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An Evaluation of Pre-lekking Vocalization Behaviors of Adult Long-Tailed Manakins in Monteverde, Costa Rica

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ABSTRACT

Long-tailed manakins (*Chiroxiphia linearis*) have many distinct vocalization sounds as part of their pre-lek call repertoire. The possible existence of patterns within the pre-lek call sequences, and rate of "toledo" calls within a given sequence were examined. Lek arenas were observed, and calls were recorded continuously in the sequence in which they were made by the manakins. Numbers of initial alpha male calls, "toledo" calls, and the actions that did (or did not) result from the calls, were recorded. There did not appear to be significant difference in the initial and "toledo" call analyses; this is most likely due to natural variation that exists in many bird species' vocalizations. Different combinations of specific pre-lek call elements were also analyzed and did not show a significant difference. In addition, the rate of "Toledos" per second was compared between three lek arenas. However, the rate of "Toledos" per second was found to be significantly different between perches, suggesting that more productive or favored sites have a faster rate of "toledos" than less productive or not favored sites.

RESUMEN

Saltarín toledos (*Chiroxiphia linearis*) tienen muchos sonidos distintos que son parte de los cantos que ocurren antes del baile de cortejo. Se estudiaron la posible existencia de patrones dentro de los cantos que ocurren antes del baile de cortejo y la cantidad de cantos "toledo" dentro de las secuencias. Se observaron los lugares donde ocurren los cortejos y se anotaron las llamadas continuamente en la secuencia que los toledos cantaron. Se anotó el número de las llamadas iniciales, el número de cantos "toledo" y las acciones que resultaron (o no resultaron) de los cantos. No se encontró diferencias significativas en los análisis de las llamadas iniciales y cantos "toledo"; probablemente es el resultado de variaciones naturales que existe en muchos especies de pájaros. Se analizaron las diferentes combinaciones de los elementos en las llamadas y compare la frecuencia de los cantos "toledo" por segundo entre tres lugares. No se encontró diferencias significativas en los análisis de las diferentes combinaciones de los elementos en las llamadas. Sin embargo, la frecuencia del canto "toledo" por segundo fue significativamente entre diferentes lugares. Esto sugiere que los lugares que son más productivos o populares tienen la frecuencia de cantos "toledo" más rápidas que los lugares que son menos productivos o impopulares.

INTRODUCTION

Populations of the long-tailed manakin (*Chiroxiphia linearis*; Pipridae) can be found from southern Mexico to Costa Rica in dry to humid forests which contain abundant undergrowth and tall secondary growth. The long-tailed manakin is a subsocial passerine frugivore, which sallies to pluck fruits from understory trees (Foster 1987). The adult male is mostly black, with a glossy crimson crown and sky blue back. It also has long, thin central

rectrices. Immature males undergo several plumage stages over the course of three to four years before acquiring full adult plumage. Female long-tailed manakins are mostly olive-green with a paler and grayer underparts, orange legs, and somewhat elongated central rectrices (Stiles and Skutch 1989).

The dual-male courtship display of long-tailed manakins has previously been well studied in Guanacaste, Costa Rica (Foster 1977), and in Monteverde, Costa Rica (McDonald 1989, McDonald and Potts 1994, Trainer et al. 2002). Foster (1977) observed that a pair of adult males display in an arena, which consists of several courts. Each court has, "a display site consisting of a low display perch and associated vines and branches". The pair of males will give a synchronous call to attract female manakins to the display arena, which sounds like the word "toledo". Once a female arrives, one male solicits the other to begin the display dance. Solicitation leads to the "Jump Display", which consists of two variants. In the "Up-Down Variant", one male jumps up off the display branch facing the female, hovers momentarily, and lands back on the branch. When the first male lands, the second male jumps, and so the dance continues. When each male jumps he makes a "buzzee" call. In the "Cartwheel Variant", the two birds alternately jump forward and backward on the branch, each time taking the place of the other male-creating a moving circle or reverse leapfrog sequence. Finally, one male will leave the display perch, and the remaining male will perform a "Solo Butterfly Display" for the female and if she accepts him they will copulate (Foster 1977).

