INCREASE OF PARENTAL EFFORT WITH BROOD SIZE IN A NIDIFUGOUS BIRD

MARTIN SCHINDLER AND JÜRG LAMPRECHT[1]

Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen, West Germany

ABSTRACT.—Positive correlations of brood size with some parental activities [vigilance (in females), approaching young (in males and females), and attack (in males)] and a negative correlation of female feeding time with brood size were found in a sample of 23 semicaptive Bar-headed Goose (*Anser indicus*) families. Detailed examination of these correlations suggests that some components of parental care in geese represent "shared parental investment" (Lazarus and Inglis 1978, 1986). The benefits of parental care are divided among the offspring, so that in precocial birds, as in altricial birds, clutch size may be adapted to selection pressures that act after the young hatch. *Received 27 October 1986, accepted 4 May 1987.*

CLUTCH size in altricial birds appears to be a compromise between the number of young that could be raised to breeding age and the costs of parental care in terms of the parents' future reproduction or survival (Perrins 1965, Charnov and Krebs 1974, Stearns 1976, Drent and Daan 1980). Models usually assume an increase of parental effort with brood size. They seem inapplicable to the post-hatching period in precocial birds that do not feed their young and for which parental care after hatching is generally assumed to be "unshared" (Lazarus and Inglis 1978, 1986). In this case the total benefit of a parental act (vigilance, defense, etc.) is gained simultaneously by each of the young. Unshared components of parental care should thus be independent of brood size. Wittenberger (1979) used the terms "shareable" (for "unshared") and "non-shareable" (for "shared"), which may give rise to serious semantic confusion. We adhere to the terminology of Lazarus and Inglis.

In the precocial Semipalmated Sandpiper (*Calidris pusilla*) the number of hatchlings the parents can raise is limited (Safriel 1975), but there is still no clear evidence that the amount of parental activities varies with brood size in precocial birds. Such variation can indicate shared components of parental care where the benefit of a parental act is divided among the offspring so that each receives only a portion of it. Trends of increased parental vigilance and decreased feeding time with brood size were reported for Greater White-fronted Geese (*Anser albifrons*; Madsen 1981) and for the Southern Lapwing (*Vanellus chilensis*; Walters 1982), but no such relationships were found in the Pink-footed Goose (*Anser brachyrhynchus*; Lazarus and Inglis 1978) (for a review see Winkler and Walters 1983).

We sought correlations between parental activities and brood size in Bar-headed Geese (*Anser indicus*) to test the assumption of unshared post-hatching parental care. Pains were taken to differentiate between parental ability influencing brood size and parental effort consequent upon brood size.

METHODS

The semicaptive flock of about 100 individually banded, unpinioned birds lived on the Max Planck Institute lake (7.2 ha) in southern West Germany. A fenced area of about 1,000 m² of grazing land was available, and *ad libitum* pellet food provided in a trough was located near the lake (further details were given by Lamprecht 1986).

Summer correlations.—We watched the tame birds from 10–20 m distance from May to July. Time-budget data for 14 pairs were collected in 1981 and for 9 pairs, including 4 from the previous year, in 1982. For each of the 23 pairs, 3-h observations were made at 4-day intervals from day 2 to day 30 after the brood hatched, then at 5-day intervals until day 50, when the young were close to fledging. Thus, each pair was observed for 36 h in total. Roughly equal morning and afternoon observations were assigned for each pair to avoid any effects of diurnal activity changes.

