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FOOD SUPPLY AND NEST TIMING OF BROAD-TAILED HUMMINGBIRDS IN THE ROCKY MOUNTAINS

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Natural selection may favor animals which synchronize their activities in such a way that peak demands for given resources correspond with peak supplies. With this in mind, Lack (The Natural Regulation of Animal Numbers, Oxford, Clarendon Press, 1954) and Perrins (Ibis 112:242, 1970) considered the synchronization of breeding seasons of birds to food abundance. Perrins recognized that reproduction must often begin as soon as food supplies allow, and well before they peak, so as to anticipate the energetic costs of brooding and feeding chicks, which exceed those of incubating eggs. Accurate timing relative to resources should be clearest where demand is high, for example among hummingbirds breeding in temperate zones (Stiles, *Univ. California Publ. Zool.* 97, 1972). Especially in high, cool mountains, seasonal food sources must support an intense metabolism of these small homeotherms (Calder, *Ecology* 54:127, 1973; Lasiewski and Dawson, *Condor* 69:13, 1967; Pearson, *Condor* 52:145, 1950).

Breeding Broad-tailed Hummingbirds (*Selasphorus platycercus*) in the vicinity of the Rocky Mountain Biological Laboratory (Gothic, Colorado; 2900 m elevation), devote an average of 11.3% of their time foraging for flower nectar, as opposed to only 1.2% fly-catching for insects (total 18 hr 18 min daylight time-budget observation of two males and one female; unpubl. data). Predominantly taken are nectars of four flowers: *Delphinium nelsoni* Greene, *D. barbeyi* Huth., *Ipomopsis aggregata* (Pursh) V. Grant, and *Castilleja miniata* Dougl. My intention is to demonstrate (1) that the start of hummingbird reproduction at Gothic corresponds in time and space with flowering of the earliest nectar source, *D. nelsoni*; (2) that

peak brooding activity in Gothic nests corresponds well with the peak density of the other three main hummingbird food plants (as listed above); and (3) that the total duration of summertime flowering of the four main food plants is implicated as a force that compresses the initiation of nesting toward the earliest possible date, because reproductive success of "late nesters" may be depressed in occasional years.

In the summers of 1972 and 1973, I followed 23 and 12 Broad-tailed Hummingbird nests, respectively, in 50 ha of aspen and conifer forest around Gothic. Qualitative notes only were taken on the condition of flowering during the first summer. In 1973, I counted blossoms of the four main hummingbird plants within 34 2 m × 2 m plots placed throughout the study area.

Figures 1 and 2 indicate the timing of flowering and of incubation in nests successfully brought to fledge in 1972 and 1973 (represented by the number of nests in the first ten days of their incubation activity). First incubation in Gothic followed *D. nelsoni* blooming by about 12 days in 1972, and by 7 days in 1973. Observations of May, 1973, suggest that male hummingbirds were frequent pre-season visitors who assumed residence just as the first *D. nelsoni* appeared. Also, females were first detected in a daily census of forests just as *D. nelsoni* blossomed in 1973 (fig. 2).

Figures 1 and 2 also show the period of brooding activity in successful nests in 1972 and 1973 (represented by the number of nests in the first ten days after hatch, ten days being roughly half the hatch-fledge interval). This period covered about five weeks, during which three of the four main hummingbird plants flowered, and blossom counts peaked as well (1973 data only; fig. 2). This suggests a close fit of the costliest period of the nesting season with that of the highest flower abundance.

Nest location, in addition to nest timing, reflected the pattern of flower appearance around Gothic. *D. nelsoni* and *I. aggregata* grew mostly along interfaces

