

## Body Size and Fecundity in Lesser Snow Geese

RAY T. ALISAUSKAS<sup>1,3</sup> AND C. DAVISON ANKNEY<sup>2</sup>

Davies et al. (1988) concluded that body size did not directly influence annual fecundity in Lesser Snow Geese (*Chen c. caerulescens*, hereafter called Snow Geese). This disagrees with Ankney and MacInnes (1978) who showed that there was a positive correlation between culmen length and body mass in pre-laying female Snow Geese, and that heavier females laid more eggs than did lighter females. A reanalysis of Ankney's and MacInnes's (1978) data by Davies et al. (1988: 645) confirmed that larger (as distinct from heavier) females in fact had higher annual fecundity. Davies et al. (1988) suggested that this disparity occurred because they excluded younger birds from their data set whereas Ankney and MacInnes did not. We view this exclusion not as an explanation, but as a problem.

We think that intraspecific variation in body size is an important influence on fecundity of arctic geese. Davies et al. (1988) ignored some crucial facts about Snow Goose biology, which led to inappropriate analyses of a uniquely appropriate data set, and we believe that the influence of body size on fecundity, and possibly survivorship, is a fact that remains buried as a result of facts Davies et al. excluded. Our concern with the analyses of Davies et al. (1988) stems from their failure to distinguish body *mass* from body *size*, their pooling of data over years, and their omission of data from young, but mostly small, females.

*Background.*—Ankney and MacInnes (1978) demonstrated the importance of nutrient reserves to Snow Goose fecundity and suggested that nutritional state, and thereby fecundity, was largely determined environmentally. Findlay and Cooke (1987) estimated that repeatability of clutch size in Snow Geese was 0.26, which confirmed that most variation is due to nongenetic effects. They used deviations from annual mean clutches to calculate this estimate "to eliminate variation arising from differences in conditions between years" (Findlay and Cooke 1983: 726). This procedure inflated repeatability estimates because it removed some environmental variation. Mean clutch size at La Perouse Bay varies annually depending primarily on chronology of nesting (Davies and Cooke 1983, Hamann and Cooke 1989); mean clutch size is lower in years when nesting is relatively late (Davies

and Cooke 1983). Because nesting geese are exposed to both within-year and among-year environmental effects, repeatability of clutch size should be calculated from data that include this annual variation. Had Findlay and Cooke (1983, 1987) not "corrected" for among-year effects, their estimate of clutch size repeatability would have been lower than 0.26. Regardless, most variance in clutch size cannot be accounted for by major and direct genetic influences. Rather, the interplay between feeding conditions and energy expenditure during the latter part of spring migration (Harvey 1971, Alisauskas 1988), and energy expenditure by prenesting geese on the breeding grounds (Barry 1962, Ryder 1970, Ankney and MacInnes 1978, Davies and Cooke 1983, Hamann and Cooke 1989) are likely the most important influences on annual fecundity in Snow Geese.

Although not stated by Davies et al. (1988), we suggest that the functional significance of body size on clutch size of Snow Geese is that body size limits how much nutrient reserve females can acquire during spring migration and transport to arctic nesting colonies (Ryder 1970, Ankney and MacInnes 1978, Alisauskas 1988: 189). Thus, in intraspecific investigations, body size should not be confused with body mass. This is particularly true for species such as Snow Geese that show great seasonal variation in body mass (Ankney 1982) and even greater seasonal variation in nutrient reserves (Alisauskas 1988). An unambiguous definition of body size ideally should refer to the structural or skeletal size of the animal. Aside from ontogenetic variation, body size of an individual bird has little measurable day-to-day or year-to-year variation (but see Smith et al. 1986). Alternatively, body mass of birds can be extremely dynamic and may even show diurnal variation. Variation in body mass of an individual reflects its nutritional state, or mass of nutrient reserves, as well as ingesta and plumage mass. Besides reflecting these sources of variation, variation in body mass among individuals can be due to differences in their structural size (e.g. Alisauskas and Ankney 1987). For an individual, the limits to variation in body mass may be determined by body size, but body size of an adult is not influenced by its current body mass.

*Body size and body mass.*—To index body size, Davies et al. (1988) used principal components analysis (PCA) with body mass, culmen, head length, and tarsus length as variables. Although not stated by Davies et al., we assume that the PCA was done with the correlation matrix of these four variables. They showed that these four variables were positively and about equally correlated with the first principal component (PC1), thereby justifying their use of PC1 as an index of overall body *size*. Although their PC1 contains in-

<sup>1</sup> Delta Waterfowl and Wetlands Research Station, Rural Route 1, Portage la Prairie, Manitoba R1N 3A1, Canada.

<sup>2</sup> Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada.

<sup>3</sup> Present address: Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada.

