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Annual variation in the timing of breeding of the Monk Parakeet in relation to climatic factors.—The timing of breeding of a species is regarded as adaptive. According to Lack (1950), natural selection normally favors those individuals rearing offspring during the season that maximizes productivity and/or minimizes mortality.

Most birds have evolved a hereditary response to environmental changes (proximate factors, sensu Baker 1938) that predicts the favorable season well in advance. The variation in day length, at middle and high latitudes, is the primary signal to induce the basic physiological and behavioral preparations for breeding (Lack 1950, Immelmann 1971, Murton and Westwood 1977). However, additional factors are generally required to adjust the onset of egg laying to slight variations in ecological conditions (Immelmann 1971).

The Monk Parakeet (*Myiopsitta monachus*) has a breeding season restricted to spring and summer. The mean date of onset of laying has been found to vary among years within a 19-day range from late October to mid November (Navarro et al., unpubl. data). The regularity in timing of breeding suggests that the increasing day-length may be the basic environmental cue controlling this species' breeding season. However, the year-to-year variation indicates that other factors also may influence the onset of breeding in the Monk Parakeet.

This paper is focused on the role of proximate factors (other than photoperiod) that may induce slight annual shifts in the timing of breeding in the Monk Parakeet. We used correlation analysis to investigate the potential effects of rainfall and temperature on the date of initiation of egg laying.

Study area and methods.—The information presented here was collected during a long-term study of the breeding biology of the Monk Parakeet, conducted in a 610-ha area located close to the town of Jesús María in Córdoba Province, Argentina. Detailed descriptions of the study area and procedures of data collection are presented in Navarro et al. (1992).

During six years (1983 to 1988), we inspected all accessible Monk Parakeet nests in the study area at 7- to 12-day intervals, from the pre-laying period in October to early the end of the breeding season in March. The dates of laying refer below to first clutches only (i.e., females laying their first egg of the season). The beginning of laying was estimated for each clutch by back-dating, based on the average interval between successive eggs and the average incubation period (2.2 and 24 days, respectively) for this species (Navarro 1989). The age of nestlings, calculated by a growth curve equation (Navarro and Bucher 1990), was also used for back-dating when necessary. We excluded from the analysis all clutches in which no accurate laying date could be estimated. Climatic data were recorded at the Córdoba airport 26 km south of the study area. Average mean, maximum, and minimum daily temperatures, rainfall, and number of rainy days and those with heavy rain (≥ 5 mm) were calculated for periods of different ending dates and length.

We used the two correlation techniques applied by Slagsvold (1976) to detect those periods during winter and spring that showed the strongest correlations between climatic data and dates of clutch initiation: (1) By varying the length of the analyzed period, with every one ending on the same fixed date. The periods tested were increments of five days between 10 and 100 days before the fixed ending date, respectively. The terminal date (1 November) was established as four days before the overall average date of onset of laying in the population (Navarro et al. 1992). The four-day interval represents an estimate of the time required to produce an egg; this interval was not available for the Monk Parakeet and was taken from other bird species (Slagsvold 1976, Orell and Ojanen 1983), and (2) By varying the ending date of the analyzed period using a certain period length. We analyzed every interval of a length mentioned in (1) successively, throughout the 100-day interval before 1 November.

Results.—On average, 26 first-clutches (range 14–32) were used to calculate the mean laying date of each year. The daily maximum temperature showed the highest significant negative correlation with the mean date of onset of egg laying (i.e., an advance in the time of breeding is associated with higher temperatures). When the mean laying dates were compared with the average daily maximum temperature recorded during periods of varying length, each ending on 1 November (method A), the period providing the highest significant correlation ($r = -0.962$; N = 6; $P < 0.01$) was 50 days, from 13 September onwards (Fig. 1). Method B gave the strongest significant correlation for the average of daily maximum temperatures in the 55-day period between 31 August and 24 October ($r = -0.996$; N = 6; $P < 0.01$). Averages of daily maximum temperatures during this period ranged from 23.0 to 24.2°C.

