

This is an English translation of a German paper from 1948. I made this translation in the 1970s when I was doing graduate research on the Broad-tailed Hummingbird (*Selasphorus platycercus*) at the Rocky Mountain Biological Laboratory, in the Colorado Rocky Mountains. To facilitate access to the paper by future researchers I have obtained permission (see below) from the publisher of this journal (now absorbed by Zoologischer Anzeiger - A Journal of Comparative Zoology) to post both a copy of the original article and my translation. Dr. Nick Waser made some corrections and additions to the translation in April 2010.

Nick and I think that the author may have misinterpreted some of what he saw, although it's also possible that the population of birds he studied is truly different from the one we have studied in Colorado. See our footnotes in a few places. My recollection is that Dr. Willam Calder, who looked for the species in the mountains in Mexico in a few winters in the 1980s, concluded that the species does not reproduce during the winter, only in the summer. Lorene Calder, who worked with Bill Calder on those trips to Mexico, wrote to Nick in April 2010: "I ferreted out a Xerox copy of Bulletin 176, U.S. National Museum in which a Maj. Bendire (1895) writes that the broad-tails raise one brood in the lower foothills and then "retire to higher altitudes in the mountain parks...here they raise their second broods under nearly similar conditions as the first". R. B. Rockwell in 1908 (Mesa County, CO) says it "frequents the timber along the streams from 6000 ft. up and raises two broods in a season and possibly three". To this, Bill wrote in the margins – "b.s. and how did they determine?" I think "they" didn't factor in the timing and availability of resources."

– David Inouye, June 2010, University of Maryland

Wagner, H. O. 1948. Die Balz des Kolibris *Selasphorus platycercus*. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie, und Geographie der Tiere 77:267-278.

Translation by David W. Inouye, with help from Nick Waser. Original paper and translation posted by permission of publisher. (see at end)

The Courtship Display of the Hummingbird *Selasphorus platycercus*.

The small (approximately 3 gram) hummingbird *Selasphorus platycercus platycercus*¹ (Swainson) occurs in the mountainous west of the United States, the Sierra Madre Orientale and the central highlands of Mexico. In the area around Mexico City, where the following observations were primarily made, it lives in montane oak forests interspersed with pine and cypress between 2300 and 3000m. Higher up, in the adjoining fir forests, it only occurs in places where fir and oak are intermixed. In the region of sparse pine woodlands between 3500m and timberline, *Selasphorus* appears to be completely absent.

¹ The Broad-tailed Hummingbird.

1. Length of Stay in Central Mexico

Selasphorus platycercus platycercus is a migratory bird. The majority arrive in central Mexico in August. From July I have only four observation dates; three of these are of adult males. The earliest date known to me, 27 June, is on the labels of two faded males in the collection of the Biological Institute in Mexico City.

During November the number of these hummingbirds steadily declines; the last leave us in the first days of December. As the adult males are the first to appear, so are they also the first to leave.

Where do these birds come from then, that stay with us about four months, raise a brood and then wander on? I am of the opinion, that these are the same animals that breed in spring in the USA, where they arrive in droves from the middle of April until May and mostly leave again in August, and this follows from the statements that Bent (1940) has put together on egg dates.

Arizona – 20 nests, 8 May – 30 July (of which 10 are between 11 June and 16 July)

Colorado – 18 nests, 22 May – 17 July (of which 9 are between 13 June and 26 June)

Utah – 10 nests, 6 June – 23 July

Probably also in the USA only one brood is raised. Bendire (1895) assumes two broods; this is contradicted however by the shortness of the stay, in connection with the length of the breeding cycle, which from the beginning of nest construction until fledging of young amounts to about 60 days. Late broods are in fact invariably replacement broods, which hummingbirds are always inclined to begin, until the migration urge sets in.

Where *Selasphorus platycercus* wanders to from the Mexican highland is unknown. In the coastal regions and in the temperate zone below 1800m I have never seen one. The habitat that they search for, therefore, presumably resembles that which they occupy in the USA and in the area around Mexico City. During January I saw and heard males in the surroundings of San Cristobal (Ciudad de las Casa, Chiapas), in oak-fir forests above 2000m. They appeared, judging by their flight noise, to be in reproductive state at this time². Whether these are the same birds, which earlier in the year one encounters further north, would surely prove very difficult to ascertain.

