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LARGE POPULATION SIZE PREDICTS THE DISTRIBUTION OF ASEXUALITY IN SCALE INSECTS

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Received February 8, 2012

Accepted July 13, 2012

Understanding why some organisms reproduce by sexual reproduction while others can reproduce asexually remains an important unsolved problem in evolutionary biology. Simple demography suggests that asexuals should outcompete sexually reproducing organisms, because of their higher intrinsic rate of increase. However, the majority of multicellular organisms have sexual reproduction. The widely accepted explanation for this apparent contradiction is that asexual lineages have a higher extinction rate. A number of models have indicated that population size might play a crucial role in the evolution of asexuality. The strength of processes that lead to extinction of asexual species is reduced when population sizes get very large, so that the long-term advantage of sexual over asexual reproduction may become negligible. Here, we use a comparative approach using scale insects (Coccoidea, Hemiptera) to show that asexuality is indeed more common in species with larger population density and geographic distribution and we also show that asexual species tend to be more polyphagous. We discuss the implication of our findings for previously observed patterns of asexuality in agricultural pests.

KEY WORDS: General purpose genotype, parthenogenesis, polyphagy, population size, scale insects.

Understanding why some organism reproduce by sexual reproduction while others reproduce asexually remains an important unsolved problem in evolutionary biology (Otto 2009). In a demographic sense, asexual reproduction is much more efficient than sexual reproduction due to the cost of producing males (Lively and Lloyd 1990). Asexuals also save the costs of mate finding and courtship, and avoid the risk inherent in breaking up successful gene combinations (Agrawal 2006; Otto 2009). And yet the majority of multicellular organisms have sexual reproduction, in spite of its inefficiency and its risks. Although asexual lineages can be highly successful in the short run, they appear to have a

higher extinction rate than sexual lineages (Maynard Smith 1978), and very few persist long enough to diversify into higher taxa (Normark et al. 2003). The cause of the extinction of asexual lineages is not known, but may be due to accumulation of unconditionally deleterious mutations (Muller 1964; Lynch et al. 1993; Henry et al. 2012), or to a failure to accumulate unconditionally beneficial mutations (Fisher 1930; Muller 1932), or to a failure to adapt when the fitness consequences of alleles change rapidly due to coevolving enemies (Jaenike 1978; Hamilton 1980; Lively 2010; Morran et al. 2011).

These population-genetic processes that might result in the extinction of asexual lineages are all strongly affected by population size. Although the accumulation of deleterious mutations may lead to the extinction of individual asexual lineages,

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when the population size is sufficiently large there are always lineages that by chance have fewer mutations (Lynch et al. 1993). In the same way, in a sufficiently large population, all possible combinations of mutations would occur, so sex would not be necessary to bring together advantageous mutations (Otto 2009). So the long-term advantage of sexual over asexual reproduction (lower extinction rate) is dependent on the effective population size and may become negligible when population size gets very large, irrespective of whether deleterious mutations or environmental changes are the main source of selection favoring sex (Keightley and Otto 2006; Otto 2009). Indeed, the effect of sexuality versus asexuality on the fate of alleles in a population can be modeled as equivalent to a larger versus smaller population size (Rice and Friberg 2009).

This leads to the prediction that the distribution of asexuality across taxa should be correlated with population size, with species having larger populations being more likely to be asexual or have asexual populations (Normark and Johnson 2011). Large population size might also help to explain why, although most asexual lineages are of relatively recent origin, some taxa do show signs of ancient asexuality (Rice and Friberg 2009). The realization that population size might affect the extinction rates of asexual species is not a new idea, but it has received relatively little attention outside of the theoretical literature (Normark and Johnson 2011). This may be due to the fact that it is very difficult to estimate (effective) population sizes for a large number of taxa, especially as asexuality is predominantly found in small and hard-to-census species (White 1973; Bell 1982; Suomalainen et al. 1987; Normark 2003). However, it might be possible to test the effect of population size on the phylogenetic distribution of asexuality by focusing on factors that are easier to measure and that are expected to be correlated with population size. Here, we consider three such factors: geographic range, host range, and status as an economic pest. The correlation of each of these factors with parthenogenesis has previously been hypothesized, with some empirical support, but previous authors have generally assumed that parthenogenesis is the cause and that broad geographic range and niche breadth and pest status are the effects (Vandel 1928; Lynch 1984; Hoffmann et al. 2008; Vrijenhoek and Parker 2009). The larger geographic range of parthenogenetic lineages has been explained by their superior colonizing ability (Vandel 1928; Vrijenhoek and Parker 2009). Their larger niche width, when observed, has been explained by the varied selection experienced by clonal genotypes (Lynch 1984; Vrijenhoek and Parker 2009). And the overrepresentation of parthenogenetic species among pests has been explained by their ability to colonize and thrive in disturbed, low-diversity agricultural environments (Hoffmann et al. 2008).