TABLE 1. Principal components analyses using correlation matrices of three linear measurements with body mass ( $PC1_{mass}$ ) and without body mass ( $PC1_{no\ mass}$ ) for Lesser Snow Geese.

Input variables	$PC1_{mass}$				$PC1_{no\ mass}$			
	1983		1984		1983		1984	
	$a^a$	$r^b$	$a$	$r$	$a$	$r$	$a$	$r$
Body mass <sup>c</sup>	0.25	0.66	0.28	0.74	—	—	—	—
Culmen	0.33	0.88	0.32	0.87	0.40	0.92	0.41	0.92
Tarsus length	0.30	0.79	0.29	0.78	0.34	0.75	0.34	0.76
Head length	0.34	0.89	0.33	0.89	0.40	0.92	0.40	0.91
Eigenvalue	2.62		2.69		2.30		2.26	
% variance explained	66		67		77		75	

<sup>a</sup> Standardized scoring coefficients.  
<sup>b</sup> Correlations between first principal component score and original variables.  
<sup>c</sup> Dash = not included in analysis.

formation about structural size, its utility as an index of structural size is weakened by inclusion of body mass (which includes information about nutritional state, ingesta mass, and plumage mass). We analyzed a sample of Snow Geese collected during winter and spring migration (Alisauskas 1988) to show why the inclusion of body mass in intraspecific comparisons of body size is not desirable. We deliberately chose data that included geese that were storing fat, protein, and mineral reserves during spring migration (Ankney 1982, Alisauskas 1988) to illustrate this.

Snow Geese with adult plumage (Bellrose 1976) were collected from January to May at three locations in 1983 and 1984: southeast Texas (January) near the town of Garwood (1983, 20 females, 13 males; 1984, 15 females, 12 males), in southeastern South Dakota (March) near the town of Bridgewater (1983, 13 females, 22 males; 1984, 30 females, 18 males), and in southern Manitoba (May) near Portage la Prairie (1983, 12 females, 15 males; 1984, 13 females, 12 males). Culmen was measured on the day of collection, after which each goose was weighed and frozen. When geese were thawed, they were dissected, ingesta was removed and weighed, and head and tarsus lengths were measured (Alisauskas 1988). Ingesta mass was subtracted from body mass to yield ingesta-free body mass. Davies et al. (1988) measured body mass of live

geese, and so their measurement included ingesta mass.

Body mass, culmen, head length, and tarsus length were used for PCA (PROC FACTOR, SAS 1985). For geese collected in 1983 and 1984, two PCAs were done with correlation matrices as input—one matrix contained four variables to get the first principal component ( $PC1_{mass}$ ), and one matrix contained only three variables, as body mass was excluded ( $PC1_{no\ mass}$ ). Thus, each goose was assigned two scores for body size indices,  $PC1_{mass}$  and  $PC1_{no\ mass}$  (PROC SCORE, SAS 1985). Correlation structure was very similar between years, both for PCAs that included, and those that excluded, body mass (Table 1). This indicates that sample sizes were sufficient to produce stable scoring coefficients.

Two-way analysis of variance (PROC GLM, SAS 1985) showed that when body size was indexed by  $PC1_{mass}$ , this index was unstable over time as geese migrated north (Table 2). But, when indexed by  $PC1_{no\ mass}$ , body size did not vary significantly among the three groups of geese. These results were consistent between years. Our analysis shows that inclusion of body mass with a set of metric variables in a PCA can produce an index that reflects both size variation and, to a large extent, the nutritional state of the animal.

We suggest that the body mass (i.e. nutritional state) of geese during molt (when Davies et al. [1988] mea-

TABLE 2. Analyses of variance in first principal component scores as determined from three measurements and mass ( $PC1_{mass}$ ), and as determined from only the three measurements ( $PC1_{no\ mass}$ ), taken from Lesser Snow Geese collected during January, March, and May of 1983 and 1984.

Effect	df	Dependent variable							
		$PC1_{mass}$				$PC1_{no\ mass}$			
		1983		1984		1983		1984	
		F	P	F	P	F	P	F	P
Sex	1	35.7	0.0001	60.0	0.0001	23.7	0.0001	51.7	0.0001
Month	2	3.6	0.03	7.8	0.0007	1.7	0.19	1.5	0.23
Sex × month	2	0.0	0.97	0.5	0.64	0.0	0.98	0.0	0.98

