A high incidence of parthenogenesis in agricultural pests

Ary A. Hoffmann^{1,2,3,*}, K. Tracy Reynolds^{1,2,3}, Michael A. Nash^{1,2,3}
and Andrew R. Weeks^{1,2,3}

¹*Centre for Environmental Stress and Adaptation Research*, ²*Department of Genetics*, and ³*Department of Zoology*,
The University of Melbourne, Parkville, 3052 Victoria, Australia

Parthenogenetic species are assumed to represent evolutionary dead ends, yet parthenogenesis is common in some groups of invertebrates particularly in those found in relatively constant environments. This suggests that parthenogenetic reproduction might be common in pest invertebrates from uniform agricultural environments. Based on the evaluations of two databases from North America and Italy, we found that parthenogenetic species comprised 45 per cent (North America) or 48 per cent (Italy) of pest species derived from genera where parthenogenesis occurred, compared with an overall incidence of 10 per cent or 16 per cent in these genera. In establishing these patterns, we included only genera containing at least some member species that reproduced by parthenogenesis. The high incidence of parthenogenesis in pest species is spread across different families and several insect orders. Parthenogenetic reproduction may be favoured in agricultural environments when particular clones have a high fitness across multiple generations. Increasing the complexity and variability of agricultural environments represents one way of potentially controlling parthenogenetic pest species.

Keywords: parthenogenesis; reproduction; agricultural pests; asexuality; insects

1. INTRODUCTION

Sexual reproduction predominates in the animal kingdom (Maynard Smith 1978) and there are many elegant explanations for the advantage of sexual reproduction (Williams 1975; Maynard Smith 1978; Kondrashov 1988; West *et al.* 1999; Otto & Lenormand 2002). Nevertheless, in some groups of organisms there is a high incidence of parthenogenetic reproduction (e.g. Welch & Meselson 2000), and several groups have recently been shown to evolve for long periods of time in a strictly parthenogenetic mode (Welch & Meselson 2000; Heethoff *et al.* 2007). Interestingly, parthenogenetic taxa are often associated with ecological factors and, in particular, a lack of disturbance in environments (Williams 1975; Vrijenhoek & Pfeiler 1997; Kearney 2003; Silvertown 2008).

Quantitative genetic models show that sexuality is favoured when there are periods of directional selection in environments that vary, whereas asexuality may be favoured under constant conditions (Burger 1999). This may help explain the high incidence of parthenogenesis in environments such as stable forest soils when compared with other types of habitat (Domes *et al.* 2007). Experimental manipulations support the notion that parthenogenetic species have relatively higher success under constant and favourable areas than under stressful and changing conditions. For instance, Domes *et al.* (2007) found that parthenogenetic oribatid soil mites suffered more from resource depletion than sexual taxa when tested in microcosms. Likewise, Maraun *et al.*

(2004) found that parthenogenetic mites were more susceptible to mechanical disturbance of soil than sexual taxa. Parthenogenetic invertebrates may also be at an advantage where frequent colonization events occur because populations can be initiated from single individuals, whereas sexual species require the presence of males and females. This could provide an advantage when there is long-distance migration into a favourable or novel environment (Karako *et al.* 2002; Mondor *et al.* 2007).

Both stable conditions and colonization following long-distance dispersal might place parthenogenetic species at an advantage in agricultural landscapes exploited by pests. Orchards, vineyards, pastures, crops and plantations provide relatively uniform environments where ongoing selection for the production of new genetic variants through sexual reproduction is likely to be weaker than in more variable natural landscapes. Some lineages of parthenogenetic species could thrive in agricultural environments at the expense of sexual relatives, particularly given the twofold advantage that parthenogens can have over individuals reproducing sexually (Maynard Smith 1978).

Here, we test whether parthenogenetic organisms are relatively more common among agricultural invertebrate pests. We link databases on parthenogenetic insect taxa with those on pests, and consider the relative incidence of pests in North America and Italy. Some general implications for agricultural pest control are then discussed.

2. MATERIAL AND METHODS

A list of asexual insect species was obtained from Normark (2003). The list was considered complete based on published information and included asexual species identified on the

* Author and address for correspondence: Department of Genetics, The University of Melbourne, Parkville, 3052 Victoria, Australia (ary@unimelb.edu.au).

basis of a lack of males as well as cytologically, although there are likely to be many undescribed asexual insects not included in the list. Asexual taxa that undergo a periodic bout of sex (e.g. aphids), often called cyclic parthenogens, were treated here as sexual organisms. Only genera containing at least one asexual species were considered in this compilation because the absence of sex in the other genera might represent a phylogenetic constraint rather than being related to the effects of selection.

