

# On the fate of sexual traits under asexuality

Casper J. van der Kooi and Tanja Schwander<sup>\*,†</sup>

*Center for Ecological and Evolutionary Studies, University of Groningen, 9700CC, Groningen, The Netherlands*

## ABSTRACT

Environmental shifts and life-history changes may result in formerly adaptive traits becoming non-functional or maladaptive. In the absence of pleiotropy and other constraints, such traits may decay as a consequence of neutral mutation accumulation or selective processes, highlighting the importance of natural selection for adaptations. A suite of traits are expected to lose their adaptive function in asexual organisms derived from sexual ancestors, and the many independent transitions to asexuality allow for comparative studies of parallel trait maintenance *versus* decay. In addition, because certain traits, notably male-specific traits, are usually not exposed to selection under asexuality, their decay would have to occur as a consequence of drift. Selective processes could drive the decay of traits associated with costs, which may be the case for the majority of sexual traits expressed in females. We review the fate of male and female sexual traits in 93 animal lineages characterized by asexual reproduction, covering a broad taxon range including molluscs, arachnids, diplopods, crustaceans and eleven different hexapod orders. Many asexual lineages are still able occasionally to produce males. These asexually produced males are often largely or even fully functional, revealing that major developmental pathways can remain quiescent and functional over extended time periods. By contrast, for asexual females, there is a parallel and rapid decay of sexual traits, especially of traits related to mate attraction and location, as expected given the considerable costs often associated with the expression of these traits. The level of decay of female sexual traits, in addition to asexual females being unable to fertilize their eggs, would severely impede reversals to sexual reproduction, even in recently derived asexual lineages. More generally, the parallel maintenance *versus* decay of different trait types across diverse asexual lineages suggests that neutral traits display little or no decay even after extended periods under relaxed selection, while extensive decay for selected traits occurs extremely quickly. These patterns also highlight that adaptations can fix rapidly in natural populations of asexual organisms, in spite of their mode of reproduction.

*Key words:* trait decay, regressive evolution, sexual traits, asexuality, parthenogenesis.

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## I. INTRODUCTION

Studies on how natural selection favours adaptations typically focus on the evolution of novel traits (e.g. Cracraft, 1990; Moczek, 2008; Brakefield, 2011; Moczek *et al.*, 2011).

However, the fate of traits that no longer contribute to fitness can also highlight the importance of natural selection for the maintenance of adaptations (Fong, Kane & Culver, 1995; Wiens, 2001; Porter & Crandall, 2003; Lahti *et al.*, 2009). Formerly adaptive traits may become

\* Author for correspondence (Tel: +41 21 692 4151; E-mail: tanja.schwander@unil.ch).

† Present address: Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

non-functional, or even maladaptive, as a consequence of environmental shifts or changes in life history, accompanied by changes in selective pressures (Fong *et al.*, 1995; Lahti *et al.*, 2009). Such traits often decay, i.e. become reduced or disappear completely, a process sometimes referred to as vestigialization.

Vestigialization is a form of regressive evolution, which may be an order of magnitude more frequent than the evolution of novel traits (Fong *et al.*, 1995). Prominent examples for vestigialization are found in the parallel eye and pigment loss in a range of cave-dwelling organisms (Wilkins & Strecker, 2003; Jeffery, 2009; Protas, Trontelj & Patel, 2011), reduced wings of flightless birds (McNab, 1994), or loss of innate defence behaviours in the absence of the relevant threats (e.g. Coss, 1999; Lahti, 2006). Less conspicuous than vestigialization of morphological or behavioural traits, regressive evolution has also been uncovered for physiological and metabolic pathways. For example, fat synthesis has decayed in parallel in different parasitoid wasps, most likely because the constant availability of host-produced lipids rendered the parasitoids' own synthesis pathways redundant (Visser *et al.*, 2010). Other 'cryptic' examples of regressive evolution stem from hosts becoming dependent on formerly parasitic bacteria for such fundamental processes as oocyte development or sex differentiation (Dedeine *et al.*, 2001; Zchori-Fein, Borad & Harari, 2006; Timmermans & Ellers, 2008; Kageyama, Narita & Watanabe, 2012).

Trait decay is not necessarily accompanied by degeneration of the molecular pathways underlying the development of its functional version. Maintenance of pathways may stem, for example, from pleiotropy where the same gene networks function in several processes (Fong *et al.*, 1995). Thus, even if a character is phenotypically absent, the genetic information responsible for its development can remain quiescent, occasionally resulting in character expression.

## II. PROCESSES UNDERLYING TRAIT DECAY

A trait can decay *via* different processes, depending on whether the formerly adaptive trait is neutral or maladaptive in the new selective environment (Fong *et al.*, 1995; Hall & Colegrave, 2008). In the first case, the trait would be under relaxed selection whereby trait-affecting mutations that would have been removed by selection under the past conditions may accumulate and fix *via* drift (e.g. Lande, 1978; Hall & Colegrave, 2008; Lahti *et al.*, 2009). This process of decay, often referred to as neutral mutation accumulation, would be expected to proceed slowly (Teotónio & Rose, 2000; Hall & Colegrave, 2008).

In the second case, if a formerly adaptive trait becomes maladaptive in a new selective environment, the trait would be expected to regress rapidly, driven by selection for reduced trait expression (Hall & Colegrave, 2008). Decay would then proceed until the character is gone, or simplified to an intermediate stage where further reduction is no longer

adaptive (Prout, 1964; Fong *et al.*, 1995; Zuk, Rotenberry & Tinghitella, 2006). Such trait reduction could also be selected for indirectly if the reduction of a useless trait releases constraints on functions that contribute to fitness and/or allows for reallocation of limited resources (Prout, 1964; Regal, 1977; Fong *et al.*, 1995; Eckert, 2001; Dorken, Neville & Eckert, 2004).

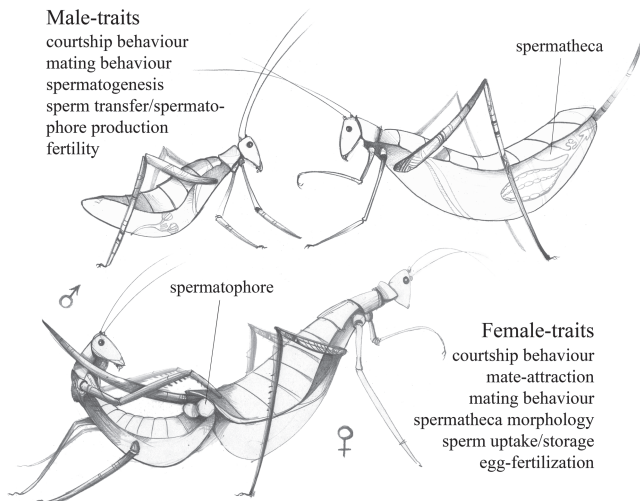
A major challenge for studies of trait decay in natural populations has been to disentangle neutral from selective processes driving the reduction of specific traits. A successful approach to demonstrating selective processes has been the analysis of traits with variable expression whereby selection-driven decay is revealed by fitness benefits in individuals with strongly reduced expression (Eckert, 2001; Dorken *et al.*, 2004). In many cases however, there is little variation among individuals in the level of trait reduction, and a similar approach could not provide positive evidence for decay driven by neutral mutation accumulation.

