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Neriman Alemdar
Ataturk University

Ronda McIntyre
University of Nebraska-Lincoln

Ho-Chi Chang
University of Notre Dame

Dwight D. Miller
University of Nebraska - Lincoln

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BIOLOGICAL AND MEDICAL SCIENCES

THE INFLUENCE OF WINGLESSNESS ON MATING FREQUENCY IN SPECIES OF THE *DROSOPHILA AFFINIS* SUBGROUP

Neriman Alemdar*, Ronda McIntyre, Ho-Chi Chang†, and Dwight D. Miller

School of Life Sciences
University of Nebraska-Lincoln
Lincoln, Nebraska 68588

Certain *Drosophila* species that cannot mate in darkness have also been shown to be unable to mate in the light if their wings have been removed, perhaps due to the fact that wings provide visual signs and signals for courtship. To determine the influence of winglessness on mating in light-dependent *Drosophila algonquin* and its relatives, we determined mating frequencies in combinations of winged and wingless individuals of the six widespread American *Drosophila affinis* subgroup species *D. affinis*, *D. algonquin*, *D. athabasca*, *D. azteca*, *D. narragansett*, and *D. tolteca*. In no case did winglessness of either females or males prevent mating altogether, though there were varying reductions of mating frequency with winglessness. Wingless males of *D. algonquin* mated with winged females as well as winged males, while wingless females of this species mated with winged males significantly less often than did winged females. It does not appear that the male courtship wing display of *D. algonquin* provides an essential visual stimulus for mating. On the other hand, it seems likely that the female's appearance, including presence of wings, is important for the male's orientation just before copulation. Our data also suggest that winglessness influences mating by impairing auditory signals and, perhaps, by reducing mobility and coordination.

† † †

INTRODUCTION

Mating in *Drosophila* is usually preceded by a pattern of behavior called courtship. In species of the *Drosophila affinis* subgroup (*D. obscura* group, Subgenus *Sophophora*) the male orients himself towards the female, extends and vibrates one or both wings, circles about the female, and eventually approaches the female's posterior to mate. It may be surmised that the male's appearance and actions provide signs and signals that induce the female to mate. Though the female displays little overt behavior during courtship, her appearance

may nevertheless be important, perhaps as a guide for the male's final approach to copulation. The fact that certain *Drosophila* species cannot mate in darkness makes it seem that visual cues are needed for mating. Moreover, interference with mating in such light-dependent species by removal of their wings is interpretable as meaning that the appearance and/or movements of the wings produce needed visual signs and signals. Grossfield (1968) discovered that the Asiatic species *D. auraria*, which cannot mate in darkness, is prevented from mating in the light if females have had their wings removed, and another light-dependent Old World species, *D. subobscura*, is kept from mating in the light if males have been made wingless. The native American species *D. algonquin* fails to mate in the dark, and other New World species of the *D. affinis* subgroup have been found to mate with reduced frequencies in darkness (Curtright and Miller, 1979). We have recently determined mating frequencies in the light in combinations of six *D. affinis* subgroup species: *D. affinis*, *D. algonquin*, *D. athabasca* (semispecies "eastern A," "eastern B," and "western-northern"), *D. azteca*, *D. narragansett*, and *D. tolteca*. These determinations have been supplemented by direct observations of courtship behavior in these species and by observations of amplified male courtship sounds.

MATERIALS AND METHODS

Table I identifies the geographical sources of laboratory strains. Except for *D. athabasca* "eastern A" and "eastern B" and *D. tolteca*, these are identical to those employed by Curtright and Miller (1979) in their study of mating frequencies in light and darkness. Stocks were maintained in half-pint (ca. 236 ml) glass bottles containing yeasted cornmeal-molasses-agar-Tegosept medium and kept in a stock room at about 18 C. Young virgin adults were etherized, separated by sex,

*Present Address: Biology Department, Atatürk University, Erzurum, Turkey.

†Present Address: Biology Department, University of Notre Dame, Notre Dame, Indiana 46556.