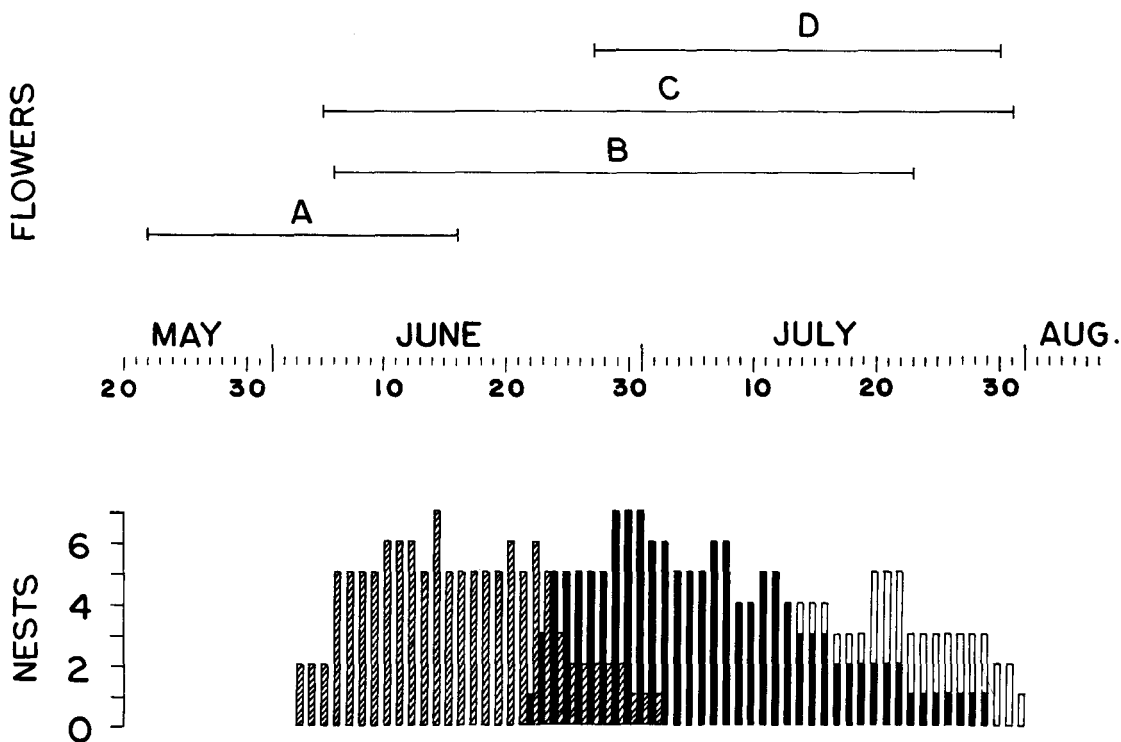


FIGURE 1. The 1972 breeding season. Top: flowering phenology; A = *D. nelsoni*; B = *I. aggregata*; C = *C. miniata*; D = *D. barbeyi*. Bottom: nest incubation and brooding activity; ordinate indicates the number of nests involved. Hatched bars = incubation activity (number of successful nests in first ten days of incubation); solid bars = brooding activity of successful nests (number of successful nests in first ten days after hatch); open bars (to the far right) = brooding activity of "late-nesters" (number of nests that subsequently failed, in first ten days after hatch).

of meadows and aspen forests, whereas *C. miniata* was concentrated near streams. Nests were generally built on the outskirts of aspen forests, or else in conifers close to streams. Some meadows were equally accessible to aspen and conifer forests. Flowers in these meadows may influence nest placement in both forest types. For instance, the first hummingbird flowers in 1973 were *D. nelsoni* in meadows, and the first nest was in a conifer stand on a streambank opposite the meadows. In riparian areas far from meadows and *D. nelsoni*, nests appeared only later, as *C. miniata* flowered.

The order and interrelationship of events within the two hummingbird breeding seasons were similar, even though overall flower timing seemed influenced by macroclimate. The mild 1972 winter allowed an earlier season than in 1973, but did not really alter the flowering sequence of the four main food plants. In 1972, *D. nelsoni* flowering was earlier by 15 days than in 1973; *I. aggregata* by 24 days; *D. barbeyi* by 8 days; and *C. miniata* by 26 days. Hummingbird activities paralleled this shift in timing. I observed feeding at *D. nelsoni* 13 days earlier in 1972 than in 1973; early morning activity, which implies overnight roosting, 15 days earlier; and courtship 10 days earlier. First nests were begun and last nests ended 11 days earlier in 1972 than in 1973, so that overall nesting seasons were of identical length (64 days), despite shifts in timing. This indicates high synchrony between individual nesting cycles, within repeatable

flowering seasons that are not quite twice as long as a single nesting cycle (flowering seasons: about 70 days in 1972, 80 in 1973. Mean nesting cycles from laying to fledge: 38 days in 1972, 41 in 1973).

Finally, figure 1 includes the brooding activity in all 1972 nests that failed after hatch (represented by the number of nests in the first ten days after hatch; all nests failed within these first ten days). These nests all belonged to "late-nesting" females, defined as those beginning incubation less than one complete nesting cycle (38 days) before 1 August, 1972. Food resources declined around 1 August, before "late-nesters" were well into the final stages of their nesting cycles. "Late-nesters" were only 28% successful ($n = 7$) as opposed to 71% ($n = 16$) for all other Gothic nests (these proportions differ statistically at an 8% significance level, using an exact multinomial test after R. A. Fisher, *Statistical Methods for Research Workers*, Edinburgh, Oliver & Boyd, 1950, p. 96). Most of these late-season failures resulted from female abandonment of nests as flower supplies declined (Calder, *Wilson Bull.* 85: 283, 1973).

