

GEOGRAPHICAL ECOLOGY OF CLUTCH SIZE VARIATION IN NORTH AMERICAN WOODPECKERS¹

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Abstract. Clutch sizes of North American woodpeckers exhibit strong positive latitudinal gradients. There is no overall effect of either estimated first egg date or proximity to the coast on clutch size. However, mean clutch size varies inversely with an index of winter productivity and estimates of breeding densities of all woodpecker species combined; clutch size is uncorrelated with summer productivity. These results support Ashmole's hypothesis that geographic trends in fecundity are determined, at least in part, by seasonality of resources.

Key words: Ashmole's hypothesis; clutch size; geographic variation; Picidae; woodpeckers.

INTRODUCTION

Since Lack (1947, 1948) first focused attention on clutch size as a major topic of ornithological interest, geographical variation has served an important role in testing theories that seek to explain the evolution of clutch size (e.g., Cody 1966). Here I examine clutch size in North American woodpeckers (Picidae) with the aim of both describing the geographic patterns of variation and of relating those patterns to hypotheses concerning the evolution of clutch size. I discuss elsewhere clutch size variation within this taxon with respect to morphology and diet (Koenig, unpubl.); thus, here I focus primarily on geographic and climatic correlations.

A primary goal of the analyses performed here investigating the correlation between clutch size and climate is to examine Ashmole's hypothesis (Ashmole 1961, 1963). This hypothesis suggests that clutch size is determined by resource abundance during the breeding season relative to breeding population density. Ashmole further proposed that breeding population density was determined by winter resource abundance; hence, clutch size should be positively correlated with seasonality of resources (i.e., the ratio of summer to winter resources) rather than absolute resource abundance during any one season. Ashmole's hypothesis has been shown to be a powerful predictor of geographic patterns of clutch size variation both in a series of passerine communities (Ricklefs 1980) and in the Northern Flicker *Colaptes auratus* (Koenig 1984a), and has also been implicated as being important in a variety of other taxa (Grant and Grant 1980, Cockburn et al. 1983; see also Boyce 1979).

Species within the family Picidae are widely distributed and often common throughout North America. Furthermore, despite a fair degree of ecological diversity within the family, all species are altricial, cavity nesting, and (except for the Acorn Woodpecker *Melanerpes formicivorus*) monogamous, and thus the importance of these life-history features as sources of clutch size variation are minimized.

MATERIALS AND METHODS

Data on clutch size were obtained from collections in North American museums and from an ongoing study of the Acorn Woodpecker at Hastings Reservation, Monterey Co., California (Koenig and Mumme, in press). In both cases, I used only clutches which were known or thought to be complete based on information given in the collector's original data cards. For each clutch I determined latitude, longitude, estimated date of clutch initiation, and location in relation to a coastline (whether the clutch was collected within 1° of a coast or inland). Date of clutch initiation was estimated as the collection date, minus the number of eggs in the clutch, minus a correction factor based on an 11- to 14-day incubation period (Jackson 1977) and the estimated age of the clutch as determined by the stage of incubation listed by the collector. For further details on this estimator, see Koenig (1984a).

Data were handled in two ways depending on the goals of the analysis. First, individual clutches were used as independent data points for analyses in which it was desirable that intraspecific or intrageneric variation be preserved intact. Second, clutches of the same species collected within the same 1° block of latitude and longitude (latilong block) were combined. Means of clutch sizes collected from all species within a particular latilong block were averaged to obtain a mean for all woodpecker species occurring within that latilong

¹ Received 14 February 1986. Final acceptance 12 June 1986.

