Evolutionary Ecology Research, 2009, **11**: 43–55

Asexual species of oribatid mites do not have a local-scale colonization advantage over sexual species

Jennifer M. Cianciolo

Biology Department, Indiana University, Bloomington, Indiana, USA

ABSTRACT

Hypothesis: Asexual species have a colonization advantage relative to sexual species. Such an advantage may allow asexuals to escape from local-scale selection pressures, such as those from competition with sexual species, and permit co-existence of the two reproductive modes.

Organisms: Species of soil mites in the suborder Oribatida with one of three reproductive types: ancient asexual, recent asexual or sexual. Taxonomic relationships indicate that these are likely to be close competitors.

Methods: Small colonizable enclosures, representing both new and defaunated habitat, were placed in a temperate forest and sampled, together with soil cores representing the surrounding habitat, at 2-month intervals over 2 years. Binary logistic regression was used to determine whether mites have a colonization advantage, defined as having a higher prevalence in colonized litter bags than in nearby source soil cores.

Results: Only the most abundant of 17 recent asexual species was found to have a colonization advantage; the rest were the poorest colonizers. Ancient asexuals had moderate colonization rates and sexual species the highest colonization rates. This pattern is opposite to the prediction that asexuals have a colonization advantage.

Keywords: colonization advantage, competition, maintenance of sexual reproduction.

INTRODUCTION

Asexual organisms are expected to be better colonizers than sexual organisms, primarily because they can populate new habitats without mates (Williams, 1975; Bell, 1982). Asexuals often occur in more northerly habitats than their close sexual relatives, a pattern called ‘geographic parthenogenesis’, first described for plants (Vandel, 1928), and they also often have broader distributions than their close sexual relatives (e.g. Moritz, 1991) or they occur in isolated habitats (Cuellar, 1994). These patterns are consistent with the hypothesis that asexuals are better colonizers than sexuals. Although colonization in plants has been studied extensively (e.g. Eppley and Pannell, 2007), colonization ability in animals has rarely been compared directly

---

Correspondence: J.M. Cianciolo, Biology Department, Indiana University, 1001 East 3rd Street, Bloomington, IN 47405, USA. e-mail: jciancio@indiana.edu

between taxonomically related sexual and asexual lineages, except in laboratory settings (e.g. Domes *et al.*, 2007).

Greater colonization ability of asexuals relative to sexual progenitors or sexual relatives could reduce some purported evolutionary costs of asexual reproduction. One such cost, resulting from the lack of genetic diversity generated by recombination, is the reduced ability of asexuals to respond to selection pressures (Weismann, 1904), such as those generated by competition with sexuals or co-evolution with parasites. A colonization advantage should allow asexual individuals to leave the shared environment, where competitive pressures and parasitism are strong, and colonize extreme or empty habitats where such pressures are weak or absent (e.g. Tooby, 1982; Tripet *et al.*, 2002). Although colonization does not directly affect mutation load, it can reduce the effects of deleterious mutations if those are exacerbated by stressful environments (Robert, 2006) or pressures from competition and parasitism.

This hypothesized colonization advantage to asexuals is usually viewed as a large-scale geographic phenomenon, but the advantage of escape from local competition could also be achieved through local-scale dispersal. Selection pressures imposed by local antagonists occur on shorter time-scales than those required for regional-scale colonization. Additionally, when organisms occur in patchy environments, colonization among patches may enhance the co-existence of sexuals and asexuals if sexual species have wider niche breadth and asexuals have greater colonization ability (Slatkin, 1974; Rodriguez *et al.*, 2007).

I tested the local-scale dispersal abilities of oribatid mites, free-living soil arthropods, with respect to reproductive mode over a 2-year period (from 2004 to 2006) in forest habitat in southern Indiana. [I will primarily discuss competitive interactions instead of parasite avoidance, because little is known about oribatid mite parasites, other than that there are many (e.g. Purrini, 1980).] Most oribatid mites are generalist plant-saprophages and fungivores in organic layers of soil (Schuster, 1956; Harding and Stuttard, 1974; Wallwork, 1983; Schneider *et al.*, 2004). Sexual and asexual oribatid species co-exist locally in soil patches that likely induce a meta-population or meta-community structure (see Koteja *et al.*, 1994). Variability in both abundance and species richness can be very high among shallow soil cores taken within any habitat, ranging from tens to hundreds of individuals, and from few to tens of species. Microhabitat conditions, such as humidity, moisture, and availability of resources, can vary considerably even at very small distances (Mitchell, 1979; Maraun *et al.*, 1999). Oribatid mite species are sometimes considered close competitors with each other due to generally similar niche requirements (Anderson, 1975), and because they are abundant and diverse when sampled at very small scales (e.g. forest floor samples). Additionally, some asexual oribatid mites occur in genera, families, and superfamilies without known sexual species and are considered ancient asexuals, as explained in greater detail below. Asexuals in primarily sexual genera are considered to be more recently derived. Although greater reproductive potential on the part of asexuals can be interpreted as a competitive advantage, that advantage is likely to be decreased by the reduced ability of aseuxals to respond to selection pressures. In oribatid mites, comparisons of reproductive potential are difficult to address because there is no variation in reproductive mode, so comparisons are restricted to heterospecifics (e.g. Ermilov and Łochyńska, 2008). Most existing data relate to eggs per female, rather than the more relevant oviposition rates, which are more difficult to obtain. Because oribatid mites are considered to be k-selected (Norton, 1994), and reproductive rates do not appear to be high, I assume sexuals are better competitors due to an enhanced potential to respond to selection from recombination.