The molting season of *Selasphorus platycercus* is unknown to me. The only molting bird I examined was a female, which was collected on 6 May 1934 in Xochicoatlan (Hidalgo), and in which the fifth and sixth primaries were pin feathers.

² It's not clear here whether he means that he heard just the flight noise, or heard the initial stages of courtship, the big U-shaped dives over females (who are usually perching on or close to the ground, in my observations in Colorado). Either of these could be heard at some distance without spotting the male.

In conclusion, I hold it not unlikely that *Selasphorus platycercus platycercus* raises two broods during the year and in between switches to a migration that takes it to the alternative breeding area, that just then provides a rich food source. In the USA flowers and insect life develop especially richly in June and July, whereas in the highlands of Mexico this occurs in September and October (the second half of the rainy season).

2. The Courtship

I have from time to time turned my particular attention to the courtship of *Selasphorus platycercus*. The segments into which it can be organized are already well known, to be sure, but the biological meaning of many actions has been misjudged, so badly so that Pitelka (1942), in his summary description, asserts that “The frequent claims of amorous intent attached to the display flights of hummingbirds by various observers are largely nonsense.”

The confusion has primarily arisen because play flight in not only this, but also other species of hummingbirds, was not recognized as such, which is all the easier to understand since in many details it strongly resembles the true courtship flight.

In hummingbird courtship two sharply separated segments must be distinguished:

- 1) The actions of the male that serve to attract the attention of a female ready to mate,
- 2) The true courtship display, in which both sexes actively participate.

Whereas the attraction actions are constantly repeated during the whole year (with the exception of interruption by molting season and migration), the true mating display only occurs once in each reproductive cycle.

a) The Attraction of a Female

Selasphorus does not join in marriage. After the female has prepared the nest, she seeks a mate only for fertilization. In many hummingbird species the male attracts the attention of the other sex through song or a call note; *Selasphorus* however uses a loud flight noise for this.

In the fully colored male the first primary feather is modified for sound production (Fig. 1) with which a noise is produced in the gliding phase of the wave-like attraction flight. This resembles the chirp of a katydid (Tettigoniidae) and is rendered as syrrrr-syrrrr³. The flight speed in the attraction flight amounts to between 20 and 25 meters/sec.

To the human ear the flight noise is easily perceptible at 50 m. The outer hearing limit for me was about 75 m. The *Selasphorus* female probably hears this noise from even greater distances.

³ See Wagner's Fig. 2



Abb. 1.

Abb. 1. Flügel mit distal verschmälertem Schallschwinge eines alten Männchens von *Selasphorus platycercus*.

Fig. 1. Wing with distal reduced acoustical tip of a mature male of *Selasphorus platycercus*.

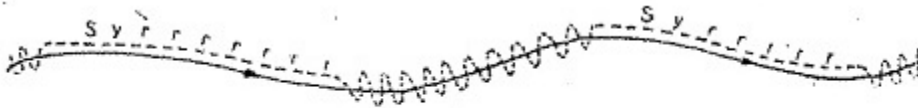


Abb. 2. Flugbahn (—) und Flügelschlag (---) beim Lockflug des Männchens. In den Gleitphasen entsteht ein Fluggeräusch (syrrrrr).

Fig. 2. Flight path (solid line) and wing beats (.....) during attraction flight of males. In the glide phase a flight noise (syrrrrr) is produced⁴.

Each male occupies a permanent territory. Often such territories abut directly on each other. The border appears to be mutually respected. I have only once observed a battle for territory possession. In this case the presumed occupant drove away an intruder from his territory, whereby he followed him at a distance of about 1 m to the apparent boundary of his territory. Both thereby produced the flight noise. Since I made this observation on 25 August, at the time when birds arrive from the north, I hold it quite likely that the pursued bird was a newcomer, who was still searching for his own territory.

⁴ He has this reversed; the flight noise is produced while the wing is beating.

Clark, C. J. 2008. Fluttering wing feathers produce the flight sounds of male streamertail hummingbirds. *Biology Letters* 4:341-344.

Hunter, T. A. 2008. On the role of wing sounds in hummingbird communication. *The Auk* 125:532-541.

As a territory for the duration of his stay in the central highlands of Mexico each male chooses an open place, either a clearing in the oak forest or oak-fir forest, but also maize, wheat and oat fields that adjoin woods, with groups of trees or shrubs on their edges.