Part of the difficulty in identifying processes underlying trait decay stems from a lack of information on the costs of traits and genetic correlations among them, as well as a lack of parallel trait losses (Lahti *et al.*, 2009). Here, we show that regressive evolution of sexual traits in parthenogenetic all-female lineages (hereafter referred to as asexual lineages) can provide insights into both decay *via* drift and selective processes. Indeed, the many independent origins of asexual lineages from sexual ancestors in a broad range of taxa allow for comparative studies of trait decay. In addition, an exceptionally large range of sexual traits, including physiological, behavioural and morphological traits should be affected by transitions to asexuality. As a consequence, the fate of (putatively) neutral as well as highly costly traits can be investigated.

## III. DECAY OF SEXUAL TRAITS IN ASEQUAL LINEAGES

In the transition from sexual reproduction with separate male and female sexes to asexuality in all-female lineages, many formerly adaptive traits should lose their adaptive value (Carson, Chang & Lyttle, 1982). These sexual traits range from traits involved in mate location and attraction, to courtship and copulation behaviours, to traits specific to the male sex (e.g. Carson *et al.*, 1982; Pannebakker *et al.*, 2004; Lehmann *et al.*, 2011; Fig. 1).

Because certain sexual traits are not expressed at all in asexuals, these traits should only decay as a consequence of drift. Prime candidates for such neutral traits would be any trait specific to males. Most asexual lineages either produce no males at all, or if they do, the extremely rare 'accidental males' appear to have no mating opportunities or success in natural populations (e.g. Gottlieb & Zchori-Fein, 2001; Schön, Rossetti & Martens, 2009; Mirab-Balou & Chen, 2010; Schwander *et al.*, 2013). Thus, male-specific traits are either not expressed, or are only expressed in individuals that have zero fitness (the males). In both cases, male-specific



**Fig. 1.** Sexual traits expected to be under relaxed or negative selection in asexuals. Drawings courtesy of Laurent Bes.

traits are not exposed to selection and could therefore only regress at a neutral rate.

In contrast to the male-specific traits, female-expressed traits formerly involved in mate attraction are unlikely to be neutral in asexuals. In addition to energy costs associated with the production of mate-attraction signals, pheromones and acoustic signals are prime targets for predators and parasitoids to locate their prey (e.g. Zuk & Kolluru, 1998; Zuk *et al.*, 2006). Thus, the production of such signals should be under strong negative selection in asexual females, where mate attraction is superfluous.

Here, we review the fate of sexual traits in animal species characterized by asexual reproduction. A literature survey for descriptions of male and/or female sexual traits in asexual lineages allowed us to obtain information for 93 asexual lineages, representing a diversity of taxa from 11 different hexapod orders, diplopods, arachnids, crustaceans and molluscs (Table 1). By investigating different trait categories across independently derived asexual lineages, we develop insights into trait decay *via* drift and selection. We focus on asexual all-female species deriving from sexual ancestors with separate sexes, to standardize comparisons between the male and female sex. We further exclude cases of asexuality where successful reproduction is dependent on individuals of the opposite sex, as is the case for different types of sperm-dependent parthenogenesis (e.g. Lamatsch & Stöck, 2009) or male asexuality (e.g. Foucaud *et al.*, 2007; Hedtke *et al.*, 2008). In these cases, individuals of the asexual lineage still need to attract individuals of the opposite sex and mate, such that costs and benefits associated with sexual traits in these species should be more similar to sexual species than to typical sperm-independent asexuals. We use unexpressed traits, which are associated with little or no costs, to predict the level of trait decay expected in the absence of selective processes. By identifying parallel and rapid trait reductions across organisms from very different ecological contexts,

we then highlight sexual traits that are universally costly in natural populations of asexual lineages.

#### IV. TESTING FOR DECAY OF SEXUAL TRAITS

It is not possible to evaluate the functionality of a trait that is not expressed (as is the case for male traits in asexual lineages where no males are known and where male production cannot be induced). For expressed sexual traits, two approaches are used to investigate their decay in an asexual lineage. First, it is sometimes possible to examine a specific character directly *via* functional assays (for example testing for sperm motility; Gottlieb & Zchori-Fein, 2001; Zchori-Fein *et al.*, 2001) or detailed histological examinations (for example in spermathecae, evaluating the presence of specific glandular tissues required for functional storage of sperm; Gotoh *et al.*, 2012). Alternatively, trait values for asexuals are compared to corresponding values in the closest sexual relatives whereby it is relevant to use appropriate sexual references. Appropriate references are particularly important when traits involving interactions between males and females are assessed, which concerns many, if not most, sexual traits. For example, to assess the production of mate-attraction signals by asexual females, sexual males are used as signal responders (Gottlieb & Zchori-Fein, 2001; Adachi-Hagimori, Miura & Abe, 2011; Schwander *et al.*, 2013). This may pose a problem in some cases, given that sexual traits can diverge rapidly between populations, such that reduced sexual attractiveness of females to sexual males may be due to population divergences rather than to reduced signal production (i.e. decay) as a consequence of asexuality. In such cases, comparisons among different sexual populations can be useful to disentangle the effect of asexuality from between-species divergences (Schwander *et al.*, 2013).

Complementary information on sexual traits involving interactions between females and males can be obtained from males produced by females of some asexual species (see Section V). In this case, detailed behavioural and morphological observations are often necessary to distinguish whether an apparent lack of a sexual function stems from regressive evolution in females, males or both sexes such that comparisons with sexual relatives may still be pertinent. In addition, obtaining enough such asexually produced males for replicated tests may be impossible, as often only a few male individuals are known to occur in entire species (e.g. Smith, Kamiya & Horne, 2006; Baur, 2010; Mirab-Balou & Chen, 2010).

A notable exception to such sample limitation stems from hymenopteran species in which asexuality is induced by infection with bacterial endosymbionts (e.g. Stouthamer, Luck & Hamilton, 1990a; Pannebakker *et al.*, 2005; Kremer *et al.*, 2009). In sexual hymenopterans, unfertilized (haploid) eggs develop into males whereas diploid eggs develop into females (haplo-diploid sex determination). Thus virgin sexual females produce exclusively haploid eggs giving rise to sons. Females infected with parthenogenesis-inducing

Table 1. Case studies reporting on the functionality of sexual traits in asexual lineages deriving from sexual ancestors with separate sexes