TABLE I. Frequencies of insemination of winged and wingless females in combinations of either five winged *or* five wingless male; with five winged females *and* five wingless females. Cohabitations lasted seven days. Chi-squares in “winged males” and “wingless males” columns are based on frequencies of winged and wingless females inseminated in the same vial; those in “Chi-square” column are based on frequencies of winged *or* wingless females inseminated by winged and wingless males in separate vials. Symbols: ns = “not significant,” * = “significant at 5% level,” and ** = “highly significant at 1% level.”

<i>Drosophila</i> Species, Stock	Insemination Frequencies		
<i>D. affinis</i> Nebraska (Nebraska National Forest, Halsey)			
	winged males	wingless males	Chi-square
winged females	105/118 (89.0%)	86/121 (71.7%)	10.851**
wingless females	106/117 (90.6%)	103/118 (87.3%)	0.340ns
Chi-square	0.046ns	8.564**	
<i>D. algonquin</i> Minnesota (Halstad)			
	winged males	wingless males	Chi-square
winged females	94/118 (79.7%)	78/110 (79.9%)	1.920ns
wingless females	43/118 (36.4%)	13/112 (11.6%)	17.992**
Chi-square	43.501**	78.203**	
<i>D. athabasca</i> “eastern A” New York (Ithaca)			
	winged males	wingless males	Chi-square
winged females	101/135 (74.8%)	8/128 (6.3%)	124.195**
wingless females	29/118 (24.6%)	4/112 (3.6%)	19.054**
Chi-square	61.492**	0.427ns	
<i>D. athabasca</i> “eastern B” Indiana (Bloomington)			
	winged males	wingless males	Chi-square
winged females	61/109 (56.0%)	15/116 (12.9%)	44.686**
wingless females	54/100 (54.0%)	15/104 (14.4%)	34.011**
Chi-square	0.019ns	0.014ns	
<i>D. athabasca</i> “western-northern” Colorado (Rocky Mt. Biological Lab., Gothic)			
	winged males	wingless males	Chi-square
winged females	98/112 (87.5%)	15/106 (14.2%)	114.175**
wingless females	52/107 (48.6%)	5/109 (4.6%)	51.760**
Chi-square	36.637**	4.667**	
<i>D. azteca</i> Arizona (Bigelow Mt., Tucson)			
	winged males	wingless males	Chi-square
winged females	96/101 (95.1%)	56/101 (50.9%)	40.427**
wingless females	72/101 (71.3%)	51/109 (46.8%)	11.893**
Chi-square	18.708**	1.221ns	

TABLE I (continued).

<i>Drosophila</i> Species, Stock	Insemination Frequencies		
<i>D. narragansett</i> Indiana (Bloomington)			
	winged males	wingless males	Chi-square
winged females	101/113 (89.4%)	32/109 (29.4%)	80.735**
wingless females	58/106 (54.7%)	27/115 (23.5%)	21.362**
Chi-square	31.461**	0.722 ^{ns}	
<i>D. tolteca</i> Colombia (Medellín)			
	winged males	wingless males	Chi-square
winged females	97/107 (90.7%)	82/115 (71.3%)	12.020**
wingless females	85/104 (81.8%)	61/107 (57.0%)	13.899**
Chi-square	2.821 ^{ns}	4.310*	

and half of each sex de-winged with dissecting needles, leaving about 10% or less of the area of each wing. Females and males were then aged in isolation one week. Following the example of Grossfield (1968), two kinds of mating combinations were then established: 1) five wingless males with five winged females and five wingless females, and 2) five wingless males with five winged females and five wingless females. At the end of one week's cohabitation the flies were etherized, the males discarded, and the females of each kind dissected and examined microscopically for the presence of sperms in their seminal receptacles. Both aging and mating were done in 35 ml vials containing a slant of sucrose agar (sucrose-agar-Tegosept) on which had been placed a small rectangular block of unyeasted *Drosophila* medium. These vials were kept inside loosely closed transparent plastic boxes (ca. 15 cm x 30 cm x 8 cm) on the shelves of an incubator maintained at 23 C. To ensure adequate and uniform illumination, a 15 W light bulb was kept burning continuously inside the incubator, and to keep relative humidity high, each box contained a dish of water beside the vials. Insemination frequency determinations continued until the total of females dissected exceeded 100 for each kind of female in each combination for every species and semispecies. Pooled data are given in Table I.

