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Lek Behavior as the Mating Strategy of *Setellia* sp. (Diptera: Richardiidae)

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A field study revealed that the mating system of the richardiid Setellia *sp. meets even the most stringent definition of lek behavior. Males remain on the upper surface of the leaves of* Saranthe *aff.* klotzchiana *(Maranthaceae), where they perform ritualized displays related to courtship and territorial behavior. Correlational data support the existence of reproductive dominance hierarchies, which are based on both male vs. male and female vs. female agonistic interactions. Curiously, the behavioral acts performed by* Setellia *sp. show remarkable similarities to other nonrelated dipteran lekkers. Aspects of evolution and convergence of these behaviors in the Acalyptratae are considered.*

KEY WORDS: mating system; courtship behavior; agression; lek behavior; Richardiidae; *Setellia*.

INTRODUCTION

Lek is the mating strategy in which (1) males do not provide any parental care, (2) only a limited portion of the habitat is used as the mating encounter site, and (3) males defend exhibition territories in these sites, which lack any essential resource to the females (Bradbury, 1985; Thornhill and Alcock, 1983). This strategy usually appears when resources required by females do not occur in economically defendable patterns (Dodson, 1986). It can be found, with some variations, in a variety of taxa, including birds, mammals, and insects (Höglund and Alatalo, 1995). Despite being taxonomically diverse, lekking is considered to be rare in its occurrence (Höglund and Alatalo, 1995; Dodson, 1986). In the Diptera, the vast majority of the known examples are restricted to a few dis-

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tinct groups, like the Hawaiian drosophilids and the Mediterranean tephritids (Höglund and Alatalo, 1995; Burla, 1990; Shelly, 1988; Dodson, 1986). Burk (1981) suggested that, for Acaliptratae dipterans, the highest complexity of signals related to reproductive behavior would be found in lekking species. Accordingly, the study of this kind of mating system can provide important cues for the understanding of the evolution of reproductive behavior among the Diptera.

The Richardiidae is a muscoid dipteran family about which very little is known, due mainly to their rareness (Borror *et al.*, 1991; Steyskal, 1987; Oldroyd, 1964). Consequently, very little information is available about their natural history and reproductive behavior. The species studied here belongs to the genus *Setellia* and is currently being described by A. P. Prado (Departamento de Parasitologia, Universidade Estadual de Campinas) and voucher specimens are deposited in the Museu de História Natural da Universidade Estadual de Campinas (ZUEC). The sexes are easily distinguished in the field by the external genitalia and because males are smaller than the females.

This report aims (1) to describe the behavioral displays related to courtship, copulation, and conflict between individuals of *Setellia* sp., (2) to investigate the formation of dominance hierarchies through this conflict, and (3) to discuss the mating system of *Setellia* in the context of the Acalyptratae.

MATERIALS AND METHODS

Study Site

Fieldwork was carried out from 22 to 30 July 1996 at the Atlantic Rainforest Reserve of Linhares (19°6′S and 39°4′W), Espírito Santo state, Southeast Brazil. The study site had a relatively high and open canopy (≈20 m), with a sparse understory containing few lianas (details given by Peixoto and Gentry, 1990). The herbaceous vegetation is dominated by Maranthaceae herbs, such as the abundant *Saranthe* aff. *klotzchiana* (*Koernicke*) Eichler, on whose leaves lek behavior by *Setellia* was observed.

Behavior Observations

Observations made from July 22 to 25 were done to characterize the main behavioral acts and to register their daily frequencies in the exhibition arena (0800–1700 h). From 26 to 28 July the flies were marked with small dots on the thorax made with enamel paint (Testors Co., Rockford, IL). Different color codes were used to discriminate the flies and assess individual performances during the contests.

RESULTS

General Behavior

Males of this species of *Setellia* can remain for several hours on the patch of *Saranthe* elected as the exhibition arena. I found no apparent trait in the patch (location, luminosity, abundance of *Saranthe*, etc.) that could be promptly regarded as the one used by the richardiids for choosing it as an exhibition site. I was able to distinguish two behavioral phases when males were alone: the *stationary* and the *patrolling* phases. In the stationary phase the males stood on the adaxial surface of the leaves of *Saranthe*, usually in the proximal third of the foliar blade, with their heads facing the base of the leaf. During this time they continuously wave their wings on the saggital plane, keeping them parallel to the leaf surface. A common behavior during this period is self-grooming, which is performed using the legs. Under rainy conditions, stationary males may seek shelter under the leaf. The patrolling behavior consists of walking on neighboring leaves, returning or not to the original leaf of the stationary phase. This tour can eventually include other leaves from adjacent vegetation. When patrolling, the fly can also oscillate the halteres and touch the leaf repeatedly with the extremity of the abdomen.

