



Contents lists available at ScienceDirect

Journal of Insect Physiology

journal homepage: www.elsevier.com/locate/jinsphys

Sexual dimorphism in cuticular hydrocarbons of the Australian field cricket *Teleogryllus oceanicus* (Orthoptera: Gryllidae)

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ARTICLE INFO

Article history:

Received 11 March 2008

Received in revised form

10 April 2008

Accepted 15 April 2008

Keywords:

Cuticular hydrocarbons

Sexual dimorphism

Sexual selection

Teleogryllus oceanicus

ABSTRACT

Sexual dimorphism is presumed to reflect adaptive divergence in response to selection favouring different optimal character states in the two sexes. Here, we analyse patterns of sexual dimorphism in the cuticular hydrocarbons of the Australian field cricket *Teleogryllus oceanicus* using gas chromatography. Ten of the 25 peaks found in our chromatographs, differed in their relative abundance between the sexes. The presence of sexual dimorphism in *T. oceanicus* is discussed in reference to a review of sexual dimorphism in cuticular hydrocarbons of other insects. We found that this trait has been examined in 103 species across seven different orders. Seventy-six of these species (73%) displayed sex specificity of cuticular hydrocarbons, the presence/absence of which does not appear to be directly linked to phylogeny. The occurrence of sexual dimorphism in cuticular hydrocarbons of some but not other species, and the extent of variation within genera, suggest that this divergence has been driven primarily by sexual selection.

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1. Introduction

Hydrocarbons are major constituents of cuticular waxes that are found on the exoskeleton of most insects. While the primary function of these compounds has been identified as providing water-proofing and protection against environmental stresses, it is now well recognized that cuticular hydrocarbons also play a central role in insect communication (Howard and Blomquist, 2005). Interspecifically, cuticular hydrocarbons have been shown to function in species recognition, and predator deterrence or avoidance (Hoffmann et al., 2006). Intraspecifically, cuticular hydrocarbons are known to function in social communication and short-range sexual communication, facilitating recognition of sexual partners, and in some cases acting as a courtship inhibitor to reduce the attractiveness of mated females (Ferveur, 2005; Howard and Blomquist, 2005).

In field crickets, mate choice is composed of several distinct elements, including contact chemoreception. Although males generally attract females over long distances by singing, once individuals are in close contact, chemical signals, or cuticular hydrocarbons, can play a central role in mate selection. For example, chemosensory cues enable female crickets to preferentially mate with novel males (Ivy et al., 2005), to favour unrelated males (Simmons, 1991), and choose dominant males over

subordinates (Kortet and Hedrick, 2005). Although mate choice experiments in crickets focus primarily on female choice, male crickets can also discriminate between females using chemosensory cues. For example, males of the Australian field cricket, *Teleogryllus oceanicus*, are known to display prudent ejaculate allocation in response to a female's mating status (Thomas and Simmons, 2007), and this discrimination could be based on chemical signals transferred from males to females during mating.

Sexual dimorphism of cuticular hydrocarbons has been previously found in a number of species of Orthopterans; however, not all the Orthopterans studied display this trait (Appendix). Here, we examine patterns of variation in cuticular composition between genders of *T. oceanicus* to determine if, and how this species cuticular composition varies between the sexes. We use quantitative analyses of gas chromatography profiles to compare individuals of the same age but different sex. As many insect species are sexually dimorphic for cuticular composition, we discuss our results in reference to a review of this literature. In particular, we focus our discussion on the evolutionary processes that may have led to divergence between the sexes in *T. oceanicus*, and other insect taxa.

2. Materials and methods

The parental generation of experimental crickets was the offspring derived from individuals collected from a banana plantation in Carnarvon, northwestern Australia. Newly hatched

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first generation nymphs were raised in 5 L plastic containers with 30 full siblings. Sexes were separated before the adult moult. After adult eclosion, crickets were isolated in individual boxes ($7 \times 7 \times 5$ cm) for 14 ± 3 days until sexually mature, before their cuticular hydrocarbons were extracted. All crickets had access to cat chow and water ad libitum, and were kept in a constant temperature room, at 25°C with a 12:12 h light–dark cycle.

