

Geographic variation in calcium and clutch size

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For over a half century numerous hypotheses have surfaced aimed at explaining a key life history trait, the evolution of clutch size in birds. A principal goal has been to explain why clutch size generally increases with latitude both within species and among closely related species. Most hypotheses have stressed food limitation, predation, or seasonality. I present a novel hypothesis to explain geographic variation: a limitation of calcium resulting from broad scale variation in this element. Because the storage capacity of avian medullary bone is limited or nonexistent, during egg formation, female birds must intake supplemental calcium. Yet calcium and other exchangeable bases are much rarer in tropical soils. I briefly review the abundant experimental and observational evidence supporting how calcium limitation affects clutch size and other life history traits, and I present a series of predictions (and apparent support for them), stemming from the calcium variation and limitation hypothesis. The balance of evidence suggests that variability in availability of environmental calcium plays a proximate and ultimate role in the evolution of clutch size. Although this hypothesis is not mutually exclusive with others, it highlights another factor that needs to be considered in studies of the geographic variation in clutch size.

Reproductive output is a fundamental target of natural selection and is thus a key to our understanding of evolution. Yet we lack consensus on what constitutes the principal factors determining variation in reproductive output within a species. In the case of avian clutch size, numerous hypotheses have been formulated to explain variation in clutch size across the range of a species or among species (Klomp 1970, Winkler and Walters 1983, Godfray et al. 1991, Monaghan and Nager 1997). These hypotheses fall into three main groups: morphological (e.g., parents can incubate only a certain number of eggs), ecological (e.g., parents can care for only a certain number of nestlings), and physiological (e.g., the female is limited by her ability to produce eggs). Morphological and physiological factors have been neglected—even called “unpopular” (Cody 1966)—largely because ecological factors have received by far the most attention and thus have shaped most of our thinking about clutch size evolution (Klomp 1970).

In 1947, David Lack proffered the most well known of the ecological hypotheses (summarized in Lack

1954). Even in its modern form, modified to account for current thinking in life history evolution (Godfray et al. 1991), Lack’s premise is that a clutch corresponds to the number of viable offspring the parent(s) can raise, a number that often varies geographically. On the basis of his extensive field experience in Central America, Alexander F. Skutch (1949) challenged Lack’s hypothesis, asserting that variation in clutch size was determined by variation in nest depredation rates. He reasoned that laying smaller clutches mitigated against the greater likelihood of predation from increased feeding effort, thus explaining the generally smaller clutch sizes in the tropics, where there are many more predators. N. Philip Ashmole (1963) presented a third key explanation, hypothesizing that increased relative productivity in the shortened breeding seasons of northern latitudes placed a premium on laying larger clutches there.

Each of these hypotheses focuses on ultimate causes, suggesting principal selective factors that shape evolution of clutch size, but proximate factors also affect clutch size (Meijer et al. 1990, Patten and Rotenberry

1999, Coe and Rotenberry 2003). After all, the degree of heritability of clutch size is debatable, with some authors suggesting it is fairly high (Klomp 1970, Perrins and Jones 1974), others fairly low (Murphy and Haukioja 1986), attributing most variation to the environment rather than additive genetics (Findlay and Cooke 1983, Krogstad et al. 1996). Only four items constitute an avian egg (Perrins 1996): water, fat, protein, and calcium (as CaCO_3). If any one is in short supply, clutch size will suffer. Time allocation, energy expenditure, and nutrient reserves have been implicated as limiting reproduction (Deerenberg et al. 1996), with the last factor related to food availability immediately prior to, rather than during, the breeding effort (Selman and Houston 1996). For several species of passerines, researchers have found a positive correlation between clutch size and the abundance of natural foods (Hussell and Quinney 1987, Boutin 1990).