TABLE 1. Mean and latitudinal correlations of clutch size in North American woodpecker species and genera.^a

Species	Latitudinal range of sample	Mean \pm SD	Correlation with latitude (r_s)	<i>n</i> clutches
<i>Colaptes auratus</i>	26–54 (28°)	6.20 \pm 1.56	0.58***	468
<i>Melanerpes carolinus</i>	25–43 (18°)	4.31 \pm 0.76	0.14	61
<i>M. aurifrons</i>	14–34 (20°)	4.65 \pm 0.80	0.29*	55
<i>M. uropygialis</i>	24–38 (14°)	3.75 \pm 0.93	-0.02	69
<i>M. erythrocephalus</i>	29–44 (15°)	4.82 \pm 0.80	0.10	71
<i>M. formicivorus</i>	32–39 (7°)	5.06 \pm 1.06	0.14*	224
<i>M. lewis</i>	33–46 (13°)	5.88 \pm 1.19	0.32*	51
All <i>Melanerpes</i>	14–46 (32°)	4.81 \pm 1.39	0.24***	531
<i>Sphyrapicus varius</i>	38–55 (17°)	4.93 \pm 1.02	0.42***	46
<i>S. ruber</i>	34–46 (12°)	4.69 \pm 0.72	0.22	42
<i>S. nuchalis</i>	36–45 (9°)	4.77 \pm 1.09	—	17
<i>S. thyroideus</i>	34–46 (12°)	5.67 \pm 0.85	0.12	49
All <i>Sphyrapicus</i>	34–55 (21°)	5.08 \pm 0.98	0.03	154
<i>Dryocopus pileatus</i>	26–55 (29°)	3.80 \pm 0.77	0.24*	92
<i>Picoides villosus</i>	28–62 (34°)	3.93 \pm 0.72	0.26***	159
<i>P. pubescens</i>	28–61 (33°)	4.81 \pm 0.78	0.27***	205
<i>P. scalaris</i>	25–34 (9°)	3.81 \pm 0.76	-0.25	58
<i>P. nuttallii</i>	33–40 (7°)	4.34 \pm 0.77	-0.05	88
<i>P. stricklandi</i>	32 (0°)	3.50 \pm 0.84	—	6
<i>P. borealis</i>	28–36 (8°)	3.68 \pm 0.69	0.16	25
<i>P. albolarvatus</i>	33–46 (13°)	4.35 \pm 0.73	0.09	98
<i>P. arcticus</i>	43–55 (12°)	3.89 \pm 0.85	0.32	27
<i>P. tridactylus</i>	41–61 (20°)	3.87 \pm 0.64	—	15
All <i>Picoides</i>	25–62 (37°)	4.28 \pm 0.85	0.18***	681
All species	14–62 (48°)	4.93 \pm 1.45	0.22***	1,926

^a Correlations with latitude given only when the sample size is >25 clutches.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

block. Mean latilong clutch size data were then used in analyses involving climate and population density, as these latter variables could not be independently calculated for every clutch, but could be reasonably determined for geographic areas on the order of latilong blocks.

For each latilong block, I added the following two climatic variables as determined from the nearest station listed in Thornthwaite Associates (1964): mean "summer" actual evapotranspiration (AE), defined as the combined AE values for the three consecutive months yielding the highest total, and mean "winter" AE, defined as the combined AE values for the three consecutive months yielding the lowest total. Actual evapotranspiration is defined as precipitation minus runoff and percolation (Sellers 1965) and is directly related to primary productivity in terrestrial environments (Rosenzweig 1968). When combined into "summer" and "winter" values, AE data has a theoretically straightforward relationship to seasonality of resources and is thus appropriate for testing Ashmole's hypothesis (Ricklefs 1980; Koenig 1984a; but see below and Hussell 1985). Indeed, AE values have been previously shown to be a good predictor of geographic variation in clutch size in both passerine communities (Ricklefs 1980) and in the Northern Flicker (Koenig 1984a).

Data on the comparative abundance of populations was determined from the North

American breeding bird survey program administered by the U. S. Fish and Wildlife Service (Bystrak 1981). Mean abundance values were calculated for each species within each latilong block from over 18,000 surveys conducted over several thousand different routes. I assumed that woodpeckers constitute a reasonably cohesive "guild" (Root 1967), and thus, that the major competitors of woodpeckers are likely to be conspecifics. Accordingly, I combined the abundances of all woodpecker species in analyses involving breeding densities. Further details can be found in Koenig (1984a).

Taxonomy follows the AOU (1983, 1985). In all, a total of 1,926 complete clutches from 21 species of North American woodpeckers was analyzed. The Northern Flicker was excluded from some of the family-wide analyses because I have analyzed it in detail elsewhere (Koenig 1984a, b), and because the strong latitudinal trends and relative abundance of this taxon might otherwise unduly influence the results of analyses performed here.

