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MALE-MALE INTERACTIONS IN CARIBBEAN FRUIT FLIES, *ANASTREPHA SUSPENSA* (LOEW) (DIPTERA: TEPHRITIDAE): TERRITORIAL FIGHTS AND SIGNALLING STIMULATION

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Abstract

Laboratory experiments were made on 2 aspects of male-male interactions in Caribbean fruit flies, *Anastrepha suspensa* (Loew). Observations of males involved in territorial contests on a lab-caged grapefruit tree revealed that large size and residence gave males advantages in fights; large intruders usually were able to oust small residents. In a second experiment, groups of individually-caged males began to emit sex pheromone and produce acoustic signals earlier in the daily sexual display period when in contact with other males than when isolated from them.

Resumen

Se hicieron experimentos en el laboratorio sobre 2 aspectos del comportamiento entre machos del "Caribbean fruit flies", *Anastrepha suspensa* (Loew). Observaciones de machos, en un árbol de toronja enjaulado en el laboratorio, envuelto en disputas territoriales, revelaron que los residentes de mayor tamaño y tenían ventaja en las peleas; los intrusos de mayor tamaño usualmente podían sacar a los pequeños residentes. En un segundo experimento, en su diari despliegue sexual, machos individualmente en-

jaulados comensaban a emitir feromonas sexuales y a producir señales acústicas más temprano cuando estaban en contacto con otros machos que cuando estaban aislados de ellos.

Males of the Caribbean fruit fly, *Anastrepha suspensa* (Loew), aggregate under leaves in trees in the late afternoon. While within these aggregations, males occupy and defend single-leaf territories (Dodson 1982, Burk 1983), release an airborne sex pheromone (Nation 1972, Perdomo 1974), produce calling songs via rapid wing vibration (Webb, et al. 1976), and court and copulate with attracted females (Perdomo 1974, Dodson 1982, Burk 1983). Such aggregations of sexually signalling males are called leks (see Thornhill and Alcock 1983); the evolution of this mating system in *A. suspensa* and other tephritids is discussed by Prokopy (1980) and Burk (1981).

Males in lekking species interact in 3 main ways (Thornhill and Alcock 1983): (1) Males are attracted to the sexual signals of other males so as to locate centers of mating activity; (2) Males engage in signalling interactions such as mutual stimulation or inhibition, or chorusing (Greenfield and Shaw 1983); (3) Males engage in aggressive interactions over possession of signalling territories. In *A. suspensa*, males in field situations are known to be as strongly attracted as virgin females to the airborne sex pheromone of other males (Perdomo et al. 1976). No information is available on male signalling interactions. Males engage in territorial threat confrontations and butting contests (Dodson 1982) in which resident males have a significant advantage (Burk 1983). This paper describes 2 laboratory experiments on interactions between *A. suspensa* males that demonstrate significant mutual signalling stimulation and a significant size advantage in territorial contests.

METHODS

Flies used were obtained from the laboratory colony maintained at the U.S.D.A. Insect Attractants, Behavior, and Basic Biology Laboratory in Gainesville, Florida, where the experiments were conducted. Flies used were virgin males and females, 9-11 days post-emergence. Flies were maintained under a 12:12 light cycle and were tested in their subjective "late afternoon" (hours 9-11 of the photophase). Temperature and relative humidity were 25 ± 1°C and 50 ± 10%.

TERRITORIAL ENCOUNTER EXPERIMENT—Twenty-four males were released in the morning onto a 1.8 m tall grapefruit tree caged in a 2 m tall, 2.5 m diameter field cage. Lighting above the tree was provided by flourescent plant grow lights. Observations of male aggressive interactions were made in the late afternoon while sitting quietly on a stool inside the cage. Observations on the effect of size on territorial outcomes were made on flies that had been pre-selected as small or large. Males were cold-anesthetized and weighed on an electronic balance. Large males were those weighing more than 12 mg, small males were those weighing less than 10 mg. Large and small males were also marked with single small dots of white or pale blue typewriter correction fluid, with the size class marked with a particular color alternating between days. Observations were made in May through July, 1981. Results were analyzed using chi-squared tests (Siegel 1956).

Signalling Stimulation Experiment—Ten individually caged males were placed adjacent to one another on a laboratory bench at the beginning of the ninth hour of the photophase (males had been placed in cages 2 hours previously). Every 15 minutes I recorded for each male whether or not he had begun to release sex pheromone ("puff") or produce calling song ("call"). Observations were continued for 3 hours. Ten replicates of each of 3 treatments were made. Isolated males (I males) were housed in 12-1/2 x 10 x 4 cm solid plastic cages with a cork-plugged hole in the top. Stiff gray cardboard partitions were placed between the cages of adjacent males. A second treatment (VC males) was similar but without cardboard partitions; males were thus in visual but not acoustic or olfactory contact. The third treatment (VAOC males) had males housed in plastic mesh cages, so that they were in acoustic, olfactory, and (slightly impaired) visual contact. Results were analyzed using Mann-Whitney U tests (Siegal 1956).

