

## SHORT COMMUNICATIONS

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### THE BREEDING SYSTEM OF THE ORANGE-CROWNED MANAKIN<sup>1</sup>

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**Abstract.** I studied the lek organization and courtship displays of the Orange-crowned Manakin (*Heterocercus aurantiivertex*) in undisturbed, lowland rain forest in northeastern Peru. The majority of leks were in seasonally flooded or swampy forest, and most were situated around the borders of old ox-bow lakes. Males maintain loosely packed courts inside exploded leks or “quasi leks,” which may extend for more than 1 km. Within leks, males vocalize throughout the day and occasionally perform two distinctly different solitary displays. One is a spectacular aerial performance that begins above the canopy. The “log display” is performed just above ground- or water-level and consists of a series of short, ritualized jumps.

**Key words:** *breeding behavior, courtship, display, female choice, Heterocercus aurantiivertex, lek, Orange-crowned Manakin.*

**Resumen.** La organización del lek y las exhibiciones del cortejo nupcial del Saltarín de Cresta Naranja (*Heterocercus aurantiivertex*) fueron estudiadas en selva virgen lluviosa del nororiente peruano. La mayoría de los leks estaban en bosque estacionalmente inundable o bosque pantanoso, localizados por lo común en las orillas de lagos fluviales antiguos. Los machos defienden “arenas” bastante dispersas, dentro de leks disgregados o “quasi leks,” que pueden alcanzar más de 1 km de extensión. Dentro de los leks, los machos vocalizan durante todo el día y ocasionalmente ejecutan en solitario dos exhibiciones nupciales claramente diferenciadas. Una es una espectacular exhibición aérea que empieza sobre el dosel del bosque. La otra exhibición, terrestre, es ejecutada a poca altura sobre el suelo o el agua, y consiste en una serie de saltos cortos y ritualizados.

The Orange-crowned Manakin (*Heterocercus aurantiivertex*) is one of three species in a genus whose natural history and mating system are poorly known (Prum 1990, Ridgely and Tudor 1994, Prum et al. 1996). *H. aurantiivertex* is known from a few localities in a restricted region of southeastern Ecuador and, prior to this study, a single locality, Chamicuro on the Río Huallaga, in northern Peru. In fact, *H. aurantii-*

*vertex* is a common bird in its preferred habitat (Alvarez 1994), and I made extensive observations on the natural history and courtship behavior of this bird, as fascinating as it is poorly known.

#### METHODS

Observations (totaling approximately 400 hr) were conducted between June 1993 and February 1996 at 17 leks, principally along the middle and lower course of the Río Tigre in northern Peru. The primary study site was the “Lago Napo” lek near Intuto, on the middle Tigre (03°29'S, 74°46'W). Observations were made during all months except August and September. The general habitat is humid tropical forest, largely undisturbed, with annual precipitation of 2,500–3,000 mm, and with no well-defined dry season; however, rains generally are most intense April–June and October–December. I observed leks primarily from a canoe along the margins of ox-bow lakes and in flooded forest, commencing at about 1 hr after first light and continuing until about 17:30, when manakin activity generally ceased. Tape recordings of vocalizations were made with an Aiwa TP-650 recorder and Vivanco EVM-298 microphone.

#### RESULTS

##### HABITAT AND SPATIAL DISTRIBUTION OF LEKS AND COURTS

Nine of 16 leks visited along the Río Tigre were situated in seasonally flooded, blackwater forest around the margins of old, very deep, tannic ox-bow lakes; I found no leks around the margins of whitewater courses or young ox-bows. The tannic lakes have more or less permanently swampy margins, or at least one such margin, dominated by *Ficus* species (Moraceae), primarily *F. lauretana* and *F. killipii*, with lesser numbers of *Virola* sp. (Myristicaceae), *Symphonia* sp. (Clusiaceae), and *Campsiandra* sp. (Leguminosae). A variety of palms (Arecaceae), especially *Mauritia flexuosa*, *Astrocaryum macrocalyx*, *Iriarteia deltoidea*, *Sheelea basleriana*, and *Socratea exorrhiza*, were abundant at some leks, and single leks on the ríos Tigre and Corrientes were situated in *Mauritia* palm swamps. Lianas and other epiphytic growth also were common. *Ficus* fruits were important foods of *H. aurantiivertex*, and the presence of leks was strongly correlated with the distribution of stands of *F. lauretana* and *F. killipii*. Most leks were in seasonally flooded forest with a can-

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opy height of 20–35 m with numerous tree falls forming light gaps, but the understory was relatively open and free of herbaceous growth. B. Whitney (pers. comm.) observed a lek in similar habitat along the blackwater Río Cuyabeno in Sucumbios Province, Ecuador.