During the 3-h observations we recorded the following activities for each parent after each 5-min interval: *feeding* (head low with intermittent pecking at grass or food pellets), *head up* (head raised, bill held horizontal or lower), *threatening* (all neck positions from extreme head up with bill raised high to head-
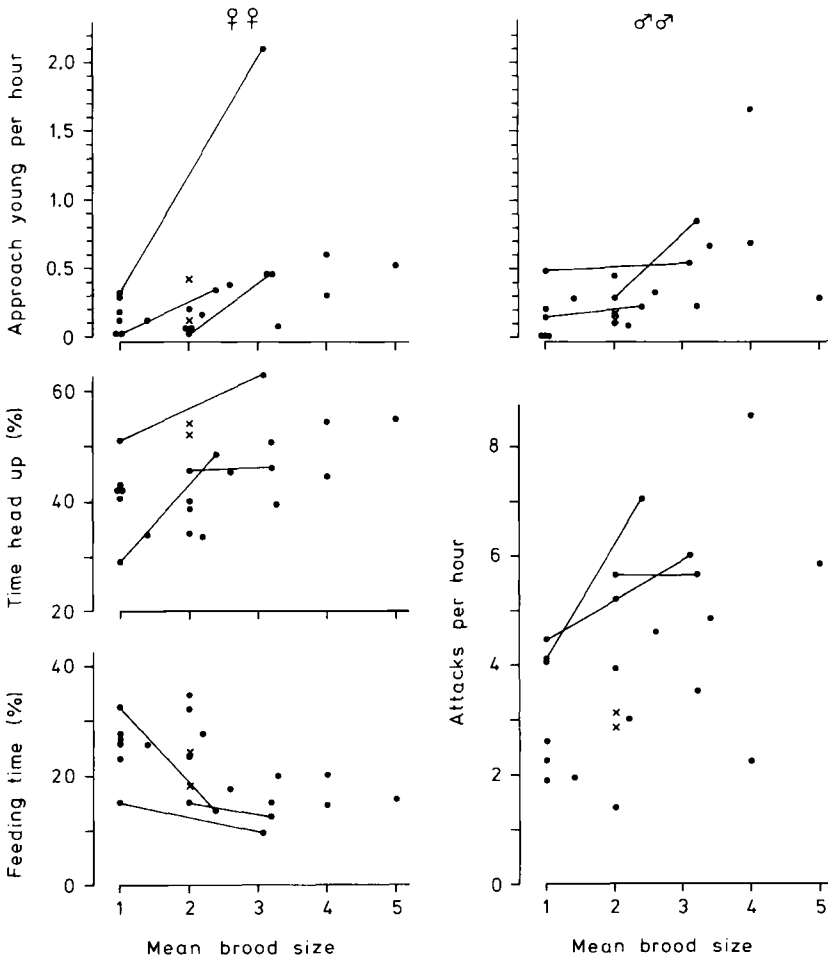

Fig. 1. Significant relationships of activities of female (left) and of male (right) parents with mean brood size. Each dot or cross represents the data of one parent. Solid lines connect data points of the three pairs in different years; crosses refer to a fourth pair with the same brood size in both years. For correlation coefficients see Table 1.

forward posture directed toward another bird), *preening, sleeping* (bird motionless, underside of bill touching breast or back), *brooding* (covering young with wings), *swimming, walking, standing,* and *lying.* The last four categories were not exclusive of the others.

We determined the percentage of each activity in all 12 observations for each parent (i.e. 36 h; Table 1, Fig. 1) or in different intervals of the entire rearing period (Table 2). This provided a relative measure of the time attributed to the various activities. Short-term events like *attacks* (dash at another bird with head held forward) and *approach young* (clearly oriented movement toward own offspring more than 2 m away or distress calling) were recorded as they occurred, and frequencies per hour determined for each parent.

Finally, we correlated the duration of long-lasting behaviors and the frequencies of short-term events with the mean number of young that accompanied each pair on all observation days (Table 1) or during the respective intervals (Table 2). Brood size was not constant because some goslings died.

One to 4 well-developed eggs (which later hatched in an incubator) were removed from three nests. In contrast to this reduction of brood size, one pair did not hatch young but adopted 4 goslings (3 survived), another pair adopted 2 young in addition to their own 3, and a third pair with 3 young adopted 1 gosling. An estimate of a pair's "potential mean brood size" was obtained by adding the number of surviving incubated goslings to the actual mean brood size, and subtracting the number of young adopted. Thus,

TABLE 1. Spearman rank correlations between mean brood size and parental behaviors during the rearing period.[a] Values in parentheses are correlations with the estimated potential mean brood size.

Behavior	Males	Females
Feeding	−0.13	−0.57*** (−0.31)
Head up	0.21	0.43* (0.34)
Threatening	−0.34	−0.20
Preening	0.24	−0.08
Sleeping	0.17	0.24
Brooding	—	0.15
Walking	−0.004	−0.04
Standing	−0.29	−0.15
Lying	0.30	0.21
Swimming	−0.03	−0.002
Attacks	0.49** (0.19)	0.31
Approach young	0.64*** (0.39)	0.54*** (0.49**)

[a] * = $P < 0.05$, ** = $P < 0.02$, *** = $P < 0.01$.

actual brood size differed from potential brood size in 6 pairs, actual to potential mean brood size being 1 to 2, 1 to 3, 1 to 5, 3.36 to 3, 4 to 3.14, and 3.1 to 0. The durations and frequencies of parental behavior significantly related to actual mean brood size were correlated with potential brood size. This was to test whether these behaviors were predictive of potential rather than actual brood size, thus indicating parental ability rather than brood-size-dependent parental effort.