We examined the distribution of asexual and sexual species in North America and Italy, where complete lists of insects were available on the World Wide Web. Two web-based databases were used for lists of species in the two regions: www.nearctica.com for North America and www.faunaitalia.it for Italy. These sites were used to develop the lists of species present in the different countries.

We then determined the pest status of the sexual and parthenogenetic species in these lists. The source of information for pest status was the 'Pest Directory', compiled by the International Society for Pest Information (Griesheim, Germany). All species recorded as being a pest were noted and compared to the above lists, regardless of the impact or type or amount of information available for a particular pest. We included all pests listed regardless of whether they were classified as agricultural, garden or forestry pests.

In a few cases, asexual species were undescribed and were not considered in the comparison as they could not be checked against species lists. We then checked to see if there were pest species in a genus. We excluded those genera which did not contain recognized pests because differences among groups might then reflect their propensity to form pests rather than being a consequence of asexual reproduction. We also excluded genera without asexual species in the two regions (North America and Italy) because the absence of asexual species might then reflect biogeographic reasons rather than the potential of asexual or sexual species to be pests.

Some bias is unavoidable in our comparisons. Pest species tend to be common and well studied, and the list of parthenogens compiled by Normark (2003) includes species for which the only evidence of parthenogenesis is a lack of males. If pest species had been sampled more intensively and widely than non-pest species, this might increase the chances of finding males in pest species, and decrease the likelihood of pest species being recorded as parthenogens. Conversely, evidence for parthenogenesis in some species is based on the cultures reared in the laboratory because pests are more likely to be reared successfully in the laboratory than non-pests; this could increase the likelihood of pest species being recorded as parthenogens.

3. RESULTS

Overall in North America, there were 119 genera across eight orders with asexual species. These figures include only genera with both pest and parthenogenetic species in the region being considered. A full list of the number of species in the different genera is provided in table 1. The genera considered included 2048 sexual species, of which 202 were pest species. For the parthenogens, the equivalent numbers were 220 overall, of which 163 were pest species. The relative abundance of parthenogenetic reproduction among the pest species was therefore high; while parthenogens comprised 10 per cent of the

species in the genera selected, they comprised 45 per cent of the pest species in these genera. Because a few genera that have only parthenogenetic species might bias these results, we also examined the distribution of sexuals and parthenogens after removing genera that did not have any sexual species within the region. With this adjustment, the percentage of species that were parthenogenetic overall (8%) was still much lower than the percentage that was a pest (39%).

The relative abundance of parthenogenetic and sexual species across different families for the genera in North America is plotted in figure 1*a*. The abundance of parthenogens was relatively higher in the pests of all families except in four families where only one pest parthenogen was present (Blaberidae, Dermestidae, Phylloxeridae and Torymidae), in three dipteran families where the incidence of parthenogenesis was extremely low and in the Trogidae which included two sexual pest species and one parthenogen that was not a pest species. Thus, while the majority of parthenogens are Hemiptera, there is a tendency in most groups for parthenogens to be relatively more common in pests than in non-pests. This is clearly indicated when the incidence of parthenogens in pest species is plotted against the overall species incidence for each family (figure 2). Based on a sign test, there are significantly ($p=0.001$) more families with a higher proportion of parthenogens in pest organisms compared with non-pest organisms.

In Italy, there were 101 genera across seven orders, and are listed in table 2. There were a total of 997 sexual species and 197 parthenogens in these genera with 142 sexually reproducing pests, compared with 133 parthenogenetic pests. The proportion of parthenogenetic species overall (17%) was therefore much lower than the proportion in the pest group (48%). This difference persisted (14% versus 42%) when genera that had only parthenogenetic species within the region were excluded.

The distribution of parthenogens across families in Italy (figure 1*b*) suggests a similar pattern to that seen in North America. The proportion of parthenogens was higher in pest groups of a range of families. There were five families with only a single parthenogenetic pest species (Chrysomelidae, Cryptococcidae, Margarodidae, Lymantriidae and Psyllipsocidae). Parthenogens were most common in the Hemiptera and the only pest families where sexuals were more abundant were the Trogidae, Agromyzidae and Adelgidae. As in the case of North America, a sign test indicates significantly ($p=0.005$) more families with a higher proportion of parthenogens among pest organisms compared with non-pest organisms (figure 2).

We also had access to the total number of pest species in families in Italy, and used this information to compute the overall incidence of parthenogenetic pests within those insect families that contained at least one parthenogenetic species. In total, there were 707 pest species in these families, compared with the 133 parthenogenetic species. Thus, the overall incidence of parthenogenesis among families that contained pests and at least one parthenogenetic species was 19 per cent, which is lower than the figure of 48 per cent given above owing to the inclusion of genera in the families that contained no parthenogenetic species.

