GEOGRAPHIC VARIATION IN CLUTCH SIZE IN THE NORTHERN FLICKER (*COLAPTES AURATUS*): SUPPORT FOR ASHMOLE'S HYPOTHESIS

WALTER D. KOENIG

Hastings Reservation and Museum of Vertebrate Zoology, University of California, Star Route Box 80, Carmel Valley, California 93924 USA

ABSTRACT.—The Northern Flicker (*Colaptes auratus*), a common hole-nesting North American woodpecker, exhibits a highly significant latitudinal increase in clutch size. Using preserved clutches and information on climatic conditions and breeding densities of confamilial species, I examined the hypothesis that this geographic trend is the result of seasonal fluctuations in resources ("Ashmole's hypothesis"; Ashmole 1961, 1963; Ricklefs 1980). Clutch size is significantly correlated both with the ratio of summer productivity to estimated breeding densities of all woodpecker species and with the ratio of summer to winter productivity, supporting Ashmole's hypothesis. In addition, a substantial portion of the latitudinal gradient can be directly explained by the seasonality of resources, primarily because of an inverse correlation between clutch size and winter productivity. These results provide the first corroboration of Ashmole's hypothesis from an examination of intraspecific clutch-size variation and suggest that geographic trends in fecundity in some cases may be largely attributable to trends in seasonal fluctuations of resources. *Received 5 December 1983, accepted 2 April 1984.*

DESPITE challenges and numerous modifications (see Stearns 1976, Winkler and Walters 1983), there is general agreement that clutch size is ultimately adjusted to the food supply by natural selection to reflect the number that, when considered over the lifetime of the individual, results in the most young surviving to maturity and attaining reproductive status (Williams 1966). Consensus breaks down, however, when the environmental and ecological factors that influence clutch-size variation are considered. Variables such as daylength (Lack 1954); population stability (Slagsvold 1981); habitat stability (Cody 1966, MacArthur and Wilson 1967); risk of nest predation (Slagsvold 1982a); allocation of time and energy among competing activities, including antipredator tactics and interspecific competition (Cody 1966, Ricklefs 1970); and seasonality of resources (Ashmole 1961, 1963; Boyce 1979; Ricklefs 1980) have all been suggested to be crucial in determining the patterns of clutch-size variation that correlate with various geographical and ecological gradients.

These hypotheses are not necessarily mutually exclusive, but to test them simultaneously would require extensive data gathered over a wide geographic area, not only on clutch size but on demography, competitive and predatory community interactions, and climatic conditions. In lieu of obtaining such comprehensive information, it is possible to examine any particular hypothesis only by comparing the consistency of geographic trends with the specific predictions that stem from it. Here, I focus on "Ashmole's hypothesis" (Ashmole 1961, 1963; Ricklefs 1980), which suggests that geographic variation in clutch size is primarily determined by absolute resource abundance relative to breeding population density. This hypothesis has recently been supported by Ricklefs (1980) through his analysis of the mean clutch size of several passerine communities. I examine this hypothesis by using data from a single altricial species, the Northern Flicker (*Colaptes auratus*). This hole-nesting woodpecker was chosen because of its wide distribution and the large number of clutches available for it. Specifically, I (1) analyze geographic trends in clutch size in this species and (2) investigate factors controlling clutch size, primarily with respect to Ashmole's hypothesis, by comparing these trends with climatic data and estimates of the breeding population densities of competing taxa.

METHODS

Clutch-size data were gathered from various North American museum collections; all forms of the *Colaptes auratus* complex were included except for the "Gilded" Flicker (*C. a. chrysoides*), whose clutch size is so different from that of other flickers (Koenig 1984)

