Evolutionary Ecology Research, 2003, **5**: 977–997

Geographic parthenogenesis in the Australian arid zone: II. Climatic analyses of orthopteroid insects of the genera *Warramaba* and *Sipyloidea*

Michael Kearney[1]* and Adnan Moussalli[2]

[1] School of Biological Sciences, Heydon Laurence Building A08, The University of Sydney,
Sydney, NSW 2006 and [2]Department of Zoology and Entomology,
University of Queensland, Brisbane, QLD 4072, Australia

ABSTRACT

The Australian arid zone harbours a surprising number of parthenogenetic organisms, including the well known case of the grasshopper *Warramaba virgo*. Less well known is the case of the stick insects of the *Sipyloidea* complex, which, despite its presence in the literature for over 15 years, has gone entirely unnoticed by workers in the field. We draw attention to the remarkable similarities between the evolution of parthenogenesis in *Warramaba* and *Sipyloidea* and analyse the geographic distributions of parthenogenetic and sexual forms with respect to six climatic variables. We provide evidence that a combination of climatic and vegetative barriers are responsible for the current distribution patterns in these taxa. Comparisons are also made with patterns of geographic parthenogenesis in lizards of the *Heteronotia binoei* complex. In general, there has been a strong tendency for parthenogenesis to originate via hybridization in the western part of the arid zone with subsequent eastward spread throughout mulga woodlands and mallee shrublands where rainfall is both low and aseasonal. We propose that the hybridization events leading to parthenogenesis in these diverse taxa were driven by a common biogeographic process – that is, by range shifts associated with changes in aridity during the late Pleistocene.

Keywords: arid zone, Australia, climate, grasshopper, parthenogenesis, stick insect.

INTRODUCTION

The most interesting aspect of parthenogenesis is its rarity; only one in a thousand species is obligately parthenogenetic (White, 1978). Despite their taxonomic rarity, parthenogenetic organisms can be successful under special circumstances and evolutionary biologists have devoted considerable effort to understanding why (Maynard Smith, 1978; Bell, 1982; Case and Taper, 1986; Suomalainen *et al.*, 1987; Vrijenhoek, 1998). By studying these exceptions to the rule of sex, we may develop a better understanding of the advantages and

---

* Author to whom all correspondence should be addressed. e-mail: mkearney@bio.usyd.edu.au

disadvantages of parthenogenetic and sexual breeding systems as well as the constraints involved in their evolution.

The Australian arid zone is a region where parthenogenesis (or 'apomixis', as it is known in plants) is particularly frequent, having evolved independently in a diversity of animals and plants. These include, in order of discovery, the grasshopper *Warramaba virgo* (White *et al.*, 1963), shrubs of the genus *Senna* (formerly *Cassia nemophila*: Randell, 1970; Holman and Playford, 2000), geckos of the *Heteronotia binoei* complex (Moritz, 1983), stick insects of the genus *Sipyloidea* (John *et al.*, 1987), trees of the *Acacia aneura* complex (Andrew *et al.*, 2003) and scincid lizards of the *Menetia greyii* complex (Adams *et al.*, in press). While the latter two cases have only recently come to light and the first three cases are well known, the case of *Sipyloidea* has remained uncited and presumably unnoticed since its publication over 15 years ago. The aims of this paper are threefold: (1) to draw attention to the similarity between the evolution of parthenogenesis in *Warramaba* and *Sipyloidea*; (2) to analyse the climatic environments occupied by these two taxa; and (3) to compare the observed patterns on a broader scale with those found in an analysis of *Heteronotia* (Kearney *et al.*, this issue).

THE ORGANISMS

Parthenogenesis in *Warramaba* was discovered by the cytologist M.J.D. White (White *et al.*, 1963). *Warramaba* is a green, wingless morabine grasshopper that lives and feeds on shrubs of the genus *Acacia* and is the only grasshopper from the suborder Caelifera that naturally reproduces by obligate thelytoky (i.e. the parthenogenetic production of females; White, 1980). It has a highly disjunct distribution, occurring in the semi-arid scrublands of eastern and western Australia with a 1600 km gap in between (White *et al.*, 1973) (Fig. 1). The western populations occur in close proximity to two related sexual species, currently undescribed and known only as P169 and P196 (their code numbers in the Australian National Insect Collection), which were shown to have given rise to the parthenogenetic forms via hybridization (Hewitt, 1975; White *et al.*, 1977; Atchley, 1978; Webb *et al.*, 1978; White, 1980; Dennis *et al.*, 1981; White and Contreras, 1982).

Almost 25 years after the discovery of *Warramaba virgo*, a cytological analysis was published of three new stick insect species of the genus *Sipyloidea* (John *et al.*, 1987). The authors noted that these green insects also live and feed on *Acacia* and *Senna* shrubs, that females are incapable of flight and that some populations are capable of parthenogenetic reproduction. They occur in the same region in Western Australia as the sexual and parthenogenetic forms of *Warramaba* (Fig. 1) and in some cases feed on the same species of *Acacia* and *Senna*. Surprisingly, the authors made no connection with *W. virgo* and, as a consequence, this remarkable convergence has been overlooked. The reason for this oversight is revealed in the original description where the authors indicate that they were one step removed from the material they had analysed: 'In the two years immediately before his death, Michael White had begun a study of the population cytogenetics of the Australian phasmatid genus *Sipyloidea* . . . Sadly this work was never completed. We have, therefore, taken the opportunity to carry out a detailed analysis of the material he collected' (John *et al.*, 1987, p. 603).

Although cytological analyses of *Sipyloidea* are preliminary at this stage (John *et al.*, 1987), a high degree of structural heterozygosity in parthenogenetic individuals is

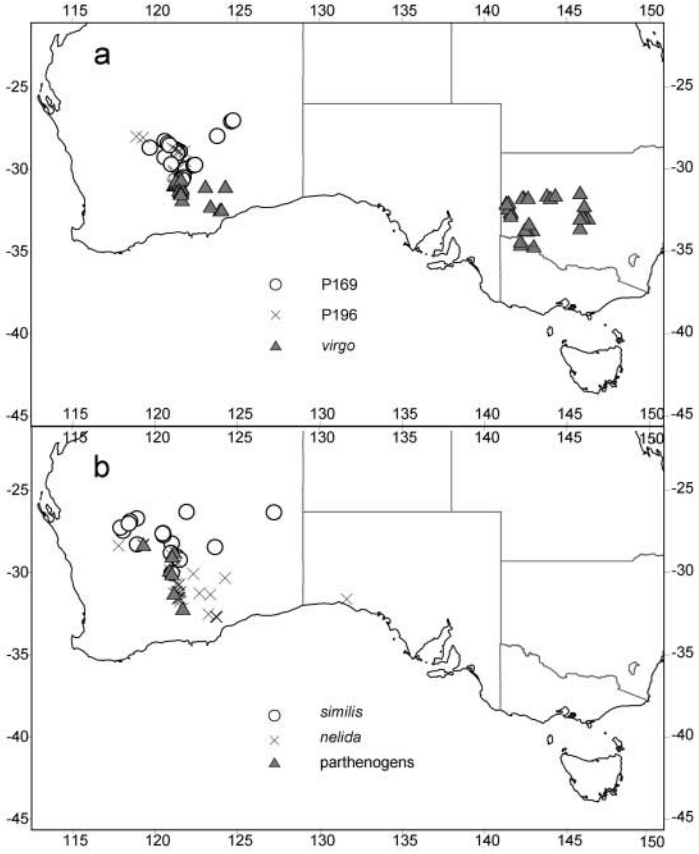

Fig. 1. Distribution of sexual and parthenogenetic races of (a) *Warramaba* and (b) *Sipyloidea*.

supportive of a hybrid genotype. Two bisexual species with extremely similar karyotypes, *S. nelida* and *S. similis*, co-exist with the parthenogenetic forms (Fig. 1) and are the most likely parental candidates. In contrast to parthenogenetic *Warramaba*, which are diploid, chromosome counts of parthenogenetic *Sipyloidea* are approximately 1.5 that of the two sexual forms, which suggests triploidy, as occurs in parthenogenetic *Heteronotia binoei*. In the remainder of this paper, we analyse the climatic environments occupied by parthenogenetic and sexual forms of *Warramaba* and *Sipyloidea* and use this information to infer the biogeographic forces leading to the origin and maintenance of parthenogenesis generally in the Australian arid zone.