I tested oribatid mite colonization abilities in forest communities in central Indiana by distributing two kinds of mite-free substrates across 25 hectares of a natural forest and examining differences in numbers of individuals colonizing these experimental environments relative to numbers in the surrounding habitat estimated from adjacently collected soil cores. If asexual species have a colonization advantage on local scales, they should be more prevalent in experimental environments than in the soil cores, while sexuals should be less prevalent in experimental environments than in soil cores. Because long-term costs of asexual reproduction such as mutation accumulation and an inability to respond to changing environments appear to be overcome by ancient asexuals, the expectation of their reduced ability to compete with sexuals may be false. Therefore, I anticipated recent asexuals to be better colonizers than ancient asexuals because it is likely that they experience greater competitive pressure from closely related sexual species, from which they were derived and therefore share greater niche overlap.

MATERIALS AND METHODS

Study species

Oribatid mites are free-living soil arthropods of significant morphological diversity and small size (mostly 300–500 μm long). Nearly 10,000 species are named (Schatz, 2002; Subias, 2004), likely representing only 1–10% of the extant fauna (Walter and Proctor, 1999). In temperate regions, several hundred thousand individuals, often representing over 100 species, are found per square metre. They have very low dispersal rates; for example, two species traced radioactively travelled 4.1 and 1.7 cm per day (Berthet, 1964). They have long generation times of 1–2 years or more and usually low fecundity, with about a couple dozen eggs per female per lifetime (Luxton, 1981; Norton, 1994).

Nearly 10% of known oribatid mite species are obligately asexual: females produce diploid eggs that develop into females. Most of these occur in genera and families – some containing more than 100 species – without known sexual species (see Norton *et al.*, 1993 and references therein; Maraun *et al.*, 2004). This pattern implies that speciation has occurred repeatedly in an asexual mode. Genetic evidence is accumulating that species in these groups can be very old – that is, ancient asexuals (Heethoff *et al.*, 2007). Other asexual species are scattered within predominately sexual clades (Norton *et al.*, 1993). These are likely to be recent asexual offshoots from sexual progenitors. As a working definition, I considered asexual species with congeneric sexual relatives to be 'recent' asexuals and those without to be 'ancient' asexuals, although the former may not be recent in the literal sense. The variation in reproductive type creates opportunities for comparative studies among sexuals, recent asexuals, and ancient asexuals, that is not possible with other taxa (Cianciolo and Norton, 2006). The term 'asexual' alone is used where recent and ancient asexuals are combined in statistical analyses.

Experimental design

To produce mite-free habitat for colonization, 100 soil cores were collected from forest habitat at Moore's Creek, Monroe County, Indiana across approximately 25 hectares throughout July 2004. Moore's Creek is a mature oak–beech–maple forest preserve that surrounds Monroe Lake with no formal land management. It has a steeply dissected ridge and ravine topography. Soil was collected with a cylinder made from PVC pipe, 3 cm in height with a diameter of 5.5 cm; this device was filled three times with contents combined to represent one soil core. Mites were extracted into 70% ethanol using Berlese funnels and the mite-free soil material was used as one type of habitat in the colonization experiments.

Each mite-free soil core (SC) was placed into a 'litter-bag' made of fibreglass window-screen (each 13 × 11 × 2 cm). In addition, I created a second type of colonization habitat by filling an additional 100 litter bags with leaves from fallen tree branches (primarily *Acer* species). These leaves also represent new habitat as there were no signs of decomposition and no mites appeared in Berlese-funnel extracts of a subset of the leaves. Colonization ability should be consistent between these two substrate types if movement is not due to differences in habitat preference. From 4 to 11 August, each soil-core-filled litter bag (LBC) was placed on the ground at its place of origin. A 'new'-leaf-filled litter bag (LBN) was paired with each LBC. Litter bags were placed end to end and affixed to the ground with a steel-staked vinyl flag.

Litter bags were collected 13 times at 1- to 2-month intervals starting in October 2004 and ending in August 2006. On each collection date, seven pairs of litter bags were randomly chosen and collected and a new soil core was taken at each pair location for a total of 21 samples per collection and 273 samples for the entire study. Each set of three samples (LBC, LBN, and SC) was given a 'set' number for unique identification.

After collection, each sample was placed in a Berlese funnel, and mites were extracted for 4 days. Adult oribatid mites were identified to species or morphospecies, except for those in the genus *Suctobelbella*, a specious asexual genus where pooling of discrete morphotypes into species can be somewhat arbitrary. Mites were identified to genus using Balogh and Balogh (1992); R.A. Norton verified or identified species.