that it was excluded from the analyses. (All proce-
dures were also run with the inclusion of *C. a. chry-
soides,* and the results differ only in detail from those
presented here.) Original data cards were consulted
to obtain the locality, date of collection, stage of in-
cubation, and the number of eggs of each clutch.
Clutches for which incubation was reported to have
been "slight," "just begun," or "one-quarter or be-
yond" were considered to be complete; those for
which the incubation stage was either unknown or
stated to have been "fresh" or "none" were consid-
ered to be potentially incomplete. For the analysis of
the influence of first-egg date on clutch size, the first-
egg date was taken to be the date of collection, minus
the number of eggs in the set, minus a correction for
the stage of incubation. The incubation period of
flickers is 11–14 days (Jackson 1977), and the assumed
clutch-initiation date was corrected by subtracting the
following number of days for the associated stage of
incubation: 2 ("slight," "just begun," "¼," or "2–5
days"), 4 ("begun," "commenced," or "started"), 7
("small embryo," "well begun," "½," or "5–7 days"),
10 ("advanced," "large embryo," or "well ad-
vanced").

For each clutch, information on geographic posi-
tion, climate, and population density were added as
follows.

Geographic position.—The latitude and longitude of
each locality, to the nearest degree, as well as wheth-
er the locality was coastal (insular or within 1° of
longitude of the coast) or inland (not within 1° of
longitude of the coast), were added to each clutch
record.

Climate.—The station nearest each locality for which
climatic water-balance data are given by Thorn-
thwaite Associates (1964) was determined; stations
were usually within 50 km of collecting localities.
From monthly data on mean precipitation (PPT) and
actual evapotranspiration (AE), the following vari-
ables were recorded: (1) overall mean annual PPT,
(2) overall mean annual AE, (3) combined PPT for
April, May, and June, (4) combined AE for April,
May, and June, (5) the maximum AE for 3 consecu-
tive months in the year, and (6) the minimum AE for
3 consecutive months in the year.

AE, defined as PPT minus runoff and percolation
(Sellers 1965), is qualitatively related to the amount
of vascular plant activity (primary productivity) in
terrestrial environments (Rosenzweig 1968) and is
thus probably a consistent estimate of overall re-
source availability for virtually any animal, regard-
less of exact diet or trophic level (see Discussion).
Following Ricklefs (1980), I added the three highest
consecutive monthly AE values for an estimate of
"summer" AE and the 3 lowest consecutive values
for "winter" AE.

Population density.—Census data from the North
American breeding-bird-survey program adminis-
tered by the United States Fish and Wildlife Service
were used as estimates of the breeding-population
densities of woodpeckers. These surveys are done
throughout the United States and Canada and consist
of censusing the breeding birds for 3 min at a series
of 50 stops 0.8 km apart along a road transect (Bys-
track 1981). Data from these surveys were condensed
as follows. First, the number of individuals of each
species of woodpecker recorded along each route was
averaged over all years that the survey was run (this
varied from 1 to 16 yr). Then, the latitude and lon-
gitude of each route was rounded to the nearest de-
gree, and census values for a route were averaged
with others within the same 1° block of latitude and
longitude ("latilong"). Finally, the mean census val-
ues for all species of woodpeckers combined were
added to each clutch-size record. In all, data from
over 18,000 censuses covering several thousand routes
were used. These estimates, although rough, are
nonetheless obtained in a uniform way and are thus
likely to be comparable throughout the large geo-
graphic region of interest.

Data analysis.—The combined clutch-size, geo-
graphic, climatic, and population-density data were
analyzed in two ways. First, each clutch-size record
was considered independently; in all, 1,164 clutches
of *Colaptes auratus* were obtained, of which 411 were
complete. Only these 411 complete clutches were
used. Second, I combined all complete clutches from
each latilong and used the means for each latilong as
a single datum. These values were then recombined
with the geographic, climatic, and census data. This
modification minimized the statistical difficulties re-
sulting from repeated use of the same climatic and
census data for all clutches near a particular locality
(within the same latilong block). Hence, these results
are used whenever the climatic or census data are
involved. Logarithmic transformation was used when
the ratio of two variables was of interest, as this
transformation, followed by a multiple regression,
provides a convenient way to assess interrelation-
ships of variables.

