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# Courtship of *Drosophila*, with a special interest in courtship songs

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This paper reviews the courtship behaviour of *Drosophila*, focusing on courtship songs and types and patterns of sounds in a variety of species with regard to phylogeny. Courtship song is one of the most important signals from males to females during courtship. In most species, males emit one or two types of courtship song, such as a pulse song and a sine song. Some species produce two types of pulse songs, some a pulse song and a sine song, and others a pulse song but no sine song. In the *montium* species subgroup of the *Drosophila* (*Sophophora*) *melanogaster* species group, copulatory courtship songs are reported; some species produce before and after mounting but others only after mounting. In the *Drosophila* (*Drosophila*) *virilis* species group and *Zaprionus*, both sexes produce songs. Breeding sites, sex pheromones and other courtship signals are also examined. Mate recognition in relation to the role of courtship elements are discussed from an evolutionary point of view.

## 1. Introduction

Courtship behaviour in *Drosophila* was first reported by Sturtevant (1915), who used *Drosophila* (*Sophophora*) *melanogaster* (*D. ampelophila*) and described several courtship elements, including vibration, scissors movement, circling and licking. Wing vibration was pointed out as “the most noticeable act” in the courtship described in that report. A sound is produced by the vibration, which was not known at the time, but now the importance of courtship songs is widely acknowledged.

More than 4,000 species are described in Drosophilidae and more than 1,000 belong to a single genus, *Drosophila*. Although there are differences in quality (behavioural elements) and quantity of courtship behaviour between species, an outline of the courtship behaviour of a particular species is helpful for understanding the function and diversity of courtship of *Drosophila*. Here, like Sturtevant, we are concerned with *D. melanogaster*.

Courtship begins with the orientation of the male. He slows down his movements and points his head

toward a female at a distance of one to two body lengths. He approaches her and when she moves, follows her. Vision is one of the most important modalities in orientation and following. In *D. melanogaster*, the frequency of and time spent on orientation decline in the dark (Willmund and Ewing, 1982; Sakai et al., 1997). When the male moves close to the female, he touches her with his foreleg (tapping). There are taste-type chemosensory bristles on the fore tarsi. He senses cuticular hydrocarbons on her body by tapping. After several rounds of tapping, he vibrates his wing at 90 degrees and produces a courtship song (Fig. 1A). The vibrating wing is, in most cases, the one closest to the female. Although it is less frequently observed, the male vibrates both wings as scissors (scissoring, Fig. 1B). Then he licks her genitalia after and/or with vibration. If the female is receptive, she moves slowly, stops walking, and spreads her vaginal plates. The male curls his abdomen and tries to grasp her abdomen with his forelegs and middle legs to copulate (a copulation attempt). If she does not reject him, genitalic coupling is achieved. If the female rejects him, she escapes from him (decamping), kicks him with her hindlegs (kicking), or moves both her wings (fluttering).

In real observations, the sequence of courtship is

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not always the linear process mentioned above. In some cases, a male repeats several behavioural elements back and forth. In other cases, especially when the male is sexually excited, some elements are omitted. If the female escapes from the male, he

ceases courting.

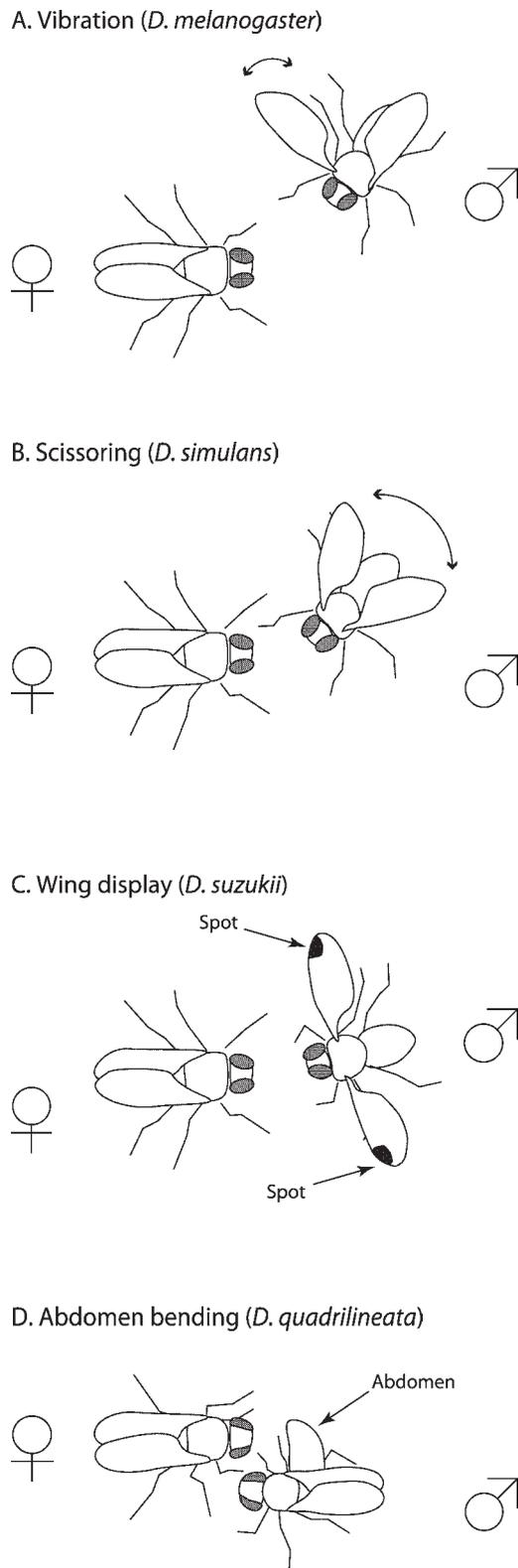
Courtship elements are species specific. Some species have elements that are different from *D. melanogaster*. Others do not have some of the elements observed in *D. melanogaster*. Quantitative differences between strains or species also exist. Therefore, in order to compare courtship between species in detail, the observer may sequentially record when all the courtship elements begin and end. Data can be summarized as an ethogram or a diagram that shows transition probabilities from one element to others and also can be used for several statistical analyses.

Although vibration is the most remarkable behaviour in *Drosophila* courtship as Sturtevant (1915) described, it was about a half century before Shorey (1962) reported sounds produced by vibration (Fig. 2). Since then, courtship songs of many species have been described in *Drosophila*. In general, courtship songs are species specific, especially between sympatric species, playing an important role in the courtship of *Drosophila* and affecting the female's decision of whether or not to accept the courting male.

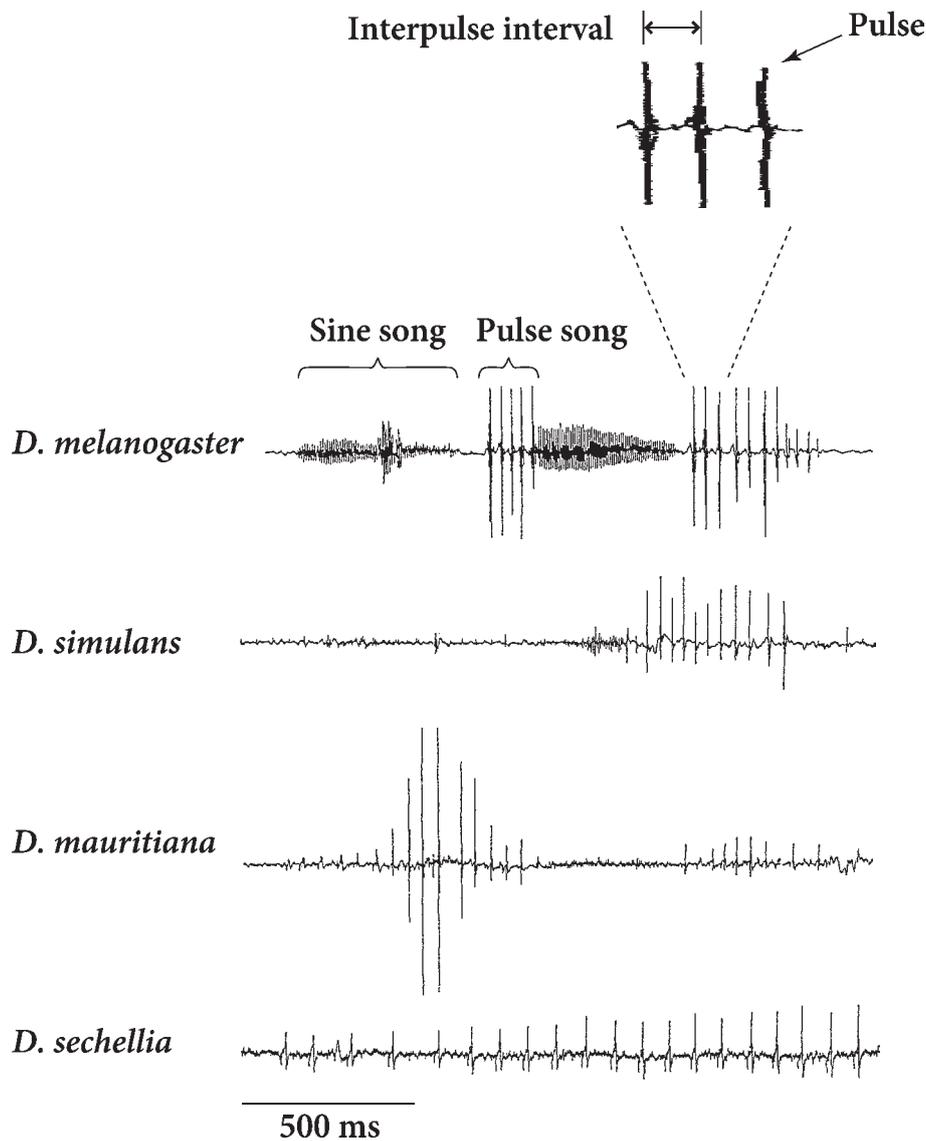
This review summarizes the courtship behaviour of *Drosophila* and provides an up-to-date catalog of *Drosophila* songs. Since phylogenetic constraints are one of the most important factors in the evolution of behaviour, we will discuss the behaviour in relation to the phylogeny of species of *Drosophila*. Hawaiian picture-winged *Drosophila* exhibit diversified biological traits including courtship behaviour (Spieth, 1984). The diversity and evolution of the Hawaiian species are quite interesting, but we deal with these species only as a special topic.

## 2. Breeding sites

A wide variety of breeding sites are used by *Drosophila*, including plants, fungi, fruits, fermenting sap (slime fluxes), cacti, flowers and crabs (Spieth, 1951; Carson, 1971; Powell, 1997). Although many species can be collected on rotting fruits and by banana bait traps, there may exist host specificity or preference. Some species use secondary host plants and host switching may have played an important role in the separation of lineages (Magnacca et al., 2008). In *D. melanogaster*, courtship and mating usually take place at feeding locations, rotting fruits, where females oviposit. Both sexes are attracted to the



**Figure 1** : Wings used in courtship. Vibration in *Drosophila melanogaster* (A), scissoring in *D. simulans* (B), wing display in *D. sukikii* (C) and abdomen bending in *D. quadrilineata* (D).



