

Response to Alisauskas and Ankney

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We appreciate Alisauskas and Ankney's (1990) comments, which shed additional light on the intriguing question of the relationship among body size, fecundity, and survival. The two key issues are the partitioning of body size into a structural component and a "condition" component, and the ways in which these two components affect fecundity.

Ankney and MacInnes (1978) wrote a seminal paper which documented that female Snow Geese (*Chen caerulescens*) with larger prelaying body reserves in spring laid larger clutches on average. They also found a positive correlation between the body mass of prelaying geese and culmen length, from which they concluded that structurally larger females were able to sequester larger body reserves and could thus lay larger clutches. We agree that geese which have accumulated more reserves lay larger clutches. Our own work confirms this (Hamann and Cooke 1989). What is at issue, and what we were attempting to test, was whether there was a positive correlation between structural size (as opposed to prelaying reserve) and clutch size (as a measure of fecundity), as was suggested by Ankney and MacInnes's (1978) correlations.

Alisauskas and Ankney (1990) restate their hypothesis as follows: "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." This is a reasonable hypothesis and is consistent with Ankney and MacInnes's (1978) findings of a positive correlation between culmen length and body mass in arriving females. However, it is inconsistent with our more extensive data base, which indicates no correlation between body size and clutch size. It also ignores the fact that, interspecifically at least, large birds have higher metabolic and flight costs than small birds (Kendeigh 1972).

Alisauskas and Ankney suggested ways that the inconsistency between our conclusions and theirs could be due to methodological factors. We do not believe this to be the case. Their criticisms of our findings fall into three categories: our failure to distinguish between body mass and body size, pooling

of data over years, and exclusion of data from young females.

Body mass and body size.—The structural size of an adult Snow Goose is determined by a combination of its genetic constitution (evidenced by the relatively large heritability values (Davies et al. 1988)) and its growth environment during development before fledging (Cooch et al. MS). There is little seasonal or lifetime variation in structural size once adult size is reached. Body mass on the other hand can vary as a result of genetic composition and developmental conditions, but it can also vary considerably during the life of the bird both within and between seasons (at least at certain times of the year). Clearly, as geese put on weight before nesting, their body mass increases but their structural size does not (Alisauskas and Ankney 1990: table 2). Many authors make use of this seasonal variation in body mass to calculate a condition measure which is some function of body mass divided by structural size (e.g. Moser and Rusch 1988).

The question at issue in our paper is whether body mass at molt should be included in our PCI value that is used as a measure of body size, when body mass at other times of the year has been clearly shown to vary and also must vary depending on whether the bird has recently eaten or not. This is a valid question. We decided to include body mass in our PCI measure, based on the assumption that when we measured our birds (ca. 5 weeks after hatch), body mass variation mainly reflected genetic and developmental variation rather than seasonal or diurnal variation. In support of this contention, we found strong positive correlations between body mass values and the other structural size measurements. The Pearson correlation coefficients between female body mass at molt and tarsus, culmen, and head length are 0.49, 0.44, and 0.54, respectively; these compare with 0.35 between tarsus and culmen, 0.42 between tarsus and head length, and 0.70 between culmen and head length. Ankney and MacInnes (1978) also found a correlation between culmen and body mass at this time in the season but interpret it differently. Second, there was little systematic change in adult body mass during the course of the measurement period (ca. 8 days). Third, we found a high repeatability of body-mass measurements (Davies 1985: table 2.3) when the same birds were measured in different years.

It seems logical that structurally larger birds will have a larger body mass due to simple allometry. However, some body-mass differences may be due to local circumstances such as whether the birds recently fed and how recently the birds completed incubation. For body mass during molt, we believe that variation due to these factors is small relative to the variation

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due to genetic and developmental factors. In our data set, there is no correlation between any of the structural size measurements which make up the PC1 and total clutch size. Correlation coefficients between total clutch size and tarsus, head length, and culmen are 0.04, 0.001, and -0.07 , respectively. None of these is significant (see Davies 1985: appendix c4). In Table 1 we present the relevant results of principal component analyses performed on a subset of our data. The analyses extract the first principal component and attendant statistics for measures of this subset both with and without body mass. The subset includes only one set of measures per individual but maximizes the age variation among individuals (see below). This is possible because many of the females were measured in several years and thus at several ages (Davies et al. 1988). Considering both the proportion of variance due to PC1, and the loadings between the PC1 estimates and the actual body measures, it is clear that the inclusion of mass in the extraction of general body-size measure has no substantial effect. The failure to find a correlation with structural measures alone suggests that variation due to condition of the birds does not influence the conclusion that structural size is not correlated with clutch size.

Alisauskas and Ankney (1990) seem to be under the impression that we are attempting to assess the effect of both structural size and nutrient storage on clutch size. We have attempted to do only the former in the Davies et al. paper; the effect of nutrient storage on clutch size was dealt with in the paper by Hamann and Cooke (1989) and confirms the findings of Ankney and MacInnes (1978).

