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CLUTCH SIZE OF THE GILDED FLICKER

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Since Short's (1965) extensive work on the genus *Colaptes*, all North American members of this genus have been considered conspecific with *C. auratus* (Mayr and Short 1970, Short 1982, American Ornithologists' Union 1983). The status of the five groups nonetheless remains open to question, particularly that of the *chrysoides* group (the Gilded Flicker) in southwestern United States and adjacent Mexico. Here I present data showing that Gilded Flickers have a markedly smaller clutch size than *C. a. auratus* and *C. a. cafer*. The difference is not explainable by the climatic or geographic factors that have been shown to influence geographic patterns in other species. Inasmuch as clutch size has a strong genetic basis (Van Noordwijk et al. 1980, Flux and Flux 1982), the magnitude and pattern of the difference suggest a discontinuity in the life histories of these taxa that may be indicative of reproductive isolation.

Clutch sizes were obtained from various North American oological collections (see below). Only clutches for which incubation was recorded to have been "slight," "just begun," or beyond, were used in order to ensure that the clutches were likely to be complete. I obtained data from 467 clutches, of which 57 were from *chrysoides* (primarily from Arizona) and the remainder from either the *auratus* or *cafer* groups (referred to below simply as *auratus*). Latitude and longitude of each locality were determined to the nearest degree. Climatic data, including total mean

annual precipitation (PPT), total mean annual actual evapotranspiration (AE), combined PPT for April, May, and June, combined AE for April, May, and June, maximum AE for three consecutive months in the year ("summer" AE), and minimum AE for three consecutive months in the year ("winter" AE) were derived for stations as close as possible (usually within 50 km) to each locality from the data given in Thornthwaite Associates (1964). AE is an index of primary productivity in terrestrial environments (Rosenzweig 1968); for details on the interpretation of AE values see Ricklefs (1980).

Clutch sizes were analyzed either by considering each clutch an independent sample or by combining all clutches for each degree of latitude and longitude (a latilong block) and using mean clutch size for clutches collected within the latilong. The latter procedure ensures greater independence of data involving the climatic variables, as the same climatic data were often used for all clutches within a particular latilong block.

The mean clutch size for the entire *auratus* sample was 6.5 eggs compared with 4.2 eggs for *chrysoides* (Table 1). This difference is highly significant by an analysis of variance, and remains so even after controlling for latitude in an analysis of covariance. Differences were similar when using the mean latilong clutch data (Table 1). As an additional control, I compared individual clutches of *auratus* and *chrysoides* taken from Arizona only; despite small sample sizes the difference between the two forms was still highly significant (Table 1). These latter data included clutches collected in 6 different years for *auratus* and 26 different years for *chrysoides*; thus they were not likely to have been the fortuitous result of yearly variation in clutch size.

Geographic variation in clutch size has been shown to be correlated with climatic variables, specifically winter AE, in both passerine communities (Ricklefs 1980) and in *C. auratus* (Koenig, unpubl.). Spearman rank correlations of all six climatic variables considered here with

TABLE 1. Comparison of clutch size of the Gilded Flicker with other forms of North American *Colaptes*.

| | A | | B | | A/B ratio | F-value* | df |
|---------------------------------|----------------|------|-----------------------|-------|-----------|----------|-------|
| | Gilded Flicker | (n) | Other <i>Colaptes</i> | (n) | | | |
| All individual clutches | | | | | | | |
| Mean | 4.20 | (57) | 6.49 | (410) | .65 | 139.4*** | 1,465 |
| Mean adjusted for latitude | 4.84 | (57) | 6.39 | (409) | .76 | 68.8*** | 1,463 |
| Arizona clutches only | | | | | | | |
| Mean | 4.19 | (37) | 5.25 | (8) | .80 | 7.7** | 1,43 |
| Mean adjusted for latitude | 4.16 | (37) | 5.42 | (8) | .77 | 11.0** | 1,42 |
| Using mean latilong clutch data | | | | | | | |
| Mean | 4.37 | | 6.75 | | .65 | 38.2*** | 1,133 |
| Mean adjusted for latitude | 5.10 | | 6.66 | | .77 | 18.6*** | 1,131 |
| Mean adjusted for winter AE | 4.62 | | 6.72 | | .69 | 35.9*** | 1,131 |