It is currently impossible to distinguish the hypotheses for each of these factors from the general role of large population size,

especially as most studies to date have just focused on one factor separately. In addition, previous studies often had relatively small sample sizes (number of taxa considered) and did not correct for phylogenetic relatedness. Here, we will use data from one specific group of insects, the scale insects (Hemiptera: Coccoidea) in a formal comparative analysis to simultaneously test the effect of geographic range, host range, and pest status on reproductive mode.

Methods

TAXON SAMPLING

Scale insects, a group of small plant-feeding insects, are ideally suited for the proposed analysis as they are characterized by a dazzling array of reproductive and genetic systems (Ross et al. 2010), including frequent asexual reproduction (Nur 1971, 1990). Scale insects also display an extreme variation in host plant specificity, with some species only able to use a few plant species while others can feed on over a hundred different plant families (Ben-Dov et al. 2011c; Normark and Johnson 2011). In addition there is large variation in geographic range sizes, with several species having a nearly cosmopolitan distribution, while others are confined to a single country (Gullan and Kosztarab 1997; Ben-Dov et al. 2011a). Finally, many scale insects are economically important pest species that attack both ornamental and crop plants (Ben-Dov et al. 2011b). Another reason why scale insects are suitable for this analysis is that parthenogenetic lineages remain diploid, like their sexual relatives (Nur 1971). This is not the case for parthenogens in many other taxa, where asexual lineages are often polyploid and it has proven difficult to disentangle the effects of polyploidy from that of parthenogenesis per se (Lundmark and Saura 2006).

DATA COLLECTION

Data on reproductive mode (sexual vs. asexual) was collected from the literature. The main source for information on the reproductive mode of scale insects was a recent review by Gavrilov (2007), which lists published information on the reproduction of scale insects. Another important source was ScaleNet (Ben-Dov et al. 2011d), an online database that collects an extensive amount of data on scale insect biology and is also an important source for literature on scale insects. In addition, new references were identified via Web of Science and Google Scholar as well as by inspecting the references of all papers of interest and by searching for citations of key papers. For the main analysis, we only included species for which authors explicitly stated the reproductive mode based on direct evidence (e.g., breeding experiments, cytological evidence, extensive field, and laboratory observations) and we excluded cases where asexuality was assumed simply due to the absence of males (although we do include these for illustrative

purposes in Fig. 1 and use them to test for publication bias, see below). For some species both asexual and sexual populations are found. For our analyses, we scored these as asexual. In total, we obtained data on reproductive mode of 396 species, Table S1 shows a list of all species included with references. The data on host plant range, geographic distribution, and number of publications in which a species was mentioned were taken from ScaleNet and were available for all species for which we have data on reproductive mode. Finally, the pest status of each species was determined by its absence or presence in the Pest Directory (2009), as compiled by the International Society for Pest Information (Griesheim, Germany) following Hoffmann et al. (2008).

PHYLOGENETIC RECONSTRUCTION

We estimated relationships among 401 scale insect species from alignments of cytochrome oxidase subunits I and II, elongation factor 1- α , nuclear small ribosomal subunit 18S, and three nonoverlapping fragments of nuclear large ribosomal subunit 28S. Phylogenetic clusters of DNA sequence data were downloaded as unaligned Fasta files from GenBank via PhyLoTA 1.5 (Sanderson et al. 2008). Table S2 shows a list of the taxa for which data was obtained from GenBank and shows which genome regions were available for each taxon.

We also added a number of unpublished sequences (see Table S2). These sequences were obtained from specimens that were preserved in 100% ethanol and stored at -20°C freezer (see Table S2 for collection information). Total genomic DNA from individual specimens was isolated using Qiagen DNeasy Blood & Tissue kit (Qiagen, Valencia, CA). Each insect was punctured with a 000 insect pin and digested overnight in the lysis buffer. The undigested cuticles were retrieved from the lysate using a sterile wide mouth micropipette tip and stored in water at 4°C for later slide mounting and species identification. The remainder of the Qiagen protocol was followed, except at the first elution only 60 μl of buffer AE was used. Polymerase chain reaction (PCR) was performed to amplify regions of the mitochondrial genes cytochrome c oxidase I and II (COI and COII, ~ 850 bp) and nuclear protein-coding gene elongation factor 1- α (EF1- α , ~ 1000 bp) as described in Morse and Normark (2006) and Andersen et al. (2010). Amplification products were purified with an ExoSAP-IT PCR Product Clean-Up enzyme digest (Affymetrix, Cleveland, OH) and sequenced directly using an ABI-3130XL Genetic Analyzer at the University of Massachusetts Genomics Resource Laboratory.