The distributions of both clutch-size data sets were
significantly non-normal by the Kolmogorov-Smir-
nov goodness-of-fit test (Sokal and Rohlf 1981); thus,
Spearman rank tests were used to assess correlations.
In lieu of comparable nonparametric tests, however,
regressions and analyses of variance were performed
when the interrelationships of several variables were
of interest. Cochran (1947) and Donaldson (1968)
conclude that F-tests, used here, are robust to modest
violations of normality. Nonetheless, results from
these analyses must be taken with caution. Two-tailed
tests are employed, and P values less than 0.05 are
considered significant.

RESULTS

The mean size of the 411 complete clutches
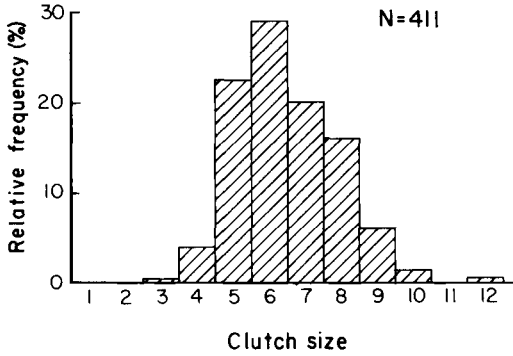used in the analyses was 6.5 eggs (SD = 1.4).

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Fig. 1. The distribution of clutch sizes among complete clutches of the Northern Flicker, exclusive of *C. a. chrysoides*. Mean ± SD = 6.5 ± 1.4 eggs.

The distribution ranged from 3 to 12 eggs, with the majority being between 4 and 9 (Fig. 1). Two geographic and one temporal trend were examined for their influence on clutch size.

First, using either all complete clutches or the lumped latilong data, I found a highly significant positive correlation between clutch size and latitude (Fig. 2, Table 1). In both cases, mean

clutch size increases by slightly over 1 egg for every 10° increase in latitude. Second, after adjusting for the stage of incubation (see above), I found that clutch size increases significantly with date (Spearman rank $r_s = 0.15$; $n = 405$; $P < 0.01$). Finally, I found that there is a tendency for clutches collected near the coast to be smaller than those obtained inland. Inland clutches average 6.9 eggs ($n = 197$), compared with 6.1 eggs for coastal clutches ($n = 207$); this difference is significant (Mann-Whitney U-test, $z = 5.2$; $P < 0.001$). In a multiple regression of clutch size on both date and latitude, however date is not significant ($F = 0.03$; df = 1,404; ns). Similarly, the coastal influence disappears when latitude is controlled for in an analysis of covariance (F-value for coastal effect controlled for latitude = 2.8; df = 1,401; ns). Refining the coastal category to include only clutches collected either within ½° or ⅛° of longitude of the coast fails to alter the significance of this difference. Thus, although these variables may be important in particular cases or within individual populations, neither date nor proximity to the coast has a detectable effect on clutch size independent of latitude on the macrogeographic scale under consideration here.
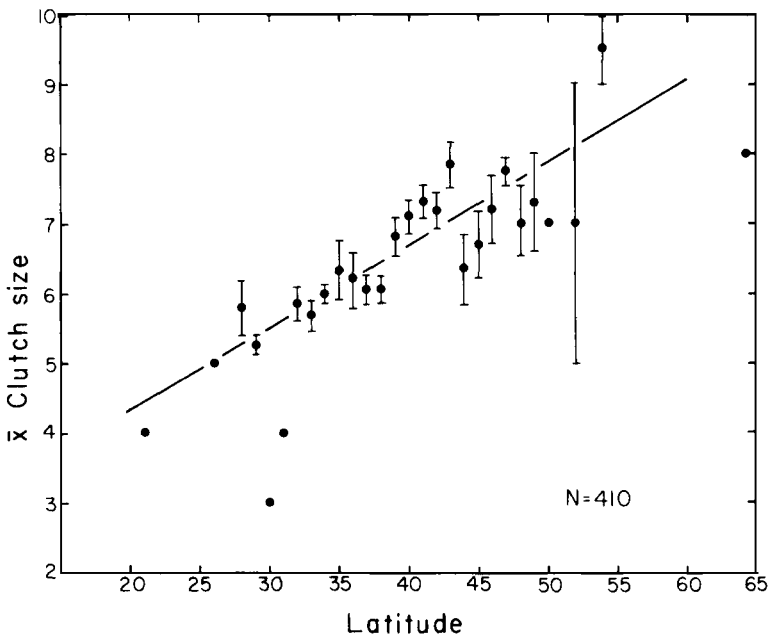

Fig. 2. Mean clutch size ± SE by latitude for *Colaptes auratus*. Sample sizes for each degree of latitude vary from 1 to 77. Regression (using individual clutches) is: clutch size = 0.118 (latitude) + 1.97 ($r^2 = 0.21$; $F = 106.81$; df = 1,408; $P < 0.001$).