One critical aspect of the male display pair is that of dominance. In each pair there exists one dominant alpha male and an assisting beta male. Although the older alpha male will perform virtually all the copulations in the arena, he cannot attract females without the assistance of a younger beta male (McDonald 1989). Female long-tailed manakins copulate multiple times in a single arena in one year, and have shown site fidelity from year to year (McDonald and Potts 1994). Beta males rarely have the opportunity to mate (4 of 263 copulations in McDonald's 1989 study). However, if a beta assists an alpha in creating a high performance arena, he will benefit in the future as an alpha male because at that point a superior population of females will be attending the lek site (McDonald 1989).

Despite the wealth of knowledge on lekking behavior, little research has been published on the pre-lek vocalization patterns of the male long-tailed manakins. It is possible that there are patterns in the pre-lek calling sequences, either in the order of specific elements, or in frequency of individual elements. These patterns may be affected by the productivity of an individual arena. It has also been observed that birds will have "listen and respond" dialogues, and may overlap songs and signals with neighbors. In addition, birds will sing autonomously in well-established territories (Todt and Hultsch 1996). Thus, there are a number of possible vocalization interactions that manakins may use in their calling patterns.

This study investigates possible patterns in manakin pre-lek calls, both in numbers of specific call elements and in rates of "toledo" calling between lek arenas. The hypothesis of this study is that there are patterns in element order and rates in pre-lek calling, and that those patterns should be fairly consistent across lek sites.

MATERIALS AND METHODS

Study Sites.— This study took place from April 13, 2002, to May 2, 2002 in Monteverde, Puntarenas, Costa Rica (10° 18'N, 84° 48'W). The two primary study areas were in premontane tropical moist forest (Holdridge 1967), at around 1300 m elevation, in the Cordillera de Tilaran mountain range. The first, which contained two major lekking arenas (Cat 1 and Cat 2), was located on the Arevalo land, which is west of the Monteverde Cloud Forest Reserve (and next to the Stuckey Farm where McDonald conducted long-tailed manakin research from 1981 through 1987). The second study area, which contained three major lekking arenas (Eco 5, Eco 6, and Eco 11), was located in the Finca Ecológica Monteverde, in Cerro Plano, Monteverde.

Field Methods. — Observations were made at one lek site on the Arevalo land from a blind. Observations at other sites were made without the use of a blind. Data were taken for four hours each day, from approximately 9:30 A.M. to 11:30 A.M., and 12:00 P.M. to 2:00 P.M.; approximately two weeks were spent at each of the study areas (the Arevalo land, and the Finca Ecológica Monteverde). The lekking sites within each study area were visited randomly, both in the morning and afternoon hours. Data were recorded using a series of eleven distinct alphabetical symbols, each representing a different sound, or sound combination, of the pre-lek call behaviors. The different calls recorded were: "toledo"; whine; pop; initial call; gargle; three, four, five, and six note monotone sequences; tweet (any other singular sounds); and lekking sounds. The calls were recorded continuously in the sequence in which they were made by the manakins; both the identity of the call, and the number of times the call was made were recorded. In addition, a random selection of "toledo" sequences was timed to obtain data on the average number of "toledos" per second for any given series at the three Finca Ecológica Monteverde sites, using a Casio Forester stopwatch.

Data analysis— The data were broken into specific groupings for analysis. The initial calls from all five major lek sites were separated into two categories (the beta male responded to the calls and "toledos" commenced, or the beta male did not respond to the calls), and summed for each calling segment (block of calling separated by some extensive period of silence). The initial call category averages were then compared using an unpaired t-test.

The "toledo" calls from all five major lek sites were separated into two categories as well (those which resulted in a lek dance, and those which did not result in a lek dance), and summed for each calling segment. The "toledo" call category averages were then compared using an unpaired t-test. An unpaired t-test was also performed for the two categories of "toledo" calls using only the data collected at the three Finca Ecológica Monteverde sites.