Figure 1. Incidence of parthenogenesis in the families of insects from (a) North America and (b) Italy, with species considered overall (open bars) or only if they are pests (hatched bars).

Figure 2. Plot of incidence of parthenogenesis in the pests and species overall in different families of insects from (a) North America and (b) Italy. If parthenogenesis is as frequent in pest species as in non-pest species, then a straight line with a slope of 1 is expected.

4. DISCUSSION

This compilation indicates that parthenogenesis is much more common among insect pests than related non-pest insect species. The same pattern may occur for

other groups of organisms. For instance, there are a number of pest mites that reproduce parthenogenetically. These include the earth mites belonging to the Penthalidae that comprise pasture and crop pests

Table 1. Number of species in the insect genera from North America, which contain pest and sexual/asexual species.

order	family	genus	total		pests	
			sexual	asexual	sexual	asexual
Blattodea	Blaberidae	<i>Pycnoscelus</i>		1		1
Coleoptera	Anobiidae	<i>Ptinus</i>	36	1	3	1
	Chrysomelidae	<i>Bromius</i>		1		1
		<i>Calligrapha</i>	26	1	1	1
		<i>Longitarsus</i>	42	1	1	
		<i>Altica</i>	58	1	2	
	Curculionidae	<i>Atrichonotus</i>		1		1
		<i>Callirhopalus</i>		1		1
		<i>Calomycterus</i>		1		1
		<i>Cercopedius</i>		1		1
		<i>Lissorhoptrus</i>	5	1		1
		<i>Listroderes</i>		2		1
		<i>Otiorrhynchus</i>	8	9	2	8
		<i>Sciaphilus</i>		1		1
		<i>Sciopithes</i>	5	1		1
		<i>Reesa</i>		1		1
Diptera	Elateridae	<i>Aeolus</i>	17	1		1
	Agromyzidae	<i>Phytomyza</i>	19	2	4	
	Ceratopogonidae	<i>Culicoides</i>	145	1	16	
	Chironomidae	<i>Paratanytarsus</i>	11	1		1
		<i>Tanytarsus</i>	33	1	2	
Hemiptera	Simuliidae	<i>Prosimulium</i>	42	1	2	
	Adelgidae	<i>Adelges</i>	8	2		2
	Adelgidae	<i>Pineus</i>	5	6	1	3
	Aleyrodidae	<i>Trialeurodes</i>	29	1	6	1
	Aphidae	<i>Acyrtosiphon</i>	23	2	2	2
		<i>Aloephagus</i>		1		1
		<i>Amphorophora</i>	12	1	1	1
		<i>Anoecia</i>	6	1	1	
		<i>Aphis</i>	144	6	1	6
		<i>Aulacorthum</i>	3	2		2
		<i>Brachycaudus</i>	6	2	4	2
		<i>Cavariella</i>	11	1		1
		<i>Cerataphis</i>	2	1	2	1
		<i>Chaetosiphon</i>	5	2	1	1
		<i>Cinara</i>	143	8	16	5
		<i>Coloradoa</i>	4	1	1	1
		<i>Dysaphis</i>	5	5	4	4
		<i>Eriosoma</i>	8	1	2	1
		<i>Essigella</i>	12	1		1
		<i>Forda</i>		2		1
		<i>Hyalopterus</i>	1	1	1	1
		<i>Hysteroneura</i>		1	1	1
		<i>Illinoia</i>	37	3	1	
		<i>Macrosiphoniella</i>	14	1	3	1
		<i>Macrosiphum</i>	77	3	1	3
		<i>Megoura</i>		1		1
		<i>Myzocallis</i>	28	1	4	
		<i>Myzus</i>	13	5	2	4
		<i>Nearctaphis</i>	12	1		1
		<i>Neotoxoptera</i>	1	2		1
		<i>Ovatus</i>	4	1		1
		<i>Pemphigus</i>	21	3	3	3
		<i>Pentalonia</i>		1		1
		<i>Pleotrichophorus</i>	48	1		1
		<i>Rhodobium</i>		1		1
		<i>Rhopalosiphonius</i>	3	2		1
		<i>Rhopalosiphum</i>	8	5	1	4
		<i>Schizaphis</i>	7	2		1
		<i>Semiaphis</i>		1		1
		<i>Sipha</i>	3	1	1	1
		<i>Smynthuroides</i>		1		1

(Continued.)