RESULTS

Territorial Encounter Experiment—As previously noted for wild populations of *A. suspensa* (Burk 1983), resident males were usually successful in aggressive encounters, remaining in sole occupation of their grapefruit leaf following 59% of 280 encounters ($X^2 = 27.6$, df=1, p<0.005) (Table 1A). Large size also had a significant effect: of 76 fights where different-sized males interacted, the larger male solely occupied the leaf after 68% ($X^2 = 17.8$, df=1, p<0.005) (Table 1B). The size and residency effects interacted in an interesting way (Table 1C). Residents were very successful when

TABLE 1. *Anastrepha suspensa* territorial fight observations.[1]

A. Residency effect:

	N Encounters	%
R stays	166	59
I stays	83	30
Both leave	25	9
Both stay	6	2

B. Size effect:

	N Encounters	%
L stays	52	68
S stays	17	22
Both leave	5	7
Both stay	2	3

C. Size-residency interaction:

Males: Resident	Intruder	R stays (%)	N encounters: I stays	Both leave	Both stay
Large	Small	30 (86%)	5	0	0
Large	Large	28 (64%)	13	2	1
Small	Small	25 (71%)	7	2	1
Small	Large	11 (31%)	21	3	1

[1]R = resident male, I = intruder male, L = large male, S = small male.

interacting with equal or smaller males (large resident vs. small intruder, $X^2=17.87$, df$=1$, p<0.005; large resident vs. large intruder, $X^2=5.48$, df$=1$, p<0.025; small resident vs. small intruder, $X^2=10.12$, df$=1$, p<0.005). But large intruders usually ousted small residents ($X^2=3.12$, df$=1$, $0.10<$p<0.05).

Intruding males apparently did not evaluate size of resident prior to arriving on the resident's leaf. Encounters were evenly distributed among the 4 possible classes of resident-intruder interactions ($X^2 = 1.53$, df $= 1$, N.S.) (Table 1C).

On the last 4 days of observations, I noted which males were puffing or calling in territories at the end of the observation period. There were 21 large and only 8 small males displaying ($X^2 = 5.82$, df $= 1$, p <0.025).

SIGNALLING STIMULATION EXPERIMENT—The percentage of sexually mature male *A. suspensa* that emitted sex pheromone and called was not significantly different for isolated males as compared with males in contact with other males (Table 2). However, isolated males had significantly longer latencies for the onset of puffing or calling than males in contact with others. All calling males previously puffed; however, not all puffing males go on to call. In this experiment, the percentage of puffing males that did go on to call was similar in all 3 groups (90% for I males, 92% for VC males, 90% for VAOC males). The latency from onset of puffing to onset of calling was not significantly longer in the isolated groups; this suggests that the significantly longer latency to onset of calling is due mainly to the original longer latency for the onset of puffing in isolated males.

DISCUSSION

The results of these experiments show that there is a strong size effect on the outcome of male-male encounters in *A. suspensa*, and that the presence of nearby males stimulates males to begin sexual advertisement earlier than they otherwise would. An advantage to large males in insect territorial contests has been demonstrated in a number of species (see review in

TABLE 2. OUTCOME OF MALE CHORUSING EXPERIMENT (N = 100 MALES IN EACH TREATMENT).

	% Puffing	% Calling	Mean puffing latency[1]	Mean calling latency	Mean puff-to-call latency
Isolated Males	84	76	4.38[2]	7.56[3]	3.22
Males in Visual Contact	91	84	3.20	5.71	2.20
Males in Visual, Acoustic, & Olfactory Contact	88	79	3.27	6.18	3.06

[1]Latencies are given in number of 15-minute observation periods. For example, if a male was first observed to puff after 60 minutes and to call after 90 minutes, his puffng latency = 4, his calling latency = 6, and his puff-to-call latency = 2.
[2]I vs. VAOC, p<0.01; I vs. VC, p<0.05 (Mann-Whitney U test). Where not stated otherwise, comparisons were not statistically significant.
[3]I vs. VAOC, p<0.05; I vs. VC, p<0.05 (Mann-Whitney U test).

Thornhill and Alcock 1983). A distinct residence effect has been shown less often, although Davies (1978) found that resident males won 100% of contests in the speckled wood butterfly (*Pararge aegeria* L.), and Burk (1979) found that all resident male field crickets (*Teleogryllus oceanicus* LeGuillou), regardless of size, won a majority of contests. More often, as in *A. suspensa*, small residents are frequently ousted by large intruders, with the result that large males eventually constitute the majority of territory holders. It should be remembered, though, that in the present study males were pre-selected so as to be quite different in size; a "resident-wins" rule might be followed more often where size differences were smaller.

The results of this study show that large males are at an advantage in intrasexual selection. Previously, Burk and Webb (1983) had shown that large males are at an advantage in intersexual selection: virgin females prefer to mate with larger males. Differences between large and small males have been found in several song parameters by Burk and Webb (1983) and Webb et al. (1984), and females respond more strongly to songs characteristic of large males (Sivinski et al. 1984).

A. suspensa males begin sexual display sooner when other males are nearby, even when no females are nearby (of course, the presence of females may have an additional stimulating effect). The experimental design used in this study is not adequate to identify the exact stimulus which causes aggregated males to display. The clear plastic cages were designed to allow visual contact only: the plastic was quite transparent and *A. suspensa* has excellent vision. Acoustic signals in *A. suspensa* are airborne and are received by antennae (Sivinski and Webb, USDA, ARS, Gainesville, FL, unpublished data), but I cannot entirely rule out the possibility that males in plastic cages detected substrate-born vibrations from adjacent males (I attempted to mitigate this possibility by not placing adjacent cages in direct physical contact, but all cages were in contact with the laboratory bench surface). Further experiments are necessary to identify the exact stimulus or stimuli involved; but this experiment does demonstrate that male-produced signals stimulate display by nearby males. Thus a group of simultaneously displaying males, or lek, is established.

Left uninvestigated in this study are the possible signalling interactions of males once simultaneous displaying is underway. The calling song of *A. suspensa* occurs in discrete pulses, but the type of detailed interaction present seems likely to be what Greenfield and Shaw (1983) call "unsynchronized chorusing," rather than synchronization or alternation of pulses. That is, males seem to begin calling when others do, and pause when they pause, but fail to precisely space their song pulses when calling. This suggestion is based entirely on passive observations, however, and detailed studies will need to be made before the exact nature of signalling interactions by *A. suspensa* males is known.

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