Actual sequences of calls from all five major lek sites were put into three or four call combinations of the most common arrangements, each including a "toledo" sequence as part of the combination. The groupings were as follows: PTP, WTW, PTW, WTP, IPT, IWT, IWPT, and IPWT (Table 1). The average frequencies of the three most common combinations (the first three combinations listed above) were then compared using an unpaired t-test.

The data from the timed "toledo" sequences were then compared using the average number of "toledos" per second in a one-way ANOVA test.

All statistical analyses were performed using STATVIEW statistical software (SAS Institute Inc. 1998, Cary, North Carolina, USA).

RESULTS

Initial Calls. – When the beta male responded to the alpha male's initial request calls, and "toledos" commenced, the number of initial calls varied from a low of one call to a high of 39 calls per calling segment. When the beta male did not respond to the alpha male's initial request calls, the number of initial calls per calling segment varied from a low of one call to a high of 44 calls per calling segment (Table 2). The number of initial calls given as a function of beta male response showed no significant difference (ANOVA, $F=1.735$; $P=0.1929$) (Fig. 1).

"Toledos". –Between all five sites, when "toledos" resulted in a lek dance, the number of "toledo" calls varied from a low of one call to a high of 512 calls per calling segment. When the "toledos" did not result in a lek dance, the number of "Toledo" calls varied from a low of one call to a high of 695 calls per calling segment (Table 2). There was no significant difference between the number of "Toledo" calls which resulted in a lek dance and the number of "toledos" which did not result in a lek dance (ANOVA, $F=0.091$; $P=0.7637$) (Fig. 2).

At the three Finca Ecológica Monteverde sites, when the "toledos" resulted in a lek dance, the number of "Toledo" calls varied from a low of one call to a high of 512 calls per calling segment. When the "toledos" did not result in a lek dance, the number of "Toledo" calls varied from a low of seven calls to a high of 695 calls per calling segment (Table 2). There was no significant difference between the number of "Toledo" calls which resulted in a lek dance and the number of "toledos" which did not result in a lek dance (ANOVA, $F=0.003$; $P=0.9592$) (Fig. 3).

Combination calls. – The number of occurrences for each of the three most common call combinations per calling segment varied from a low of zero to a high of 24 occurrences for PTP; the number of occurrences per calling segment varied from a low of zero to a high of 24 occurrences for PTW; the number of occurrences per calling segment varied from a low of zero to a high of 14 occurrences for WTW (Table 2). There was no significant difference between the amounts of the three most common combinations of calling sounds (ANOVA, $F=0.802$; $P=0.4513$). There was also no significant difference in any of the possible combinations (Post-hoc test, PTP and PTW, $P=0.5193$; PTP and WTW, $P=0.2084$; PTW and WTW, $P=0.5368$) (Fig. 4).

Rate of "toledos". – The rate of the number of "toledos" per second at Eco 11 varied from a low of 0.202 to a high of 0.600 "toledos" per second; the rate at Eco 5 varied from a low of 0.351 to a high of 0.800 "toledos" per second; the rate at Eco 6 varied from a low of 0.299 to a high of 0.750 "toledos" per second (Table 2). There was a significant difference between the rates of "toledos" per second between the three different sites (ANOVA, $F=$

16.957; $P < 0.0001$). The post-hoc tests show a significant difference between the combination rates (Post-hoc test, Eco 11 and Eco 5, $P < 0.0001$; Eco 11 and Eco 6, $P = 0.0074$; Eco 5 and Eco 6, $P = 0.0007$) (Fig. 5).

DISCUSSION

Initial and "toledo" calls.— Initial alpha male manakin call data show very large amounts of variation (Table 2). The "toledo" call amount data for both five site combined data, and the three Finca Ecológica Monteverde sites, show great amounts of variation as well (Table 2). It does not seem that a response (or lack thereof) will limit the number of calls a long-tailed manakin will make. The amount of calls the birds make before terminating a calling sequence may be determined by some other factor outside of the number of calls made without a response, either from a beta male, or a female at the display site.

