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THE PROXIMATE EFFECTS OF RAINFALL ON CLUTCH SIZE OF THE CALIFORNIA GNATCATCHER¹

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Abstract. It has been hypothesized that clutch size in bird species occurring in arid habitats is influenced by annual rainfall. We propose an alternative hypothesis that avian clutch size in resident species should be more strongly associated with rainfall in the short-term (during egg-formation) than during the long-term (cumulative across the season). We tested this hypothesis with museum egg-sets for California Gnatcatcher (*Poliottila californica*) nests taken in southern California combined with rainfall data from the geographically closest weather station to nest collection site. Clutch size was independent of laying date. Seasonal rainfall was not a good predictor of clutch size; rainfall during egg formation was a better predictor. Using isotonic regression, we detected a strong positive trend in the association between clutch size and cumulative rainfall, with cumulative rainfall across 1 month prior to the estimated month of clutch completion having the strongest positive association. These data support the hypothesis that smaller clutches result from more immediate conditions, not from the wet-year/dry-year dichotomy.

Key words: *California Gnatcatcher, clutch size, isotonic regression, nutritional constraints, Poliottila californica, rainfall.*

In arid environments, the availability of energy and nutrients essential for egg formation in birds, namely fats, proteins, calcium, and water (Perrins 1996), often varies in direct proportion to rainfall. As a result, variation in the timing of egg-laying and clutch size in many species often is strongly associated with precip-

itation (Newton 1998). In some arid regions, however, precipitation is strongly seasonal, concentrated in one portion of the year and alternating with a dry period, frequently with no rain at all. Furthermore, the onset, duration, and quantity of precipitation that occur during the wet season are usually highly variable from year to year, frequently with little temporal autocorrelation across years (Rotenberry and Wiens 1991). Thus, favorable conditions also may be ephemeral. It follows that birds living in such environments are most likely under strong selection for flexibility to lay the number of eggs that closely matches current and predicted future conditions. Although the physiological mechanisms by which this prediction and matching might be achieved are not known, it must involve the integration of internal and external conditions over some previous period of time. The question arises, then, over what period of time does this integration and response occur?

Traditionally, the statistical assessment of clutch size variation in birds inhabiting such seasonal environments is based on a correlation between clutch size and total precipitation accumulated across the rainy season (Newton 1998); larger clutches are expected in wetter years. This analysis implicitly assumes that the clutch size "decision" is based on conditions summed over the entire period, which may be up to 6 months long. However, it is reasonable to assume that if desert species have been selected to respond appropriately to possibly ephemeral conditions, then the relevant period for assessing that response may be shorter than the full wet season. In this case, clutch size should be better predicted by rainfall in a much shorter term, perhaps just that during the period of egg formation itself, just prior to laying.

To test these alternatives, we examined data from museum egg-sets for the California Gnatcatcher (*Po-*

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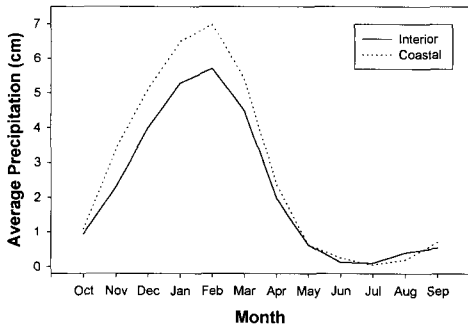


FIGURE 1. Average rainfall by month at representative interior (Riverside, 1 December 1927–31 July 1998) and coastal (Laguna Beach, 1 March 1928–31 July 1998) sites in cismontane southern California. Data are from the Western Regional Climate Center, Reno, Nevada (www.wrcc.dri.edu/cgi-bin/cliMAIN.pl) and are presented to illustrate seasonality and matching of rainfall patterns.

lioptila californica), a small insectivorous passerine endemic to California and Baja California. Specifically, we were interested in testing the hypothesis that clutch size in this species is a response to the amount of rainfall received throughout the winter prior to the onset of breeding vs. the hypothesis that precipitation in a period shortly before clutch completion date is important. Thus, our objective is to examine differences in immediate vs. season-long effects of rainfall on clutch size in the California Gnatcatcher.