Reproductive mode was determined from the literature, where possible, or from sex-ratio analysis. The validity of the latter method has been established by numerous lines of previous work (Schaefer *et al.*, 2006). For example, Palmer and Norton (1992) studied nine asexual species in the taxon Desmonomata, all with strong female-biased sex ratios; analysis of allozyme variability found no evidence for recombination, both because of fixed levels of heterozygosity and a rarity of complete homozygosity. *Mucronothrus nasalis*, the species with the highest percentage of males (9%) found in the study, had the lowest calculated genetic diversity. Numerous asexual desmonomatan species have been collected over continents and seasons with no significant variation in the observed female-biased sex ratios (Palmer and Norton, 1991), indicating that male production and outcrossing do not occur in restricted ecological or geographic circumstances. Additionally, asexual reproduction has been documented in 27 species by culturing (Taberly, 1987; Palmer and Norton, 1991; J.M. Cianciolo, unpublished); each of these species has a highly biased female sex ratio (96–100% female), while sexual oribatid mites tend to have even sex ratios (Luxton, 1981). When examined, rare males appeared to be sexually non-functional (Taberly, 1988).

Statistical analyses

The degree to which sampling of each habitat treatment represented the standing community was assessed by calculating S_1, the Chao 1 richness estimator ($S_1 = S_{\mathrm{obs}} + a^2/2b$, where S_1 = Chao 1 richness indicator, S_{obs} = observed richness, a = the number of species represented by one individual, and b = the number of species represented by two individuals) (Chao, 1984). This equation corrects the observed richness for the occurrence of rare species in the data set. Richness was then plotted against collection date to visualize the sampling of the community. Richness was compared across SC, LBC, and LBN by rarefaction in which the data are re-sampled assuming the lowest common abundance using the program EcoSim (Gotelli and Entsminger, 2001).

Colonization ability was determined by comparing the numbers of individuals of a particular reproductive mode as they occurred in litter bags relative to natural soil cores. Good colonizers should be present in the source and abundant in both types of litter bags. Binary logistic regression was used with habitat (SC, LBC, LBN) as the dependent variable and reproductive mode, collection date, and set number and season included as independent variables. Each species and its abundance comprised one line of data with its corresponding dependent and independent variables. Regressions were carried out in SPSS 14.0 for Windows (SPSS, Inc., Chicago, IL).

RESULTS

In total, 48,918 individuals in 104 species were extracted, counted, and identified from the core and litter bag samples combined (see Online Appendix at evolutionary-ecology.com/data/2360appendix.pdf). Asexuals represented 78.5% of all individuals sampled but only 44.9% (44/98) of the identified species collected. There were 16,991 ancient asexual individuals in 25 species and 21,386 recent asexuals in 17 species. There were 9668 sexual individuals in 54 species. Mites of unknown reproductive mode were excluded from the analysis; these comprised only 1.8% of individuals ($n = 873$) and 5.8% of species in the study ($n = 8$). Within each reproductive mode, one taxon was clearly the most abundant: the sexual species *Zygoribatula* sp., the recent asexual *Oppiella nova* (Oudemans), and ancient asexual individuals in the genus *Suctobelbella*. Analyses were done with and without these species included, and with only these species included.

Sampling effort was effective as the Chao 1 indicator showed 97% of species were represented in the soil core data (97 observed of 100.13 estimated species present) and 94% in LBC (97 observed, 101.9 estimated) and 95% in LBN (92 observed, 96.5 estimated). The reduction in the number of species added over time (Fig. 1) also indicated that sampling was near complete. Richness was not significantly different across treatments as indicated by rarefaction, suggesting that colonization of the litter bags was complete.

Collection date, set number, and season had no predictive role as determined by Cox and Snell R^2 values and did not contribute to the models as determined by Hosmer-Lemeshow goodness-of-fit tests (Table 1).

Sexual individuals were found in greater frequencies in both litter bag types relative to soil cores, whether the data were analysed with individuals from all species (Fig. 2a), individuals from all species with common species excluded (Fig. 2b), or individuals of the most common species only (Fig. 2c). More sexual individuals were found in LBC than in SC and more in SC than in LBN (Fig. 2d). The species-level pattern (Fig. 3) was similar to that when individuals of all species were included (Fig. 2a). For simplicity, cross-tabulation tables (Table 2a, b) show analyses with all species only. In these tables, the standardized residuals give the direction of difference that is of interest. For example, in Table 2a, the value 39.8 for sexuals in LBN indicates that there were more sexuals in that habitat than expected by independence. Statistical independence for a 2 × 2 contingency table is defined as follows: the probability of being in a particular habitat, given the individual's reproductive mode, equals the probability of being in that particular habitat.