Depending on the perceptual constraints of the bird, different calling patterns can be perceived in distinct ways depending on the circumstances. For example, different calling patterns may be perceived as the same message, or conversely, similar calling patterns may convey different meanings depending on the context (Horn and Falls 1996, Hailman and Ficken 1996). The categorization of different song elements seems to be a dynamic, rather than static process. In other words, different sounds signify different meanings in different contexts, instead of one sound always denoting one meaning. There are different features and implications of calls depending on the function of the task being performed (Todt and Hultsch 1996). Displays are defined relative to one another, with changing meanings depending on the situation (Horn and Falls 1996). It is possible that the type of vocalization that the bird makes functions only as a carrier signal, and variations in the signal may communicate some useful information about the physical state, or intentions of the caller (Hailman and Ficken 1996).

Call variation has been noted many times in different avian species. Petrels (Procellariiformes), a nonpasserine group, show characteristic vocalization patterns for food-begging, copulation, *agonistic* calls, distress calls, contact calls, and other major calls (Bretagnolle 1996). Some birds have different call patterns to communicate information about predators. Male chickens (*Gallus gallus*; Phasianidae) have been shown to have variable physical and vocal responses to different types of predators. In this way, their alarm calls are thought to be "functionally referential" (Evans et al. 1993). Because many species of animals, especially birds, have specific vocalization patterns depending on the context and intent of the call, it is very possible that the variation in manakin pre-lek calls can be explained by this same pattern. It is conceivable that a manakin would vary the length of calling bouts depending on different messages it wanted to send to the other manakins in the area.

It is also possible that different pairs of manakins had different ability levels of song matching depending on the length of time that they had been singing together. The pairs of males which have better matched sound frequencies in "toledo" sequences will receive more visits by females; the longer the partnership between manakins is formed, the more matched their singing will be (Trainer et al. 2002). In addition, long-tailed manakins do not track each other's songs. Therefore, some inconsistency results from slight variations in individual partner vocalizations (Trainer et al. 2002). It is likely that some variability, at least in "toledo" patterns, results from variation in different aptitudes for song matching between different pairs.

Combination calls. — Since there is no significant difference in the occurrence of the three most common combinations of calls, it may seem that there are a few messages which are frequently communicated during pre-lek calling. There are also a number of less common combination patterns (see Methods: Data Analysis), which may be communicating less prevalent messages in long-tailed manakin pre-lek call sequences.

Birds are known to be sensitive to different combinations of song types, especially in territorial birds (Horn and Falls 1996). Different variations of vocalizations are used in different situations (Horn and Falls 1996). In addition, courtship and male/male singing are usually more complex than territorial singing. The sequences of song types in avian vocalizations tend to be more variable than the sequences of elements within each song (Todt and Hultsch 1996). Therefore, despite the variation in different call combinations performed by the joint male singing, it remains that there are a few combinations that are consistently more common than others.

Information being communicated between birds can be changed by the physical structure of the calling sequence. Order of sequences can be specialized, and combinations of calls can be controlled by modifying transition flexibility (Kroodsma 1978), by varying the length of calling sections, or by singing different sound combinations (Smith 1996). For that reason, the existence of such a variety of different sound combinations in long-tailed manakin pre-lek call patterns does not seem surprising.

Rate of "toledos". — There was a significant difference between the rates of "toledos" per second of the three Finca Ecológica Monteverde sites. The rate was more rapid at Eco 5 than at Eco 6, and the rate was more rapid at Eco 6 than at Eco 11. A possible explanation for this, besides the inherent variability in birdcalls (as described above), is that some sites appear to be more productive lekking arenas than others. McDonald (1989) also identified productive lekking arenas by, "persistent, high rates of dual-male calling." Another observation was that there seemed to be more active birds at Eco 5 than at either of the other sites. Concurrently, there seemed to be more birds, making more calls at Eco 6, than at Eco 11. At Eco 11, there were usually only two or three birds at any given time, and generally less calling and flitting around than at either of the other two sites. Therefore, it could also be that the more long-tailed manakins present at any given site, the more rapid the calling at that site will be. Other site-specific factors may also influence the rate of calling at that site.