Sequences from each locus were aligned with MAFFT (Katoh and Toh 2008). Hypervariable regions of ribosomal alignments were purged with Gblocks (Castresana and Talavera 2007; Talavera and Castresana 2007), with the allowed gap positions parameter set to half, the minimum length block parameter set to 5, and the maximum number of contiguous nonconserved posi-

tions parameter set to 12. Mesquite 2.74 (Maddison and Maddison 2011) was used to delimit codon positions, exclude introns, and concatenate alignments (total alignment length 3972 positions). We partitioned the DNA dataset by genome and codon position, and estimated values of a HKY + G model of nucleotide substitution independently across partitions. We used BEAST version 1.6.1 (Drummond and Rambaut 2007) to estimate the joint posterior probability of a set of phylogenetic relationships and divergence times given the mixed HKY + G model of nucleotide substitution, a Yule model of phylogenetic branching, and a set of prior probability densities on the ages of specific nodes. We placed an exponential prior, with a zero offset of 117 Ma and a mean of 11.7 Ma on the crown node of Putoidae (Koteja and Azar 2008). We placed a second exponential prior, with a zero offset of 89 Ma and a mean of 8.9 Ma on the crown node of the neococcoids, excluding Pseudococcidae (Koteja 2000). The MCMC analysis was run for 10G generations, sampling trees every 1K generations. Parameter estimate traces were examined with Tracer version 1.5 (Drummond and Rambaut 2007), and trees sampled before parameter values had reached the stationary distribution were discarded. TreeAnnotator (part of BEAST package) was used to find the maximum clade credibility tree (the sampled tree with the highest product of posterior probabilities).

EXTINCTION ANALYSIS

It has been widely assumed that asexual lineages have higher extinction rates than closely related sexual lineages (Muller 1964; Otto 2009). We test this assumption for scale insects with a maximum likelihood approach, comparing the fit of nested Binary State Speciation and Extinction (BiSSE: Maddison et al. 2007) models of diversification using likelihood ratio tests (LRT) in the R package diversitree (FitzJohn et al. 2009). Specifically, we compare (1) a model with five free parameters in which the rate of trait transformation from asexual to sexual (q_{01}) was set to zero, to (2) a model with four free parameters in which the extinction rates of asexual and sexual lineages (μ_0 and μ_1) were constrained to be equal. To account for incomplete phylogenetic sampling, diversitree allows users to specify state-specific sampling fractions. We used the fraction of asexual and sexual species present in our phylogenetic data as compared to our complete dataset (asexual 29/93; sexual 103/389).

COMPARATIVE ANALYSIS

To test for the relationship between asexuality and host range, geographic range and pest status we used a binary mixed model, with reproductive mode (sexual vs. asexual) as the binary response. We use two different approaches to correct for nonindependence due to shared ancestry (Felsenstein 1985). First of all we use a formal phylogenetic comparative approach, namely the phylogenetic mixed model (Lynch 1991) as described in Hadfield (2010a).



Figure 1. Estimated scale insect phylogeny based on maximum likelihood analysis of alignments of GenBank DNA sequence data. The boxes at the tip of the phylogeny represent the reproductive mode of a species (solid boxes, sexual; empty boxes, asexual) and the shape of the box represent the strength of support for the reproductive mode (squares, reproductive mode confirmed; circles, reproductive mode assumed). Bars next to tip names are proportional to geographic range size, estimated by the number of countries in which the species is known to occur.

We estimated a phylogenetic tree using 401 species (see section Phylogenetic reconstruction) and then pruned the species for which no information about reproductive mode was available (see Fig. 1). Because sequence data were only available for a subset of the species for which we were able to obtain data on reproductive mode (125 spp.), we decided to also present a model where nonindependence due to shared ancestry is corrected for by taxonomy (taxonomic mixed model: Cluttonbrock and Harvey 1977), by including family and genus as random effects, following the methods of Hadfield (2010b).