**Figure 2** : Oscillogram of courtship songs in *Drosophila melanogaster*, *D. simulans*, *D. mauritiana* and *D. sechellia*. Both pulse and sine songs are observed in *D. melanogaster*, *D. simulans* and *D. mauritiana*, but only pulse song in *D. sechellia*. Interpulse interval is a time interval between pulses. The original figure is from Tomaru and Oguma (2003) and modified for this review.

odours. Some species have a specific host, for example, *Gecarcinus ruricola* (black or mountain crab) for crab fly, *D. carcinophila* of the *mercatorum* species subgroup of the *D. (D.) repleta* species group and *D. endobranhia* of the *D. (D.) canalinea* species group (Carson, 1971); *Morinda citrifolia* for *D. sechellia* of the *D. (S.) melanogaster* species subgroup (Lachaise et al., 1988; R'Kha et al., 1991; Higa and Fuyama, 1993; Jones, 1998); cacti for cactophilic species of the *repleta* group (Krebs and Bean, 1991; Powell, 1997); and flowers for many species in a variety of groups, for example, *D. florum* of the *D. (D.) bromeliae* species group, species of the *D. (D.) flavopilosa* species group, *D. (Phloridosia) lutzii* (Carson, 1971), *D. oshimai* of the *suzukii* species subgroup of the *D. (S.) melanogaster* species group (Choo and Nakamura, 1973), and species

of the *D. (S.) elegans* species subgroup of the *melanogaster* group (Sultana et al., 1999; Kimura and Hirai, 2001).

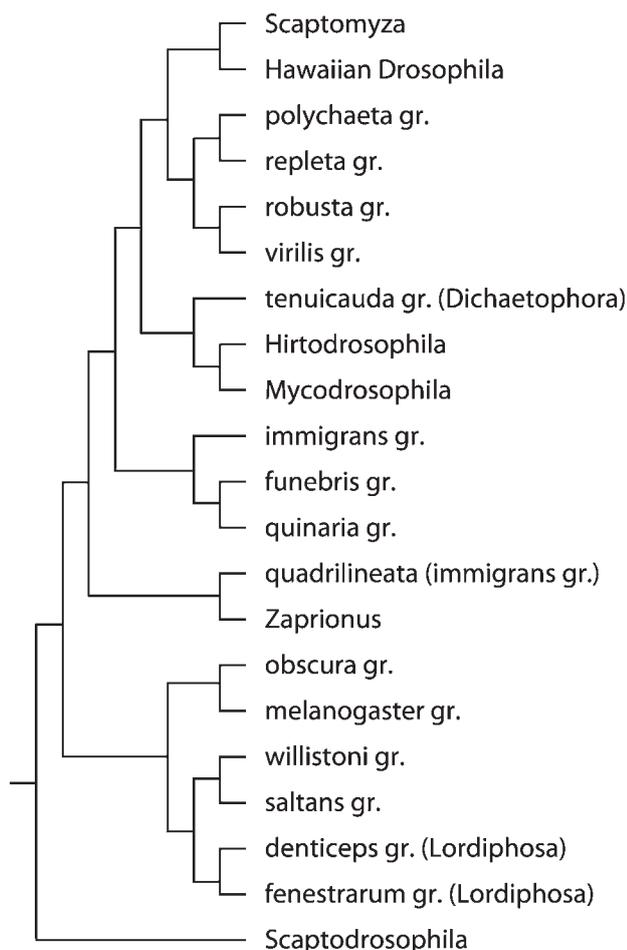
Feeding, mating and ovipositing do not always take place at the same site in a lot of species (Carson, 1971). Males of *D. elegans* hold territories on morning glory (*Ipomea*) flowers (Hirai and Kimura, 1997; Kimura and Hirai, 2001). In the early morning males disperse to newly opened flowers from withered flowers where they spent the night. Aggressive behaviour or fighting with intruding males is observed. A series of courtship behaviours is performed on flowers. The number of males on a single flower increases from morning to evening and the males can no longer defend their territories. In the evening, the flies stay and spend the night. Females

lay eggs on flowers in the daytime. Species of Hawaiian picture-winged *Drosophila* court and mate not at the feeding sites but on leks (Spieth, 1984). For example, males make leks on tree trunks, the under-surface of trees, or shrub stems. A female visits the leks and chooses a male to mate. In cactophilic *D. (D.) mojavensis*, males are distributed across the necrotic cactus arms in the morning and courtship and mating are observed there. The site of ovipositing is not the necrotic arms but different parts of the cacti (Krebs and Bean, 1991).

### 3. Courtship songs

#### 3.1 Two types of courtship songs

Males of most species in the genus *Drosophila* emit sounds (courtship songs) toward females by vibrating their wing(s) during courtship rituals (Table 1, where the species are arranged according to their phylogenetic relationships shown in Fig. 3). Some



**Figure 3** : Phylogenetic relationships of *Drosophila*. The diagram is based on the consensus tree of Katoh et al. (2000) and has been modified for the *Drosophila immigrans* species group (Katoh et al., 2007). Genera or species groups not listed in Table 1 are also presented.

species produce sounds by one wing, some by both wings and others use one or both wings in a species specific manner. Furthermore, males of some species vibrate wings differently for each song repertoire even in a species (Asada et al., 1992; Demetriades et al., 1999). Courtship songs of *Drosophila* can be classified into two types based on the waveforms of the sounds. The major type, “pulse song”, is observed in most species producing songs. The other type is “sine song” (or “humming sound”). Both types are common in species of the genus *Drosophila*, although different names have been sometimes used to describe similar songs of different species by different authors.

A pulse song consists of a series of separate pulses (Fig. 2); although sometimes the pulses are connected without intervals. Each pulse is composed of several cycles of waves. A series of pulses is called a “burst” or “train”. Pulse songs are characterized by several parameters such as cycle length, cycle number per pulse, pulse length, intrapulse frequency, interpulse interval, pulse number per burst, intraburst frequency and interburst interval. Different terms may be used to describe song parameters by different authors and the same terms are sometimes defined differently. Thus, one should be careful when comparing songs between species, since different terms sometimes refer to the same parameter. Sine songs are sounds without pulse structure (Fig. 2); the name “sine song” comes from the waveform which is similar to a sine wave. There are many species in which males do not produce this type of song (Table 1). Sine songs are characterized by the frequency and length of the song.

#### 3.2 Song repertoires

Concerning song repertoires, some species have only one song and others have two or more song types. In the former case, the songs are usually pulse songs. In the latter case, combinations include two types of pulse songs, a pulse song and a sine song, or two types of pulse songs and a sine song. Thus, some species have several types of pulse songs. To date, a species with three song types (two pulse plus one sine) is *D. siamana* of the *hypocausta* species subgroup, the *D. (D.) immigrans* species group (Asada et al., 1992).

Several different terms for more than two pulse songs have been used and there are also differences how to classify the pulse songs. Two species in the *D. (S.) pseudoobscura* species subgroup (*D. pseudo-*

*obscura* and *D. persimilis*) have two pulse songs, a high rate repetition song (HRR) and a low rate repetition song (LRR), which differ in rates of repetition in a burst (Ewing, 1969). Similarly, five species in the *D. (S.) affinis* species subgroup (*D. affinis*, *D. algonquin*, *D. athabasca*, *D. azteca* and *D. tolteca*) have two pulse songs, high and low pulse repetition rate sounds (Chang and Miller, 1978). Species in these two species subgroups (the *pseudoobscura* and the *affinis* subgroups) have similar two type songs and both subgroups belong to the same species group, the *D. (S.) obscura* species group. Two species in the *D. (D.) funebris* species group (*D. multispina* and *D. macrospina*) have two pulse songs, primary and secondary songs, the latter being characterized by polycyclic pulses and long interpulse interval (Ewing, 1979). Twelve species in the *repleta* group (*D. anceps*, *D. meridiana*, *D. navojoa*, *D. peninsularis*, *D. stalkerii*, *D. mercatorum*, *D. canapalpa*, *D. limensis*, *D. melanopalpa*, *D. hydei*, *D. eohydei* and *D. neohydei*) have two pulse songs, A and B songs; A songs consist of simple, short pulse trains produced towards the start of courtship, while B songs tend to be more complex and occur later (Ewing and Miyan, 1986). Four species in the *biplectinata* species complex of the *D. (S.) ananassae* species subgroup of the *melanogaster* group (*D. biplectinata*, *D. parabiplectinata*, *D. pseudoananassae* and *D. malerkotliana*) have two pulse songs, short and long songs (Crossley, 1986).

In the *melanogaster* subgroup, six species have both pulse and sine songs: *D. melanogaster*, *D. simulans*, *D. mauritiana*, *D. erecta*, *D. teissieri* and *D. orena* (Ewing and Bennet-Clark, 1968; Cowling and Burnet, 1981; Cobb et al., 1989), whereas *D. sechellia*, *D. yakuba* and *D. santomea* have no sine songs (Cobb et al., 1989; Watson et al., 2007; Blyth et al., 2008). Although *D. yakuba* and *D. santomea* have no sine song, they have two types of pulse songs (Demetriades et al., 1999; Watson et al., 2007; Blyth et al. 2008): primary and secondary songs that differ in interpulse interval and intrapulse frequency (Blyth et al. 2008). Even though these two species are close relatives in this species subgroup (Llopart et al., 2002), song parameters are clearly different. Primary and secondary songs were first named as clack and thud songs, respectively, by Demetriades et al. (1999), but there is a confusion surrounding the terminology of song types (Blyth et al., 2008). Therefore, here we use new terminology, primary and secondary songs,

which are reclassified by Blyth et al. (2008). Two closely related species, *D. birchii* and *D. serrata* of the *D. (S.) montium* species subgroup of the *melanogaster* group (Hoikkala and Crossley, 2000), three species of the *lini* clade in the *D. (S.) kikkawai* species complex of the *montium* subgroup (*D. lini*, *D. ohnishii* and *D. ogumai*) (Wen et al., 2011), two species in the *D. (D.) virilis* species group (*D. littoralis* and *D. flavomontana*) (Hoikkala, 1985; Suvanto et al., 1994) and one species, *Hirtodrosophila mycetophaga* (Crossley, 1989) also have both pulse and sine songs. The order of pulse songs and sine songs in courtship is also species specific; species in the *melanogaster* species subgroup usually produce sine songs before pulse songs. Songs of *H. mycetophaga* look like those of *D. melanogaster*, that is, sine song followed by pulse song. On the other hand, three species of the *lini* clade produce pulse songs followed by sine song. A male of *D. littoralis* usually produces pulse songs but he produces a humming sound while circling around a female when the female does not spread her wings (acceptance posture).

Courtship songs are, in general, species specific. As mentioned in the previous section, song repertoires and structures are similar among species in the same species subgroup or species complex; in this sense, courtship songs reflect phylogenetic relationships. But parameters, such as interpulse interval and intrapulse frequency, are diverged even between closely related species. Since species of *Drosophila* producing courtship songs have at least one pulse song and a part of the species have sine song, pulse song in the genus *Drosophila* seems to be a single origin, whereas sine song is likely to have multiple origins because species producing sine song belong to different groups (Crossley, 1990). Pulse songs are often critical for species recognition for females, and therefore, it is difficult to lose. In contrast, sine songs are not species identifiers in most cases, suggesting that they are easily lost. The sound characteristics and wing movements of sine songs are similar to those of when flying (von Schilcher, 1976b; Crossley, 1990). Therefore, sine songs are easier to generate than pulse songs. An exception is the *lini* clade, where sine song seems to be more important than pulse song (Wen et al., 2011).