Contrary to the males, females of this species of *Setellia* do not remain in the arena for a long time, usually for just some minutes. The wing and haltere displays as well as the movement with the extremity of the abdomen are also included in the behavioral repertoire of the females.

Courtship and Copulation

The males seem to court every approaching female indiscriminately in the arena. First, the female lands on a nearby or on the same leaf as the male. As the male perceives her presence, he waves the wings more vigorously, more or less perpendicularly to the leaf, keeping them briefly in an upright position, a behavior designated wing flicking (Fig. 1). Wing flicking has approximately half the frequency of normal wing waving, which is approximately 2 movements per s. During wing flicking the male walks with sudden, rapid pulses from one side to the other, describing small half-circles. After some of these movements, the male interrupts the wing flicking, walks quickly toward the female, and mounts, holding the female by her abdomen with his second pair of legs. The female lays her genitalia on the leaf, which is reached by the male genitalia. During copulation both male and female continue to wave their wings, but in males the frequency of this movement is increased and assumes a higher amplitude toward the abdomen. Immediately after the beginning of the copulation, the female begins to push the male with her third pair of legs and with her wings.

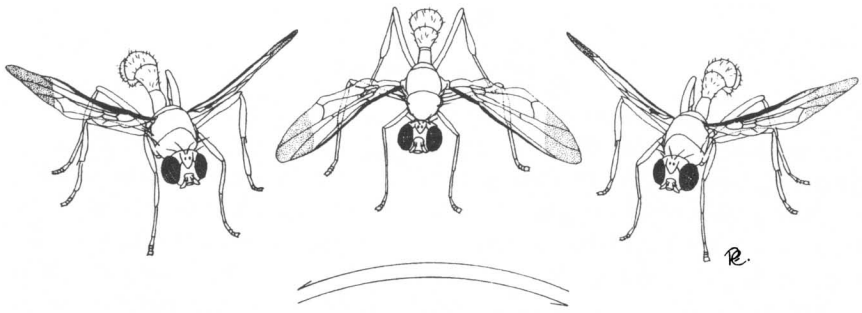

Fig. 1. Wing flicking behavior performed by males of *Setellia* sp. during courtship and male–male agonistic interactions.

If there is no disruption, the copulation can last as long as 20 min (mean ±SD = 15.1 ± 5.66 min; $N = 9$ records). After copulation the male resumes wing flicking until the female departs from the leaf.

The daily frequency distribution of courtships is clearly bimodal, beginning at approximately 0800 h and finishing around 1700 h, with a sharp decrease in frequency between 1100 and 1300 h (Fig. 3). Copulations were observed only during the morning, from 0900 to 1200 h. Curiously, a great number of courtships occurred during the afternoon, when no copulation was registered. Only 33.8% of the courtships observed ($N = 169$) succeeded, 23.8% resulted in the chasing of the courting male by the female, and in the remaining 32.4% the female simply flew away. The chase of a courting male by a female is identical to the female–female contest described below.

Male–Male Contests

Male–Male conflict is very similar to the early stages of the courtship display. One individual approaches the resident male by landing on a nearby or on the same leaf. One of the males begins the wing flicking behavior, which is promptly followed by the same reaction from its opponent. Subsequently, one or both males rotate their wings, holding them at an almost-perpendicular angle to the thorax and to the leaf, slightly directed to the opponent (Fig. 2). The wing rotation occurs as the male approaches the opponent, until they touch each other with the wings. Both males then distend their legs and elevate their bodies, grappling and pushing each other with the first pair of legs as if "measuring forces." After a couple of seconds in this position a vigorous wrestle begins, often resulting in one or both males falling from the leaf to the ground. The males can fly back again to the leaf and resume the contest. No injury was ever observed during contests between males. One male can give up at any stage of the contest, which may last from a few seconds to more than 3 min.

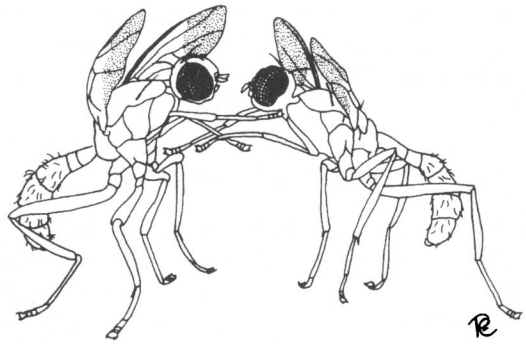

Fig. 2. Stance during male–male agonistic interactions in *Setellia* sp. See text for details.

The daily frequency distribution of male–male agonistic interactions also has a clear bimodal pattern and a considerable number of contests occurred in the afternoon, when no copulation was recorded (Fig. 3). Contests occurred independently of the presence of females in the arena.