To test for possible collinearity between host and geographic range we used a taxonomic model with a Gaussian error structure using the nlme package (Pinheiro et al. 2007) in the R software environment (R Development Core Team 2010). All generalized linear mixed models (both the phylogenetic and taxonomic models) were implemented using the Bayesian mixed model package MCMCglmm (Hadfield 2010a). We used parameter expanded priors for the variances of the random effects for the taxonomic model, which are relatively uniform for the standard deviations (Gelman 2006; Hadfield 2010b). And we used a χ^2 -squared prior with one degree of freedom (as advocated by de Villemereui et al., Methods in Ecology and Evolution, in review) as a relative uniform prior for the intraclass correlation for binary data in the phylogenetic models. The residual variances were fixed at one because they are not identifiable in binary models and we used slice sampling (Damien et al. 1999; Hadfield 2010b) to improve the mixing efficiency of the chain. All models were run for 1 million iterations with a burn-in of 200,000 iterations. R code for prior and model specification can be found in Table S3. We checked for convergence of the chain by visual inspection of the trace plots and by calculating the autocorrelation statistics (according to Hadfield 2010b). For the fixed effects we present the posterior mode (PM) with the credibility interval (CI) and the pMCMC. The latter is defined as two times whichever is smaller: the probability that the coefficient is negative or the probability that the coefficient is positive. All these values were obtained using the summary function in MCMCglmm (Hadfield 2010b). We calculated the phylogenetic signal of reproductive mode, as the intraclass correlation, which describes the correlation between the estimated phenotype of two species within the same family/genus (for the taxonomic mixed model):

$$\frac{\sigma^2_{family}}{\sigma^2_{genus} + \sigma^2_{family} + \sigma^2_{residual} + \pi^2/3} \text{ and } \times \frac{\sigma^2_{genus}}{\sigma^2_{genus} + \sigma^2_{family} + \sigma^2_{residual} + \pi^2/3}$$

and the phylogenetic signal (for the phylogenetic analysis)

$$\frac{\sigma^2_{phylogeny}}{\sigma^2_{phylogeny} + \sigma^2_{residual} + \pi^2/3}.$$

Finally, we did an additional analysis intended to provide information about the temporal sequence of origins of parthenogenesis vs. geographic range expansion: we compared the average geographic range of sexual species in genera that do or do not contain at least one asexual species, using a general linear model with a Gaussian error structure.

PUBLICATION BIAS

A common problem with comparative and meta-analyses is that particular findings are more likely to be published, and that species sampling might not be random (Møller and Jennions 2001). In this analysis this might pose a problem, because species that are particularly common are more likely to be considered pests, and species with a wide host range or wide geographic range are more likely to have been studied more thoroughly and therefore asexuality might have been noticed more often in those species. To control for this possible bias, we included the number of published articles that mention a given species as a covariate in the analysis. In addition, we also performed the analysis including taxa for which asexuality was merely assumed because males were not observed (a scenario more likely for poorly studied taxa) and found no difference in the results, something that would not be expected if the patterns we find are driven by observation bias. For simplicity, we only report the results for taxa where asexuality has been confirmed (see section on Data collection above).

Results

EXTINCTION RATES

The phylogenetic pattern of asexuality among scale insect lineages may result from either (1) asymmetrical rates of trait transformation that are heavily biased toward change from asexual to sexual, or (2) asymmetrical trait-dependent extinction rates that are much higher in asexual lineages. If we assume that asexual lineages do not regain sex ($q_{01} \sim 0$), then our data strongly support higher rates of extinction for asexual lineages ($\mu_0 = 2.93 \times 10^{-1}$; $\mu_1 = 3.92 \times 10^{-8}$; LRT P -value < 0.001).

COMPARATIVE ANALYSIS

In this analysis, we considered the effect of host range, geographic distribution, and pest status on the distribution of asexuality, because we expected these factors to be correlated with population size. But first we tested for correlations between our explanatory variables. We found a strong correlation between host range and geographic distribution ($t = 16.69$, $P < 0.001$, see Table 1 and Fig. 2) and found that this correlation was strong for both sexual and asexual species, although the slope was slightly but significantly less steep for sexual species (asexual: $R^2 = 0.72$, sexual: $R^2 = 0.58$, $t = -2.68$, $P = 0.008$, see Table 1 and Fig. 2). Due to this strong collinearity between two of our explanatory factors it

Table 1. Summary table of a general linear mixed model with host range as the response variable, geographic range, and reproductive mode as explanatory variables and genus and family as random effects.