METHODS

Locality records for the different sexual and parthenogenetic races of *Warramaba* and *Sipyloidea* were collated from the available literature and from museum records. The number of localities used for each taxon is shown in Table 1. For *Sipyloidea*, we used only localities where males had been located as sexual data points because the occurrence

Table 1. Number of localities for the various taxa used in the analyses

Form	Localities (*n*)
P169	20
P196	16
Warramaba virgo	52
Sipyloidea similis	20
Sipyloidea nelida	10
Parthenogenetic *Sipyloidea*	7

of parthenogenesis had not been ascertained in all female specimens. We analysed the distributions of these taxa with respect to six climatic variables for which we constructed continent-wide interpolated surfaces based on weather station data (>30 years): mean annual temperature, mean annual humidity, mean annual rainfall, temperature seasonality, rainfall seasonality and inter-annual rainfall variability (hereafter referred to as rainfall variability). Construction of climate surfaces and statistical analyses were undertaken as previously described in a study on *Heteronotia binoei* to which we refer the reader for more detail (Kearney *et al.*, this issue). As in the previous study, we based the rainfall variability surface on the coefficient of rainfall variability calculated only over the summer months (see Kearney *et al.*, this issue, for justification). We used the GIS program ArcView to query the climatic conditions at localities where *Warramaba* and *Sipyloidea* were sampled and then used these data in three different kinds of analyses of the climatic environments currently occupied by the different sexual and parthenogenetic forms. We first compared the mean environments of the different taxa for each climatic variable separately using analyses of variance (ANOVA) to test for differences between parthenogens and sexuals. Second, we used discriminant function analysis to determine how well the various taxa could be distinguished based on the climatic environments in which they occur, and which climatic variables provide the best discrimination (Green, 1971). Finally, we used logistic regression to model the geographic distribution of the various taxa as a function of the six climatic covariates. For this analysis, all-subset fitting in conjunction with AICc model averaging was used both to determine the relative importance (AICc weights) for each of the six climatic variables and to develop a predictive model (Burnham and Anderson, 1998). In the latter analysis, we used 660 randomly allocated points across continental Australia as pseudo-absence points (Zaniewski *et al.*, 2002) and down-weighted their contribution to coefficient estimation such that they were weighted to the same extent as the known presence records.

Logistic regression analyses were conducted using the statistical package SAS 8.02, specifically PROC LOGISTIC for performing logistic regression, and SAS/IML and SAS/MACRO languages for automating all subset fitting, AICc determination and subsequent model-averaged calculations. Spatial interpolation was based on model-averaged coefficients and applied using ArcView. All other statistical analyses were conducted using SYSTAT 9.0 with a criterion of $P < 0.05$ for statistical significance.

RESULTS

Comparison of mean environments

For *Warramaba*, we compared the mean climatic environments occupied by the two parental sexual taxa, P196 and P169, and eastern and western populations of *W. virgo*, using ANOVA and *post-hoc* multiple comparisons (Tukey's test) (Fig. 2). The parental sexual taxa were not significantly different for any of the six climatic traits considered. Both populations of *W. virgo* occupied cooler environments with lower rainfall seasonality and higher humidity than either of the sexual forms. The eastern populations of *W. virgo* occupied lower rainfall seasonality environments than the western populations, and occupied environments of higher rainfall than P196, P169 and the western populations of *W. virgo*. The western populations of *W. virgo*, however, occurred in an environment of lower temperature seasonality than the two sexual species and the eastern *W. virgo*. Finally, eastern populations of *W. virgo* occupied lower rainfall variability environments than P169, P196 and western populations of *W. virgo*. In contrast, for *Sipyloidea*, there were significant differences between the putative parental sexual taxa for all climatic variables except for rainfall variability (Fig. 3). *Sipyloidea nelida* occupied a cooler, wetter and more humid environment than *S. similis* with lower temperature and rainfall seasonality. In fact, *S. nelida* differed from *S. similis* in a roughly similar manner to the way sexual *W. virgo* differed from its parental sexual taxa (Figs 2, 3). The parthenogenetic populations of *Sipylodiea* were intermediate to the two sexual species for all six climatic variables (Fig. 3).

Multidimensional comparisons

The first discriminant analysis of *Warramaba* contrasted populations of the two sexual races with all parthenogenetic populations of *W. virgo*. The two discriminant functions calculated for this comparison significantly discriminated among the taxa based on the six climatic variables (Wilks' $\lambda_{6,2,85} = 0.265$, $F_{12,160} = 12.582$, $P < 0.0001$). However, tests of the residual roots indicated the second discriminant function (DF2) was not statistically significant ($\chi^2_5 = 7.894$, $P = 0.162$). Rainfall and humidity loaded positively on the first discriminant function (DF1), while rainfall seasonality and temperature loaded negatively on this discriminant function (Table 2). A scatter plot of the scores for the two discriminant functions demonstrates clear separation between *W. virgo* and both its sexual progenitor species P169 and P196, but there is considerable overlap of the climatic envelopes of the latter two taxa (Fig. 4a). These patterns are reiterated by the success of the discriminant function in classifying these taxa, with the two sexual taxa often being misclassified as each other but *W. virgo* only rarely being misclassified as P196 (Table 3a). The climatic envelope of *Warramaba virgo* thus differs from those of its two sexual parents P169 and P196 in being cooler and wetter with lower rainfall seasonality and lower temperature seasonality.

The second discriminant analysis of *Warramaba* contrasted the combined climatic envelope of the two sexual races with the eastern and western parthenogenetic populations of *W. virgo*. This analysis also significantly discriminated among these taxa (Wilks' $\lambda_{6,2,85} = 0.020$, $F_{12,160} = 88.414$, $P < 0.0001$) and tests of residual roots indicated that both the discriminant functions were statistically significant (all $P < 0.05$). Rainfall seasonality,

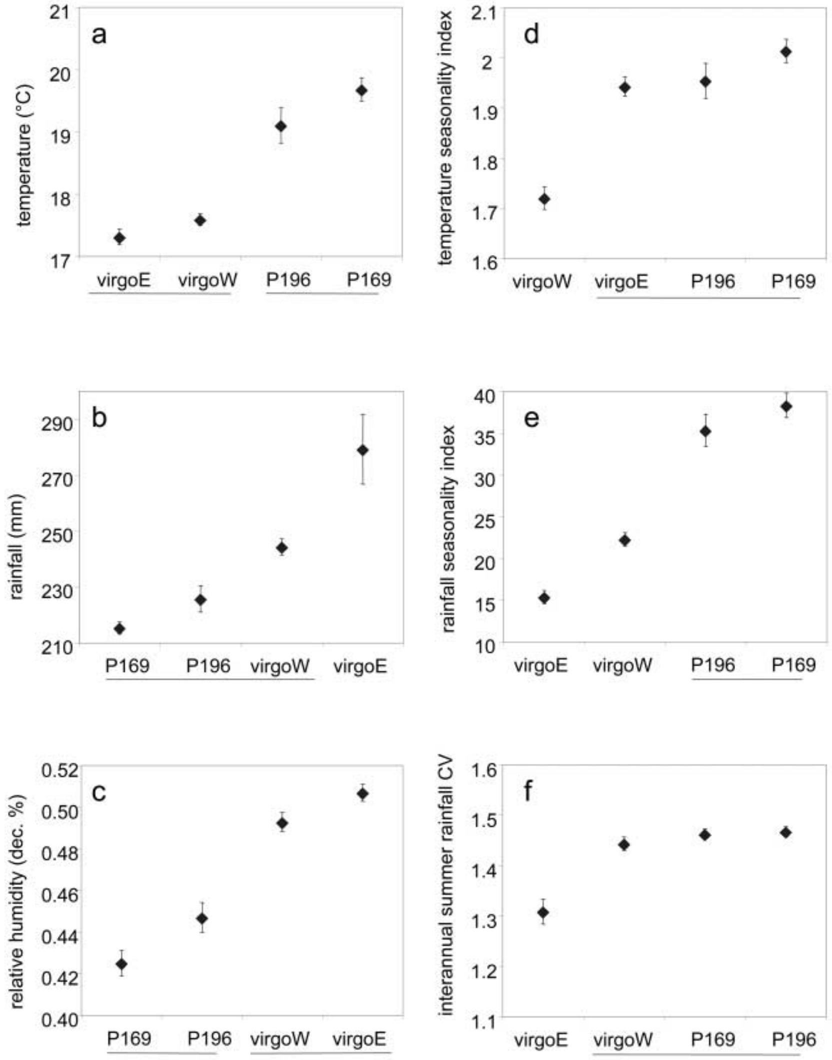

Fig. 2. Mean values (± standard error) of (a) annual temperature, (b) annual rainfall, (c) annual relative humidity, (d) seasonality of temperature, (e) seasonality of rainfall and (f) inter-annual variation in summer rainfall for the two sexual species of *Warramaba*, P169 and P196, as well as the eastern (virgoE) and western (virgoW) populations of the parthenogenetic species *W. virgo*. Taxa are ranked in increasing order of mean value. Lines under taxon names on the x-axes indicate those comparisons that did not differ significantly for *post-hoc* multiple comparisons (Tukey's test) following univariate analysis of variance.