Spring correlations.—We investigated whether behavioral differences between pairs in spring could be used to predict brood size. We collected time-budget data for pairs in March 1983, before laying. Three to 5 times daily, with intervals of at least 1 h, each pair was located in a pre-set order and the activity (feeding, head up, attack, or threat) of each mate noted after 1 min. Any threats or attacks were also noted during the following minute. Each was observed for 60–80 min. We expressed head up and feeding as the percentage of observation minutes starting with this behavior, and the frequencies of attacks and threats as the percentage of observation minutes containing at least one such event. The behavior durations or frequencies in the 13 successfully breeding pairs were correlated with subsequent brood size measured when the family left the nest.

All *P*-values for Spearman rank correlation coefficients are two-tailed.

RESULTS

Summer correlations.—Brood size correlated positively and significantly with approach young and attack rates in male parents and with time spent head up and rate of approach young in females, and negatively with female feeding time (Table 1). These relationships also

TABLE 2. Spearman rank correlations between some parental behaviors in summer and actual brood size in different intervals of the rearing period.[a] $n = 23$ pairs.

Behavior	Age of young (days)		
	2–14	18–30	35–50
Female			
Feeding time (%)	−0.54***	−0.49**	−0.12
Head up time (%)	0.55***	0.24	0.38
Approach young/h	0.20	0.52**	0.40
Male			
Attacks/h	0.41	0.36	0.30
Approach young/h	0.64***	0.62***	0.31

[a] ** = $P < 0.02$, *** = $P < 0.01$.

applied to all three pairs with different brood sizes in the 2 yr (connected points in Fig. 1). The values of one pair that had the same number of young in both years tended to be remarkably similar. Except for approach young in females, Spearman correlations for the five parental behaviors above with potential brood size were not significant ($P > 0.05$; Table 1) and were lower than the correlation between actual and potential brood size ($r_s = 0.56$, $n = 23$, $P < 0.01$).

For these five parental behaviors, correlations with mean actual brood size were calculated separately for three parts of the rearing period (Table 2). Except for female approach young, correlations were higher when goslings were young.

Spring correlations.—Only female head up and threats correlated significantly with subsequent brood size (Table 3). All other correlations were not significant.

DISCUSSION

Parental age was not related to actual or potential brood size (maximum Spearman correlation coefficient $r_s = 0.16$, $P > 0.2$) and cannot account for our results. Correlations with brood size do not indicate directly that behavior durations or frequencies are *consequences* of brood size. This interpretation is suspect if a spring behavior correlated significantly with *future* brood size just as it did in summer, and if the behavior in summer correlated higher (or equally high) with *potential* than with actual brood size. We found that only three parental behaviors, female feeding time, male attack rate, and male rate of approaching young, met these criteria. They are more likely to be conse-

quences than determinants of actual brood size, and their dependence on brood size is indicative of shared components of parental effort (see introductory paragraphs). Only these three behaviors will be discussed further.

Relationships between parental effort and brood size will affect clutch size only if the parents incur costs in terms of survival, future reproductive success, or both. Male approaches toward young and attacks were infrequent (Fig. 1). Although these activities expend energy, and attacks may also induce injury, male parental costs may be too small to affect the evolution of clutch size. In females, however, brood-size-dependent costs of parental care may be linked with substantially reduced feeding time (see Fig. 1) and thus induce a slower or incomplete replacement of nutrients lost during incubation. In some goose species, female feeding rates and nutrient reserves are important for subsequent reproductive success (Ryder 1970, Harvey 1971, Ankney and MacInnes 1978, Aldrich and Raveling 1983, Prop et al. 1984, Teunissen et al. 1985). Reduced feeding time in large families does not mean necessarily that females eat less. At least three alternatives exist.

(1) Females feeding more efficiently may build up more reserves, and consequently lay larger clutches (Ankney and MacInnes 1978), breed more effectively (Aldrich and Raveling 1983), or both. Such birds would have more young while needing less time to feed. We found that clutch size did not correlate with brood size ($r_s = 0.04$, $n = 23$; see also Lamprecht 1986). Further, the body mass of paired females measured in January (1982 and 1983) or March (1983) did not correlate with the number of young leaving the nest in early summer (January 1982: $r_s = 0.03$, $n = 24$; January 1983: $r_s = -0.08$, $n = 29$; March 1983: $r_s = 0.19$, $n = 27$). We believe this lack of correlation was due to a superabundance of food.

(2) If females with large families selected the more nourishing pellet food over grass, they could reduce feeding time. The correlation between the number of young and the proportion of time females fed on pellet food (measured only in 1982) was not significant ($r_s = -0.10$, $n = 9$) and contrary to expectation.