Taxonomic groups and species names	Species information		Summary		Male traits				Female traits				References				
	Common name	Parthenogenesis	Sex determination in sexual sister groups	Male	Female	Male production	Normal morphology	Courting behaviour/attraction	Access to females	Mating behaviour	Sperm transfer/spermatophore production	Functional sperm		Normal spermatheca; seminal receptacles	Male attraction; response to courtship	Normal copulation behaviour; sperm/spermatophore uptake	Egg fertilization
<b>ARTHROPODA</b>																	
<b>BRANCHIOPODA</b>																	
<i>Anostraca</i>																	
<i>Artemia parthenogenetica</i>	Brine shrimp	A	ZW:ZZ	?	D	Y	Y	—	Y	Y	Y	N?	—	Y	N	MacDonald & Browne (1987) and Browne (1992)	
<b>MALACOSTRACA</b>																	
<b>Isopoda</b>																	
<i>Trichoniscus pusillus (elsabethae)</i>	Woodlouse	A	Unknown <sup>a</sup>	D	D	Y	Y	—	Y	Y	N	N	—	Y	N	Vandel (1931, 1934)	
<b>OSTRACODA</b>																	
<i>Limnocythere inopinata</i>		obl	XX:XO?	F?	?	Y	Y	—	—	—	—	—	—	—	—	Greiger <i>et al.</i> (1998)	
<i>Vestalenula cornelia</i>		obl	XX:XO?	D?	?	Y	Y	—	—	—	N <sup>b</sup>	—	—	—	—	Smith <i>et al.</i> (2006) and Schön <i>et al.</i> (2009)	
<b>ARACHNIDA</b>																	
<b>Araneae</b>																	
<i>Codoles togolaceras</i>	Spider	obl	XX:XO	?	D	N?	—	—	—	—	—	—	N <sup>c</sup>	—	—	Shimojima & Nishihira (2000)	
<i>Dysdera hungarica</i>	Spider	A	XX:XO	?	F?	N?	—	—	—	—	—	—	Y	—	—	Korenko <i>et al.</i> (2007, 2009)	
<i>Thobina minutissimus</i>	Spider	obl	XX:XO	?	D	N?	—	—	—	—	—	—	N <sup>c</sup>	—	—	Edwards <i>et al.</i> (2003)	
<i>Triaris stenaspis</i>	Spider	obl	XX:XO/XX:XY	?	F?	N?	—	—	—	—	—	—	Y	—	—	Burger (2009) and Korenko <i>et al.</i> (2009)	
<b>IXODIDA</b>																	
<i>Haemaphysalis longicornis</i> (3n strain)	Tick	A	XX:XO	D	D	Y	Y	—	N	—	N	—	—	N	—	Oliver (1971) and Oliver <i>et al.</i> (1973)	
<b>SARCOPTIFORMES</b>																	
<i>Platynothrus peltifer</i>	Oribatid mite	obl	Unknown <sup>a</sup>	D	D	Y	Y <sup>d</sup>	0 <sup>c</sup>	0 <sup>c</sup>	0 <sup>c</sup>	N <sup>c</sup>	—	—	N	—	Tabery (1987, 1988)	
<i>Noldrus pallidus</i>	Oribatid mite	obl	Unknown <sup>a</sup>	F	D	Y	Y	0 <sup>c</sup>	0 <sup>c</sup>	0 <sup>c</sup>	—	—	—	N	—	Tabery (1987, 1988)	
<i>Noldrus sylvestrus</i>	Oribatid mite	obl	Unknown <sup>a</sup>	F?	D	Y	Y	0 <sup>c</sup>	0 <sup>c</sup>	0 <sup>c</sup>	—	—	—	N	—	Tabery (1987, 1988)	
<i>Tritylobothonius tectorum</i>	Oribatid mite	obl	Unknown <sup>a</sup>	D	D	Y	Y <sup>d</sup>	0 <sup>c</sup>	0 <sup>c</sup>	0 <sup>c</sup>	N <sup>c</sup>	—	—	N	—	Tabery (1987, 1988)	
<b>TROMBIDIFORMES</b>																	
<i>Byobia praetiosa</i>	Clover mite	obl <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	—	Y	—	—	—	—	Y	N	Weeks & Breuwer (2001)	
<i>Brevipalpus californianus</i>	Flat mite	obl <sup>f</sup>	Haplodiploid	F?	D	Y <sup>f</sup>	Y	—	—	—	—	—	—	—	N	Groot & Breuwer (2006)	
<i>Brevipalpus obovatus</i>	Flat mite	obl <sup>f</sup>	Haplodiploid	D	D	Y <sup>f</sup>	Y	—	Y	N	N	—	—	Y	N	Groot & Breuwer (2006)	
<i>Brevipalpus phoeniceus</i>	False spider mite	obl <sup>f</sup>	Haplodiploid	F?	D	Y <sup>f</sup>	Y	—	—	—	—	—	—	—	N	Pijnacker <i>et al.</i> (1981) and Groot & Breuwer (2006)	
<b>DIPLOPODA</b>																	
<i>Nemasona varicorne</i>	Millipede	A	XX:XO/XX:XY	F	D	Y	Y	—	Y	Y	Y <sup>g</sup>	N <sup>c</sup>	—	—	—	Enghoff (1967)	
<b>HEXAPODA</b>																	
<b>Collembola</b>																	
<i>Folsomia candida</i>	Springtail	A	XX:XO	D	D	Y	Y	Y?	—	—	N	—	—	N	N?	Kiauta (1970) and Buono (2011)	
<b>COLEOPTERA</b>																	
<i>Cix fusipes</i>	Beetle	A	XX:XY?	?	D	Y <sup>h</sup>	Y <sup>h</sup>	—	—	—	—	—	—	N	N	Lawrence (1967)	
<b>Diptera</b>																	
<i>Drosophila mercatorum</i>	Fruitfly	A	XX:XY	?	D	N?	—	—	—	—	—	—	—	—	—	Carson <i>et al.</i> (1982)	
<b>Ephemeroptera</b>																	
<i>Ameletus ludens</i>	Mayfly	obl	XX:XO?	F?	?	Y	Y	—	—	—	—	—	—	—	—	Funk <i>et al.</i> (2006)	
<i>Centropilum triangulifer</i>	Mayfly	obl	XX:XO?	F?	D	Y	Y	—	—	—	—	—	—	—	—	Funk <i>et al.</i> (2006)	
<b>Hemiptera</b>																	
<i>Rhopalosiphum padi</i>	Aphid	con	XX:XO	F <sup>b</sup>	?	Y	Y	Y	Y	Y	Y	Y	—	—	—	—	Delmotte <i>et al.</i> (2001)