The size of the territory depends on the circumstances. In the forest they are often just openings of less than 50 m diameter. In such places the male has two favored perches 3 to 5 m high, on the forest edge, sometimes only a single one. This is an isolated (often dead) thin twig that he returns to after two to four round trip flights. He remains there one to two minutes before he begins a new round trip, so as to let his flight noise be heard⁵. If the territory is in a field, it is considerably larger. In one case the distance paced off between two perches amounted to over 300m. Also the number of favored perches is larger here, usually 3–4. Twigs of bushes at the field edge, or agaves, usually serve as such. In contrast to the small forest territory, here the bird makes no round trip flight, rather as a rule flies in more or less a straight line when changing perches.

During the entire day one can see and hear the attraction flight of the males; even with advanced dusk I hear them occasionally. If they search for blossoms in the neighborhood of a perch, that is where this search begins. They also return to the perch, often for only a few seconds, before they begin a new attraction flight⁶.

The males begin with attraction flights as soon as they arrive from migration. I have not been able to ascertain an increase in intensity during the time of their stay. I observed the latest attraction flight of the year on 15 October. I have gained the impression that the males perform their attraction flight up until the time of their abrupt migration away. I have not ascertained fat deposits before the departure.

I have only heard song twice in the oak forest, and both times from young males (the one only had slightly colored throat feathers, the other a throat patch of small extent). It consisted of low, somewhat strained, tones juxtaposed quickly, which are probably without any meaning in the sex life⁷. In the attraction flight I have never perceived any vocal sound.

b) The Courtship Display

The courtship proper is correctly described by Skutch (1940) and Linsdale (1938). I myself have only been present at five courtship flights in the course of seven years; it is only performed once in each breeding cycle, and its observation is therefore always dependent on a

⁵ For more on the role of the wing whistle in territoriality, see Miller, S. J. and D. W. Inouye. 1983.

Roles of the wing whistle in the territorial behaviour of male broad-tailed hummingbirds (*Selasphorus platycercus*). *Animal Behaviour* **31**:689-700.

⁶ Maybe better described as an advertising flight, if the birds are not mating in Mexico.

⁷ In fact, true song is not described in the Broad-Tailed Hummingbird

lucky chance⁸. I cannot say with certainty where the courtship flight occurs, whether in the territory of the male, in the territory of the female, or in a third place. In three cases I had the impression that it occurred in an area that appealed to the female as a nesting site. In the other two cases it was uncertain, since the locality matched the claims of the male as well as the female. In a male's territory in an open field, as frequently encountered in cultivated landscapes, I have never observed a courtship flight. All of this agrees with the hypothesis that the male, after making the acquaintance of the female, follows to the area of the nest. This is further supported in that the female takes the lead in the following mating act.



Abb. 3. Balz, 1. Phase. Flugbahn des Männchens (—).

Fig. 3. Courtship display, first phase. Flight path of the male (—)

⁸ The fact that he observed this so rarely is additional evidence that these birds are not mating in Mexico. I have seen this several times a day while watching birds at feeders in Colorado in June.

The courtship flight of the male apparently has the goal of increasing the sexual readiness of the female and thereby ensuring fertilization. This increase expresses itself in the behavior of the female during the courtship display. At the same time I have been unable to ascertain any change in the degree of excitation of the male.

The behavior of the female, which changes with increasing sexual excitation, has motivated me to organize the courtship schematically into three steps, although without maintaining that the courtship display always goes through these three phases (never more or fewer). Important individual differences in susceptibility to stimulation may manifest themselves thereby. The courtship flight of a pair is not repeated in the same airspace, therefore it is impossible to follow all events by eye in broken terrain, and I found myself obliged to reconstruct the entire event from fragments. Only once after observing a courtship flight did I see another one about ten minutes later in the same area, which presumably was made by the same pair, and it was the change in behavior of the female established thereby that motivated me to divide the courtship into the following phases.

1st Phase (Fig. 3)

The female sits quietly on a separate twig of a bush. The male repeatedly makes 2–3 headfirst dives before the female. In the pause between the two dives the male sits 1–3 minutes on an adjacent tree. Without visible cause the female flies away, followed by the male.⁹

2nd Phase (Fig. 4)

I have observed this stage only in its second section, because I arrived only after the courtship had already begun. The male came shooting down in a dive. Before he reached the female, she flew somewhat toward him, in order to climb suddenly to a height at his side and then fly off with him.