Female–Female Contests

When females meet, they can also engage in contests, which, however, are less ritualized than those involving males. The interacting females approach each

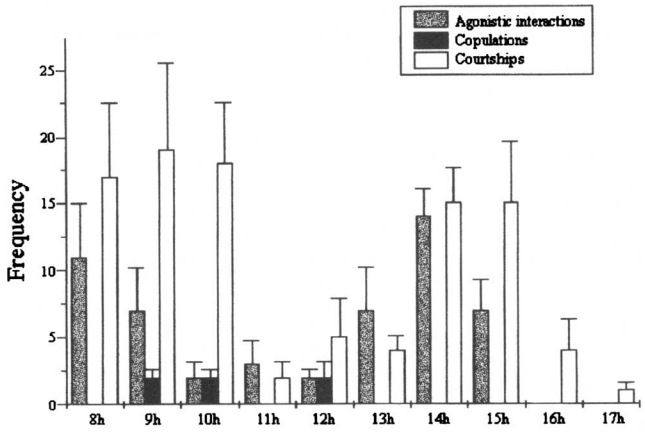

Fig. 3. Daily frequency distributions of courtships, copulations, and male–male agonistic interactions. The data were collected in 59 h of focal observations in a single lek, between July 22 and July 30. The columns display the cumulative frequencies plus standard errors.

other frontally, slow down or stop the wing waving, and one or both chase the other, causing the defeated female to leave the leaf. The sequence can also be interrupted before the chase. This behavior was observed irrespective of the presence of the male.

Dominance Hierarchies

A clear dominance hierarchy is established among males of *Setellia* (Table I). The males that won more agonistic interactions were also those that had more courtships (Spearman's $r_s = 0.920$, $P = 0.0245$) and copulations (Spearman's $r_s = 0.0182$, $P = 0.0183$) (Table II). The top-ranking male (RED) alone accounted for 60% of the copulations recorded ($N = 10$ observations).

Table I. Dominance Hierarchy Between Males of *Setellia* sp. Constructed from Observations of 63 Agonistic Interactions in a Single Lek over 30 h 15 min; Males Without Any Agonistic Interactions Were Excluded

Dominant male	Subordinate male						
	RED	BLU	BLUGRA	REDBLU	BLURED	REDGRA	Total
RED	×		16	11	2	1	30
BLU	10	×	6	1	1		18
BLUGRA	6		×	4			10
REDBLU	1		2	×			3
BLURED	1				×		1
REDGRA			1			×	1
Total	18	0	25	16	3	1	63

Table II. Male Dominance Hierarchy in *Setellia* sp. Based on Agonistic Interactions and Courtships[a]

Male	Wrestles won	Presentations won	Courtships	Copulations
RED	5	26	43	6
BLU	5	13	20	2
BLUGRA	1	9	15	1
REDBLU	0	3	14	1
GRE	0	0	4	0
BLURED	0	1	0	0
REDGRA	0	1	4	0
Total	11	53	100	10

[a]Presentations are the conflicts that did not result in direct wrestling. The data were collected in 30 h 15 min of focal observations in a single lek.

Table III. Dominance Hierarchy Between Females of *Setellia* sp. Constructed from Observations of 11 Agonistic Interactions in a Single Lek over 30 h 15 min; Females Without Any Agonistic Interactions Were Excluded

Dominant female	Subordinate female							
	GRABLU	GRARED	GREBLU	GRAGRE	GREGRA	BLUGRE	GRA	Total
GRABLU	×	3			1		1	5
GRARED	3	×				1		4
GREBLU		1	×					1
GRAGRE			1	×				1
GREGRA					×			0
BLUGRE						×		0
GRA							×	0
Total	3	4	1	0	1	1	1	11

Table IV. Female Dominance Hierarchy in *Setellia* sp. Based on Agonistic Interactions and Courtships[a]

Female	Received chases	Performed chases	Courtships	Copulations
GRABLU	3	5	22	2
GRARED	4	4	23	2
GREBLU	1	2	43	2
GRAGRE	0	1	2	1
GREGRA	1	0	3	1
REDGRE	0	0	2	1
NEW[b]	0	0	0	1
BLUEGRE	1	0	3	0
GRA	1	0	2	0
GREGRE	0	0	2	0
Total	11	12	102	10

[a]Chases refer only to female–female agonistic interactions. The data were collected in 30 h 15 min of focal observations ina single lek.
[b]An unmarked female.

Although not as clear as among males, the data also suggest a dominance hierarchy among females (Table III), with a significant correlation between performed chases and courtships (Spearman's $r_s = 0.736$, $P = 0.0199$) and copulations (Spearman's $r_s = 0.855$, $P = 0.0069$) (Table IV).

