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Permeability of Magpie and Blackbird Eggshells to Water Vapor: Variation Among and Within Nests of a Single Population

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Circumstantial evidence from studies of domestic fowl indicates that permeability of avian eggshells is a genetically controlled character (Smith 1973, Wangensteen et al. 1974). If permeability of an avian eggshell is, in fact, largely an expression of the genome of the female producing the egg, it is likely that the majority of the variation in permeability in a sample of eggs (and in the population from which the sample is drawn) is attributable to genetic differences among various females. Consequently, it may be that little new information about the population can be obtained by collecting more than one egg laid by a single female (Sokal and Rohlf 1969: 206ff).

To evaluate the hypothesis that most of the variation in permeability of eggs in a population stems from differences among clutches as opposed to differences among eggs within clutches, we collected three eggs from each of 10 nests of Black-billed Magpies (*Pica pica*) located east of Fort Collins, Colorado (T8N, R67W, S36, Weld County; elevation 1,554 m). Three eggs also were collected from each of 10 nests of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) nesting at Latham Reservoir near Greeley, Colorado (T4N, R65W, S1-2, Weld County; elevation 1,402 m). In the laboratory the eggs were placed randomly in vented desiccators above anhydrous calcium sulfate to maintain a dry atmosphere (Ar et al. 1974). The desiccators were held in a constant temperature cabinet at 25°C, a temperature too low for embryogenesis to proceed (White and Kinney 1974). Each egg was weighed six times on an analytical balance at intervals of 24 h, and the rate of weight loss—which is attributable largely to the escape of water vapor (Ar et al. 1974, Rahn et al. 1976)—was computed using a linear regression procedure. Subsequently, the volume of each egg was determined by displacement of water (Lynn and von Brand 1945), and surface area was calculated using the equation derived by Hoyt (1976).

Since vapor pressure inside the eggs approximated the vapor pressure of pure water at 25°C (i.e. 3.167 kPa; Lomholt 1976, Taigen et al. 1978), and since vapor pressure of the atmosphere inside the desiccators was zero, the permeability of eggshells to water vapor was calculated using the equation

$$K_{H_2O} = \dot{M}_{H_2O}/(\Delta P_{H_2O} \cdot A)$$

where K_{H_2O} is permeability of an eggshell to water vapor ($\mu g \cdot day^{-1} \cdot Pa^{-1} \cdot cm^{-2}$), $\dot{M}_{H_2O}$ is the rate of water loss in the desiccator ($\mu g \cdot day^{-1}$), ΔP_{H_2O} is the gradient in vapor pressure across the eggshell (Pa), and A is the surface area of the eggshell (cm^2). All values for permeability were adjusted to sea level conditions (barometric pressure = 101.325 kPa).

Data for eggs of both magpies and blackbirds were subjected to one-way analysis of variance, Model II (Sokal and Rohlf 1969), which revealed that variation in permeability of eggshells to water vapor is significantly larger among clutches than within clutches (Table 1). We subsequently partitioned the variance using methods outlined by Sokal and Rohlf (1969), and found that fully 85% of the total variation in permeability of magpie eggs could be assigned to the "among clutch" component. For eggs of Yellow-headed Blackbirds, 56% of the total variation in permeability stemmed from differences among clutches. [Similar analyses were performed on data for conductance of magpie and blackbird eggs to water vapor ($\bar{\bar{x}}$ = 8.566 and 9.091 $\mu g \cdot d^{-1} \cdot Pa^{-1}$, respectively), and on surface area of eggs ($\bar{\bar{x}}$ = 22.5 and 12.9 cm^2, respectively), and similar results were obtained in every instance.]

TABLE 1. One-way Analysis of Variance (Model II) of data for permeability of eggs of Black-billed Magpies and Yellow-headed Blackbirds to water vapor [grand means ($\mu g \cdot day^{-1} \cdot Pa^{-1} \cdot cm^{-2}$): magpie = 0.410; blackbird = 0.703]