	Value	Std. error	DF	<i>t</i> -value	<i>P</i> -value
(Intercept)	0.965	2.058	209	0.469	0.640
Geographic range	0.719	0.043	209	16.685	<0.001
Reproduction	0.286	2.200	209	0.130	0.897
Geographic range: reproduction	−0.142	0.053	209	−2.690	0.008

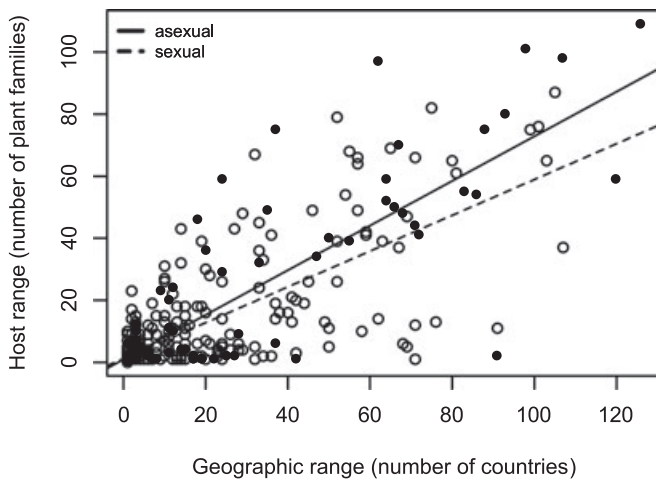


Figure 2. Correlation between host range and geographic range. Circles show the raw data for asexual (filled circles) and sexual (open circles) species. The lines show the regression coefficient for asexual (solid line) and sexual (dashed line) species.

was not possible to test both factors in the model simultaneously, as collinearity leads to strongly inflated standard errors (Zuur et al. 2009). We therefore chose to only include geographic range, because it showed the strongest effect size in the full model (Geographic range: posterior mean = -0.646 , host range: posterior mean = -0.531), although both factors are significant when fitted on their own.

TAXONOMIC MIXED MODEL

Data on reproductive mode was available for 396 species. Sexual reproduction showed a strong negative correlation with geographic range (PM = -0.78 , CI = -1.41 to -0.18 , pMCMC = 0.014 , Fig. 3A, Table 2), with species reported from a large number of countries being more likely to reproduce asexually than those with a small geographic range. We also show that species that are reported to be pests are more likely to have asexual reproduction (PM = -1.2 , CI = -2.31 to -0.12 , pMCMC = 0.03 , Fig. 3A, Table 2). We did, however, not find that more thoroughly

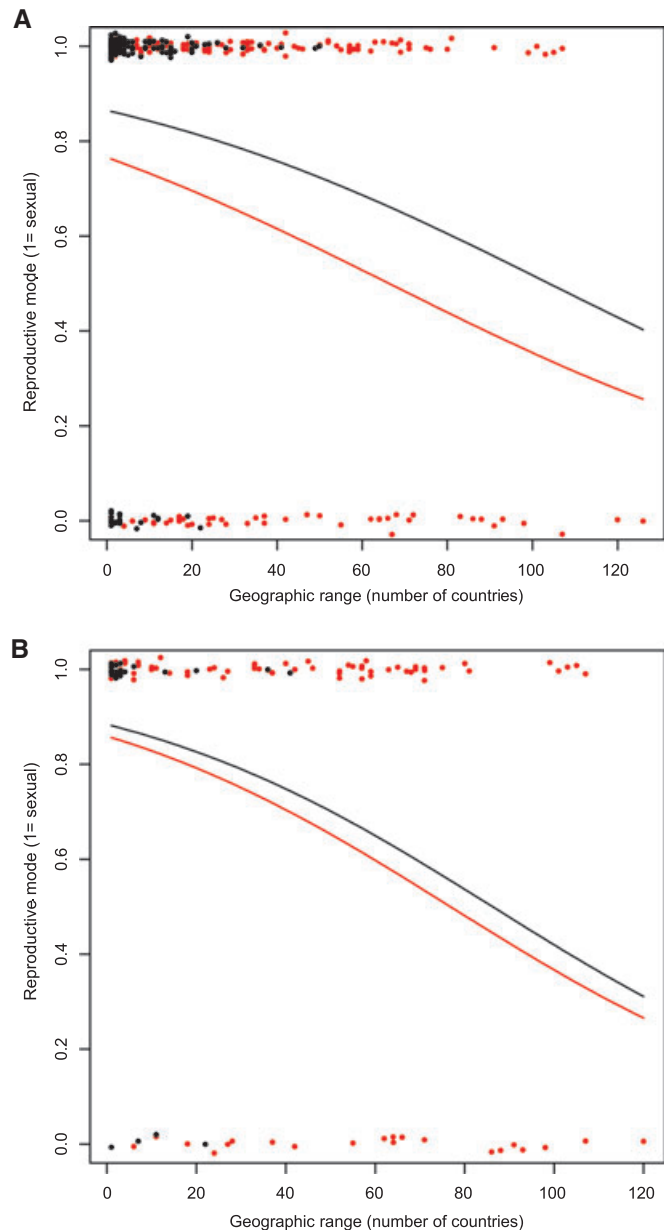


Figure 3. Correlation between reproductive mode (0 = asexual, 1 = sexual) and geographic range. Pest species are represented by red dots and nonpest species by black dots. The lines plot predicted values of from two models: (A) the taxonomic mixed model (396 species included); (B) the phylogenetic mixed model (125 species included).