Some direct observations of courtship and mating behavior were also made to determine whether there were any striking variations of such behavior with winglessness. Although all species were observed, special emphasis was put on *D. affinis*, *D. algonquin*, and *D. athabasca* "eastern A," which had been found (Table I) to contrast with each other regarding effect of winglessness on mating frequencies. Flies were prepared as for the mating vials. One male, either winged or

wingless, and one winged female and one wingless female were introduced without etherization (by means of an aspirator) into a cylindrical observation chamber about 12.7 mm in diameter and 5 mm in depth inside a Plexiglas block. Observation under a dissecting microscope lasted 30 minutes, and each minute was scored for manifestations of courtship directed towards either or both of the females—namely, orientation, circling, and wing extension and vibration. Also noted were attempted copulations (the male lunging at the female's posterior without establishing connection) and copulations, though the latter were infrequent in the 30-minute observation periods. Ambient temperatures during observations averaged about 24 C and varied from 22 C to 26 C. Pooled data for *D. affinis*, *D. algonquin*, and *D. athabasca* "eastern A" are presented in Table II.

Sounds accompanying courtship of winged and wingless males and females of all species were amplified and recorded, using the apparatus and procedure of Chang and Miller (1978), including the dynamic microphone observation chamber of Miller *et al.* (1975). Special attention was given to *D. athabasca* "eastern A," in which it had been found that the mating frequencies of wingless males were much lower than those of winged males (Table I). Temperatures during observations averaged about 25.5 C and ranged from 23 C to 28 C. Data from *D. athabasca* "eastern A" were gotten from matched pairs of observations of winged and wingless males made on the same day under similar conditions. Following the procedure of Chang and Miller (1978), sonograms were prepared from recordings of courtship sounds of winged and wingless males of this semispecies, pulse repetition rates determined from the sonograms, and mean interpulse intervals calculated.

TABLE II. Direct observations of courtship and mating in combinations of one winged *or* wingless male and one winged female *and* one wingless female during 30 minutes. Numbers in “courtship” and “copulation attempted” columns are pooled numbers of minutes (of 30 per male) of the indicated activity. Copulations are those begun in the observation periods. Chi-squares are based on an expected equality for the two kinds of females. Symbols are as in Table I; differences of small numbers are not significant (binomial expansion).

<i>Drosophila</i> Species, Stock (number of trials)	Courtship Activity	Copulation Attempted (but not achieved)	Number of Copulation
<i>D. affinis</i> (Nebraska)			
winged males (11)			
winged female	30	12	4
wingless female	26	10	2
	$X^2 = 0.161ns$	$X^2 = 0.046ns$	
wingless males (9)			
winged female	42	13	3
wingless female	30	7	2
	$X^2 = 1.681ns$	$X^2 = 1.250ns$	
<i>D. algonquin</i> (Minnesota)			
winged males (10)			
winged female	47	2	0
wingless female	38	0	0
	$X^2 = 0.753ns$		
wingless males (10)			
winged female	44	0	2
wingless female	32	1	0
	$X^2 = 1.592ns$		
<i>D. athabasca</i> “eastern A” (New York)			
winged males (8)			
winged female	106	29	2
wingless female	82	15	0
	$X^2 = 2.814ns$	$X^2 = 3.841^*$	
wingless males (8)			
winged female	97	27	0
wingless female	80	4	0
	$X^2 = 1.446ns$	$X^2 = 15.631^{**}$	