Two leks along the Tigre were located in “brushy forest” characterized by a dense growth of rather low-stature trees with a canopy height of 10–15 m. One site was seasonally flooded, and the other was on a white sand area on *terra firma*. This habitat is patchy and especially poorly known in Peru, but physiognomically similar to the “caatinga forest” of the upper Rio Negro region (also blackwater) of northwestern Brazil (B. Whitney, pers. comm.). Two other leks were located along the margins of blackwater streams. One lek near Intuto had no standing water in the vicinity but was in a poorly drained spot dominated by palms. One lek near Lores, on the Río Tigre below Intuto, was in secondary *terra firma* forest with an abundance of Melastomataceae.

Male *H. aurantiivertex* defended individual territories, or courts, within exploded leks or quasi leks (terms defined in Gilliard 1969, Foster 1983). Courts were approximately 8–15 m in diameter, and extended to 15–25 m diameter when log display sites were included. At the “Lago Napo” lek, most courts were 100 to 300 m (rarely 400 m) from the closest neighbor. The two courts nearest each other were separated by a small arm of the lake, approximately 65 m apart. The entire lek was approximately 1.2 km long, but some other leks that were not measured may have been more extensive. Males perched in courts were not in visual contact with even their closest neighbors. However, neighboring males easily could hear each other’s advertisement calls (audible to me for up to about 200 m), and flight displays were audible at 400–500 m under favorable climatic conditions, especially when the forest was flooded.

Leks and courts of *H. aurantiivertex* appear to persist from year to year, as is typical of other manakins (Sick 1967, Bradbury 1981, Robbins 1985). Courts located in 1993 were occupied in 1994 and 1995, although I was not able to determine whether the same individual males were present. Courts were occupied and defended outside the reproductive season, even while the defending bird was in molt, although birds performed no displays. Fidelity to lek courts persisted even after significant local disturbance to vegetation. In the Lago Napo lek, a court remained occupied even after two large trees were cut in 1994, and after another tree on the opposite side of the court fell in a wind-storm in 1995, leaving the male particularly exposed and visible. Subsequently, fishermen frequently camped for periods of 3–4 days within 10 m of the male’s favorite perches, but he persisted at the site. At a different court, a male was collected after suffering a mist-net injury on 2 January 1995, and this court remained unoccupied for at least four months. When I revisited this site in February 1996, another male was present.

#### ATTENDANCE OF MALES AT COURTS

Male *H. aurantiivertex*, with some individual variation, spend from 70–90% of the day at their courts. A

single male in Napo, Ecuador observed over a period of 7 days was in attendance on its court 92% of the time (R. Prum, pers. comm.). When not displaying, feeding, or physically interacting with other individuals, males in this study perched on three or four favored branches between about 0.5 and 12 m above ground or water level. Most males spent 50–60% of the time on one or two particular perches, delivering advertisement calls and occasionally performing brief foraging sallies for insects or fruit. Height above ground varied with canopy height: birds perched in the subcanopy of the court trees, so in courts with taller trees birds chose higher perches. The birds were quiescent for much of the time on their courts, regularly passing 10–15 min without moving, and giving only occasional advertisement calls. Once I observed a male remain completely immobile for 19 min. Movements were quite sudden and rapid, especially during intra-specific chases. At all seasons of the year, birds allowed me to observe them from only a few meters distant, continuing displays and calls normally, even when I made such movements as slapping mosquitoes or putting on rain gear.

#### VOCALIZATIONS

*H. aurantiivertex* makes at least nine distinct types of vocalizations, primarily by males at their courts, although given the difficulties of distinguishing the sexes under field conditions (especially away from display courts) my attribution of calls to one sex or the other may require revision.

*Advertisement call.* This call was delivered only by the displaying male from perches inside the court and probably represents an advertisement to females, as well as possibly acting to repel other males (Sick 1967). It was one of the most frequently given vocalizations from June to February. A typical call was a thin meandering trill (Fig. 1A), sometimes introduced by weak, rapidly delivered whistles of slightly lower frequency. Males delivering this call maintained a normal perching posture and did not open the bill especially wide. This call was emitted throughout the day, usually at intervals of 1–6 min, but more sporadically through midday. During molt and the months following, mostly March to June, the advertisement call rarely was given.