There is clearly high variability in long-tailed manakin pre-lek calls. Hailman (1996) states that researchers often have problems recording vocalizations because of the difficulty involved in distinguishing and identifying distinct calls, due to a great deal of variability in frequency, length, general identity, and amplitude of calls. In order to infer further information about the specific meaning of different call sequences, playback experiments would need to be completed to observe the specific responses to various song combinations. According to Horn and Falls (1996), playbacks are the most important test to see if the design of the call pattern actually affects the behavior of the receivers. Therefore, further, more specific studies would need to be completed in order to gain a greater understanding of the pre-lek call patterns of the long-tailed manakins.

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Table 1. Definitions of codes for the most common long-tailed manakin pre-lek call combinations heard in Monteverde, Puntarenas, Costa Rica.

Code	Meaning of Code
PTP	A series of pops, followed by a series of “toledos”, followed by a series of pops
WTW	A series of whines, followed by a series of “toledos”, followed by a series of whines
PTW	A series of pops, followed by a series of “toledos” followed by a series of whines
WTP	A series of whines, followed by a series of “toledos” followed by a series of pops
PTT w	A series of pops, followed by a series of “toledos”, followed by a series of tweets
IPT	A series of initial calls, followed by a series of pops, followed by a series of “toledos”
IWT	A series of initial calls, followed by a series of whines, followed by a series of “toledos”
IWPT	A series of initial calls, followed by a series of whines, followed by a series of pops, followed by a series of “toledos”
IPWT	A series of initial calls, followed by a series of pops, followed by a series of whines, followed by a series of “toledos”.

Table 2: Results for low and high numbers of calls per calling segment, and standard deviations for call data.

Call/Response	Mean No. Calls/Rate	Standard Deviation	Low Number Calls	High Number Calls
Initial-Beta Shows	10.147	10.694	1	39
Initial Beta No Show	13.889	11.423	1	44
All Toledo Dance	123.864	135.625	1	512
All Toledo No Dance	135.833	152.532	1	695
Eco Toledo Dance	127.250	140.019	1	512
Eco Toledo No Dance	124.562	173.088	7	695
PTP	4.062	5.267	0	24
PTW	3.312	4.721	0	24
WTW	2.594	3.809	0	14
Eco 11 Toledo/sec	.307	0.076	0.202	0.600
Eco 5-Toledo/sec	.555	0.180	0.351	0.800
Eco 6- Toledo/sec	.397	0.112	0.299	0.750

