTING

Although no explicit estimation formulae can be derived for the fixed and variance/covariance parameters of the HLM, maximum likelihood estimates are obtained via an iterative estimation procedure, for which different algorithms are available. We have used ML3 (Prosser *et al.* 1991) based on iterative generalized least-squares estimation. In ML3 it is also possible to obtain unbiased estimates of the variance/covariance parameters using the method of restricted

maximum likelihood, but for our large enough data set this was not necessary. The advantage of using software especially designed for HLMs is that it can deal with unbalanced data, as we have here: unequal numbers of goslings per family.

The model-building process will usually consist of consequent steps of adding available explanatory variables, first fixed and then random. Generally, a forward selection process is advisable. As in all statistical analyses, model building is best guided by theoretical insights and considerations. But of course we can also use statistical guidelines such as significance of the parameters and other measures related to goodness-of-fit. The intraclass correlation coefficient [$\rho = \tau_0^2 / (\tau_0^2 + \sigma^2)$] measures the proportion of level 2 variance and can be interpreted as the proportion of variance that is present between higher-order units.

Fixed parameters can be tested with the familiar *t*-ratio of parameter estimate over standard error. For the *t*-ratio a *t*-distribution is assumed, with a number of degrees of freedom that depends on the level to which the variable, the effect of which is tested, belongs. This is especially important for the explanatory variables at the second level, when a relative small amount of higher order units are available. For large samples, we can approximate the *t*-distribution with a normal distribution. For testing the significance of random parameters, i.e. the variance and covariance parameters, *t*- or *Z*-test statistics are not appropriate. The likelihood ratio test, or deviance test, a well known general test, is used instead. The deviance

(minus two times the log-likelihood logarithm of the likelihood value) is a relative measure of (negative) goodness-of-fit, implying that the deviance of a model in itself cannot be interpreted, but that it can be interpreted relative to other nested models. A model 0 with m_0 parameters is said to be nested within model 1 if model 1 has the same m_0 parameters plus m_1 different parameters. By definition, the deviance of model 1, D_1 , will not be larger than the deviance of model 0, D_0 . The difference in deviance of these two models, fitted to the same data, $D_0 - D_1$, can be used as a test statistic with an approximate χ^2 -distribution with m_1 degrees of freedom.

MODELLING GOSLING GROWTH

In Tables 2 and 3, the results of a hierarchical linear model on gosling growth are given. The null model gives the grand mean of gosling size (PC1) and the variance at the family level (τ^2) and at the gosling level (σ^2). Much more variation is found at the family level (i.e. between goslings within families). The final model is the result of a forward selection process, first adding age and age² as basic variables, next the other explanatory variables. Except sex, all of the explanatory variables are at the family level. In the final model, both variances have significantly decreased, especially the between-family variance (τ^2) that is now smaller than the within-family variance (σ^2). No random slope for sex was found, implying that its effect does not vary over families.