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Geographic parthenogenesis in the Australian arid zone: I. A climatic analysis of the *Heteronotia binoei* complex (Gekkonidae)

Michael Kearney,[1]* Adnan Moussalli,[2] Jared Strasburg,[3] David Lindenmayer[4] and Craig Moritz[5]

[1] *School of Biological Sciences, Heydon Laurence Building A08, The University of Sydney, Sydney, NSW 2006, Australia,* [2]*Department of Zoology and Entomology, University of Queensland, Brisbane, QLD 4072, Australia,* [3]*Department of Biology, Washington University, St Louis, MO 63130, USA,* [4]*Centre for Resource and Environmental Studies, Australian National University, Canberra, ACT 0200, Australia and* [5]*Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA*

ABSTRACT

Patterns of geographic parthenogenesis can provide insight into the ecological implications of the transition from sexual to parthenogenetic reproduction. We analysed quantitatively the environmental niches occupied by sexual and parthenogenetic geckos of the *Heteronotia binoei* complex in the Australian arid zone. This complex consists of two independently derived maternal lineages of hybrid parthenogens, which, in turn, include two different triploid races that resulted from reciprocal backcrossing with the parental sexual taxa. The sexual progenitors are still extant and occupy very distinct environmental niches. The triploid parthenogenetic races are biased in their environmental niche towards those of the sexual races for which their genomes are biased and this dosage effect is apparent in both maternal lineages. Thus triploidy may have benefited the parthenogens through partial recovery of the parental niches. Although the parthenogens have a broader geographic distribution than their sexual progenitors, their environmental niche is narrower and biased towards one of the sexual races. In keeping with general patterns of geographic parthenogenesis, parthenogenetic *H. binoei* occupy a harsher environment than the sexual forms, occurring in regions of persistently low rainfall. Bioclimatic modelling suggests patterns of rainfall are important in limiting the distribution of sexual and parthenogenetic taxa, and extrapolation from the current bioclimatic profiles indicates potential for further eastward range expansion by the parthenogens.

Keywords: arid zone, Australia, climate, gecko, parthenogenesis.

INTRODUCTION

Parthenogenetic organisms have received considerable attention from evolutionary biologists, especially from the standpoint of understanding the advantages and disadvantages

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

of sexual reproduction. To test hypotheses for the maintenance of sex, special attention has been paid to the ecological circumstances under which parthenogenesis occurs (Bell, 1982). One frequently observed pattern is that the geographic distributions of parthenogenetic organisms diverge in some manner from those of related sexual species, a phenomenon called 'geographic parthenogenesis' (Vandel, 1928). In general, parthenogenesis is observed to be more common than sex at higher latitudes and altitudes, in xeric environments, on islands or in island-like habitats, and in habitats variously described as disturbed, transient, ecotonal and marginal (see reviews by Suomaleinen, 1950; Cuellar, 1977; Glesener and Tilman, 1978; Bell, 1982; Lynch, 1984; Bierzychudek, 1985; Suomalainen *et al.*, 1987).