RESULTS

It may be seen from Table I that there was some mating in all combinations of winged and wingless flies of all species, including those with wingless individuals of either or both sexes of light-dependent *D. algonquin*. On the other hand, mating occurred with reduced frequencies in nearly all combinations of wingless flies compared with winged ones. Contingency Chi-squares (with Yates' Correction) were calculated for the numbers of inseminated winged and wingless females in each combination involving winged males or wingless males, and these are given in the "winged males" and "wingless males" columns of Table I. Likewise, contingency Chi-squares were determined for numbers of inseminations of winged females by winged males or wingless males and of wingless females by winged males or wingless males (hence, in separate vials in each case) and these are given in the "Chi-square" column of Table I.

Most deviations were either significant or highly significant (23 of 32 comparisons), with winglessness, of either or both sexes, associated with reduced mating frequencies. However, mating frequency differences varied widely. *D. algonquin* was the only species in which wingless males inseminated winged females with a frequency as high as that of winged males. In the other species there were increasing reductions of insemination frequencies of winged females by wingless males in the following order: *D. affinis*, *D. tolteca*, *D. azteca*, *D. narragansett*, *D. athabasca* "eastern B," *D. athabasca* "western-northern," and *D. athabasca* "eastern A." Comparing data from wingless females that mated with winged males to those of winged females mating with winged males, it may be seen that wingless *D. affinis* females mated as well with winged males as did winged females, followed by increasing reductions of mating of wingless females in the order: *D. athabasca* "eastern B," *D. tolteca*, *D. azteca*, *D. narragansett*, *D. athabasca* "western-northern," *D. algonquin*, and *D. athabasca* "eastern A." It seems noteworthy that light-dependent *D. algonquin*, with no reduction of mating frequency of wingless males with winged females, had a strong reduction of mating frequency of wingless females with winged males. Comparisons of mating frequencies of wingless females by wingless males vs. winged females by winged males show that *D. affinis* was least disturbed by winglessness of both sexes, with a frequency of 87.3% compared to 89.0% (a non-significant difference), followed by increasing reductions of mating frequency in the order: *D. tolteca*, *D. azteca*, *D. narragansett*, *D. athabasca* "eastern B," *D. algonquin*, *D. athabasca* "western-northern," and *D. athabasca* "eastern A."

The following impressions stand out. Mating in *D. affinis* was little affected by winglessness of either sex. Mating in *D. algonquin* was not reduced by winglessness of males but strongly affected by winglessness of females—suggestive of

Grossfield's (1968) finding in light-dependent *D. auraria*, though in the latter species wingless females were reported not to mate at all. Regarding the mating of wingless males, *D. algonquin* contrasted with nearly light-dependent (Curt-right and Miller, 1979) *D. athabasca* "western-northern" and *D. narragansett*, in both of which wingless males mated much less than winged males. Mating in *D. athabasca* "eastern A" was strongly reduced by winglessness of either sex—but there is no evident relation of this to an influence of darkness, since darkness actually inhibited mating in this semispecies less (Curt-right and Miller, 1979) than in the other two kinds of *D. athabasca*.

Direct observations of the behavior of a winged or wingless male in the presence of a winged and a wingless female failed to reveal any striking difference of behavior of such males with respect to the two kinds of females—nor of total courtship activity of the two sorts of males, the wingless males courting as vigorously as the winged ones, including extension and vibration of their wing stubs. However, copulation in these species was achieved in only a minority of cases in the 30-minute observation period (no more than one-fourth of combinations of winged male and winged female), thus providing little opportunity to observe behavioral details that might influence chances of achieving copulation. Table II presents data from *D. affinis*, *D. algonquin*, and *D. athabasca* "eastern A." For each kind of male and each kind of female, the number of minutes scored for the presence of courtship activity (*i.e.* orientation, circling, and wing extension and vibration) and attempted copulation is recorded (pooled from the several observations), as well as total number, if any, of copulations achieved. Although, for each species and kind of male, the number of minutes scored for courtship of winged females exceeded that for wingless females, differences are not significant at the 5% level. In *D. affinis*, attempted copulations by either kind of male did not occur significantly more often with winged than with wingless females. However, in *D. athabasca* "eastern A," winged males attempted copulation more often with winged females than with wingless females at the borderline of significance, and the difference between numbers of minutes of attempted copulation scored for wingless males with winged females compared to that for wingless males with wingless females was highly significant.