To quantify cuticular hydrocarbons, we immersed freshly freeze-killed individual crickets in 4 ml of hexane for 5 min. We injected $1 \mu\text{L}$ of this sample into a gas chromatograph and mass spectrometer (Shimadzu GCMS QP2010) operating in the split mode (ratio 10:1), and fitted with a Stabilwax column of 30×0.25 mm internal diameter (i.d.) using helium as a carrier gas (total flow rate of 13.2 mL/min). We optimized separation of the extract by using a column temperature profile in which the analysis began at a temperature of 50°C for 1 min, and rose to 250°C for 20 min. The transfer line from the GC to the mass spectrometer was set at 250°C . We analysed washes derived from 28 unmated males and 26 unmated females.

We also analysed washes from an additional 10 crickets (five males and five females) on an RTX-5MS column (30×0.25 mm i.d.) using the same gas chromatograph and mass spectrometer. This is because the Stabilwax column used in the analysis described earlier has a maximum temperature of 260°C ; a temperature not high enough to determine if there are hydrocarbons in the C36–C40+ range. We optimized separation of these extracts using a column temperature profile that began at 50°C for 1 min, rose to 250°C for 20 min and rose again to 320°C for 10 min. We again used helium as the carrier gas (total flow rate 11.5 mL/min).

For data analysis, peaks were labelled by peak number, which corresponded to their retention times (Fig. 1, Table 1). Individual hydrocarbons were identified using a custom GCMS library based on authentic standards, NIST library and other published data (Blomquist et al., 1976). For data analysis, we used proportional peaks, because absolute peaks are often subject to large experimental errors (Blows and Allan, 1998; Rundle et al., 2005; Savarit and Ferveur, 2002). Proportional peaks were calculated by

dividing the area of each peak in a given sample by the sum of all peak areas in that sample. We used a log contrast transformation to remove the problem of non-independence introduced into the analysis by using proportions (Blows and Allan, 1998; Rundle et al., 2005; Simmons et al., 2003). Log contrasts were calculated by dividing an arbitrarily chosen peak (peak 5) by the proportional peak area, and then taking the log of the new variables. $\text{Log}(1+x)$ was used because not all individuals contained every compound. We performed a principal components analysis on these new variables following Neems and Butlin (1995).

3. Results

Using the Stabilwax column, we were able to distinguish 25 peaks that ranged in chain length from 29 to 35 carbons (Table 1). The RTX-5MS column yielded no additional peaks. The samples run on this column are excluded from the following analysis.

The principal component analysis returned 24 components. We considered only those components where the eigenvalue was greater than 1 (Norman and Streiner, 1994) in the multivariate data set. Five components had an eigenvalue greater than 1, and collectively explained 83% of the variance in cuticular hydrocarbon blends. The percentage of variance explained was 39.95, 22.36, 9.68, 5.77 and 5.01 for components 1–5, respectively.

Univariate analysis of variance of the individual peaks revealed that principal component one (PC1) showed significant differences between the sexes (Table 2, Fig. 2). To examine the relative contribution of each peak, we used correlations between the original variables and the PC scores (Table 3). Cuticular hydrocarbons with correlations greater than 0.7 times the largest correlation were considered to have contributed significantly to the PC (Mardia et al., 1979). Ten peaks were found to contribute to PC1. Examination of the raw concentrations of these 10 peaks show that the strongest component was peak 22 representing 32% of the total cuticular hydrocarbons present on males, but only 24% of the total cuticular hydrocarbons present on females (Table 1).