The pattern for ancient asexuals is less clear. When all species were included in the

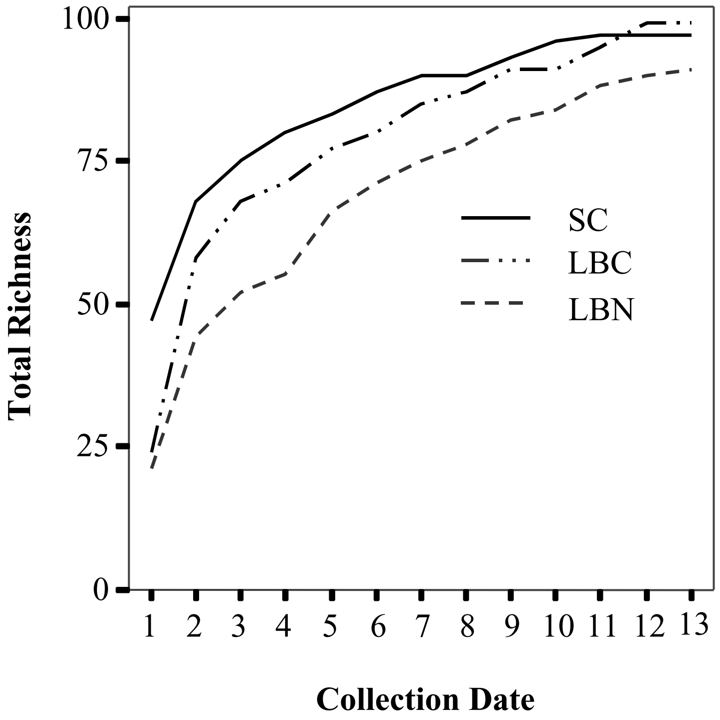

Fig. 1. Increase in oribatid mite species richness by collection date (1 = October 2004; 2 = November 2004; 3 = December 2004; 4 = February 2005; 5 = April 2005; 6 = June 2005; 7 = August 2005; 8 = October 2005; 9 = December 2005; 10 = February 2006; 11 = April 2006; 12 = June 2006; 13 = August 2006) for each habitat type (SC = soil core; LBC = litter bag core; LBN = litter bag 'new' leaves).

analysis, the proportion of ancient asexuals in the cores did not differ from that in either litter bag type (Fig. 2a). With the most common species excluded, the proportion of ancient asexuals in the litter bags was greater than in the cores (although less different from expected than for sexuals; see Fig. 2b). With only the most common species included, ancient asexuals were less frequent in the litter bags than in the soil cores (Fig. 2c). Fewer individuals occurred in both litter bag types than in soil cores.

In general, recent asexuals were less frequent in litter bags than in soil cores (Fig. 2a, b, d). Only the most common species, *O. nova*, was more frequent in LBN than in the soil cores (Fig. 2c).

DISCUSSION

Asexual oribatid mites do not appear to have a colonization advantage relative to sexual oribatid mites, and recent asexuals appear to be poorer colonizers than ancient asexuals. Although the model fits were poor (for low Cox and Snell R^2 values across the regressions, see Table 1), the data suggest that sexuals are better colonizers than asexuals, allowing the rejection of the hypothesis that asexuals avoid local selection pressures through colonization advantage. Because these differences were consistent between litter bag types,

Table 1. Binary regression of oribatid mite reproductive mode, collection date, season, and set number on habitat

(a) All species included

	Step 1	Step 2	Step 3	Step 4
SC vs. LBC				
Factor added	Reproductive mode	Collection date	Season	Set number
H & L Test[a]	1.000	0.000	0.000	0.000
Cox & Snell R^2	0.053	0.075	0.081	0.083
Change in C&S R^2		0.022	0.006	0.002
SC vs. LBN				
Factor added	Reproductive mode	Season	Collection date	Set number
H & L Test[a]	1.000	0.000	0.000	0.000
Cox & Snell R^2	0.068	0.104	0.114	0.115
Change in C&S R^2		0.036	0.01	0.001

(b) Most common species not included

	Step 1	Step 2	Step 3	Step 4
SC vs. LBC				
Factor added	Reproductive mode	Season	Collection date	Set number
H & L Test[a]	1.000	0.000	0.000	0.000
Cox & Snell R^2	0.068	0.090	0.101	0.105
Change in C&S R^2		0.022	0.011	0.004
SC vs. LBN				
Factor added	Reproductive mode	Season	Collection date	Set number
H & L Test[a]	1.000	0.000	0.000	0.000
Cox & Snell R^2	0.125	0.156	0.164	0.168
Change in C&S R^2		0.031	0.008	0.004

(c) Most common species only included

	Step 1	Step 2	Step 3	Step 4
SC vs. LBC				
Factor added	Reproductive mode	Collection date	Season	Set number
H & L Test[a]	1.000	0.000	0.000	0.000
Cox & Snell R^2	0.062	0.094	0.100	0.101
Change in C&S R^2		0.032	0.006	0.001
SC vs. LBN				
Factor added	Reproductive mode	Season	Collection date	Set number
H & L Test[a]	1.000	0.000	0.000	0.000
Cox & SnellR^2	0.060	0.122	0.142	0.143
Change in C&S R^2		0.062	0.02	0.001

Note: SC = soil core; LBC = litter bag core; LBN = litter bag 'new' leaves.

[a] Hosmer and Lemeshow test.