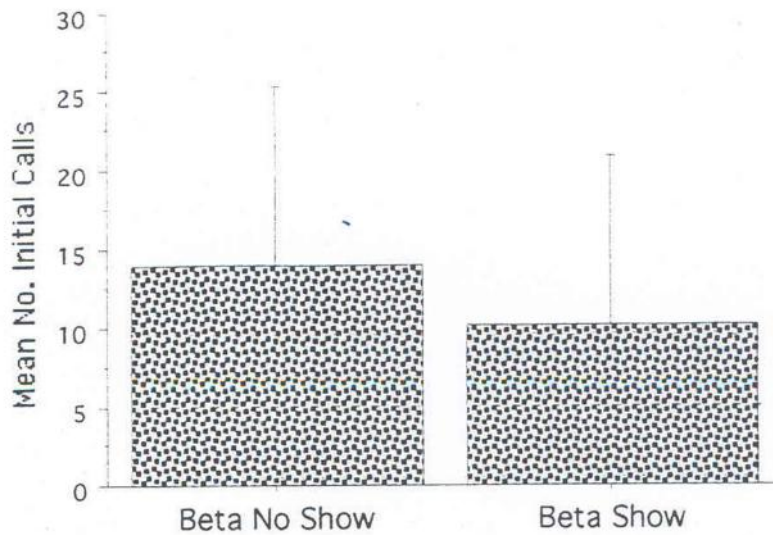


FIGURE 1. Average number of initial alpha male manakin calls in a calling segment, in which the beta male responded to the calls and "toledos" commenced (Beta Show), or the beta male did not respond to the calls (Beta No Show) (ANOVA, $F = 1.735$; $P = 0.1929$). (Means ± 1 SD are reported.)

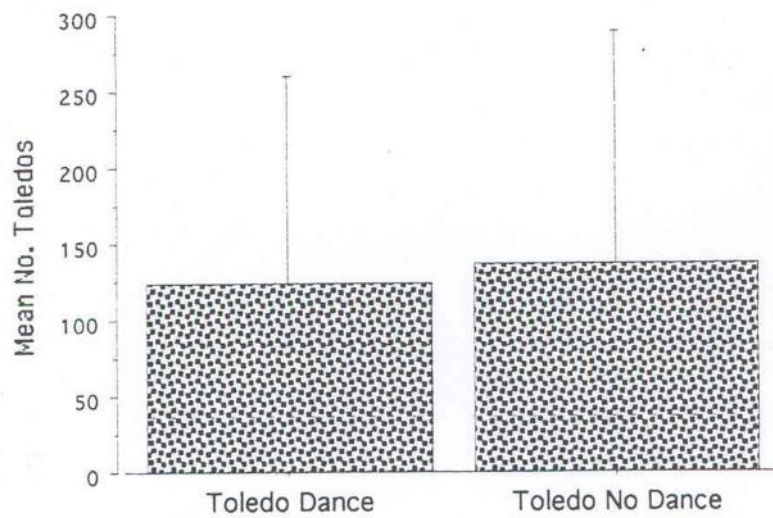


FIGURE 2. Average number of "toledos" in a calling segment, in which "toledos" resulted in a lek dance (Toledo Dance), or "toledos" did not result in a lek dance (Toledo No Dance), for all sites combined (ANOVA, $F = 0.091$; $P = 0.7637$). (Means ± 1 SD are reported.)

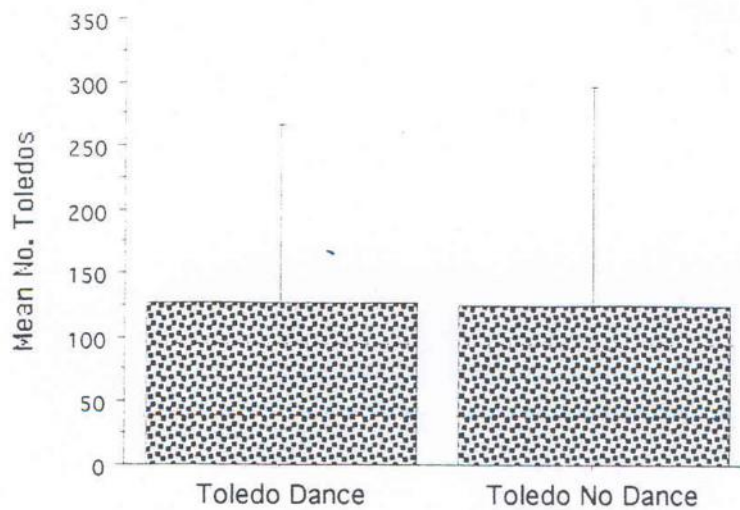


FIGURE 3. Average number of "toledos" in a calling segment, in which "toledos" resulted in a lek dance (Toledo Dance), or "toledos" did not result in a lek dance (Toledo No Dance), for the three Finca Ecologica Monteverde sites (ANOVA, $F = 0.003$; $P = 0.9592$). (Means ± 1 SD are reported.)