Rainfall showed a non-significant correlation with egg-laying dates, based on method A (Fig. 1). However, number of rainy days resulted in significant positive correlations by method B, the highest ($r = 0.864$; N = 6; $P < 0.05$) being for the 40-day period between 17 September and 26 October. Moreover, when only days with heavy rains (≥ 5 mm) were considered, there was a closer correlation for the 35-day interval between 2 September and 6 October ($r = 0.926$; N = 6; $P < 0.01$).

In a further step, we tried to partial out the effect of temperature on the relationship between days with heavy rains and average date of beginning of egg laying. We calculated partial correlation coefficients between average date of start of egg laying and the two climatic variables: number of days with heavy rains (from 2 September to 6 October) and average of daily maximum temperatures (31 August to 24 October). The temperature showed a significant negative correlation with date of start of breeding when the number of days of heavy rains was held constant ($r = -0.970$; N = 6; $P < 0.01$). On the other hand, for a

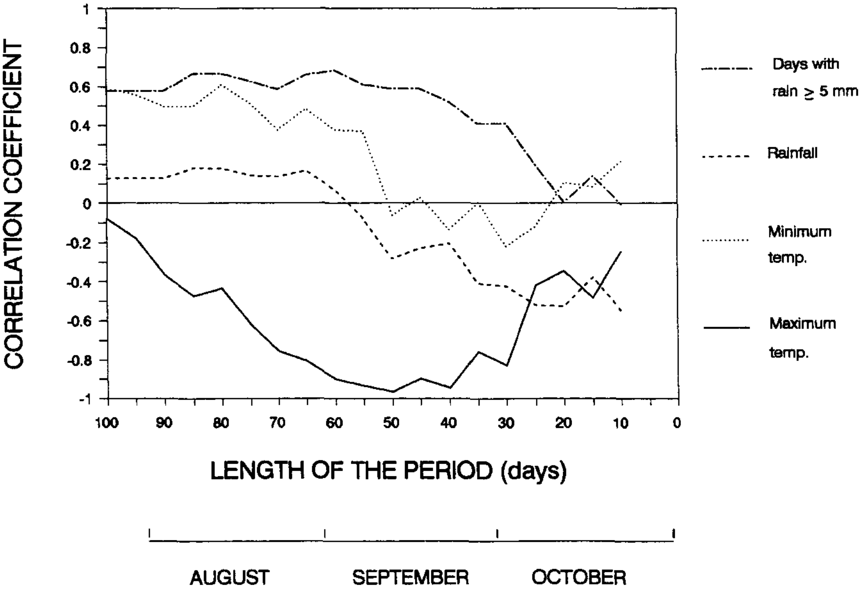

FIG. 1. Variation in the correlation coefficient obtained for the relationship between date of start of egg laying in Monk Parakeets and climatic factors occurred during periods of different length ending on a fixed date (1 November). Notice that a negative correlation means that earlier breeding attempts are associated with higher values of the climatic factor.

fixed maximum temperature, number of days with heavy rains and date of start of breeding were not significantly correlated ($r = 0.244$; N = 6; $P > 0.05$).

Discussion.—Higher maximum temperatures experienced in late-winter to mid-spring are correlated strongly with earlier breeding in the Monk Parakeet. Therefore, although the regularity in the timing of breeding suggests that photoperiod may be the principal factor setting the breeding season in Monk Parakeets, maximum temperatures also may exert some influence. In contrast with the results obtained by Lofts and Murton (1966) in the Wood-Pigeon (*Columba palumbus*), a sharp rise in temperature seems not to advance egg laying in the Monk Parakeet, as the period in which this species is sensitive to that climatic factor is of considerable length.

The influence of temperature on the initiation of laying has been well documented in Eurasian tits (*Parus* spp.), in which breeding begins earlier during mild springs than during cold ones (Perrins 1965, 1973; Slagsvold 1976; Murton and Westwood 1977; O'Connor 1978; Orell 1983; Orell and Ojanen 1983).