But rather than food availability *per se*, the important determinant of clutch size is the availability of nutrients (Bolton et al. 1992, Monaghan et al. 1995, Selman and Houston 1996, Ramsay and Houston 1998), particularly calcium (Reynolds et al. 2004), a crucial requirement for egg formation and nestling development that is poorly represented in most foods birds consume (Barclay 1994, Graveland and van Gijzen 1994). If the ability to produce eggs (or nestlings) limits clutch size (Monaghan et al. 1995), then geographic variation of any one of the four constituents of an egg—water, fat, protein, or calcium—would lead to geographic variation in clutch size. Food and water vary across the landscape and may vary consistently across broader scales; however, starting with the importance of nutrients in egg formation (Monaghan et al. 1995, Ramsay and Houston 1998), I present a novel hypothesis that geographic variation in environmental calcium is a chief determinant of geographic variation in avian clutch size. If this hypothesis be true, then the following predictions relating available calcium to clutch size should hold.

Calcium during oögenesis

Reproductively active females should seek supplemental calcium during egg formation (oögenesis). Most birds are income breeders (Langin et al. 2006). Although species vary (Dhondt and Hochachka 2001), there is an abundance of evidence that female birds consume supplemental calcium during the breeding season but not at other times (Simkiss 1975, Graveland 1990, Reynolds 1997). This point provides *prima facie* support for the notion that calcium availability limits reproductive output. Because most foods are poor sources of calcium (Barclay 1994, Graveland and van Gijzen 1994, Bureš and Weidinger 2000), females must obtain elsewhere the calcium needed to form eggs;

indeed, food intake generally does not increase during oögenesis (Bolton et al. 1992, Houston et al. 1995), but species may differ in their ability to find supplemental calcium (Eeva and Lehikoinen 2004). Williams (1996) noted that endogenous reserves make only a minor contribution to egg production, so a strong relationship between clutch size and body condition is not expected (cf. Pettifor et al. 2001). In essence, provided a female is obtaining enough food and water—above that needed for survival—the constraint on reproductive output must lie elsewhere.

Calcium during nestling development

Calcium limitation during oögenesis may set a proximate ceiling on clutch size, but it may be an ultimate control as well, with selection against thin-shelled eggs—and thickness diminishes across a given clutch (Gosler et al. 2005). Likewise, calcium is needed to produce young capable of fledging, meaning that calcium availability is limiting at the nestling stage (Monaghan and Nager 1997, Tilgar et al. 2005), providing a second ultimate control. As a result, *supplemental calcium (or foods rich in calcium) should be sought for growing nestlings.* As noted above, females seek calcium-rich items (e.g., snail shells, isopods, and millipedes) through the breeding cycle (see also Graveland and Drent 1997, Bureš and Weidinger 2000). Both sexes search extensively for such items if they are not available readily, and search effort declines after skeletal growth has peaked (Bureš and Weidinger 2003). Offering further support, in a supplementation study parents with nestlings “use[d] offered calcium-rich material more frequently” in regions with reduced environmental calcium, in this case acidified areas (Bureš and Weidinger 2001). In an ultimate sense, then, clutch size also depends on parental ability to furnish nestlings with sufficient calcium.

Clutch size and calcium decreases or increases

If calcium is limiting, then a prediction and its corollary ought to hold. First, *if available calcium is decreased, then clutch size should decrease.* Graveland and his colleagues (Graveland 1990, Graveland et al. 1994) documented that, across a suite of passerine species, reproductive output is reduced in areas with increased acidification from acid rain and similar environmental perturbations that reduce available calcium. Clutch size decreases in at least some of these studies (Graveland 1990). Although this pattern may not be universal (Ramsay and Houston 1999), clutch size and other

reproductive parameters are limited on soils with naturally poor abundances of exchangeable bases (Glooschenko et al. 1986, Graveland et al. 1994, Graveland and Drent 1997, Mänd et al. 2000), suggesting that the pattern is real and general.