*Interaction vocalizations.* These vocalizations were delivered by males principally when an outside male approached a court, but also in response to calls from another male, or when a different species of bird passed close to a court. In the early stages of the breeding season, this vocalization was given frequently, more often than the advertisement call, but it was heard only irregularly through the bulk of the reproductive period. Thus, these vocalizations may function primarily to establish and maintain a display site. The principal vocalization, with some variation, consisted of a series of syllables appearing much like the advertisement call but with a decided metallic quality (Fig. 1B). I observed a female give a similar vocalization several times from or near the nest.

*Agonistic vocalizations.* During aggressive chases and other encounters between males, a loud, rapid, chattering series that rises and falls was given (Fig.

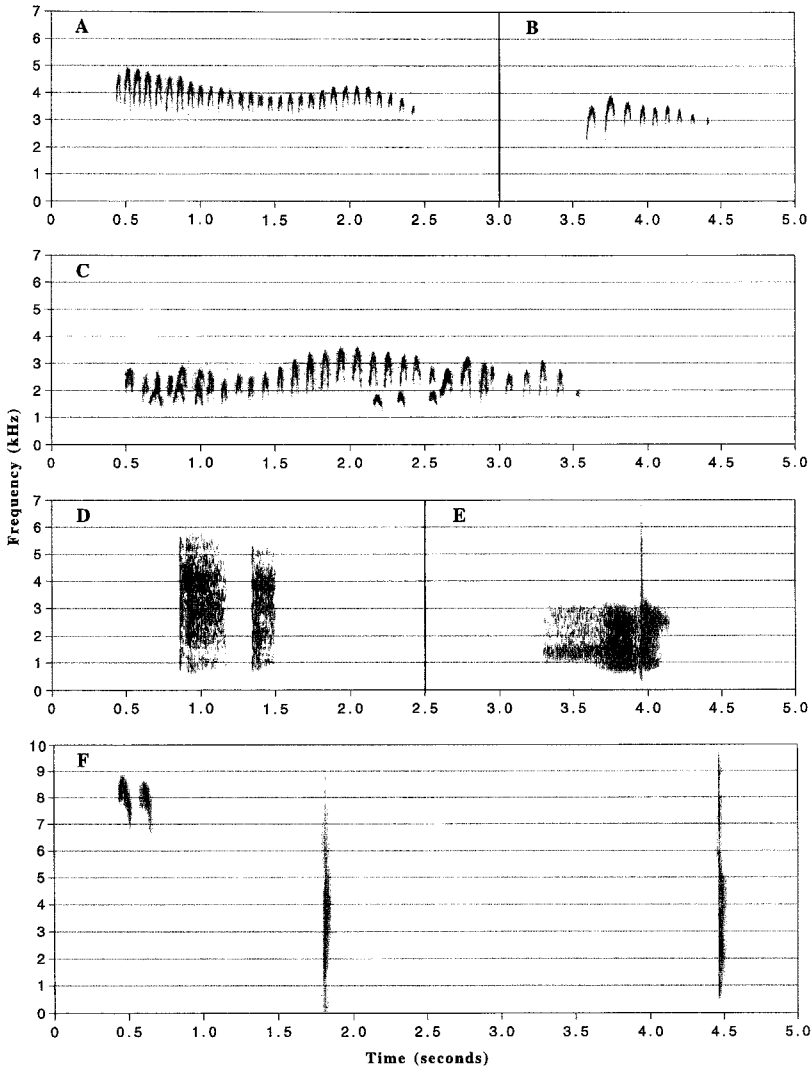


FIGURE 1. Some characteristic vocalizations of *Heterocercus aurantiivertex*. (A) Advertisement call, a thin trill: *che'che-tree'e'e'e'e'e'e'e'e'e'e* (Lago Napo, June 1995). (B) Interaction vocalization (Lago Napo, June 1995). (C) Agonistic call, a loud rapid chatter: *chi-chi-che-che-che-chee-chee* (Sachacochoa, upper Río Tigre, February 1994). (D) Agonistic call, given when highly agitated; in this case, attacking a stuffed specimen: a metallic, vibrating *tingg-tingg* (Lago Napo, February 1995). (E) Flight display, with hissing sound and final explosive *pop* (vertical line), probably produced by the spreading of the tail and wings (Mishana, bajo Nanay, September 1998). (F) Bisyllabic display call (*sche sche*) and two mechanical *pop* sounds (vertical lines at about 1.7 and 3.9 sec), probably produced by the wings, employed in the log display (Napo, Ecuador, August 1992). Sound spectrograms were produced by Phyllis Isler using Canary 1.2 of the Bioacoustics Research Program of the Cornell Laboratory of Ornithology, and Canvas of Deneba Software, Miami, Florida.

1C). When encounters were especially aggressive, the male sometimes terminated this vocalization with strange, vibrating, metallic calls (Fig. 1D). For example, these complete vocalizations were given repeatedly by a male as it furiously pecked at the head of a stuffed specimen placed in its court. When a female specimen was placed in another male's court, the male emitted the *chi-chi* series of vocalizations but not the

hyper-aggressive metallic calls, and he repeatedly attempted copulation. Immediately afterwards, the male performed an extended log display and, a few minutes later, an aerial display. These hyper-aggressive vocalizations appeared to be reserved for male-male interactions.

*Chattering*. This vocalization is similar to the agonistic call described above but is not as metallic in

quality. A female gave it when another species of bird (unidentified) passed near her fledglings. I also heard this chattering during chases on leks, but was not able to determine whether it was given by males, females, or both.