Table 1. (Continued.)

order	family	genus	total		pests	
			sexual	asexual	sexual	asexual
Hymenoptera	Asterolecaniidae	<i>Takecallis</i>		3		1
		<i>Tetraneura</i>	1	2		2
		<i>Therioaphis</i>	3	1	2	1
		<i>Toxoptera</i>		2		2
		<i>Tuberculatus</i>	1	3	3	
		<i>Uroleucon</i>	88	2	2	1
		<i>Asterolecanium</i>	1	3		2
	Coccidae	<i>Ceroplastes</i>	8	3	4	3
		<i>Coccus</i>	2	5	1	5
		<i>Eucalymnatus</i>		1		1
		<i>Milviscutulus</i>		1		1
		<i>Parasaissetia</i>		1		1
		<i>Parthenolecanium</i>	2	5	2	3
		<i>Physokermes</i>	4	1		1
		<i>Protopulvinaria</i>		1		1
		<i>Pulvinaria</i>	19	3	6	1
		<i>Saissetia</i>	1	3	1	3
	Diaspididae	<i>Abgrallaspis</i>	1	1		1
		<i>Aspidiotus</i>	6	2	3	2
		<i>Chionaspis</i>	22	1	1	1
		<i>Chrysomphalus</i>	2	1	2	1
		<i>Diaspis</i>	12	1	2	1
		<i>Fiorinia</i>	4	1	2	1
		<i>Hemiberlesia</i>	4	3		3
		<i>Howardia</i>		1	1	1
		<i>Ischnaspis</i>		1	1	1
		<i>Kuwvanaspis</i>	2	1		1
		<i>Lepidosaphes</i>	15	1	6	1
		<i>Neopinnaspis</i>		1		1
		<i>Odonaspis</i>	8	1	1	1
		<i>Parlatoria</i>	8	1	5	1
		<i>Pinnaspis</i>		3		3
		<i>Quadraspidiotus</i>	8	1	1	
	Magarodidae	<i>Matsucoccus</i>	15	2		1
	Ortheziidae	<i>Orthezia</i>	23	1		1
	Pseudococcidae	<i>Antonina</i>	5	1	2	1
		<i>Dysmicoccus</i>	27	1	3	1
		<i>Ferrisia</i>	4	1		1
		<i>Phenacoccus</i>	35	1	9	1
		<i>Rhizoecus</i>	31	1	4	1
Hymenoptera	Phylloxeridae	<i>Daktulosphaira</i>		1		1
	Cepidae	<i>Cephus</i>	1	1	1	1
	Cynipidae	<i>Diplolepis</i>	3	8	1	3
	Cynipidae	<i>Plagiotrochus</i>		1		1
	Tenthredinidae	<i>Heterarthrus</i>		1		1
		<i>Nematus</i>	81	1	3	1
		<i>Pontania</i>	41	1	2	1
		<i>Pristiphora</i>	43	2	2	1
		<i>Megastigmus</i>	23	1	6	1
Lepidoptera	Torymidae	<i>Alsophila</i>		1		1
	Lymantriidae	<i>Orgyia</i>	9	1	3	1
Psocoptera	Ectopsocidae	<i>Ectopsocus</i>	7	1		1
	Liposcelidae	<i>Liposcelis</i>	22	1	7	1
	Psyllipsocidae	<i>Psyllipsocus</i>	1	1		1
	Trogiidae	<i>Lepinotus</i>	2	1	2	
Thysanoptera	Thripidae	<i>Scirtothrips</i>	12	1	1	1
		<i>Taeniothrips</i>	9	1	1	1
		<i>Thrips</i>	57	2	7	2

Table 2. Number of species in the insect genera in Italy, which contain pest and sexual/asexual species.