METHODS

SPECIES AND STUDY AREA

Our study included only California Gnatcatchers in southern California, and thus only nominate *P. c. californica*. In southern California, this species is restricted to coastal sage scrub associations in cismontane valleys, low-elevation foothills, and coastal bluffs. Rainfall in cismontane southern California is associated with single, large storm events, such that rainfall in the region is distinctly spatially autocorrelated month-to-month (Fig. 1). Furthermore, rainfall is highly seasonal, being concentrated in late fall and winter (November through March), with virtually none in the mid-summer (June through August; Fig. 1).

CLUTCH SIZE DETERMINATION AND RAINFALL

We examined all available egg-set data cards ($n = 117$) from the Western Foundation of Vertebrate Zoology (Camarillo, California), the San Bernardino County Museum (Redlands, California), the Museum of Vertebrate Zoology (University of California, Berkeley), the Santa Barbara Museum of Natural History (Santa Barbara), and the San Diego Natural History Museum (San Diego). Although there are potential biases in egg set data (McNair 1987), most collectors waited until clutch completion before collecting a nest (L. F. Kiff, pers. comm.), so these clutch-size data should be sound. After discarding ambiguous records or records from localities that could not be readily associated with

a weather station, there remained a total sample of 105 California Gnatcatcher clutches available for analysis, all from Orange, Riverside, San Bernardino, and San Diego Counties, California, spanning from 1883 to 1959. Clutch size data were taken directly from the card. Clutch completion date was estimated using the correction method described by Patten and Campbell (1994).

Monthly rainfall data were gathered from the Department of Water Resources (1980). Rainfall was used for the weather station nearest the nest collection locality. For seasonal rainfall, we used rainfall totals for the 6 months immediately prior to the month in which the clutch was completed; for example, if a clutch completion date was estimated to be 5 April 1914, then we used cumulative rainfall from October 1913 through March 1914. We similarly calculated cumulative rainfall for 3 months and 1 month prior to the clutch completion month.

STATISTICAL ANALYSES

Linear regression analysis, with rainfall as the predictor and clutch size as the criterion, was conducted for each cumulative rainfall amount. Cumulative rainfall data were transformed by $\log_{10}(x + 1)$. Simple descriptive statistics, correlation analyses, and ANOVA were conducted to examine the concordance between this data set and previous studies, and to uncover potential sampling biases in the data, such as between clutch size and collection date.

Our alternative hypothesis was that clutch size would be more strongly influenced by rainfall in the short-term. Thus, we predicted that cumulative rainfall 1 month prior to clutch completion would have a stronger association with clutch size than would cumulative rainfall 3 months prior to clutch completion; similarly, we predicted that 3 months would show a stronger association than 6 months. Linear regression and ANOVA may have low power when the alternate hypothesis is one-tailed. As a result, we employed isotonic regression (Gaines and Rice 1990) on Spearman rank correlation coefficients for each of the cumulative rainfall periods. This technique can be thought of as a one-tailed ANOVA. Under the isotonic regression model, our H_0 was $r_{s1} = r_{s3} = r_{s6}$, whereas our ordered expectation H_A was $r_{s1} \geq r_{s3} \geq r_{s6}$, with at least one strict inequality.

The isotonic regression statistic with sample variances (\bar{E}^2) is a ratio of between-groups sums of squares and total sums of squares (Barlow et al. 1972, Gaines and Rice 1990). Tabled critical values for \bar{E}^2 are generally only for few groups, small n , and equal sample sizes. Whereas we had few groups ($k = 3$) and equal sample sizes ($n = 105$), our degrees of freedom were fairly high ($\nu = N - k = 312$, where N is the total sample, or kn). As a result, we transformed this value to an S statistic (Robertson et al. 1988), where $S = \nu \bar{E}^2 / (1 - \bar{E}^2)$, and used tabled critical values of S (Robertson et al. 1988) to determine statistical significance.

Variance estimates for Spearman rank correlation coefficients were obtained through a resampling procedure. We used the bootstrap rather than the jackknife procedure because the latter overestimates variance for nonlinear functions such as correlation coefficients

(Efron and Tibshirani 1993). We performed 100 bootstrap replications. Statistical analyses were performed using commercial software (BMDP Statistical Software 1990, SAS Institute 1996) and a custom-designed C language program. Values presented are means \pm SD.