A corollary is that, all other things being equal, *if available calcium is increased, then clutch size should increase*. More studies are needed, as direct evidence in support of this prediction—from both field and laboratory studies—has emerged only recently. In the field, relative to a control group, clutch size tended to increase in a population of house wrens *Troglodytes aedon* provided with supplemental calcium (Johnson and Barclay 1996), and clutch size increased in great tits *Parus major* supplemented with calcium relative to tits not receiving supplements (Tilgar et al. 2002). Even if clutch size was not affected, calcium supplementation of other populations of wild birds increased shell thickness and egg volume (Graveland and Drent 1997, Tilgar et al. 1999, Mänd and Tilgar 2003). In the laboratory, Reynolds (2001) found that “dietary calcium appears to be of paramount importance in providing sufficient calcium for clutch formation” for zebra finches *Taeniopygia guttata*, although the effect on clutch size *per se* was marginal. Additional studies of wild and captive birds should strive to understand the effects of supplement calcium on clutch size, particu-

larly in light of expected tradeoffs between egg volume and egg number. Effects may be indirect, with calcium supplementation increasing female condition (Mänd and Tilgar 2003) and female condition increasing clutch size (Pettifor et al. 2001).

Geographic variation in calcium

Taken together, this evidence suggests that calcium limits reproductive output of birds. In particular, that parents seek supplemental calcium during the breeding cycle but not other times implies a need for calcium beyond that acquired in normal diet. Decreases and increases in available calcium lead to concomitant changes in clutch size and other aspects of reproductive output. If there is any relationship between calcium limitation and geographic variation in clutch size, then *environmental calcium must vary geographically on a broad scale*. In general, soils in temperate zones are eutrophic whereas those in tropical zones are oligotrophic (Jordan and Herrera 1981). A principal distinction between these soils types lies in their ability to retain nutrients, especially calcium and other exchangeable bases (Brady and Weil 2002). Tropical soils have notoriously low levels of calcium (Fig. 1; Richter and Babbar 1991), typically differing by an