RESULTS

THE LATITUDINAL GRADIENT

Mean clutch sizes (\pm SD) for the 21 species of woodpeckers considered are given in Table 1. Also listed in Table 1 are the latitudinal ranges

TABLE 2. Analysis of covariance of clutch size for individual species and for genera of North American woodpeckers excluding *Colaptes auratus*.

Variable	Regression slope	F-value	df
<i>Species</i>			
Covariates			
Latitude	0.026	35.3***	1, 1173
Est. first egg date	0.000	0.9	1, 1173
Main effects			
Species	—	22.9***	19, 1173
Proximity to the coast ^a	—	0.1	1, 1173
Explained ($R^2 = 0.286$)	—	12.8***	39, 1173
<i>Genera</i>			
Covariates			
Latitude	0.023	23.8***	1
Main effects			
Genus	—	57.8***	3
Explained ($R^2 = 0.120$)	—	49.3***	4

^a Whether the clutch was collected inland or within 1° of the coast.

over which clutches for each taxon were obtained and correlation coefficients for clutch size with latitude for each taxon for which I was able to find 25 or more complete clutches. Of the 18 species in this category, correlation coefficients were positive for 15 species (significantly so for 8 species spread throughout all 5 genera), and negative for only 3 species (none significantly so).

Examination of Table 1 suggests that the significance of the latitudinal correlation for individual species depends in part on the range over which clutches were collected and on the sample size. The first of these relationships was confirmed by a Mann-Whitney *U*-test comparing the latitudinal range for each species according to whether the latitudinal correlation with clutch size was significant at the 0.05 level or not; a highly significant difference was found (z -value = 5.04, $P < 0.001$). The second was tested by dividing species into three categories based on the number of clutches obtained ($N > 100$, 51 to 100, and 25 to 50). All

four species (100%) in the first category yielded significant correlations with latitude, while only two of six (33%) in the second category and one of four (25%) in the third category did so ($\chi^2 = 6.7$, $df = 2$, $P < 0.05$). These results indicate that the interspecific differences in the correlation between clutch size and latitude listed in Table 1 are largely an artifact: the likelihood that a significant correlation occurs is a function of the sample size and the latitudinal range over which samples were obtained.

Table 1 also lists mean clutch size for each genus under consideration. Clutch sizes of all five genera correlate positively with latitude, and only that for sapsuckers (*Sphyrapicus*) is not significant. (The sample size and latitudinal range for *Sphyrapicus* is large enough to suggest that this may reflect a real generic difference.) Using all individual clutches combined (either including or excluding *C. auratus*), there is also a highly significant latitudinal gradient. Analyses of covariance similarly indicate the importance of latitude as a predictor of clutch size within the family, even when *C. auratus* is excluded (Table 2).

The data in Table 2 also indicate that, at least on a familywide basis, neither estimated first egg date nor proximity to the coast significantly influence clutch size. In both the analyses in Table 2 the covariates (including latitude) were controlled prior to consideration of the main factors. Thus, there remain highly significant interspecific and intergeneric differences in clutch size after controlling for latitude.

ASHMOLE'S HYPOTHESIS

Ashmole's hypothesis predicts that geographic variation in clutch size is correlated with seasonality of resources (Ashmole 1961, Ricklefs 1980). Prior analyses (Ricklefs 1980, Koenig 1984a) have tested for such a correlation by comparing clutch size with the ratio of summer to winter actual evapotranspiration. As pointed out by Hussell (1985), however, a stricter interpretation of Ashmole's hypothesis suggests that the appropriate test is between clutch size and $(S - W)/W$, where S = summer and

TABLE 3. Spearman rank correlations between variables using mean values for each latilong block. $n = 297$ latilongs except for correlations involving breeding density, for which $n = 262$ latilongs.

