

FIGURE 1. Lateral view of albinistic (right) and normal color phase (left) of immature male Blue Grouse.

TERRITORIAL AND FEEDING ACTIVITY OF BROAD-TAILED HUMMINGBIRDS (*SELASPHORUS PLATYCERCUS*) IN *IRIS MISSOURIENSIS*

DAVID L. LYON

Department of Biology
Cornell College
Mt. Vernon, Iowa 52314

Hummingbird territorial systems are often organized around food resources, usually nectar, and hummingbird-flowered plants are the usual source of the nectar. The territorial system described here is organized around a bee-flowered species, *Iris missouriensis*, and some theoretical implications of hummingbird feeding activity under these conditions for the evolution of a hummingbird flower from a bee flower are discussed.

Rustler Park in the Chiricahua Mountains in Arizona lies at approximately 2560 m elevation. Portions of the park, about 2 ha and a few similar, smaller outlying areas, are open meadows which support heavy stands of *Iris missouriensis* during late May and June. *Iris* has a typical gullet-type bee-pollinated flower (Faegri and van der Pijl 1966); the blossom is so constructed that large-bodied bees (*Bombus* spp. and *Xylocopa* spp.), in forcing their way between the ventral tepal and dorsal petalous stamen, contact stigmas and anthers.

During the May-June period of peak *Iris* flowering, male Broad-tailed Hummingbirds (*Selasphorus platycercus*) used the blossoms frequently and established territories in the large meadow. They sometimes fed "legitimately" and effected some pollination, but most often exploited blossoms "illegitimately" by probing

it possible that more pale Blue Grouse occur in wild populations but are selected against through lack of cryptic coloration.

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at the juncture of the tepals just above the blossom receptacle (table 1). Various lepidopterans also secured nectar "illegitimately" in a similar manner, but fed from a stationary position near the base of the receptacle. *Bombus* and *Xylocopa* also frequented the blossoms; thus there appeared to be considerable competition for nectar. Rivoli's Hummingbird (*Eugenes fulgens*) and the Blue-throated Hummingbird (*Lampornis clemenciae*) were also present occasionally at the edges of the meadows, but were never observed feeding on *Iris*.

Female *S. platycercus* did not establish territories but were sighted occasionally at the edge of the meadow. Less often, they were observed within the meadow where, upon discovery, they were usually attacked by the territorial males. No mating displays were observed. During the study period, females were most often seen feeding in smaller open areas where *Iris* was less abundant, more dispersed, and therefore less likely to be dominated by territorial males. Outside the meadows, a few territorial males were observed defending flowering single shrubs or small trees of *Robinia neomexicana* or clumps of *Echinocereus triglochidiatus*. Otherwise, except for an occasional early-blooming *Penstemon barbatus*, blossoms of other species did not appear to be utilized by either sex during the study period.

During the period of observation, 2-24 June 1971, eight territories were maintained in the large *Iris* meadow, four by recognizable individuals (fig. 1). Territories were usually contiguous, but where *Iris* density was low and territorial interaction sporadic or absent, precise boundaries could not be determined. Otherwise, boundaries were well defined and exclusion of conspecifics was complete. Chases were the most obvious territorial activity, but vocal and visual displays were also common. Perched or feeding

TABLE 1. Illegitimate vs. legitimate utilization of *Iris* by *Selasphorus platycercus*. Legitimate uses effected some pollination, while illegitimate uses did not.

| Bird | No. of feeding forays | No. of blossoms utilized | | |
|------|-----------------------|--------------------------|------------|----------------|
| | | Illegitimate | Legitimate | % illegitimate |
| 1 | 4 | 92 | 16 | 85.2 |
| 2 | 2 | 24 | 8 | 75.0 |
| 3 | 4 | 52 | 24 | 68.4 |
| 4 | 5 | 72 | 18 | 80.0 |
| 5 | 5 | 29 | 20 | 59.2 |
| | 20 | 269 | 86 | 75.8 |

territorial individuals often gave a characteristic metallic "chittering," presumably a threat signal, when the boundary of the territory was approached by a feeding bird from an adjacent territory. When males of adjacent territories were simultaneously perched and in close proximity, yet each within its own territory, one or both engaged in vocal display, sometimes for periods up to 15 min. Visual display was restricted to dive or flight displays and was most often observed at the termination of pursuit flights.