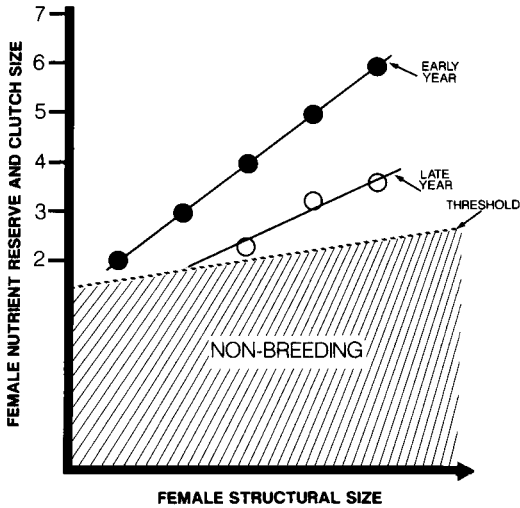


Fig. 1. Relationship between body size and clutch size in prelaying Lesser Snow Goose females. The dashed line represents a nutrient reserve threshold below which females will not attempt to nest.

sured their Snow Geese) as it relates to clutch size is irrelevant because clutch size is influenced by nutritional state of geese *before* the clutch is laid (Ankney and MacInnes 1978, Alisauskas et al. 1987). The mean and variance of Snow Goose nutrient reserves and body mass are greater for samples of prelaying Snow Geese than they are for molting Snow Geese (cf. Ankney and MacInnes 1978, Ankney 1979). However, an individual's structural size measured during molt should reflect its structural size before egg laying. This leads to the hypothesis that structurally larger females have greater fecundity than smaller females because large females have a greater capacity for nutrient storage. Therefore, the effects of size and nutrient reserves on fecundity must be evaluated separately. Davies et al. (1988) could properly evaluate only the effect of structural size on clutch size, but not the effect of nutrient stores. Finally, the technique used for banding geese involves holding them in pens, with significant declines in body mass becoming greater as geese are held longer (A. Dzubin, Canadian Wildlife Service, pers. comm.). We hope that Davies et al. will recalculate PC1 scores using only linear measures.

*Annual variation.*—Nesting by Snow Geese is delayed by inclement weather or snow cover, and the longer the interval between arrival and nesting, the lower the average clutch size (Davies and Cooke 1983). This likely occurs because females use some nutrient reserves for existence energy while waiting to nest, thereby leaving less reserve available for egg production (cf. Barry 1962, Ryder 1970, Hamann and Cooke 1989). We suggest that relations between body

size and fecundity are year-specific. Assume, for simplicity, that such relations are examined in both an early year (when females nest immediately after arrival) and a late year (when females wait 2 weeks for snow to clear to allow occupation of nest sites). Assume also that the influence of body size is an important determinant of clutch size, and that females arrive on nesting colonies with maximum reserves constrained only by their structural size, a situation not unlike that found by Ankney and MacInnes (1978). It is apparent that pooling data across years would obscure relations between body size and annual fecundity (Fig. 1). Davies et al. (1988) pooled data from at least 4 years.

Besides a reduction in clutch size in late years, a greater proportion of birds forego nesting in such years (Davies and Cooke 1983). Given the importance of nutrient reserves to fecundity, the model (Fig. 1) predicts that it is the smallest birds that do not breed in late years. Clutches of 0, of course, cannot be recorded, and thus data from late years will more likely bias data for large females (by reducing overall their estimated mean clutch size if data are pooled across years) than for small females. Also, the slope that describes such a relationship likely varies among years, as would the variation about the line. It follows that the relationship should be strongest when feeding conditions during spring migration are good and when geese nest immediately after arrival on nesting areas. This underscores the need to examine body size-fecundity relationships by year rather than by pooling data across years. Some measure of chronology must be involved in the analysis.

If the model (Fig. 1) is correct, then it has relevance to Findlay and Cooke's (1987) estimate for heritability of clutch size. Clutch size may have no direct genetic basis. Rather clutch size may be simply a correlated phenotypic trait of body size, but body size appears to be partly genetically determined (Davies et al. 1988). We suggest that Findlay and Cooke's (1987) heritability estimate for clutch size reflects the influence of body size on clutch size.

*Omission of young females.*—Davies et al. (1988: fig. 4) showed positive covariation between body size and age in their sample of nesting females, and argued convincingly that this occurred because small geese start to breed at an earlier age than large geese. Before examining the relation between annual fecundity and body size, they cited Rockwell et al. (1983), who showed that clutch size in Snow Geese covaried with female age. Subsequently they omitted females less than four years old from their sample. They found no relation between size and fecundity. When they included all nesting females, Davies (1988: 645) found positive correlations between size and each of their four indices of fecundity, despite the biases due to an undesirable index of body size and to pooling of data across years. They suggested that the disparity between their result and the finding (Ankney and

MacInnes 1978) that fecundity is related to body size existed because of the different age structures of the two samples. By not excluding two- and three-year-old females, Ankney and MacInnes (1978) maintained a sample of geese that was representative of the population.

