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An evolutionary view on courtship behavior of *Drosophila*: From a comparative approach

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Courtship behavior is highly divergent in Diptera, especially in *Drosophila*. The typical courtship of *Drosophila melanogaster* is an elaborate repertoire including elements of orienting, tapping, scissoring, circling, wing-vibrating, licking and attempting to copulate, in which males and females send and receive visual, chemical, tactile and acoustic signals from each other. The divergence of courtship behavior reflects the phylogeny to some extent. Loss or gain of certain elements, which cause qualitative differences in courtship behavior among species, are very common in *Drosophila*. On the other hand, rapid quantitative changes in sexual signals tend to occur between sympatric, closely related species but not between allopatric, close relatives. In this review, we assemble available information on courtship behavior, compare its behavioral elements across 135 species of 30 species groups from three genera of the Drosophilidae, excepting the Hawaiian picture-wing *Drosophila* with a bizarre courtship pattern, and discuss functions of each element in relation to its loss or gain and possible evolutionary mechanisms underlying the sexual signal divergence.

1. Introduction

Mating success mainly relies on Specific Mate Recognition System (SMRS). Every sexually reproducing species possesses its own distinct SMRS that controls the exchange of sensory information sent and received by both sexual partners during interplay (Paterson, 1985). *Drosophila* courtship is an elaborate ritual which involves specific types of activity (certain elements), such as orienting, tapping, scissoring (scissor-like opening and closing of both wings without courtship song), circling, wing vibrating (one wing or both wings rapidly up and down with production of courtship song), licking and attempting to copulate, from both sexes. Visual, chemical and acoustic signals derived from these certain elements make up SMRS and the divergence of each element is the important factor contributing to premating isolation and speciation.

Courtship behavior is one of characters which have derived from the ancestor and then diverged to be adapted to environmental changes or evolved

through sexual selection and speciation. Mating in flight is the ancestral Dipteran behavioral pattern and is common in most primitive families such as mosquitoes, of which males have the auditory plumose antenna sensitive to the flight tone of the female and the enlarged specialized eye to capture the female (Downes, 1969). However, such behavior is rare in the derived Acalypteratae with the dichoptic eyes (McAlpine and Munroe, 1968). In the Drosophilidae, mating behavior is highly interactive between males and females especially before mounting. The drosophilid matings typically occur on some types of food substrates, associated with more or less species-specific courtships or epigamic displays making use of posture, movements or display of patterns before attempting to mount and copulate (Spieth, 1952). The great variety of environmental and food conditions has mainly determined the way in which flies can meet and mate, and explains the diversity of mating behaviors (Wicker-Thomas, 2007). Such a drosophilid mating system appears to possess adaptive advantages: males could ascertain many females with small expenditure of time and energy; unreceptive females could repel males during feeding; receptive females could excise sexual selection on several

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males. The diurnal feeding shortly on a small discrete food mass is the key factor responsible for the selective pressure on the evolution of this courtship pattern (Spieth, 1974).

Certain elements of mating behavior are widespread across various species, but it is also obvious that qualitative as well as quantitative interspecific differences exist. A few, if any, quantitative differences are observable between closely related species, while more distantly related species invariably display qualitative differences. In *Drosophila* courtship, the male is primarily responsible for sexual isolation and the female for sexual selection (Spieth, 1952, 1974; Brown, 1965). Closely related species or races derived from allopatric localities are often less sexually isolated than those derived from sympatric sites, the former displaying an identical courtship pattern but the latter distinct ones (Ehrman, 1965; Spieth, 1978). This suggests the reinforcement of divergence in courtship signals between sympatric species/races (Chang and Miller, 1978; Wen et al., 2011). To understand the evolutionary mechanism of courtship behavior, i.e., how and why the relevant characters have reached their present forms, one must combine comparative ethological works with studies on the function, origin and genetics of behavior (Hinde and Tinbergen, 1958; Brown, 1965). It is important to examine roles of courtship in mate selection and reproductive isolation. The initial observations of *Drosophila* mating behavior were made by geneticists interested in evolutionary problems (Ewing, 1983). Before Spieth's (1952) pioneer work on courtship behavior of 101 *Drosophila* species belonging to 21 species groups, mating behavior of *D. melanogaster*, *D. pseudoobscura*, *D. persimilis*, *D. affinis*, *D. algonquin*, and some species of the *D. willistoni* species group and the *D. virilis* species group had already been documented by various investigators (Sturtevant, 1915; Spieth, 1947, 1948; Miller, 1950; Spieth, 1951). Hitherto, courtship behaviors of more than 135 species belonging to 30 species groups and some Hawaiian picture-wing *Drosophila* species have been observed by many investigators. Thus accumulated information makes comparison of courtship behaviors possible across the largest genus *Drosophila* in the Drosophilidae. Tomaru and Yamada (2011) thoroughly reviewed courtship behaviors of *Drosophila*, mainly focusing on their courtship songs of acoustic stimuli. In this review, therefore, we provide infor-

mation on other behavioral elements, especially those related to visual and chemical stimuli, from a viewpoint of how certain elements of courtship have diverged along the evolutionary process. Since in *Drosophila* courtship males are more active and play vital roles for successful mating, we concentrate mainly on male courtship. The elements present or absent in each species are summarized in Table 1 from selected references, excepting some others having failed to observe some behaviors in some species by careless observation or using different strains (Ewing, 1983). We exclude Hawaiian picture-wing *Drosophila* species from the comparison in this review, because an aberrant type of courtship behavior and advertising behavior in a small territory or lek was displayed by these endemic species (Spieth, 1974).