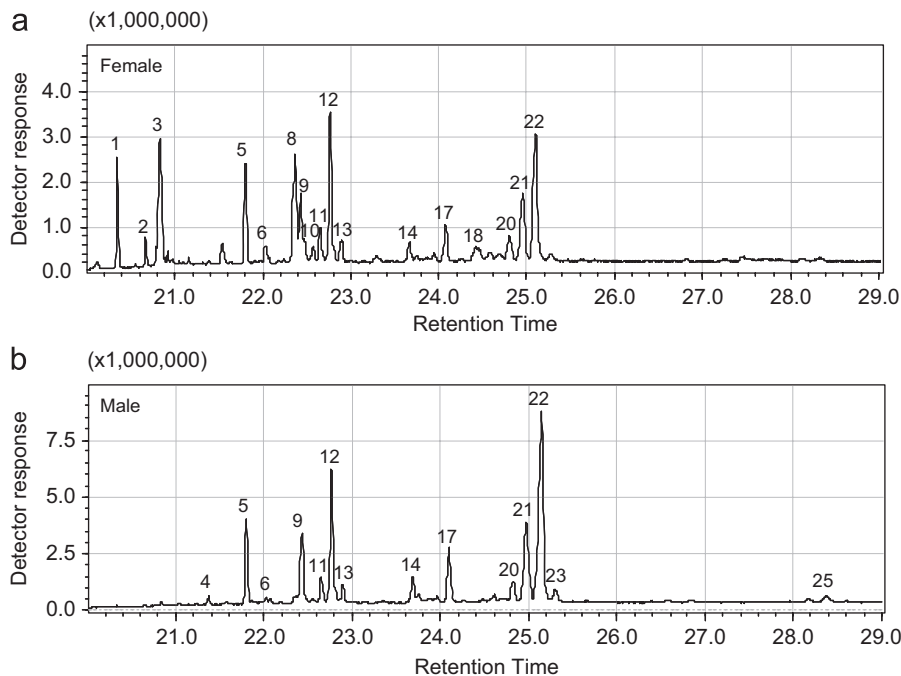


Fig. 1. A typical GC profile of (a) female and (b) male crickets (*Teleogryllus oceanicus*). The X-axis shows the retention time and the Y-axis the ionization detector response. The figures have different values on the Y-axes. Peak numbers are indicated (see Table 1 for more detail). Note not all peaks were found in every cricket.

Table 1
The relative contribution of the 25 cuticular hydrocarbon peaks identified from hexane washes of male and female *T. oceanicus*

Peak	Retention time	Molecular weight	Hydrocarbon	Concentration (%±S.E.)	
				Male	Female
1	20.33		Unresolved	0.000±0.358	1.267±0.372
2	20.66	408	C ₂₉	0.000±0.119	0.409±0.124
3	20.84	406	C _{29:1}	0.109±0.602	1.807±0.625
4	21.37		Unresolved	0.660±0.066	0.225±0.069
5	21.80	436	x-meC ₃₁	6.617±0.431	9.841±0.448
6	22.02		Unresolved	0.543±0.078	0.771±0.081
7	22.08	434	C _{31:1}	0.286±0.035	0.048±0.037
8	22.34	434	C _{31:1}	0.966±0.866	5.78±0.898
9	22.43	434	C _{31:1}	7.638±0.577	4.648±0.599
10	22.55	432	C _{31:2}	0.249±0.112	0.341±0.116
11	22.65	432	C _{31:2}	2.906±0.175	1.859±0.181
12	22.77	432	C _{31:2}	15.851±0.812	9.197±0.843
13	22.89	432	C _{31:2}	2.252±0.180	0.783±0.187
14	23.68	464	x-meC ₃₃	2.541±0.931	9.091±0.966
15	23.75		Unresolved	0.209±0.051	0.082±0.052
16	23.95	462	C _{33:1}	0.670±0.491	5.046±0.509
17	24.09	462	C _{33:1}	6.509±0.381	1.764±0.396
18	24.42	462	C _{33:1}	0.000±0.275	1.493±0.286
19	24.60	462	C _{33:1}	0.649±0.064	0.085±0.067
20	24.82	460	C _{33:2}	2.476±0.174	2.100±0.181
21	24.96	460	C _{33:2}	13.326±0.525	12.570±0.545
22	25.14	460	C _{33:2}	32.669±1.153	24.019±1.197
23	25.29	460	C _{33:2}	2.132±0.175	1.054±0.181
24	27.19	492	C ₃₅	0.000±0.724	2.736±0.752
25	28.36	488	C _{35:2}	0.740±0.660	2.981±0.685

Table 2
Univariate ANOVAs using the principal component scores of the five components with eigenvalues greater than 1 (PC1–5)

Component	d.f.	SS	F	p
<i>PC1</i>				
Model	1	359.11	125.34	<0.001
Error	52	148.99		
<i>PC2</i>				
Model	1	0.15	0.03	0.87
Error	52	284.28		
<i>PC3</i>				
Model	1	1.23	0.52	0.47
Error	52	121.93		
<i>PC4</i>				
Model	1	0.01	0.003	0.95
Error	52	73.33		
<i>PC5</i>				
Model	1	0.71	0.59	0.45
Error	52	63.02		

Significant value is in bold.