* Comparisons by ANOVA; ** = $P < 0.01$, *** = $P < 0.001$.

clutch size of *C. auratus* confirm that only winter AE is significant ($r_s = -0.48$, $n = 121$, 2-tailed $P < 0.001$). However, an analysis of covariance comparing the clutch size of the two taxa while controlling for winter AE still fails to significantly decrease the difference between them; mean clutch size of *chrysooides* is still only 69% of that of *auratus* (Table 1). A similarly significant difference remains in an analysis of covariance controlling for minimum, maximum, and total mean annual AE (F -value = 21.7; $df = 1, 129$; $P < 0.001$). Thus, the markedly smaller clutch size of the Gilded Flicker is not interpretable as a simple result of latitude or the climatic variables considered. Because these climatic variables probably have a strong ultimate effect on clutch size (e.g., via seasonal fluctuations in resources: Ricklefs 1980; Koenig, unpubl.) and undoubtedly correlate with other geographic patterns not tested here (e.g., altitude), their inability to explain the small clutch size of *chrysooides* is particularly significant.

These results suggest that the fecundity and life histories of Gilded Flickers differ markedly from those of other contiguous flicker populations. The significant difference in clutch size must be compensated by higher survivorship, younger age at first breeding, or higher incidence of second nesting in *chrysooides* compared with *auratus*. The museum data analyzed here are inadequate to discriminate among these alternatives. Published information (Bent 1939) does not suggest a prolonged breeding season in *chrysooides*, whereas *auratus* raises two broods a season in at least some areas. Thus, either delayed reproduction in *auratus* or higher survivorship of eggs, nests, fledglings, or adults in *chrysooides* is probably involved.

Taken by itself, the difference of 25 to 35% in clutch size between the two forms is not extraordinary. However, the failure of geographic or climatic variables to account for the difference suggests that it may be more than simple clinal variation. Rather, since the discontinuity remains even between adjacent Arizona populations, the difference in clutch size suggests that the taxa may be genetically distinct.

Alternatively, the difference in clutch size may not be genetic at all but primarily the result of differences in food supply, the woodlands inhabited by *auratus* presumably being more productive (or fluctuating more seasonally) than the saguaro cactus desert inhabited by *chrysooides*. A population study would be necessary to evaluate this possibility, and indeed, is critical to the resolution of the taxonomic dilemma posed by these forms.

The smaller clutch size of the Gilded Flicker thus distinguishes it from other forms of *C. auratus*. Other information gathered by Short (1965) on the hybridization status of this form is ambiguous (Johnson 1969): contact between *chrysooides* and *auratus* is limited during the breeding season because they prefer different habitats, and all but one of the hybrid zones studied by Short support stabilized hybrid swarms with little or no genetic contact with either parental type. A thorough study of the status of *chrysooides*, using modern molecular techniques, would seem to be useful in assessing the degree of introgression currently occurring with other forms of *Colaptes*.

Data used in these analyses were collected from the American Museum of Natural History, California Acad-

emy of Sciences, Delaware Museum of Natural History, Denver Museum of Natural History, Field Museum of Natural History, Florida State Museum, Milwaukee 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, University of Wisconsin (Madison), and the Western Foundation of Vertebrate Zoology; I extend my thanks to the staff members who assisted me in using these collections. Janet Conley, Nancy Joste, Ron Mumme, and Pam Williams aided with various aspects of data acquisition and coding. I performed the analyses while I was with the Moore Laboratory of Zoology and Department of Biology, Occidental College, whose facilities are gratefully acknowledged. The manuscript was improved by the comments of Ned Johnson, Lloyd Kiff, Frank Pitelka, Steve Russell, Pam Williams, and Bob Zink. Financial assistance came from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and from National Science Foundation grant DEB81-09128 to F. A. Pitelka.

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