(3) If large families tended to feed in less exploited areas, the females might need less time to become satiated. Time spent in less frequented areas with higher grass was not correlated with brood size ($r_s = 0.05$, $n = 23$), however.

TABLE 3. Spearman rank correlations between parental behaviors in March and subsequent brood size.[a]

Behavior	Males	Females
Feeding	0.20	-0.03
Head up	-0.21	0.65**
Threats	-0.18	0.57*
Attacks	-0.09	-0.27

[a]* = $P < 0.05$, ** = $P < 0.02$.

None of the alternative explanations hold, and we believe females with more young have higher nutritional costs that may limit brood size to a level below the maximum possible.

It would be inappropriate to generalize results from one field population to another when environmental conditions are different. We thus cannot be confident that our results, obtained under conditions of semicaptivity and superabundance of food, also apply to geese in the wild. In fact, the superabundance of food in our flock apparently obscured the positive relationship between female feeding time in spring and subsequent reproductive success, which was demonstrated for Barnacle Geese (*Branta leucopsis*) in the field (Prop et al. 1984). We also found no relationship between male attack rate in spring and future brood size (Table 3), but it is difficult to imagine how, under the same conditions, the dependence of brood size on female feeding time and male attack rate could arise as an artifact in summer. Some justification for a more general validity of our results comes from the few field studies available.

The correlations of parental vigilance and feeding with brood size reported for Greater White-fronted Geese and Southern Lapwings agree with our findings, in spite of the low numbers of individuals and possible influence of parental ability. In addition, the "sitting time" of parents decreased with brood size in Snow Geese (*Chen caerulescens caerulescens*) (Lessells in press). Lazarus and Inglis (1978) found no such correlations in a field study of Pink-footed Geese, probably because observations began at a gosling age of about 4 weeks. We found that correlations of female feeding time and head up and of male attacks and approach young with brood size tended to be higher early in the rearing period and decreased over time (Table 2).

Brood sizes observed in the two years of our study (see Fig. 1) were within the normal range of the flock, for which brood size upon leaving

the nest averaged 2.58 young (range 1–6, n = 130 broods in 1975–1986). Mean gosling mortality until fledging was 22.3%. Field records of brood sizes in Bar-headed Geese are rare: Schäfer (1938) counted 3–8 well-developed eggs per clutch and observed that only 1–3 young (more rarely 4–5) fledged. Clutch sizes of 4–8 eggs (mostly 4–6) were reported by Dementiev and Gladkov (1967) and of 2–10 eggs (mostly 4–5) by Kydyraliew (1967), but no information on brood size or hatching rate was given.

Lessells (1986) found in Canada Geese (*Branta canadensis*) that from one molt to the next, females with larger broods had lost more mass (or gained less) than those with smaller broods. She was unable to show, however, that brood size affected parental survival or future fecundity in the stationary population studied.

In the migratory Tundra Swan (*Cygnus columbianus bewickii*) both males and females accompanied by cygnets had a lower return rate to the wintering grounds than adults with no offspring (Scott 1980: table 2). Although these differences were not quite significant, they suggest some survival costs of parental care. Proof is still wanting, but in migrating populations brood-size-dependent energy costs and food deficits may lower the parents' survival, future reproductive success, or both. Clutch size in such nidifugous birds may be adapted to selection pressures acting after hatching, as is apparently true in altricial birds.

In geese, selection pressures that limit clutch size might be counteracted by the effect that larger families tend to be more dominant in wild flocks (Boyd 1953, Hanson 1953, Raveling 1970). In competitive situations females of dominant pairs feed more and will breed more successfully in the following season (Teunissen et al. 1985, Lamprecht 1986). Successful adults, however, do not adopt stray goslings to increase family size. Orphans older than a few days are always rejected by other families, indicating that the optimum brood size is smaller than maximum (Black and Owen 1984). As no effect of sibling competition was found (Black and Owen 1984, Lessells 1986), reluctance to adopt goslings may be due to the costs involved in rearing additional young.

LITERATURE CITED

ALDRICH, T. W., & D. G. RAVELING. 1983. Effects of experience and body condition on incubation behavior of Canada Geese. Auk 100: 670–679.

ANKNEY, C. D., & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance in female Lesser Snow Geese. Auk 95: 459–471.

BLACK, J. M., & M. OWEN. 1984. Importance of the family unit to Barnacle Goose *Branta leucopsis* offspring—a progress report. Norsk Polarinst. Skr. 181: 79–85.

BOYD, H. 1953. On encounters between White-fronted Geese in winter flocks. Behaviour 37: 291–319.