2. Behavioral elements and their functions in *Drosophila* courtship

Apart from endemic Hawaiian picture-wing *Drosophila* species which mate on their leks or territories, most *Drosophila* species display courtship during feeding on a food mass. *Drosophila* courtship is very diverse among species, and requires visual, acoustic, and chemical cues (Wicker-Thomas, 2007). Each species possesses a species-specific repertoire of signals associated with unique movements. Homologous signals are quite different between distinct species, but similar, with some quantitative differences, between closely related species.

Drosophila male courtship is commonly composed of the elements of orientation, tapping, wing flicking, wing waving, wing semaphoring, wing scissoring, wing vibration, leg vibration, leg rubbing, circling, licking, mounting and countersignaling (Spieth, 1974). Each element has its function for leading to successful copulation (Spieth, 1952, 1974; Ewing, 1983). Males and females send and/or receive several stimuli, such as visual, chemical, tactile or acoustic ones, from each other during courtship. Males' dancing by flicking, waving, scissoring or rowing of one or two wings and circling is a visual language to females; chemical signals and tactile stimuli are transmitted between males and females by males' tapping and licking on females; acoustic signals, probably visual signals as well, are produced by vibrating one or two wings. In many species, the role of visual signals is less species-

specific than the roles of chemical or acoustic signals (Markow and O'Grady, 2005).

2.1 Courtship elements related to visual stimuli

Visual stimuli are one of the major factors in the initiation of courtship (Spieth, 1952). At the beginning of courtship, a male orients a moving female and then taps her. Few *Drosophila* females are so receptive that they will accept a male as soon as he taps (Manning, 1960). After tapping, the male performs some wing display behaviors or circling to let the female slow down. Wing displays include wing waving, flicking, scissoring, rowing, or vibrating which probably produces both visual and acoustic signals. Thus, such visual signals are sent from males to females and should be received by females under light.

2.1.1 Light dependency

Light is required for *Drosophila* to receive visual stimuli from environmental factors or individuals of conspecific or alien species. In *Drosophila*, some species fail to mate or reduce mating success without light, while some others are able to mate in the darkness; i.e., the former is dependent but the latter independent on light for mating. It has been well documented that the extent of light-dependency for mating varies among *Drosophila* species.

According to the classification by Grossfield (1971), light-independent species (8 spp.) are less than light-dependent ones (12 spp. being somewhat light-dependent and 22 spp. completely dependent). For the light-independent species, such as *D. melanogaster*, *D. busckii*, *D. ananassae*, *D. montium*, *D. pseudoobscura*, *D. affinis*, *D. funebris*, *D. virilis*, *D. hydei*, *D. replete* and *D. immigrans*, visual stimuli by wing display or circling might be dispensable but courtship might more rely on chemical stimuli by tapping/licking and/or acoustic stimuli by wing vibration (Table 1). For some completely light-dependent species, such as *D. subobscura*, *D. munda*, *D. palustris*, *D. phalerata* and *D. guttifera*, which produce no acoustic stimuli, courtship might mainly rely on visual stimuli by wing display and/or circling and subsequently following elements (Table 1). Other more or less light-dependent species use both visual and chemical/acoustic stimuli for courtship.

2.1.1.1 *D. subobscura*

Drosophila subobscura is one of species which completely depend on light for courtship (Grossfield, 1971). While a male and a female are moving face to

face, the male gradually opens his wings, and spreads them when he stops to move. This "wing-dance" is the only effective courtship element in this species. Brown (1965) conducted two experiments to test the importance of visual stimuli of this "wing-dance" for mating success. The first was to remove the male wings completely or the distal half of them. The results indicated that the number of successful mating pairs was significantly reduced in both wing removal treatments, which made females walk away from the wing-removed males. The second was to show a black spherical "Plasticine" model moving side by side or an etherized female to a virgin male. In response to the moving experimental object, some virgin males tapped, orientated, wing-danced and even tried to copulate with the moving model. Some virgin males ignored the etherized female until she began to move. Thus, the first experiment revealed that the display of wing opening and spreading was important for the female to keep staying with the male. The second experiment suggested that a side-by-side moving article was the cue for male to pay attention to court. Interestingly, the wing vibration is very rare in this species, suggesting that any acoustic signal is not used as a cue to stimulate its partner. *Drosophila subobscura* is the only species that does not sing any courtship songs but performs the unique wing-dancing in the *D. obscura* species group (Table 1). *Drosophila subobscura* occurs in a variety of habitats from woodlands, pastures, even to moorlands. It has a good deal of genetic heterogeneity, and this might serve to adapt it to a wide variety of habitats (Brown, 1965). There is a light-independent strain selected from a geographic population. This strain shows the totally modified courtship lacking the wing-dance; the males rape the females without preceding courtship. The females seem to be rather passive and do not resist atypical copulation attempts by the males. The behavioral differences between the light-dependent and -independent strains are genetically determined by a polygenic system involving all four autosomes but not the X-chromosome (Pinsker and Doschek, 1980). It seems likely that this genetically determined variation of courtship seen in wild populations is the consequence of natural selection under different environments.