4. Discussion

Consistent with previous research in insects (Fig. 3, Appendix), our result demonstrates sexual dimorphism in the cuticular hydrocarbon profiles of *T. oceanicus*. In our multivariate analysis, 10 of the 25 peaks were found to differ between the genders in their relative concentrations (Table 3). Although the functional significance of this sexual dimorphism in *T. oceanicus* remains to be tested, our result suggests that it is a blend of cuticular compounds, rather than a single compound, which would be important for sex discrimination, as is the case in the cricket *Gryllus bimaculatus* (Tregenza and Wedell, 1997).

While we found gender specific differences in cuticular hydrocarbons in *T. oceanicus*, not all Orthopterans display this trait (Fig. 3). In fact, little or no gender differences in cuticular

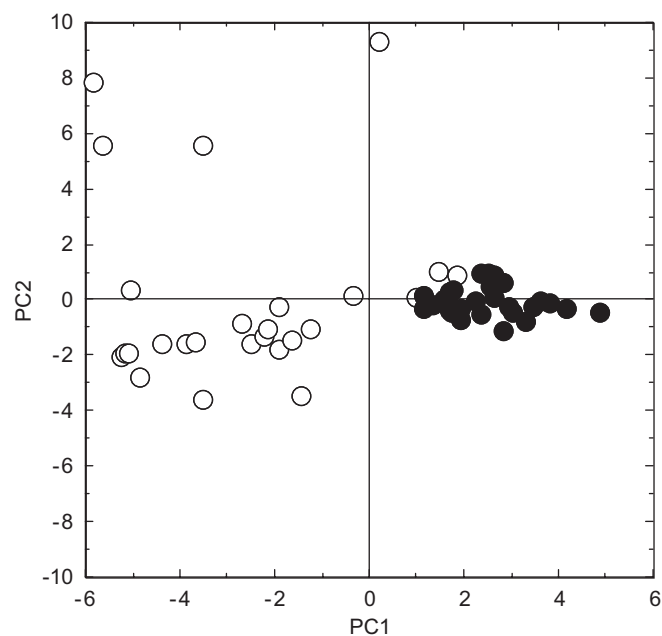


Fig. 2. Separation of male (closed circles) and female (open circles) *Teleogryllus oceanicus* cuticular hydrocarbon extracts based on the first two principal components (PC) extracted from the principal component analysis.

hydrocarbons have been found in three species of Acrididae (Appendix). Indeed, there are also numerous examples of species in other taxa where there appears to be no sex specificity of cuticular hydrocarbons (Appendix). A lack of sexual dimorphism in some species could simply reflect methodological limitations. For example, most studies use gas chromatography retention times to analyse difference between the sexes, but there are many aspects of variation in hydrocarbon composition that are not

Table 3
Correlations between relative concentrations of cuticular hydrocarbon peaks and the five components extracted from the principal components analysis

Peak	Retention time	Principal component				
		1	2	3	4	5
1	20.33	-0.12	0.38	0.15	0.07	0.03
2	20.66	-0.12	0.38	0.13	0.03	0.05
3	20.84	-0.08	0.39	0.17	0.08	-0.03
4	21.37	0.24	0.15	0.08	0.14	-0.29
6	22.02	0.03	0.11	0.21	0.63	0.10
7	22.08	0.21	0.01	-0.15	0.13	0.48
8	22.34	-0.16	0.32	0.10	0.01	0.02
9	22.43	0.26	0.13	0.01	-0.08	-0.08
10	22.55	0.03	0.33	0.04	0.02	-0.15
11	22.65	0.29	0.08	-0.05	-0.01	0.10
12	22.77	0.30	0.06	-0.09	-0.02	0.03
13	22.89	0.28	0.09	-0.15	-0.11	0.02
14	23.68	-0.20	-0.24	0.13	0.27	-0.15
15	23.75	0.15	-0.01	0.01	0.29	0.53
16	23.95	-0.18	-0.26	0.23	0.09	0.07
17	24.09	0.27	0.07	-0.05	0.14	-0.06
18	24.42	-0.19	0.16	0.34	-0.19	0.20
19	24.6	0.21	0.08	0.09	0.15	-0.43
20	24.82	0.23	0.00	0.36	-0.01	0.17
21	24.96	0.23	-0.19	0.30	0.09	-0.01
22	25.14	0.26	-0.17	0.20	0.00	-0.09
23	25.29	0.23	-0.09	0.34	-0.11	-0.15
24	27.19	-0.16	-0.13	-0.16	0.50	-0.19
25	28.36	-0.07	-0.19	0.47	-0.16	0.06

Peaks that contribute significant amounts to the principal components are in bold.