### 3.3 Role of courtship songs

Courtship songs have been suggested to: (1) lower female locomotor activity and increase female recep-

Table 1 : Phylogenetic relationships and courtship song characteristics in *Drosophila*

Genus	Subgenus	Species group	Species subgroup/phyliad	Species complex	Species	Description	Pulse song		Sine song		Duet/female song	Copulatory song	References		
							IPI (ms)	IPF	Description	Frequency					
<i>Drosophila</i>	<i>Idiomya</i>	picture wing (Hawaiian)	<i>pilimana</i> subgroup		<i>D. glabripes</i>	Pulse-structured high frequency clicking sounds.	16.4 (20-21°C)	10000-14500 cps (20-21°C)					Hoikkala et al. (1989)		
					<i>D. lineosetae</i>	Pulse-structured high frequency clicking sounds.	90.0 (20-21°C)	8300-12500 cps (20-21°C)					Hoikkala et al. (1989)		
					<i>D. fasciculisetae</i>	Pulse-structured high frequency clicking sounds.	9.2 (20-21°C)	frequency range: 500 to > 10000 Hz, dominant frequency: 5500-6000 Hz, 4600-5600 cps (20-21°C)					Hoy et al. (1988), Hoikkala et al. (1989)		
			<i>grimskawai</i> subgroup		<i>D. affinisjuncta</i>	Pulse-structured high frequency clicking sounds.	5.8 (20-21°C)	10100-14100 cps (20-21°C)					Hoikkala et al. (1989)		
					<i>D. disjuncta</i>	Pulse-structured high frequency clicking sounds.	7.3 (20-21°C)	5200-6600 cps (20-21°C)					Hoikkala et al. (1989)		
					<i>D. digressa</i>	Pulse-structured high frequency clicking sounds.	5.6 (20-21°C)	5600-12800 cps (20-21°C)					Hoikkala et al. (1989)		
			<i>planitibia</i> subgroup		<i>D. cyrtoloma</i>	Pulse-structured song and trill (long series of stereotyped sound cycles).	165.64	85.08 Hz							Hoy et al. (1988)
					<i>D. silvestris</i>	Pulse song (generated by abdominal vibrations) and tone song.	45.0-65.9 (20±1°C)	175 Hz		Tone song		169.5 Hz, 90-222 Hz (20±1°C)	Duet		Hoy et al. (1988), Hoikkala and Welbergen (1995)
					<i>D. planitibia</i>	Pulse and humming sounds.	55.2-81.9 (20±1°C)	400-500 Hz (18-19°C)		Humming sound		109-260 Hz (20±1°C), 120-300 Hz (18-19°C)		Hoikkala and Welbergen (1995), Hoikkala and Kaneshiro (1997)	
			<i>repleta</i> group		<i>D. heteroneura</i>		54.5-76.2 (20±1°C)					203-250 Hz (20±1°C)			Hoikkala and Welbergen (1995)
					<i>D. hydei</i>	Two pulse songs (A and B song).	A: 13.6, B: 13.6 (25.5°C)								Ewing (1979), Ewing and Miyan (1986)
					<i>D. eohydei</i>	Two pulse songs (A and B song).	A: 12.6, B: 12.6 (25.5°C)								Ewing (1979), Ewing and Miyan (1986)
<i>D. neohydei</i>	Two pulse songs (A and B song).	A: 11.1, B: 11.1 (25.5°C)										Ewing (1979), Ewing and Miyan (1986)			

<i>Drosophila</i>		<i>Drosophila</i>				
<i>repleta</i> group	<i>mercatorum</i> subgroup	<i>D. mercatorum</i>	Two pulse songs (A and B song). A: 8.2-9.4, B: 52.7-59.5 (25°C), A: 8.6, B: 8.6 (25.5°C)	412.501 Hz (25 ± 1°C)	Ewing (1979), Ikeda et al. (1980), Ewing and Miyan (1986)	
		<i>D. paranaensis</i>	Complex pulse trains. 6.9, 14.4, 19.2 (25.5°C)		Ewing (1979), Ewing and Miyan (1986)	
		<i>D. peninsularis</i>	Two pulse songs (A and B song). A: 14.7, B: 6.8 (25.5°C)		Ewing (1979), Ewing and Miyan (1986)	
	<i>fasciola</i> subgroup	<i>moju</i> complex	<i>D. moju</i>	Simple pulse song. 50.859 (25 ± 1°C)		Costa and Sene (2002)
			<i>D. coroica</i>	Simple pulse song. 99.050-109.101 (25 ± 1°C)	305.459-314.364 Hz (25 ± 1°C)	Costa and Sene (2002)
		<i>D. ellisoni</i>	Short pulses followed by a trill. 97.473 (25 ± 1°C)	251.358 Hz (25 ± 1°C)	Costa and Sene (2002)	
		<i>D. fascioloides</i>	Short pulses followed by a trill. 125.757 (25 ± 1°C)	362.901 Hz (25 ± 1°C)	Costa and Sene (2002)	
		<i>D. onca</i>	Short pulses followed by a trill. 508.091 (25 ± 1°C)	289.26 Hz (25 ± 1°C)	Costa and Sene (2002)	
		<i>D. rosinae</i>	Simple but duplicated pulses. 72.34 (25 ± 1°C)	306.624 Hz (25 ± 1°C)	Costa and Sene (2002)	
	<i>mulleri</i> subgroup	<i>eremophila</i> complex	<i>D. metleri</i>	Pulse song. 35 (24 ± 1°C)		Alonso-Pimental et al. (1995)
			<i>D. eremophila</i>	Pulse song. 32 (24 ± 1°C)		Alonso-Pimental et al. (1995)
			<i>D. micrometleri</i>	Pulse song. 24 (24 ± 1°C)		Alonso-Pimental et al. (1995)
<i>anceps</i> complex		<i>D. nigrospiracula</i>	Pulse song. <10 (24 ± 1°C)		Alonso-Pimental et al. (1995)	
		<i>D. anceps</i>	Two pulse songs (A and B song). A: 9.6, B: 9.6, 23.6, 35.5 (25.5°C)		Ewing (1979), Ewing and Miyan (1986), Alonso-Pimental et al. (1995)	
		<i>D. leonis</i>	Pulse song. <10 (24 ± 1°C)		Alonso-Pimental et al. (1995)	
<i>mojavensis</i> complex		<i>mulleri</i> complex	<i>D. mulleri</i>	Simple pulse trains. 25.9 (25.5°C)		Ewing and Miyan (1986)
			<i>D. aldrichi</i>	Simple pulse trains. 15.8 (25.5°C)		Ewing and Miyan (1986)
		<i>buzzatii</i> complex	Complex pulse trains. 8.1, 12.4 (25.5°C)		Ewing and Miyan (1986)	
		<i>longicornis</i> complex	Simple pulse trains. 6.8 (25.5°C)		Ewing and Miyan (1986)	
		<i>ritae</i> complex	No patterned song.		Ewing and Miyan (1986)	
		<i>mojavensis</i> (arizonae)	Simple pulse trains. 19.8 (25.5°C)		Ewing and Miyan (1986)	

Genus	Subgenus	Species group	Species subgroup/ phylad	Species complex	Species	Description	Pulse song		Sine song		Duet/ female song	Copulatory song	References			
							IPI (ms)	IPF	Description	Frequency						
<i>Drosophila</i>	<i>Drosophila</i>			<i>mojavensis</i> complex	<i>D. mojavensis</i>	Simple pulse trains.	16.8 (25.5°C)						Ewing and Miyan (1986), Etges et al. (2006)			
					<i>D. navojoa</i>	Two pulse songs (A and B song).	A: 9.8, B: 29.7 (25.5°C)					Ewing and Miyan (1986)				
				<i>multeri</i> subgroup	<i>D. stalkerii</i>	Two pulse songs (A and B song).	A: 8.4, B: 17.5 (25.5°C)						Ewing and Miyan (1986)			
					<i>D. meridiana</i>	Two pulse songs (A and B song).	A: 11.0, B: 15.7, 28.7 (25.5°C)						Ewing and Miyan (1986)			
				<i>repleta</i> group	<i>D. meridionalis</i>	Complex pulse trains.	169.80-200.84 (25°C)	433.21-503.91 Hz (25°C)					Costa et al. (2000)			
					<i>D. martensis</i>	Simple pulse trains.	7.1 (25.5°C)						Ewing and Miyan (1986)			
					<i>D. repleta</i>	Simple pulse trains.	11 (25.5°C)						Ewing and Miyan (1986)			
				<i>virilis</i> group	<i>repleta</i> subgroup	<i>D. canapalpa</i> (synonym of <i>neorepleta</i> )	A and B songs	A: 11.6, B: 29.9 (25.5°C)								Ewing and Miyan (1986)
						<i>D. limensis</i>	A and B songs	A: 12.0, B: 12.5 (25.5°C)								Ewing and Miyan (1986)
						<i>D. melanopalpa</i> (synonym of <i>releta</i> )	A and B songs.	A: 12.4, B: 12.4, 25.1, 37.5 (25.5°C)								Ewing and Miyan (1986)
						<i>D. montana</i>	Pulse song.	39.9, 32 (19±1°C)	259 Hz (19±1°C)				Sometimes female song.			Donegan and Ewing (1980), Hoikkala and Lumme (1987), Hoikkala and Suvanto(1999)
				<i>virilis</i> group	<i>montana</i> phylad	<i>D. littoralis</i>	Pulse song and sine song.	323 (21-22°C), 318.9	346 Hz (21-22°C), 278-345 cps (20.5-21.5°C)			The secondary songs classified as sine song.				Donegan and Ewing (1980), Hoikkala and Lumme (1987), Hoikkala and Lumme (1987)
						<i>D. flavomontana</i>	Pulse song and sine song.	99.0			The secondary songs classified as sine song.		Sometimes female song.		Donegan and Ewing (1980), Hoikkala and Lumme (1987), Suvanto et al. (1994)	
						<i>D. lacicola</i>	Pulse song.	81.4							Donegan and Ewing (1980), Hoikkala and Lumme (1987)	



Genus	Subgenus	Species group	Species subgroup/ phylad	Species complex	Species	Description	Pulse song		Sine song		Duet/ female song	Copulatory song	References	
							IPI (ms)	IPF	Description	Frequency				
<i>Drosophila</i>	<i>Drosophila</i>	<i>funnebrus</i> group	<i>funnebrus</i> subgroup		<i>D. funnebrus</i>	One type of pulse songs (primary song).	8.4 (25.5 ± 0.5°C)						Ewing (1979)	
						One type of pulse songs (secondary song).	8.6 (single cycle pulses interspersed in intervals between secondary song), 138.8 (secondary song) (25.5 ± 0.5°C)					Ewing (1979)		
		<i>funnebrus</i> group	<i>macrospina</i> subgroup		<i>D. m. macrospina</i>	Two types of pulse songs (primary and secondary songs).	Primary song: 12.3, Secondary song: 75.0 (25.5 ± 0.5°C)							Ewing (1979)
						Two types of pulse songs (primary and secondary songs).	Primary song: 10.7, Secondary song: 64.4 (25.5 ± 0.5°C)					Ewing (1979)		
						Two types of pulse songs (primary and secondary songs).	Primary song: 9.9, Secondary song: varied 26.7–17.1–41.6–52.6 (25.5 ± 0.5°C)					Ewing (1979)		
						Only one type of song. Copulatory song.	367.55 (21 ± 1°C)	263.19 Hz (21 ± 1°C)			Sing during copulation and little singing before mounting.	Neems et al. (1997)		
		<i>quinaria</i> group			<i>D. kuntzei</i>	Only one type of song.	12.71–14.33 (21 ± 1°C)	255–270 Hz (21 ± 1°C)						Neems et al. (1997)
						Only one type of song.	14.76–16.39 (21 ± 1°C)	245–265 Hz (21 ± 1°C)				Neems et al. (1997)		
						Only one type of song.	29.51–40.56 (21 ± 1°C)	292–306 Hz (21 ± 1°C)				Neems et al. (1997)		
						No wing vibration/display.						Tomaru et al. (2006)		
<i>Zaprionus</i>	<i>Zaprionus</i>	<i>armatus</i> group	<i>tuberculatus</i> subgroup		<i>Z. tuberculatus</i>	Type 1 (monocyclic), Type 2 (mono or polycyclic).	Type 1: 12.4 (18–20°C) Type 2: 26.6 (18–20°C) Type 1: 10.7 (24–26°C) Type 2: 28.9 (24–26°C)	Type 2: 170 Hz (24–26°C)			Two types of songs, pulse and continuous tone sound.	Bennet-Clark et al. (1980)		