2.1.1.2 The *D. melanogaster* species complex

Drosophila melanogaster is the only light-

Table 1: Elements of male courtship behavior in the Drosophilidae

Genus	Subgenus	Species-group	Species	Before mounting				Being or after mounting		References***				
				Chemical stimuli		Visual stimuli		Acoustic stimuli	Male:female courtship		(A±B)** signal divergence between closely related species			
				tapping	licking	circling	scissoring/flicking/waving/rowing					light dependency	wing vibration*	
<i>Scaptodrosophila</i>		<i>victoria</i>	<i>S. victoria</i>	+	-	-	-	N/A	V3-5	+	-	N/A	1	
		<i>ruffrons</i>	<i>S. lebanonensis</i>	+	-	-	-	N/A	V3-5	+	-	N/A	1	
		<i>latifasciaeformis</i>	<i>S. latifasciaeformis</i>	+	+	+	-	N/A	V90	-	-	N/A	1	
<i>Hiridrosophila</i>			<i>H. dancani</i>	+	-	-	-	N/A	-	-	-	N/A	1	
		<i>saltans</i>	<i>D. prosaltans</i> <i>D. saltans</i>	+	+	+	-	N/A	V20-40, V90 V90	-	-	N/A	1	
<i>Drosophila</i>		<i>startevanti</i>	<i>D. rectangularis</i>	+	+	+	-	N/A	V20-40	-	-	N/A	1	
		<i>elliptica</i>	<i>D. emarginata</i>	+	+	+	F	N/A	-	-	-	N/A	1	
		<i>willistoni</i>	<i>D. willistoni</i>	+	+	-C	F, S	N/A	V70-90	-	-	N/A	4; 1; 5	
			<i>D. equinoxialis</i>	+	+	-C	F	N/A	V70-90	-	-	N/A	4; 1; 5	
			<i>D. paulistorum</i>	+	+	-C	F	N/A	V70-90	-	-	N/A	1; 5	
			<i>D. tropicalis</i>	+	+	-C	F	N/A	V70-90	-	-	N/A	1; 5	
		<i>boathensis</i>	<i>D. sacinea</i>	+	+	-C	F	N/A	V70-90	-	-	N/A	4; 1	
			<i>D. capricorni</i>	+	+	-C	F	N/A	V70-90	-	-	N/A	4; 1	
			<i>D. fumipennis</i>	+	+	-C	W, S	N/A	-	-	-	N/A	4; 1	
			<i>D. nebulosa</i>	+	+	-C	W, S	N/A	-	-	-	N/A	4; 1	
		<i>melanogaster</i>	<i>D. melanogaster</i>	+	+	+	S (rare)	I	V90	-	+	-	N/A	1; 6; 7; 8; 3
			<i>D. simulans</i>	+	+	+	S (many), R1/2	II	V90 (rare)	-	+	-	N/A	1; 6; 7; 8; 3
		<i>D. sechellia</i>	+	+	+	S, R1	II	V	-	+	-	N/A	8;	
		<i>D. mauritiana</i>	+	+	+	S, R2 (many)	II	V90 (rare)	-	+	-	N/A	9; 8	
		<i>D. yakuba</i>	+	+	+	S, R2	II	V	-	+	-	N/A	8; 10	
		<i>D. santomea</i>	+	+	+	S, R2	II	V	-	+	-	N/A	11; 10	
		<i>D. teissieri</i>	+	+	+	S, R2	II	V	-	+	-	N/A	8	
		<i>D. erecta</i>	+	+	+	S	II	V	-	+	-	N/A	8	
		<i>D. oreana</i>	+	+	+	S	II	V	-	+	-	N/A	8	
	<i>suzukii</i>	<i>D. biarmipes</i>	+	+	+	S	N/A	V	-	+	-	N/A	12	
	<i>elegans</i>	<i>D. elegans</i>	+	-	+	W180	N/A	-	-	+	-	N/A	13	
		<i>D. gannigcola</i>	+	-	+	W30	N/A	-	-	+	-	N/A	13	
	<i>takahashii</i>	<i>D. takahashii</i>	+	-	+	W	II	V90	-	+	-	N/A	14; 1; 3	
	<i>ananassae</i>	<i>D. ananassae</i>	+	-	+	S	I	V5-15	-	+	-	N/A	14; 1; 3; 15; 16	
		<i>D. pallidosa</i>	+	-	+	S	N/A	V50-90	-	+	-	N/A	17; 15; 16; 18	
		<i>D. malerkhottiana</i>	+	+	+	S	N/A	V	-	+	-	N/A	19	
		<i>D. bipunctata</i>	+	-	N/A	N/A	N/A	V5-15	-	+	-	N/A	20	
	<i>montium</i>	<i>D. avarria</i>	+	-	-	-	II	rare	-	+	+	N/A	14; 1; 21; 22	
		<i>D. triarvria</i>	+	-	-	-	II	rare	-	+	+	N/A	21; 22	
		<i>D. bicarvria</i>	+	-	-	-	III	rare	-	+	+	N/A	21; 22	
		<i>D. sabauvria</i>	+	-	-	-	N/A	rare	-	+	+	N/A	23	
		<i>D. quadraria</i>	+	-	-	-	N/A	rare	-	+	+	N/A	23	
		<i>D. rufa</i>	+	-	-	-	II	-	-	+	+	N/A	14; 1; 3	
		<i>D. montium</i>	+	-	-C	-	I	-	-	+	+	N/A	14; 1; 3	
		<i>D. serrata</i>	+	-	rare	-	N/A	rare	-	+	+	N/A	14; 1; 3	
		<i>D. birchii</i>	+	-	rare	-	N/A	rare	-	+	+	N/A	24; 25	
		<i>D. lini</i>	+	-	-	-	N/A	rare	-	+	+	N/A	24; 25	
		<i>D. ogatai</i>	+	-	-	-	N/A	-	-	+	+	N/A	26; 27	
		<i>D. ohnishi</i>	+	-	-	-	N/A	-	-	+	+	N/A	26; 27	
		<i>D. kibakawai</i>	+	-	-	-	N/A	-	-	+	+	N/A	26; 27	
		<i>D. leontia</i>	+	-	-	-	N/A	-	-	+	+	N/A	28; 42	
		<i>D. bocki</i>	+	-	-	-	N/A	-	-	+	+	N/A	28; 42	