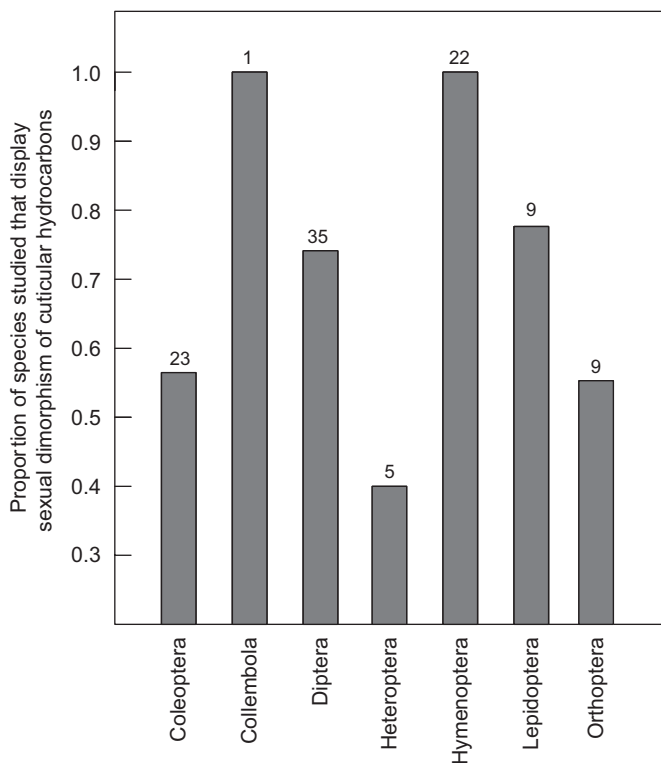


Fig. 3. The proportion of species investigated that display sexual dimorphism in cuticular hydrocarbons. Species are grouped by order, and the total number of species investigated in each order for this trait is shown above the bars. See Appendix for more details.

revealed by this approach (i.e. the position of double bonds or an enantiomeric composition of hydrocarbons). Furthermore, differences in cuticular hydrocarbons between the sexes can change in

relation to a number of biological states, such as age and reproductive status; differences between sexes can be more marked in older than younger individuals (Caputo et al., 2005), and mated females often produce hydrocarbons that are the same as the major hydrocarbon component of mature males (Andersson et al., 2000; Kukuk, 1985; Scott, 1986; Sreng, 2006). In studies using field-collected samples, it is often difficult to know the biological state of specimens. Despite these methodological limitations, it is clear from our review that differences between the sexes are not directly linked to phylogeny. For example, three members of the *melanogaster* subgroup of *Drosophila* species display marked sexual dimorphism in cuticular hydrocarbons, while five other species in the group do not (Cobb and Jallon, 1990). Moreover, some species of *Drosophila* display qualitative differences between the sexes (Cobb and Jallon, 1990), while males and females of other species contain the same hydrocarbons, but differ in the relative abundance of compounds (Blows and Allan, 1998). This divergence in the presence/absence of sexual dimorphism across taxa suggests that sexual selection may be a strong driving force in the evolution of this trait.

Sexual selection could drive differentiation of cuticular hydrocarbons, if the chemical composition of the cuticle is used as a contact pheromonal signal in mate choice. Confirmation of the use of cuticular hydrocarbons in mate choice comes from a large number of studies that have demonstrated that particular compounds produced by one sex stimulate sexual behaviour of the other, or that gender specific ratios of cuticular hydrocarbons can influence mate choice (Appendix). Furthermore, most sexually selected traits related to mate choice, show delayed maturation (Delhey et al., 2007), and a number of studies have demonstrated that differences in the cuticular hydrocarbons between sexes can be more marked in older than younger individuals (Caputo et al., 2005; Mpuru et al., 2001; Brown et al., 1992). But perhaps the most convincing evidence that sexual selection can drive cuticular hydrocarbon evolution comes from studies of *Drosophila*, where cuticular hydrocarbons have been formally examined in this context. Chenoweth and Blows (2005) reported strong directional sexual selection on male and female cuticular hydrocarbons in *D. serrata*, but the strength of sexual selection differed between the sexes. In this species, the evolution of sexual dimorphism appears to have been achieved by sex-limited expression of traits controlled by genes on the X chromosome (Chenoweth and Blows, 2003).