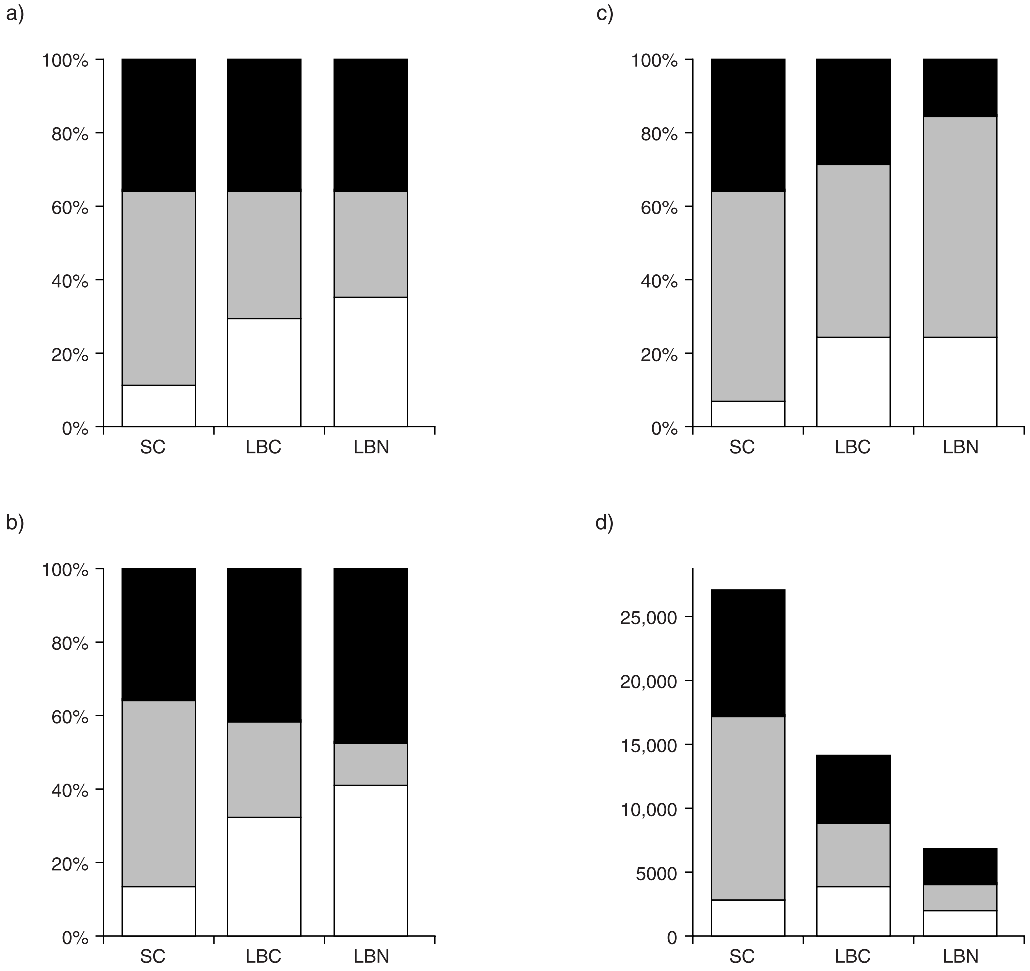

Fig. 2. Changes in oribatid mite abundance by reproductive mode across each habitat (SC = soil core; LBC = litter bag core; LBN = litter bag 'new' leaves). Black shading represents ancient asexuals, grey shading recent asexuals, and white sexuals. In (a) the percentages of individuals in all species are compared; in (b) the percentages of individuals in all species excluding those in the one most common taxon from each reproductive mode are compared; in (c) the percentages of individuals only within those most common species are compared; and in (d) the total numbers of individuals in all species are compared.

the pattern likely represents general local colonization movements or dispersal, rather than differences in habitat preference.

Recent and ancient asexuals appear to differ slightly in their colonization ability. Recent asexuals tended to be poorer colonizers, and ancient asexuals appear to be moderately good colonizers, indicated by their equal frequencies in litter bags relative to soil cores when all species were analysed. This might be expected if movement between patches enhances long-term persistence, but it does not support the idea that competition with sexuals is greater for recent asexuals than for ancient asexuals. Despite the moderate rate of

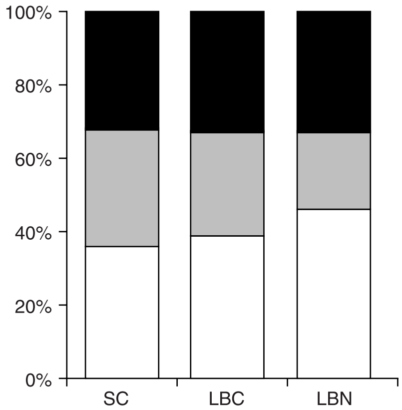

Fig. 3. Percentages of oribatid mite species by reproductive mode in each habitat (SC = soil core; LBC = litter bag core; LBN = litter bag 'new' leaves). Black shading represents ancient asexuals, grey shading recent asexuals, and white sexuals.

colonization of ancient asexuals overall, individuals in the genus *Suctobelbella* appear to be among the poorest colonizers: compared with only the very common recent asexual, *O. nova*, and the very common sexual, *Zygoribatula* sp., suctobelbellids were the worst colonizers. When suctobelbellids were excluded from the analysis, ancient asexuals were more common in litter bags than in soil cores. Future research should address the role such ecological differences among asexual species play in the success of asexuality as a reproductive mode. Adaptive hypotheses, such as the avoidance of parasite co-evolution, as well as explanations due to chance, such as historical contingency, should also be tested.