Genus	Subgenus	Species-group	Species	Before mounting				Being or after mounting		References***							
				Chemical stimuli	Visual stimuli	Acoustic stimuli	Male-male courtship	Acoustic stimuli	(A+B)** signal divergence between closely related species								
				tapping	licking	circling	scissoring/flicking/waving/rowing	light dependency	wing vibration*	Male-male courtship	Acoustic stimuli	wing vibration					
<i>Drosophila</i>	<i>Drosophila</i>	<i>tamidiarsus</i>	<i>D. repletales</i>	+	-	-	-	N/A	-	-	-	-	N/A	I			
			<i>D. immigrans</i>	+	-	+	F, S	I	-	-	-	-	-	N/A	I		
			<i>D. sulfurigaster</i>	+	-	+	W	N/A	-	-	-	+	-	-	N/A	I	
			<i>D. funebris</i>	+	+	-	F	I	V	V	+	+	-	-	N/A	1; 3; 43	
			<i>D. subfanebris</i>	+	+	-	-	N/A	V	V	+	+	-	-	N/A	1; 43	
			<i>D. m. macroshina</i>	+	+	-	-	N/A	V	V	+	+	-	-	N/A	1; 43	
			<i>D. m. limpiensis</i>	+	+	-	-	N/A	V	V	+	+	-	-	N/A	1; 43	
			<i>D. m. ohioensis</i>	+	+	-	-	N/A	-	-	+	+	-	-	N/A	I	
			<i>D. trispina</i>	+	-	-	F	N/A	-	-	+	+	-	-	N/A	I	
			<i>D. cardini</i>	+	+	+	-	N/A	-	-	-	-	-	-	N/A	I	
			<i>D. cardinoides</i>	+	+	-	F	N/A	-	-	-	-	-	-	N/A	I	
			<i>D. neocardini</i>	+	+	-	W, F	N/A	-	-	-	+	-	-	N/A	I	
			<i>D. polymorpha</i>	+	+	+	-	-	-	-	N/A	V	N/A	-	N/A	I	
			<i>D. quinaria</i>	+	-	-	F	N/A	-	-	N/A	-	+	-	-	N/A	I
			<i>D. munda</i>	+	+	-	-	III	-	-	III	-	-	-	-	N/A	1; 3
<i>D. occidentalis</i>	+	+	-	F	II	-	-	II	-	+	-	-	N/A	1; 3			
<i>D. suboccidentalis</i>	+	+	-	F	N/A	-	-	N/A	-	+	-	-	N/A	I			
<i>D. palustris</i>	+	+	+	F	III	-	-	III	-	+	-	-	N/A	1; 3			
<i>D. subpalustris</i>	+	+	-	-	II	-	-	II	-	+	-	-	N/A	1; 3			
<i>D. quinaria</i>	+	+	-	-	N/A	-	-	N/A	-	+	-	-	N/A	I			
<i>D. tenebrosa</i>	+	+	+	F	N/A	-	-	N/A	-	few	-	-	N/A	I			
<i>D. phalerata</i>	+	+	+	F	III	-	-	III	-	+	-	-	N/A	1; 3; 34			
<i>D. t. transversa</i>	+	+	-	-	N/A	-	-	N/A	V20-30	+	-	-	N/A	1; 3; 34			
<i>D. t. subquararia</i>	+	+	+	-	-	-	-	N/A	-	+	-	-	N/A	I			
<i>D. guttifera</i>	+	+	+	-	-	-	-	III	-	+	-	-	N/A	I			
<i>D. testacea</i>	+	+	+	-	-	-	-	N/A	-	+	-	-	N/A	I			
<i>D. tripancleta</i>	+	+	-	-	-	-	-	III	V75-90	+	-	-	N/A	1; 3			
<i>D. crocina</i>	+	+	+	-	-	-	-	N/A	V15-20	+	-	-	N/A	I			
<i>D. guarami</i>	+	+	+	-	-	-	-	III	V5	-	-	-	N/A	1; 3			
<i>D. rubrifrons</i>	+	+	+	-	-	-	-	N/A	V90	+	-	-	N/A	I			
<i>D. castanea</i>	+	+	+	-	-	-	-	N/A	V5	-	-	-	N/A	I			

+: present; -: absent; N/A: no information available; -C: males circle non-receptive females; rare: males rarely display the behavior; many: male's behavior is abundant; W: wing waving, F: wing flicking, S: wing scissoring, R1: one wing rowing, R2: two wings rowing; I: light-independent, II: somewhat light-dependent, III: completely light-dependent.

* The number indicates the degree of wing extension from the body axis.

** (A+B) indicates sympatric species A and B; (A-B) indicates allopatric species A and B.

*** 1. Spieth (1952); 2. Bixler et al. (1992); 3. Grossfield (1971); 4. Spieth (1947); 5. Ritchie and Gleason (1995); 6. Manning (1960); 7. Ewing et al. (1968); 8. Cobb et al. (1989); 9. Robertson (1983); 10. Blyth et al. (2008); 11. Llopert et al. (2002); 12. Hegde et al. (2005); 13. Yeh et al. (2006); 14. Spieth and Hsu (1950); 15. Yamada et al. (2002a); 16. Yamada et al. (2002b); 17. Futch (1973); 18. Yamada et al. (2008); 19. Hegde and Krishna (1997); 20. Ewing and Bennet-Clark (1968); 21. Oshima et al. (1984); 22. Oshima et al. (1996); 23. Tomaru and Oguma (1994); 24. Hoikkala et al. (2000); 25. Hoikkala and Crossley (2000); 26. Oshima et al. (1995); 27. Wen et al. (2011); 28. Baimai et al. (1980); 29. Brown (1965); 30. Noor and Aquadro (1998); 31. Miller (1950); 32. Chang and Miller (1978); 33. McRobert and Tompkins (1987); 34. Neems et al. (1997); 35. Stalker (1942); 36. Hoikkala and Lumme (1984); 37. Wasserman et al. (1971); 38. Wasserman and Zweig (1991); 39. Markow (1981a); 40. Krebs and Bean (1991); 41. Alonso-Pimentel et al. (1995); 42. Li and Wen (unpublished data); 43. Ewing (1979).