Genus	Subgenus	Species group	Species subgroup/ phylad	Species complex	Species	Description	Pulse song		Sine song		Duet/ female song	Copulatory song	References		
							IPI (ms)	IPF	Description	Frequency					
<i>Drosophila</i>	<i>Sophophora</i>	<i>affinis</i> subgroup			<i>D. toleuca</i>	Two types of sounds (Low and High pulse repetition rate sounds).	Low pulse repetition rate sound: 507.9–666.7 Hz, High pulse repetition rate sounds: 727.7 Hz (22–26°C)						Chang and Miller (1978)		
						One type of pulse song (low rate repetition sound).	437.5–509.8 Hz (22–26°C)				Chang and Miller (1978)				
						Similar to that of <i>D. pseudoobscura</i> .	171, 38.4 (25°C)			Ewing and Bennet-Clark (1968)					
		<i>obscura</i> group	<i>obscura</i> subgroup		<i>D. pseudoobscura</i> subgroup		<i>D. ambigua</i>	LRR & HRR.	186, 37.9 (25°C) HRR: 42.6, LRR: 15 pulses/s (23°C)					Ewing and Bennet-Clark (1968), Ewing (1969)	
								LRR & HRR.	53.7 (25°C), HRR: 66.8, LRR: omitted or very few pulses (23°C)				Ewing and Bennet-Clark (1968), Ewing (1969)		
								Wing spread horizontally, but no vibration/sound detected.				Ewing and Bennet-Clark (1968)			
		<i>melanogaster</i> group	<i>subobscura</i> subgroup		<i>ananassae</i> complex		<i>D. subobscura</i>	Pulse song.	10.30–11.27 (25±1°C), 3–11 (25°C)						Ewing and Bennet-Clark (1968), Yamada et al. (2002b)
								Pulse song.	10.25–11.22 (25±1°C)				Yamada et al. (2002b)		
								Two pulse songs (short and long songs).	8.38 (25°C), Short song: 10.1, Long song: 11.0 (22±1°C)				Ewing and Bennet-Clark (1968), Crossley (1986)		
		<i>melanogaster</i> group	<i>ananassae</i> subgroup		<i>bipunctinata</i> complex		<i>D. bipunctinata</i>	Two pulse songs (short and long songs).	Short song: 12.8, Long song: 14.1 (22±1°C)						Crossley (1986)
								Two pulse songs (short and long songs).	Short song: 13.6, Long song: 11.0 (22±1°C)				Crossley (1986)		
								Two pulse songs (short and long songs).	Short song: 9.2, Long song: 9.6 (22±1°C)				Crossley (1986)		
		<i>melanogaster</i> group	<i>elegans</i> subgroup				<i>D. malerkotliana</i>	Spotted wings. Wing display.							Kopp and True (2002)
								Pulse and sine songs.	33.8 (25°C), 30.8 (25±0.5°C)				169.9 Hz (25 ± 0.5°C)	Ewing and Bennet-Clark (1968), Cowling and Burnet (1981)	



Genus	Subgenus	Species group	Species subgroup/ phylad	Species complex	Species	Description	Pulse song		Sine song		Duet/ female song	Copulatory song	References				
							IPI (ms)	IPF	Description	Frequency							
<i>Drosophila</i>	<i>Sophophora</i>	<i>melanogaster</i> group	<i>auraria</i> complex	<i>auraria</i> complex	<i>D. quadraria</i>	Pulse song, copulatory song.	15.6 (24–25°C)	128.9 Hz (24–25°C)				before mounting and during/after mounting	Tomaru and Oguma (1994a)				
					<i>D. lini</i>	Pulse and sine songs, copulatory song.	82.85 (23±1°C)			253.4 Hz (23±1°C)				Only during/after mounting	Wen et al. (2011)		
					<i>D. ohmishii</i>	Pulse and sine songs, copulatory song.	86.75 (23±1°C)				193.0 Hz (23±1°C)				Only during/after mounting	Wen et al. (2011)	
			<i>montium</i> subgroup	<i>kikkawai</i> complex	<i>D. ogumai</i>	Pulse and sine songs, copulatory song.	88.91 (23±1°C)							Only during/after mounting	Wen et al. (2011)		
					<i>D. birchii</i>	Most males produced only one song that is no-pulse structured, resembled sine song more than pulse song. Some males had a clear pulse structure sounds.	14 (24–26°C)	400–450 Hz (24–26°C)		150–160 Hz (24–26°C)				Only during/after mounting	Hoikkala and Crossley (2000)		
					<i>D. serrata</i>		28.0–35.5 (24–26°C)	400–450 Hz (24–26°C)		140 Hz (24–26°C)				Only during/after mounting	Hoikkala and Crossley (2000)		
			<i>suzukii</i> subgroup	<i>serrata</i> complex	<i>D. suzukii</i>	Spotted wings. Wing display, but no vibration.										Kopp and True (2002)	
					<i>D. pulchrella</i>	Spotted wings. Wing display. High amplitude, nonrhythmic “foot” sounds, 422–479 Hz.											Kopp and True (2002), Lai et al. (2009)
					<i>D. biarmipes</i>	Spotted wings. Wing display. High amplitude, nonrhythmic “foot” sounds, 259–352 Hz.											Kopp and True (2002), Lai et al. (2009)
					<i>D. prostipennis</i>	Spotted wings. Wing display. Short, high frequency pulse structured song. All species have pulse song, but some species have multiple song types.	4	520 Hz									Kopp and True (2002), Lai et al. (2009)
			<i>willisloni</i> group													Gleason and Ritchie (1998)	



tivity (Bennet-Clark and Ewing, 1967; von Schilcher, 1976a, b; Crossley and Bennet-Clark 1993; Crossley et al., 1995), (2) increase male activity (von Schilcher, 1976a; Crossley et al., 1995; Eberl et al., 1997), (3) act as an indicator for sexual selection, (4) provide species specific signals for mating with an appropriate partner.

Although the first role is suggested in both sine and pulse songs in *D. melanogaster* (von Schilcher, 1976a, b; Crossley et al., 1995), pulse song acts as a critical signal in species recognition. As shown by playback song experiments, species specific interpulse interval is a parameter fascinating to females in the *melanogaster* subgroup (Bennet-Clark and Ewing, 1969; von Schilcher, 1976a, b), the *D. (S.) auraria* species complex of the *montium* subgroup (Tomaru et al., 1995) and the *virilis* group (Isoherranen et al., 1999b; Saarikettu et al., 2005). These findings mean that the interpulse interval is one of the critical signals to maintain species and isolate different species. Although mate recognition is performed by both sexes, usually males act first in the courtship of *Drosophila*. Males choose a mate by assessing signals emitted from females; a well-known signal is female cuticular hydrocarbons that function as a sex pheromone. The females then decide to accept or reject male courtship by examining a male-producing signal; a well-known signal is male courtship songs.

Interpulse intervals are reported to vary within a series of songs in the species of the *melanogaster* subgroup and the *pseudoobscura* subgroup (Kyriacou and Hall, 1980; Alt et al., 1998; Noor and Aquadro, 1998; Demetriades et al., 1999). The fluctuating cycle of interpulse interval variation within an individual is thought to be important for mating in the *melanogaster* subgroup (Kyriacou and Hall, 1982; Ritchie et al., 1999), but not likely in the *pseudoobscura* subgroup (Noor and Aquadro, 1998).

Importance and effects of conspecific and heterospecific songs differ depending on the species. In some cases, heterospecific songs are more important to avoid an inappropriate mate and conspecific song is not necessarily needed for a successful mating, for example, a species pair of *D. (S.) ananassae* and *D. (S.) pallidosa* (Yamada et al., 2002a, 2008), the *auraria* complex (Tomaru et al., 1995, 1998), *D. virilis* and *D. littoralis* (Hoikkala and Aspi, 1993; Isoherranen et al., 1999a). Even in such species, conspecific acoustic signals have a role in enhancing female receptivity.

In some other cases, the priority of conspecific song is very high, for example, *D. (D.) montana* (Liimatainen et al., 1992; Hoikkala and Aspi, 1993), *D. (D.) ezoana* (Hoikkala and Aspi, 1993), *D. (Dorsilopha) busckii* (Bixler et al., 1992), *D. sechellia* (Tomaru et al., 2000, 2004) and one of the strains of *D. pallidosa* (Doi et al., 2001); they do not mate without conspecific songs. In other cases, species specificity in song parameters is not critical but facilitates faster mating.

### 3.4 Copulating songs

Males of the majority of *Drosophila* species produce songs during courtship rituals before mounting females. Some species, however, are known to show copulatory courtship (Spieth, 1952); they produce songs during mounting (when a male is trying to get on a female) and after mounting (when he is completely on her). Most of the species showing copulatory courtship belong to the *montium* subgroup, including the species of the *auraria* complex (Tomaru and Oguma, 1994a, 1994b), of the *lini* clade in the *kikkawai* complex (Wen et al., 2011) and of the *D. (S.) serrata* species complex (Hoikkala and Crossley, 2000). Outside the *montium* subgroup, copulating songs are reported in *D. (S.) algonquin* from the *affinis* subgroup (Chang and Miller, 1978). Copulating songs were also reported in two species from the *melanogaster* subgroup, *D. sechellia* and *D. orena*, but it is not clear which sex produces the sounds (Cobb et al., 1989).

Within the species producing copulating songs, some species produce songs before and during/after mounting and the others only during/after mounting. Those which produce songs before and during/after mounting are species of the *auraria* complex (Tomaru and Oguma, 1994a, 1994b) and *D. algonquin* (Chang and Miller, 1978). In contrast, three species of the *lini* clade and two species of the *serrata* complex usually do not produce songs before mounting, but do only during/after mounting. In these species, a female receives acoustic signals only after mounting. If she judges that a mounting male is not an appropriate mate, she refuses him physically, for example, by fluttering and kicking. The situation in species of the *serrata* complex and the *lini* clade looks the same, but the significance of the songs is very different. Courtship song is unlikely to be a critical factor in the discrimination between *D. serrata* and *D. birchii*, because the females discriminate against wingless males (i.e., no wing vibrations, no songs) during copulation (Hoikkala and Crossley, 2000). On the other

hand, in the three species of the *lini* clade, male songs emitted during/after mounting seem to be critical in mate discrimination (Oguma et al., 1995; Wen et al., 2011), even though they are produced only after mounting.

### 3.5 Rejecting sounds by females

In contrast to males, females usually do not emit specific sounds (Ewing and Bennet-Clark, 1968). Although female wing movements such as fluttering produce sounds, they are usually not a constant acoustic signal but rather irregular sound noise, often louder than male courtship songs (our observations). These sound noises are considered a signal of rejection. Such wing fluttering is observed in many species (Ewing and Bennet-Clark, 1968; Ikeda, 1985; Crossley, 1986; Paillette et al., 1991; Satokangas et al., 1994; Suvanto et al., 1994; Oguma et al., 1995; Tomaru et al., 1998; Yamada et al., 2008). Female wing fluttering was observed especially in heterospecific pairs between species of the *lini* clade in the *kikkawai* complex (Oguma et al., 1995; Wen et al., 2011), the *auraria* complex (Tomaru et al., 1998) and the *D. (S.) ananassae* species complex (Yamada et al., 2008); furthermore, the flutterings cause male courtship termination (Yamada et al., 2008). This behaviour is observed among not only females but also males (Ikeda 1985; Paillette et al., 1991; Satokangas et al., 1994; Suvanto et al., 1994; Saarikettu et al., 2005; Yamada et al., 2008). Therefore, fluttering and its effect are likely to be universal between species and sexes in *Drosophila*, but it is not known which signals emitted by the fluttering are effective among acoustic, visual and pressure sense.