	Latitude	Summer AE	Winter AE	Summer AE-winter AE	Breeding density all picids
Mean clutch size all picids	0.37***	-0.06	-0.32***	0.00	-0.17**
Latitude	—	-0.07	-0.76***	0.06	-0.24***
Summer AE	—	—	-0.05	0.97***	0.32***
Winter AE	—	—	—	-0.22***	0.22***
Summer AE-winter AE	—	—	—	—	0.31***

TABLE 4. Regressions of mean clutch size for all woodpeckers combined by latilongs on actual evapotranspiration and breeding density. Variables are log-transformed.

Variable	Regression slope	F-value	df
<i>Actual evapotranspiration</i>			
Summer AE	-0.019	0.6	1, 294
Winter AE	-0.044	31.1***	1, 294
Explained ($R^2 = 0.096$)	—	15.5***	2, 294
<i>Summer AE and density</i>			
Summer AE	-0.014	0.3	1, 259
Density	-0.112	5.0*	1, 259
Explained ($R^2 = 0.020$)	—	2.9	2, 259

W = winter AE. In Table 3 I present correlations between the mean clutch size of all picids, determined for each latilong block as described above, with latitude, S , W , and $S - W$, and the estimated breeding density of all woodpeckers. Using these data there is again a strong positive latitudinal gradient in clutch size. There is no correlation between variation in mean clutch size and either S or $S - W$, while clutch size correlates inversely with both W and breeding density. The correlation between S and $S - W$ is close to unity, indicating that Hussell's (1985) correction is unnecessary for this data set. I will thus use only S , rather than $S - W$, in the following analyses.

The top half of Table 4 presents the results of a multiple regression of $\ln[\text{mean clutch size}]$ by latilongs on $\ln[S]$ and $\ln[W]$. As expected based on the results in Table 3, W correlates inversely with mean clutch size, while there is no relationship between clutch size and S . Thus, variation in mean clutch size correlates with S/W due to the inverse correlation between clutch size and W .

On a proximate level, Ashmole's hypothesis predicts that geographic patterns in clutch size are determined by the ratio of resources available for reproduction to breeding population density. This prediction is tested in the lower half of Table 4 with the latilong data using S and the estimates of population density for all woodpeckers combined derived from the breeding bird surveys. The results indicate that clutch size again is uncorrelated with S . However, mean clutch size decreases significantly with increasing density.

Although there is a strong correlation between winter AE and latitude (Tables 3 and 4), there remains a highly significant latitudinal gradient even after controlling for winter AE (using the combined mean clutch size data, a multiple regression of $\ln[\text{clutch size}]$ on lati-

tude controlling for $\ln[W]$ yields an F -value of 10.6, $df = 1, 295$, $P < 0.01$).

DISCUSSION

There is a strong positive latitudinal gradient in clutch size among North American woodpeckers (Table 1). Fifteen of 18 species (83%) with adequate data and four of five genera (80%) yield positive correlations between clutch size and latitude, significantly so for eight species and four genera. Only three species had negative correlations between clutch size and latitude; two of these were very weak and none was significant. Furthermore, interspecific differences in the significance of the observed latitudinal trends appear to be largely a function of sample size and the latitudinal range over which clutches were obtained. Thus, North American woodpeckers join the ranks of the variety of other birds and mammals for which strong latitudinal gradients in clutch size have been described (e.g., Lack 1947, Lord 1960, Cody 1966).

I have shown elsewhere (Koenig 1984a) that there is no correlation in *C. auratus* between clutch size and either first egg date or proximity to the coast when controlling for latitude. The identical pattern holds within the family as a whole excluding *C. auratus* (Table 2). Clutch size may still decrease with date at a particular locality; however, the latitudinal gradient masks whatever date or coastal effects may be present on a finer geographic scale (see Moore and Koenig 1986).

Table 2 also indicates that there are significant interspecific and intergeneric differences in clutch size within the family even after controlling for latitudinal differences. At least some of these differences are related to differences in foraging ecology and feeding behavior, with species more dependent on wood-boring beetle larvae tending to have smaller clutches than those dependent on other resources (Koenig, unpubl.). In addition, migratory species tend to have larger clutches while species with greater sexual dimorphism in culmen length tend to have smaller clutches. Nonetheless, a major geographic gradient within the family remains even after interspecific variation is removed.