Table 1. Continued

Taxonomic groups and species names	Species information			Summary			Male traits					Female traits					References
	Common name	Parthenogenesis	Sex determination in	Male	Female	Male production	'Normal' morphology	Courting behaviour/attraction	Mating females	Sperm transfer	spermatophore production	Functional sperm	Normal spermatheca; seminal receptacles	Male attraction; response to courtship	Normal copulation behaviour; sperm uptake	Egg fertilization	
<b>Hymenoptera</b>																	
<i>Nomada japonica</i>	Bee	obl	Haplodiploid	?	D?	—	—	—	—	—	—	—	N <sup>c</sup>	—	—	—	Maeta <i>et al.</i> (1987)
<i>Cerapachys birai</i>	Ant	obl	Haplodiploid	?	D	N?	—	—	—	—	—	—	N	—	—	—	Tsuji & Yamauchi (1995) and Ravary & Jaisson (2004)
<i>Monomorium triviale</i>	Ant	obl	Haplodiploid	?	F?	N?	—	—	—	—	—	—	Y	—	—	—	Gotoh <i>et al.</i> (2012)
<i>Myocopterus smithii</i>	Ant	A	Haplodiploid	?	D	N?	—	—	—	—	—	—	N	—	—	—	Himler <i>et al.</i> (2009) and Rabeling <i>et al.</i> (2011)
<i>Pristomyrmex punctatus (pungens)</i>	Ant	obl	Haplodiploid	F	F?	Y	Y	—	—	—	Y <sup>k</sup>	Y	Y	—	—	—	Ito <i>et al.</i> (1984) and Gotoh <i>et al.</i> (2012)
<i>Pyramica membranifera</i>	Ant	obl	Haplodiploid	?	F?	N?	—	—	—	—	—	—	Y	—	—	—	Ito <i>et al.</i> (2010) and Gotoh <i>et al.</i> (2012)
<i>Diplolepis rosae</i>	Gall wasp	obl	Haplodiploid	F	D	Y	Y	Y	—	—	—	—	—	—	—	—	Stille & Dawring (1980)
<i>Aphytis diaspidis</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	—	Y	Y	Y <sup>k</sup>	Y	Y	Y <sup>l</sup>	Y	—	Zchori-Fein <i>et al.</i> (1995)
<i>Aphytis linguansensis</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	Y	—	Y	Y <sup>k</sup>	Y	Y	Y <sup>l</sup>	Y	—	Argov <i>et al.</i> (1995) and Zchori-Fein <i>et al.</i> (1995)
<i>Aphytis mytilaspidis</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	—	Y	Y	Y	—	—	—	—	—	Rossler & Debach (1973)
<i>Aphytis yanamensis</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	F?	?	Y <sup>f</sup>	Y	—	—	—	—	—	—	—	—	—	Zchori-Fein <i>et al.</i> (1995, 1998) and Burger (2009)
<i>Encarsia formosa</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	D	D	Y <sup>f</sup>	Y	Y	N <sup>c</sup>	N	Y <sup>k</sup>	Y <sup>m</sup>	—	Y?	N?	—	Zchori-Fein <i>et al.</i> (1992), Kajita (1993), and Hunter (1999)
<i>Encarsia hispidia</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	F?	?	Y <sup>f</sup>	Y	—	—	—	—	—	—	—	—	—	Hunter (1999) and Giorgini <i>et al.</i> (2009)
<i>Encarsia meritoria</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F?	Y <sup>f</sup>	Y	Y	Y	Y	Y <sup>k</sup>	Y	—	—	—	—	Giorgini (2001)
<i>Encarsia perniciosi</i>	Parasitoid wasp	A	Haplodiploid	F?	D	Y <sup>f</sup>	Y	—	—	—	—	—	—	—	—	—	Stouthamer & Luck (1991)
<i>Encarsia protansena</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	D	D	Y <sup>f</sup>	N	—	N	N	—	N	N	—	—	—	Giorgini (2001)
<i>Erimocerus mundus</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	—	—	Y	Y	Y <sup>k</sup>	Y	Y	Y?	—	—	De Barro & Hart (2001)
<i>Asobara japonica</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	N <sup>c</sup>	Y	Y	Y <sup>g</sup>	—	—	N	N	—	Kremer <i>et al.</i> (2009) and Reumer (2012)
<i>Lysiphlebus fabarum</i>	Parasitoid wasp	con	Haplodiploid	F <sup>b</sup>	?	Y	Y	Y	Y	Y	Y	—	—	—	—	—	Belshaw <i>et al.</i> (1999), Sandrock <i>et al.</i> (2011), and Sandrock & Vorburger (2011)
<i>Apanagyrus diversicomis</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	Y	Y	Y	Y <sup>g</sup>	N	—	—	N	—	Pijls <i>et al.</i> (1996)
<i>Diaphorencyrtus algeriathensis</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y	Y	—	—	—	—	Y	Y	—	Meyer & Hoy (2007)
<i>Gronotoma micranompha</i>	Parasitoid wasp	obl	Haplodiploid	F	D	Y <sup>f</sup>	Y	Y	Y	—	Y <sup>k</sup>	—	—	Y	Y	—	Arakaki <i>et al.</i> (2001)
<i>Galeopsomyia foveola</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	Y	Y	Y	Y <sup>k</sup>	Y	Y	Y?	—	—	Argov <i>et al.</i> (2000)
<i>Noachrysocentrus formosa</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F?	D	Y <sup>f</sup>	Y	—	—	—	N	—	—	—	—	—	Adachi-Hagimori <i>et al.</i> (2011)
<i>Priogato soenius</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F?	?	Y <sup>f</sup>	Y	—	—	—	—	—	—	—	—	—	Giorgini <i>et al.</i> (2010)
<i>Leptophthia clavipes</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	Y	Y	Y	Y <sup>g</sup>	N	—	Y	N <sup>c</sup>	—	Paunehakker <i>et al.</i> (2005) and Kraajjeveld <i>et al.</i> (2009)
<i>Tetrastichus coeruleus</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F?	D	Y <sup>f</sup>	Y	—	—	—	—	N	—	N	N	—	Reumer (2012)
<i>Venturia consensens</i>	Parasitoid wasp	con?	Haplodiploid	F	D	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	—	Schneider <i>et al.</i> (2003)
<i>Muscidifurax uniraptor</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	D	D	Y <sup>f</sup>	Y	Y	Y	N	N	N	N	N <sup>c</sup>	N	—	Gotlieb & Zchori-Fein (2001)
<i>Telenomus naevii</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	Y	Y	Y <sup>l</sup>	Y	Y <sup>l</sup>	Y <sup>l</sup>	—	Y	—	Arakaki <i>et al.</i> (2000) and Jeong & Stouthamer (2005)
<i>Trichogramma brevicapillum</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>l</sup>	Y <sup>l</sup>	Y <sup>l</sup>	Y	Y <sup>l</sup>	Y <sup>l</sup>	Y <sup>l</sup>	Y <sup>l</sup>	Y	Stouthamer & Werren (1993)
<i>Trichogramma thilonis</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>l</sup>	Y <sup>l</sup>	Y <sup>l</sup>	Y	Y <sup>l</sup>	Y <sup>l</sup>	—	Y <sup>l</sup>	Y	Stouthamer <i>et al.</i> (1990a,b)

