HAS BROOD PARASITISM SELECTED FOR EARLIER NESTING IN THE CALIFORNIA GNATCATCHER?

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Reconstructing past selective pressures can be a daunting task, as data are often sparse, unreliable, or inconsistently gathered. Nevertheless, museum collections provide an impressive but all too often untapped resource. Data housed in such collections provide an important window to the past and allow us to identify and explore changes in the ecology of a species or a community (Reznick et al. 1994, Smith et al. 1995, Schaffer et al. 1998). With respect to avian breeding biology, a wealth of data resides on egg-data cards, most of which are associated with egg sets and nests collected during the heyday of oölogy in the late 19th and early 20th centuries. Although egg-set cards are not without their biases and flaws (McNair 1987), they remain useful, bearing information that can be gathered and analyzed, with great potential for increasing our understanding of avian breeding biology.

We used virtually all available egg-set data to construct a picture of the historical breeding biology of the California Gnatcatcher (*Polioptila californica*). In particular, we were interested in examining changes in clutch size and clutch-completion date over the past 100 years. Whereas our results for clutch size differed not and those for clutch-completion date differed little from those of other studies (e.g., Atwood 1990, 1993), we uncovered an apparent shift toward earlier clutch completion subsequent to the establishment of the brood-parasitic Brown-headed Cowbird (*Molothrus ater*) within the range of the gnatcatcher. We therefore hypothesize that cowbird parasitism has selected for earlier nesting in the California Gnatcatcher.

METHODS

We examined all available egg-set cards (n = 117) from five California collections: the Western Foundation of Vertebrate Zoology, Camarillo (WFVZ), San Bernardino County Museum, Redlands (SBCM), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), Santa Barbara Museum of Natural History, Santa Barbara (SBMNH), and the San Diego Natural History Museum, San Diego (SDNHM). The majority of these cards represented sets collected in California; only six are for Baja California.

We did not use four cards because they contained questionable information. Two cards from Ventura County (WFVZ 43088, WFVZ 92163) were said to be from nests in an "apricot tree" and in "pasture land," respectively. From these thumbnail habitat descriptions, these nests were more likely of the Blue-gray Gnatcatcher (*P. caerulea*). A set attributed to *P. melanura* [i.e., *P. californica*] from San Luis Obispo County (MVZ 10484) pertains to the Blue-gray Gnatcatcher because the California Gnatcatcher is unknown north of Ventura County (Atwood 1980, 1988). A card from Baja California

(WFVZ uncatalogued, 20 May 1928) likely pertained to an incomplete clutch (there was only one egg in the nest). Another card from Baja California (WFVZ 103856) lacked a collection date but was used in the analysis of clutch size. Thus the number of egg-set cards usable for analysis of clutch-completion date was 112. Three nests contained Brown-headed Cowbird eggs, so we excluded them from clutch-size analyses, leaving n = 109 for that study.

Unless the card specified the exact date of laying, we estimated the clutch's completion date from its collection date and stage of incubation. The California Gnatcatcher's incubation period is about 14 days from the laying of the last egg (see Woods 1949). We used a correction similar to Koenig's (1984) to estimate clutch-completion date (Table 1; Patten and Campbell 1994). A majority of historical egg sets were collected within the first few days of the final egg's being laid (McNair 1987, L. F. Kiff pers. comm.), so we considered the incubation stage to be between "fresh" and "slight" if incubation information was not available (e.g., if nothing was indicated on the card); that is, we subtracted one day from the collection date for those few cases.

We calculated clutch-completion date and clutch size as simple means, and regressed clutch-completion date against year of collection. Clutch size was regressed (in separate tests) against clutch-completion date and against year of collection. In further regression analyses against clutch-completion date we used 1920 as a dividing point because, although an exact date cannot be set, this was approximately the year when the Brown-headed Cowbird became an established breeder in cismontane southern California (Laymon 1987, Rothstein 1994). We compared mean clutch-completion dates before and after 1920 by means of Mann–Whitney U tests with α = 0.10. Analysis of variance (ANOVA) was used to compare mean clutch size across various studies. Statistical tests were performed with BMDP statistical software (1990 version for personal computers).