As well as could be determined, territorial violations that occurred, though not frequent, were by territorial individuals already resident in the meadow and usually by birds from contiguous territories. Chases were usually initiated immediately above general blossom height, often continued across other territories, and sometimes persisted to high altitudes at some distance from either territory. Birds usually had two or more conspicuous perches at various locations within the territory. The previous year's projecting stem remnants of *Heilianthella* sp., which were abundant in most territories, were most frequently used, but projecting branches of Chiricahua Pine (*Pinus ponderosa* var. *chiricahuaensis*) 3–10 m above ground level and tall *Iris* plants were also used.

Displays and overt aggression were usually directed toward conspecifics, but bees feeding on *Iris*, especially *Bombus* and *Xylocopa*, were frequently at-

TABLE 2. Density of *Iris* blossoms on plots.

| Date | Blossoms/m ² $\bar{x} \pm SE$ |
|---------|---|
| 14 June | 15.1 \pm 1.6 |
| 18 | 14.0 \pm 1.8 |
| 21 | 10.8 \pm 2.1 |
| 22 | 7.6 \pm 0.9 |
| 24 | 5.4 \pm 0.6 |
| 1 July | 0.0 |

tacked and often successfully ejected from the territory. Feeding butterflies often appeared to be deliberately supplanted but were seldom pursued.

With the apparent exception of the Fiery-throated Hummingbird (*Panterpe insignis*) (Wolf and Stiles 1970), average territory size recorded in the present study (2040 m² or 0.2 ha) appeared substantially larger than that recorded for other species of humming birds (Pitelka 1951; Fox 1954; Legg and Pitelka 1956; Grant and Grant 1968; Wolf 1969; Lyon, unpubl.) Several factors were probably involved. Defense of territories appeared very efficient due to the openness of the meadow, the homogeneity in blossom level, and the uniform dispersion of *Iris* plants. Under these conditions, detection and ejection of trespassing birds are easier than from a heterogeneous territory which offers greater possibilities for concealment. Larger territory size, however, may also be a consequence of the smaller quantities of nectar produced by bee flowers (Faegri and van der Pijl 1966), necessarily leading to territories with relatively larger numbers of flowers.

The territorial system was very stable during all but the latter part of the observation period. When the study began, eight territories were present and no change in number (or size) of territories or territorial individuals occurred from 2 June through 20 June. [Though birds were not marked, four (those occupying territories 1, 2, 4, and 6) could be identified by distinctive plumage characteristics. Since these birds remained on territories throughout the study period, it was presumed others did also.] On 14 June, in anticipation of a rapid decline in flowering and the effects it might have on stability of the territorial system, eight 3 m \times 15 m randomly selected plots were established in the meadow to record the daily average number of *Iris* blossoms per unit area, hence to provide an index of the relative number of *Iris* blossoms available daily to *S. platycercus* (table 2). At the same time, territories were ranked in categories of high, medium, or low density by visual estimation (fig. 1). On 21 June territories 1 and 7 (medium density) and 2 and 3 (low density) were deserted. The bird in territory 6 (high) subsequently defended the combined area of territory 6 and the abandoned territory 7. Territories 4 and 5 remained intact. During this period, the average number of blossoms recorded on plots fell to 10.8 blossoms/m² (table 2). One day later only territories 6 and 8 (high) remained. Two days later the average number of blossoms fell to 5.4/m² and all territories were deserted. The territorial system thus disintegrated quickly once the number of blossoms reached 10.8/m², even though takeover of deserted territories on 21 June by the still active territorial birds would have more than compensated for the loss of nectar due to decrease in blossom number. That no birds remained to feed on *Iris*

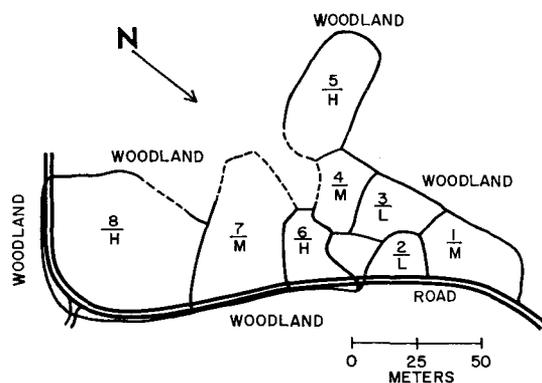


FIGURE 1. Map of *Iris missouriensis* meadow study area, Rustler Park, Chiricahua Mountains, Arizona, showing *Selasphorus platycercus* territories, June 1971. Numbers indicate territories, letters under hash marks estimated density of *Iris* blossoms (L = low; M = medium; H = high). Broken lines indicate uncertainty of territorial boundary. Birds in territories 1, 2, 4, and 6 could be identified by distinctive plumage characteristics.