When they compared clutch sizes of different age Snow Geese during specific periods of nesting, Hamann and Cooke (1989) found no significant differences in clutch size. They concluded that age per se does not influence clutch size and so the exclusion of young females from the analyses of Davies et al. (1988) was unwarranted. That exclusion introduced a serious bias if medium and large females, nesting for the first time, also lay smaller clutches than they lay in subsequent years (see Rockwell et al. 1983, above). Because age of first reproduction is greater for larger Snow Geese, many of their four-year-old females must have been medium and large females nesting for the first time. Cooke et al. (1981: 324) suggested that "the attainment of maximal clutch size [in female Snow Geese] requires at least two years of breeding experience." Thus, because most or all small four-year-olds were experienced breeders and most medium and large four-year olds were inexperienced, the mean clutch sizes of medium and large females were biased downward and that of small females was biased upward.

We ask Davies et al. to reconsider the effect that omitting young, mostly small females had on their conclusions. It is possible to assess two or more covarying traits (e.g. body size, age, or breeding experience) on a response variable if an appropriate model is chosen. For example, Alisauskas and Ankney (1987) showed that although age and size covary in breeding American Coots (*Fulica americana*), each of several effects can be assessed simultaneously on a dependent variable independently of other effects (in that case, the effects of size and age on variation in mass of somatic protein). We suspect that the influence of female body size on annual Snow Goose fecundity will become apparent if appropriate analyses are done. Body size may be more important than age in explaining Snow Goose demography, and we agree with Sauer and Slade (1987: 85) that "description of the relationships among size, age and demography of vertebrate populations should give exciting insights into the animal's life history, and provide a link between physiological and population ecology."

We thank T. W. Arnold, R. C. Bailey, A. W. Diamond, P. T. Handford, P. W. Hicklin, and D. M. Scott for their many helpful comments.

#### LITERATURE CITED

- ALISAUSKAS, R. T. 1988. Nutrient reserves of Lesser Snow Geese during winter and spring migration. Ph.D. thesis, London, Univ. Western Ontario.
- , & C. D. ANKNEY. 1987. Age-related variation in the nutrient reserves of breeding American Coots (*Fulica americana*). *Can. J. Zool.* 65: 2417-2420.
- , ———, & D. G. KREMENTZ. 1987. Body condition in Eastern Kingbirds. *Auk* 104: 546-547.
- ANKNEY, C. D. 1979. Does the wing molt cause nutritional stress in Lesser Snow Geese? *Auk* 96: 68-72.
- . 1982. Annual cycle of body weight in Lesser Snow Geese. *Wildl. Soc. Bull.* 10: 60-64.
- , & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95: 459-471.
- BARRY, T. W. 1962. Effects of late seasons on Atlantic Brant reproduction. *J. Wildl. Manage.* 26: 19-26.
- BELLROSE, F. C. 1976. Ducks, Geese and Swans of North America. Harrisburg, Pennsylvania, Stackpole Books.
- COOKE, F., M. A. BOUSFIELD, & A. SADURA. 1981. Mate change and reproductive success in the Lesser Snow Goose. *Condor* 83: 322-327.
- DAVIES, J. C., & F. COOKE. 1983. Annual nesting productivity in Snow Geese: prairie droughts and arctic springs. *J. Wildl. Manage.* 47: 291-296.
- , R. F. ROCKWELL, & F. COOKE. 1988. Body-size variation and fitness components in Lesser Snow Geese (*Chen caerulescens caerulescens*). *Auk* 105: 639-648.
- FINDLAY, C. S., & F. COOKE. 1983. Genetic and environmental components of clutch size variance in a wild population of Lesser Snow Geese (*Chen caerulescens caerulescens*). *Evolution* 37: 724-734.
- , & ———. 1987. Repeatability and heritability of clutch size in Lesser Snow Geese. *Evolution* 41: 453.
- HAMANN, J., & F. COOKE. 1989. Intra-seasonal decline of clutch size in Lesser Snow Geese. *Oecologia* 79: 83-90.
- HARVEY, J. M. 1971. Factors affecting Blue Goose nesting success. *Can. J. Zool.* 49: 223-234.
- ROCKWELL, R. F., C. S. FINDLAY, & F. COOKE. 1983. Life history studies of the Lesser Snow Goose: I. The influence of time and age on fecundity. *Oecologia* (Berlin) 56: 318-322.
- RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82: 5-13.
- SAS INSTITUTE INC. 1985. SAS user's guide: statistics, ver. 5 ed. Cary, North Carolina.
- SAUER, J. R., & N. A. SLADE. 1987. Size-based demography of vertebrates. *Annu. Rev. Ecol. Syst.* 18: 71-90.
- SMITH, J. N. M., P. ARCESE, & D. SCHLUTER. 1986. Song Sparrows grow and shrink with age. *Auk* 103: 210-212.

Received 7 July 1989, accepted 21 July 1989.