### 3.6 Female song: duet

Females of species in the *virilis* group (*D. americana*, *D. kanekoi*, *D. borealis*, *D. lummei*, *D. ezoana*, *D. montana*, *D. virilis*, *D. flavomontana*, *D. lacicola* and *D. littoralis*) are known to produce songs called “duet”, because both males and females produce songs during courtship (Donegan and Ewing, 1980; Hoikkala, 1985). Donegan and Ewing (1980) reported that the female started singing before the male. The female song has a role to induce the males to court. Actually, the female does not repel a male after producing the songs and immediately accepts a courting male (Satokangas et al., 1994). The female song observed in the *virilis* group is not common in the genus *Drosophila*, but similar female songs are known in species of the genus *Zaprionus*, a close relative of the

genus *Drosophila* (Bennet-Clark et al., 1980).

### 3.7 Sounds produced not by wing vibration

Insects are known to use various organs to produce sounds for communication (Ewing, 1989). *Drosophila* males produce courtship songs by wing vibrations, but there are exceptional instances where organs other than the wings are used. Hawaiian *Drosophila* species produce much higher carrier frequency sounds that range from 500 Hz to greater than 10 kHz (Hoy et al., 1988; Hoikkala et al., 1989), while the songs of most *Drosophila* are less than 500 Hz. In one of the Hawaiian *Drosophila* species, *D. fasciculisetae*, males vibrate their wings when they produce sounds, but those sounds are not produced by movements of the entire wing vane because the sounds were generated even when the wings were removed (Hoy et al., 1988). *Drosophila silvestris*, another Hawaiian *Drosophila*, produces pulse song and tone song; the pulse song is generated by low-amplitude abdominal vibration (Hoy et al., 1988).

The auditory organs of flies are considered to be arista and Johnston’s organs inside antennae. As the range of frequencies those organs can perceive is between 150 and 500 Hz (Ewing, 1978), the high frequencies observed in the songs of the Hawaiian *Drosophila* exceed the hearing ability by the organs. Hoikkala and Moro (2000) examined the body structures of flies by scanning electron microscopy and found several features on the legs and wings sensilla which could play a part in sound/vibration perception, although it is not known if these structures function to hear the sounds or not.

### 3.8 Genetic basis of courtship song

Courtship songs are described in many species of *Drosophila* (Table 1), but extensive analyses of behaviour, genetics and evolution have been done only in some species groups including the *melanogaster* subgroup, the *virilis* group, the *auraria* complex and the *pseudoobscura* subgroup. Mutations and the genetic basis of courtship songs were reviewed by Gleason (2005).

Here we deal with the *period* gene for an example. Fluctuation cycle of interpulse interval (IPI cycle or Kyriacou and Hall cycle [K&H cycle]) is controlled by a circadian clock gene, *period* (*per*) (Kyriacou and Hall, 1980, 1986; Demetriades et al., 1999; Ritchie et al., 1999). The IPI cycle is shorter in *per<sup>s</sup>*, an allele that shortens circadian periods, longer

in *per<sup>l</sup>*, an allele that prolongs circadian periods, and arrhythmic in *per<sup>o</sup>*, an allele of arrhythmic circadian periods. It should be noted that the *period* gene does not affect the average value of interpulse interval, indicating that interpulse interval is not determined by the *period* gene.

#### 4. Hearing of songs

Many insects produce sounds in various ways to communicate between individuals, sexes and species. Mechanisms of sound generation are classified into several types: percussion, air expulsion, vibration, tymbal mechanisms and stridulation (Ewing, 1989). A mechanism most *Drosophila* species use is the vibration of their wings. This is typical not only in the genus *Drosophila*, but also in the order Diptera (Ewing, 1989). As the characteristics of a sound depend on the organ generating it, hearing ability and character depend on the hearing organ. Major hearing organs of insects are tympanal and flagellar organs. Tympanal organs are sound pressure detectors, which are good at detecting long distance sounds and wide range of frequencies such as 3 to 150 kHz (Ewing, 1989). On the other hand, flagellar organs are particle velocity detectors suitable for detecting near field sounds (Bennet-Clark, 1971; Eberl, 1999). Crickets, one of the insects that have the tympanal organs, sing a call song that is loud and high in frequency (more than 10 kHz) from a long distance, but flies usually do not produce such a call song. Flies in the genus *Drosophila* sing small sound courtship songs that are emitted from near field distance as they can touch and that we cannot hear without amplification.

The auditory organs in *Drosophila* are the flagellar type organs consisted from an arista that is the 6th branch of antennae and Johnston's organ located inside the second segment of antennae (Todi et al., 2004). The courtship songs are low frequency sounds of less than 500 Hz. Furthermore, females whose aristae were surgically removed showed reduced sexual receptivity in conspecific crosses (Manning, 1967; Tomaru et al., 1998; Tomaru et al., 2000; Doi et al., 2001; Yamada et al., 2008). These results indicate that the aristae and Johnston's organs are the receptors for courtship songs. Direct electrophysiological experiments using *D. funebris* showed that the antennae (including the aristae and Johnston's organ) of *Drosophila* can detect acoustic signals such as sine and

pulse songs; then the organs could detect species differences in interpulse intervals (Ewing, 1978). Eberl et al. (2000) examined electrophysiological responses of the antennae using *D. melanogaster*. They can respond to simulated sine songs of 160 and 250 Hz, but their response to a 500 Hz sine song was very poor. Sine song frequencies of the species in the *melanogaster* subgroup are 100–350 Hz (Cowling and Burnet, 1981; Cobb et al., 1989). Frequency responses are well tuned by physical structures of antennae, neural inputs of sound signals and projection to the center, and highly adapted for songs (Göpfert and Robert, 2001, 2002; Kamikouchi et al., 2009; Yorozu et al., 2009). From these lines of evidence, the aristae and Johnston's organs are well tuned to detect courtship sounds, or it can be said that males produce songs tuned to female hearing ability.

#### 5. Courtship without song

Although vibration is most noticeable in the courtship of *D. melanogaster* (Sturtevant, 1915), there are a number of species in which the males do not vibrate to produce sounds (Table 1). In species without songs, it is very likely that there is a courtship signal from males to females. In some species, males have a remarkable black spot on the tip of each wing. The spots seem to be an important visual signal in courtship. Species with spotted wings are found in the *elegans*, the *rhopaloa*, the *suzukii* and the *takahashii* species subgroups of the *melanogaster* group (Kopp and True, 2002; Yeh et al., 2006). However, not all male members of these subgroups have spotted wings. During courtship, the male of a species with spotted wings spread his wings in front of the courting female as if to display the spots (Fig. 1C). In contrast, this display behaviour is less frequently found, or absent, in related species without spots. This behavioural difference suggests that the wing spots are an important visual signal during courtship. One such species is *D. suzukii*, a pest of plants, especially cherries, berries and other skinny fruits (Matsumura, 1931; Baufeld et al., 2010; Walsh et al., 2010). Males whose wing spots were surgically removed showed reduced copulation frequency compared with intact males, but there was no significant difference in copulation frequency when the experiments were done in the dark (Fuyama, 1979). Males of *D. pulchrella*, a spotted wing species of the *suzukii* subgroup, produced high

amplitude, nonrhythmic toot sounds (Lai et al., 2009), suggesting that not only a visual signal but also sounds may play a role in the courtship of this species.

In *D. (D.) quadrilineata*, the male bends his abdomen and points its tip towards a courting female (Tomaru et al., 2006). The male never vibrates or displays his wings during courtship but frequently bends his abdomen (Fig. 1D). Although the abdomen bending can be a visual signal from a male to a female, the male may discharge volatile sex pheromones while bending his abdomen. A culture vial of this species has a characteristic odour and human observers can distinguish between a vial that has been housed with males and that with females. Behavioural assays will clarify whether or not volatile male sex pheromones are involved in the courtship of *D. quadrilineata*.

In Hawaiian *Drosophila*, males' liquid pheromones seem to play a role in courtship. Males of some species excrete a liquid from their anus onto the lek substrate, and in other species males drag the tip of their abdomen to advertise their presence to females (Spieth, 1984). Again the odour can be detected by the human nose. In addition, males of some species curl the abdomen up and forward and direct its tip towards the females' face during their courtship. The droplet is, therefore, released very close to the antennae of the females. In other species, males release a liquid during courtship and vibrate their wing as if fanning the odour to the females.

## 6. Sex pheromone

Cuticular hydrocarbons cover the insect body (Blomquist, 2010). They are long chain molecules and less volatile, and protect insects from desiccation and water. The components of cuticular hydrocarbons are classified into n-alkenes, methyl-branched components and unsaturated hydrocarbons. The role of cuticular hydrocarbons, their biosynthesis, their production and their detection have been best studied in *Drosophila* (Ferveur and Cobb, 2010). The contents of cuticular hydrocarbons differ between species and/or sexes. In *Drosophila*, species specific and/or sex specific unsaturated cuticular hydrocarbons play a role in contact sex pheromones. Ferveur and Cobb (2010) recently reviewed the behavioural and evolutionary roles of cuticular hydrocarbons, and Wicker-Thomas and Chertemps (2010) did the genetics and

biosynthesis.

A female sex pheromone of *Drosophila* was first identified in *D. melanogaster* (Antony et al., 1985). It is (Z,Z)-7,11-heptacosadiene, a long chain diene (C<sub>27:2</sub>) and a major component of cuticular hydrocarbons in *D. melanogaster* females, and acts as a sex pheromone. Although some species have sexually monomorphic cuticular hydrocarbons, *D. melanogaster* is a sexually dimorphic species. A major component of males of *D. melanogaster* is (Z)-7-tricosene (C<sub>23</sub>). Sexual monomorphisms and dimorphisms do not reflect the phylogenetic relationships of the species concerned. The three species *D. simulans*, *D. mauritiana* and *D. sechellia* are closely related and members of the sister group of *D. melanogaster*. In *D. simulans* and *D. mauritiana*, both sexes have (Z)-7-tricosene (Cobb and Jallon, 1990), whereas *D. sechellia* is a sexual dimorphic species, males having (Z)-6-tricosene, a position isomer of (Z)-7-tricosene and females (Z,Z)-7,11-heptacosadiene (Cobb et al., 1989). Sex pheromones identified by using synthetic monoene or dienes are (Z)-11-pentacosene (C<sub>25</sub>) of *D. virilis* (Oguma et al., 1992; Doi et al., 1996), (Z,Z)-5,27-tritriacontadien (C<sub>33:2</sub>) of *D. pallidosa* (Nemoto et al., 1994) and (Z,Z)-5,25-hentriacontadien (C<sub>31:2</sub>) of *D. ananassae* (Doi et al., 1997). Cuticular hydrocarbons of *Drosophila* were reviewed by Ferveur (2005).

