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ARE GREATER SNOW GEESE CAPITAL BREEDERS? NEW EVIDENCE FROM A STABLE-ISOTOPE MODEL

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Abstract. The strategy of relying extensively on stored nutrient reserves for reproduction (capital breeding) was thought to be common in large-bodied birds breeding in harsh environments, such as arctic-nesting geese, but this view has been challenged recently. Our objective was to model inputs to the eggs from stored reserves and from local food plants in Greater Snow Geese (*Chen caerulescens atlantica*) breeding in the high Arctic, using a new approach based on stable-isotope signatures. Snow Geese and their eggs were collected during laying from 1999 to 2001 (N = 66 females and 110 eggs). We analyzed the isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) of egg constituents (lipid-free yolk, yolk lipid, and albumen), goose tissues (lipid-free breast muscles, abdominal fat, and whole liver), and of the food plants eaten by laying geese in the Arctic (graminoids and forbs). We applied a two-isotope mixing model approach to delineate nutrient input to eggs quantitatively. Differences in the isotopic signature of endogenous reserves and arctic food plants were relatively large (5.3–8.0‰ for $\Delta\delta^{13}C$ and 7.5‰ for $\Delta\delta^{15}N$) because reserves were accumulated in southern staging areas where geese feed in farmlands and estuarine habitats. The percentage of egg nutrients derived from exogenous sources (food consumed in the Arctic) was higher than from endogenous (body) reserves and varied little among the three years. Isotopic signatures indicated that endogenous reserves contributed 33% of lipid-free yolk nutrients, 27% of albumen, and 20% of yolk, on average. Isotopic signatures of egg constituents of individual females were more strongly related to those of liver than endogenous sources (breast muscles or abdominal fat), indicating that the endogenous isotopic signature was diluted by a dietary input in the liver. We also found evidence of seasonal variation in the use of endogenous reserves. Late-laying females apparently invested proportionally more endogenous reserves in their eggs than did early layers, but not those laying larger clutches. We conclude that Greater Snow Geese use a mixed capital/income breeding strategy. Our study shows that isotopic composition of tissues can be used to infer the contribution of exogenous vs. endogenous sources of nutrients for egg formation where inputs differ isotopically.

lipid

Key words: Arctic; capital breeder; carbon; Chen caerulescens atlantica; *fat; food plant nutrients; Greater Snow Geese; nitrogen; protein; stable-isotope mixing model; stored nutrient reserves.*

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INTRODUCTION

Partitioning energy among vital processes such as survival, growth, or reproduction is of fundamental importance to all organisms. For species living in environments where food is seasonally limited, optimal allocation of energy to these processes will be strongly affected by the annual cycle of resource availability (Masman 1986, Weathers and Sullivan 1993). Many organisms have adapted to seasonality by storing energy reserves to survive periods of reduced energy intake such as winter, or of high energy demand such as reproduction. This strategy is commonly used by species exploiting strongly seasonal environments, such as most reptiles (Naulleau and Bonnet 1996, Henen 1997, Bonnet et al. 2002) or migratory birds breeding in polar regions (Ankney and MacInnes 1978, Astheimer and Grau 1985, Parker and Holm 1990, Esler and Grand 1994). The strategy of relying extensively on stored energy or nutrient reserves for reproduction has been termed *capital* breeding, as opposed to the *income* strategy in which breeding animals use external resources directly available at that time (Drent and Daan 1980, Jönsson 1997, Meijer and Drent 1999). The capital/income breeding dichotomy should be viewed as two ends of a continuum, with most species falling somewhere in between. Nonetheless, the position of an organism along this gradient (i.e., either toward the capital or income end of the spectrum) will have a considerable influence on many life history traits such as number and size of offspring, timing of breeding, or the occurrence of semelparity (Bonnet et al. 1998).

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