The assumption that sexuals are better competitors than asexuals could be false if genetic diversity is not significantly lowered in asexuals. This could happen if clones span the genetic spectrum that sexuals cover, or if recombination occurs within asexual lineages; for example, Omilian *et al.* (2006) found that asexual *Daphnia pulex* undergo mitotic recombination. The frozen niche variation model posits that the production of asexual lineages through hybridization of sexual lineages results in a series of clones that can exploit the same resource range as sexual progenitors (Vrijenhoek, 1979). This idea does not apply to oribatid mites, because asexual females are not produced through hybridization and appear not to be continuously generated from close sexual relatives. Ancient asexuals are even less likely to retain any sampling of the original sexual genetic diversity, as radiation appears to have occurred entirely without sex (Maraun *et al.*, 2004). Nevertheless, splits between species appear to be deep (Maraun *et al.*, 2003), and genetic diversity could be high due to mutational divergence. Asexuals could also experience competitive advantage where competition is determined only by population size; however, relative reproductive rates among sexual and asexual oribatid mite species are not well understood.

Secondary production of oribatid mite species is expected to be low because of their chelicerate ancestry – that is, they are not thought to be well-adapted as decomposers; if true, the production of males could be especially costly (Norton, 2007). A model by Scheu and Drossel (2007) showed that a scarcity of resources could give an advantage to sexual reproduction, but where resources are quickly replenished, asexuality tends to predominate. Both parts of this scenario could apply to soil mites, if indeed resource utilization is

Table 2. Cross-tabulation tables of oribatid mite reproductive mode by habitat

(a) Reproductive mode by SC vs. LBN for all species

			Reproductive mode			
			Ancient asexual	Recent asexual	Sexual	Total
Habitat	SC	Count	9574	14,410	3080	27,064
		% within Habitat	35.4	53.2	11.4	100.0
		% within Reproductive mode	79.7	87.7	55.5	79.6
		% of Total	28.2	42.4	9.1	79.6
		Standardized residual	0.1	11.6	−20.2	
	LBN	Count	2442	2026	2474	6942
		% within Habitat	35.2	29.2	35.6	100.0
		% within Reproductive mode	20.3	12.3	44.5	20.4
		% of Total	7.2%	6.0	7.3	20.4
		Standardized residual	−0.2	−22.9	39.8	
Total	Count		12,016	16,436	5554	34,006

(b) Reproductive mode by SC vs. LBC for all species

			Reproductive mode			
			Ancient asexual	Recent asexual	Sexual	Total
Habitat	SC	Count	9574	14,410	3080	27,064
		% within Habitat	35.4	53.2	11.4	100.0
		% within Reproductive mode	65.8	74.4	42.8	65.8
		% of Total	23.3	35.1	7.5	65.8
		Standardized residual	−0.1	14.7	−24.1	
	LBC	Count	4975	4950	4114	14,039
		% within Habitat	35.4	35.3	29.3	100.0
		% within Reproductive mode	34.2	25.6	57.2	34.2
		% of Total	12.1	12.0	10.0	34.2
		Standardized residual	0.1	−20.4	33.4	
Total	Count		14,549	19,360	7194	41,103

Note: SC = soil core; LBC = litter bag core; LBN = litter bag 'new' leaves. Signs of standardized residuals show direction of difference from expectation.

inefficient, while resource input – for example, leaf fall and subsequent fungal colonization – provides for relatively fast replenishment with respect to their generation time. Indeed, Scheu and Drossel (2007) concluded that the narrow resource spectrum found in soil systems may explain the ubiquity of asexual reproduction there. The co-existence of sexual and asexual forms might also be facilitated by similarity in colonization abilities if neutral processes play a role in community dynamics (see, for example, Cadotte, 2007).

The local-scale pattern found here appears to be in conflict with larger-scale field data. The first few species to appear after disturbances like flooding or cultivation tend to be asexuals, and those tend to remain after the habitat stabilizes (reviewed in Norton and Palmer, 1991). When examined at such larger scales, asexual oribatid mites are usually predominant in disturbed habitats; however, they are also common in climax environments (reviewed in Norton and Palmer, 1991; Cianciolo and Norton, 2006). A microcosm study (at the local scale by definition) of recolonization found that, although asexual oribatid mites were strongly associated with early collection dates, sexuals were faster at repopulating the defaunated habitat (Domes *et al.*, 2007). I did not find a similar effect of collection date. Asexual oribatid mites likely possess a colonization advantage when moving into new habitats at regional scales, but they do not appear to accrue such an advantage at local scales. Their long-term persistence may be facilitated by this large-scale dispersal ability, but it is not facilitated by local-scale dispersal. If asexual species do indeed swamp sexuals by a reproductive advantage, local-scale colonization advantage by sexuals may help to explain how hundreds of sexual and asexual oribatid mite species co-exist locally with similar ecologies.

ACKNOWLEDGEMENTS

Thanks to Roy A. Norton for verifying mite identifications and comments on the manuscript, to Carly Willenborg and Matt Guanzon for help with fieldwork, and to Ashley Siniard for help with field and microscope work. Thanks to Adam Sheya for statistical advice and Helmut Zwölfer, Farrah Bashey-Visser, and Yaniv Brandvain for comments on the manuscript.