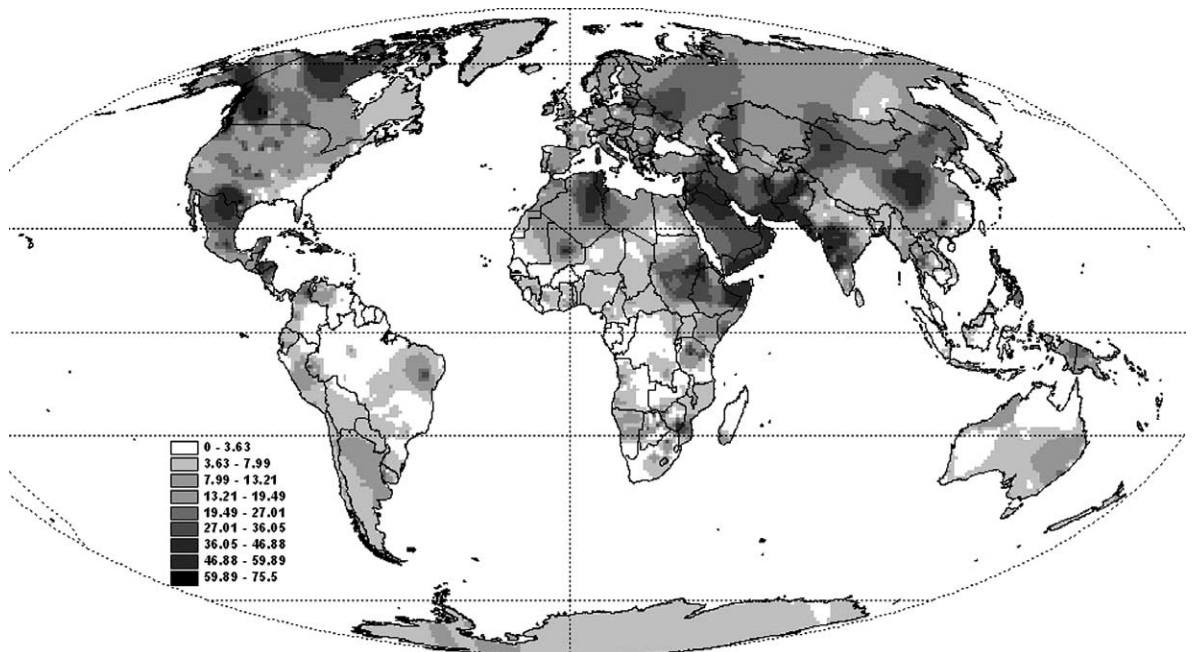


Fig. 1. A world map of exchangeable calcium (cmol/kg) in the upper horizon of the soil. The map was created in ArcView 3.3 by interpolating Ca^{2+} from 3699 sampling locations (data from Batjes 2002), then clipping the interpolation by landmasses (using Mila Grid Utilities 1.4 extension by Vincent Guissard of the Université catholique de Louvain, Belgium; <http://www.mila.ucl.ac.be/logistique/sig/sig-tools/milagrid/index.html>). Note that areas of low Ca^{2+} are concentrated between the tropic lines, whereas areas of high Ca^{2+} generally occur north of the Tropic of Cancer.

order of magnitude from temperate soils (Jordan and Herrera 1981, Brady and Weil 2002:351). The pattern is complex (Fig. 1; Huston 1993), but calcium tends to increase from the equator toward the poles; i.e., latitudinal variation is substantial (Fig. 2).

Geographic variation in clutch size

A critical relationship is whether *avian clutch size covaries with the amount of calcium available in the environment on a broad scale*. There is an abundance of evidence that avian clutch size increases with latitude (Moreau 1944, Lack 1954, Ashmole 1963, Kulesza 1990), a metric itself associated with calcium (Fig. 2). For example, mean clutch sizes of the song sparrow *Melospiza melodia* along the Pacific coast of North America increase from 3.05 eggs in Baja California to 4.17 eggs in Alaska (Johnston 1954), and clutch sizes of the northern flicker *Colaptes auratus* (Fig. 2) and the tree swallow *Tachycineta bicolor* across North America and the pied flycatcher *Ficedula hypoleuca* and the yellow wagtail *Motacilla flava* across Europe show similar increases with latitude (Koenig 1984, Jarvinen 1989, Bell 1996, Dunn et al. 2000). A variety of other bird species, both passerines and non-passerines, increase their clutches with increasing latitude (Cody 1966, Owen 1977), although the pattern may not be linear (Sanz 1998) and there are exceptions, especially among hole-nesting species that attempt single broods (Soler and Soler 1992).

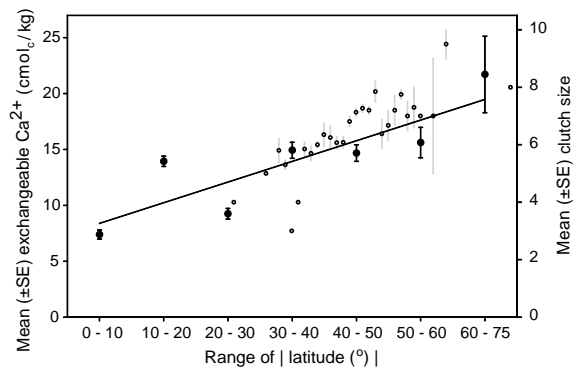


Fig. 2. The general relationship between latitude (treated as an absolute value) and exchangeable calcium in the upper horizon of the soil (filled circles). Ca^{2+} values were averaged by 10° latitudinal bands for the 3699 sampling locations compiled in Batjes (2002). The smaller number of sampling locations at high latitudes accounts for the larger standard errors there (e.g., $n = 820$ for 0–10° but $n = 39$ for 60–75°). For comparison, clutch size variation from 21° to 64° N latitude in the northern flicker *Colaptes auratus* complex, approximated from Koenig (1984: Fig. 2), is superimposed.

Of course, latitudinal variation in clutch size may have other causes, such as an increase in relative environmental productivity (Ashmole 1963, Koenig 1984, Dunn et al. 2000). Nonetheless, an apparent association between clutch size and available calcium appears in other dimensions. As noted above, geographic variation in exchangeable calcium is complex. Across eastern North America, for example, there is substantial longitudinal variation, with calcium generally increasing from the Atlantic coast to the Great Plains (Fig. 1). Thus, *if calcium is limiting, clutch size should increase accordingly*—i.e., it will not vary solely with latitude. A recent study of the eastern bluebird *Sialia sialis* supports this prediction: Dhondt and colleagues (2000) noted that, over the species’ range, longitudinal variation substantial: “All else being equal, a participant in Maine at 70° W would report a clutch size that was smaller by 0.46 eggs than a participant in North Dakota at 103° W.” Calcium likewise varies with longitude across western Europe, reaching a low on the Iberian Peninsula (Fig. 1; Huston 1993). Bell (1996) reported that the yellow wagtail clutch size increased not only with latitude but with longitude across this very gradient.