following the complete abandonment of all territories might suggest a cessation of nectar production concomitant with blossom decline, yet butterflies, *Bombus*, and *Xylocopa* continued to feed heavily on *Iris* until 1 July at which time flowering ceased. Further, the inclusion of recently abandoned territories into already existing territories might have proven too large an energy expense for assuring protection from raiding conspecifics in relation to the additional amount of nectar consumed. However, the continued stability of large territory 8, the enlargement and persistent defense for at least one day of the combined areas of territories 6 and 7, and the absence of all *S. platycercus* in the meadow after 24 June would argue against that interpretation.

One plausible explanation is related to the flowering of hummingbird-flowered plants of the region. At elevations between 1400–2200 m, flowering occurs primarily from late February–May, and above 2200 m from July–September. Species flowering in the first period include *Pentstemon superbus*, *P. subulatus*, *P. pseudospectabilis*, *P. bridgesii*, *P. parryi*, *Salvia henryii*, and *Fouquieria splendens*. Species of the later regimen include *P. pinifolius*, *Stachys coccinea*, *Bouvardia glaberrima*, *Salvia lemmonii*, *Castilleja patriotica*, *Polemonium pauciflorum*, *Aquilegia tri-ternata*, and *Silene laciniata*. Two species, *Echinocereus triglochidiatus* and *Pentstemon barbatus*, are found both above and below 2200 m. Both flower from May–September, beginning at lower elevations early and progressing to higher elevations in late summer. Only *Zauschneria californica* occurs at low elevations in the July–September period.

During the later period, *P. barbatus* is by far the most abundant hummingbird-flowered species above 2200 m, and therefore the most important nectar source for *S. platycercus*. The first blossoms in most stands do not appear until the end of June when *Iris* is nearing the end of its flowering period. The start of flowering by *P. barbatus* coincided well with the abandonment of the *S. platycercus* territories described above. Periods of observation at *P. barbatus* stands nearest the *Iris* meadow, following abandonment, indicated consistent but light usage by *S. platycercus*, but this was anticipated. Stands of this species are abundant but widely scattered and, during initial blooming, total nectar availability at any one stand was probably limited. This necessitated continued movement among stands with feeding periods of limited duration at each stand. Two weeks following abandonment, however, *P. barbatus* was flowering profusely and by then *S. platycercus* had established territories in most of the larger stands.

DISCUSSION AND CONCLUSIONS

There seems little doubt that hummingbird territoriality, at least that in which defense of food is the primary function, reaches its greatest development in association with hummingbird-flowered species of plants. Such plants are characterized by large nectar production, red tubular corollas, and exclusion of other potential pollinators. Nectar production encourages territoriality if blossom density is sufficiently high to make exclusion of other hummingbirds (including conspecifics) worth the price of the energy expenditure (Brown 1964). Infrequently, and under special conditions such as exist in the tropical dry forest of Costa Rica at times of the year when alternate nectar resources may be

scarce (Stiles and Wolf 1970), hummingbirds may depend upon and defend insect-pollinated species as a major source of nectar. In such situations hummingbirds are primarily nectar thieves, feeding “illegitimately” on flowers designed for other modes of pollination. The utilization of *Iris missouriensis* by *S. platycercus* falls into this category. Here, special conditions encouraged the exploitation of what one month earlier or later would have been an insignificant nectar source. Possibly because of its small size and lower energy requirements, *S. platycercus* is able to utilize *Iris* as an interim food source whereas the larger *Eugenes* and *Lampornis* could not secure enough nectar to pay for energy expended in feeding and territorial defense. The absence of other small hummingbirds above 2200 m during this period eliminated a second source of interspecific territorial clashes and possibly allowed for conservation of energy. Further, the relatively high density of blossoms per unit area, their uniform and extensive dispersion, and the openness of the terrain which would make defense more efficient, encouraged the establishment of territories. Finally, the scarcity of other suitable flower resources above 2200 m during May and June also probably encouraged the establishment of territories in the *Iris* meadow.