TABLE 1. Full and partial correlation coefficients of mean clutch of Northern Flickers by latilongs with geographic, climatic, and breeding-density variables. Sample size refers to latilong blocks.

	Spearman r	Pearson or partial r	P-value	n
Latitude	0.48	0.49	<0.001	121
Controlling for summer AE	—	0.49	<0.001	117
Controlling for winter AE	—	0.30	<0.001	117
Controlling for breeding density of all picidae	—	0.40	<0.001	107
Climatic variables				
Total mean annual PPT	0.03	—	ns	121
Total mean annual AE	−0.02	—	ns	121
PPT April–June only	0.09	—	ns	121
AE April–June only	0.06	—	ns	121
Summer AE	0.03	—	ns	121
Winter AE	−0.48	—	<0.001	121
Breeding density of Picidae	−0.29	—	<0.01	111

Thus, these variables were ignored in subsequent analyses.

Prediction 1: clutch size and seasonal productivity.—Ashmole's hypothesis states that clutch size is determined by resource abundance relative to breeding population density. Ashmole further postulated that populations are regulated by resources during the nonbreeding season; hence, clutch size should correlate with seasonality of resources, irrespective of absolute resource level (Ricklefs 1980). A first test of Ashmole's hypothesis is thus to correlate clutch size with climatic variables related to the seasonal availability of resources. Spearman rank
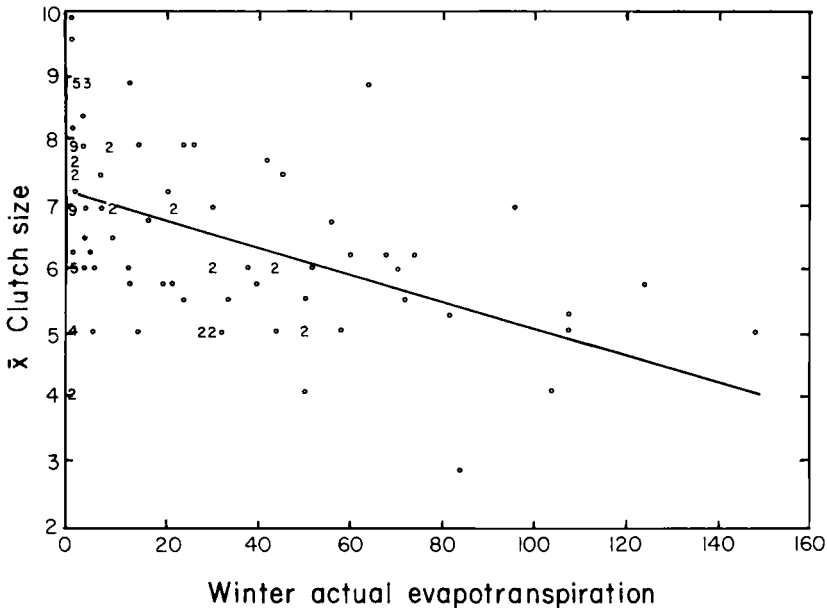

Fig. 3. Mean clutch size by latilongs versus winter AE in millimeters (lowest value of AE for 3 consecutive months; see text). Plotted numbers refer to multiple points (9 = more than 8 latilongs with the plotted value). Regression is: clutch size = −0.21 (winter AE) + 7.17 (r^2 = 0.21; F = 32.2; df = 1,119; P < 0.001).

correlations with the six climatic variables investigated here indicate that only winter productivity correlates significantly with mean clutch size (Table 1): clutch size increases as winter productivity in an area decreases (Fig. 3). No significant correlations exist between clutch size and summer or total annual productivity (Table 1).