Although there is strong evidence to suggest that sexual selection drives the evolution of sexual dimorphism in cuticular hydrocarbons, consideration must also be given to the possibility that in some species this sexual dimorphism could be a result of environmental selection, and have no associated signalling value. For example, the original function of cuticular hydrocarbons is thought to be protection against desiccation, so changes in cuticular hydrocarbon composition between the sexes could reflect divergence in microhabitat preferences of males and females. Certainly, some structural features of cuticular hydrocarbons such as chain length, degree and position of unsaturation and of methyl branching, are associated with different rates of water loss (Gibbs, 1998). Furthermore, experimental manipulation of temperatures during early imaginal life of *Drosophila melanogaster* has shown that changes in temperature can affect the ontogeny of sexually dimorphic cuticular hydrocarbons (Savarit and Ferveur, 2002). Although it seems unlikely that environmental selection influences the divergence of male and female cuticular hydrocarbons for species such as *T. oceanicus*, where there does not appear to be any gender lifestyle differences, this type of selection process should be considered for species with sex-dependent habitat preferences.

It is also possible that selective processes act on other phenotypic variances that inadvertently effect the composition of the cuticle. Learning more about the biosynthesis of cuticular hydrocarbons will certainly aid in distinguishing between direct and indirect selection within each species. For example, are the hydrocarbons in question influenced by diet, or are they synthesized in situ? Certainly, in some species, hydrocarbon synthesis is related to food intake, while in other species, critical enzymes involved in cuticular hydrocarbon biosynthesis have been isolated, and several sex determination genes clearly influence cuticular hydrocarbon profiles (see Howard and Blomquist, 2005 for review). Ultimately it could be a combination of interacting selection processes that has the greatest influence on the level of cuticular hydrocarbon expression in each sex. Certainly, in *Drosophila*, the interaction between natural and sexual selection has a greater influence on the evolution of mate recognition via cuticular hydrocarbon profiles than either process in isolation (Blows, 2002).

Whatever the evolutionary processes that led to sexually dimorphic cuticular hydrocarbons in such a wide range of insect

species, it is clear from the literature that female specific pheromones stimulate male courtship behaviour (Appendix), while male specific cuticular pheromones can influence a female's propensity to mate (Grillet et al., 2006). For example, in the cricket *G. bimaculatus*, males are known to display avoidance or aggressive behaviour to male cuticular hydrocarbons (Nagamoto et al., 2005), but courtship behaviour to female hydrocarbons (Tregenza and Wedell, 1997; Nagamoto et al., 2005). These behavioural responses by males to sex specific cuticular hydrocarbons may also be apparent in *T. oceanicus*, but have yet to be investigated.

Acknowledgements

Thanks to A. Reeder for providing access to the GCMS. This work was supported by funding from the Australian Research Council, the University of Western Australia, and the West Australian Centres of Excellence in Science and Innovation Program.

Appendix. Insect species in which sexual dimorphism of cuticular hydrocarbons has been investigated

