Reviving the calcium-from-lemmings hypothesis

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The well-known Roselaar-Summers hypothesis, states that there is a relationship between lemming abundance in the arctic tundra and the breeding productivity of waders and geese (Roselaar 1979; Summers 1986; Underhill *et al.* 1993). The birds breed more successfully in peak lemming years because predators eat abundant lemmings which may reduce redation on nesting birds. However predators eat eggs and young of birds in years during and after a decrease in lemming population size.

The Roselaar-Summers hypothesis was pre-dated by the "MacLean hypothesis" which also speculated "upon the possible dependence of sandpipers on lemmings... for reproduction", although MacLean (1974) did not have prey-switching in mind!. He suggested lemmings were a calcium source necessary for egg production and growth of juveniles. He found that, in June, 32 out of 84 (38%) stomachs of female sandpipers of four species contained lemming teeth and bones. Of these 84 females, 61 had an ovarian follicle exceeding 4 mm in diameter, 29 of the 61 (48%) had skeletal remains in the stomachs; this percentage increase to 100% (n = 10) for females with follicles greater than 15 mm or an egg in the oviduct. In contrast, he found teeth and bones in 3 out of 162 (2%) of stomachs of males in June. In July, the values were 1.6% for females (n = 61) and 0% for males (n = 79). In July 12% of the stomachs of chicks contained teeth and bones (n = 131) but only 1.3% in August (n = 76). June for adult females and July for juveniles are periods when the demand for calcium is at a peak.

MacLean (1974) noted that Dunlins *Calidris alpina* on the Finnish coast have a mean inter-laying interval of 36 hours compared with 24 in northern Alaska. He suggested that general food availability during the egg-laying period was better on the Finnish coastal mudflats compared to Alaskan upland tundra and the shorter Alaskan laying interval was attributable to abundant lemming skeletal remains there. Thus laying interval might not be regulated by overall energy availability, but rather by abundance of a limiting nutrient which, in the case of egg production, could be calcium.

The daily food intake of laying female Dunlin was estimated by Norton (1973) to be 16.5 g. The average calcium concentration of tipulid larvae, the main prey of Dunlin at this time, is 0.35%, suggesting a daily calcium intake per day of 0.06 g. A Dunlin egg contains 0.24 g of calcium. Assuming 100% efficiency of calcium assimilation (noting that 70% is the approximate retention rate in laying hens [Simkiss 1975]), it would take four days to ingest sufficient calcium from tipulid larvae to produce one egg! To put the problem into perspective, a clutch of four sandpiper eggs contains about twice as much calcium as the female which lays them. Clearly, an additional source of calcium is required for egg production, and MacLean (1974) hypothesised that this came from lemmings.

Obviously, sandpipers do not attack lemmings to eat their skeletons! But when lemmings are abundant, their bones and teeth are readily available on the tundra in the pellets of avian predators of lemmings such as skuas and Snowy Owls *Nyctea scandiaca* (MacLean 1974), and in the scats of Arctic Foxes *Alopex lagopus*. MacLean noted that lemming bones had even been found in the stomachs of laying female Lapland Buntings *Calcarius lapponicus*.

The impact of calcium deficiency on reducing breeding productivity has been demonstrated for Great Tits *Parus major* (Graveland *et al.* 1994). One of the consequences of acid rain is a leaching of calcium from soils - on poor soils the effect is so pronounced that snails, which also require large amounts of calcium for growth and reproduction, are greatly reduced in number. During the critical egg-laying period, the tits normally consume snails to provide calcium for egg production. Lack of snails results in eggs with shells that are so porous and thin that the eggs desiccate or are broken during incubation, leading to nest failure.

An analogous example of calcium deficiency during the nestling period has been described for Cape Griffon Vultures *Gyps coprotheres* in southern Africa (Houston 1978; Richardson *et al.* 1986). Here, Spotted Hyaenas *Hyaena hyaena* assume the role for vultures that lemming predators play for sandpipers on the tundra, the provision of bone fragments of manageable size. In the absence of bone-crushing hyaenas, there are no bone fragments at carcasses for parents to feed to juvenile vultures. As a result, these suffer debilitating bone deformities due to lack of calcium. Further evidence that calcium is required by developing young are provided in studies by Douthwaite (1976) of young Pied Kingfishers *Ceryle rudis* which digested fish bones whereas adults regurgitated them in pellets, and by Seastedt & MacLean (1977) of young Lapland Buntings, which were fed lemming bones and teeth and egg shell.

MacLean's calcium-from-lemmings hypothesis has apparently not been followed up. Given the renewed interest in calcium deficiencies in vultures and tits (Richardson *et al.* 1986; Graveland *et al.* 1994), it is certainly worth pursuing in relation to sandpipers. One weakness of the hypothesis is how sandpipers find sufficient calcium to breed successfully in years when there are few lemmings and fewer lemming predators, as occurred over much of the Taimyr Peninsula in 1990 (Yurlov 1993). Do the pellets and scats from previous years still persist to provide bone fragments and teeth? Likewise, it would be useful to determine the calcium budgets of female arctic-breeding geese and passerines.

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