Table 1. Continued

Taxonomic groups and species names	Species information			Summary		Male traits				Female traits								
	Common name	Parthenogenesis	Sex determination in sexual sister groups	Male	Female	Male production	'Normal' morphology	Courting behaviour/attraction	Females' fitness	Mating behaviour	Sperm transfer/sperm production	Functional sperm	Normal sperm	spermatheca; seminal receptacles	Male attraction; response to courtship	Normal copulation behaviour; sperm/spermatophore uptake	Egg fertilization	References
<i>Trichogramma canadensis</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Y <sup>f</sup>	Y <sup>f</sup>	N <sup>c</sup>	Y <sup>f</sup>	Y	Silva & Stouthamer (1997)
<i>Trichogramma deon</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Stouthamer <i>et al.</i> (1990 <i>b</i> ), Stouthamer & Luck (1993), and Stouthamer & Kazmer (1994)
<i>Trichogramma embryophagum</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F?	?	Y <sup>f</sup>	Y	—	—	—	—	—	—	—	—	—	—	Pinto & Stouthamer (1994)
<i>Trichogramma laykai</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Y	Y <sup>f</sup>	Y <sup>f</sup>	—	Y <sup>f</sup>	Y	Stouthamer & Kazmer (1994) and Hohmann <i>et al.</i> (2001)
<i>Trichogramma nr deon</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	—	—	—	—	—	—	—	—	Y <sup>f</sup>	Y	Stouthamer & Kazmer (1994)
<i>Trichogramma olae</i>	Parasitoid wasp	obl <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Stouthamer & Kazmer (1994) and Stouthamer <i>et al.</i> (1990 <i>b</i> ) and Grenier <i>et al.</i> (2002)
<i>Trichogramma plaineri</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Stouthamer <i>et al.</i> (1990 <i>a,b</i> )
<i>Trichogramma pretiosum</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Y	Y <sup>f</sup>	Y <sup>f</sup>	—	Y <sup>f</sup>	Y	Stouthamer <i>et al.</i> (1990 <i>b</i> ), Stouthamer & Luck (1993), and Stouthamer & Kazmer (1994)
<i>Trichogramma thianana</i>	Parasitoid wasp	A <sup>f</sup>	Haplodiploid	F	F	Y <sup>f</sup>	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Y	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y <sup>f</sup>	Y	Stouthamer & Werren (1993)
<b>Lepidoptera</b>																		
<i>Dalicia (Solobia) triquetrella</i> (2n strain)	Bagworm moth	A	ZOZZ;ZW:ZZ	F	VAR	Y	Y	—	Y	Y	Y	Y	Y	VAR	VAR	Y	VAR	Seiler (1960, 1963)
<i>Dalicia (Solobia) triquetrella</i> (4n strain)	Bagworm moth	obl	ZOZZ;ZW:ZZ	?	D	N	—	—	—	—	—	—	—	N <sup>c</sup>	N <sup>c</sup>	Y	N <sup>f</sup>	Seiler (1960, 1963)
<i>Dalicia (Solobia) lichellula</i>	Bagworm moth	obl	ZOZZ	?	D	N	—	—	—	—	—	—	—	—	—	Y	N	Seiler & Puchta (1956)
<i>Luffia ferchaultella</i>	Bagworm moth	obl	ZOZZ	?	D	N <sup>?</sup>	—	—	—	—	—	—	—	Y	Y	Y	N <sup>f</sup> , <sup>j</sup>	Narbel-Hofmeister (1962, 1966)
<b>Orthoptera</b>																		
<i>Poecilimon intermedius</i>	Bushcricket	obl	XX:XO	?	D	N <sup>?</sup>	—	—	—	—	—	—	—	N	N	Y	N <sup>?</sup>	Lehmann <i>et al.</i> (2007, 2011)
<i>Saga pedo</i> (4n)	Bushcricket	obl	XX:XO	F?	D	Y	Y	—	—	—	—	—	—	Y <sup>m</sup>	Y <sup>m</sup>	Y	N <sup>f</sup>	Lemonnier-Darcemont & Darcemont (2007, 2008) and Baur (2010)
<b>Phasmida</b>																		
<i>Bacillus aticus</i>	Stick insect	obl	XX:XO	F	F	Y	Y	—	—	—	—	—	—	—	—	—	Y	Scali (2009, 2013)
<i>Bacillus rositus</i>	Stick insect	A	XX:XO	F	F	Y	Y	—	—	—	Y	Y	Y	—	—	Y	Y	Scali (1968, 2009)
<i>Garaulus morosus</i>	Stick insect	obl	XX:XO	D	D	Y	Y	Y	Y	N	N	N	N	—	—	Y	N	Pijnacker (1964)
<i>Timema douglasi</i>	Stick insect	obl	XX:XO	F	D	Y	Y	Y	Y	Y <sup>g</sup>	Y <sup>g</sup>	N <sup>c</sup>	N <sup>c</sup>	N <sup>c</sup>	N <sup>c</sup>	Y	N	Schwander <i>et al.</i> (2013)
<i>Timema genericum</i>	Stick insect	obl	XX:XO	F	D	Y	Y	Y	Y	Y <sup>g</sup>	Y <sup>g</sup>	N <sup>c</sup>	N <sup>c</sup>	N <sup>c</sup>	N <sup>c</sup>	Y	N	Schwander <i>et al.</i> (2013)
<i>Timema monikensis</i>	Stick insect	obl	XX:XO	F	D	Y	Y	Y	Y	Y <sup>g</sup>	Y <sup>g</sup>	N <sup>c</sup>	N <sup>c</sup>	N <sup>c</sup>	N <sup>c</sup>	Y	N	Schwander <i>et al.</i> (2013)
<i>Timema shephardi</i>	Stick insect	obl	XX:XO	F	D	Y	Y	Y	Y	Y <sup>g</sup>	Y <sup>g</sup>	N <sup>c</sup>	N <sup>c</sup>	N <sup>c</sup>	N <sup>c</sup>	Y	N	Schwander <i>et al.</i> (2013)
<i>Timema tahoe</i>	Stick insect	obl	XX:XO	F	D	N <sup>?</sup>	—	—	—	—	—	—	—	N <sup>c</sup>	N <sup>c</sup>	Y	N	Schwander <i>et al.</i> (2013)
<b>Psocoptera</b>																		
<i>Caecilius aurantiacus</i>	Psocid	A	XX:XO	?	D	N <sup>?</sup>	—	—	—	—	—	—	—	N	N	—	—	Mockford (1971)
<i>Berkana lucifuga</i>	Psocid	obl	XX:XO	F	D	Y	Y	Y	Y	—	—	—	—	N <sup>c</sup>	N <sup>c</sup>	—	—	Mockford (1971)
<i>Lipossettis bostrychophila</i>	Psocid	obl	XX:XO?	F?	?	Y	Y	—	—	—	—	—	—	—	—	—	—	Mockford & Krushchynsky (2008) and Wang <i>et al.</i> (2008)
<i>Peripocus quadrifasciatus</i>	Psocid	A	XX:XO	?	D	N <sup>?</sup>	—	—	—	—	—	—	—	N	N	—	—	Mockford (1971)
<i>Pococ bipunctatus</i>	Psocid	A	XX:XO	?	D	N <sup>?</sup>	—	—	—	—	—	—	—	N	N	—	—	Mockford (1971)
<b>Thysanoptera</b>																		
<i>Frankliniobrips vesipiformis</i>	Thrips	obl <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	—	Y	Y	Y <sup>k</sup>	Y	Y	—	—	Y	N	Arakaki <i>et al.</i> (2001)
<i>Anaphothrips obscurus</i>	Thrips	obl	Haplodiploid	F?	?	Y	Y	—	—	—	—	—	—	—	—	—	—	Mirab-Balou & Chen (2010)

Table 1. Continued

Taxonomic groups and species names	Species information		Summary			Male traits					Female traits					References
	Common name	Parthenogenesis	Sex determination in sexual sister groups	Male	Female	Male production	'Normal' morphology	Courtship behaviour/attraction to females	Mating behaviour	Sperm transfer/spermatophore production	Functional sperm	Normal sperm/seminal receptacles	Mate attraction; response to attraction; courtship	Normal copulation behaviour; sperm/seminal receptacle uptake	Egg fertilization	
<i>Heliethrips haemorrhoidalis</i>	Thrips	obl	Haplodiploid	F?	D	Y	Y	—	—	—	—	N	—	—	Mound (1976) and Del Bene <i>et al.</i> (1998)	
<i>Hecinothrips femoralis</i>	Thrips	obl <sup>f</sup>	Haplodiploid	F	D	Y <sup>f</sup>	Y	—	Y	Y <sup>k</sup>	N <sup>c</sup>	Y	—	N	Moritz (1989) and Kumm & Moritz (2008)	
<i>Parthenothrips dracaenae</i>	Thrips	obl	Haplodiploid	F	D	Y	Y	—	—	Y <sup>k</sup>	N <sup>c</sup>	—	—	—	Lewis (1973) and Kumm (2002)	
<i>Thrips nigropilosus</i>	Thrips	A	Haplodiploid	?	D	—	—	—	—	—	—	—	N <sup>c</sup>	—	Nakao & Yabu (1998)	
<b>MOLLUSCA</b>																
<b>Gastropoda</b>																
<i>Potamopyrgus antipodarum</i> (pinkins) (5n)	Snail	A	Unknown <sup>a</sup>	F	D	Y	Y	—	—	Y <sup>k</sup>	N <sup>c</sup>	Y	Y	—	Patil (1958) cited in Bell (1982), Neiman & Lively (2005), Nelson & Neiman (2011), and Neiman <i>et al.</i> (2012)	
<i>Melanoides tuberculata</i> (5-6n)	Snail	A	Unknown	D	?	Y	Y	—	—	N	—	—	—	—	Jacob (1954, 1957)	
<i>Melanoides lineatus</i> (4n)	Snail	A	Unknown	D	?	Y	Y	—	—	N	—	—	—	—	Jacob (1954, 1957)	

Parthenogenesis: A, asexual lineages in species with both asexual and sexual strains; obl: obligately asexual species; con: contagious parthenogenesis (functional males are expected given their reproductive success in matings with sexual females). Lineages are diploid unless otherwise specified (2n: diploid, 3n: triploid, 4n: tetraploid); species and genera names in parentheses indicate synonyms. The combined evidence for different male and female traits is summarized as: D (deceased) or F (functional), Y (yes); trait is fully expressed and functional; N (no): functionality reduced or lacking; —: no information available for the trait; 0: trait does not exist for this species; ?: inference uncertain; VAR (variable): functional in some, non-functional in other strains; see footnotes and text for details.