independent species in this species complex. *Drosophila simulans*, *D. mauritiana* and *D. sechellia* depend on light to more or less extent. The decrease of mating frequency in darkness is the least in *D. simulans*, the most in *D. sechellia*, and intermediate in *D. mauritiana* (Spieth and Hsu, 1950; Grossfield, 1972; Robertson, 1983; Sakai et al., 1997). The normal courtship of *D. melanogaster* involves shortly orient-front behavior but abounding wing vibration (Manning, 1960; Markow and Hanson, 1981). Markow and Hanson (1981) dissected the courtship of *D. melanogaster* by multivariate analyses and found out that the orient-front behavior during the circling frequently happened in unsuccessful or long-bout courtships to give more visual signals for exciting the unreceptive female. In contrast, the visual information, such as scissoring, is dominant in its sympatric species, *D. simulans*, which displays more scissoring and spends less time on wing vibration. *Drosophila mauritiana*, most closely related to *D. simulans*, is light-dependent as well, spending less time for wing vibration but longer time for sending visual stimuli (Cobb et al., 1989), although it uses wing rowing rather than scissoring as a display.

The light-dependency varies also between strains of *D. simulans*. Sakai et al. (1997) found that one strain from Ogasawara, Japan was light-independent like as *D. melanogaster*. The intraspecific difference of mating frequency in darkness depends on genetic differences in the male-specific sexual behavior rather than in the locomotor or mating activity (Sakai et al., 1997).

2.1.1.3 The *D. auraria* species complex

Mating behavior of three species, *D. auraria*, *D. triauraria* and *D. biauraria*, in the *D. auraria* species complex is very similar, lacking wing-display and front-circling: a male approaches and taps a female, and then circles to her rear, and makes a running lunge when her position is appropriate to mount; having mounted and grasped the female, the male extends one wing to 90° and vibrates it, and at the same time attempts to copulate. The light-dependency varies to some extent between the species: *D. biauraria* is completely light-dependent, while *D. auraria* and *D. triauraria* are somewhat light-dependent (Spieth and Hsu, 1950; Oguma et al., 1984; Oguma et al., 1996).

Oguma et al. (1996) used an infrared camera to record courtship behavior of the *auraria* complex

under darkness, and found that tapping and subsequent elements triggered by visual signals were rarely observed under darkness. However, when flies were in close contact, males mounted females and attempted to copulate. A picture in the paper showed that a male of *D. auraria* copulating with a female vibrated his wing in darkness, and that three females near the copulating couple spread their wings in response to the wing vibration of the male. Obviously, acoustic signals should have induced female's receptive response under darkness in this species. This finding indicates that *D. auraria* can mate in the dark if partners are in close contact, although Grossfield (1971) classified this species as a completely light-dependent one.

2.1.2 Evolution of elements related to visual stimuli

Grossfield (1971) divided *Drosophila* into three classes by investigating insemination rate under light and darkness: Class I is light-independent, with species distributed worldwide or over wide geographic regions; Class II and III are somewhat and completely light-dependent, respectively, with species distributed in limited regions, except for the cosmopolitan *D. simulans* (Grossfield, 1972). Two distantly related species, *D. simulans* and *D. subobscura*, have evolved the light-dependent feature independently (Spieth and Hsu, 1950). Males of either species do not use acoustic cue but mainly wing display during courtship. Males send visual signals to females by vigorous wing display: wing-dance in *D. subobscura* and scissoring in *D. simulans*. Females have to receive these messages under light. This feature may have evolved similarly, even though independently, probably through the loss of acoustic signals in males or degeneration of hearing sensory in females, and the enhancement of visual signals by wing-dance, scissoring and/or circling in males or the gain of susceptible visual sensory in females, in these two unrelated species.

Visual stimuli are less used in the *D. montium* species subgroup. Species in this subgroup display similar courtship behavior without wing display or circling before mounting, but use more acoustic signals by wing vibration after mounting. This is a very unique and typical courtship pattern in this subgroup. The light-dependency varies among species in this subgroup: *D. biauraria* is completely dependent, *D. auraria* and *D. triauraria* highly dependent, *D. rufa* less dependent, and *D. montium* independent (Gross-

field, 1972; Oguma et al., 1996). In this subgroup, the light-dependency might have evolved as the consequence of adaptations to environments or ecological habitats where they are living.