RESULTS

Mean clutch completion for California Gnatcatcher nestings was 5 May [standard deviation (SD) 22.57, n = 112), with roughly two-thirds of pairs

Table 1 Corrections Used to Estimate Clutch-Completion Date from Egg-Set Cards[a]

Incubation stage (from the data card)	Estimated clutch-completion date
Fresh, just begun	collection date
Slight, started, begun, trace	collection date minus 2 days
Well begun, embryo taking shape	collection date minus 5 days
About half	collection date minus 9 days
Advanced, far advanced	collection date minus 12 days

[a]From Patten and Campbell (1994). Incubation time for the California Gnatcatcher is assumed to be 14 days. See the text for treatment of cards lacking incubation data.

completing their clutches between 13 April and 28 May (the mean ± one standard deviation). We define the nesting season as the time between commencement of nest building and fledging of young. Nest construction generally begins about three weeks prior to egg laying, incubation lasts 14 days, and young fledge between 9 and 15 days after hatching, with smaller broods requiring less time to fledge (Woods 1949). Average fledging time is probably 13–14 days; thus, the peak historical nesting season for the California Gnatcatcher extended from 23 March to 26 June. The earliest clutch-completion date was 22 March, indicating nesting commenced as early as about 1 March. The latest clutch-completion date was 10 July, indicating fledging as late as about 7 August. Mean clutch size was 3.85 (SD 0.49, n = 110, mode = 4). Clutch size did not decrease over the season ($r = -0.019$, not significant) nor did clutch size decrease over the years represented in this study (1883 to 1959; $r = -0.053$, not significant).

By contrast, a negative correlation of clutch-completion date with year of collection was significant (Figure 1; $r = -0.21$, $P < 0.03$). Even with the 1959 record excluded—it could be considered a late outlier (the next latest

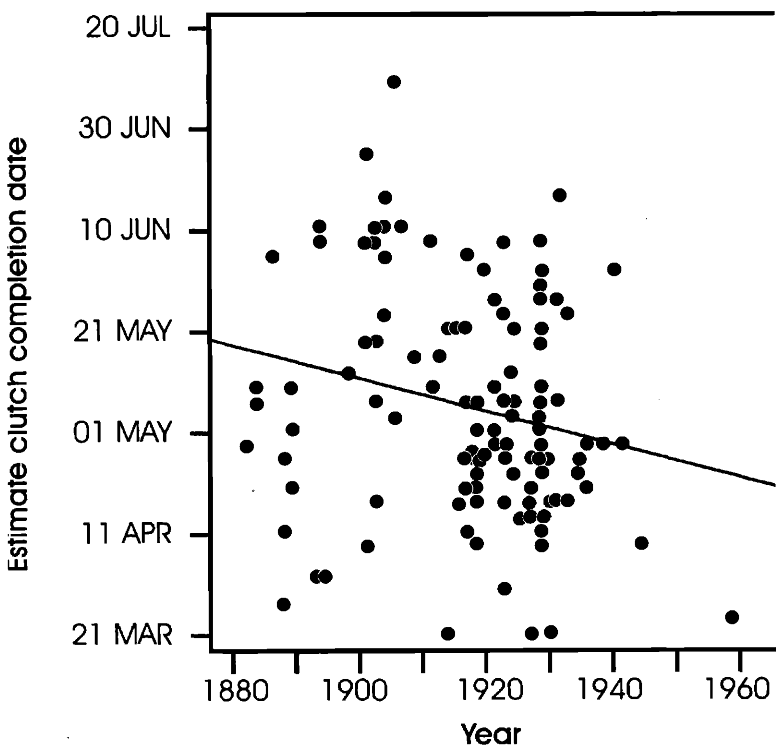

Figure 1. Estimated clutch-completion date vs. year of collection ($r = -0.21$, $P <$ 0.03).