studied taxa (as estimated by the effect of the number of publication per species) were more likely to be asexual (PM = -1.20 , CI = -0.13 to 1.14 , $P = 0.142$, see Table 2). To estimate the phylogenetic signal, we calculated the intraclass correlation for both family and genus. Family explains 13.7% (CI = 0.32 – 49%), while genus explains 22% (CI = 1.78×10^{-4} – 51.6%). However, both these estimates have very wide credibility intervals,

Table 2. Estimates for the fixed effects in the taxonomic model with family and genus included as random effects. All estimates are generated by the summary function in the R package MCMCglmm. The table shows the posterior mean with the lower and upper 95% confidence interval of the estimate, the pMCMC (probability that the estimate does not differ from zero), and the effective sample size, which is an estimate of the equivalent number of independent iterations that the MCMC chain represents.

	Posterior mean	L-95% CI	U-95% CI	Eff. samples	pMCMC
Intercept	2.84	1.60	4.25	1000	<0.001***
Geographic range	-0.78	-1.41	-0.18	1000	0.014*
Publications	0.47	-0.13	1.14	1000	0.142
Pest status	-1.20	-2.31	-0.12	1000	0.030*

Table 3. Estimates for the fixed effects from the phylogenetic model. All estimates are generated by the summary function in the R package MCMCglmm. The table shows the posterior mean with the lower and upper 95% confidence interval of the estimate, the pMCMC (probability that the estimate does not differ from zero), and the effective sample size, which is an estimate of the equivalent number of independent iterations that the MCMC chain represents.

	Posterior mean	L-95% CI	U-95% CI	Eff. samples	pMCMC
Intercept	1.67	-0.08	3.52	1000	0.066
Geographic range	-1.05	-1.97	-0.18	1128	0.012*
Publications	0.40	-0.50	1.18	1000	0.362
Pest status	-0.30	-2.16	1.52	1000	0.768

suggesting that we are not able to accurately estimate these correlations from our data.

PHYLOGENETIC MIXED MODEL

From the 401 species used to construct the phylogeny, information on the reproductive mode was available for 125 species and only these could be included in the phylogenetically controlled analysis. The results of the analysis were very similar to those obtained from the taxonomic model (see above). Again there was a strong negative correlation between geographic range and the probability of reproducing sexually (PM = -1.04, CI = -1.97 to -0.18, pMCMC = 0.012, Fig. 3B, Table 3) and no effect of the number of published papers per species (PM = 0.40, CI = -0.50 to 1.18, pMCMC = 0.362, Table 3). The only difference in results for this taxonomic model is that the effect of pest status is no longer significant in the phylogenetic analysis (PM = -0.30, CI = -2.16 to 1.52, pMCMC = 0.768, Table 3, Fig. 3B), possibly due to the sharply reduced sample size. We found that 20% of the variation in reproductive mode was explained by shared phylogeny, but the credibility interval was very large (8.64×10^{-8} –51.0%) suggesting that our model lacked the power to reliably estimate this parameter. Finally, we attempted to test if the larger geographic range of asexuals preceded or followed the evolution of large geographic range. Sexual species in genera containing asexual species have a significantly larger geographic range ($F_{1,146} = 5.18$, $P = 0.024$, Fig. 4), suggesting that large geographic range precedes

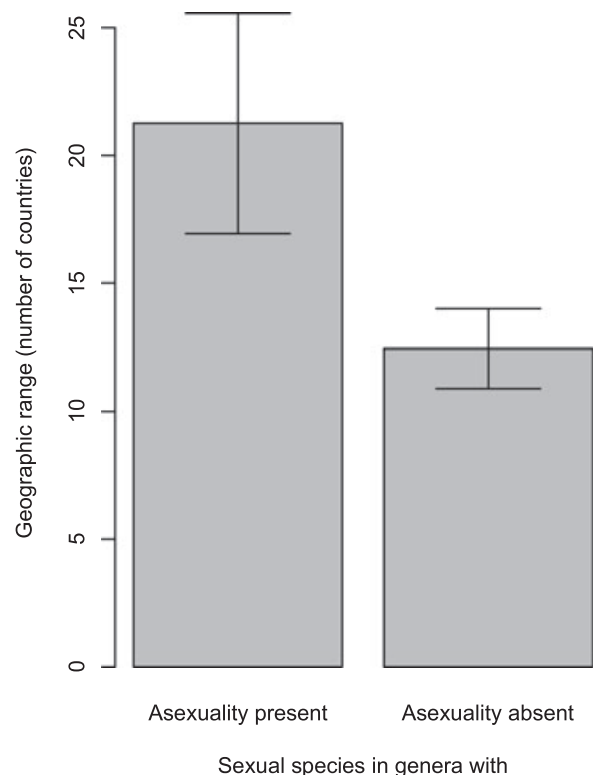


Figure 4. Average geographic range of *sexually* reproducing species in genera, which contain at least one asexual species (asexuality present), or that do not contain asexual species (asexuality absent). Error bars represent the standard error of the mean.

the evolution of parthenogenesis, and thus is not a consequence of parthenogenesis.