An important question in these studies has been the extent to which the observed patterns can be attributed to different genetic systems (i.e. sexual or asexual) or to the phenotypic effects of other genetic correlates of parthenogenesis, particularly hybridity and polyploidy (Lynch, 1984; Parker and Niklasson, 2000). For instance, the tendency for parthenogenetic organisms to occur in 'open' or sparsely populated environments, such as deserts or the Arctic, has been attributed to their colonizing ability, since only one individual is needed to found a population (Cuellar, 1994). Another major hypothesis is that sex is favoured over parthenogenesis in environments of high biotic uncertainty because recombination is necessary for effective co-evolution with predators, parasites and competitors (Jaenike, 1978; Hamilton *et al.*, 1990; Lively *et al.*, 1990); thus, parthenogenesis is restricted to sparsely populated environments where biotic interactions are weak (Glesener and Tilman, 1978; Hamilton *et al.*, 1990). However, many parthenogenetic organisms, including all known vertebrate cases, are hybrids and many are also polyploid. Although hybridization may play an important role in the origin of parthenogenesis (Moritz *et al.*, 1989), hybrids are often also phenotypically different from their parental taxa (Arnold, 1997) and parthenogenetic hybrids may be no exception. For instance, hybrid parthenogens may have intermediate phenotypes (Schlosser *et al.*, 1998) and thus occupy environments that are intermediate to those of their sexual parents – the 'intermediate niche hypothesis' (Moore, 1977). In contrast, the 'frozen-niche variation hypothesis' suggests that parthenogenetic taxa with multiple origins may consist of clones with individually narrow but diverse niches, representing genetically based phenotypic diversity captured from the sexual progenitors (Vrijenhoek, 1984). Finally, the 'general purpose genotype hypothesis' predicts parthenogens have broader environmental tolerances and thus occupy a broader range of environments, through heterosis resulting from hybridization (Schultz, 1971; Bulger and Schultz, 1979; Cullum, 1997; Schlosser *et al.*, 1998), through the evolution of polyploidy (Suomalainen, 1962; Beaton and Herbert, 1988; Soltis and Soltis, 2000) or through selection over time for generalist clones (Parker *et al.*, 1977; Lynch, 1984). Considering these additional complexities, patterns of geographic parthenogenesis should be interpreted with as much background information on the genetic relationships of the taxa being compared as possible.

The Australian arid zone is home to a remarkable diversity of parthenogenetic animals and apomictic plants, including grasshoppers, stick insects, geckos, skinks and shrubs (White *et al.*, 1963; Randell, 1970; Moritz, 1983; John *et al.*, 1987; Holman and Playford, 2000; Andrew *et al.*, 2003; Adams *et al.*, in press). In this study, we examined geographic patterns of parthenogenesis with respect to climate in a well-studied case of hybrid parthenogenesis from this region: gekkonid lizards of the *Heteronotia binoei* complex. The *H. binoei* system has a number of advantages for analysis of geographic parthenogenesis. First and foremost, both sexual progenitors are still extant and have been identified,

providing a powerful basis for comparison. Second, detailed genetic comparisons have demonstrated that extant clones arose within geographically restricted regions near the western limit of their current range, providing an important historical perspective (Moritz, 1993). Third, unlike many unisexual vertebrates, parthenogenesis in *H. binoei* is sperm-independent, providing a clearer picture of the ecological implications of hybrid parthenogenesis. We use a variety of statistical methods to ascertain if there are indeed differences in the climatic associations of the sexual and parthenogenetic forms of *H. binoei* and interpret these patterns with respect to the known genetic relationships among them. In particular, we frame our analyses around the following questions:

1. How do the climatic environments of the sexual progenitors of parthenogenetic *H. binoei* differ?
2. How do the mean climatic environments occupied by parthenogenetic and sexual *H. binoei* differ? In particular, do they occupy an intermediate environment to their sexual progenitors as predicted by the intermediate niche hypothesis?
3. Do parthenogenetic *H. binoei* occupy a broader range of climatic conditions or environmental niche (see Austin *et al.*, 1990; Peterson *et al.*, 1999) as predicted by the general purpose genotype hypothesis, or is there substantial divergence among independently derived groups of clones as predicted by the frozen-niche variation model?
4. Which climatic factors correspond most strongly with the distributions of sexual and parthenogenetic *H. binoei*?
5. Is the geographic range of parthenogenetic *H. binoei* at equilibrium or is there potential for further range expansion?

METHODS

Study system

Heteronotia binoei is a small, nocturnal, terrestrial lizard that occurs throughout continental Australia except for the cool, mesic regions of the southeast and southwest (Cogger, 2000). The genetics of this complex have been well studied throughout its distribution using comparisons of chromosomes, allozymes, nuclear ribosomal RNA genes and mitochondrial DNA (mtDNA) (summarized in Moritz, 1993). It includes at least five chromosomally distinct sexual races designated A6-2, SM6, CA6, CYA6 and EA6, which are largely indistinguishable morphologically but which occupy discrete geographic regions (Fig. 1). There are also triploid, parthenogenetic forms that are widely distributed in the central and western deserts across an area in excess of $1.5 \times 10^6 \cdot \mathrm{km}^{-2}$ (Fig. 2), where they occur in sympatry with the CA6, SM6 and EA6 sexual races.