**Display call.** A short, stuttered two (rarely one) note call virtually always was emitted immediately before performance of a bout of jumps in the log display (see below). During that display, one or two notes preceded one or two sharp, mechanically produced, *pop* sounds about 2 sec apart (Fig. 1F). Although this vocalization was delivered only in conjunction with the log display, similar notes sometimes preceded the advertisement call.

The remaining vocalizations, not described here, rarely were heard, and include food solicitation by chicks and distress calls. In addition, a thin, penetrating whistle (*tsiii*) at about 6 kHz is given occasionally, and may be an alarm call.

#### PERFORMANCE OF DISPLAYS

*H. aurantiivertex* performed two kinds of courtship displays, both of which were performed solitarily. The aerial flight display commenced as the male moved from its court perch into the canopy. It then flew upward in either a zig-zagging trajectory or in 30 to 50-m diameter spirals that become successively tighter as the bird rose, until it reached heights between 60 and 100 m above the canopy. From this point it plummeted sharply toward its court, gaining momentum through the first 15 to 20 m with rapid wing-beats, and then partially closed its wings and held them in this position, which produced a peculiar hissing sound that loudened steadily as velocity increased. At the culminating point, 2–3 m above the canopy, the bird abruptly changed its trajectory nearly 90°, producing a dry, explosive *pop* (Fig. 1E). The hissing sound probably was the result of air passing through the remiges and, perhaps, the straight, slightly stiffened outer rectrices. The explosive, terminal *pop* may result from the sudden opening of the wings and spreading of the tail as the bird breaks its descent. Finally, the bird scribed an arc, sometimes very wide, before entering the trees with great speed (Fig. 2). The complete operation lasted from 20–40 sec in the longest displays, depending on the height attained by the male. The descent phase of the display lasted from 3–4 sec. Some flight displays, especially the first flights of the morning, which tended to be shorter, may lack the explosive *pop* at the finish. Some plummets were performed at less acute angles, approximating 75°. Sometimes males performed “failed” flight displays in which no sound was produced by the point of mid-descent, and the display was aborted.

The second principal courtship display of *H. aurantiivertex* is the log display. The male descended to a roughly horizontal branch, approximately 6 to 30 (rarely 45) cm in diameter, and between 10 cm and 2 m above ground. Typically a male used various display logs within his court. Soon after landing on a display log, the male performed a series of vertical dancing jumps of 15 to 20 cm height, with the head upright and the brilliant orange crest fully erect. Each jump was accompanied by a sharp *pop* sound (Fig. 1F) like