rainfall variability and temperature loaded positively on DF1 and humidity and rainfall loaded negatively (Table 2). Temperature seasonality, temperature and rainfall seasonality loaded negatively and most strongly on DF2, while humidity loaded positively (Table 2). Scatter plots of the discriminant function scores for this analysis show clear separation

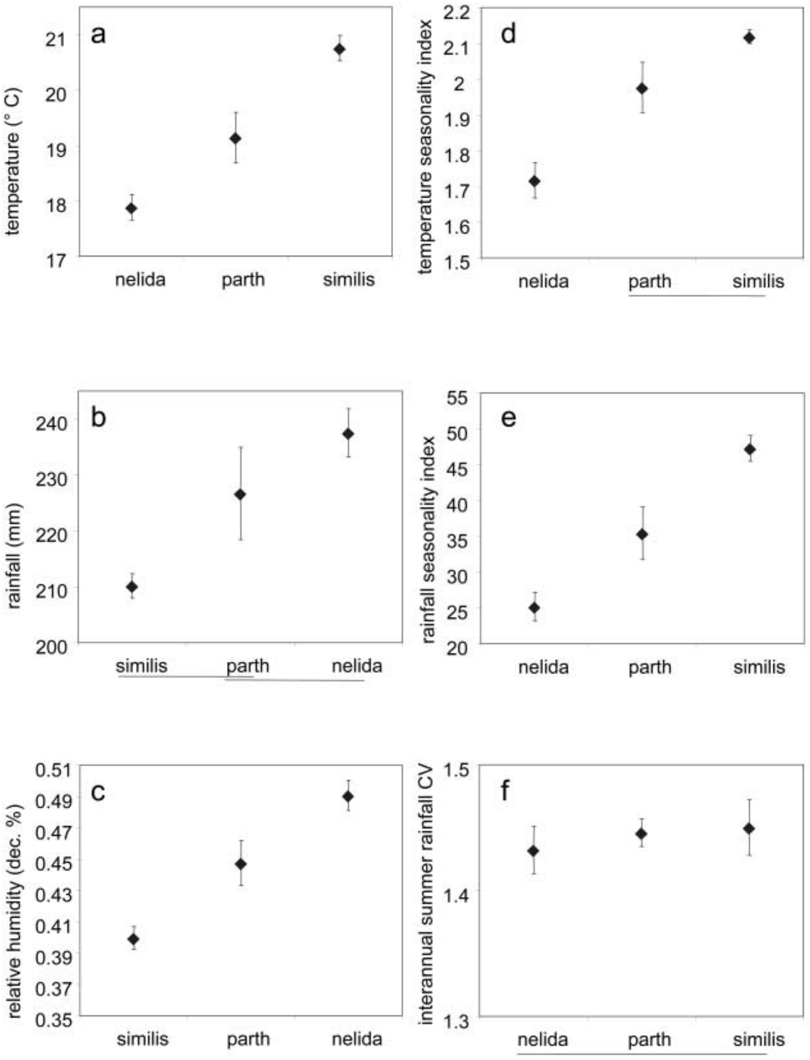

Fig. 3. Mean values (± standard error) of (a) annual temperature, (b) annual rainfall, (c) annual relative humidity, (d) seasonality of temperature, (e) seasonality of rainfall and (f) inter-annual variation in summer rainfall for the sexual forms of *Sipyloidea similis* and *S. nelida* as well as parthenogenetic *Sipyloidea*. Taxa are ranked in increasing order of mean value. Lines under taxon names on the x-axes indicate those comparisons that did not differ significantly for *post-hoc* multiple comparisons (Tukey's test) following univariate analysis of variance.

between the eastern and western populations of *W. virgo* and a minor overlap of the western populations of *W. virgo* with the sexual taxa (Fig. 4b). This pattern is reflected by the classification success of this analysis, with perfect classification success for the two parthenogenetic lineages and some sexual populations misclassified as western parthenogenetic populations (Table 3b).

Table 2. Predictor variable loadings, canonical *R*-values and eigenvalues for discriminant function analyses of different combinations of parthenogenetic and sexual *Warramaba* and *Sipyloidea*

		Correlations of predictor variables with discriminant functions	
Comparison	Predictor variable	1	2
P169, P196 and *W. virgo*	Temperature	**−0.939**	0.176
	Humidity	**0.944**	0.254
	Rainfall	**0.554**	−0.057
	Temperature seasonality	−0.396	−0.218
	Rainfall seasonality	**−0.993**	−0.040
	Rainfall variability	−0.499	−0.210
	Canonical *R*	0.842	0.302
	Eigenvalue	2.433	0.100
P169, P196, Eastern *W. virgo* and Western *W. virgo*	Temperature	**0.548**	**−0.766**
	Humidity	**−0.579**	**0.739**
	Rainfall	**−0.521**	0.261
	Temperature seasonality	−0.178	**−0.929**
	Rainfall seasonality	**0.712**	**−0.693**
	Rainfall variability	**0.649**	−0.073
	Canonical *R*	0.978	0.745
	Eigenvalue	21.450	1.249
Parthenogenetic *Sipyloidea*, *S. nelida* and *S. similis*	Temperature	**0.9443**	−0.0084
	Humidity	**−0.6845**	−0.0463
	Rainfall	**−0.8739**	0.064
	Temperature seasonality	**0.8322**	−0.3146
	Rainfall seasonality	**0.9112**	−0.05
	Rainfall variability	0.131	−0.0755
	Canonical *R*	0.8358	0.4235
	Eigenvalue	2.3171	0.2186

Note: Loadings above 0.5 are in **bold face** and the highest loading per discriminant function is underlined.

Finally, one discriminant analysis was carried out for *Sipylodiea* which contrasted the two presumed parental sexual species with the parthenogenetic forms. This analysis provided good discrimination among taxa (Wilks' $\lambda_{6,2,34} = 0.2474$, $F_{12,142} = 4.8840$, $P < 0.0001$), but tests of residual roots indicated that DF2 was not a significant contributor ($\chi^2_5 = 6.2264$, $P = 0.2848$). Temperature loaded positively and most strongly on DF1, with rainfall seasonality and temperature seasonality also loading positively and humidity and rainfall loading negatively on this axis (Table 2). A graphical representation of the discriminant function scores shows a clear separation on DF1 between sexual *S. nelida* and *S. similis*, with the parthenogenetic taxa falling neatly in-between. The discriminant function was therefore successful at discriminating among all three taxa (Table 3c).