Order	Family	Species	Dimorphic	Stimulatory role	References
Coleoptera	Cantharidae	<i>Rhagonycha fulva</i>	Yes		Jacob (1978)
	Cerambycidae	<i>Anoplophora glabripennis</i>	Yes	Yes	Zhang et al. (2003)
		<i>Anoplophora malasiaca</i>	Yes	Yes	Fukaya (2003), Fukaya et al. 2000
		<i>Megacyllene caryae</i>	Yes	Yes	Ginzel and Hanks (2003a), Ginzel et al. (2003c)
		<i>Megacyllene robiniae</i>	Yes	Yes	Ginzel et al. (2003c), Ginzel et al. (2006)
	Chrysomelidae	<i>Xylotrechus colonus</i>	Yes	Yes	Ginzel et al. (2003b)
		<i>Diabrotica barberi</i>	Yes		Golden et al. (1992)
		<i>Diabrotica longicornis</i>	Yes		Golden et al. (1992)
		<i>Leptinotarsa decemlineata</i>	Yes		Dubis et al. (1987)
	Curculionidae	<i>Caulophilus oryzae</i>	No		Howard and Perez-Lachaud (2002)
		<i>Ips confusus</i>	No		Page et al. (1997)
		<i>Ips cribricollis</i>	No		Page et al. (1997)
		<i>Ips grandicollis</i>	No		Page et al. (1997)
		<i>Ips hoppingi</i>	No		Page et al. (1997)
		<i>Ips latidens</i>	No		Page et al. (1997)
		<i>Ips lecontei</i>	Yes		Page et al. (1997)
		<i>Ips montanus</i>	No		Page et al. (1997)
		<i>Ips paraconfusus</i>	No		Page et al. (1997)
		<i>Ips pini</i>	No		Page et al. (1997)
		<i>Orthotomicus caelatus</i>	No		Page et al. (1997)
		<i>Canthon cyanellus cyanellus</i>	Yes	Yes	Ortiz-Dominguez et al. (2006), Ortiz-Dominguez et al. (2006)
		Scolytidae	<i>Hypothenemus hampei</i>	Yes	
	Staphylinidae	<i>Aleochara curtula</i>	Yes	Yes	Peschke and Metzler (1987)
Collembola	Hypogastruridae	<i>Schoettella ununguiculata</i>	Yes		Porco et al. (2004)
	Calliphoridae	<i>Chrysomya bezziana</i>	Yes		Brown et al. (1998), Brown et al. (1992)
Diptera	Calliphoridae	<i>Cochliomyia hominivora</i>	Yes	Yes	Mackley and Broce (1981), Pomonis (1989)
		<i>Lucilia cuprina</i>	Yes		Goodrich (1970)
		<i>Phormia regina</i>	No		Stoffolano et al. 1997
	Culicidae	<i>Aedes aegypti</i>	Yes		Horne and Priestman (2002)
		<i>Aedes hendersoni</i>	No		Pappas et al. (1994)
		<i>Aedes triseriatus</i>	No		Pappas et al. (1994)
		<i>Anopheles gambiae</i>	Yes		Caputo et al. (2005)
		<i>Culex quinquefasciatus</i>	Yes		Chen et al. (1990)
		<i>Drosophila birchii</i>	Yes	Yes	Blows and Allan (1998)
		<i>Drosophila erecta</i>	Yes	Yes	Cobb and Jallon (1990)
		<i>Drosophila malenogaster</i>	Yes	Yes	Cobb et al. (1990), Coyne et al. (1994)
		<i>Drosophila mauritiana</i>	No		Cobb et al. (1990), Coyne et al. (1994)
		<i>Drosophila orena</i>	No		Jallon and David (1987)
		<i>Drosophila pallidosa</i>	Yes	Yes	Nemoto et al. (1994)
	Drosophilidae	<i>Drosophila pseudoobscura</i>	No		Toolson and Kupersimbron (1989)
		<i>Drosophila sechellia</i>	Yes	Yes	Cobb et al. (1990), Coyne et al. (1994)
		<i>Drosophila serrata</i>	Yes	Yes	Blows et al. (1998), Hine et al. (2002)
		<i>Drosophila simulans</i>	No		Cobb et al. (1990), Coyne et al. (1994)
		<i>Drosophila teissieri</i>	No		Cobb et al. (1990)
		<i>Drosophila virilis</i>	Yes	Yes	Jackson and Bartelt (1986), Oguma et al. (1992)
		<i>Drosophila yakuba</i>	No		Cobb et al. (1990)