⁹ This description misses a phase that I observe commonly in Colorado. Following the large U-shaped dives (typically 2-3 of them I think) with the female at the bottom of the dive, if the female doesn't leave, the male will fly about a foot above her, swinging a few inches side to side, making a distinctive wing sound, and after several seconds of this will fly up to do more of the large U-shaped dives. I've never seen courtship proceed beyond that stage, probably because I usually observe this behavior while females are trying to get to a feeder.

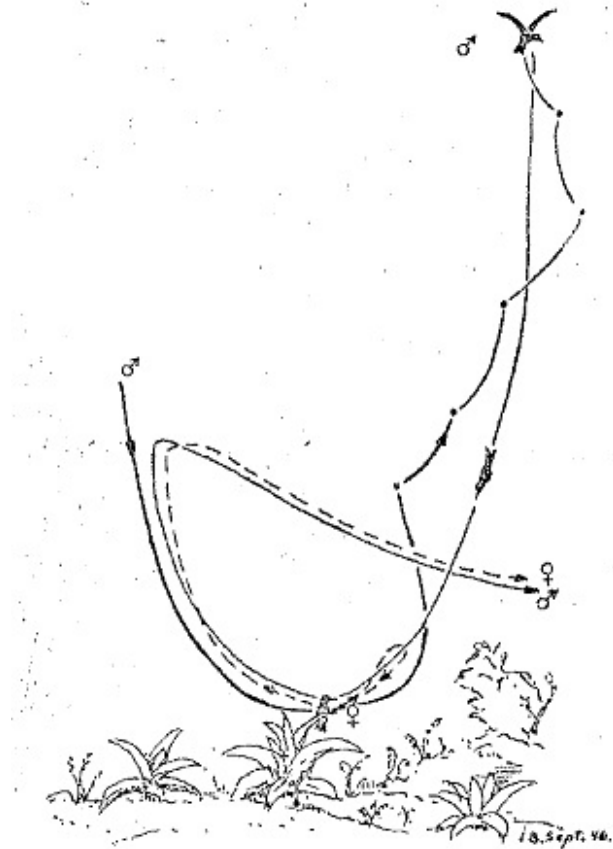


Abb. 4. Balz, 2. Phase. Flugbahn von Männchen (—) und Weibchen (---).

Fig. 4. Courtship display, 2nd phase. Flight path of the male (—) and female (...)

3rd Phase (Fig. 5)

Here the female is very active. The pair arrives together. She sits on a bush while he climbs in the air. When he shoots by her in a dive she joins him. Now both climb upward and dive together. In the case I observed a second and third mutual dive followed. After the third they did not fly up, but instead flew away close together. As the 4th Phase, which I have not observed, copulation probably follows.

I estimate the height reached during the courtship flight as about 40 m. As may be seen in the sketches, the climbing occurs stepwise. The dive with folded wings is exceedingly fast and lasts less than one second (determined with a stopwatch).