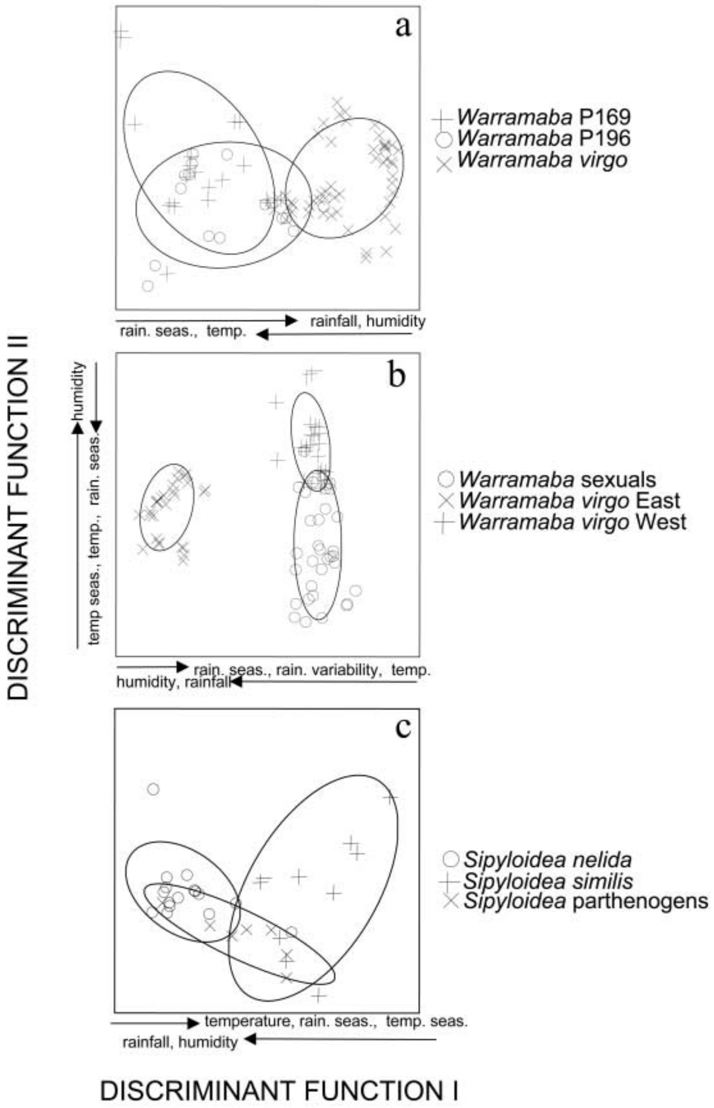

Fig. 4. Scores from discriminant function analyses plotted against discriminant function 1 and 2 for: (a) the two sexual species of *Warramaba*, P169 and P196, as well as the parthenogenetic species *W. virgo*; (b) the sexual races P169 and P196 combined compared with eastern and western populations of *W. virgo*; and (c) the sexual forms of *Sipyloidea similis* and *S. nelida* as well as parthenogenetic *Sipyloidea*. Arrows indicate direction of increase in value of those climatic variables that loaded most strongly (values greater than 0.5) on each discriminant function. Sample confidence ellipses (68%) are also shown.

Climate correlates of spatial distribution

The models fitted to the spatial distribution of the different races of *Warramaba* and *Sipyloidea* provided a good fit to the observed distribution points (Tables 4–7). In general,

Table 3. Classification success of discriminant function analyses of different combinations of parthenogenetic and sexual *Warramaba* and *Sipyloidea*

(a)	169	196	*virgo*	% correct
169	15	5	0	75
196	6	9	1	56
virgo	0	5	47	90
(b)	sexuals	*virgo* east	*virgo* west	% correct
sexuals	28	0	9	75
virgo east	0	28	0	100
virgo west	0	0	24	100
(c)	*similis*	*nelida*	parthenogenetic	% correct
similis	7	0	3	70
nelida	1	18	1	90
parthenogenetic	0	1	6	86

Note: Actual groups are in rows and predicted groups are in columns.

Table 4. Chi-square goodness-of-fit values, degrees of freedom (d.f.), P-values and R^2 range for global logistic regression models fit to the distribution of the various sexual and parthenogenetic races of *Warramaba* as a function of the six climatic covariates

Taxon	χ^2	d.f.	P	R^2
P169	0.228	1	0.633	0.70–0.94
P196	0.206	1	0.650	0.63–0.83
virgo	0.946	2	0.623	0.67–0.74
virgo east	0.202	1	0.653	0.66–0.82
virgo west	1.570	2	0.456	0.79–0.93

the distribution of all of these taxa showed a strong association with rainfall-related covariates (Fig. 5). For instance, annual rainfall was strongly and quadratically associated with all taxa except for the eastern populations of *W. virgo* and for *W. virgo* overall. All *Warramaba* models showed an association with rainfall seasonality, with quadratic associations for the sexual taxa and negative associations for the parthenogenetic forms. A negative association with rainfall seasonality was also present for *S. nelida*. Parthenogenetic *Sipyloidea* also showed a quadratic association with rainfall variability. The models for *W. virgo* showed associations with temperature-related covariates. When eastern and western populations of *W. virgo* were modelled separately, they showed associations with temperature seasonality, while the model for both of these populations combined showed a quadratic association with annual temperature. Extrapolation from these models predicts the occurrence of all western populations of *Warramaba* and *Sipyloidea* further to the east than their current distribution (Fig. 6). Similarly, the eastern populations of *W. virgo* were

Table 5. Model-averaged coefficient estimates (*β*), standard errors (SE) and *K* for linear and quadratic terms of logistic regression models fitted to the distribution of the various sexual and parthenogenetic races of *Warramaba* as a function of the six climatic covariates

Taxon	*K*		I	T	T^2	R	R^2	ST	ST^2	SR	SR^2	H	H^2	CVR	CVR^2
P169	22	*β*	−2048.442	0.711	−0.002	**15.559**	**−0.035**	0.068	0.000	**1.632**	**−0.024**	754.026	−818.992	**104.567**	−45.276
		SE	2973.897	1.214	0.003	**24.484**	**0.056**	0.181	0.000	**3.235**	**0.040**	1377.347	1393.145	**171.209**	70.379
P196	50	*β*	−345.916	−0.063	0.000	**1.181**	**−0.002**	0.018	0.000	0.819	−0.013	397.276	−449.751	208.282	−99.014
		SE	289.310	0.372	0.001	**0.969**	**0.002**	0.052	0.000	0.850	0.010	481.580	483.198	299.167	123.901
virgo	59	*β*	−443.201	**4.582**	**−0.013**	**0.072**	0.000	0.033	0.000	**0.286**	**−0.009**	109.590	−113.686	−0.207	0.685
		SE	256.697	**2.450**	**0.007**	**0.059**	0.000	0.045	0.000	**0.500**	**0.008**	156.036	128.702	4.407	1.061
virgo east	118	*β*	−212.955	1.426	−0.004	−0.018	0.000	**0.340**	0.000	**0.124**	−0.007	213.012	−175.956	−16.254	4.973
		SE	276.120	1.809	0.004	0.036	0.000	**0.575**	0.001	**0.534**	0.010	289.006	232.875	20.995	7.795
virgo west	38	*β*	−738.170	**4.289**	−0.011	**1.498**	−0.003	**2.046**	**−0.007**	**0.596**	−0.016	−19.970	−17.278	−0.063	0.564
		SE	822.664	**5.645**	0.013	**1.449**	0.003	**2.644**	**0.007**	**1.222**	0.022	112.554	67.073	9.607	1.289

Note: **Bold face** indicates those covariates with an AIC weighting greater than 0.6. I = intercept, T = temperature, R = rainfall, ST = temperature seasonality, SR = rainfall seasonality, H = humidity, CVR = rainfall variability.