order	family	genus	total		pests	
			sexual	asexual	sexual	asexual
Coleoptera	Anobiidae	<i>Pinus</i>	41	1	5	1
	Chrysomelidae	<i>Bromius</i>		1		1
		<i>Gastrophysa</i>	1	1		
		Curculionidae	<i>Eusomus</i>		1	
	<i>Liophloeus</i>		1	1		
<i>Polydrusus</i>	5		1	3		
<i>Sciaphilus</i>			1		1	
Diptera	Chironomidae	<i>Paratanytarsus</i>	9	1		1
Embioptera	Oligotomidae	<i>Haploembia</i>		1		
Hemiptera	Adelgidae	<i>Adelges</i>	1	1	1	
		<i>Pineus</i>	2	1	1	1
	Aleyrodidae	<i>Trialeurodes</i>	3	1	1	1
		Aphidae	<i>Aloephagus</i>		1	
	<i>Amphorophora</i>		2	1	1	1
	<i>Aploneura</i>		1	1		1
	<i>Baizongia</i>			1		1
	<i>Cavariella</i>		6	1		1
	<i>Coloradoa</i>		6	1	1	1
	<i>Eriosoma</i>		4	1	1	1
	<i>Hammamelistes</i>			1		
	<i>Hormaphis</i>			1		
	<i>Hyadaphis</i>		2	1	2	1
	<i>Hyalopterus</i>		1	1	1	1
	<i>Illinoia</i>			1		
	<i>Jacksonia</i>			1		
	<i>Macchiatella</i>			1		
	<i>Macrosiphoniella</i>		19	1	2	1
	<i>Megoura</i>			1		1
	<i>Melanaphis</i>		2	1	1	
	<i>Metopolophium</i>		4	1	1	1
	<i>Mimeuria</i>			1		
	<i>Myzaphis</i>		2	1		
	<i>Ovatus</i>		3	1	1	1
	<i>Pachypappa</i>		2	1		
	<i>Paracletus</i>		1	1		
	<i>Patchiella</i>			1		
	<i>Pemphigus</i>		8	1	1	1
	<i>Pentalonia</i>			1		1
	<i>Pterochloroides</i>			1		1
	<i>Rectinasus</i>			1		
	<i>Rhodobium</i>			1		1
	<i>Rhopalomyzus</i>		1	1		
	<i>Semiaphis</i>		1	1		1
	<i>Siculaphis</i>			1		
	<i>Sipha</i>		2	1	1	1
	<i>Smynthuroides</i>			1		1
	<i>Therioaphis</i>	9	1	1	1	
	<i>Toxoptera</i>		1		1	
	<i>Trama</i>		1			
	<i>Wahlgreniella</i>	1	1			
	Asterolecaniidae	<i>Asterodiaspis</i>	4	1		1
		<i>Bambusaspis</i>		1		1
		Coccidae	<i>Eucalymnatus</i>		1	
	<i>Parasaissetia</i>			1		1
	<i>Physokermes</i>		1	1	1	1
	<i>Protopulvinaria</i>			1		1
<i>Pulvinaria</i>			1		1	
<i>Rhizopulvinaria</i>	2		1			
Cryptococcidae	<i>Cryptococcus</i>			1		1
Delphacidae	<i>Muellerianella</i>		1	1		
Diaspididae	<i>Abgrallaspis</i>	1	1		1	
	<i>Chionaspis</i>	2	1		1	

(Continued.)

Table 2. (Continued.)

order	family	genus	total		pests	
			sexual	asexual	sexual	asexual
Hymenoptera		<i>Chrysomphalus</i>	1	1	1	1
		<i>Diaspis</i>	3	1	2	1
		<i>Fiorinia</i>		1		1
		<i>Hemiberlesia</i>	1	1		1
		<i>Howardia</i>		1		1
		<i>Ischnaspis</i>		1		1
		<i>Lepidosaphes</i>	9	1	3	1
		<i>Leucaspis</i>	4	1		1
		<i>Odonaspis</i>		1	1	1
		<i>Parlatoria</i>	5	1	5	1
		<i>Quadraspidiotus</i>	12	1	2	1
	Magarodidae	<i>Gueriniella</i>		1		
	Magarodidae	<i>Marchalina</i>		1		1
	Ortheziidae	<i>Orthezia</i>	1	1		1
	Phylloxeridae	<i>Aphanostigma</i>		1		1
		<i>Moritziella</i>		1		
		<i>Viteus</i>		1		1
	Pseudococcidae	<i>Antonina</i>	1	1		1
		<i>Coccura</i>		1		
	Aphelinidae	<i>Aphelinus</i>	6	1		
	Apidae	<i>Ceratina</i>	12	1		
	Braconidae	<i>Bracon</i>	95	1		
		<i>Meteorus</i>	23	1		
		<i>Pygostolus</i>	2	1		
	Cynipidae	<i>Liposthenes</i>		1		
		<i>Phanacis</i>		1		
	Encyrtidae	<i>Coccidoxenoides</i>		1		
	Ichneumonidae	<i>Venturia</i>		1		
	Mymaridae	<i>Anagrus</i>	8	1		
		<i>Anaphes</i>	11	1		
	Signiphoridae	<i>Signiphora</i>		1		
	Tenthredinidae	<i>Nematus</i>	27	1	1	1
		<i>Pontania</i>	13	1	2	1
		<i>Strongylogaster</i>	5	1		
	Torymidae	<i>Megastigmus</i>	4	1	3	1
		<i>Torymus</i>	18	1		
Lepidoptera	Gracillariidae	<i>Phyllonorycter</i>	83	1	15	1
	Lymantriidae	<i>Orgyia</i>		1		1
Orthoptera	Gryllidae	<i>Myrmecophila</i>	2	1		
	Tettigoniidae	<i>Saga</i>	1	1		
Phasmatodea	Bacillidae	<i>Clonopsis</i>		1		
Psocoptera	Caeciliidae	<i>Caecilius</i>	6	1		
	Epipsocidae	<i>Epipsocus</i>		1		
	Liposcelidae	<i>Liposcelis</i>	15	1	7	1
	Psocidae	<i>Psocus</i>		1		
		<i>Trichadenotecnum</i>	2	1		
	Psyllipsocidae	<i>Psyllipsocus</i>		1		1
	Troctopsocidae	<i>Chelyopsocus</i>		1		
	Trogiidae	<i>Cerobasis</i>	1	1		
		<i>Lepinotus</i>	2	1	2	
Thysanoptera	Thripidae	<i>Pseudodendrothrips</i>		1		1
		<i>Scirtothrips</i>	1	1	1	1
		<i>Taeniothrips</i>	1	1	1	1
Zygentoma	Ateluridae	<i>Proatelurina</i>		1		