REFERENCES

Anderson, J.M. 1975. The enigma of soil animal species diversity. In *Progress in Soil Ecology: Proceedings of the Fifth International Colloquium of Soil Zoology, 1973* (J. Vanek, ed.), pp. 51–58. Prague: Academia.

Balogh, J. and Balogh, P. 1992. *The Oribatid Mites Genera of the World*, Vols. 1 & 2. Budapest: Hungarian National Museum Press.

Bell, G. 1982. *The Masterpiece of Nature: The Evolution and Genetics of Sexuality*. Berkeley, CA: University of California Press.

Berthet, P. 1964. Field study of the mobility of Oribatei using radioactive tagging. *J. Anim. Ecol.*, **33**: 443–449.

Cadotte, M.W. 2007. Concurrent niche and neutral processes in the competition–colonization model of species coexistence. *Proc. R. Soc. Lond. B*, **274**: 2739–2744.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. *Scand. J. Stat.*, **11**: 265–270.

Cianciolo, J.M. and Norton, R.A. 2006. The ecological distribution of reproductive mode in oribatid mites, as related to biological complexity. *Exp. Appl. Acarol.*, **40**: 1–25.

Cuellar, O. 1994. Biogeography of parthenogenetic animals. *Biogeographica*, **70**: 1–13.

Domes, K., Scheu, S. and Maraun, M. 2007. Resources and sex: soil re-colonization by sexual and parthenogenetic oribatid mites. *Pedobiologia*, **51**: 1–11.

Eppley, S.M. and Pannell, J.R. 2007. Sexual systems and measures of occupancy and abundance in an annual plant: testing the metapopulation model. *Am. Nat.*, **169**: 20–28.

Ermilov, S.G. and Łochyńska, M. 2008. The influence of temperature on the development time of three oribatid mite species (Acari, Oribatida). *North-West J. Zool.*, **4**: 274–281.

Gotelli, N.J. and Entsminger, G.L. 2001. *EcoSim: Null Models Software for Ecology*, Version 7.0.

Jericho, VT: Acquired Intelligence Inc. & Kesey-Bear (http://homepages.together.net/≈gentsmin/ecosim.htm).

Harding, D.J.L. and Stuttard, R.A. 1974. Microarthropods. In *Biology of Plant Litter Decomposition* (C.H. Dickinson and G.J.F. Pugh, eds.), pp. 489–532. New York: Academic Press.

Heethoff, M., Domes, K., Laumann, M., Maraun, M., Norton, R.A. and Scheu, S. 2007. High genetic divergences indicate ancient separation of parthenogenetic lineages of the oribatid mite *Platynothrus peltifer* (Acari, Oribatida). *J. Evol. Biol.*, **20**: 392–402.

Koteja, I., Stachowicz, A. and Sgardelis, S. 1994. Metapopulation study of *Crytostigmata* inhabiting rock dwelling mosses. *Bios*, **2**: 157–161.

Luxton, M. 1981. Studies on the oribatid mites of a Danish beech wood soil: IV. Developmental biology. *Pedobiologia*, **21**: 312–340.

Maraun, M.J., Alphei, M., Bonkowski, R., Buryn, S., Migge, M., Peter, M. *et al.* 1999. Middens of the earthworm *Lumbricus terrestris* (Lumbricidae): microhabitats for micro- and mesofauna in forest soil. *Pedobiologia*, **43**: 276–287.

Maraun, M., Heethoff, M., Scheu, S., Norton, R.A., Weigmann, G. and Thomas, R. 2003. Radiation in sexual and parthenogenetic oribatid mites (Oribatida, Acari) as indicated by genetic divergence of closely related species. *Exp. Appl. Acarol.*, **29**: 265–277.

Maraun, M., Heethoff, M., Schneider, K., Scheu, S., Weigmann, G., Cianciolo, J. *et al.* 2004. Molecular phylogeny of oribatid mites (Oribatida, Acari): evidence for multiple radiations of parthenogenetic lineages. *Exp. Appl. Acarol.*, **33**: 183–201.

Mitchell, M.J. 1979. Effects of physical parameters and food resources on oribatid mites in forest soils. In *Recent Advances in Acarology*, Vol. 1 (J.G. Rodriguez, ed.), pp. 585–592. New York: Academic Press.

Moritz, C. 1991. The origin and evolution of parthenogenesis in *Heteronotia binoei* (Gekkonidae) – evidence for recent and localized origins of widespread clones. *Genetics*, **129**: 211–219.

Norton, R.A. 1994. Evolutionary aspects of oribatid mite life histories and consequences for the origin of the Astigmata. In *Mites: Ecological and Evolutionary Analyses of Life-history Patterns* (M. Houck, ed.), pp. 99–135. New York: Chapman & Hall.

Norton, R.A. 2007. Holistic acarology and ultimate causes: examples from the oribatid mites. In *Acarology XI: Proceedings of the International Congress* (J.B. Morales-Malacara, V. Behan-Pelletier, E. Ueckermann, T.M. Pérez, E.G. Estrada-Venegas and M. Badii, eds.), pp. 3–20. Mexico City: Universidad Nacional Autónoma de México.