Males' cuticular hydrocarbons are species specific and sexual dimorphisms are found in some species. Therefore, cuticular hydrocarbons of males can act as a sex pheromone. In *D. melanogaster*, (Z)-7-tricosene, a major component of cuticular hydrocarbons of males, affects mating of females (Grillet et al., 2006). Mating was enhanced by larger amounts of (Z)-7-tricosene from males with a GS10164 insertion driven by GAL4 compared with reduced (Z)-7-tricosene from *desat1<sup>1573-1</sup>* mutant males. Females whose antennae were surgically removed showed reduced mating, suggesting that females perceive male sex pheromones via antennae.

## 7. Mounting position and copulation

Spieth (1952) named two mounting positions, forward and rearward, and unnamed for a few exceptional species. The forward position is a type observed in *D. melanogaster*. A male places his forelegs at the base of the wings of a female or grasps her

thorax with his forelegs, grasps her abdomen with his middle legs, and lays his hindlegs on the substrate or grasps her abdomen. This mounting position seems to be primitive. The other type, the rearward position, is thought to be derived and seen in most species of the subgenus *Drosophila* and some species of the subgenus *Sophophora*. A male grasps a female's abdomen or wing tips with his forelegs and grasps her abdomen with his middle and/or hindlegs. Although there have been many reports describing the courtship behaviour, the mounting position is poorly described and clear descriptions were not found in many cases.

Positions of mounting and copulation are symmetric, that is, the axis of both sexes coincides. However, in *D. melanogaster*, the removal of a single sensillum of male genitalia affects the mating position and results in a contralateral asymmetry in the male's mating posture (Acebes et al., 2003). Although this sensillum affects the symmetry of the mounting position, the male seems to mount in the forward position, judging from the photograph in Figure 2 in Acebes et al. (2003).

Copulation or intromission is achieved before or after a male mounts a female. In the description of Spieth (1952), all species belonging to the subgenus *Drosophila* are classified as intromission after mounting, or no description. Most species of subgenus *Sophophora* are in the intromission before mounting or at the same time. Exceptional species in *Sophophora* are those belonging to the *montium* subgroup, *D. auraria*, *D. rufa* and *D. montium*, and *D. ananassae* of the *ananassae* subgroup; they are the species of the intromission after mounting. Copulation after mounting was observed in other species (*D. serrata*, *D. birchii*, *D. lini*, *D. ohnishii* and *D. ogumai*) of the *montium* subgroup (Hoikkala and Crossley, 2000; Wen et al., 2011).

Spieth (1952) suggested that there is a relationship between the male's grasping of the female and the presence of spines that species of the *immigrans* group have on the inside of the fore femur. Similar spines on the fore femur are also found in the genus *Zaprionus*. In the courtship behaviour of *D. silvestris*, a Hawaiian *Drosophila*, Carson (2002) argued for the importance of tactile stimulus from the male. The male of *D. silvestris* actively drums the tibial bristles (cilia) on the dorsal surface of the female's abdomen. Males of *D. mojavensis* drum continuously upon the underside of the female's abdomen using their fore

tarsi (Krebs and Bean, 1991), suggesting the importance of tactile stimuli as well as courtship songs in this species.

## 8. Conclusion

The female does not play a passive role in courtship as was pointed out in the first report of courtship behaviour in *Drosophila* (Sturtevant, 1915). Since the male behaviour is a response to female sex pheromones, a male may be evaluated by a female in his ability of wing vibrations and following (Ferveur and Cobb, 2010). Before mounting, a female moves slowly as if the courting male can easily approach her. In response to courtship songs, a female spreads both her wings when she accepts the courting male in some species (Ikeda et al., 1981; Oguma et al., 1996; Vuoristo et al., 1996). In contrast, sometimes the female moves rapidly and escapes from the male. The female often kicks the male and/or produces rejecting sounds when he attempts to copulate. Females of the *virilis* group produce a song when accepting a courting male. In species in which the males hold territories, females visit a territory or a lek to choose their partner. Decision making based on a male's visual signal is also shown in *D. suzukii* females. In species in which the males produce sounds during courtship, songs seem to be a critical signal affecting the female's decision making. The females do not learn how to choose a partner; decision making to choose partners and its species specificity are genetically determined (Pifheiro et al., 1993; Isoherranen et al., 1999a; Doi et al., 2001).

The general structure and/or overall shape of courtship songs are similar within closely related species but the song parameters differ. For example, between *D. melanogaster* and *D. simulans*, some song parameters, such as interpulse interval, intrapulse frequency and sine song frequency, differ. In some cases, a gain or loss of song type is found. In the *melanogaster* subgroup, males emit a pulse song and a sine song, but *D. sechellia*, *D. yakuba* and *D. santomea* do not have a sine song. In the *virilis* group, male songs are polycyclic and females also sing. In contrast, a different but similar structure is found in distantly related species. The males of *D. lini* and related species in the *kikkawai* complex produce pulse and sine songs, although the overall shape of the courtship song of the *lini* clade is different from that

of *D. melanogaster*. In most cases, songs are species specific in terms of parameters (Table 1). In the case of closely related species that share similar values of sound parameters, they are allopatrically distributed (Tomaru et al., 1994a; Wen et al., 2011). Based on circumstantial evidence, courtship songs play an important role in sexual isolation between sympatric species and could be shaped by the process of reinforcement and/or reproductive character displacement.

Courtship songs are related not only to species recognition between species but also to sexual selection within species. Female choice based on the male's signal is observed, but it is not easy to figure out the evolutionary cause of female choice. Cost of mating is reported in *Drosophila* (e.g., Ueyama and Fuyama, 2003); however, it is poorly known how the females evaluate the quality of the courting males based on the male's signal (Chapman, 2006). Experiments were carried out to compare mating frequencies between intact males and males whose wings were partly removed in *D. melanogaster* (Robertson, 1982), *D. littoralis*, *D. montana* and *D. ezoana* (Hoikkala and Aspi, 1993). Females preferred intact or long-winged males better. Examination with wild caught females also showed preference to males that produced short pulses with high frequency songs (Aspi and Hoikkala, 1995). Variations are observed in male song parameters and in mate preference of females within species (Ritchie et al., 2005). Playback tests using artificially synthesised songs revealed that *D. montana* females preferred songs with a short pulse length and high pulse frequency (Ritchie et al., 1998). Furthermore, their preferences were not absolute but rather relative (Hoikkala and Aspi, 1993). Females choose males with high frequency songs (Hoikkala and Suvanto, 1999) and egg-to-adult survival rates positively correlate with the pulse frequency of the father's song in *D. montana* (Hoikkala et al., 1998); these results indicate that females obtain an indirect benefit by choosing males based on songs. Song divergence is not correlated with genetic divergence in the *D. (S.) willistoni* species complex, suggesting rapid evolution of song parameters (Gleason and Ritchie, 1998). Sexual selection seems to contribute, at least partly, to the evolution of species specific courtship songs.

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## References

- Acebes, A., M. Cobb, and J.-F. Ferveur (2003) Species-specific effects of single sensillum ablation on mating position in *Drosophila*. *J. Exp. Biol.*, **206**, 3095–3100.
- Alonso-Pimentel, H., H. G. Spangler, and W. B. Heed (1995) Courtship sounds and behaviour of the two saguaro-breeding *Drosophila* and the relatives. *Anim. Behav.*, **50**, 1031–1039.
- Alt, S., J. Ringo, B. Talyn, W. Bray, and H. Dowse (1998) The *period* gene controls courtship song cycles in *Drosophila melanogaster*. *Anim. Behav.*, **56**, 87–97.
- Antony, C., T. L. Davis, D. A. Carlson, J.-M. Pechine, and J.-M. Jallon (1985) Compared behavioral responses of male *Drosophila melanogaster* (Canton S) to natural and synthetic aphrodisiacs. *J. Chem. Ecol.*, **11**, 1617–1629.
- Asada, N., K. Fujiwara, H. Ikeda, and F. Hihara (1992) Mating behavior in three species of the *Drosophila hypocausta* subgroup. *Zool. Sci.*, **9**, 397–404.
- Aspi, J., and A. Hoikkala (1995) Male mating success and survival in the field with respect to size and courtship song characters in *Drosophila littoralis* and *D. montana* (Diptera: Drosophilidae). *J. Insect Behav.*, **8**, 67–87.
- Baufeld, P., G. Schrader, and J.-G. Unger (2010) Die Kirschessigfliege - *Drosophila suzukii* - Ein neues Risiko für den Obst- und Weinbau (The Cherry vinegar fly - *Drosophila suzukii* - An emerging risk for fruit and wine growing). *J. Kult. pflanzen*, **62**, 2–5. (With an English abstract)
- Bennet-Clark, H. C. (1971) Acoustics of insect song. *Nature*, **234**, 255–259.
- Bennet-Clark, H. C., and A. W. Ewing (1967) Stimuli provided by courtship of male *Drosophila melanogaster*. *Nature*, **215**, 669–671.
- Bennet-Clark, H. C., and A. W. Ewing (1969) Pulse interval as a critical parameter in the courtship song of *Drosophila melanogaster*. *Anim. Behav.*, **17**, 755–759.
- Bennet-Clark, H. C., Y. Leroy, and L. Tsacas (1980) Species and sex-specific songs and courtship behaviour in the genus *Zaprionus* (Diptera-Drosophilidae). *Anim. Behav.*, **28**, 230–255.
- Bixler, A., J. B. Jenkins, L. Tompkins, and P. McRobert (1992) Identification of acoustic stimuli that mediate sexual behavior in *Drosophila busckii* (Diptera; Drosophilidae). *J. Insect Behav.*, **5**, 469–478.
- Blomquist, G. J. (2010) Structure and analysis of insect hydrocarbons. In: Blomquist, G. J., and A.-G. Bagnères (eds) *Insect Hydrocarbons: Biology, Biochemistry, and Chemical Ecology*: 19–34. Cambridge University Press,