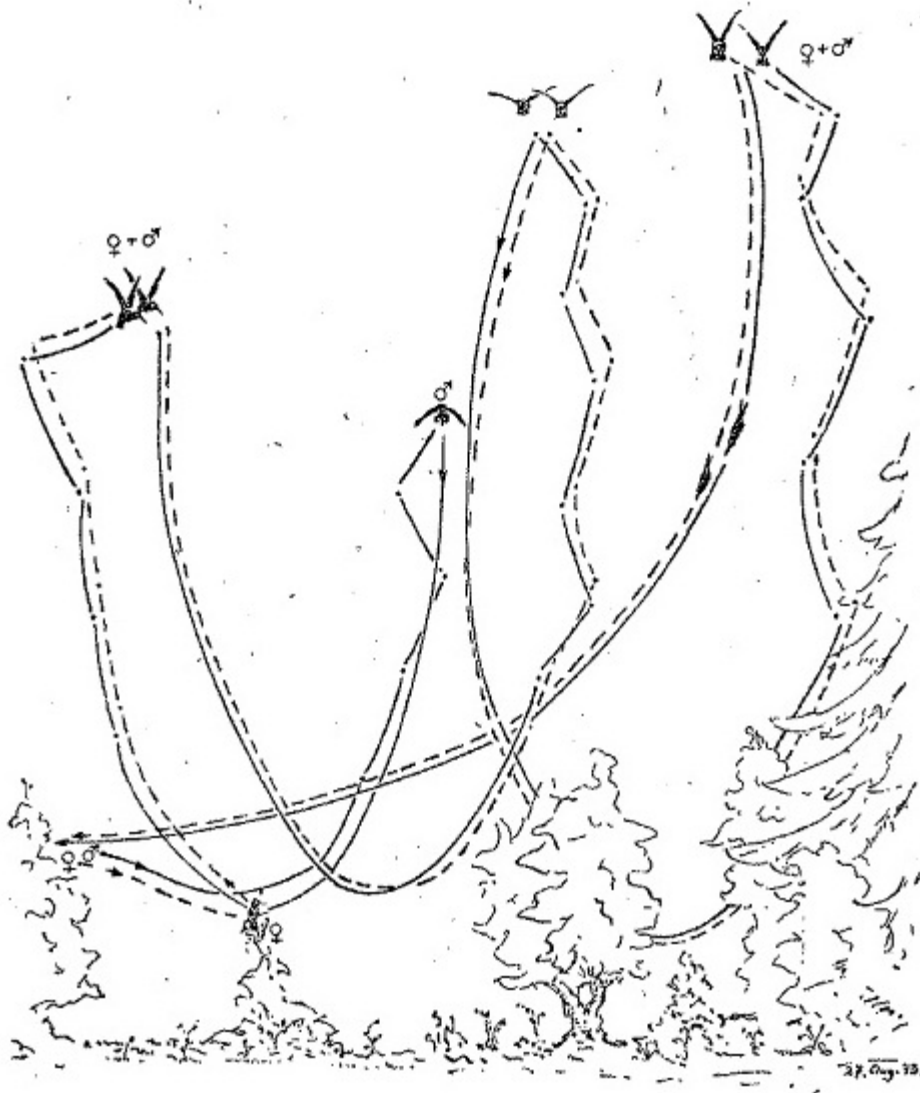


Abb. 5. Balz, 3. Phase. Zeichen wie in Abb. 4.

Fig. 5. Courtship display, 3rd phase. Symbols as in Fig. 4.

All the courtship flights at which I was present occurred in the morning hours (2–4 hours after sunrise). How long a time passes between the encountering of a partner and copulation is unknown; I assume 1–2 hours.

3. The Play Flights

In the Mexican highlands one often sees play flights of *Selasphorus*, primarily performed by young birds. How widely adult females participate therein cannot be confirmed without shooting, because female and young males are similarly colored. A faded adult male was only once observed participating. The young birds are probably those that were raised in the summer in the USA and follow the adults from one breeding ground to the other, although they have not

yet proceeded to reproduction. In the course of their stay in this locale the frequency of the play flights increases. They are performed singly or in pairs. Only once did I see 4 birds participating together.

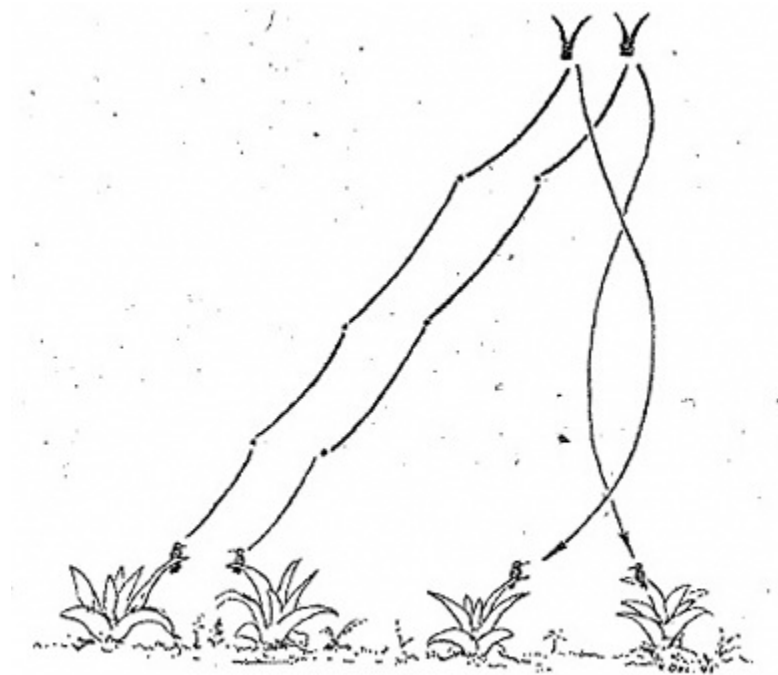


Abb. 6. Spielflug von zwei Gefährten. Beobachtet Herbst 1941.

Fig. 6. Play flight of two companions. Observed in autumn of 1941.