Mean clutch size of North American woodpeckers varies inversely with winter AE (W) and with the breeding density of all picids but does not correlate with summer AE (S) or with $S - W$. These results are further supported by multiple regressions (Table 4). Insofar as AE values represent seasonal availability of resources, these results thus support all four predictions of Ashmole's hypothesis (including the proposition that winter resources limit breed-

ing population size) delineated by Møller (1984, see also Hussell 1985): (1) clutch size is inversely correlated with winter resources (Table 3), (2) clutch size is positively correlated with resources per breeding pair (lower half of Table 4), (3) clutch size is positively correlated with the ratio of summer to winter resources (upper half of Table 4), and (4) clutch size is uncorrelated with summer resources (Table 3).

These results, along with the community-wide analysis of Ricklefs (1980) and my earlier analysis of *C. auratus* (Koenig 1984a), all lend support to the role of seasonality of resources in determining geographic variation in clutch size. There are, however, several reasons to continue investigation of the factors influencing geographic trends in fecundity. First, seasonality of resources can explain only a small fraction (2.0 to 9.6% based on the R^2 values in Table 4) of the total variance in clutch size, and there remains a strong, highly significant latitudinal gradient even after controlling for winter AE. Similar results were found for *C. auratus* alone (Koenig 1984a). Thus, at best, Ashmole's hypothesis would appear to be able to explain only a fraction of the geographic variation in clutch size within North American woodpeckers.

Second, the analyses performed here, as well as the earlier studies of Ricklefs (1980) and Koenig (1984a), also involve several shortcomings. The tests performed are only indirect, some of the data (in particular, the breeding bird surveys) are only rough approximations, and no alternative hypotheses for the observed geographic patterns have been rigorously tested (Koenig 1984a). In addition, as pointed out by Hussell (1985), even the fulfillment of the above predictions of Ashmole's hypothesis cannot be considered definitive inasmuch as many environmental and biological variables correlate with latitude, and therefore with clutch size as well. I agree with Hussell (1985) that evidence beyond the correlations detected here and in prior studies will be necessary before firm conclusions concerning the evolution of geographic variation in clutch size can be drawn.

One approach that goes beyond the analyses presented here is the investigation of interseasonal variation in clutch size as a function of population density and food resources. Such an analysis for the Acorn Woodpecker indicates that yearly variation in clutch size within a population correlates significantly with the resources available for breeding per individual as indicated by the number and energetic content of stored acorns per bird (Koenig and Mumme, in press). Because it involves a single

population, this finding eliminates the confounding effects of latitudinal correlates such as varying daylength. Nonetheless, even this analysis fails to go beyond simple correlations, and it obviously fails to directly address the issue of geographic variation in clutch size. Thus, experimental manipulation and consideration of time-activity budgets, as suggested by Hussell (1985), are desirable to test alternative hypotheses of clutch size variation.

Seasonality of resources is unlikely to solve the problem of geographic variation in clutch size (see also Møller 1984). However, its relative success in a spectrum of analytical levels suggests that it influences clutch size in a variety of taxa. Ashmole's hypothesis clearly deserves careful consideration in all studies of geographic variation in fecundity.

ACKNOWLEDGMENTS

Data used in these analyses were collected from the American Museum of Natural History, California Academy of Sciences, Chicago Academy of Sciences, Delaware Museum of Natural History, Florida State Museum, Milwaukee County Public Museum, Moore Laboratory of Zoology, Museum of Vertebrate Zoology, National Museum of Natural History, San Bernardino County Museum, Santa Barbara Museum of Natural History, and Western Foundation of Vertebrate Zoology; I thank those who aided and abetted my data collecting forays to these collections. Janet Conley, Nancy Joste, Ron Mumme, Pam Williams, and especially Maria Pereyra helped with various aspects of data collecting, coding, and analysis. D. Bystrak provided the breeding bird census data, and Occidental College provided access to computer facilities. Numerous helpful comments were provided by Jon Greenlaw and Dennis Paulson. Financial assistance came from the Frank M. Chapman fund of the American Museum of Natural History. Field work on the Acorn Woodpecker at Hastings Reservation has been supported by NSF grant BSR8410809.

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