As a result of the inverse correlation between clutch size and winter AE, clutch size is significantly correlated with the seasonality of resources, as indexed by the ratio of summer to winter AE (transforming all three variables logarithmically and performing a multiple regression yields an F-value of 16.9; df = 2,118; $P < 0.001$), but this is mostly due to the inverse relationship between clutch size and winter AE (partial correlation coefficient = -0.41; $F = 33.5$; df = 1,118; $P < 0.001$); summer AE is unrelated to clutch size (partial correlation coefficient = -0.09; $F = 0.9$; df = 1,118; ns).

Prediction 2: clutch size and breeding-bird density.—Ashmole's hypothesis can be examined more directly by using estimates of population size derived from the breeding-bird-census data. Needed are relative estimates of the densities of all individuals competing for generally similar resources. I used the breeding density of all species of woodpeckers combined on the assumption that, at least as a first approximation, woodpeckers can be considered a "guild" (Root 1967) and that the largest competitive influence on flickers is likely to come from other woodpeckers, including conspecifics. The correlation of flicker clutch size with the estimated breeding-bird density of all woodpeckers combined is significantly negative (Table 1). Furthermore, clutch size correlates significantly with the ratio of the density of all woodpeckers combined to summer productivity, as indicated by a multiple regression using the two transformed variables (F-value = 4.7; df = 2,108; $P < 0.05$). This correlation appears to be largely the result of the inverse relationship between clutch size and total breeding density (partial correlation coefficient = -0.27; $F = 8.7$; df = 1,108; $P < 0.01$); summer AE is again unrelated to clutch size (partial correlation coefficient = 0.06; $F = 0.4$; df = 1,108; ns).

Ashmole's hypothesis and the latitudinal gradient.—Of particular interest is the extent to which Ashmole's hypothesis can explain the strong latitudinal gradient in clutch size of the Northern Flicker. I examined this question by use of partial correlation analyses (Table 1). Controlling for winter AE results in a partial correlation coefficient of 0.30 between latitude and clutch size. This value, although highly significant, is only 61% of the simple correlation coefficient of 0.49 between the two variables (Table 1). Controlling for summer AE has no influence on the correlation between latitude and clutch size, and controlling for breeding density of woodpeckers decreases the partial correlation coefficient to 0.40. Thus, controlling for winter AE or breeding-population density, important components of Ashmole's hypothesis, reduces the correlation between clutch size and latitude by up to 40%.

DISCUSSION

Similar to a variety of other birds and mammals (e.g. Lack 1947, Lord 1960, Cody 1966), Northern Flickers exhibit a highly significant latitudinal increase in clutch size (Table 1, Fig. 2). I examined the hypothesis that this trend ultimately results from a direct relationship between clutch size and seasonal fluctuation of resources, an hypothesis suggested by Ashmole (1961, 1963) and supported on theoretical grounds more recently by Boyce (1979). Ashmole further suggested (anticipating Fretwell 1972) that populations are limited during the nonbreeding season, when resources are scarce. Given this hypothesis, a correlation should exist between winter resources and breeding population density. Hence, two correlations are predicted: first, between clutch size and a seasonal fluctuation in resources independent of absolute resource abundance and, second, between clutch size and the ratio of summer resources to breeding population density. This latter correlation is, in turn, dependent on the assumed correlation between winter productivity and breeding-bird density (see Ricklefs 1980, Fig. 1, for a graphical representation of Ashmole's hypothesis).

Ricklefs (1980) tested Ashmole's hypothesis by using mean clutch sizes of passerine communities in several disjunct localities. His results support the above predictions: a strong relationship both between mean clutch size and the ratio of summer AE to winter AE (due to a strong inverse correlation between clutch size and winter AE) and between clutch size and the ratio of summer AE to local breeding densities of passerines (as measured by population

censuses in five localities) was found. Ashmole's hypothesis has also been suggested to be important in explaining the relatively large clutches among Darwin's finches (*Geospiza*) compared with other finches on the adjacent Ecuadorian mainland (Grant and Grant 1980), as well as the geographic variation in brood size in the marsupial genus *Antechinus* (Cockburn et al. 1983).