<sup>a</sup>Diplo-diploid sex determination but no known sex chromosomes.

<sup>b</sup>Males most likely do not produce sperm at all.

<sup>c</sup>Traits are still present but reduced or altered; for example asexually produced males are less attractive than sexual males, or courting is rarer or reduced in comparison to sexual males; sperm-storage organs are present but smaller/altered shape relative to sexual strains.

<sup>d</sup>Some 'males' have intersexual characteristics.

<sup>e</sup>No courting or mating behaviour in these species; spermatophores are deposited and left unattended by males and picked up (or not) by females.

<sup>f</sup>Parthenogenesis is endosymbiont induced; production of males after antibiotic or heat treatment, usually also at a low rate in natural/unreated populations.

<sup>g</sup>Sperm from asexually produced males is functional in crosses with sexual females, but fertilization efficiency is reduced in comparison to sexual males - notice that in these cases it is not possible to disentangle the effect of asexuality from an effect of incompatibility between diverged populations and species/cryptic female choice.

<sup>h</sup>Reported males are probably from sexual strains.

<sup>i</sup>Fertilized eggs: low viability and intersex development.

<sup>j</sup>Very low rate of fertilization (sometimes only paternal gene leakage).

<sup>k</sup>Sperm motile and appeared functional in assays, but functionality was not confirmed *in situ* crosses with sexual females.

<sup>l</sup>Functionality of the trait is not directly documented in studies but inferred, given the successful fertilization of sexual females/reversibility of asexuality.

<sup>m</sup>Trait state uncertain because no comparison with sexual relatives available.

endosymbionts also lay haploid eggs, but these eggs become diploid *via* gamete duplication and develop into females (Stouthamer & Kazmer, 1994). If such infected asexual females are cured from their endosymbionts (for example *via* antibiotic treatment) they produce sons instead of daughters, given that their haploid eggs remain haploid and develop into males. For these species it is thus possible to obtain large numbers of males from all-female asexual lineages (e.g. Stouthamer *et al.*, 1990a; Pannebakker *et al.*, 2005; Kremer *et al.*, 2009).

## V. FATE OF MALE-SPECIFIC TRAITS IN ASEQUAL LINEAGES

For asexual lineages that do not produce any males (and for which male production cannot be induced by antibiotic treatment), it is impossible to distinguish whether male phenotypes are simply not expressed, or whether the pathways underlying male development have decayed. In other words, the functionality of male sexual traits can only be investigated in the subset of lineages that maintain the developmental pathways leading to the differentiation of males.

Among the 93 asexual lineages for which any information on sexual traits (male or female expressed) is available, at least 74 are able to produce males even though they are most likely obligately asexual (Table 1). Males in a minority of these lineages (3 out of the 74) regularly mate with females of related sexual lines and thereby generate new asexual lineages ('contagious parthenogenesis'; Delmotte *et al.*, 2001; Paland, Colbourne & Lynch, 2005; Sandrock, Schirmer & Vorburger, 2011). In these cases, the maintenance of male functionality is expected, given the mating success of asexually produced males. For the remaining 71 lineages, the absence of mating opportunities for asexually produced males should result in relaxed selection on male traits, which may then decay as a consequence of drift. In these lineages, males are considered to be developmental accidents, whereby their production occurs too rarely to be associated with measurable costs, at least in species with high reproductive output (Neiman *et al.*, 2012). Given that trait decay as a consequence of drift is expected to proceed slowly, relatively little decay would be expected for male-specific traits in asexuals overall, and more extensive decay in old as compared to young asexual lineages. Consistent with these predictions, studies report little or no evidence for morphological decay of males in the lineages known to produce accidental males, with functional decay of males in only 13 lineages (Table 1). Although the unknown age of most asexual lineages makes it impossible to assess whether the 13 lineages with decayed male traits are relatively old compared to the lineages with functional males, two lines of evidence are suggestive that this may be the case. First, two of the species with reported decay of male traits are oribatid mites, a group hypothesized to have been asexual for 100 million years (Maraun *et al.*, 2003; Domes *et al.*, 2007; Heethoff *et al.*, 2007). Second, for

11 of the 13 lineages with decayed male traits, there is also information available on the functionality of female sexual traits, which are strongly reduced in nine cases. Additional information for more lineages on the time passed since the inception of asexuality would provide insights into the time frame required for the neutral decay of male traits.

The male traits to decay first under asexuality appear to be largely linked to fertility and sperm production. Courtship behaviours and morphological traits generally remain fully functional and equivalent to behaviours and trait values in related sexual males. Thus, in 11 of the 13 species with evidence for decay of male traits, males produce immotile sperm or have otherwise dysfunctional spermatogenesis (Table 1). Similarly, in at least eight asexual lineages where asexually produced males appear fully functional, these males are characterized by lower fertilization efficiency of eggs from sexual females when compared to sexual males. Although this may also stem from sexual–asexual hybrid incompatibilities or cryptic female choice (see Schwander *et al.*, 2013), this pattern is consistent with traits linked to spermatogenesis being the first to decay.

A rapid decay of sperm functionality relative to other male traits may stem from two non-exclusive processes. First, the genetic architecture underlying sperm functionality traits may be such that there are many possible targets for loss of function mutations. Indeed as noted 40 years ago, mutations causing male sterility in *Drosophila melanogaster* appear to be 10–15% more frequent than mutations causing lethality (Lindsley & Lifschytz, 1972). Second, gene networks underlying spermatogenesis may involve more male-specific elements without pleiotropic effects in females than male morphological and behavioural traits. Genes expressed in testis of *Drosophila melanogaster* and *Anopheles gambiae* males are among the most highly tissue specific (Chintapalli, Wang & Dow, 2007; Baker *et al.*, 2011) suggesting that their alteration may indeed be devoid of consequences in females.

The mechanisms underlying accidental male production by asexual females depend on the sex-determination system present in the sexual ancestors. In the species where parthenogenesis is induced by endosymbiotic bacteria, male development has been hypothesized to occur in individuals with low bacterial titres, or in lineages where the efficiency of host reproductive manipulation by the bacteria is lower than 100% (e.g. Huigens & Stouthamer, 2003; Koivisto & Braig, 2003; Reumer, van Alphen & Kraaijeveld, 2012; notice that eggs unaffected by bacterial manipulation will develop into males given the haplodiploid sex-determination system in these species). In asexuals deriving from species with XX:XO sex determination (females have two, males only one X chromosome), males can develop as a consequence of accidental sex chromosome losses *via* non-disjunction (Scali, 1968, 2013; Baur, 2010). Such sex chromosome losses are less likely to generate functional males in species with XX:XY sex determination (and functional genes on the Y), and indeed there are no known instances of male production by asexual lineages deriving from sexual ancestors characterized by this sex-determination system (though XY chromosomal



sex determination, with the gene content on the Y unknown, remains possible in several cases where the sex-determination system in sexual sister groups is uncertain; Table 1).

There are only a few documented cases of accidental male production by asexual females in taxa with female heterogamety (females are ZW or ZO, males ZZ; Table 1). In many of these species, especially in different asexual bagworm moths, reproduction occurs *via* a meiotic type of parthenogenesis, where two of the four meiotic products fuse to re-establish the maternal ploidy levels (reviewed in Suomalainen, Saura & Lokki, 1987). This fusion does not occur at random but is always between the two central nuclei, which results in offspring having the same chromosome complement as their mother (Suomalainen *et al.*, 1987). Thus, this mechanism also maintains the ZW (or ZO) chromosomal constitution, leading to the production of daughters. It seems plausible that errors during meiosis could rarely lead to the fusion of two different nuclei, which would generate ZZ individuals that would develop into males (Suomalainen *et al.*, 1987). However, the karyotype of accidental males in these species has not been investigated thus far, such that male development may also stem from other processes.