Discussion

Here we have shown that three likely correlates of population size—geographic range, host range, and pest status—are all correlated with the probability of asexual reproduction. Scale insect species with a larger geographic and host range are more likely to be asexual, although due to the strong correlation between host range and geographic range, it is not possible to determine which of these factors is most important. Our taxonomic model indicates that species recorded as agricultural pests have an increased tendency to asexuality, though this effect was not significant under our phylogenetic model. These findings are consistent with our prediction that only asexual lineages with a high effective population size are able to avoid extinction, as large population size increases the effectiveness of natural selection and can thereby compensate for a lack of recombination and sex (Rice and Friberg 2009; Normark and Johnson 2011).

We have framed this article around the theoretical expectation that large population size reduces the adaptive advantage of sex over asex. In our view this is the best explanation for the patterns we have documented, but we cannot entirely rule out alternative hypotheses. There are two general classes of alternative explanations. First, the arrow of causality might point in the opposite direction: successful parthenogenesis might cause large population size, rather than large population size causing successful parthenogenesis. Second, some other feature of large population size, rather than more efficient natural selection and consequent increased longevity of parthenogenetic lineages, might lead to the evolution of parthenogenesis. Below we consider each of these possibilities.

ARROW OF CAUSATION: LARGE POPULATION SIZE ==> PARTHENOGENESIS, OR VICE VERSA?

The biggest source of ambiguity in interpreting our findings is the inference of causality, given the arrow of causation connecting large population size or large geographic range to asexuality can point either way. Most authors have interpreted parthenogenesis as the cause and wide geographic distribution as the effect. In the short term, the causal effects of parthenogenesis are undeniable: parthenogenetic populations often have a much broader geographic range than conspecific sexual populations, and it would be very hard to explain this without invoking their increased colonizing ability and reproductive efficiency (Vandel 1928; Vrijenhoek and Parker 2009). But in our view this short-term consequence of parthenogenesis has obscured a larger pattern: that species already having a large population size are more likely to give

rise to parthenogenetic populations that persist long enough to be observed.

A species is more likely to be parthenogenetic if it is widespread, or polyphagous, or a pest. But parthenogenesis is uncommon, and it is nonetheless the case that most widespread, highly polyphagous species of scale insects are sexual (Fig. 2), and that almost all of these widespread, highly polyphagous, sexual species are pests (Miller 2005; Miller et al. 2005; Normark and Johnson 2011). Even within species here classified as asexual, many have sexual populations, and in most cases these are also highly polyphagous and widespread (Gerson 1990; Nur 1990; Miller et al. 2005; Provencher et al. 2005). The fact that the syndrome of traits (extreme polyphagy, wide geographic distribution, pest) occurs with or without parthenogenesis implies that parthenogenesis is not a critical factor in the origin of the syndrome, but rather that these traits present in the ancestral sexual population have facilitated the success of asexual descendants. This view is supported by our finding that sexual species in genera that also contain asexuals have larger geographic ranges than sexual species in genera where parthenogenesis is absent (Fig. 4).

In our view, the most parsimonious interpretation is that large population size is a critical causal factor in this syndrome that arises earlier than parthenogenesis. It has been argued that large population size is causally connected to broad host range in a positive feedback loop (Normark and Johnson 2011). A similar argument could be made for a synergy between large population size and broad geographic range. Although geographic ranges of scale insects have expanded dramatically in recent centuries due to human action, cosmopolitan, and invasive scale insect species are typically widespread and abundant in their native range and natural habitats (Schowalter and Ganio 2003; Miller et al. 2005; Schowalter and Zhang 2005; Gwiazdowski et al. 2011; GE Morse, AO and BBN, unpubl. data). Our results offer further support for the empirical finding by Hoffman et al. (2008) that parthenogenesis is correlated with pest status, but our interpretation of the cause of this correlation is very different. Hoffman et al. (2008) hypothesized that parthenogenetic pests have become abundant in certain environments (agricultural areas), and that this abundance is, in part, a consequence of parthenogenesis. In contrast, we argue that these species are abundant in many environments, not just agricultural and human-altered environments, and that high abundance precedes the origin of parthenogenesis.