2.2 Elements related to chemical stimuli

Two elements, tapping and licking, are associated with chemical stimuli, although tactile stimuli might be involved as well. Courtship of many species in the *melanogaster* subgroup is initiated by male's tapping on female with his fore tarsi where chemoreceptors are located, and then other elements, such as following, circling, wing display and wing vibration, take place. After wing vibration, the male licks the female's genitalia with his proboscis and then attempts to copulate (Ewing and Bennet-Clark, 1968). Spieth (1952) amputated the male fore tarsi in four species of the *virilis* group and confirmed that stimuli were received by the male via his fore tarsi and that differences existed in this factor between strains of the same species. When males tap other males, some species, such as those of the *D. mulleri* species subgroup of the *D. repleta* species group and the *D. saltans* and *D. willistoni* species groups, stop courtship immediately (Table 1), suggesting that they discriminate between conspecific males and females based on chemical/tactile signals obtained by tapping. However, some other species continue male-male courtship even after tapping. In *D. melanogaster*, tapping with correct gustatory inputs is necessary for males to induce the species-specific hallmark of unilateral wing vibration, because the flies deprived of gustatory inputs become to perform bilateral wing extension during courtship (Koganezawa et al., 2010). Thus, the pheromone input by tapping from the foreleg of courting male shapes the courtship song pattern. The licking action after wing vibration of the male obviously stimulates the female. It is possible that chemical stimuli are involved in this action (Spieth, 1952). Tapping is, however, absent in many species of the *montium* and the *obscura* subgroups, and licking is totally omitted in all investigated species of these subgroups (Table 1). Commonly seen male-male courtships in the *montium* subgroup might be due to the lack of tapping and/or licking elements. Other elements, such as wing vibration after mounting, play a very important role in discriminating mates in this subgroup, for example in *D. lini*, *D. ogumai* and *D. ohnishi* (Wen et al., 2011).

The tapping and licking elements of courtship

might have evolved along with female sex pheromones. The first *Drosophila* sex pheromone was identified from *D. melanogaster* (Antony and Jallon, 1982). Since then, a variety of cuticular hydrocarbon molecules have been identified from females and males in a number of *Drosophila* species (see Ferveur, 2005; for a review). Recently, Ferveur and Cobb (2010) have reviewed behavioral and evolutionary roles of cuticular hydrocarbons, and Wicker-Thomas and Chertemps (2010) have done the genetics and biosynthesis of them.

3. Timing of courtship: precopulatory courtship vs. copulatory courtship

The timing of male courtship should be an important factor to be considered for understanding the evolution of courtship behavior. Copulatory courtships, i.e., courtships occurring after intromission, are very common in insect (Eberhard, 1991). However, elaborated courtships in most *Drosophila* species are of typical precopulatory one. Only a few species of the *D. quinaria* species group and the *mulleri*, the *affinis* and the *montium* species subgroups have been reported to perform copulatory courtships with some variation (Miller, 1950; Spieth, 1952; Wasserman et al., 1971; Tomaru and Oguma, 1994; Neems et al., 1997; Wen et al., 2011).

3.1 *D. pegasus*

Drosophila pegasus is the first species which was reported to have no precopulatory courtship in *Drosophila*. When a male detects a female, he immediately climbs upon her abdomen and rides on her for a long period (Wasserman et al., 1971). The extended riding of male on female was called "grasping behavior" or "mate grasping" (Wasserman et al., 1971; Wasserman and Zweig, 1991; Gronlund et al., 2002). Females play only a passive role in mounting, but males can clearly distinguish mates, preferring females, upon initial grasping. Male-male grasping occurs when no female is present, but such a male usually releases his hold soon. It is still unknown what signals are used for males to differentiate between males and females, because the cuticular hydrocarbon composition is the same in both sexes (Gronlund et al., 2002). Males can distinguish even females reared on different types of food or from different localities, preferring females reared on the original host cactus media or from the

same local population, respectively (Wasserman and Zweig, 1991). In *D. pegasus*, this grasping behavior has evolved along with the complete loss of other elements that are commonly seen in the normal courtship of *Drosophila*.

3.2 *D. algonquin* and *D. phalerata*

Drosophila algonquin is a sibling species of *D. affinis* in the *affinis* subgroup of the *obscura* group. They are widely distributed in the United States east of the Rocky Mountains, with the overlapped range in the western Great Plains and in the northeastern States. Sex combs of *D. algonquin* are larger than those of *D. affinis* (Miller, 1950). In both species, courtship is usually very brief, being followed quickly by copulation. While males of *D. algonquin* sometimes continue to buzz during copulation, such a behavior is not found in *D. affinis* and other species of the *affinis* subgroup. Each burst of buzz was produced by vibration of both wings extended about 45° and lasted about a third of one second; 66 buzzes were counted in a copulation lasting for almost 5 min (Miller, 1950; Chang and Miller, 1978).

Drosophila phalerata feeds on fungi, usually together with *D. transversa*, *D. limbata* and *D. kuntzei* of the *quinaria* group in different combinations. All four species produced courtship songs by vibrating one or both wings in their courtships. Males of *D. phalerata* produce most of their songs during rather than prior to copulation, whereas males of the other three species remain silent during copulation. The song of *D. phalerata* consists of unstructured pulses with 260 Hz of carrier frequency (Neems et al., 1997), being similar to the sine songs in the *D. lini* clade (Wen et al., 2011).

The copulatory courtship with wing vibration after mounting has independently evolved only once in *D. algonquin* and in *D. phalerata* among relatives of the *affinis* subgroup and of the *quinaria* group, respectively.

3.3 The *D. auraria* and the *D. serrata* species complexes

The *auraria* complex consists of four sympatric species, *D. auraria*, *D. bauraria*, *D. triauraria* and *D. subauraria*, and one allopatric species, *D. quadraria* (Kimura, 1987). The courtship behavior of five species is similar. When a male finds a female, he orients to her, then follows and taps her body. Wing vibration is observed during following in most cases. Males produce less courtship songs before copulation

and at attempted copulation but more during copulation (Tomaru and Oguma, 1994). Thus, both precopulatory and copulatory courtships are performed, but with different intensities, by these species.

Drosophila birchii and *D. serrata* are sympatric sibling species which are endemic to Australia. Males of these two species court their females mainly during copulation, singing after mounting and during copulation. Females of both species discriminate against wing-removed conspecific males which do not sing (Hoikkala et al., 2000), strongly suggesting that their copulatory courtship song is an essential cue for mating success.