Table 6. Chi-square goodness-of-fit values, degrees of freedom (d.f.), *P*-values and R^2 range for logistic regression models fit to the distribution of the various sexual and parthenogenetic races of *Sipyloidea* as a function of the six climatic covariates

Taxon	χ^2	d.f.	*P*	R^2
similis	1.2097	3	0.7507	0.66–0.90
nelida	0.4533	4	0.9779	0.69–0.85
parthenogenetic	1.4229	3	0.7002	0.24–0.78

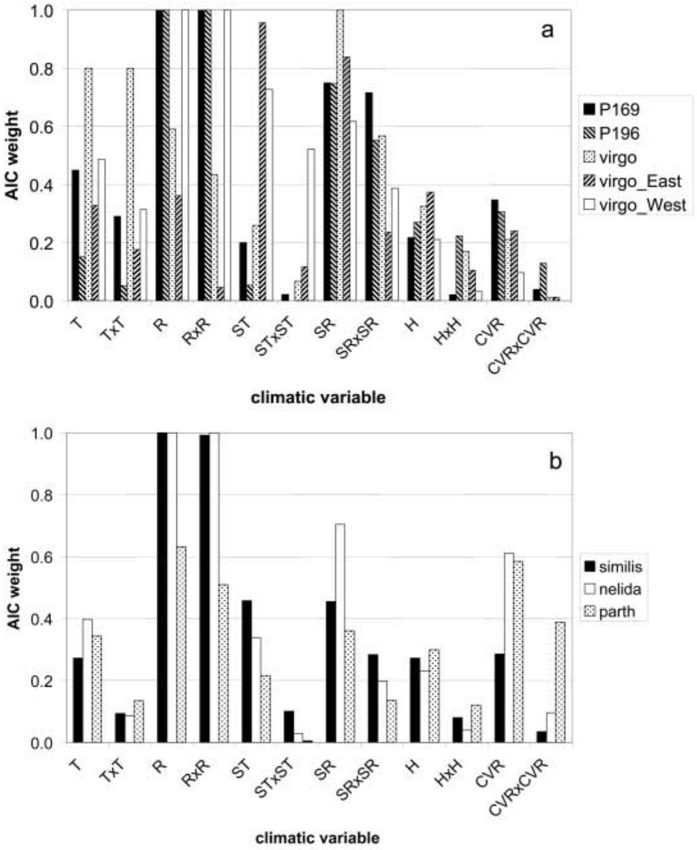

Fig. 5. Model-averaged AICc weightings of the coefficients estimated for the six climatic variables (as linear and quadratic terms) in logistic regression modelling of the distribution of (a) two sexual species of *Warramaba*, P169 and P196, as well as the parthenogenetic species *W. virgo* overall and separated into eastern and western populations, and (b) the sexual forms of *Sipyloidea similis* and *S. nelida* as well as parthenogenetic *Sipyloidea*. T = temperature, R = rainfall, ST = temperature seasonality, SR = rainfall seasonality, H = humidity, CVR = rainfall variability.

Table 7. Model-averaged coefficient estimates (β), standard errors (SE) and *K* for linear and quadratic terms of logistic regression models fit to the distribution of the various sexual and parthenogenetic races of *Sipyloidea* as a function of the six climatic covariates

Taxon	*K*		I	T	T^2	R	R^2	ST	ST^2	SR	SR^2	H	H^2	CVR	CVR^2
similis	53	β	−1463.923	0.589	−0.001	**11.510**	**−0.027**	1.011	−0.002	1.391	−0.015	76.561	−86.972	9.813	−2.444
		SE	1734.967	1.183	0.003	**13.735**	**0.032**	2.192	0.004	2.586	0.024	147.414	165.775	26.476	10.049
nelida	46	β	−128.111	0.115	0.000	**0.933**	**−0.002**	−0.023	0.000	**−0.061**	−0.001	8.819	−5.345	**10.562**	1.697
		SE	97.627	0.291	0.001	**0.638**	**0.001**	0.045	0.000	**0.167**	0.001	21.332	14.841	**27.020**	8.596
parthenogenetic	99	β	−302.986	0.371	−0.001	**0.466**	−0.001	0.016	0.000	0.101	−0.002	65.647	−69.088	**399.294**	−202.568
		SE	405.375	0.647	0.001	**0.619**	0.001	0.033	0.000	0.246	0.003	96.425	91.475	**591.139**	265.305

Note: **Bold face** indicates those covariates with an AIC weighting greater than 0.6. I = intercept, T = temperature, R = rainfall, ST = temperature seasonality, SR = rainfall seasonality, H = humidity, CVR = rainfall variability.

predicted, with low probability, further to the west in a region where western populations of *W. virgo* currently occur (Fig. 6).

DISCUSSION

Analysis of the geographic distribution of a parthenogenetic organism is most informative when the parental forms are available for comparison. For *Warramaba virgo*, extensive evidence indicates the sexual taxa P196 and P169 gave rise to *W. virgo* through hybridization. These two sexual taxa occupy similar climatic environments, and there are no differences between the means of any of the six climatic variables we considered (Fig. 4a). The discriminant function analysis frequently misclassified these taxa as each other, particularly P196 as P169 (Table 3a).

Warramaba virgo, however, typically occupies environments that are climatically distinct from its sexual parents (Figs 2, 4). Nowhere is *W. virgo* sympatric with its parental sexual forms, but instead is biased to higher latitudes, a common pattern of geographic parthenogenesis (Glesener and Tilman, 1978). In contrast to the parental sexual forms of *W. virgo*, the putative parental forms of parthenogenetic *Sipyloidea*, *S. nelida* and *S. similis*, occupy very distinct climatic environments (Figs 3, 4c). For instance, *S. nelida* occurs in an environment that is cooler, wetter and more humid with less temperature and rainfall seasonality than that of *S. similis* (Fig. 3). Also in contrast to *Warramaba*, the distribution of parthenogenetic *Sipyloidea* is nested within that of its two presumed parental forms (Fig. 1b) and, accordingly, the parthenogens occupy an almost precisely intermediate climatic environment (Figs 3, 4c).

What processes are responsible for these different geographic patterns among *Warramaba* and *Sipyloidea*? There is good evidence that the allopatry between *W. virgo* and its sexual progenitors is at least partly the result of destabilizing hybridization (Lynch, 1984), since males of both parental forms will readily mate with *W. virgo*, producing allotriploids of low viability (White *et al.*, 1977). It is thus possible that *W. virgo* was forced to ‘escape’ soon after its origin into habitat not occupied by its sexual parental forms (White and Contreras, 1979). Why is overlap possible between sexual and parthenogenetic *Sipyloidea* but not sexual and parthenogenetic *Warramaba*? The answer to this may lie in the different ploidy levels in the parthenogenetic forms. Parthenogenetic *W. virgo* are diploid, but parthenogenetic *Sipyloidea* have chromosome counts approximately 1.5 times those of the sexual forms (John *et al.*, 1987), which strongly suggests triploidy. This may have led to reproductive isolation between parthenogenetic and sexual *Sipyloidea*. Triploidy in *Sipyloidea* could have arisen through backcrossing of the original diploid parthenogens with sexual males, as occurred in *Heteronotia binoei*, which also overlaps with its sexual progenitors.

If destabilizing hybridization were the major cause of parapatry between parthenogenetic and sexual *W. virgo*, one might expect the eastern populations of *W. virgo* to occupy a climatic envelope more similar to that of the parental sexual forms, since the latter are absent in the east. Although there are some distinct differences in the climatic environments of the eastern and western populations of *W. virgo* (Figs 2, 4b), the evidence that the eastern populations of *W. virgo* have returned to a similar climatic envelope to their sexual progenitors is inconclusive. For example, the discriminant function analysis indicates a shift in the eastern populations of *W. virgo* towards the sexual forms along the second discriminant function (Fig. 4b). However, when mean environmental conditions are considered, when-