Heteroptera	Glossinidae	<i>Glossina austeni</i>	Yes	Yes	Carlson et al. (2005), Nelson and Carlson (1986)	
		<i>Glossina brevipalpalis</i>	Yes	Yes	Nelson et al. (1988), Sutton and Carlson (1997)	
		<i>Glossina fuscipes fuscipes</i>	Yes		Nelson et al. (1988)	
		<i>Glossina morsitans morsitans</i>	Yes	Yes	Langley et al. (1975), Nelson et al. (1986)	
		<i>Glossina pallidipes</i>	Yes	Yes	Carlson et al. (1984), Nelson et al. (1986)	
		<i>Glossina palpalis gambiensis</i>	Yes		Nelson et al. (1988)	
		<i>Glossina palpalis palpalis</i>	Yes		Nelson et al. (1988)	
		<i>Glossina tachinoides</i>	Yes	Yes	Carlson et al. (1998), Nelson et al. (1988)	
		Muscidae	<i>Hydrotaea aenescens</i>	Yes		Carlson et al. (2001)
			<i>Musca autumnalis</i>	Yes		Jurenka et al. (1998)
<i>Stomoxys calcitrans</i>	Yes			Carlson and Mackley (1985), Muhammed et al. (1975)		
Hymenoptera	Musco domesticus		Yes	Yes	Adams et al. (1995), Carlson et al. (1971), Nelson et al. (1981)	
		Simuliidae	<i>Wilhelmia equina</i>	Yes		Büda et al. (2003)
		Reduviidae	<i>Dipetalogaster maxima</i>	No		Juárez et al. (2002)
			<i>Triatoma barberi</i>	No		Juárez et al. (2002)
			<i>Triatoma dimidiata</i>	Yes		Juárez et al. (2002)
			<i>Rhodnius prolixus</i>	No		Juárez et al. (2001)
		Pentatomidae	<i>Bagrada hilaris</i>	Yes		De Pasquale et al. (2007)
		Anthophoridae	<i>Amegilla dawsoni</i>	Yes		Simmons et al. (2003)
			Bethyidae	<i>Cephalonomia stephanoderis</i>	Yes	
		<i>Cephalonomia tarsalis</i>		Yes		Howard (1998)
<i>Cephalonomia waterstoni</i>	Yes			Howard (1992)		
<i>Laelius utilis</i>	Yes			Howard (1992)		
Lepidoptera	Braconidae	<i>Ascogaster quadridentata</i>	Yes		Espelie and Brown (1990)	
		<i>Cardiochiles nigriceps</i>	Yes	Yes	Syvvertsen et al. (1995)	
		Cephiidae	<i>Cephus cinctus</i>	Yes		Bartelt et al. (2002)
		Colletidae	<i>Colletes cucicularius</i>	Yes	Yes	Mant et al. (2005)
		Eucharitidae	<i>Kapala sulcifacies</i>	Yes		Howard et al. (2001)
		Eulophidae	<i>Diglyphus isaea</i>	Yes		FinidoriLogli et al. (1996)
		Eurytomidae	<i>Eurytoma amygdali</i>	Yes	Yes	Krokos et al. (2001)
		Myrmicinae	<i>Cardiocondyla obscurior</i>	Yes	Yes	Cremer et al. (2002)
		Perilampinae	<i>Perilampus fluvicornis</i>	Yes		Espelie et al. (1990)
		Orthoptera	Pteromalidae	<i>Lariophagus distinguendus</i>	Yes	Yes
<i>Muscidifurax raptor</i>	Yes				Bernier et al. (1998)	
<i>Muscidifurax raptorellus</i>	Yes				Bernier et al. (1998)	
<i>Muscidifurax zaraptor</i>	Yes				Bernier et al. (1998)	
<i>Nasonia vitripennis</i>	Yes			Yes	Steiner et al. (2006)	
<i>Pteromalus cerealellae</i>	Yes				Howard (2001)	
Sphecidae	<i>Eurcerceris conata</i>			Yes		Clarke et al. (2001)
	<i>Eurcerceris rubripes</i>			Yes		Clarke et al. (2001)
Noctuidae	<i>Anticarsia gemmatalis</i>			Yes	Yes	Heath et al. (1983)
	Noctuoidae			<i>Helicoverpa armigera</i>	Yes	
<i>Helicoverpa zea</i>		Yes		Carlson et al. (1991)		
<i>Heliiothis subflexa</i>		No		Carlson et al. (1991)		
<i>Heliiothis virescens</i>		Yes		Carlson et al. (1991)		
Nymphalidae	<i>Lasiommata megera</i>	Yes		Dapporto (2007)		
	<i>Lasiommata paramegaera</i>	Yes		Dapporto (2007)		
Papilionidae	<i>Papilio polytes</i>	Yes		Ômura and Honda (2005)		
	Tortricidae	<i>Cydia pomonella</i>	No		Espelie et al. (1990)	
Orthoptera	Acrididae	<i>Chorthippus parallelus</i>	Yes		Neems and Butlin (1994), Tregenza et al. (2000)	
		<i>Chortoicetes terminifera</i>	No		Hooper et al. (1996)	
		<i>Locusta migratoria cinerascens</i>	No		Genin et al. (1986)	
		<i>Schistocerca americana</i>	No		Espelie et al. (1994)	
		<i>Schistocerca shoshone</i>	Yes		Chapman et al. (1995)	
		Gryllidae	<i>Acheta domesticus</i>	Yes		Warthen and Uebel (1980)
			<i>Gryllus bimaculatus</i>	Yes	Yes	Tregenza and Wedell (1997)
		Trigonidiidae	<i>Laupala makaio</i>	Yes		Mullen et al. (2007)

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