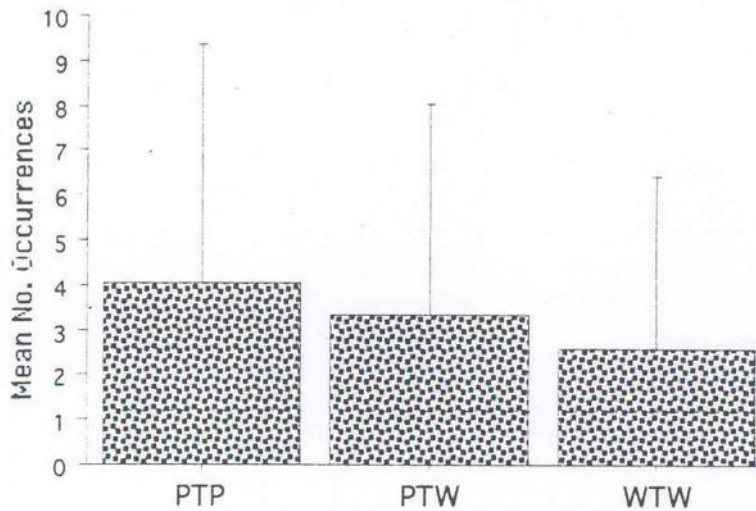


FIGURE 4. Average number of occurrences of each of the three most common manakin call combinations in a calling segment: PTP, PTW, and WTW (ANOVA, $F = 0.802$; $P = 0.4513$) (Post-hoc test, PTP and PTW, $P = 0.5193$; PTP and WTW, $P = 0.2084$; PTW and WTW, $P = 0.5368$). (Means ± 1 SD are reported.)

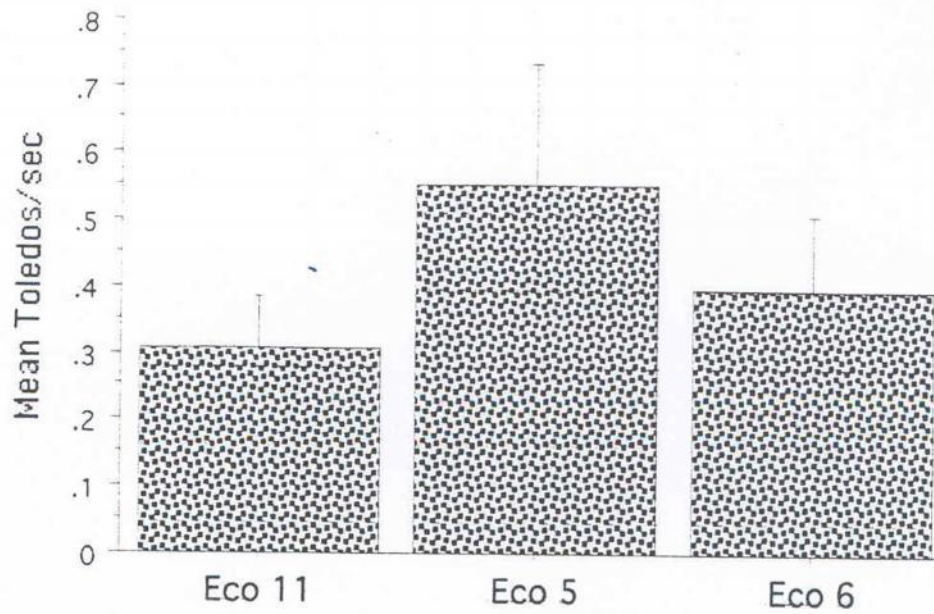


FIGURE 5. Average rate of number of "toledos" per second at each of the three Finca Ecologica Monteverde long-tailed manakin major lek sites (ANOVA, $F = 16.957$; $P < 0.0001$) (Post-hoc test, Eco 11 and Eco 5, $P < 0.0001$; Eco 11 and Eco 6, $P = 0.0074$; Eco 5 and Eco 6, $P = 0.0007$). (Means \pm 1 SD are reported.)