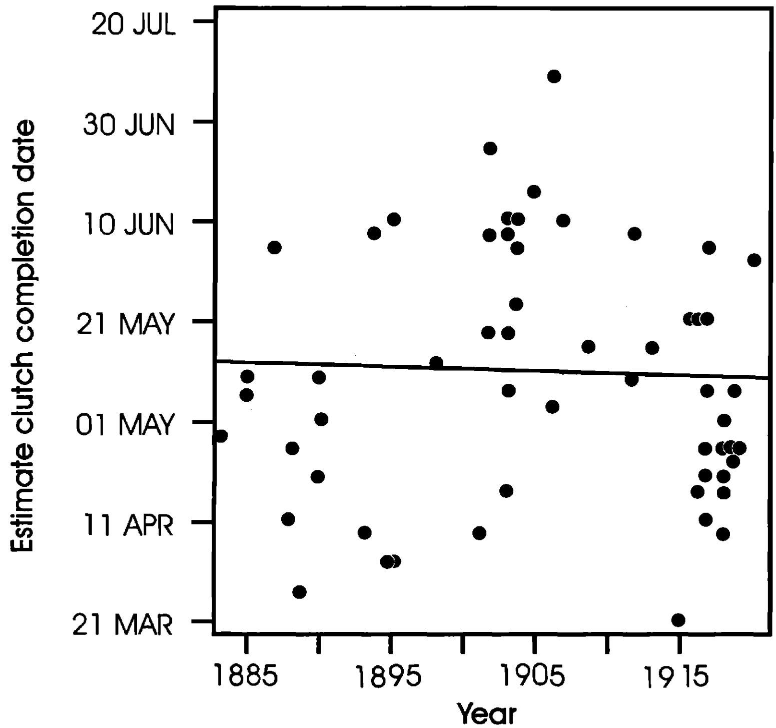

Figure 2. Estimated clutch-completion date vs. year of collection for egg sets collected from 1883 through 1920, inclusive (r = –0.06, P > 0.60, n = 54).

collection was in 1945)—the negative relationship persists (r = –0.17, P < 0.08). With the data set divided by the year 1920, clutch-completion date from 1883 through 1919 was not significantly correlated with year of collection (Figure 2; r = –0.06, P > 0.60, n = 54) but that from 1920 through 1959 was (Figure 3; r = –0.23, P < 0.08, n = 58).

The mean clutch-completion date from 1883 through 1920 was 10 May (SD 24.52), whereas from 1921 through 1959 it was 1 May (SD 19.86). These means differ significantly (U = 1885, P < 0.07) and, coupled with the strong negative correlation between clutch completion date and year of collection, the difference suggests a shift toward earlier clutches after 1920 (i.e., after the Brown-headed Cowbird became established in cismontane southern California). Nest-card data do not alter the nesting period described by Atwood (1988, 1990, 1993) and extended by Patten and Campbell (1994). Likewise, clutch sizes from the museum egg sets were strictly comparable (ANOVA, $F_{3,222}$ = 1.30, P > 0.25) to previously published means of 3.84 (SD 0.57, n = 61; Atwood 1988), 3.67 (SD 0.61, n = 27; Roach 1989), and 3.88 (SD 0.23, n = 33; Bontrager 1991).

