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This Week's Citation Classic

Ankney CD & Maclnnes C D. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459-71, 1978.
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Female Snow Geese that arrive at Arctic breeding grounds with larger nutrient reserves (lipid, protein, calcium) lay, on average, larger clutches. Lipid and protein reserves not used for egg production are critical for successful incubation: females that deplete their reserves during late incubation either desert their nests or starve to death. Thus, to reproduce successfully, a female Snow Goose can only commit to egg production those reserves that are surplus to her maintenance requirements for incubation. [The SC/® indicates that this paper has been cited in more than 240 publications, making it the most-cited article published in this journal.]

Nutrient Reserves and Clutch Size

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A question that has intrigued ecologists and evolutionary biologists is "What, both proximately and ultimately, determines how many offspring an organism produces per breeding attempt?" David Lack first formalized this question.[1,2] Lack originally dealt with birds that feed their young and hypothesized that clutch size in such species has evolved to correspond to the maximum number of young for which parents could, on average, find food.

This hypothesis clearly didn't apply to birds like waterfowl, that don't feed their young. Thus, Lack later hypothesized[3] that clutch size of waterfowl had evolved in relation to the average amount of food available to the laying hen. Shortly thereafter, John P. Ryder modified this hypothesis to account for clutch size evolution in Arctic-nesting geese.[4] Ryder assumed that these birds don't feed after arrival to the breeding grounds, and thus he proposed that clutch size was determined by the size of a female's "energy reserves" relative to the amount of those reserves required to complete incubation.

So, when I arrived at the University of Western Ontario in 1970 to become part of Charlie D. MacInnes's team working at the large Snow Goose colony at McConnell River, N.W.T., the time was "ripe" for someone to test these ideas. I broadened Ryder's terminology from "energy" reserves to "nutrient" reserves so as to include lipid, protein, and calcium reserves, as they are the macronutrients in eggs. Also important in my thinking was the seminal paper by Harold C. Hanson[5] showing that, on an annual basis, these reserves fluctuate markedly in Canada Geese. Finally, I took to heart Hanson's advice to me: "The answers will only be found by freely sacrificing (shooting) birds on the breeding grounds."

The only time that I regretted following Hanson's advice was when our freeze-dryer broke down (as I recall, it cost Charlie's research grant $3,000 to fly in a refrigerator repairman from Churchill, Manitoba!). Anyway, my assistant, Larry Patterson, and I each had to backpack 60 pounds of frozen goose samples 30 miles to Eskimo Point where we begged and borrowed freezer space.

Although other articles on the importance of nutrient reserves to Arctic Geese have since appeared, including one of my own on Atlantic Brant,[6] none has so clearly shown the relation between nutrient reserves and clutch size that I found in Snow Geese. This is primarily because Hanson's advice (above) wasn't followed; i.e., sample sizes were sufficient to show the major use of reserves by breeding geese, but too small for analyzing the relation between clutch size and reserve size. The Arctic Goose research subsequently stimulated much research on the importance of nutrient reserves to temperate-breeding ducks. This research has shown that reliance on reserves by breeding females is ubiquitous among species. There is, however, considerable controversy about whether protein or lipid is the most limiting nutrient in duck reproduction. Regardless, it is now clear[7] that the weight of evidence overwhelmingly supports Lack's original hypothesis about clutch size of waterfowl.

Ironically, the first paper from my Snow Goose research that I submitted to *Auk* (confirming that egg-laying and incubating geese feed little or not at all) was nearly rejected because one reviewer and the editor thought that waterfowl papers should be in *Journal of Wildlife Management*! Fortunately, John Wiens, who edited this paper, knew better.

I have always had one regret about the research: David Lack died a year before I completed my PhD thesis and I didn't have the pleasure of sending him a copy. But, given his tremendous insight, I wouldn't be surprised if he knew anyway.

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2. ---------- . The significance of clutch size. 3. Some interspecific comparisons. *Ibis* 90:25-45. 1948.
3. ---------- . The significance of clutch size in waterfowl. *Wildfowl* 18:125-8. 1967.
4. **Ryder J P.** A possible factor in the evolution of clutch size in Ross Goose. *Wilson Bull.* 82:5-13. 1970.
5. **Hanson H C.** The dynamics of condition factors in Canada Geese and their relation to seasonal stresses. *Arct. Inst. North Am. Tech. Pap.* 12:1-68. 1962.
6. **Ankney C D.** Nutrient reserve dynamics of breeding and molting Brant. *Auk* 101:36l-70, 1984.
7. **Ankney C D. Afton A D & Alisauskas R T.** The role of nutrient reserves in limiting waterfowl reproduction. *Condor* 93:1029-32. 1991.

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