In contrast to the above studies, the analyses performed here involve intraspecific clutch-size variation. Nonetheless, the trends relating clutch size in flickers to the degree of seasonal fluctuation in resources as measured by AE values and by breeding-bird densities are strikingly similar to the patterns derived by Ricklefs (1980) using mean clutch sizes of entire communities. First, there is a significant positive correlation between clutch size in the Northern Flicker and the ratio of summer to winter AE, and, as in Ricklefs' data, this is due to a strong inverse correlation between clutch size and winter AE (Table 1, Fig. 3); clutch size and summer AE are unrelated. Second, clutch size in this species is directly correlated with the ratio of summer productivity to breeding density of all woodpecker species combined; this relationship stems, at least in part, from a highly significant correlation between winter productivity and estimated breeding population density ($r_s = 0.33$; $n = 223$; $P < 0.001$).

Thus, Ashmole's hypothesis is supported by geographic patterns in clutch size in the Northern Flicker. Not only are seasonal fluctuations in resources highly correlated with clutch size, but the strong inverse correlation of clutch size with winter productivity (coupled with the lack of significant correlations between clutch size and either breeding-season or total yearly productivity) lends support to Ashmole's suggestions that breeding populations are regulated by winter resources and that fecundity is ultimately linked to seasonality rather than to absolute resource abundance. As in the data analyzed by Ricklefs (1980), breeding-season production is simply too uniform geographically to cause the major trends in clutch size documented here in the Northern Flicker.

The latitudinal gradient, however, is not completely explicable on the basis of Ashmole's hypothesis; a significant latitudinal trend remains after controlling for either seasonality or breeding densities of woodpecker species

(Table 1). This failure of Ashmole's hypothesis to account more completely for the latitudinal gradient is not surprising, given the many other factors that may influence clutch size. For example, such diverse factors as predation rates on nests (Ricklefs 1977a, b; Slagsvold 1982a), population stability (Slagsvold 1981), population density (Klomp 1970), and adult mortality (Ricklefs 1977a, b) have been suggested as partial causes of geographic trends. To the extent that any or all of these variables may be important, it is unrealistic to expect any single hypothesis to account for geographic patterns in clutch size completely. Similarly, given the multitudes of factors that have been identified as influencing intrapopulational variation in clutch size [e.g. female age (Klomp 1970), female condition (Askenmo 1982, Loman 1982), age of the pair bond (Cullen 1968), nest size (Karlsson and Nilsson 1977, Slagsvold 1982b), territory quality (Högstedt 1980), season (Kluijver 1951, Lack 1954, Yom-Tov 1974), year (Lack 1954), and local differences in food abundance (Kluijver 1951, Lack 1954)], it is unlikely that any single variable, such as latitude, will explain all or even the majority of variance in clutch size in any species.

Nonetheless, clutch size appears to have a strong heritable basis (Klomp 1970, Yom-Tov 1974, Perrins and Jones 1974, van Noordwijk et al. 1980, Findlay and Cooke 1983); thus, geographic patterns are likely to reflect, at least in part, adaptive variation. In the Northern Flicker, latitude accounts for 21% of the variance in all individual clutches (Fig. 2). It is thus of considerable importance to determine the factors that appear to be playing a significant role in producing this trend. As stated by Ricklefs (1980: 38), the direct relation between clutch size and latitude is so general as to be the pattern "... by which all hypotheses about clutch size are ultimately tested." In both Ricklefs' analysis involving passerine communities and in this analysis involving an intraspecific comparison, Ashmole's hypothesis emerges as a powerful tool in understanding geographic patterns in clutch-size variation.

There are, however, several limitations to these data. First, it is not clear what effect, if any, can be expected from the migratory patterns of some flicker populations. Seasonal migration might tend to obscure the predicted correlation between winter AE and breeding population density, as the breeding population

in an area to which or from which many birds migrate would not necessarily reflect winter productivity. Where important, migration might thus destroy any correlation between clutch size and the ratio of summer to winter productivity. The fact that there is nonetheless a strong correlation between clutch size and winter productivity (Fig. 3) suggests that winter AE correlates well with actual breeding population density despite this apparent shortcoming.