- Cambridge.
- Blyth, J. E., D. Lachaise, and M. G. Ritchie (2008) Divergence in multiple courtship song traits between *Drosophila santomea* and *D. yakuba*. *Ethology*, **114**, 728–736.
- Carson, H. L. (1971) The ecology of *Drosophila* breeding sites. *Harold L. Lyon Arboretum Lecture No.2*, 1–27.
- Carson, H. L. (2002) Female choice in *Drosophila*: evidence from Hawaii and implications for evolutionary biology. *Genetica*, **116**, 383–393.
- Chang, H.-C., and D. D. Miller (1978) Courtship and mating sounds in species of the *Drosophila affinis* subgroup. *Evolution*, **32**, 540–550.
- Chapman, T. (2006) Evolutionary conflicts of interest between males and females. *Curr. Biol.* **16**, R744–R754.
- Choo, J. K., and K. Nakamura (1973) On a new species of *Drosophila* (*Sophophora*) from Japan (Diptera). *Kontyû*, **41**, 305–306.
- Cobb, M., B. Burnet, R. Blizard, and J.-M. Jallon (1989) Courtship in *Drosophila sechellia*: its structure, functional aspects, and relationship to those of other members of the *Drosophila melanogaster* species subgroup. *J. Insect Behav.*, **2**, 63–89.
- Cobb, M., and J.-M. Jallon (1990). Pheromones, mate recognition and courtship stimulation in the *Drosophila melanogaster* species subgroup. *Anim. Behav.*, **39**, 1058–1067.
- Costa, C. T. A., G. C. S. Kuhn, and F. M. Sene (2000) Low courtship song variation in South and *Drosophila meridionalis* (Diptera, Drosophilidae). *Rev. Bras. Biol.*, **60**, 53–61.
- Costa, C. T. A., and F. M. Sene (2002) Characterization of courtship sounds of species of the subgroup *fasciola* (Diptera, Drosophilidae, *Drosophila repleta* group): interspecific and interpopulational analyses. *Braz. J. Biol.*, **62**, 573–583.
- Cowling, D. E., and B. Burnet (1981) Courtship songs and genetic control of their acoustic characteristics in sibling species of the *Drosophila melanogaster* subgroup. *Anim. Behav.*, **29**, 924–935.
- Crossley, S. A. (1986) Courtship sounds and behaviour in the four species of the *Drosophila bipectinata* complex. *Anim. Behav.*, **34**, 1146–1159.
- Crossley, S. A. (1989) The place of insect behaviour genetics in psychology with a special emphasis on teaching. In: Bond, N. W., and D. A. T. Siddle (eds) *Psychobiology: issues and applications*: 549–559. Elsevier Science Publishers, Amsterdam.
- Crossley, S. A. (1990) *Drosophila* pulse and sine songs and their evolution. *Behav. Genet.*, **20**, 714.
- Crossley, S., and H. C. Bennet-Clark (1993). The response of *Drosophila parabiplectinata* to simulated courtship songs. *Anim. Behav.*, **45**, 559–570.
- Crossley, S., H. C. Bennet-Clark, and H. T. Evert (1995) Courtship song components affect male and female *Drosophila* differently. *Anim. Behav.* **50**, 827–839.
- Demetriades, M. C., J. R. Thackeray, and C. P. Kyriacou (1999) Courtship song rhythms in *Drosophila yakuba*. *Anim. Behav.*, **57**, 379–386.
- Doi, M., M. Matsuda, M. Tomaru, H. Matsubayashi, and Y. Oguma (2001) A locus for female discrimination behavior causing sexual isolation in *Drosophila*. *Proc. Natl. Acad. Sci., USA*, **98**, 6714–6719.
- Doi, M., T. Nemoto, H. Nakanishi, Y. Kuwahara, and Y. Oguma (1997) Behavioral response of males to major sex pheromone component, (Z,Z)-5,25-hentriacontadien, of *Drosophila ananassae* females. *J. Chem. Ecol.*, **23**, 2067–2078.
- Doi, M., M. Tomaru, H. Matsubayashi, K. Yamanoi, and Y. Oguma (1996) Genetic analysis of *Drosophila virilis* sex pheromone: genetic mapping of the locus producing (Z)-11-pentacosene. *Genet. Res.*, **68**, 17–21.
- Donegan, J., and A. W. Ewing (1980) Duetting in *Drosophila* and *Zaprionus* species. *Anim. Behav.*, **28**, 1289.
- Eberl, D. F. (1999) Feeling the vibes: chordotonal mechanisms in insect hearing. *Curr. Opin. Neurobiol.*, **9**, 389–393.
- Eberl, D. F., G. M. Duyk, and N. Perrimon (1997) A genetic screen for mutations that disrupt an auditory response in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci., USA*, **94**, 14837–14842.
- Eberl, D. F., R. W. Hardy, and M. J. Kernan (2000) Genetically similar transduction mechanisms for touch and hearing in *Drosophila*. *J. Neurosci.*, **20**, 5981–5988.
- Etges, W. J., K. F. Over, C. C. De Oliveira, and M. G. Ritchie (2006) Inheritance of courtship song variation among geographically isolated populations of *Drosophila mojavensis*. *Anim. Behav.*, **71**, 1205–1214.
- Ewing, A. W. (1969) The genetic basis of sound production in *Drosophila pseudoobscura* and *D. persimilis*. *Anim. Behav.*, **17**, 555–560.
- Ewing, A. W. (1978) The antenna of *Drosophila* as a 'love song' receptor. *Physiol. Entomol.*, **3**, 33–36.
- Ewing, A. W. (1979) Complex courtship songs in the *Drosophila funebris* species group: Escape from an evolutionary bottleneck. *Anim. Behav.*, **27**, 343–349.
- Ewing, A. W. (1989) *Arthropod Bioacoustics: Neurobiology and Behaviour*. Cornell University Press, New York.
- Ewing, A. W. and H. C. Bennet-Clark (1968) The courtship songs of *Drosophila*. *Behaviour*, **31**, 288–301.
- Ewing, A. W., and J. A. Miyan (1986) Sexual selection, sexual isolation and the evolution of song in the *Drosophila repleta* group of species. *Anim. Behav.*, **34**, 421–429.
- Ferveur, J.-F. (2005) Cuticular hydrocarbons: their evolution and roles in *Drosophila* pheromonal communication. *Behav. Genet.*, **35**, 279–295.
- Ferveur, J. F., and M. Cobb (2010) Behavioral and evolutionary roles of cuticular hydrocarbons in Diptera. In: Blomquist G. J., and A.-G. Bagnères (eds) *Insect Hydrocarbons: Biology, Biochemistry, and Chemical Ecology*: 325–343. Cambridge University Press, Cambridge.
- Fuyama, Y. (1979) A visual stimulus in the courtship of *Drosophila suzukii*. *Experientia*, **35**, 1327–1328.
- Gleason, J. M. (2005) Mutations and natural genetic variation in the courtship song of *Drosophila*. *Behav. Genet.*,

- 35, 265-277.
- Gleason, J. M., and M. G. Ritchie (1998) Evolution of courtship song and reproductive isolation in the *Drosophila willistoni* species complex: Do sexual signals diverge the most quickly? *Evolution*, **52**, 1493-1500.
- Göpfert, M. C., and D. Robert (2001) Turning the key on *Drosophila* audition. *Nature*, **411**, 908.
- Göpfert, M. C., and D. Robert (2002) The mechanical basis of *Drosophila* audition. *J. Exp. Biol.*, **205**, 1199-208.
- Grillet, M., L. Dartevielle, and J.-F. Ferveur (2006) A *Drosophila* male pheromone affects female sexual receptivity. *Proc. R. Soc. B*, **273**, 315-323.
- Higa, I., and Y. Fuyama (1993) Genetics of food preference in *Drosophila sechellia*. I. Responses to food attractants. *Genetica*, **88**, 129-136.
- Hirai, Y., and M. T. Kimura (1997) Incipient reproductive isolation between two morphs of *Drosophila elegans* (Diptera: Drosophilidae). *Biol. J. Linnean Soc.*, **61**, 501-513.
- Hoikkala, A. (1985) Genetic variation in the male courtship sound of *Drosophila littoralis*. *Behav. Genet.*, **15**, 135-142.
- Hoikkala, A., and J. Aspi (1993) Criteria of female mate choice in *Drosophila littoralis*, *D. montana*, and *D. ezoana*. *Evolution*, **47**, 768-777.
- Hoikkala, A., J. Aspi, and L. Suvanto (1998) Male courtship song frequency as an indicator of male genetic quality in an insect species, *Drosophila montana*. *Proc. R. Soc. B: Biol. Sci.*, **265**, 503-508.
- Hoikkala, A., and S. A. Crossley (2000) Copulatory courtship in *Drosophila*: behavior and songs of *D. birchii* and *D. serrata*. *J. Insect Behav.*, **13**, 71-86.
- Hoikkala, A., R. R. Hoy, and K. Y. Kaneshiro (1989) High-frequency clicks of Hawaiian picture-winged *Drosophila* species. *Anim. Behav.*, **37**, 927-934.
- Hoikkala, A., and K. Y. Kaneshiro (1997) Variation in male wing song characters in *Drosophila planitibia* (Hawaiian picture-winged *Drosophila* group). *J. Insect Behav.*, **10**, 425-436.
- Hoikkala, A., and J. Lumme (1984) Genetic control of the difference in male courtship sound between *Drosophila virilis* and *D. lummei*. *Behav. Genet.*, **14**, 257-268.
- Hoikkala, A., and J. Lumme (1987) The genetic basis of evolution of the male courtship sounds in the *Drosophila virilis* group. *Evolution*, **41**, 827-845.
- Hoikkala, A., and S. Moro (2000) SEM Search for sound production and sound perception organs in a variety of *Drosophila* species. *Microsc. Res. Tech.*, **50**, 161-168.
- Hoikkala, A., and L. Suvanto (1999) Male courtship song frequency as an indicator of male mating success in *Drosophila montana*. *J. Insect Behav.*, **12**, 599-609.
- Hoikkala, A., and P. Welbergen (1995) Signals and responses of females and males in successful and unsuccessful courtships of three Hawaiian lek-mating *Drosophila* species. *Anim. Behav.*, **50**, 177-190.
- Hoy, R. R., A. Hoikkala, and K. Y. Kaneshiro (1988) Hawaiian courtship songs: evolutionary innovation in communication signals of *Drosophila*. *Science*, **240**, 217-219.
- Ikedo, H. (1985) Nature of the sound produced by courtship-inhibiting behavior of the male *Drosophila marcatrum*. *Experimentia*, **41**, 1197-1199.
- Ikedo, H., H. Idoji, and I. Takabatake (1981) Intraspecific variations in the threshold of female responsiveness for auditory stimuli emitted by the male in *Drosophila mercatorum*. *Zool. Mag.*, **90**, 325-332.
- Ikedo, H., I. Takabatake, and N. Sawada (1980) Variation in courtship sounds among three geographical strains of *Drosophila marcatrum*. *Behav. Genet.*, **10**, 361-375.
- Isoherranen, E., J. Aspi, and A. Hoikkala (1999a) Inheritance of species differences in female receptivity and song requirement between *Drosophila virilis* and *D. montana*. *Hereditas*, **131**, 203-209.
- Isoherranen, E., J. Aspi, and A. Hoikkala (1999b) Variation and consistency of female preferences for stimulated courtship songs in *Drosophila virilis*. *Anim. Behav.*, **57**, 619-625.
- Jones, C. D. (1998) The genetic basis of *Drosophila sechellia*'s resistance to a host plant toxin. *Genetics*, **149**, 1899-1908.
- Kamikouchi, A., H. K. Inagaki, T. Effertz, O. Hendrich, A. Fiala, M. C. Göpfert, and K. Ito (2009) The neural basis of *Drosophila* gravity-sensing and hearing. *Nature*, **458**, 165-171.
- Katoh, T., D. Nakaya, K. Tamura, and T. Aotsuka (2007) Phylogeny of the *Drosophila immigrans* species group (Diptera: Drosophilidae) based on Adh and Gpdh sequences. *Zool. Sci.*, **24**, 913-921.
- Katoh, T., K. Tamura, K., and T. Aotsuka (2000) Phylogenetic position of the subgenus *Lordiphosa* of the genus *Drosophila* (Diptera: Drosophilidae) inferred from alcohol dehydrogenase (Adh) gene sequences. *J. Mol. Evol.*, **51**, 122-130.
- Kimura, M. T., and Y. Hirai (2001) Daily activity and territoriality of *Drosophila elegans*. *Tropics*, **10**, 489-495.
- Kopp, A., and J. R. True (2002) Evolution of male sexual characters in the oriental *Drosophila melanogaster* species group. *Evol. Devel.*, **4**, 278-291.
- Krebs, R. A., and K. L. Bean (1991) The mating behavior of *Drosophila mojavensis* on organ pipe and agria cactus. *Psyche*, **98**, 101-109.
- Kyriacou, C. P., and J. C. Hall (1980) Circadian rhythm mutations in *Drosophila melanogaster* affect short-term fluctuations in the male's courtship song. *Proc. Natl. Acad. Sci., USA*, **77**, 6729-6733.
- Kyriacou, C. P., and J. C. Hall (1982) The function of courtship song rhythms in *Drosophila*. *Anim. Behav.*, **30**, 794-801.
- Kyriacou, C. P., and J. C. Hall (1986). Interspecific genetic control of courtship song production and reception in *Drosophila*. *Science*, **232**, 494-497.
- Lachaise, D., M.-L. Cariou, J. R. David, F. Lemeunier, L. Tsacas, and M. Ashburner (1988) Historical biogeography of the *Drosophila melanogaster* species subgroup. *Evol. Biol.*, **22**, 159-225.