(Umina *et al.* 2004), the Bryobia mites that are pests of pasture and crop plants (Weeks & Breeuwer 2001; Arthur *et al.* in press) and false spider mites that are pests of citrus (Kitajima *et al.* 2007). Unfortunately, the mode of reproduction of insufficient numbers of mites is known to undertake a general comparison of the incidence of parthenogenetic reproduction in pest and non-pest mites.

Several factors may contribute to the high incidence of parthenogenesis among pests. The most likely reason is that agricultural environments are stable and uniform with an abundance of resources. In these environments, the same genotype may be continuously favoured by selection; this leads to a selective advantage of some parthenogenetic lineages over a sexual population, whereas sexual reproduction is favoured in variable environments with periods

of directional selection (Burger 1999). Empirical data on invertebrate groups such as oribatid mites support the notion that parthenogens are more likely to have an advantage over sexuals in constant than in variable environments (Domes *et al.* 2007).

Another factor is that environmental cues leading to sexual reproduction may be absent in agricultural ecosystems. Cyclical parthenogens such as aphids that reproduce sexually on some occasions, but not others, often require specific hosts to trigger a sexual phase and these hosts might be absent, particularly if the aphids have invaded agricultural areas from other regions. If the environmental cues are missing for long enough, then the sexual reproduction might be lost permanently when there is DNA decay in genes essential for sexual reproduction (Wilson & Sunnucks 2006). In grape phylloxera, there is also evidence that lineages in viticultural regions away from the native range of phylloxera have become asexual (Corrie *et al.* 2002), in contrast to patterns of reproduction where different hosts are available (Downie *et al.* 2000).

Finally, sporadic colonization might favour parthenogenesis in ephemeral agricultural crops. Colonization is unlikely to favour parthenogenesis in pastures, perennial crops, forests and orchards, but may be important in some horticultural and broad acre crops that are re-sown annually in a patchy arrangement. Some genetic studies suggest that colonization of these crops by pests might involve only a small number of invaders (Daly & Gregg 1985; Vialatte *et al.* 2007), and these invaders may have difficulty in finding mates. However, we suspect that this factor is less important than the others already discussed because many of the groups in table 1 with high numbers of parthenogens—such as the Coccidae, Curculionidae and Diaspididae—are pests of woody plants rather than annual crops.

Parthenogenetic species are often thought to represent general purpose genotypes capable of having a high fitness across different environments (Lynch 1984), but it is now recognized that they can also contain high levels of genetic variability and comprise specialist genotypes adapted to different conditions (Vrijenhoek 1984; Harshman & Futuyma 1985; Fox *et al.* 1996; Weeks & Hoffmann 1998). Genotypes can predominate on different hosts or at different times of the year. Parthenogenetic lineages appear capable of exploiting specific niches (Vrijenhoek 1984; Weeks & Hoffmann 1998), and the agricultural environment potentially provides a stable distribution of such niches.

Pests are nevertheless faced with unique sets of selection pressures in agricultural environments. In particular, the application of agricultural chemicals provides novel selection pressures to which pests have to adapt. Although parthenogenetic lineages can differ in susceptibility to pesticides (Umina & Hoffmann 1999), the rates of adaptation will be slower than in sexual species. Therefore, insecticide resistance development is likely to be of less concern in parthenogenetic species, particularly if the resistance involves multiple loci as opposed to single mutational steps. Parthenogens may even have higher inherent rates of resistance to pesticides, as in the case of parthenogenetic earth mites when compared with their close sexual relatives (Umina *et al.* 2004), but ongoing evolutionary responses are likely to be slower. Given that sexual reproduction is thought to be at least partly selected

through parasites and pathogens (West *et al.* 1999; Jokela *et al.* 2003; Kumpulainen *et al.* 2004), parthenogenetic pests might be particularly susceptible to control by *Metarhizium* and other biological control agents. In natural populations, sexual forms of species appear to be more persistent in environments where there is a high load of pathogens and parasites (Jokela *et al.* 2003), and this factor might be exploited in controlling parthenogenetic pests.