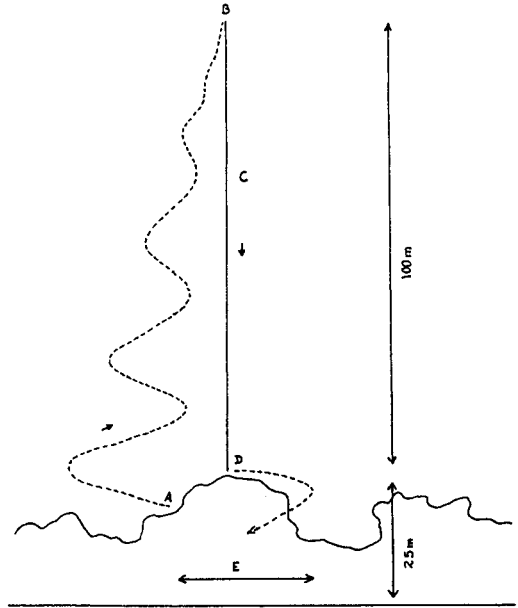


FIGURE 2. Schematic representation of the spectacular flight display of *Heterocercus aurantiivertex*. A–B: the male rises from the canopy above its terrestrial court, spiraling or weaving upward toward the apex of the ascent. B–C: several rapid, momentum-building wing-beats are given as the bird begins the descent phase. C–D: the main descent phase involves a steep plummet toward the forest canopy with partially spread wings, producing a loud hissing sound that increases in amplitude with the velocity of the diving bird (and is perhaps produced in part by the passage of air through the rectrices) and terminates with an explosive *pop* as the bird flares the wings and tail to break its descent 2–3 m above the treetops. D–E: at the finish of the display, the male often scribes a wide, horizontal arc over the canopy before returning to its terrestrial court.

that made by cracking a thin, dry branch, and apparently much like display sounds described for *Corapipo gutturalis* (Prum 1986, Théry 1990), *C. altera* (Aldrich and Bole 1937, Wetmore 1972), and *C. leucorrhoea* (Skutch 1967, Sick 1967). *Corapipo* produces the sound with a slap of the wings, as probably does *H. aurantiivertex*. The male's posture was perpendicular to the substrate but its jumps were interspersed with occasional 90° aerial pirouettes after which it landed briefly in various positions, sometimes about-facing. If the male landed other than perpendicularly to the substrate, he regained that orientation with a short jump. Figure 3 shows principal postures adopted during the log display. Pirouettes may be performed with the tail erect and the head down, causing the bird to resemble a bundle of feathers as it spun in the air. A variation has males hovering to display height in a horizontal position, with shallow wing beats.

The number of jumps per bout varied from 1–13 ( $x = 4.6 \pm 3.3$ ,  $n = 38$ ), and jumps usually were per-

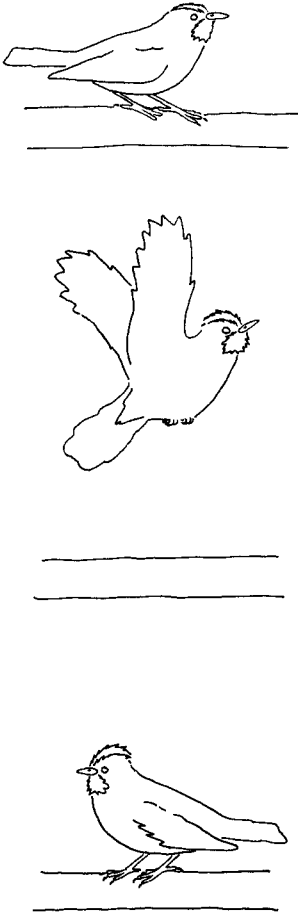


FIGURE 3. Principal phases of the log display of *Heterocercus aurantiivertex*. Uppermost figure: in the calling phase, the male delivers the display call, often bisyllabic (two notes on left side of Fig. 1F). Middle figure: with the crest erect, a series of vertical, dancing jumps of approximately 15–20 cm height is performed, each jump accompanied by one or two sharp *pop* sounds presumably produced by the wings (two vertical marks on right side of Fig. 1F). Jumps are interspersed with occasional 90° aerial pirouettes, performed with the tail erect and head down. Lowermost figure: the bird lands on the display log, sometimes about-facing.