Given the mechanisms underlying accidental male production in species with XX:XO sex determination, the maintenance of male functionality in many asexual lineages is somewhat paradoxical. In asexual females, all loci occur exclusively in a diploid (or polyploid) state such that recessive deleterious alleles are constantly masked and could therefore accumulate. In asexually produced males however, recessive alleles present on the X chromosome would be expressed in diploid asexuals, given the hemizygous state of this chromosome in males – assuming that there was enough time for the build-up of a recessive load. It remains possible that the few documented male individuals represent the tip of an iceberg of XO eggs, most of which would die in the course of their development due to recessive deleterious mutations on the X. However, this would require chromosomal non-disjunctions to be quite frequent, entailing significant fertility costs for females. Interesting questions for future studies are thus whether gene conversion or some other mechanism can reduce the accumulation of recessive deleterious alleles in asexuals, and if some of the dysfunctional traits in asexually produced males stem from the expression of recessive alleles.

In comparison to species with XX:XO sex determination, male phenotypes in haplodiploid groups with endosymbiont-induced parthenogenesis should be less affected by the expression of recessive alleles. This is because asexual females are fully homozygous, given their development from haploid eggs that undergo gamete duplication. Perhaps this is the main reason for why particularly many such asexual species are known to produce males and why these males typically show a complete lack of decay (Table 1).

Overall the ubiquitous maintenance of male traits across the majority of asexual lineages would be best explained by neutral decay requiring millions of years to result in significant phenotypic effects, a time frame rarely reached by asexual lineages (Schurko, Neiman & Logsdon,

2009). In addition, male developmental and physiological pathways may consist almost exclusively of components with pleiotropic effects in both sexes, which would prevent these elements from degenerating. When by some rare accident the male developmental pathway is triggered, it would therefore still generate functional males. Alternatively, the development of functional males may indicate that lineages presumed to be asexual have some low level of cryptic sex. However, although formally demonstrating the lack of sexual reproduction in a lineage is challenging (Schurko *et al.*, 2009), this explanation is difficult to reconcile with the decay of female sexual traits reported in the vast majority of asexual lineages, including most cases with functional males (see Section VI).

## VI. FATE OF FEMALE SEXUAL TRAITS IN ASEXUALS

In contrast to the maintained male traits, female-linked sexual traits show evidence for decay in the majority (82%) of asexual lineages. Among the 73 asexual lineages for which a range of female traits were investigated, a significant reduction of at least one, but typically several, sexual traits was reported in 60 cases (Table 1). Such broad-scale trait decay should severely impede reversals to classical forms of sexual reproduction. Sexual trait decay could thus provide a positive line of evidence (*sensu* Schurko *et al.*, 2009; Birky, 2010) for obligate asexuality in a lineage, provided that decayed traits are fixed rather than phenotypically plastic and that the sample of analyzed asexual females allows excluding the occurrence of extremely rare females (i.e. those occurring at frequencies similar to the frequency of rare males among asexual females) with functional sexual traits.

Among the 60 lineages with female sexual trait decay, the ability to use sperm for egg fertilization is completely lacking or at least strongly reduced in all 38 species where this trait was investigated. Thus, for 31 out of these 38 lineages (Table 1), sperm was not integrated into eggs and there was no evidence for any paternal genetic contribution to offspring. In the seven remaining species, there is occasional fertilization of small egg fractions, whereby in at least two cases, individuals developing from fertilized eggs are developmentally unstable and often display intersexual traits (Table 1). This pattern strongly suggests selective mechanisms driving the trait shift. Egg fertilization could be very costly for asexuals, for example if ploidy elevation reduces egg or offspring viability, as suggested by developmental abnormalities in the species where partial fertilization of asexual eggs occurs. Alternatively, this trait could be linked to the origin of asexuality *per se*. For example, gene flow from sexual strains could prevent the initial establishment of a new asexual lineage lacking strong barriers to paternal genetic contributions (Lynch, 1984). Such a barrier is described in the asexual bushcricket *Saga pedo*: eggs have a reduced number of micropyles (pores in the ovum membrane through which sperm enter) as compared to sexual

relatives, limiting the chances of egg–sperm interactions (Sanger & Helfert, 1994). Mutations allowing for asexual embryo development may also entail correlated changes constraining egg–sperm interactions. This could explain why fertilization ability is only maintained in hymenopteran species with endosymbiont-induced asexuality (Table 1), where transitions to asexuality do not involve modifications of egg types laid (both virgin sexual and asexual females lay haploid eggs). In this sense, the absence of egg fertilization in asexuals may not always indicate decay of a sexual trait. Further research in incipient asexual lineages and their interactions with sexual populations may provide insights into the evolutionary process underlying the loss of egg fertilization ability in asexuals.

Parallel losses also occur for traits involved in mate location or copulation propensity, consistent with the idea of selection acting to reduce such traits to diminish costs linked to exposure to predators and diseases. The best evidence for selection-driven decay stems from traits underlying mate location and attraction, given that these traits have regressed in parallel in groups using different signalling systems (notably based on olfactory or auditory signals) and independently of whether females are the emitting or responding sex. For example in sexual bushcricket species, females are the responding sex and are attracted by males with songs (Gwynne, 2001). The asexual bushcricket *P. intermedius* has completely lost phonotaxis within fewer than 200000 years and displays a morphological reduction of hearing-related structures (Lehmann, Strauss & Lakes-Harlan, 2007; Lehmann *et al.*, 2011).

Among insect species using chemical communication, however, females are typically the signalling rather than the responding sex and emit pheromones and other olfactory cues to attract males (Greenfield, 2002). Here, females in several asexual stick insect species produce either no cues or cues that are not attractive to males (Schwander *et al.*, 2013). A lack of pheromones eliciting male courtship or a lack of female sexual behaviour is also reported in species with endosymbiont-induced parthenogenesis (e.g. Pijls, Van Steenberghe & van Alphen, 1996; Silva & Stouthamer, 1997; Pannebakker *et al.*, 2005; Kremer *et al.*, 2009). An additional line of evidence supporting selective rather than neutral regression of mate-attraction traits stems from asexual stick insect lineages, where the extent of attractiveness loss depends less on the age of the asexuals than on distribution patterns; young asexuals overlapping with their sexual counterparts display more extreme decay than old asexuals isolated from sexual species (Schwander *et al.*, 2013). Although *Potamopyrgus antipodarum* snails, where females appear to play a passive role in mate finding and copulation, may represent an exception to this pattern (Nelson & Neiman, 2011), these parallel and rapid losses of different female traits involved in mate attraction and mating suggest that selective mechanisms, rather than drift, are driving trait changes.

Similar to the preserved male traits, female sexual traits not exposed to selection also tend to be maintained, even in species with extensive trait decay overall. For example in the

asexual bushcricket with reduced phonotaxis and hearing organs, no decline in female mating behaviour has been observed when asexual females are confined with males of related sexual species (Lehmann *et al.*, 2011). Since without phonotaxis, asexual females are not attracted to males and will therefore typically not encounter them under natural conditions, copulation behaviour in asexual females is no longer expressed and could therefore only regress *via* drift.