A salient feature of these data is the fact that *D. affinis*, *D. algonquin*, and *D. athabasca* "eastern A" were essentially alike regarding frequencies with which their males (winged or wingless) courted wingless females. Thus, on the basis of these observations of early courtship, it does not seem that a difference of relative times spent by the males courting wingless females can account for the fact that although *D. affinis* experienced no reduction of mating frequency of wingless females by winged males in seven-day cohabitations, *D. algonquin* and *D. athabasca* "eastern A" had large reductions

of mating of wingless females. On the other hand, data on attempted copulations in *D. affinis* and *D. athabasca* "eastern A" suggest that, in the latter species, male behavior initiating copulation is responsible for the fact that wingless females mated less often than winged ones.

As reported by Miller *et al.* (1975), courtship sounds of wingless males in the three semispecies of *D. athabasca* did not appear to be different from those produced by males with wings. Similarly, in all six *D. affinis* subgroup species of this investigation, sounds accompanying the courtship of wingless males were not perceptibly different from those of winged males (nor were there differences related to winglessness of females). Moreover, in *D. athabasca* "eastern A," ten winged males had a mean interpulse interval of 29.58 ± 2.08 msec while ten wingless males had an interpulse interval averaging 28.05 ± 1.38 msec, and the difference is not significant (according to the t-test for matched pairs). Our results failed to confirm the finding of Kan (1977) that interpulse intervals in the sounds of wingless *D. athabasca* "eastern A" were longer than those of winged males (based on a small number of observations of a different strain).

DISCUSSION

Descriptions of courtship and mating in *D. affinis* subgroup species have been made by Miller (1950), Spieth (1952), Ensign (1960), Miller *et al.* (1975), and Chang and Miller (1978). The male typically orients towards the female, usually her anterior end—though behind the female (Ensign, 1960) in *D. affinis* and *D. tolteca*. Sometimes courtship is initiated by the male's tapping the female with a foretarsus (Spieth, 1952; Ensign, 1960). After orientation the male, moving sideways, circles about the female, describing an arc with the female at the center. During orientation and circling the male repeatedly extends and vibrates one or both wings, and these wing movements are accompanied by characteristic sounds (Miller *et al.*, 1975; Chang and Miller, 1978). As reported by Ensign (1960), Miller *et al.* (1975), and Chang and Miller (1978), males of *D. affinis*, *D. algonquin*, and *D. athabasca* "eastern A" extend and vibrate both wings, while in the other species (and the other two *D. athabasca* semispecies) males extend and vibrate only one wing. As courtship continues, the male assumes a position to the rear of the female, approaches her genital region, spreading her wings, and attempts intromission. The effort to achieve copulation may fail, in which case the male may return to orientation, circling, and wing display. On the other hand, if intromission takes place, the male mounts the female, spreading her wings still further. Attempted copulation and the initiation of copulation may be accompanied by additional sounds, though wing vibration is not conspicuous at these times. In some *Drosophila* species (e.g. the *D. willis-toni* group) a receptive female spreads her wings before the male approaches, but this behavior has not been observed in

the *D. affinis* subgroup. Non-receptive females may produce a "rejection sound" (Ewing and Bennet-Clark, 1968; Miller *et al.*, 1975; Chang and Miller, 1978), but this is not accompanied by wing extension, though vibration of the unextended wings has been observed (Chang and Miller, 1978).