In summary, parthenogenesis appears to be relatively more common among pests than among non-pest groups of insects and mites, at least in those taxa where asexual and sexual species are found. This is consistent with the advantages parthenogenetic organisms are likely to have over sexuals in stable and resource-rich environments. Different control strategies might be implemented against parthenogenetic pests than for sexual species, such as through pesticides where resistance mechanisms require responses through multiple genes and/or biopesticides. This might eventually produce shifts in pest complexes away from parthenogenetic pests in crops that are sprayed or that carry multiple gene resistance mechanisms.

We thank Ben Normark for his several insightful comments. A.A.H. held a Federation fellowship from the ARC while completing this work.

REFERENCES

- Arthur, A., Hoffmann, A. A., Umina, P. A. & Weeks, A. R. In press. Emerging pest mites of grains (*Balaustium medicagoense* and *Bryobia* spp.) show high levels of tolerance to currently registered pesticides. *Aust. J. Exp. Agric.*
- Burger, R. 1999 Evolution of genetic variability and the advantage of sex and recombination in changing environments. *Genetics* **153**, 1055–1069.
- Corrie, A. M., Crozier, R. H., van Heeswijck, R. & Hoffmann, A. A. 2002 Clonal reproduction and population genetic structure of grape phylloxera, *Daktulosphaira vitifoliae*, in Australia. *Heredity* **88**, 203–211. (doi:10.1038/sj.hdy.6800028)
- Daly, J. C. & Gregg, P. 1985 Genetic variation in *Heliothis* in Australia: species identification and gene flow in the 2 pest species *Heliothis armigera* (Hübner) and *Heliothis punctigera* Wallengren (Lepidoptera, Noctuidae). *Bull. Entomol. Res.* **75**, 169–184.
- Domes, K., Scheu, S. & Maraun, M. 2007 Resources and sex: soil re-colonization by sexual and parthenogenetic oribatid mites. *Pedobiologia* **51**, 1–11. (doi:10.1016/j.pedobi.2006.11.001)
- Downie, D. A., Granett, J. & Fisher, J. R. 2000 Distribution and abundance of leaf galling and foliar sexual morphs of grape phylloxera (Hemiptera: Phylloxeridae) and *Vitis* species in the central and eastern United States. *Environ. Entomol.* **29**, 979–986.
- Fox, J. A., Dybdahl, M. F., Jokela, J. & Lively, C. M. 1996 Genetic structure of coexisting sexual and clonal subpopulations in a freshwater snail (*Potamopyrgus antipodarum*). *Evolution* **50**, 1541–1548. (doi:10.2307/2410890)
- Harshman, L. G. & Futuyma, D. J. 1985 The origin and distribution of clonal diversity in *Alsophila pometaria* (Lepidoptera: Geometridae). *Evolution* **39**, 315–324. (doi:10.2307/2408365)
- Heethoff, M., Domes, K., Laumann, M., Maraun, M., Norton, R. A. & Scheu, S. 2007 High genetic divergences indicate ancient separation of parthenogenetic lineages of