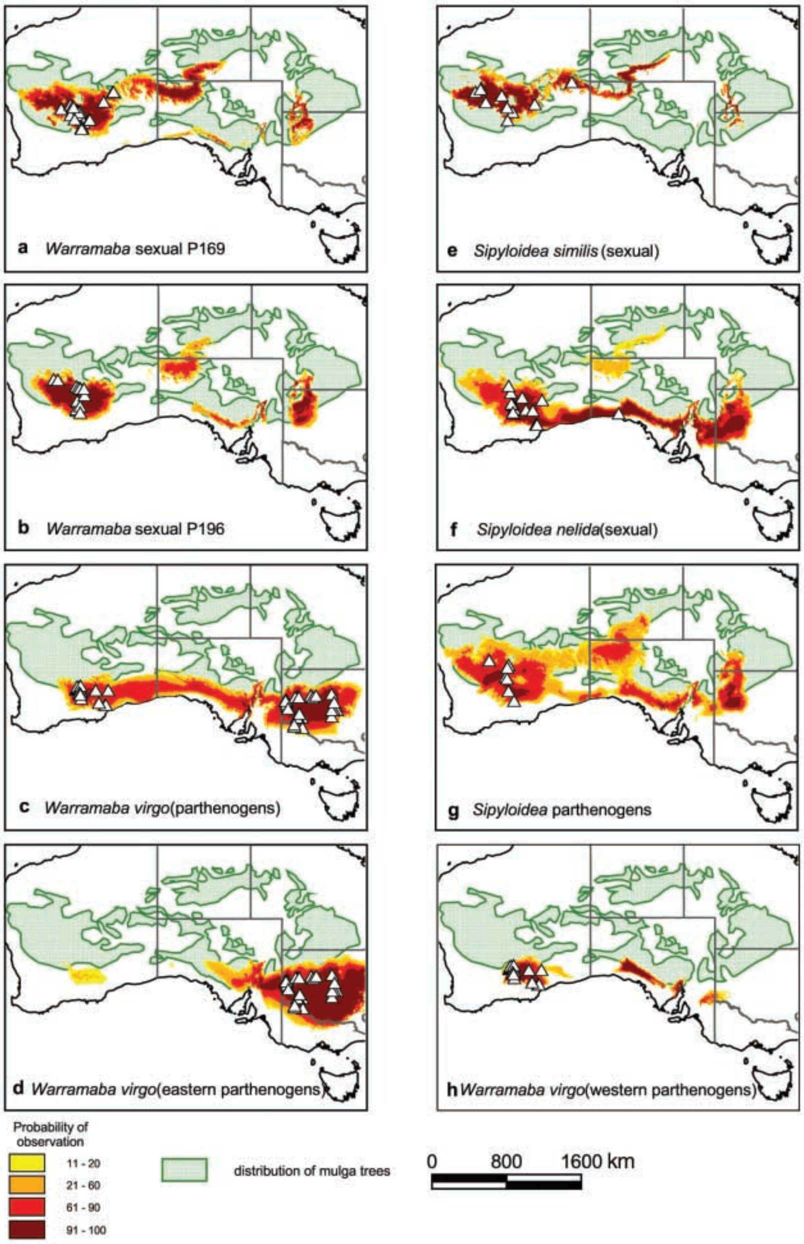

Fig. 6. Predicted distributions of the various sexual and parthenogenetic forms of *Warramaba* and *Sipyloidea* based on logistic regression models of probability of occurrence as a function of six climatic variables: annual temperature, annual rainfall, annual relative humidity, seasonality of temperature, seasonality of rainfall and inter-annual variation in summer rainfall. All-subset fitting in conjunction with AICc model averaging was used to develop predictive models. The distribution of mulga woodland is also shown (after Nix and Austin, 1973).

ever eastern and western *W. virgo* differ, the western populations are usually more similar to the parental sexuals, with the exception being temperature seasonality (Fig. 2). Although extrapolation from the current climatic environment of the sexuals predicts populations further east, these predictions lie north of the eastern populations of *W. virgo* in mulga habitat (Fig. 6a,b). Climatic extrapolation of the eastern *W. virgo* populations similarly predicts a small, moderately suitable area in the west only to the south of the current distribution of the sexual progenitors, precisely where the western populations of *W. virgo* currently occur (Fig. 6d). The apparent conservancy in the climatic envelope of *W. virgo* may reflect a bias in the original clones that were formed at the time of origin to those that could exist outside the niche of the parental sexual forms. There may have been little subsequent evolutionary change in these clones after migration to the east, despite the absence of the sexual forms there. It should also be considered, however, that P196 has actually been displaced by *W. virgo* from the southern part of its geographic range in Western Australia. The current distribution of the other sexual form, P169, shows good correspondence with that of *S. similis* and it is possible that P196 once had a distribution similar to that of *S. nelida*, which currently overlaps strongly with *W. virgo* (Figs 1, 6f). Indeed, *W. virgo* and P196 are quite distinct in appearance and size from P169 but are very similar to each other and are quite difficult to discern in the field (White *et al.*, 1977; Atchley, 1978). If this similarity between *W. virgo* and P196 extends to other features of their ecology, it may also explain the southern bias of the distribution of *W. virgo*.

Two of the strongest patterns of parthenogenesis in the Australian arid zone are the tendency for western origins and the association with hybridization. Parthenogenetic *Warramaba* and *Sipyloidea* probably originated in the west, since this is the only region where the parental sexual forms occur (Fig. 1). In the case of *Heteronotia*, where the sexual progenitors occur in both the west and the east, genetic analyses also support a western origin (Moritz, 1991; Moritz and Heideman, 1993). Hybridization appears to play an important role in initiating many cases of parthenogenesis (Cole, 1975; Moritz *et al.*, 1989) and there is strong evidence for a hybrid origin in *Warramaba* (Atchley, 1981; Dennis *et al.*, 1981; White and Contreras, 1981, 1982; Honeycutt and Wilkinson, 1989) and *Heteronotia* (Moritz, 1983; Moritz and Heideman, 1993) as well as the recently discovered Australian scincid lizard *Menetia greyii* (Adams *et al.*, in press). Although evidence for a hybrid origin in *Sipyloidea* is only suggestive at this stage (John *et al.*, 1987), it appears more likely in light of the aforementioned taxa. Moreover, hybridization between the trees *Acacia aneura* and *A. craspedocarpa* may also have occurred in the region where parthenogenetic *Warramaba* and *Sipyloidea* arose, with hybrids, backcrosses and parental forms all co-existing, although it is unknown if these hybrids reproduce through apomixis (Miller *et al.*, 2002).

These patterns strongly suggest that the hybridization events leading to parthenogenesis in these taxa resulted from the same biogeographic processes. We propose that the repeated formation of an unsuitably low rainfall region extending southeast from the coastal town of Carnarvon during the hyper-arid times of the Pleistocene periodically divided taxa into northern and southern isolates, creating ideal conditions for hybridization – the ‘Carnarvon suture zone’ hypothesis (Fig. 7a). This zone consists of a low-rainfall trough extending from the interior of Australia to the Western Australian coastline. Annual rainfall records over the past 100 years indicate significant variability in the aridity of this zone, which is reflected by the coefficient of variation of summer rain; and the zone of overlap between the sexual progenitor taxa of parthenogenetic *Warramaba*, *Heteronotia* and *Sipyloidea* is closely associated with this region (Fig. 7a). This contention is also supported in *Heteronotia* and