The opposite results obtained from linear and partial correlation analysis between rainy days and date of breeding suggest that rainy days seem to produce only an indirect influence on the date of onset of breeding. Therefore, the apparent relationship between these variables could well be due to chance or to lower temperatures caused either by the lack of sunshine or by the rain, and not to a direct hindering of the courtship and nest-reconditioning behavior or foraging activities.

Although average maximum temperatures of above 23°C seem to work as a secondary factor that advances breeding in Monk Parakeets, the relationship between temperature and the onset of laying is probably complex. As earlier breeders have a higher breeding success within the population (Navarro and Bucher, unpubl. data), many pairs would presumably raise more young if they could begin egg laying earlier than they do. Females may produce their eggs when another limiting factor (possibly food supply) allows. In the absence of data on the association between climate and food resources for Monk Parakeets, it is not easy to establish if the onset of egg laying results from the direct effect of the preceding temperature, by a linked factor such as an improvement in the availability or quality of food, or via some modification in the aspect of the landscape.

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Capsaicin effects on consumption of food by Cedar Waxwings and House Finches.—Capsaicinoids (e.g., N-vanillyl-n-nonamide, norcapsaicin, nordihydrocapsaicin, capsaicin, dihydrocapsaicin, homocapsaicin, homodihydrocapsaicin; Hoffman 1983) are aromatic amides and the pungent principles in Capsicum peppers. Although these substances are strong chemical irritants for most mammals (e.g., Rozin et al. 1979), the available data suggest that they are inoffensive to some birds. For example, European Starlings (*Sturnus vulgaris*) and Rock Doves (*Columba livia*) are unresponsive to these compounds, even when concentrations greatly exceed those which mammals avoid (Szolcsanyi et al. 1986; Mason et al., in press).

The present studies were designed to explore further the apparent taxonomic specificity of capsaicin. We also measured the capsaicin levels present in wild fruits and used that concentration in our behavioral tests.

Materials and methods.—To determine an ecologically valid concentration of capsaicin to use in behavioral tests, we determined the average amount of capsaicin present in wild peppers (*Capsicum annuum*). Fruits were collected during the summers of 1990 and 1991 at the Audubon Sabal Palm Sanctuary, Cameron County, Texas. Fresh specimens were frozen immediately and shipped to the Monell Chemical Senses Center, Philadelphia, Pennsylvania. Upon arrival, capsaicin concentrations were determined according to the method of Hoffman et al. (1983). Fruits were weighed, ground to a paste, and extracted with 95% ethanol at 65–75°C for five h. Suspended material was allowed to settle, and the supernatant was transferred to Teflon-lined screw-capped vials. Samples of fluid (50 μl) were injected into a Waters Associates ALC/GPC high performance liquid chromatograph (HPLC) system with a 10 μl Bondapak C_{18} column and a guard column of Bondapak C_{18}/Corasil (Waters Associates) with detection at 280 nm (Hoffman et al. 1983).

Five male Cedar Waxwings (*Bombycilla cedrorum*) were mist-netted near Gainesville, Florida, and shipped by air to the Monell Center. Five male House Finches (*Carpodacus mexicanus*) were funnel trapped in the Philadelphia area. All birds were caged individually (dimensions: 61 cm × 36 cm × 41 cm) under a 12:12 light-dark cycle (lights on 07:00–19:00 h EST).

During a two-week period of adaptation to captivity, canary-finch feed (AVN®, Purina Mills, Inc., St. Louis, Mo.; hereafter referred to as feed) and tapwater were provided ad libitum. Because waxwings are frugivorous, their diet was supplemented with mashed bananas and blueberries every third day.

A five day pretreatment period immediately followed adaptation. On each pretreatment day, birds were food deprived overnight (18:00–08:00 h). Between 08:30 and 09:00 h, one cup containing 20 g of control feed was placed in each cage. Control feed samples were prepared by spraying plain feed with diethyl ether 24 h before testing, and then placing the feed under a fume hood to evaporate the ether (Jakubas et al. 1991). Consumption, spillage, body mass, and dry feces mass for each bird were measured at the end of each test. After testing and until lights out, all birds were provided free access to plain feed and tapwater.

A five-day treatment period immediately followed pretreatment. During treatment, birds