Source of variation	df[a]	Sum of squares	Mean squares	F-ratio	Expected mean squares	Estimate of variance component	% total variation
				Black-billed Magpie			
Among nests	9	1.0643	0.1182	16.82 ($P < 0.001$)	$\sigma_W^2 + 2.79\sigma_A^2$	$\sigma_A^2 = 0.0398$	85.04
Within nests	18	0.1268	0.0070		σ_W^2	$\sigma_W^2 = 0.0070$	14.96
				Yellow-headed Blackbird			
Among nests	9	0.6081	0.0676	4.62 ($P < 0.005$)	$\sigma_W^2 + 2.79\sigma_A^2$	$\sigma_A^2 = 0.0190$	56.54
Within nests	18	0.2632	0.0146		σ_W^2	$\sigma_W^2 = 0.0146$	43.46

[a] The total df is 27, instead of 29, because 2 eggs were damaged in transit to the laboratory

Permeability of avian eggshells to water vapor may increase during incubation (Sotherland et al. 1979), perhaps as a result of small decreases in thickness of eggshells attending recovery of calcium from shells by developing embryos (Simkiss 1967). Thus, it is possible that a portion of the variation in permeability among clutches we sampled is attributable to differences in the amount of time the various clutches had been incubated and in the amount of development that had occurred before eggs were collected. However, since none of the magpie eggs contained an embryo with a chorioallantois, it is not likely that variation in permeability among clutches could have been caused by ontogenetic changes in permeability of eggshells (Sotherland et al., ms). Therefore, the largest portion of the variation in permeability of magpie eggshells to water vapor probably can be traced to individual (genetically based?) differences among the females producing the eggs.

Eggs in many of the blackbird nests had undergone considerable incubation prior to collection, and were characterized by advanced embryos and well-developed chorioallantoic membranes. Thus, we cannot attribute inter-nest variation in permeability of blackbird eggshells to water vapor solely to genetic differences among females in the nesting population, because a portion of the variation in permeability may have resulted from ontogenetic changes in the eggshells.

Since there frequently are limits to the number of eggs that may be collected and/or handled conveniently in the laboratory, experiments must be designed carefully in order to extract the largest possible amount of useful and reliable information from the samples. Data summarized in Table 1 indicate that eggs of a single clutch are more similar than eggs from different clutches (particularly in the case of the magpies), and therefore that collecting more than one egg from nests such as these yields relatively little new information about the population in question (Sokal and Rohlf 1969). Furthermore, when there is a limit to the number of eggs that may be collected, the probability of making an inaccurate prediction about the population is increased by taking more than one egg from each nest, rather than by collecting one egg from each of many more nests. Figure 1A represents the most probable result of collecting eggs from three nests in a population. Values grouped in such a manner provide an accurate estimate of the population mean, but at the same time underestimate the population variance. Figure 1B represents the next most probable result of collecting eggs from three nests in a population. Although this procedure yields accurate estimates of both the population mean and the population variance, the effective sample size is very small (see beyond). Figure 1C illustrates the least probable outcome of collecting eggs from three nests in a population; the procedure provides inaccurate estimates of both the population mean and the population variance. If only one egg is taken from a nest, eggs may be collected from many more nests, and there will be a greater probability of obtaining accurate estimates of the population parameters (Figure 1D).

Another disadvantage of collecting several eggs from each of a few nests is that there are fewer degrees of freedom obtained by collecting eggs in this way than by collecting the same number of eggs but taking only one egg from each of several nests. Eggs collected by deliberately taking more than one egg from a nest cannot be considered statistically to be independent samples from a population: only the mean values for the nests from which eggs were taken can be considered as independent samples from the population. However, eggs collected by taking one egg from each of several nests are independent samples