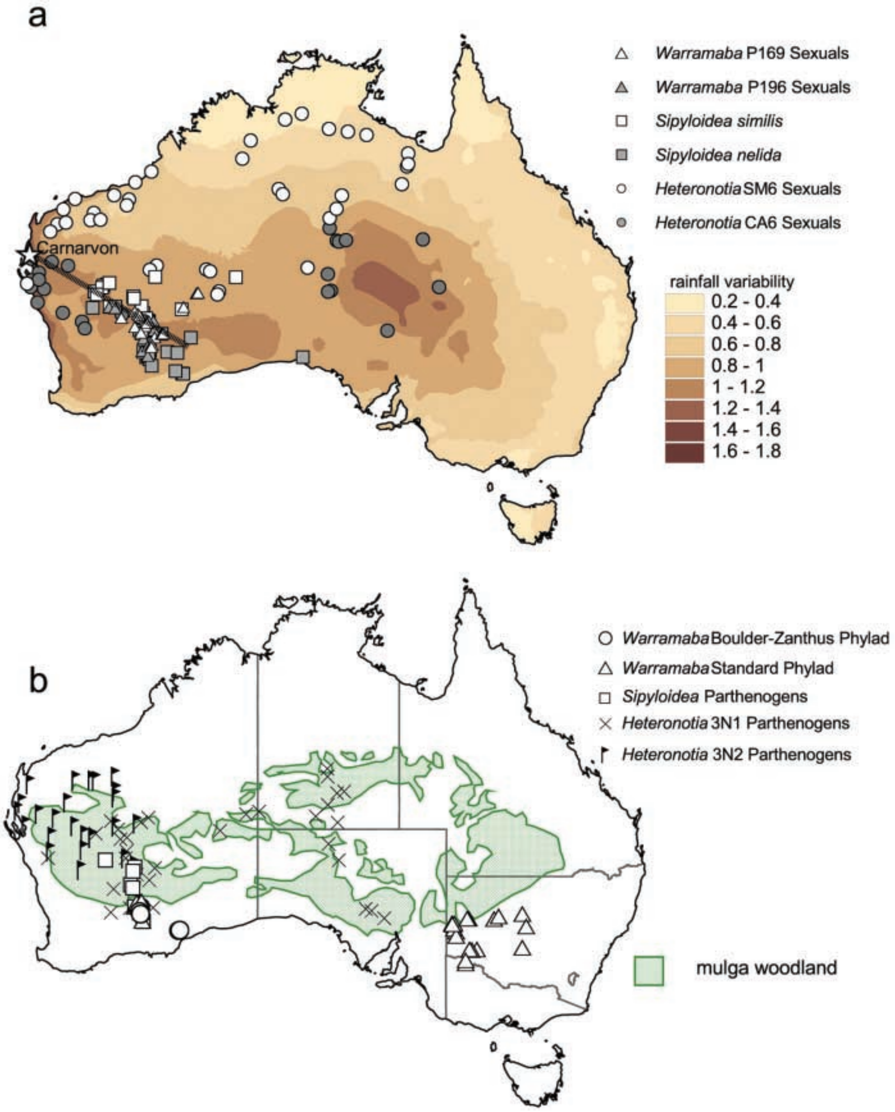

Fig. 7. Broad biogeographic patterns of sexual and parthenogenetic *Warramaba, Sipyloidea* and *Heteronotia*. (a) Association of zone of overlap of hybridizing sexual taxa of the three genera with a highly variable low rainfall zone that we have called the 'Carnarvon suture zone' (dotted line). The coefficient of inter-annual summer rainfall variability is shown in the background. (b) Distributions of parthenogenetic lineages of the three genera with respect to mulga woodland (mulga distribution based on Nix and Austin, 1973).

Sipyloidea by the distinct climatic environments occupied by the parental sexual forms, especially the strong association of their distributions with rainfall-related variables (see Fig. 6b and Kearney *et al.*, this issue).

Detailed genetic analyses of *Warramaba* and *Heteronotia* provide evidence for independent origins of parthenogenesis in both space and time. For instance, in *Heteronotia* mtDNA analysis reveals two maternal lineages, the more widespread 3N1 lineage occurring in eastern and central regions of the arid zone and the more restricted 3N2 lineage occurring only in the west (Fig. 7b). Similarly, two 'phylads' of *W. virgo* have been identified, the 'standard' phylad occurring in the east and west and the 'Boulder-Zanthus' phylad occurring only in the west (Fig. 7b). There is good evidence that these phylads arose through hybridization at different areas of overlap between P196 and P169 and it is likely that the geographically more restricted 'Boulder-Zanthus' phylad had a more recent origin (Dennis *et al.*, 1981; White and Contreras, 1981; Honeycutt and Wilkinson, 1989). This may also be true of *Heteronotia* and may mean that parthenogenesis in *Sipyloidea* originated concurrently with the latest origins in *Warramaba* and *Heteronotia*.

A further geographic tendency in parthenogenetic *Warramaba* and *Heteronotia* is an eastward spread following western origins. Eastern populations of *W. virgo* are separated by a gap of 1600 km from the western populations and an important question is whether this occurred by vicariance following an initial range extension or through passive dispersal across the gap. The prevailing winds of southern Australia do blow from west to east, but White (1980) has suggested that the extremely fragile nature of *W. virgo* and its eggs render passive dispersal by wind highly unlikely. Extrapolation from the current climatic envelope of *W. virgo* indicates a continuous band of moderately suitable climate extending between the eastern and western populations along the south coast (Fig. 6c). This is also true for sexual *S. nelida* (Fig. 6f) and for the parthenogenetic *Sipyloidea* (Fig. 6g), which are currently restricted to Western Australia, thus climate *per se* may not be preventing eastward spread of the western populations. There is a strong association of *Warramaba*, *Sipyloidea* and *Heteronotia* with the 'mulga' habitat type (Fig. 6) and also with 'mallee' habitat on the southern periphery of the mulga zone, and these habitat types include some of the host plants of the former two genera. The conspicuous absence of 'mulga' habitat on the Nullarbor Plain (Fig. 7b), which consists of a broad plain of chenopod shrubland, is thus likely to be an important factor limiting eastward expansion. There is only one record of *S. nelida* from the mulga habitat on the eastern side of the Nullarbor Plain. It may be telling that this individual was a male, since only male *Sipyloidea* have the capacity for flight.

Why is parthenogenesis so common in the Australian desert? It does appear that biogeographic forces in the western part of the arid zone may have led to a high chance of origin via hybridization, but successful origin is only the first hurdle facing the evolution of parthenogenesis; what selective forces allow persistence? This study and that of Kearney *et al.* (this issue) have shown that parthenogenetic *Heteronotia*, *Warramaba* and *Sipyloidea* are all strongly associated with low-rainfall environments, one of the classic patterns of geographic parthenogenesis (Glesener and Tilman, 1978). It has been suggested that sexual reproduction is an adaptation to cope with the uncertainty of biotic interactions (Jaenike, 1978; Hamilton *et al.*, 1990; Lively *et al.*, 1990), and Glesener and Tilman (1978) proposed that parthenogenetic taxa occupy low-productivity environments such as arid zones and regions of high latitude and altitude because in such places biotic interactions are weak. However, this is a hypothesis for the advantage of sex and does not explain what it is about parthenogenesis that favours its evolution from sexual taxa in environments such as the Australian arid zone. Perhaps the advantage of parthenogenesis in low-productivity, and hence low-density, environments simply lies in the ability to reproduce without the costs of finding a mate (Gerritson, 1980). An interesting alternative is that the desert environment is somehow promoting the fixation of specialized or novel genotypes. The generation of a diverse array of clones through multiple hybridization events and allopolyploidy may provide a means to rapidly diversify and colonize an 'open' environment or 'ecological vacuum' (Stebbins, 1950; Randell, 1970; Roughgarden, 1972; Vrijenhoek, 1978, 1984). Parts of the Australian arid zone may have been inhospitable to many taxa during the hyper-arid glacial maxima of the Pleistocene, and thus may have presented 'open' environment for newly generated clonal genotypes to colonize. Of course, the long-term persistence of narrowly adapted clones would require relatively constant environments through time or recurrent origins of clones, as well as some density- or frequency-dependent selection, if extinction of specialized clones is to be avoided (Weeks, 1993). Kearney *et al.* (this issue) have noted that the environments occupied by parthenogenetic *Heteronotia* are characterized by persistently low rainfall. An additional level of constancy may be true for *Warramaba* and *Sipyloidea* which feed on *Acacia* trees, including mulga. A mulga tree may live for over a hundred years, supporting many generations of these insects (*Warramaba* is annual but the generation time of *Sipyloidea* is unknown). The apparent existence of apomixis in these plants (Miller *et al.*, 2002; Andrew *et al.*, 2003), as well as their other food plant *Senna* (Randell, 1970; Holman and Playford, 2000), would provide a further level of stability. Tests of co-adaptation to host plants in *Warramaba* and *Sipyloidea* through reciprocal transplant experiments would be very informative in this respect.

ACKNOWLEDGEMENTS

We thank Peter Miller for help obtaining locality records for *Sipyloidea*, Joe Miller and Mark Adams for kindly sharing unpublished manuscripts with us and Nelida Contreras, James F. Crow, Joe Miller, Craig Moritz, Curt Lively, Nicole Kearney and Graham Webb for discussion and comments on the manuscript.

REFERENCES

Adams, M., Foster, R., Hutchinson, M.N., Hutchinson, R.G. and Donnellan, S.C. in press. The Australian scincid lizard *Menetia greyii*: a new instance of widespread vertebrate parthenogenesis. *Evolution*.

Andrew, R., Miller, J.T., Peakall, R., Crisp, M.D. and Bayer, R.J. 2003. Genetic, cytogenetic and morphological patterns in a mixed mulga population: evidence for apomixis. *Austr. Syst. Bot.*, **16**: 69–80.

Atchley, W.R. 1978. Biological variability in the parthenogenetic grasshopper *Warramaba virgo* (Key) and its sexual relatives. II. The western Australian taxa. *Evolution*, **32**: 375–388.

Atchley, W.R. 1981. Chromosomal evolution and morphometric variability in the thelytokous insect *Warramaba virgo* (Key). In *Evolution and Speciation: Essays in Honour of M.J.D. White* (W.R. Atchley and D.S. Woodruff, eds), pp. 371–379. New York: Cambridge University Press.