Removal of the wings may be expected to hinder or prevent mating of drosophilas in several possible ways. Wing display by the male may serve to produce a signal to the female causing her to submit to mating—perhaps a visual signal, chemical stimulation (by way of induced air currents), or an auditory signal (Spieth, 1952) or some combination of these. Winglessness might, of course, be expected to interfere with the production and transmission of such a signal. On the other hand, absence of wings might so alter visible form that the other individual lacks a sufficient basis for recognition or guidance to accomplish mating—e.g. the male may require the female's wings to orient himself to complete his final movements to achieve copulation. Still another possibility is that winglessness of either or both sexes may impair mobility, coordination of movements, or ability to respond to the other individual, resulting in reduced mating frequency.

Several studies have shown that wingless *Drosophila* males mate less effectively than normal males. Bastock (1956) reported that *D. melanogaster* males without wings, though courting vigorously, mate less often than winged males, whether in light or darkness. Ewing (1964), who used several methods to reduce wing size in *D. melanogaster* males (low temperature during development, selective breeding, and amputation), found that males with large wings mated more successfully than those with small or amputated wings. The influence of male winglessness has been reported to vary between closely related species. Manning (1959) found the effect of winglessness in males to be less in *D. simulans* than in *D. melanogaster*.

The failure of *Drosophila* species to mate in darkness is *prima facie* evidence of the importance of some visual factor in mating. Spieth (1952) reported that light-dependent *D. auraria* and *D. subobscura* males do not vibrate their wings during courtship, though the *D. subobscura* male postures in front of the female without wing vibration. Ewing and Bennet-Clark (1968) described a pattern of wing extensions and movements in the male courtship behavior of *D. subobscura* and concluded that the male's display does appear to provide a visual stimulus. As already stated, if made wingless, *D. subobscura* males do not mate (Grossfield, 1968). However, light-dependent *D. algonquin*, in which males extend and vibrate both wings during courtship, is neither hindered nor prevented from mating by winglessness of males. It therefore does not seem that the courtship wing display of *D. algonquin* males provides a necessary visual stimulus and that the failure of this species to mate in darkness is due to the female's inability to see the display.

There is much evidence that auditory signals accompanying wing movements of courting *Drosophila* males are important factors promoting mating (Shorey, 1962; Waldron, 1964; Ewing and Bennet-Clark, 1968). Such sounds may differ strikingly between closely related species and presumably provide a basis for species discrimination and reproductive isolation. The semispecies of *D. athabasca* are distinguishable by their male courtship sounds (Miller *et al.*, 1975), and all the *D. affinis* subgroup species of this investigation have their characteristic courtship sounds (Chang and Miller, 1978). Bennet-Clark and Ewing (1967) showed that wingless *D. melanogaster* males were enabled to mate with increased frequencies by accompanying their courtship with artificial sounds simulating those of courting winged males and by an air current directed towards the females. Bennet-Clark and Ewing (1969) demonstrated that artificial male courtship sounds promoted the mating of wingless *D. melanogaster* males if the interval between sound pulses was adjusted to match that of the natural sounds, thus indicating that interpulse interval is a critical parameter in the sounds of courting males. In their study of various *Drosophila* species, Ewing and Bennet-Clark (1968) detected no sound during courtship in light-dependent *D. subobscura*, though related *D. obscura* group species did produce such sounds; as already stated, they did observe wing movements interpretable as visual signals in this species.

Efforts have been made to determine the effect of winglessness on sounds produced by courting males of several *Drosophila* species. Waldron (1964) found that wingless *D. persimilis* males made sounds "as loud, steady, and sustained as those produced by normal males, and of about the same pitch and temporal patterning." Miller *et al.* (1975) observed that *D. athabasca* males with wings partly or nearly all removed produced sounds during courtship very similar to those of males with wings intact. However, Waldron (1964) used a crystal microphone and Miller *et al.* (1975) used a dynamic microphone, in both of which sound is transmitted through a membrane on which the courting flies stand, so as suggested by Waldron (1964), it is probable that much of the sound of these males was transmitted, from the vibration of body and legs, through the sub-stratum as well as through the air. On the other hand, Schilcher (1976), using a ribbon (or velocity) microphone, reported that courting *D. melanogaster* wingless males were "completely mute," evidence that the air-borne component of the male's sound, to which this microphone responds and which can be received by the female's antennae (Bennet-Clark, 1971), is prevented by removal of the male's wings. Thus, evidence from pressure-sensitive microphones (*i.e.* crystal or dynamic microphones) that a courting male's sound is essentially unchanged by winglessness does not constitute proof that the male's sound is unaltered.