RESULTS

Clutch size data were not biased. For example, mean clutch size from the museum egg-set data of 3.87 ± 0.46 eggs ($n = 105$) did not differ (ANOVA, $F_{3,222} = 1.30$, $P > 0.25$) from previously published mean clutch sizes of 3.84 ± 0.57 ($n = 61$; Atwood 1988), 3.67 ± 0.61 ($n = 27$; Roach 1989), and 3.88 ± 0.23 ($n = 33$; Bontrager 1991). Atwood (1988) used many of the same egg sets, so the lack of difference was not surprising, but the other values are from field studies. Likewise, the mean estimated clutch completion date (6 May \pm 22 days) was generally consistent with nesting dates provided by Atwood (1988, 1993). Furthermore, there was no relationship between clutch size and estimated clutch completion date ($r = -0.10$, $P > 0.3$), and clutch size did not decrease over the years represented in this study (1883 to 1959, $r = -0.05$, $P > 0.5$).

Cumulative rainfall 6 months prior to the month in which the clutch was completed was a marginal predictor of clutch size ($r^2 = 0.03$, $F_{1,103} = 3.28$, $P > 0.07$). Thus, the hypothesis that smaller clutches are produced in dry years and larger clutches are produced in wetter years was not strongly supported by these data. However, cumulative rainfall more immediately prior to the month in which the clutch was completed was a significant predictor of clutch size, both for 3 months ($r^2 = 0.05$, $F_{1,103} = 4.97$, $P < 0.03$) and 1 month ($r^2 = 0.08$, $F_{1,103} = 9.29$, $P < 0.003$) prior to clutch completion, although with a low variance explained in both cases.

There was no association between cumulative rainfall for 1 month and 6 months ($r_s = -0.06$, $P > 0.5$) prior to clutch completion date. However, there were significant autocorrelations between cumulative rainfall for 1 month and 3 months ($r_s = 0.42$, $P < 0.001$) and for 3 and 6 months ($r_s = 0.52$, $P < 0.001$) across the 105 clutch completion dates. There was a significant degree of association between clutch size and cumulative rainfall both 1 month and 3 months prior to the month in which the clutch was completed (Table 1). The ordered expectation of increased degree of association between clutch size and short-term cumulative rainfall levels was strongly supported by our data. Because we estimated variances around values of r_s with bootstrap resampling, each run produced a slightly different estimate of E^2 . Even so, E^2 values were always > 0.17 ; thus, $S > 63.5$ in all cases, meaning $P \ll 0.01$ ($S_{2,312} \approx 7.0$ at $\alpha = 0.01$; Robertson et al. 1988) for the probability of type I error in rejecting H_0 in favor of the H_A with ordered expectations.

DISCUSSION

Seasonal rainfall does not significantly affect clutch size in the California Gnatcatcher, yet more immediate rainfall does. These results call into question the idea of larger clutches in "wet years" and smaller ones in "dry years" (Grishaver et al. 1998). Instead, clutch

TABLE 1. Association between clutch size and three periods of cumulative rainfall. Significance of Spearman rank correlation coefficient values (r_s) is under the H_0 of no association ($n = 105$). Variance estimates were obtained from bootstrap resampling with 100 replications. These estimates were consistent with the variance for r_s under a normal approximation, where $\sigma^2 = 1/(n - 1)$ (Kendall and Gibbons 1990).

	Cumulative rainfall \times months prior to month of clutch completion		
	1 month	3 months	6 months
r_s	0.27	0.21	0.13
P	<0.006	<0.03	0.20
S_r^2	0.008	0.01	0.009

size was reduced when rainfall was low during egg formation, but was modal when rainfall was average during this period. That female passerines require more water at the onset of egg-laying than at other times (Reynolds and Waldron 1999) suggests a cause for this observed relationship. Furthermore, at least based on the museum egg-set data, clutch size in the California Gnatcatcher did not decrease over the breeding season, a pattern contrary to that found in other species (Williams 1996, Winkler and Allen 1996), but perhaps consistent with apparent flexibility of their response to short-term rainfall.

The fact that clutch size is better predicted by more immediate factors is of general interest for the evolutionary ecology of avian reproduction and suggests that the ability to produce eggs can limit clutch size (Monaghan et al. 1995). The degree of heritability of clutch size is debatable. Although most authors have indicated that it is fairly high (Klomp 1970), others have suggested that it is quite low (Murphy and Haukioja 1989), with most variation in clutch size resulting from environmental factors rather than additive genetic effects (Williams 1996). Factors such as time allocation, energy expenditure, and nutrient reserves of the parents have been implicated as limiting reproduction in birds (Deerenberg et al. 1996), although only the last factor is likely related to food availability immediately prior to, rather than during, the breeding effort (Selman and Houston 1996).