Norton, R.A. and Palmer, S.C. 1991. The distribution, mechanisms and evolutionary significance of parthenogenesis in oribatid mites. In *The Acari: Reproduction, Development and Life History Strategies* (R. Schuster and P.W. Murphy, eds.), pp. 107–136. London: Chapman & Hall.

Norton, R.A., Kethley, J.B., Johnston, D.E. and O'Connor, B.M. 1993. Phylogenetic perspectives on genetic systems and reproductive modes of mites. In *Evolution and Diversity of Sex Ratio in Insects and Mites* (D. Wrensch and M. Ebberts, eds.), pp. 8–99. New York: Chapman & Hall.

Omilian, A.R., Cristescu, M.E.A., Dudycha, J.L. and Lynch, M. 2006. Ameiotic recombination in asexual lineages of *Daphnia. Proc. Natl. Acad. Sci. USA*, **103**: 18638–18643.

Palmer, S.C. and Norton, R.A. 1991. Taxonomic, geographic and seasonal distribution of thelytokous parthenogenesis in the Desmonomata (Acari: Oribatida). *Exp. Appl. Acarol.*, **12**: 67–81.

Palmer, S.C. and Norton, R.A. 1992. Genetic diversity in thelytokous oribatid mites (Acari; Acariformes: Desmonomata). *Biochem. Syst. Ecol.*, **20**: 219–231.

Purrini, K. 1980. On the incidence and distribution of parasites of soil fauna of mixed coniferous forests, mixed leaf forests, and pure beech forests of lower Saxony, West Germany. In *Soil Biology as Related to Land Use Practices: Proceedings of the 7th International Colloqium on Soil Zoology* (D. Dindal, ed.), pp. 561–582. Washington, DC: US Environmental Protection Agency.

Robert, A. 2006. Negative environmental perturbations may improve species persistence. *Proc. R. Soc. Lond. B*, **273**: 2501–2506.

Rodriguez, A., Jansson, G. and Andren, H. 2007. Composition of an avian guild in spatially structured habitats supports a competition–colonization trade-off. *Proc. R. Soc. Lond. B*, **274**: 1403–1411.

Schaefer, I., Domes, K., Heethoff, M., Schneider, K., Schön, I., Norton, R.A. *et al.* 2006. No evidence for the 'Meselson effect' in parthenogenetic oribatid mites (Oribatida, Acari). *J. Evol. Biol.*, **19**: 184–193.

Schatz, H. 2002. Die Oribatidenliteratur und die beschriebenen Oribatidenarten (1758–2001) – Eine Analyse. *Abhandlungen und Berichte des Naturkunde Museums Görlitz*, **74**: 37–45.

Scheu, S. and Drossel, B. 2007. Sexual reproduction prevails in a world of structured resources in short supply. *Proc. R. Soc. Lond. B*, **274**: 1225–1231.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A. *et al.* 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios (N-15/N-14). *Soil Biol. Biochem.*, **36**: 1769–1774.

Schuster, R. 1956. Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. *Zeitschrift für Morphologie und Ökologie der Tiere*, **45**: 1–33.

Slatkin, M. 1974. Competition and regional coexistence. *Ecology*, **55**: 128–134.

Subias, L.S. 2004. Listado sistemático, sinonímico y biogeográfico de los Ácaros Oribátidos (Acarifomes, Oribatida) del mundo (1748–2002). *Graellsia*, **60**: 3–305.

Taberly, G. 1987. Recherches sur la parthénogénèse thélythoque de deux espèces d'Acariens Oribates: *Trhypochthonius tectorum* (Berlese) et *Platynothrus peltifer* (Koch). I. *Acarologia*, **28**: 187–198.

Taberly, G. 1988. Recherches sur la parthénogénèse thélythoque de deux espèces d'acariens oribatides: *Trhypochthonius tectorum* (Berlese) et *Platynothrus peltifer* (Koch). IV: Observations sur les males ataviques. *Acarologia*, **29**: 95–107.

Tooby, J. 1982. Pathogens, polymorphism, and the evolution of sex. *J. Theor. Biol.*, **97**: 557–576.

Tripet, F., Jacot, A. and Richner, H. 2002. Larval competition affects the life histories and dispersal behavior of an avian ectoparasite. *Ecology*, **83**: 935–945.

Vandel, A. 1928. La parthénogénèse géographique: contribution à l' étude de la parthénogénèse naturelle. *Bull. Biol. Fr. Belg.*, **62**: 194–281.

Vrijenhoek, R.C. 1979. Factors affecting clonal diversity and coexistence. *Am. Zool.*, **19**: 787–797.

Wallwork, J.A. 1983. Oribatids in forest ecosystems. *Annu. Rev. Entomol.*, **28**: 109–130.

Walter, D.E. and Proctor, H.C. 1999. *Mites: Ecology, Evolution and Behavior*. Sydney, NSW: University of New South Wales Press.

Weismann, A. 1904. *The Evolutionary Theory*. London: Edward Arnold.

Williams, G.C. 1975. *Sex and Evolution*. Princeton, NJ: Princeton University Press.