DISCUSSION

Setellia sp. fulfills all the conditions of the most conservative definition of lek proposed by Bradbury (1985): (1) the males remain in the arena most of

the time and do not follow their females after copulation, therefore it can be reasonably stated that they do not provide any parental care; (2) the arenas were found in restricted patches inside the herbaceous vegetation, being much more restricted than the distribution of *Saranthe*; and (3) there was no resource in the arena, other than copulations, to be searched for by the females. We can also detect a male dominance hierarchy which is consistent with the general case in leks, where one or few of the males usually execute most of the copulations (Höglund and Alatalo, 1995).

Among the dipterans, the occurrence of this kind of mating strategy, although considered to be rare, has already been described for other acaliptrate muscoid dipterans, such as the Otitidae, Tephritidae, and Drosophilidae (Höglund and Alatalo, 1995, and references therein; Burla, 1990; Dodson, 1986). Curiously, many of the features of the leks described for these families find correlates in the behavior of *Setellia*.

The patrolling behavior of *Setellia* resembles that found in *Drosophila silvestris*, *D. planitibia*, and *D. heteroneura*, including wing waving (Hoikkala and Welbergen, 1995). This behavior is well known from the Tephritidae, in which it has been pointed out as an intraspecific recognition behavior (Burk, 1981; Zwolfer, 1974). Another feature present in *Setellia* sp. that also occurs repeatedly in dipteran lekkers is the wing (which bears color patterns), which is displayed during the sequence of ritualized behaviors in male–male agonistic interactions and courtships (Hoikkala and Welbergen, 1995; Burla, 1990; Shelly, 1987, 1988; Parsons, 1977). The female effort to dislodge the male during copulation using the legs and wings was also reported for several species of *Drosophila* (Spieth, 1974).

The wing movements displayed by *Setellia* sp. also look similar to those observed in dipterans known as "stalkeyed," belonging to at least eight families characterized by having the eyes in the extremity of long stalks (McAlpine, 1979). Features like stalkeyes and patterned wings have been pointed out as ways of assessing the size of the opponent (Burla, 1990; Thornhill and Alcock, 1983).

The sequence of displays involved in the male–male agonistic interaction also has striking similarities with other dipteran lekkers, despite clearly evolving independently in the various lineages. The sequence head to head orientation–wing flicking–wing presentation–grapples with the forelegs–wrestle present in *Setellia* sp. is very similar to the sequences described for other lekkers (for examples see Batra, 1979; Dodson, 1986; Shelly, 1987, 1988; Burla, 1990). Moreover, individual components of the sequence also appear very similar [for instance, compare the wing rotation behavior performed by *Setellia* sp. and the fighting stance depicted by Spieth (1981)]. All these similarities clearly suggest the existence of similar constraints underlying the evolution of lek behavior among these groups. Which are these constraints, whether developmental, selective, phylogenetic, or whatever, is an open question. When females cannot count on paternal care or nutrition, it is expected that they will select males of higher

genetic quality (Trivers, 1972), as indicated by phenotypic vigor—the "good genes" (Thornhill and Alcock, 1983, Alcock and Pyle, 1979; but see Whittier and Kaneshiro, 1995). In these cases, as was recorded in *Setellia* sp., the beginnings of courtship and of male–male agonistic interactions are identical. This could enable the females of *Setellia* to evaluate indirectly the performance of the courting male face in an intrasexual conflict, since the beginning of the conflict is the phase in which more than 70% of them are resolved. Inasmuch as (1) one female can be courted several times by many males until copulation is achieved and (2) on many occasions there is chasing of the courting male, it seems reasonable to consider the existence of a selection component from the females on the males in the arena, and that this selection is based on vigor characteristic presented in courtship. This could also be reinforced by the fact that, in the female dominance hierarchy, 85.7% of copulations are confined to the apparently more vigorous male, even in the presence of other males in the lek. However, to demonstrate that females are using the courtship displays as indicators of male quality, Boake (1986) suggested that the average attractiveness and fitness of the males need to be measured, and a correlation between the two components need to be established. Males, on the other hand, do not provide any evidence of choosing females, since they court indiscriminantly every female that approaches. Therefore, there is evidence of intrasexual selection among both males and females, based on dominance hierarchies, and unidirectional intersexual selection, where females would be selecting more vigorous males. The existence of a female dominance hierarchy in animals with such limited cognitive capabilities such as flies provides a very interesting model to test the selection of parental ability to adjust the offspring sex ratio to the position in the reproductive hierarchy (Trivers and Willard, 1973).

This is the first report of reproductive behavior of a richardiid fly, probably the first detailed survey of any behavior for the entire family. Further studies are still indispensable for solid generalizations about the evolution of mating strategies in the Richardiidae. On the other hand, the occurrence of this kind of mating behavior in a richardiid seems to indicate that leks may be more common among insects than has been previously recognized.

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