formed about once per second, often in pairs or in a series of four, with several seconds between. Thus, the characteristic sound produced during the display was a paired *pop-pop* clearly audible at distances of 20 to 30 m. I never observed a log display that lasted longer than 2 min; the log displays of *Corapipo gutturalis* are much longer (Prum 1986). In approximately 200 hours observing male *H. aurantiivertex* at courts, I observed the log display only 38 times (although I heard the characteristic *pop-pop* on a few other occasions without seeing the displaying bird). I observed 23 of these

performances in 12 days between October and December 1995, from a male at a lek near Intuto in a palm swale in *terra firma* far from the river or any standing water. Observations of courts near water during the same months in this and previous years produced few instances of log displays. Determination of whether these apparent differences in the frequency of log displays are related to individual variation, habitat differences (i.e., proximity of water or water levels), proximity of females, or other factors requires further study. At most leks I observed log displays considerably less frequently than flight displays. However, the male that performed 23 log displays performed only 8 flight displays during the same period.

During the most intense activity at the leks, from about mid-May to January, males often performed 1–5 flight displays between about 06:45 and 11:00, and another 1–3 between 14:00 and 17:30. Flight displays were highly weather dependent: on calm, sunny days activity began earlier and was more intense than on windy or rainy days, when sometimes there were no displays; males often performed only one or two displays per morning when skies were overcast. Frequency of flight displays apparently also diminished over time within the display season, as suggested by one male's performance of 23 flight displays in 11 days in July and only 3 displays in 6 days during November–December of the same year. Inter-display intervals of individual males were highly variable for both flight and log displays. One male performed three flight displays with less than 1 min interval between them, but intervals of most males varied greatly, with lapses of up to 1 to 2 hr. Similarly, I observed one male perform log displays 5 times in one day, but most males performed log displays a maximum of 3 times per day, some passing complete days without log displaying. The mechanical sounds produced in both the flight and log displays were most clearly audible and penetrating when the forest was flooded; the reflective surface of the water may propagate the sound.

#### DISCUSSION

The only manakins known to perform elaborate flight displays are *Corapipo* (Aldrich 1937, Davis 1982, Prum 1986), and *Heterocercus* (Prum et al. 1996; B. Whitney, pers. comm.; this study), which also are unique among manakins in possessing a silky-white ruff. These shared, apparently derived behavioral and morphological features suggest a sister relationship for *Heterocercus* and *Corapipo*. Phylogenetic analysis of manakin display behavior (Prum 1990) and of syrinx characters (Prum 1992), however, have indicated that these genera belong to different clades within Pipridae. Therefore, Prum et al. (1996) concluded that the similarities in display between *Heterocercus* and *Corapipo* were homoplastic. A new phylogenetic analysis based on display elements that incorporates the data now available from *Heterocercus*, or on an independent data set (e.g., molecular characters) might be useful.

Bradbury (1981) suggested that exploded lek species do not establish territories over resources, but select sites offering advantages for signal transmission and predator avoidance. *H. aurantiivertex* apparently

uses the audio-reflective surface of water to amplify its display message, and performs terrestrial displays within a spatially complicated maze of woody roots and trunks, that may be difficult for some predators, such as *Accipiter* and *Micrastur* species, to negotiate rapidly. Another characteristic of the micro-habitat of *H. aurantiivertex*, however, is the proximity of fruiting food plants to males on courts. Fruit availability frequently is unpredictable and randomly dispersed in the tropics (particularly *Ficus* species; Fleming 1979), and it is to be expected that males of exploded lek species would maintain territories near potential crossroads for females (Bradbury 1981). I suspect that *H. aurantiivertex* has evolved a combination of these strategies.

In the exploded lek or quasi-lek, polygynous breeding system of *H. aurantiivertex*, flight-displaying males are in auditory contact with several other males. Terrestrial courts are widely separated (65 to 400+ m) but almost all males remain in auditory contact with at least one other male through advertisement and interaction vocalizations. Males holding courts are intolerant of other males when these are visually detected. Therefore, it is not possible for females to evaluate male display performance on terrestrial courts in concert, as it is, for example, in most species of *Pipra* manakins.

My limited data suggest that most male *Heterocercus aurantiivertex* invest more time and energy into conspicuous flight displays than in the relatively quiet and isolated log displays. There are appreciable differences in the frequency and quality of males' flight displays, which is the most visually and audibly most conspicuous, and probably the most energetically expensive, performance in the display repertoire of *H. aurantiivertex*. Therefore, it is possible that males performing the most vigorous flight displays, or the most frequent flight displays, are optimally demonstrating their greater fitness to potential mates. It remains to be determined which elements of displays are the most important in this regard.

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