PARTHENOGENESIS IN LARGER POPULATIONS: HIGH ORIGINATION RATE, LOW EXTINCTION RATE

Even if one concedes that large population size precedes the origin of parthenogenesis, there are still alternative possible explanations for this. We have focused on extinction, implicitly assuming that

the distribution of parthenogenesis reflects troughs in the distribution of extinction risk for parthenogenetic lineages (Maynard Smith 1978; Bell 1982). An alternative interpretation of our extinction rate analysis is that reversions from parthenogenesis to sex are much more common than origins of parthenogenesis. We cannot rule out this possibility, but we agree with the conventional wisdom that regards it as implausible (Bull and Charnov 1985), as genes involved in aspects of male reproductive function or female sexual behavior have been shown to degenerate rapidly in several parthenogenetic insect species (Normark et al. 2003). Additionally, one of the few detailed studies on the phylogenetics of sexual and parthenogenetic lineages in a scale insect species (Provencher et al. 2005) found a single origin and no evidence for the loss of parthenogenesis. Another alternative possibility is that the distribution of parthenogenesis reflects peaks in the distribution of origination rate of parthenogenetic lineages. And there is a plausible mechanism connecting large population size to a high origination rate for parthenogenetic lineages: if origins of parthenogenesis are rare, they are more likely to occur in large populations than small ones (Normark and Johnson 2011).

First, we concede that differences in origination rate may have played a significant role in shaping the patterns we describe in this article. But we argue that differences in extinction rate are also likely to be part of the explanation for the patterns. Our analysis finds support for the hypothesis that asexual scale insects have a higher extinction rate than sexuals. More broadly, the hypothesis that parthenogens have a higher extinction rate than sexuals helps to explain major features of the taxonomic distribution of parthenogenesis, while the hypothesis that the distribution of parthenogenesis is limited by rarity of origination fails to explain the “tippy” distribution of parthenogenesis in taxonomies and phylogenetic trees (Maynard Smith 1978).

Conclusions

The hypothesis that large population size ought to protect an asexual population from extinction is an old one (Muller 1964) that is currently ascendant on theoretical grounds (Keightley and Otto 2006; Otto 2009; Rice and Friberg 2009). To our knowledge, this is the first study that provides comparative statistical support for this hypothesis. Clearly, population size is not the only factor that affects the distribution of parthenogenesis. If it were, there would be many parthenogenetic marine organisms, whereas in fact these are almost entirely absent (Bell 1982; Suomalainen et al. 1987). Nonetheless, it may be an important factor both at the broadest scales (small vs. large organisms) and within particular groups. The association of parthenogens with “marginal” habitats (e.g., high altitude, high latitude, xeric, island) (Glesener

and Tilman 1978; Bell 1982; Bierzychudek 1985) may reflect large geographic range, associated with large population size. Although theory provides us with a general expectation that sex becomes less important at higher population sizes, theorists have not been able to put numbers on this and predict the actual population size at which such effects become important (how large is “large?”)—the effects of sexuality on extinction risk are too sensitively dependent upon unknown quantities like the spectrum of selection coefficients of new mutations. This study, however, suggests a way of empirically estimating the critical population size, by investigating the census and genetic population sizes of the scale insect species represented as points in Figure 3A, B. Further phylogenetic study may also permit us to investigate the ages of the parthenogenetic lineages and the extent to which they are experiencing an accumulation of deleterious mutations (Paland and Lynch 2006; Neiman et al. 2010; Henry et al. 2011). Unusual things happen when population sizes get very large. It is appropriate that we should use common pests to study such phenomena, which can yield practical knowledge applicable to pest management along with potentially fundamental insights into the evolution of genetic systems.

ACKNOWLEDGMENTS

We would like to thank J. Hadfield and S. Otto for their help with the statistical analysis. This research was supported by US National Science Foundation (NSF) (DEB-0447880), the USDA National Institute of Food and Agriculture (2009–02310), and the Royal Society. The manuscript was improved by the comments of N. Johnson, D. Fairbairn, N. Perrin, and two anonymous reviewers. The authors are unaware of any conflict of interest.

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Associate Editor: N. Perrin

Supporting Information

The following supporting information is available for this article:

Table S1. Table with all taxa for which data on reproductive system was available and the reference from which the information was obtained.

Table S2. Table with all taxa used to construct the phylogeny for which sequence information was available from Genbank.

Table S3. Table with all taxa for which unpublished sequences were included in the analysis.

Supporting Information may be found in the online version of this article.

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