- the oribatid mite *Platynothrus peltifer* (Acari, Oribatida). *J. Evol. Biol.* **20**, 392–402. (doi:10.1111/j.1420-9101.2006.01183.x)
- Jokela, J., Lively, C. M., Dybdahl, M. F. & Fox, J. A. 2003 Genetic variation in sexual and clonal lineages of a freshwater snail. *Biol. J. Linn. Soc.* **79**, 165–181. (doi:10.1046/j.1095-8312.2003.00181.x)
- Karako, S., Achituv, Y., Perl-Treves, R. & Katcoff, D. 2002 *Asterina burtoni* (Asteroidea; Echinodermata) in the Mediterranean and the Red Sea: does asexual reproduction facilitate colonization? *Mar. Ecol. Prog. Ser.* **234**, 139–145. (doi:10.3354/meps234139)
- Kearney, M. R. 2003 Why is sex so unpopular in the Australian desert? *Trends Ecol. Evol.* **18**, 605–607. (doi:10.1016/j.tree.2003.09.021)
- Kitajima, E. W., Groot, T. V. M., Novelli, V. M., Freitas-Astua, J., Alberti, G. & de Moraes, G. J. 2007 *In situ* observation of the *Cardinium* symbionts of *Brevipalpus* (Acari: Tenuipalpidae) by electron microscopy. *Exp. Appl. Acarol.* **42**, 263–271. (doi:10.1007/s10493-007-9090-1)
- Kondrashov, A. S. 1988 Deleterious mutations and the evolution of sexual reproduction. *Nature* **334**, 435–440. (doi:10.1038/336435a0)
- Kumpulainen, T., Grapputo, A. & Mappes, J. 2004 Parasites and sexual reproduction in psychid moths. *Evolution* **58**, 1511–1520. (doi:10.1554/03-567)
- Lynch, M. 1984 Destabilizing hybridization, general purpose genotypes and geographic parthenogenesis. *Q. Rev. Biol.* **59**, 257–291. (doi:10.1086/413902)
- Maraun, M., Heethoff, M., Schneider, K., Scheu, S., Weigmann, G., Cianciolo, J., Thomas, R. H. & Norton, R. A. 2004 Molecular phylogeny of oribatid mites (Oribatida, Acari): evidence for multiple radiations of parthenogenetic lineages. *Exp. Appl. Acarol.* **33**, 183–201. (doi:10.1023/B:APPA.0000032956.60108.6d)
- Maynard Smith, J. 1978 *The evolution of sex*. Cambridge, UK: Cambridge University Press.
- Mondor, E. B., Tremblay, M. N. & Messing, R. H. 2007 Morphological and ecological traits promoting aphid colonization of the Hawaiian Islands. *Biol. Invasions* **9**, 87–100. (doi:10.1007/s10530-006-9010-z)
- Normark, B. B. 2003 The evolution of alternative genetic systems in insects. *Annu. Rev. Entomol.* **48**, 397–423. (doi:10.1146/annurev.ento.48.091801.112703)
- Otto, S. P. & Lenormand, T. 2002 Resolving the paradox of sex and recombination. *Nat. Rev. Genet.* **3**, 252–261. (doi:10.1038/nrg761)
- Silvertown, J. 2008 The evolutionary maintenance of sexual reproduction: evidence from the ecological distribution of asexual reproduction in clonal plants. *Int. J. Plant Sci.* **169**, 157–168. (doi:10.1086/523357)
- Umina, P. A. & Hoffmann, A. A. 1999 Tolerance of cryptic species of blue oat mites (*Penthaleus* spp.) and the redlegged earth mite (*Halotydeus destructor*) to pesticides. *Aust. J. Exp. Agric.* **39**, 621–628. (doi:10.1071/EA99028)
- Umina, P. A., Hoffmann, A. A. & Weeks, A. R. 2004 Biology, ecology and control of the *Penthaleus* species complex (Acari: Penthaleidae). *Exp. Appl. Acarol.* **34**, 211–237. (doi:10.1007/s10493-004-1804-z)
- Vialatte, A., Plantegenest, M., Simon, J. C. & Dedryver, C. A. 2007 Farm-scale assessment of movement patterns and colonization dynamics of the grain aphid in arable crops and hedgerows. *Agric. For. Entomol.* **9**, 337–346. (doi:10.1111/j.1461-9563.2007.00347.x)
- Vrijenhoek, R. C. 1984 Ecological differentiation among clones: the frozen niche variation model. In *Population biology and evolution* (eds K. Wöhrmann & V. Loeschcke), pp. 217–231. Berlin, Germany: Springer.
- Vrijenhoek, R. C. & Pfeiler, E. 1997 Differential survival of sexual and asexual *Poeciliopsis* during environmental stress. *Evolution* **51**, 1593–1600. (doi:10.2307/2411211)
- Weeks, A. R. & Breeuwer, J. A. J. 2001 *Wolbachia*-induced parthenogenesis in a genus of phytophagous mites. *Proc. R. Soc. B* **268**, 2245–2251. (doi:10.1098/rspb.2001.1797)
- Weeks, A. R. & Hoffmann, A. A. 1998 Intense selection of mite clones in a heterogeneous environment. *Evolution* **52**, 1325–1333. (doi:10.2307/2411302)
- Welch, D. M. & Meselson, M. 2000 Evidence for the evolution of bdelloid rotifers without sexual reproduction or genetic exchange. *Science* **288**, 1211–1215. (doi:10.1126/science.288.5469.1211)
- West, S. A., Lively, C. M. & Read, A. F. 1999 A pluralist approach to sex and recombination. *J. Evol. Biol.* **12**, 1003–1012. (doi:10.1046/j.1420-9101.1999.00119.x)
- Williams, G. 1975 *Sex and evolution*. Princeton, NJ: Princeton University Press.
- Wilson, A. C. C. & Sunnucks, P. 2006 The genetic outcomes of sex and recombination in long-term functionally parthenogenetic lineages of Australian Sitobion aphids. *Genet. Res.* **87**, 175–185. (doi:10.1017/S0016672306008202)