The nesting synchrony of Gothic Broad-tailed Hummingbirds relative to flowers suggests that fluctuating energetic demands during reproduction, and predictably fluctuating food levels, are in close conformity. Presumably, such conformity may be produced by only slight, or occasional, differences in the

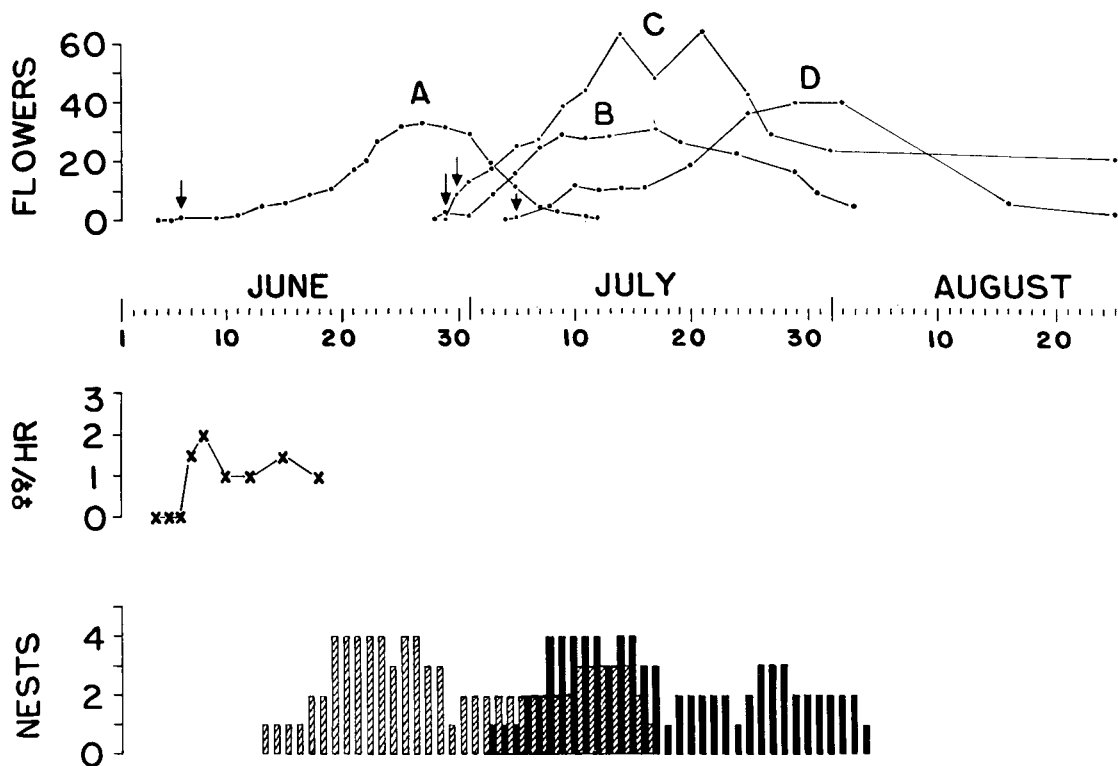


FIGURE 2. The 1973 breeding season. Top: as in figure 1; except that ordinate indicates the average number of blossoms per $2\text{ m} \times 2\text{ m}$ plot; arrows denote first appearances of respective flower types. Bottom: as in figure 1; except that no open bars (brooding activity of "late-nesters") are shown. Middle, left: census of forests; ordinate indicates the average number of female Broad-tailed Hummingbirds detected per census hour.

fitness of nesting females. An abrupt end to a nesting season, as happened in 1972, may exemplify the latter sort of difference.

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DURATION OF FEEDING BOUTS AND RESPONSES TO SALT SOLUTIONS BY HUMMINGBIRDS AT ARTIFICIAL FEEDERS

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The feeding methods of hummingbirds depend upon the characteristics of the flowers from which they feed, nectar quantity and quality, crop volume, and rate of absorption from the gut (Skutch 1952, Grant and Grant 1968, Hainsworth and Wolf 1972, Snow and Snow 1972, Wolf et al. 1972, Hainsworth 1973). In this paper, I report on interspecific differences in feeding bout duration in seven species of hummingbirds. Most observations were made at artificial feeders, but a few birds were observed feeding from

flowers. Certain other aspects of feeding behavior are described (see also Broom 1975).

Two of my experiments were prompted by Bacon's (1973) observation of a hummingbird hovering over the sea and apparently drinking. The hummingbird may have been responding to its reflection or drinking to obtain water or salt. I therefore tested the preferences of hummingbirds for salt solutions of different concentrations in artificial feeders.

Hummingbirds of 10 species were observed feeding from 15 artificial feeders at a home in Aripo Valley, Trinidad, between October and December 1972. A few birds of three species feeding from hibiscus flowers were observed with binoculars from a distance of 20 m. The duration of each feeding bout, i.e. the time that the bill tip was inside the flower, was recorded. In Experiment 1 bouts were timed with a stopwatch from distances of 4 to 10 m. In Experiments 2 and 3, hummingbird consumption of liquid