3.4 The *D. kikkawai* species complex

Three sibling species, *D. lini*, *D. ohnishii* and *D. ogumai*, form a clade in the *D. kikkawai* species complex of the *montium* subgroup (Wen, 2004). *Drosophila lini* and *D. ogumai* are allopatric, and *D. ohnishii* is distributed in the intermediate region, parapatrically with each of the other two species (Oguma et al., 1995; Zannat and Toda, 2002; Wen et al., 2011). Males follow moving flies and attempt to mount without tapping, circling or wing display before mounting. Immediately after mounting a female, the male extends either of his wings to 45–90° from the body axis, vibrates it, and attempts to copulate. Males produce sine songs with different frequencies, high (about 250 Hz) in the two allopatric species, *D. lini* and *D. ogumai*, but low (about 190 Hz) in *D. ohnishii* (Wen et al., 2011). Very interestingly, this difference in the sine song frequency exactly corresponds to the presence or absence of sexual isolation between the species; i.e., there is strong sexual isolation between the parapatric pairs of species, *ohnishii/lini* and *ohnishii/ogumai*, but no isolation between the allopatric pair, *lini/ogumai*. Playing back low frequency sine songs to *D. lini* and *D. ogumai* or high frequency songs to *D. ohnishii* has induced female repelling behavior (Li et al., in preparation), strongly suggesting that the frequency of sine song produced in copulatory courtship is an important sexual signal for mate recognition in these sibling species.

Three other sibling species, *D. kikkawai*, *D. leontia* and *D. bocki*, form another clade in the *kikkawai* complex (Wen, 2004). The distribution range of *D. leontia* overlaps with those of the other two species (Baimai et al., 1980). We observed their courtship behavior and found that they also displayed copulatory courtships like as the *lini* clade. Mounting of an

alien species male also induced female repelling behavior (Li et al., unpublished data).

4. Sexual signal divergence in sympatric closely related species

Natural selection strengthens sexual isolation in response to maladaptive hybridization following secondary contact of two species/subspecies/populations through the process known as reinforcement (Noor, 1999). Sexual isolation may result from divergence in sexual signals and receiver preferences between closely related species, so that speciation will be influenced by changes in signals and preferences (Butlin and Ritchie, 1994). Sexual signal divergence is sometimes seen in some courtship elements between sympatric closely related species: for example, in locomotory activity, wing display and pulse song between *D. melanogaster* and *D. simulans*, in circling and wing display between *D. elegans* and *D. gunungcola*, in pulse song among species of the *auraria* complex, between *D. serrata* and *D. birchii*, between *D. yakuba* and *D. santomea*, and between *D. pseudoobscura* and *D. persimilis*, and in timing of singing and song type between *D. affinis* and *D. algonquin* (Table 1). On the other hand, sexual signals are usually similar between allopatric close relatives: for example, the sine song frequency is similar between *D. lini* and *D. ogumai* (Wen et al., 2011).

4.1 Scissoring in *D. melanogaster* and *D. simulans*

Drosophila melanogaster and *D. simulans* are sympatric, cosmopolitan close relatives. Although they commonly meet and compete for food under natural conditions (Manning, 1960), they differ to some extent in their niches and behavior: *D. simulans* prefers lower temperatures than *D. melanogaster* does; *D. melanogaster* appears more active but *D. simulans* sluggish; and *D. melanogaster* pupates frequently on the walls of culture bottles but rarely on the food surface, while *D. simulans* does conversely. The commonest sequence of courtship is orientation-scissoring-vibration-licking in *D. simulans* and *D. melanogaster*, but scissoring is almost omitted from this sequence in *D. melanogaster* while *D. simulans* spends less time in wing vibration (Manning, 1960; Cobb et al., 1986). The amount of scissoring increased with courtship duration in *D. simulans* (Cobb

et al., 1986). Given *D. simulans* males with *D. melanogaster* females, the *D. simulans* males act as *D. melanogaster* males, omitting scissoring after orientation. On the other hand, given *D. melanogaster* males with etherized *D. melanogaster* females, they display scissoring to the immobile females. These facts suggest that the repertoire of intrinsic courtship elements is common to both species (Manning, 1960). However, courtship is an interaction between two individuals, and changes in levels of excitation are necessary in both sexes. For more active females of *D. melanogaster*, visual stimuli by wing rowing and scissoring would be apt to be out of female's field of view and therefore ineffective, but wing vibration may have an effect in reducing female's locomotor activity (Cobb et al., 1986). Males of *D. simulans* may send more visual stimuli by scissoring their wings to excite conspecific females that are more sluggish, i.e., having a higher threshold for response, than *D. melanogaster* females (Manning, 1960). Interestingly, probably in relation to the shift of courtship to using more visual stimuli in *D. simulans*, the eyes of *D. simulans* are larger, with 5% more eye facets, than those of *D. melanogaster* (Manning, 1960).

4.2 Pulse song in the *D. pseudoobscura* species complex

Drosophila pseudoobscura and *D. persimilis* are sibling species with identical morphological characters and broadly sympatric across western North America. Females of these species discriminate against heterospecific males as mates, but males court heterospecific females as quickly and readily as they do conspecific females in the laboratory (Noor, 1996; Noor and Aquadro, 1998). Differences in the interpulse interval (IPI) and the intrapulse frequency (IPF) of courtship song have been detected between the two species. These differences are controlled by both X-chromosomal and autosomal loci (Noor and Aquadro, 1998).