- Lai, Y., J. Gleason, and J. True (2009) Acoustic analyses of two undocumented sound patterns in the *Drosophila suzukii* and *D. takahashii* species subgroups. *J. Acoust. Soc. Am.*, **125**, 2710.
- Lakovaara, S., and A. Hoikkala (1979) Analysis of the male courtship sounds of certain species of the *Drosophila virilis* group. *Aquilo Ser. Zool.*, **20**, 94-99.
- Liimatainen, J. O., A. Hoikkala, J. Aspi, and P. Welbergen (1992) Courtship in *Drosophila montana*: the effects of male auditory signals on the behaviour of flies. *Anim. Behav.*, **43**, 35-48.
- Llopart, A., S. Elwyn, D. Lachaise, and J. A. Coyne. (2002) Genetics of a difference in pigmentation between *Drosophila yakuba* and *D. santomea*. *Evolution*, **56**, 2262-2277.
- Magnacca, K. N., D. Foote, and P. M. O'Grady (2008) A review of the endemic Hawaiian Drosophilidae and their host plants. *Zootaxa*, **58**, 1-58.
- Manning, A. (1967) Antennae and sexual receptivity in *Drosophila melanogaster* females. *Science*, **158**, 136-137.
- Matsumura, S. (1931) *Illustrated Insects of Japan-Empire*. Toukou Shoin, Tokyo. (In Japanese)
- Neems, R. M., K. Dooher, R. K. Butlin, and B. Shorrocks (1997) Differences in male courtship song among the species of the *quinaria* group of *Drosophila*. *J. Insect Behav.*, **10**, 237-246.
- Nemoto, T., M. Doi, K. Oshio, H. Matsubayashi, Y. Oguma, T. Suzuki, and Y. Kuwahara (1994) (Z,Z)-5,27-tritriacontadien: Major sex pheromone of *Drosophila pallidosa* (Diptera: Drosophilidae). *J. Chem. Ecol.*, **20**, 3029-3027.
- Noor, M. A. F., and C. F. Aquadro (1998) Courtship songs of *Drosophila pseudoobscura* and *D. persimilis*: analysis of variation. *Anim. Behav.*, **56**, 115-125.
- Oguma, Y., J.-M. Jallon, M. Tomaru, and H. Matsubayashi (1996) Courtship behavior and sexual isolation between *Drosophila auraria* and *D. triauraria* in darkness and light. *J. Evol. Biol.*, **9**, 803-815.
- Oguma, Y., T. Nemoto, and Y. Kuwahara (1992) (Z)-11-pentacosene is the major sex pheromone component in *Drosophila virilis* (Diptera). *Chemoecology*, **3**, 60-64.
- Oguma, Y., S. Wen, M. Tomaru, H. Matsubayashi, and T. Peng (1995) Reproductive isolation between *Drosophila lini* and its siblings. *Jpn. J. Genet.*, **70**, 311-320.
- Paillette, M., H. Ikeda, and J.-M. Jallon (1991) A new acoustic signal of the fruit-flies *Drosophila simulans* and *D. melanogaster*. *Bioacoustics*, **3**, 247-254.
- Piñeiro, R., M. C. Carracedo, J. I. Izquierdo, and P. Casares (1993) Bidirectional selection for female receptivity in *Drosophila melanogaster*. *Behav. Genet.*, **23**, 77-83.
- Powell, J. R. (1997) *Progress and Prospects in Evolutionary Biology: The Drosophila Model*. Oxford University Press, Oxford.
- Ritchie, M. G., E. J. Halsey, and J. M. Gleason (1999) *Drosophila* song as a species-specific mating signal and the behavioural importance of Kyriacou and Hall cycles in *D. melanogaster* song. *Anim. Behav.*, **58**, 649-657.
- Ritchie, M. G., R. M. Townhill, and A. Hoikkala (1998) Female preference for fly song: playback experiments confirm the target of sexual isolation. *Anim. Behav.*, **56**, 713-717.
- R'Kha, S., P. Capy, and J. R. David (1991) Host-plant specialization in the *Drosophila melanogaster* species complex: a physiological, behavioral, and genetical analysis. *Proc. Natl. Acad. Sci. USA*, **88**, 1835-1859.
- Robertson, H. M. (1982). Female courtship summation in *Drosophila melanogaster*. *Anim. Behav.*, **30**, 1105-1117.
- Saarikettu, M., J. O. Liimatainen, and A. Hoikkala (2005) The role of male courtship song in species recognition in *Drosophila montana*. *Behav. Genet.*, **35**, 257-263.
- Sakai, T., K. Isono, M. Tomaru, and Y. Oguma (1997) Light-affected male following behavior is involved in light-dependent mating in *Drosophila melanogaster*. *Genes Genet. Syst.*, **72**, 275-281.
- Satokangas, P., J. O. Liimatainen, and A. Hoikkala (1994) Songs produced by the females of the *Drosophila virilis* group of species. *Behav. Genet.*, **24**, 263-272.
- Shorey, H. H. (1962) Nature of the sound produced by *Drosophila melanogaster* during courtship. *Science*, **137**, 677-678.
- Spieth, H. T. (1951) The breeding site of *Drosophila lacicola* Patterson. *Science*, **113**, 232.
- Spieth, H. T. (1952). Mating behavior within the genus *Drosophila* (Diptera). *Bull. Amer. Mus. Natur. Hist.*, **99**, 395-474.
- Spieth, H. T. (1984) Courtship behaviors of the Hawaiian picture-winged *Drosophila*. *Univ. California Publ. Entomol.*, **103**, 1-92.
- Sturtevant, A. H. (1915) Experiments on sex recognition and the problem of sexual selection in *Drosophila*. *J. Anim. Behav.*, **5**, 351-366.
- Sultana, F., M. T. Kimura, and M. J. Toda (1999) Anthophilic *Drosophila* of the *elegans* species-subgroup from Indonesia, with description of a new species (Diptera: Drosophilidae). *Entomol. Sci.*, **2**, 121-126.
- Suvanto, L., A. Hoikkala, and J. O. Liimatainen (1994) Secondary courtship songs and inhibitory songs of *Drosophila virilis*-group males. *Behav. Genet.*, **24**, 85-94.
- Todi, S. V., Y. Sharma, and D. F. Eberl (2004) Anatomical and molecular design of the *Drosophila* antenna as a flagellar auditory organ. *Microsc. Res. Tech.*, **63**, 388-399.
- Tomaru, M., M. Doi, H. Higuchi, and Y. Oguma (2000) Courtship song recognition in the *Drosophila melanogaster* complex: heterospecific songs make females receptive in *D. melanogaster*, but not in *D. sechellia*. *Evolution*, **54**, 1286-1294.
- Tomaru, M., H. Matsubayashi, and Y. Oguma (1995) Heterospecific inter-pulse intervals of courtship song elicit female rejection in *Drosophila biauraria*. *Anim. Behav.*, **50**, 905-914.
- Tomaru, M., H. Matsubayashi, and Y. Oguma (1998) Effects of courtship song in interspecific crosses among the species of the *Drosophila auraria* complex (Diptera: Drosophilidae). *J. Insect Behav.*, **11**, 383-398.

- Tomaru, M., and Y. Oguma (1994a) Differences in courtship song in the species of the *Drosophila auraria* complex. *Anim. Behav.*, **47**, 133-140.
- Tomaru, M., and Y. Oguma (1994b) Genetic basis and evolution of species-specific courtship song in the *Drosophila auraria* complex. *Genet. Res.*, **63**, 11-17.
- Tomaru, M., and Y. Oguma (2003) Courtship behaviour and song in *Drosophila*. *The Iden*, **57**, 80-84. (In Japanese)
- Tomaru, M., Y. Oguma, and M. Watada (2006) Courtship in *Drosophila quadrilimeata* with a unique male behavioral element, abdomen bending. *J. Ethol.*, **24**, 133-139.
- Tomaru, M., H. Yamada, and Y. Oguma (2004) Female mate recognition and sexual isolation depending on courtship song in *Drosophila sechellia* and its siblings. *Genes Genet. Syst.*, **79**, 145-150.
- Ueyama, M., and Y. Fuyama (2003) Enhanced cost of mating in female sterile mutants of *Drosophila melanogaster*. *Genes Genet. Syst.*, **78**, 29-36.
- von Schilcher, F. (1976a) The role of auditory stimuli in the courtship of *Drosophila melanogaster*. *Anim. Behav.*, **24**, 18-26.
- von Schilcher, F. (1976b) The function of pulse song and sine song in the courtship of *Drosophila melanogaster*. *Anim. Behav.*, **24**, 622-625.
- Vuoristo, M., E. Isoherranen, and A. Hoikkala (1996) Female wing spreading as acceptance signal in the *Drosophila virilis* group of species. *J. Insect Behav.*, **9**, 505-516.
- Walsh, D. B., M. P. Bolda, R. E. Goodhue, A. J. Dreves, J. Lee, D. J. Bruck, V. M. Walton, S. D. O'Neal, and F. G. Zalom (2010) *Drosophila suzukii* (Diptera: Drosophilidae): invasive pest of ripening soft fruit expanding its geographic range and damage potential. *J. Integ. Pest Mngmt.*, (in press).
- Watson, E. T., E. Rodewald, and J. A. Coyne (2007) The courtship song of *Drosophila santomea* and a comparison to its sister species *D. yakuba* (Diptera: Drosophilidae). *Eur. J. Entomol.*, **104**, 145-148.
- Wen, S.-Y., H. Yamada, Y.-F. Li, M. T. Kimura, Y. Oguma, K. Sawamura, and M. J. Toda (2011) Copulatory courtship behavior and sine song as a mate recognition cue in *Drosophila lini* and its sibling species. *Zool. Sci.*, (in press).
- Wicker-Thomas, C., and T. Chertemps (2010) Molecular biology and genetics of hydrocarbon production. In: Blomquist G. J., and A.-G. Bagnères (eds) *Insect Hydrocarbons: Biology, Biochemistry, and Chemical Ecology*: 53-74. Cambridge University Press, Cambridge.
- Willmund, R., and A. W. Ewing (1982) Visual signals in the courtship of *Drosophila melanogaster*. *Anim. Behav.*, **30**, 209-215.
- Yamada, H., M. Matsuda, and Y. Oguma (2002a) Genetics of sexual isolation based on courtship song between two sympatric species: *Drosophila ananassae* and *D. pallidosa*. *Genetica*, **116**, 225-237.
- Yamada, H., T. Sakai, M. Tomaru, M. Doi, M. Matsuda, and Y. Oguma (2002b) Search for species-specific mating signal in courtship songs of sympatric sibling species, *Drosophila ananassae* and *D. pallidosa*. *Genes Genet. Syst.*, **77**, 97-106.
- Yamada, H., M. Tomaru, M. Matsuda, and Y. Oguma (2008) Behavioral sequence leading to sexual isolation between *Drosophila ananassae* and *D. pallidosa*. *J. Insect Behav.*, **21**, 222-239.
- Yeh, S.-D., S.-R. Liou, and J. R. True (2006) Genetics of divergence in male wing pigmentation and courtship behavior between *Drosophila elegans* and *D. gunungcola*. *Heredity*, **96**, 383-395.
- Yorozu, S., A. Wong, B. J. Fischer, H. Dankert, M. J. Kernan, A. Kamikouchi, K. Ito, and D. J. Anderson (2009) Distinct sensory representations of wind and near-field sound in the *Drosophila* brain. *Nature*, **458**, 201-205.