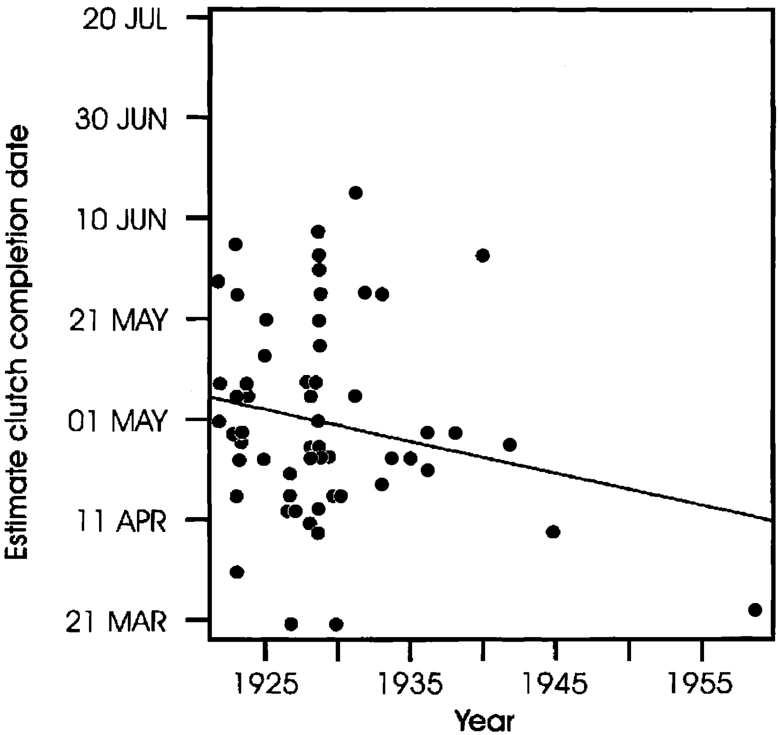

Figure 3. Estimated clutch-completion date vs. year of collection for egg sets collected after 1920, the approximate year in which Brown-headed Cowbirds became established in cismontane southern California (Laymon 1987, Rothstein 1994; $r = -0.23$, $P < 0.08$, $n = 58$).

Three California Gnatcatcher nests in our data set were parasitized by Brown-headed Cowbirds. All three were collected between 25 and 30 May in the years 1929 to 1933. We calculated the mean laying date for Brown-headed Cowbird to be 22 May (SD = 18.77, $n = 256$; data from Norris 1947, Berger 1951), indicating a primary laying period from 3 May through 10 June, a finding consistent with other studies (Payne 1973, Verner and Ritter 1983, Kiff and Irwin 1987). Note that all three parasitized nests fall within this window. Our analyses of clutch-completion date excluded these parasitized nests, although there is no *a priori* reason to assume that parasitism affects anything other than clutch size for a given nest. With all cases included, we calculated the same negative trend both for all data ($r = -0.23$, $P < 0.02$) and for post-1920 data ($r = -0.23$, $P < 0.10$, $n = 54$). Furthermore, mean clutch-completion date for post-1920 nests was earlier (30 April) and means of pre-1920 and post-1920 nests differed significantly ($U = 1840$, $P = 0.03$).

DISCUSSION

Museum egg-set data are subject to several potential biases and limitations. Nest searches by egg collectors were usually not random through the year or across habitats. Collectors were not distributed randomly and tended to search more heavily close to home. Their searches were generally intended to maximize the number of nests found, either across or within species. Still, mean clutch sizes in egg-set data are usually not seriously biased (McNair 1987). Whereas early dates are well represented, late dates tend to be poorly represented. Species that regularly nest late may be under-represented and have data skewed to one end of the nesting season. Because California Gnatcatcher eggs were collected at a fairly even rate for 60 years and throughout the species' California range, we feel that biases in these data are minimal, giving no reason to expect biases to shift through time.