The *S. platycercus*-*Iris* relationship suggests particular interactions that might be involved in the evolution of the hummingbird flower. Although it appears well established that most bird-pollinated flowers in temperate areas have evolved from bee flowers (Grant 1961), the specific kinds of conditions under which this might occur, and especially the incipient stages in the process, seem poorly understood. Though *Iris missouriensis* has a very specialized bee-pollinated blossom and would not be expected to respond readily to even intense selection pressures from hummingbird pollination, the complex of factors described above could be effective in initiating the process of evolution from bee to hummingbird pollination if, rather than *Iris missouriensis*, the species involved was a more generalized bee flower. Under such circumstances the following schema is suggested:

1. Initial establishment and persistence of a species of small hummingbird in the pollination system (territorial or nonterritorial), perhaps through range extension triggered by climatic changes, whose nectar demands are subsequently lower than those of larger species perhaps already present.
2. Presence of an unspecialized bee-pollinated species with a relatively dense growth pattern and large blossom (hence possibly more nectar), and flowering out of phase with all or the most important of the flowering species in the hummingbird pollination syndrome. *Echinocereus triglochidiatus*, for example, though seldom abundant, is a large-blossomed local hummingbird flower equal in size to *Iris*, which probably evolved from a bee-pollinated ancestor.
3. Increased usage and pollination by hummingbirds relative to bees and thus greater selection pressure by hummingbirds, leading eventually to blossom adaptations for hummingbird pollination. The total number of floristic components in the bird syndrome would thereby be increased and the syndrome possibly protracted temporally.

S. platycercus probably does not qualify as a recent addition to the bird fauna of the Chiricahuas since it ranges from Central America to southern Montana (Bent 1940). Though *Eugenes fulgens* and *Lampornis clemenciae* are too large to fit the conditions of the schema, the ranges of both reach their northernmost extension in southern Arizona (Marshall 1957), illustrating how, under the right bird-flower conditions, range extension alone might serve as the initial impetus as indicated in the schema. The schema would also apply to situations in which bees, birds, and their respective flowers were already present if, instead of or in addition to range extension, environmental changes occur. For example, Cruden (1972) suggests that increased daily periods of inclement weather, which substantially decrease bee activity but have little effect on feeding activity by hummingbirds, increase hummingbird pollination relative to bee pollination.

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UNUSUAL ATTACK OF INTRUDING MALE ON A NESTING PAIR OF PILEATED WOODPECKERS

LAWRENCE KILHAM

Department of Microbiology
Dartmouth Medical School
Hanover, New Hampshire 03755

The following observations were made on Sapelo Island while I was a guest of the Marine Institute of the University of Georgia. Although they are concerned mainly with an attack in which an intruding male (IM) drove an established pair of Pileated Woodpeckers (*Dryocopus pileatus*) from their nearly completed nest hole, events during the days preceding and immediately following are given to gain perspective. Recognition of individuals was by behavioral differences.

The nest hole was located about 22 m high in a dead pine. It was deep enough on 15 March 1972 for the resident male (RM) to roost in it at night. He continued excavating, however, over the next week. When I approached the pine at 06:45 on 21 March, RM was resting on another dead pine not far from the nest tree, but 3 m from an intruding Pileated Woodpecker that was drumming. After a few minutes, the intruder flew to the nest tree. The female woodpecker, who was inside the hole, then flew at and attacked the intruder. There was much flapping

of wings, both while in the air and while clinging to the trunk of the pine, as the two birds circled to strike each other. When this ended, the female left to fly in an apparent attack on her mate who had been perching higher up in the nest tree. He flew off and she followed. The intruder was then alone. It perched almost motionless for the next 15 min until 07:05 when the RM returned and hitched upward toward it in a bill-waving threat dance (Kilham, *Condor* 61:377, 1959). I then heard the female drumming. The intruder flew toward her and this was the last time I saw it. Unfortunately, I was unable to be sure of its sex against a dark grey sky.

The work of excavating the hole, carried on almost entirely by RM, continued over the next few days. On 23 and 24 March, it appeared that events were close to the time of copulation and egg-laying, for the female entered the nest hole soon after sunrise and I heard tapping and low *woicks* (Kilham, *Condor* 61:377, 1959) when the male looked in at her. The male remained in trees not far from the hole on 24 March. When he flew toward the nest at 07:35, I noted an IM flying toward it at the same time. At first, the two males flew at each other while circling in a combination of flying and clinging to the trunk 3 m below the hole. IM, however, broke away to ascend to the hole, where he met the female. The two jabbed at each other in the entrance. After a few moments, the intruder backed down to attack RM as before, then flew back to the hole. The jabbing of bills was more intense as the intruder forced