Lastly, if this pattern of coordinate variation between clutch size and calcium availability is general, then it should not be restricted to birds. Accordingly, another prediction will hold: *litter size in mammals or clutch size in fish or reptiles, for example, will also covary with environmental calcium*. Data in support of this prediction are similarly inferential, yet latitudinal variation parallel to that noted in birds has been documented in salmon (Fleming and Gross 1990) and turtles (Iverson et al. 1993). Moreover, Barclay (1994) argued that litter sizes in bats, and perhaps in other small mammals, are limited by calcium availability.

Rates of oögenesis and fledging time

Diminution of available calcium has another predictable consequence for egg formation. As noted above, females need supplemental calcium to produce eggs (see Reynolds 1997). *If little calcium is available, then egg formation should proceed at a slower rate*. Although hardly universal, this prediction is supported in part by the high incidence of egg laying ever other day in Neotropical suboscines, such as species in the families Thamnophilidae, Formicariidae, Tyrannidae, and Pipridae (Stutchbury and Morton 2001: 34), yet their temperate counterparts (i.e., in the Tyrannidae) lay daily, fitting the “expected” pattern. Increasing exposure of a nest (e.g., to predators, to harsh weather) has little conceivable adaptive value. I suggest that delayed laying is the result of being unable to form eggs faster. Likewise, lengthy nestling periods, often

resulting from increased frugivory in the tropics, may be associated with lower calcium availability, and there is even evidence that nestlings of tropical birds refuse excessive fruit but readily consume foods that promote development (Stutchbury and Morton 2001: 114–116).

Conclusions

The calcium hypothesis does not exclude potential effects that food (i.e., protein and fat) or water (Lack 1954, Patten and Rotenberry 1999, Coe and Rotenberry 2003) may have on clutch size. Instead it suggests a general explanation for geographic variation in clutch size, one that does not depend on different processes functioning in different ecosystems (cf. Martin et al. 2000). In essence, I hypothesize that calcium availability determines mean clutch size within a species across geographic scales, but local differences in food, water, or predation change the variance around that mean—e.g., variation in nest predation influences clutch size within a latitude, seemingly through an optimized reaction norm (Julliard et al. 1997), but does not explain differences among latitudes (Martin et al. 2000).

Calcium availability plays both a proximate and an ultimate role in the selection of mean clutch size. At the proximate level, a female unable to locate extrinsic calcium cannot produce as many eggs as a female able to do so. However, a reduction in calcium may not manifest itself immediately in a reduction of clutch size. Evidence from a variety of studies (Glooschenko et al. 1986, Graveland 1990, Graveland et al. 1994, Graveland and Drent 1997, Tilgar et al. 1999, Mänd et al. 2000, Reynolds 2001, Reynolds et al. 2004) strongly implies that reduced calcium often manifests itself in thinner eggshells or fewer fledglings, not smaller clutches. Thus, at the ultimate level, because thinner eggs break more easily, a sustained reduction in calcium should select for smaller clutches, as should an inability to fledge full-grown nestlings. Species breeding in areas impacted heavily by acid rain or other acidification may not have reduced clutch size yet, but if conditions persist natural selection will favor individuals that lay fewer eggs with thicker shells or that limit the number of nestlings. By contrast, the latitudinal gradient in environmental calcium (Jordan and Herrera 1981, Richter and Babbar 1991, Huston 1993) has existed for eons, allowing ample time for a matching gradient in clutch size to evolve. Researchers would do well to account for calcium limitation in studies involving variation in clutch size. Future work should incorporate tests of the effects of calcium, latitude, predation, food, and seasonality combined in

multivariate or model comparison analyses to determine the relative strength of these predictors.

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