Published extreme historical nesting dates for the California Gnatcatcher are from 10 April to 30 May in western Riverside County (Hanna 1934) and from 28 March to 12 July throughout the species' range (Bendire 1888, Woods 1949). More general accounts based on historical data paint a comparable portrait: in Los Angeles County the nesting season was reported as "late March to early July" with the "best month" being April (Kiff and Irwin 1987), rangewide as "late February through July," with the mean date for nest initiation being 5 May (Atwood 1988, 1990, 1993). Our results are generally comparable to these previous studies, although mean dates for the most thorough analyses (by Atwood) differ markedly, for we estimated a date of 5 May for mean *clutch completion*, whereas his 5 May date was for mean *nest initiation*. Assuming three weeks between nest initiation and egg laying (see above), we calculated a mean nest-initiation date of about 15 April. Two recent studies slightly expanded the early portion of the nesting window, with the breeding season extending from the last two weeks of February through the first week of July at a San Diego County site (Roach 1989) and nest construction as early as 26 February with "all nest activity ... concluded by mid-July" at an Orange County site (Bontrager 1991). Furthermore, the late end of the breeding season has been extended to late August (Patten and Campbell 1994).

Historically, brood parasitism of the California Gnatcatcher by cowbirds has been recorded infrequently (Hanna 1934, Friedmann et al. 1977, Friedmann and Kiff 1985), although it has been suggested that parasitism may be responsible for the species' "decline or absence in some areas where suitable habitat remains" (Atwood 1980). Currently, cowbird parasitism plays a major role in gnatcatcher nest failure, at least locally (Braden et al. 1997), and probably has for quite some time. Our data suggest that cowbird parasitism may have altered the California Gnatcatcher's breeding biology, selecting for earlier nesting. Recent late-season nesting records (Patten and Campbell 1994) may indicate an overall protraction of its nesting period. Most pairs of gnatcatchers have at least two broods each season and, given the early commencement of gnatcatcher nesting and the comparatively late laying of the Brown-headed Cowbird, we suspect that the majority of gnatcatcher nests parasitized by cowbirds hold at least the second clutch of the season. Assuming a shift toward earlier nesting is heritable, we hypothesize that California Gnatcatchers that fledge their first brood before the onset of cowbird parasitism are more fit, i.e., leave more progeny.

Selection over so short a time, while apparently not common, has been demonstrated in Darwin's finches and guppies (Gibbs and Grant 1987, Reznick et al. 1990, Weiner 1995). Smith et al. (1995) described selection in response to altered food sources within the past century affecting bill length in the Iiwi (*Vestiaria coccinea*). That a shift toward earlier gnatcatcher nesting is a selective response is difficult to corroborate, although predicting such a response is reasonable given that lower nesting success of some hosts is correlated with synchronous laying of host and cowbird eggs (McGeen 1971). As noted above, egg collectors could unwittingly but substantially bias data they gathered, but it seems unlikely that bias toward collecting early-season egg sets would take place only after 1920. Data sets both before and after 1920 are close to equal in size, so we doubt that sample sizes are responsible for the apparent pattern in post-1920 data. Egg-set data for other species nesting in cismontane southern California could test this hypothesis, with both common hosts such as the Song Sparrow (*Melospiza melodia*), where the same pattern would be predicted, and uncommon hosts such as the Wrentit (*Chamaea fasciata*), where the pattern would not be predicted.

It is impossible to prove, from available information, whether the proximate cause of the earlier mean nesting date is earlier nest initiation, a decrease in the incidence of multiple brooding, or both. We favor the first possibility, as currently the gnatcatcher's nesting season is at least as long as it was earlier this century. In either case, but particularly if fewer birds are attempting multiple brooding, other ultimate causes are possible, especially a decrease in resource quality or availability (e.g., habitat degradation). Such a decrease might cause fewer nesting attempts per season or could even affect the seasonality of nest predation through its effects on other species or on vegetative cover.

SUMMARY

We used virtually all available nest cards for the California Gnatcatcher ($n = 112$) to analyze historical patterns of its nesting schedule and clutch size. Year of collection ranged from 1883 to 1959, with the majority from 1885 to 1940. Mean clutch size was 3.85, with a mode of four. Clutch-completion dates extended from 23 March to 26 June, with a mean of 5 May. The mean clutch-completion date has become progressively earlier, particularly since 1920. This shift corresponds to the appearance of the brood-parasitic Brown-headed Cowbird within the range of the gnatcatcher.

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