4.3 Timing of singing and pulse song in the *D. quinaria* species group

Drosophila phalerata, *D. transversa*, *D. limbata* and *D. kuntzei* are fungal breeders and are distributed with overlap in parts of the United Kingdom and the near-continent. Several pulse song parameters are different between *D. transversa*, *D. limbata* and *D. kuntzei*: for example, the mean interpulse interval, IPI, is about 30 ms in *D. transversa*, 15 ms in *D. limbata*, but 13 ms in *D. kuntzei*. *Drosophila phalerata* is

very different in the timing and the type of courtship song from the other three species. It is the only species that sings during copulation and invests very little time in singing before mounting. It produces single pulses with no structural grouping but unimodal IPIs around the mean 370 ms. Each pulse is made up of 2 to 20 cycles and lasts 23 ms on average (Neems et al., 1997).

4.4 Female acceptability in the *D. mojavensis* species complex

Drosophila mojavensis and *D. arizonae* are sibling species and partially sympatric in northern Sinaloa, Sonora and in parts of southern Arizona. They utilize different rotting cacti species as primary substrates for breeding and occasionally meet together on the same host plant (Wasserman and Koepfer, 1977). Sympatric *D. mojavensis* females are much less receptive than its allopatric females to court by *D. arizonae* males, suggesting that selection on sympatric *D. mojavensis* has caused the range of female-acceptable male mating behaviors to move away from the range of *D. arizonae* behaviors (Wasserman and Koepfer, 1977; Markow, 1981a). However, *D. arizonae* males persist in courting *D. mojavensis* females under sympatry, even though they are unable to elicit an acceptance gesture (Markow, 1981a).

4.5 Courtship pattern in the *D. anceps* and the *D. eremophila* species complexes

Among three species of the *D. anceps* species complex (*D. anceps*, *D. leonis* and *D. nigrospiracula*), *D. nigrospiracula* is the first branched-off species and allopatric to the other two partially sympatric species. Courtship elements lost or gained in this complex are tapping and circling lost in *D. nigrospiracula*, and tapping and flicking lost in *D. leonis*; *D. anceps* show all these elements. The pulse burst length is significantly different between the sympatric species, *D. anceps* and *D. leonis*, but not between an allopatric pair of *D. nigrospiracula* and *D. anceps* (Alonso-Pimentel et al., 1995). On the other hand, three allopatric species, *D. eremophila*, *D. mettleri* and *D. micromettleri*, of the *D. eremophila* species complex belonging to the same *repleta* group have similar courtship patterns and courtship song parameters (Alonso-Pimentel et al., 1995).

5. Conclusion

Premating isolation may develop more rapidly than postmating isolation (Markow, 1981b). The basic similarity and the diversity of mating behavior displayed by various species of the Drosophilidae leave no doubt that there has been evolution of mating behavior in the family. Observing courtship behaviors of 101 *Drosophila* species, Spieth (1952) pointed out that tapping is an invariable element at the initial phase of mating sequence and therefore must have been present in the ancestral stocks. Most members of the subgenus *Drosophila* retain this ancestral contact feature of tapping and licking but produce no distance stimuli by wing display and vibration at the initial phase (Table 1), and therefore they are regarded as primarily contact animals. On the other hand, most members of the subgenus *Sophophora* have diverged from this ancestral pattern by becoming dependent on distance stimuli (wing display and vibration) rather than contact stimuli especially by licking (Table 1; Spieth, 1952). Of course, there are some exceptions in both subgenera, for example, female's duet song in the *virilis* group of the subgenus *Drosophila* (see Tomaru and Yamada, 2011 for a review on its features and roles) and licking in the *saltans* and the *willistoni* groups and the *melanogaster* subgroup of the subgenus *Sophophora*. The precopulatory courtship usually accompanied with distance stimuli might be the derived courtship pattern, while the copulatory courtship widespread in insects and in the *montium* subgroup might be the primary type.

Behavioral differences may arise as by-products of genetic divergence in allopatric populations (Muller, 1939) or be developed and strengthened by natural selection in the process of reinforcement when allopatric populations secondarily become contact and their hybrids are poorly adapted (Dobzhansky, 1940). It has been documented by some selection experiments using *D. melanogaster* (McDonald, 1979) and *D. subobscura* (Pinsker and Doschek, 1980) that there is genetic variation in some traits of courtship behavior of *Drosophila*. Such intraspecific genetic variation should have been under natural selection and/or sexual selection and have been the main factor leading to evolution of courtship behavior.

Gain or loss of some courtship elements in ancestral or derived populations could result in unsuccessful courtship between the populations (Kaneshiro, 1976;

Watanabe and Kawanishi, 1979; Markow, 1981b). How courtship elements are gained or lost along evolutionary processes? Why such sexual signal divergence occurs more frequently between sympatric species than between allopatric ones? A possible answer will be provided on the basis of the reinforcement or reproductive character displacement models for speciation, although a number of theoretical problems have been pointed out on these models. Very rapid evolution of premating isolation observed between sympatric forms of *Drosophila* provides indirect evidence in favor of these models (Ritchie and Gleason, 1995). Under sympatry with closely related species, sexual selection alone may lead to increased divergence in their courtship behavior, and additionally, through severe resource competition, ecological selection could favor behavioral separation between them (Coyne and Orr, 1989; Kondrashov and Kondrashov, 1999; Ritchie, 2007). Thus, interactive forces from all environmental factors, such as food, habitat, and competing species, should be taken into account to fully understand mechanisms of courtship evolution. Population-based phylogeographic, ecological, genetic and genomic studies, and conducting experimental evolution are perhaps more likely to provide conclusive evidence in this genomic and proteomic era (Ritchie, 2007). We expect that further studies especially on more species in the *montium* subgroup shall give a deeper insight into the evolution of precopulatory and copulatory courtships in the *melanogaster* group.

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