Female sperm-storage organs are also often maintained and hence appear to be associated with little or no costs. Only two studies report a decay of the ability to store sperm in asexual females (Gottlieb & Zchori-Fein, 2001; Kraaijeveld *et al.*, 2009) whereas in most cases, spermathecae in asexuals display only altered shapes relative to sexuals or more variability, indicating reduced developmental stability of the organ (Table 1). Both patterns are consistent with trait decay as a consequence of relaxed selection, but it is difficult to see why a somewhat altered shape would reduce possible costs associated with spermatheca differentiation.

Fully maintained female functionality was documented in only 13 out of the 73 asexual lineages for which a range of female traits were investigated (18%). It is notable that 11 of these 13 species are hymenopterans with endosymbiont-induced parthenogenesis, 10 from the same genus (*Trichogramma*) of parasitoid wasps (Table 1). In this genus parthenogenesis is even revertible, as stable sexual populations can be derived from asexual lines by curing the females of their endosymbionts (Stouthamer *et al.*, 1990*a,b*). The lack of sexual trait decay in these species may stem from infections being very recent and/or from ongoing gene flow between sexual and asexual lines. Consistent with these explanations, allele sharing in natural populations with alternative reproductive modes, as well as paternal genome leakage into asexual lineages in laboratory crosses between asexual females and sexual males, is documented in several *Trichogramma* species (Stouthamer *et al.*, 1990*a,b*; Stouthamer & Luck, 1993; Stouthamer & Kazmer, 1994). The two remaining asexual lineages with maintained female sexual traits are stick insects from the genus *Bacillus*, which may be facultative parthenogens (Scali, 2009).

In addition to the typical female-expressed sexual traits, there are certain taxon-specific traits that have also regressed after transitions to asexual reproduction. However, given the uniqueness of these traits, processes underlying their decay cannot be inferred from comparative approaches. One such taxon-specific trait is the use of different hosts for male and female offspring by certain groups of parasitoid wasps (the use of different hosts for the production of sons *versus* daughters is believed to originate from sex-specific optimal resource conditions and developmental requirements; Hunter, 1999). Asexual species in these groups thus only lay eggs into the female-specific host and three asexual hymenopteran species in the Aphelinidae family have lost the behaviour of switching hosts for male offspring (Hunter, 1999; Zchori-Fein *et al.*, 2001; Kenyon & Hunter, 2007). Since the behaviour to search and find hosts for male larvae is not expressed in asexual females, the trait would have regressed *via* drift,

in contrast to the general pattern that extensive sexual trait changes would stem from selective processes. However, the lack of male host usage by asexual Aphelinidae females is more likely due to changes in the hosts than in the parasitoids; co-evolutionary dynamics of hosts avoiding detection by parasitoids and parasitoids recognizing volatile and other cues emitted by the hosts is expected to drive continuous change in both hosts and parasitoids (Vinson, 1975). Thus, asexual wasps would be able to identify ancestral male-host cues present prior to the transition to asexuality, but not the contemporary version of such cues.

## VII. GENETIC ARCHITECTURE OF DECAYED TRAITS

An open question remaining is the genetic architecture underlying trait decay. Thus it is largely unknown whether trait decay typically proceeds by the accumulation of mutations with small phenotypic effects, or in large increments, for example as a consequence of major effect mutations in regulatory sequences or highly connected elements (Jeffery, 2001, 2009; Lahti *et al.*, 2009). Thus far, data on sexual trait decay point to the latter. These data stem from three studies in hymenopterans with endosymbiont-induced asexuality. In these species, the genetic architecture of decayed sexual traits can be investigated by introgressing genes from asexual into sexual lines, taking advantage of sons produced by asexual females cured of their endosymbionts (Pannebakker *et al.*, 2004; Jeong & Stouthamer, 2005; Russell & Stouthamer, 2011).

The first study to investigate the genetic basis of trait decay focused on the fertility of asexually produced males (Pannebakker *et al.*, 2004), whereby ‘fertility’ was assessed from offspring sex ratios produced by sexual females (low fertility would be indicated by male-biased sex ratios, since successfully fertilized eggs develop into females). A single, major effect locus affecting male fertility was identified *via* an elegant mapping approach, consistent with a simple genetic architecture underlying trait decay (Pannebakker *et al.*, 2004). However, hymenopteran females might adjust their offspring sex ratios according to the quality of their mates, producing more fertilized (female) eggs when mated with a high-quality male (e.g. West & Sheldon, 2002). Thus, given that male fertilization ability in this study was assessed indirectly from offspring sex ratios in crosses with females of a sexual strain, it is difficult to exclude that the uncovered locus is associated with male attractiveness to females rather than with male fertility.

The two remaining studies focused on egg fertilization ability of females and found evidence for a single locus underlying the loss of egg fertilization in asexuals, recessive in one and dominant in the other study, with additional minor-effect modifiers (Jeong & Stouthamer, 2005; Russell & Stouthamer, 2011). Similar to the earlier study, these patterns would also indicate a simple genetic architecture of trait decay. However, as noted above, the lack of egg

fertilization ability in asexuals may be linked to the origin of asexuality, rather than indicating sexual decay, such that generalizations for the genetic architecture of decayed traits are difficult.

The current evidence thus points to sexual trait decay stemming from very few mutations with relatively strong phenotypic effects. While generalizations from these studies for trait decay may be difficult, they provide guidelines for future studies investigating the genetic architecture of regressed traits. Additional such studies are thus highly warranted, especially for well-characterized traits clearly stemming from the loss of sexual reproduction, in hymenopterans as well as in other taxa. Given the fertility of asexually produced males in many asexual lineages, such approaches should be feasible even with only a handful of males available. Insights from such studies may notably inform on the influence of trait complexity on its rate of decay. A complex trait consisting of many components may display signatures of decay more rapidly than a simple trait because more targets are available for mutations with phenotypic effects. Alternatively, the opposite may be true if modifying one element is enough (Jeffery, 2001). Finally, insights into the genetic basis of trait decay may also shed light on loci underlying trait variation among sexual species.

## VIII. CONCLUSIONS

(1) Research on trait decay is important because it provides insights into the selective pressures generating and maintaining traits. Given the energy required to produce and maintain most characters, useless features may often be a disadvantage and their reduction should be favoured by natural selection (Regal, 1977).

(2) The combined evidence from studies of sexual traits in 93 independently derived asexual lineages suggests that trait decay typically only occurs if driven by selective processes. Traits expected to be under relaxed selection and decay *via* neutral mutation accumulation were generally fully functional, or displayed only minor shifts (not affecting functionality) since the abandonment of a sexual lifecycle.

(3) The ubiquitous maintenance of male traits across the majority of asexual species would be best explained by neutral decay requiring millions of years to result in significant phenotypic effects, a time frame rarely reached by asexual lineages (Schurko *et al.*, 2009), or by male developmental and physiological pathways consisting almost exclusively of components with pleiotropic effects in both sexes. The maintenance of male developmental pathways reveals that major developmental pathways can remain quiescent and functional over extended time periods.

(4) In contrast to the maintained male traits, sexual traits in asexual females display large-scale shifts relative to sexual females, often indicating decay. Traits decayed in parallel across many asexual lineages are involved in mate attraction or location, as well as copulation behaviours, as expected given the potentially considerable costs associated with the

expression of these traits. Asexual females also consistently lack the ability to fertilize eggs or include paternal genetic contributions in offspring, but this pattern may be linked to the origin of asexuality rather than being a case of trait decay.

(5) More generally, we expect that the majority of trait losses stem from selection rather than the relaxation thereof, and that losses typically occur in large increments rather than by the accumulation of small steps. There would thus be few instances of intermediate situations with traits in the process of decay, such that in modern taxa only reduced trait values are observed, for which further reduction provides no additional fitness benefits.

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