As stated above, in all *D. affinis* subgroup species of this

investigation wingless males produced sounds that did not seem different from those made by winged males—as determined with a dynamic microphone. Neither was it possible to demonstrate that the interpulse interval was significantly changed by winglessness in *D. athabasca* "eastern A." Nevertheless, it cannot be concluded that the total quality of male courtship sound in these species was unaltered by winglessness. Removal of the air-borne component of this sound may have produced an effect on mating success, the relative importance of this factor varying from species to species. It is perhaps significant that the three *D. affinis* subgroup species of our investigation least affected by winglessness (*D. affinis*, *D. algonquin*, and *D. tolteca*) are also ones in which it has been found that courtship is relatively "quiet" (Chang and Miller, 1978). This may mean that male courtship sounds in these species are less important for promoting mating than in the others—or, at least, the air-borne sounds. On the other hand, the fact that nearly light-dependent *D. athabasca* "western-northern" and *D. narragansett* had large reductions of mating frequency with male winglessness may mean that their relatively loud male courtship sounds are important and that some visual factor (perhaps pertaining to the female) is important too.

Spieth (1952) reported that courting *D. auraria* males, unlike those of *D. subobscura*, posture at the rear of the female, then lunge at the female's posterior to mate. Grossfield (1968) found that wingless males of this light-dependent species can mate, though with reduced frequency, but wingless females do not mate at all. He also observed that males of this species courting wingless females appear to be unable to proceed to mate after assuming a position behind the female and that female non-receptiveness did not appear responsible for the failure of wingless females to mate. It was concluded that the barrier to mating with wingless *D. auraria* females was the lack of a visual cue from the female, identified as a "wing-spreading 'go-ahead' signal" in that species. Our direct observations of *D. affinis*, *D. algonquin*, and *D. athabasca* "eastern A" failed to show that males of the latter two species court wingless females less persistently than do *D. affinis* males, although *D. algonquin* and *D. athabasca* "eastern A" wingless females were mated with much less often than were *D. affinis* wingless females. The available evidence on attempted copulations suggests that *D. athabasca* "eastern A" wingless females mate less often than winged ones because males attempt copulation with them less often. It may be speculated that such a difference of male behavior in the final stage of courtship is also responsible for the reduced mating frequency of wingless females in *D. algonquin*. Perhaps, as in *D. auraria*, a visual cue on the part of the female is important for the completion of mating. However, in *D. algonquin*, but not *D. auraria*, winglessness of the female impairs but does not prevent this cue, though it is abolished by darkness. Since, in *D. algonquin*, no movement on the part of the female has been

found to signal receptivity, the female's visual cue may be no more than her general appearance, which is grossly modified by winglessness.

It also remains possible that winglessness of these drosophilas reduces their chances of mating by impairing vigor, coordination, and ability to respond to stimuli during courtship. However, proof of such a basis for reduced mating frequencies is difficult to establish—at least to the exclusion of impairment of signs and signals. Grossfield (1968) concluded that the failure of wingless *D. subobscura* males to mate was due to their inability to respond to the female's courtship signals. Averhoff and Richardson (1974), who reported evidence of the importance of chemical stimulation for mating in *D. melanogaster* (but *not* related to wing movements or the presence of wings), proposed that the mating disadvantage of wingless *D. melanogaster* males is due to impaired mobility rather than to female rejection of such males. Although we have no evidence that such factors reduced mating frequencies with winglessness in the *D. affinis* subgroup species (*e.g.* wingless males courted vigorously), we cannot rule them out as contributors to reductions of mating success.

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