In a play flight the birds fly up in the air as in courtship flight and then dive down. However, the height reached is lower than in courtship flight. Often they rise up in the air only once, only to immediately perch again (Fig. 6), and it is rare that a bird flies up more than three times (Fig. 7). Two birds gladly make play flights together (Fig. 6). These differ from the courtship flight as a rule in that the partners do not shoot down closely together, rather take separate ways. Occasionally one of two participating birds remains perched, whereby the resemblance with high courtship (1st Phase) is increased. Two such hummingbirds, which I shot on 11 January 1945 while they were in play flight together, were found to be by dissection, a young male (weight 3.30 g) and a female with small ovaries¹⁰ (weight 2.55 g). In the four birds mentioned the play flight was completely irregular. One or several birds flew up at the same time or one after another. Noteworthy was that one bird only occasionally, trivially participated, and mostly sat on a branch. When this one changed perches, the others followed (observed three times). All four birds were in juvenile plumage or were females. One was recognizable as a young male by several colored feathers in its throat patch.

¹⁰ Perhaps evidence against breeding during the winter.

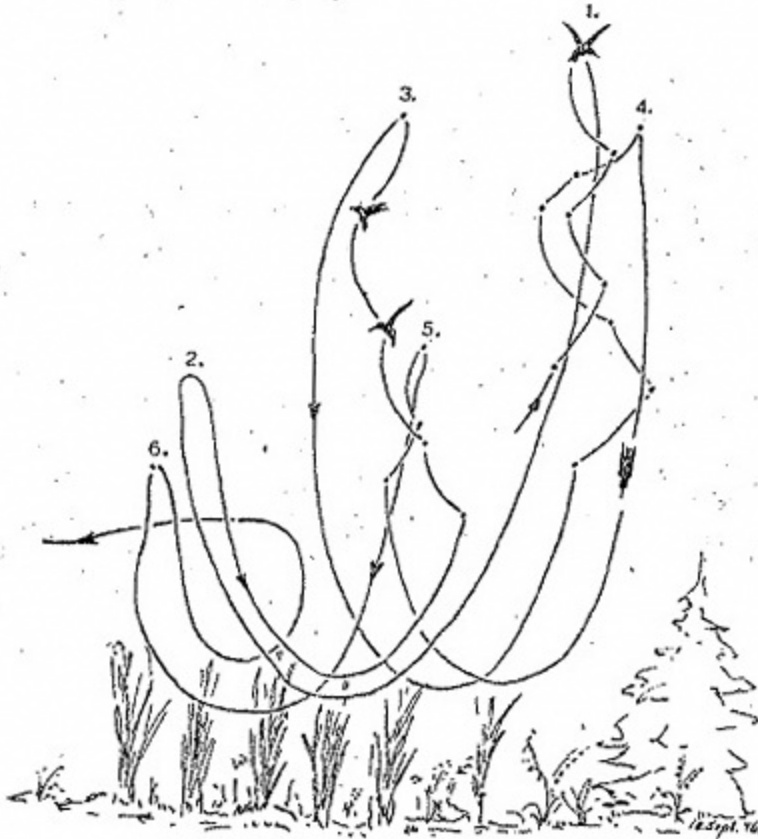


Abb. 7. Spielflug eines einzelnen Vogels. 6 Aufstiege. Beobachtet 18.9. 1946.

Fig. 7. Play flight of a single bird. 6 ascents. Observed 18 September 1946.

Such play flights have, as mentioned earlier, contributed much toward turning the estimation of the true mating behavior of hummingbirds onto false paths. I myself have only learned after some years to distinguish “play” (that is, the instinctive previous practice for the real thing) and “earnest”.

Summary.

1. From the circumstance that *Selasphorus platycercus* is found in the western states of the USA from April or May until August, and in central Mexico from August until the end of November, and in each of these regions raises only one brood (2 young), it is concluded that this hummingbird regularly moves between two widely separated breeding grounds and in such a way has two broods every year.

2. The courtship is divided into two segments, namely a) in actions that serve to attract a female: a wave-form attraction flight combined with a loud flight noise, and b) in the actions of the courtship display, which leads to the synchronization of the readiness for copulation of both partners: performance of plunging flights from a considerable height, in which the female also participates after a while.

3. Young birds (immature males and even adult females), execute play flights singly or in pairs, or even in fours, whose enactment serves as practice for the real thing later, and which distinguishes itself from courtship flight of mature animals by its lesser intensity.

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