Other limitations should also be borne in mind. As pointed out by Ricklefs (1980), these tests are indirect; the exact relationship between actual evapotranspiration and food available to flickers is unknown, and the breeding-bird-census data used here may or may not serve as anything more than a crude index of relative population densities. AE values do rank localities by their productivity, however (Whittaker and Likens 1973), and are thus likely to correlate with resources available to any but the most specialized species. Because Northern Flickers eat a wide diversity of items, including insects (dominated by ants but including many other taxa as well), fruits, mast, and seeds (Beal 1911, Neff 1928, Cruz and Johnston 1979, Short 1982), it is likely that resource abundance for this species is correlated with primary productivity and, thus, AE. Furthermore, alternatives to seasonal AE values (e.g. mean annual and seasonal PPT) were tested; these did not correlate with clutch size. As for the census figures, despite their obvious limitations there simply is no alternative set of comparable data available.

In addition, the decision to examine only the breeding densities of other woodpecker species as potential competitors was done largely for logistic reasons. Future analyses, making use of detailed ecological studies of foraging behavior and habitat preference information (neither of which is currently available for the Northern Flicker) could add significantly to our understanding of the roles of community interactions in affecting resource abundance and, ultimately, clutch size.

Finally, it should be noted that the clutch-size values analyzed here are not necessarily correlated with total annual fecundity. Northern Flickers are capable of producing more than one clutch a year, particularly at more southerly latitudes (Bent 1939). Hence, the latitudinal gradient in clutch size may not reflect a similar trend in total annual fecundity. Little is known about what geographic trends exist in this critical measure of reproductive output for any bird species.

Nonetheless, the fact that these analyses have limitations does not imply that they are weak or that the conclusions are not of general importance. Geographic patterns in clutch size are a widespread, striking, and complex phenomenon. The results presented here, along with the analyses of Ricklefs (1980), unambiguously point to the seasonality of resources as being an important, if not the dominant, determinant of geographic patterns in clutch-size variation. Clearly, Ashmole's hypothesis deserves careful scrutiny when latitudinal trends in fecundity in other taxa are examined.

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100 Years Ago in The Auk

From "A study of the singing of our birds," by Eugene P. Bicknell (1884 Auk 1: 322–332):

The song of the Northern Shrike "may be one of the first that the spring can claim; for that indefinable change that comes into the atmosphere and the sunlight on some days of late winter and leads us to look springward, seems to be as quickly felt by this hardened and cruel bird as by the most tender species which it is wont to make its victims. An unusually vocal bird was observed on February 10, 1877—a morning when winter seemed quietly relaxing from long-continued severity. Perched in the sunlight, on the topmost spray of a tall oak, on an eminence commanding an expanse of changing landscape, it was alternately singing and preening its beautiful plumage. The song was a medley of varied and rather disconnected articulations, an occasional low warble always being quickly extinguished by harsh notes, even as the bird's gentle demanor would soon be interrupted by some deed of cruelty."

"It has been claimed that the Butcher Bird attracts birds and small animals by imitating their cries, thus making them its easy prey. It is true that notes similar to the screaming of small birds and the squealing of mice are interspersed through its song; but they are uttered without method, and sometimes actually in conjunction with the most harsh and startling sounds of which the bird is capable."

From "Birds of the Lower Uruguay," by Walter B. Barrows (1884 Auk 1: 313–319):

"So many stories have been told of the breeding habits of these birds [rheas, *Rhea americana*] that I could probably add nothing of value myself, so I append the following, which was told me by a young man who was born and brought up among Ostriches [rheas]. When an Ostrich has built a nest and laid the full number of eggs, she is naturally anxious to be able to find the nest again after having wandered away to any distance. This she manages by simply laying eggs at intervals of half-a-mile or so over the adjacent country, placing each egg with its smaller end pointing directly toward the nest!"