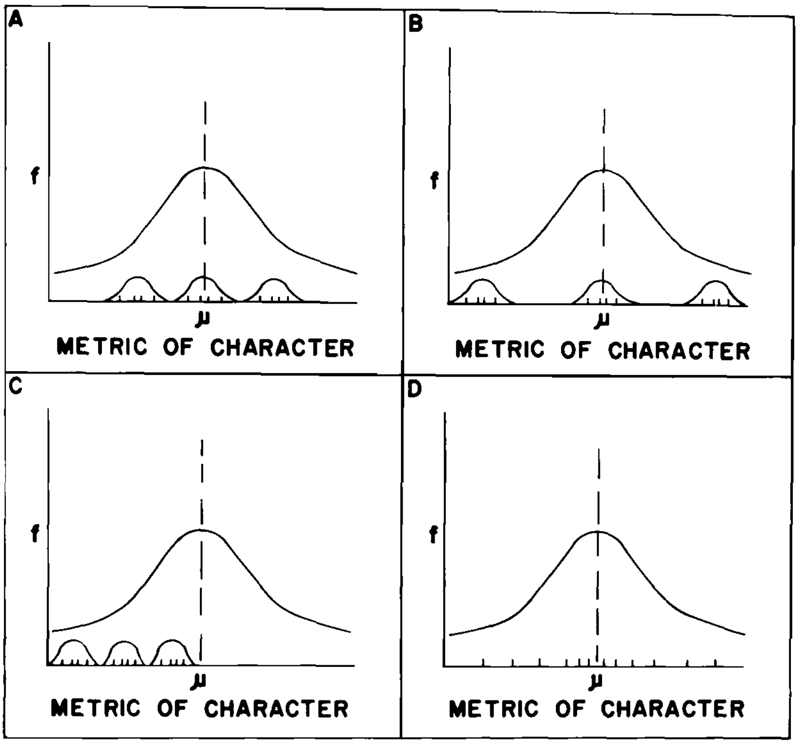

Fig. 1. Four possible results of collecting 12 eggs from a population. The large bell-shaped curves represent population frequency distributions; the three smaller bell-shaped curves in A, B, and C represent frequency distributions for individual nests. Small vertical lines along the abscissas are values of a character for individual eggs. A, B, and C are situations in which 12 eggs are collected by taking 4 eggs from each of 3 nests; D is a situation in which 12 eggs are collected by taking 1 egg from each of 12 nests. f = frequency; μ = true mean for the character.

from the population, because eggs acquired in such a manner have approximately the same probability of being collected. If each egg collected by taking several eggs from a nest is (erroneously) considered to be an independent sample from the population, the degrees of freedom will be increased artificially, and the estimate of the standard error will thereby be reduced. An inordinately low estimate of the standard error could lead investigators to conclude that a mean difference between populations is statistically significant when, in fact, no difference exists.

In summary, the majority of the variation in permeability of magpie and blackbird eggshells can be assigned to variation among clutches, which presumably reflects on genetic differences among females producing the eggs. Unless preliminary experiments have been performed to partition variation among and within clutches, it is best to assume that the "among clutch" component is the more important of the two. Thus, if a fixed number of eggs is to be collected, the most reliable sampling procedure is to take one egg from each of several nests rather than several eggs from fewer nests.

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Food-storing by Yellow-bellied Sapsuckers

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On four occasions during November and December in Nacogdoches, Texas we observed eastern Yellow-bellied Sapsuckers (*Sphyrapicus varius*) storing food. On 24 November 1977, an immature bird stored a whole pecan (*Carya illinoensis*) nut in a crevice of a dead pecan branch stub about 10 m above the ground. The sapsucker placed the nut in the crevice and pecked on it to wedge it into place. The bird had previously examined three other dead branch stubs and apparently found them unsuitable. While searching for a storage site with the pecan in its bill, the sapsucker repeatedly uttered its meow-like call.

On 8 December 1976, an adult male sapsucker removed a pecan from its covering, flew 15 m to a utility pole and wedged the pecan in a crevice 10 m above the ground near the top. He repeated the process three times.

On 13 December 1976, a juvenile male sapsucker fed on a southern magnolia (*Magnolia grandiflora*) fruit and then stored several 14 m above the ground in a crevice of an American elm (*Ulmus americana*). The next day the same bird stored red oak (*Quercus falcata*) acorns in the same elm tree. We did not observe sapsuckers preparing sites for food storage nor returning to feed on any of the stores.

Food storing has been reported in only six other North American picids, five of which are melanerpine (*Melanerpes erythrocephalus*: Kilham 1958, Wilson Bull. 70: 107–113; *Melanerpes carolinus*: Kilham 1963, Wilson Bull. 75: 227–234; *Melanerpes lewis*: Bock 1970, Univ. Calif. Publ. Zool. Vol. 92; *Melanerpes formicivorus*: MacRoberts 1970, Condor 72: 196–204; *Melanerpes aurifrons*: Martin and Kroll 1975, Wilson Bull. 87: 553). Alderson (1890, Oologist 7: 147) reported a Hairy Woodpecker (*Picoides villosus*) storing insects in an unused nest cavity. We believe this to be the first report of food storing by Yellow-bellied Sapsuckers, and it is of special interest because the genus *Sphyrapicus* belongs to the melanerpine assemblage of woodpeckers (Short and Morony 1970, Condor 72: 310–315).

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