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

Burnham, K.P. and Anderson, D.R. 1998. *Model Selection and Inference: A Practical Information-theoretic Approach*. New York: Springer-Verlag.

Case, T.J. and Taper, M.L. 1986. On the coexistence and coevolution of asexual and sexual competitors. *Evolution*, **40**: 366–387.

Cole, C.J. 1975. Evolution of parthenogenetic species of reptile. In *Intersexuality in the Animal Kingdom* (R. Reinboth, ed.), pp. 340–355. New York: Springer-Verlag.

Dennis, E.S., Peacock, W.J., White, M.J.D., Appels, R. and Contreras, N. 1981. Cytogenetics of the parthenogenetic grasshopper *Warramaba* (formerly *Moraba*) *virgo* and its bisexual relatives. VII. Evidence from repeated DNA sequences for a dual origin of *W. virgo*. *Chromosoma*, **82**: 453–469.

Gerritson, J. 1980. Sex and parthenogenesis in sparse populations. *Am. Nat.*, **115**: 718–742.

Glesener, R.R. and Tilman, D. 1978. Sexuality and the components of environmental uncertainty: clues from geographic parthenogenesis in terrestrial animals. *Am. Nat.*, **112**: 659–673.

Green, R.H. 1971. A multivariate statistical approach to the Hutchinsonian niche: bivalve molluscs of central Canada. *Ecology*, **52**: 543–556.

Hamilton, W.D., Axelrod, R. and Tanese, R. 1990. Sexual reproduction as an adaptation to resist parasites (a review). *Proc. Natl. Acad. Sci.*, **87**: 3566–3573.

Hewitt, G.M. 1975. A new hypothesis for the origin of the parthenogenetic grasshopper *Moraba virgo*. *Heredity*, **34**: 117–136.

Holman, J.E. and Playford, J. 2000. Molecular and morphological variation in the *Senna artemisoides* complex. *Austr. J. Bot.*, **48**: 569–579.

Honeycutt, R.L. and Wilkinson, P. 1989. Electrophoretic variation in the parthenogenetic grasshopper *Warramaba virgo* and its sexual relatives. *Evolution*, **43**: 1027–1044.

Jaenike, J. 1978. An hypothesis to account for the maintenance of sex within populations. *Evol. Theory*, **3**: 191–194.

John, B., Rentz, D.C.F. and Contreras, N. 1987. Extensive chromosome variation in the stick insect genus *Sipyloidea* Brunner von Wattenwyl (Phyllidae: Necrosciinae) within Australia, and descriptions of three new species. *Invertebrate Taxonomy*, **1**: 603–630.

Kearney, M., Moussalli, A., Strasburg, J., Lindenmayer, D. and Moritz, C. 2003. Geographic parthenogenesis in the Australian arid zone. I. A climatic analysis of the *Heteronotia binoei* complex (Gekkonidae). *Evol. Ecol. Res.*, **5**: 953–976.

Lively, C.M., Craddock, C. and Vrijenhoek, R.C. 1990. Red Queen hypothesis supported by parasitism in sexual and clonal fish. *Nature*, **344**: 864–866.

Lynch, M. 1984. Destabilizing hybridization, general purpose genotypes and geographic parthenogenesis. *Quart. Rev. Biol.*, **59**: 257–290.

Maynard Smith, J. 1978. *The Evolution of Sex*. Cambridge: Cambridge University Press.

Miller, J.T., Andrew, R. and Maslin, B.R. 2002. Towards an understanding of variation in the Mulga complex (*Acacia aneura* and relatives). *Conserv. Sci. West. Austr.*, **4**: 19–35.

Moritz, C. 1983. Parthenogenesis in the endemic Australian lizard *Heteronotia binoei* (Gekkonidae). *Science*, **220**: 735–736.

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.

Moritz, C. and Heideman, A. 1993. The origin and evolution of parthenogenesis in *Heteronotia binoei* (Gekkonidae): reciprocal origins and diverse mitochondrial DNA in western populations. *Syst. Biol.*, **42**: 293–306.

Moritz, C., Brown, W.M., Densmore, L.D., Wright, J.W., Vyas, D., Donnellan, S., Adams, M. and Baverstock, P. 1989. Genetic diversity and the dynamics of hybrid parthenogenesis in *Cnemidophorus* (Teiidae) and *Heteronotia* (Gekkonidae). In *Evolution and Ecology of Unisexual Vertebrates* (R.M. Dawley and J.P. Bogart, eds), pp. 87–112. Albany, NY: SUNY Press.

Nix, H. and Austin, P. 1973. Mulga: a bioclimatic analysis. *Tropical Grasslands*, **7**: 9–21.

Randell, B.R. 1970. Adaptations in the genetic system of Australian arid zone *Cassia* species (Leguminosae, Caesalpinioideae). *Austr. J. Bot.*, **18**: 77–97.

Roughgarden, J. 1972. The evolution of niche width. *Am. Nat.*, **106**: 683–718.

Stebbins, G.L. 1950. *Variation and Evolution in Plants*. New York: Columbia University Press.

Suomalainen, E., Saura, A. and Lokki, J. 1987. *Cytology and Evolution in Parthenogenesis*. Boca Raton, FL: CRC Press.

Vrijenhoek, R.C. 1978. Coexistence of clones in a heterogeneous environment. *Science*, **199**: 549–552.

Vrijenhoek, R.C. 1984. Ecological differentiation among clones: the frozen niche variation model. In *Population Biology and Evolution* (K. Wöhrmann and V. Loeschcke, eds), pp. 217–231. Heidelberg: Springer-Verlag.

Vrijenhoek, R.C. 1998. Animal clones and diversity. *Bioscience*, **48**: 617–628.

Webb, G.C., White, M.J.D., Contreras, N. and Cheney, J. 1978. Cytogenetics of the parthenogenetic grasshopper *Warramaba* (formerly *Moraba*) *virgo* and its bisexual relatives. IX. Chromosome banding studies. *Chromosoma*, **67**: 309–339.

Weeks, S.C. 1993. The effects of recurrent clonal formation on clonal invasion patterns: a Monte Carlo simulation of the frozen niche variation model. *Am. Nat.*, **141**: 409–427.

White, M.J.D. 1978. *Modes of Speciation*. San Francisco, CA: W.H. Freeman.

White, M.J.D. 1980. The genetic system of the parthenogenetic grasshopper *Warramaba virgo*. In *Insect Cytogenetics* (R.L. Blackman, M. Ashburner and G.M. Hewitt, eds), pp. 119–131. Oxford: Blackwell.

White, M.J.D. and Contreras, N. 1979. Cytogenetics of the parthenogenetic grasshopper *Warramaba* (formerly *Moraba*) *virgo* and its bisexual relatives. V. Interactions of *W. virgo* and a bisexual species in geographic contact. *Evolution*, **33**: 85–94.

White, M.J.D. and Contreras, N. 1981. Chromosome architecture of the parthenogenetic grasshopper *Warramaba virgo* and its bisexual ancestors. *Chromosomes Today*, **7**: 165–175.

White, M.J.D. and Contreras, N. 1982. Cytogenetics of the parthenogenetic grasshopper *Warramaba* (formerly *Moraba*) *virgo* and its bisexual relatives. VIII. Karyotypes and C-banding patterns in the clones of *W. virgo. Cytogenet. Cell Genet.*, **34**: 168–177.

White, M.J.D., Cheney, J. and Key, K.H.L. 1963. A parthenogenetic species of grasshopper with complex structural heterozygosity (Orthoptera: Acridoidea). *Austr. J. Zool.*, **11**: 1–19.

White, M.J.D., Webb, G.C. and Cheney, J. 1973. Cytogenetics of the parthenogenetic grasshopper *Moraba virgo* and its bisexual relatives. I. A new species of the *virgo* group with a unique sex chromosome mechanism. *Chromosoma*, **40**: 199–212.

White, M.J.D., Contreras, N., Cheney, J. and Webb, G.C. 1977. Cytogenetics of the parthenogenetic grasshopper *Warramaba* (formerly *Moraba*) *virgo* and its bisexual relatives. II. Hybridization studies. *Chromosoma*, **61**: 127–148.

Zaniewski, A.E., Lehmann, A. and Overton, J.M. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecol. Model.*, **157**: 261–280.