Annual variation.—Body-size measurements for tarsus, culmen, head length, and body mass of adult Snow Geese were highly repeatable from year to year (r^2 values from 0.71 to 0.79; Davies 1985). Because there is no systematic trend, it would seem that slight annual differences reflect measurement errors rather than real changes in the structural size of the birds. Conversely, clutch size varied considerably within birds from one year to the next ($r^2 = 0.146$; Lessells et al. 1989). If structural size has a major influence on clutch size, one would expect perhaps higher repeatabilities of clutch size or lower repeatabilities of structural size than we observe. We pooled our data over years because our sample size was insufficient to do otherwise. Nevertheless, if there were a correlation between structural size and clutch size (as predicted by Alisauskas and Ankney), we would expect it in the pooled data as well as those for individual years.

Use of 2- and 3-year-old females.—Young breeders (2- and 3-year-olds) lay smaller clutches and lay later in the season than older birds (Finney and Cooke 1978, Rockwell et al. 1983, Hamann and Cooke 1987). Alisauskas and Ankney (1990) seem to interpret Hamann and Cooke's (1989) recent paper to show that there is no correlation between clutch size and female

TABLE 1. Principal component analysis of body measures of Lesser Snow Geese (Loadings are the product-moment correlations between the PC1 score and the body measurement).

	Analysis	
	Mass included	Mass excluded
Eigenvalue	2.52	2.04
Proportion of variance	0.63	0.68
Loadings		
Mass	0.79	—
Tarsus	0.75	0.72
Head length	0.85	0.89
Culmen	0.78	0.85

age. This is due to a misunderstanding which should be cleared up before dealing with the major point. Within a season there is a strong negative covariance between laying date and clutch size. Hamann and Cooke (1989) show that although young breeders generally lay later in the season than older birds, if they do lay at the same time they will have a similar clutch size. In fact a recent more sophisticated analysis of these data shows that even controlling for laying date, young geese still lay slightly smaller clutches (E. G. Cooch unpubl.). This means that young birds lay smaller clutches mainly because of factors which result in the strong negative covariance between clutch size and laying date. As individual birds grow older (at least from the ages of 2-5), they increase their clutch size and advance their laying date. These two phenomena occur in parallel. The explanation is probably that as birds gain foraging experience, they accrue more nutrients, lay more eggs, and lay earlier in the season. They do not change in structural size, and the changes in clutch size with age cannot be attributed to structural size changes.

We excluded 2- and 3-year-old birds in our analysis because young birds lay smaller clutches, and in our sample young birds were also structurally smaller. As we show above, this correlation between structural size and clutch size is not related causally, but it is a correlation nevertheless and will complicate the interpretation of our results. As such, if we are to understand the relationship between structural size and clutch size, we must remove this additional complication. If the hypothesis is that smaller birds lay smaller clutches, this should be detectable even after the complexity caused by including young adults in the sample is eliminated. Alisauskas and Ankney argue that our sample is still biased because "most or all small four year olds were experienced breeders and most or all medium or large females were inexperienced." We have no evidence that first-time-breeding 4-year-olds lay smaller clutches than experienced breeders. We think it unlikely, because it is probably improved

foraging which influences clutch size rather than experience in previous breeding. In addition, fewer than 14% of our 4-year-olds are likely to be inexperienced breeders (Cooke and Rockwell 1988) and 4-year-olds make up <30% of our sample. Alisauskas and Ankney quote from Cooke et al. (1981) that "the attainment of maximal clutch size requires at least two years of breeding experience." This conclusion was based only on birds which nested first as 2-year-olds, and we were in error in extrapolating to all breeding females regardless of their age of first breeding. We apologize for misleading the readers of our earlier paper on this point.

An alternative to eliminating the data from 2- and 3-year-old birds from our analysis would be to have statistically adjusted the clutch size data for an age effect, as suggested by Alisauskas and Ankney. This would have allowed us use data from our entire sample. We did not pursue this approach because our sample of young females was biased towards smaller birds, and addition of data from younger birds would have added little power to our ability to detect clutch-size: body-size correlations. Because our sample of young birds was biased by size, statistical adjustment of the data under the assumption that only age was controlled would have been incorrect. Eliminating the younger birds as we did seems to be a better test of the hypothesis, although if there were a correlation of fecundity and body size only in young birds, then we would not be able to detect it.

Although it is possible that omitting 2- and 3-year-old birds from the sample may bias the sample, to leave them in definitely does so. There are difficulties in adjusting the data. If we include them without age adjustments, we may find a positive correlation between structural size and clutch size; but it would be erroneous to conclude from this that structural size is causally related to clutch size through its limitation on how much nutrient the female can acquire. Ankney and MacInnes did not know the age composition of their birds and had no way of knowing whether a nonrandom distribution of age classes in their sample accounted for the positive correlation between structural size and clutch size. We have attempted to control for the known bias in our own data by testing the hypothesis in a sample of birds where we think this bias is absent.

In conclusion, we stand by our results and will continue to investigate the fascinating question of the relationship between structural size, fecundity, and survival. The high heritability for body-size measurements suggests that the character is not under

strong directional selection, and we see no reason why large and small Snow Geese within limits should not have equal overall fitness values.

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