Food availability can influence clutch size (Greenlaw 1978, Boutin 1990), but what is probably more important is nutrient availability, including nutrients in food resources (Graveland and van Gijzen 1994, Ramsay and Houston 1998). As noted above, egg formation in birds requires fat, protein, water, and calcium. The first two of these resources are a function of diet, and in passerines this diet is typically insects and other arthropods, as even most granivorous birds become largely insectivorous when nesting. Arthropod availability is in turn directly associated with rainfall levels (Greenlaw 1978). Thus, clutch size should be constrained during oögenesis because of a reduced abundance of insects and seeds and because of the lower availability of water.

The short-term constraint on clutch size shown by the California Gnatcatcher is consistent with findings

for several other passerines in which the clutch size appears to be proximately controlled by resources at the time of oögenesis (Murphy 1978, Rotenberry and Wiens 1991). Likewise, a positive correlation between natural food abundance and clutch size has been measured in several other passerines (Greenlaw 1978, Husell and Quinney 1987). Thus, whereas mean clutch size is likely set by evolutionary factors (Lack's hypothesis), our results together with findings from other field studies and experimental manipulations (Monaghan et al. 1995, Selman and Houston 1996, Williams 1996) suggest that much of the variance in clutch size is determined by environmental conditions during egg formation. The goals of future research should be to identify the proximate physiological mechanisms responsible for producing environmental condition-dependent response to resource availability over a variety of time scales, and patterns of association between species' attributes such as body size and duration of the critical period of rainfall.

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SOCIAL DOMINANCE AND ENERGY RESERVES IN WINTERING WOODLAND BIRDS¹

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Abstract. To understand animals' tactics for surviving the winter season, we need to know how they manage their energy reserves. Fat reserves in small birds in winter generally increase with starvation risk. Studies have documented higher fat reserves in response to various sources of variability in energy intake or expenditure. Using three woodland species, Carolina Chickadee (*Poecile carolinensis*), Tufted Titmouse (*Baeolophus bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*), we tested the prediction that the more predictable food supply of socially dominant animals enables them to maintain lower energetic reserves than subordinate conspecifics. We inferred dominance from age and sex categories. The hypothesis was fully supported. In all three species, dominants carried relatively lower fat reserves than subordinates.

Key words: Carolina Chickadee, dominance, energy reserves, fatness, fat reserves, Tufted Titmouse, White-breasted Nuthatch.

During the nonbreeding season, temperate-zone birds must survive harsh conditions marked by low ambient temperatures, long nights, and unpredictable foraging success. During that period, energy reserves are required to survive both long nights and reductions in foraging success resulting from unpredictable food supplies and inclement weather. Full understanding of birds' tactics for surviving the winter season requires knowledge of how they manage their energy reserves. Because free-ranging birds carry less fat than the maximum possible (Witter and Cuthill 1993), there appears

to be some fitness cost to carrying extra fat, and predation risk has been hypothesized to be one component of such a fitness cost (Lima 1986, McNamara and Houston 1990).

Heavier birds appear to be less maneuverable when escaping a predator's attack and they also need to forage more intensively at the expense of vigilance to maintain higher fat reserves, so heavier birds should be more vulnerable to predators (Witter and Cuthill 1993). Thus, avian body mass has been proposed to represent a trade-off between risk of starvation and risk of predation (McNamara and Houston 1990), where risk of starvation selects for larger energy reserves, while risk of predation selects for lower mass and, therefore, lower energy reserves. Many experimental studies have demonstrated that an increase in variance in any variable that contributes to risk of starvation (e.g., food intake rate, day length, air temperature, etc.) causes birds to increase their fat reserves (Ekman and Hake 1990, Bednekoff and Krebs 1995, Pravosudov and Grubb 1997).

The advantages of reducing predation risk should cause birds to lower their body mass whenever it is possible to do so without increasing the risk of starvation. This shift can be seen under conditions where food becomes more predictable and available, such as in a laboratory setting with food ad libitum (Ekman and Hake 1990). We can therefore predict that birds with relatively low mass (low energy reserves) may be living under either good nutritional circumstances where they maintain low reserves by preference, or under poor nutritional circumstances where their energy reserves are low by necessity.

During the winter, many birds form social groups marked by a linear dominance hierarchy (Hogstad 1987, Koivula and Orell 1988, Ekman and Lillendahl 1993). In parids, linear dominance follows the order in which adult males are the most dominant individuals followed by juvenile males, and then by adult females

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