CHARNOV, E. L., & J. R. KREBS. 1974. On clutch size and fitness. Ibis 116: 217–219.

DEMENTIEV, P., & N. GLADKOV. 1967. The birds of the Soviet Union, vol. 4. Jerusalem, Israel Program for Sci. Transl. Pp. 316–321.

DRENT, R. H., & S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225–252.

HANSON, H. C. 1953. Inter-family dominance in Canada Geese. Auk 70: 11–16.

HARVEY, J. M. 1971. Factors affecting Blue Goose nesting success. Can. J. Zool. 49: 223–234.

KYDYRALIEW, J. 1967. Die Streifengans (*Anser indicus*) im Tienschan Gebirge. Ornitologija 8: 245–253.

LAMPRECHT, J. 1986. Social dominance and reproductive success in a goose flock (*Anser indicus*). Behaviour 97: 50–65.

LAZARUS, J., & I. R. INGLIS. 1978. The breeding behaviour of the Pink-footed Goose: parental care and vigilant behaviour during the fledging period. Behaviour 65: 62–88.

———, & ———. 1986. Shared and unshared parental investment, parent-offspring conflict and brood size. Anim. Behav. 34: 1791–1804.

LESSELLS, C. M. 1986. Brood size in Canada Geese: a manipulation experiment. J. Anim. Ecol. 55: 669–689.

———. In press. Parental investment, brood size and time budgets: behaviour of Lesser Snow Goose *Anser c. caerulescens* families. Ardea.

MADSEN, J. 1981. Post hatching behaviour of families and non-breeding Greenland White-fronted Geese. Pp. 116–122 *in* Report of the 1979 Greenland White-fronted Goose study expedition to Edalungmiut Nunat, west Greenland (A. D. Fox and D. A. Stroud, Eds.). Aberystwyth.

PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major*. J. Anim. Ecol. 34: 601–647.

PROP, J., M. R. VAN EERDEN, & R. H. DRENT. 1984. Reproductive success of the Barnacle Goose *Bran-*

ta leucopsis in relation to food exploitation on the breeding grounds, western Spitsbergen. Norsk Polarinst. Skr. 181: 87–117.

RAVELING, D. G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. Behaviour 37: 291–319.

RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Geese. Wilson Bull. 82: 4–13.

SAFRIEL, U. N. 1975. On the significance of clutch size in nidifugous birds. Ecology 56: 703–708.

SCHÄFER, E. 1938. Ornithologische Ergebnisse zweier Forschungsreisen nach Tibet. J. Ornithol. 86: 1–149 (Sonderheft).

SCOTT, D. K. 1980. The behaviour of Bewick's Swans at the Welney Wildlife Refuge, Norfolk, and on the surrounding fens: a comparison. Wildfowl 31: 5–18.

STEARNS, S. C. 1976. Life-history tactics: a review of ideas. Q. Rev. Biol. 51: 3–47.

TEUNISSEN, W., B. SPAANS, & R. DRENT. 1985. Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. Ardea 73: 109–119.

WALTERS, J. R. 1982. Parental behavior in Lapwings (Charadriidae) and its relationship with clutch sizes and mating systems. Evolution 36: 1030–1040.

WINKLER, D. W., & J. R. WALTERS. 1983. The determination of clutch size in precocial birds. Pp. 33–68 *in* Current ornithology, vol. 1 (R. F. Johnston, Ed.). New York, Plenum Press.

WITTENBERGER, J. F. 1979. The evolution of mating systems in birds and mammals. Pp. 271–349 *in* Handbook of behavioral neurobiology, vol. 3 (P. Marler and J. G. Vandenbergh, Eds.). New York, Plenum Press.

The **Deutsche Ornithologen-Gesellschaft** will hold its **100th annual meeting** as the "International 100th Annual Meeting" from **24 September through 1 October 1988** at the Museum Alexander Koenig in Bonn, West Germany. The key themes will be Zoogeography and systematics and Behavioral ecology. All interested in participating should contact **Dr. K.-L. Schuchmann, Museum Alexander Koenig, Adenauerallee 150-164, D-5300 Bonn, Federal Republic of Germany.**

Publications of the International Council for Bird Preservation are now available in North America from **Princeton University Press.** These include ICBP/IUCN Red Data Books and ICBP Technical Publications. All have been reviewed in *The Auk* (1986, Auk 103: 445, 446, 643, 645; 1987, Auk 104: 586). For information contact the **Order Department, Princeton University Press, 3175 Princeton Pike, Lawrenceville, New Jersey 08648** (phone 609-869-1344).