Genetic analyses revealed that the parthenogens are hybrids between the SM6 and CA6 sexual races. Backcrossing between the presumed original diploid hybrids (which have never been found and are possibly now extinct) and males of both parental sexual races has produced two distinct triploid forms: form A parthenogens with a double dosage of the CA6 genome, and form BC parthenogens with a double dosage of the SM6 genome (Figs 2a, 3). The chromosome and allozyme diversity of the parthenogens is extraordinarily high, presenting the possibilities that they are unusually ancient or arose by multiple hybridization events. The multiple hybrid origin theory is supported by the strong correlation

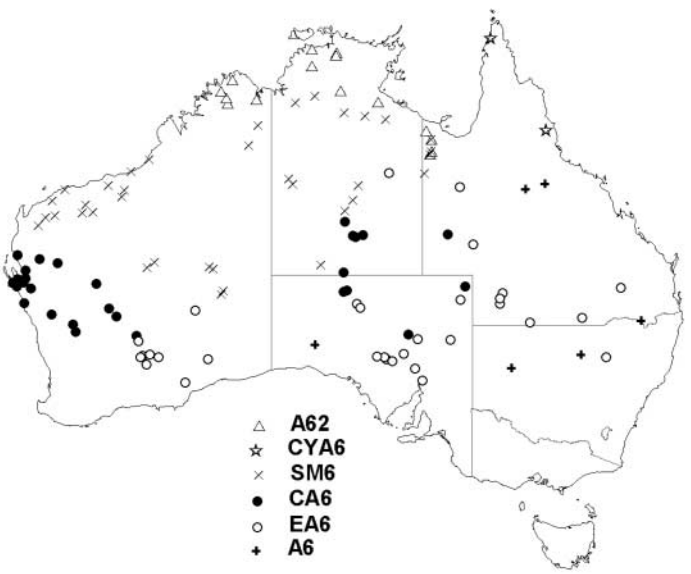

Fig. 1. Distribution of chromosomally distinct sexual races of *Heteronotia binoei*.

between expected heterozygosity in the parental taxa and that within the parthenogens, as well as the strong similarity of the allozyme polymorphisms within the sexual and parthenogenetic races. Comparison of their mtDNA with that of the parental sexual taxa supports the other evidence for multiple origins. Two distinct maternal lineages of parthenogen of reciprocal origin have been identified: 3N1 in the eastern and central part of the range with a CA6 maternal parent, and 3N2 in the western part of the range with an SM6 maternal parent (Figs 2b, 3). Significantly, the diversity of these mtDNA races is exceptionally low, of the same magnitude as that within individual populations of their respective sexual maternal progenitors. This indicates that the multiple hybrid origins were recent and geographically restricted. Moreover, both maternal lineages are genetically most closely aligned with western, but geographically separated, sexual populations of their respective maternal parents. This suggests western origins and, for the 3N1 clones in particular, a subsequent rapid spread eastward to central Australia.

Construction of climate surfaces

We analysed the distribution of sexual and parthenogenetic lineages of *H. binoei* with respect to six climatic variables that we recognize as biologically important in this region and to these organisms: mean temperature, mean relative humidity, mean rainfall, temperature seasonality, rainfall seasonality and inter-annual rainfall variability (hereafter referred to as rainfall variability). Continent-wide surfaces for these six climatic variables were interpolated from weather station data (>30 years) with the programs ANUSPLIN and ANUCLIM (Hutchinson, 1991, 2000; Hutchinson *et al.*, 1999) using a 0.05° resolution digital elevation model (DEM) (Hutchinson and Dowling, 1991). Seasonality of temperature and rainfall were calculated as the coefficient of variation of values within years, while

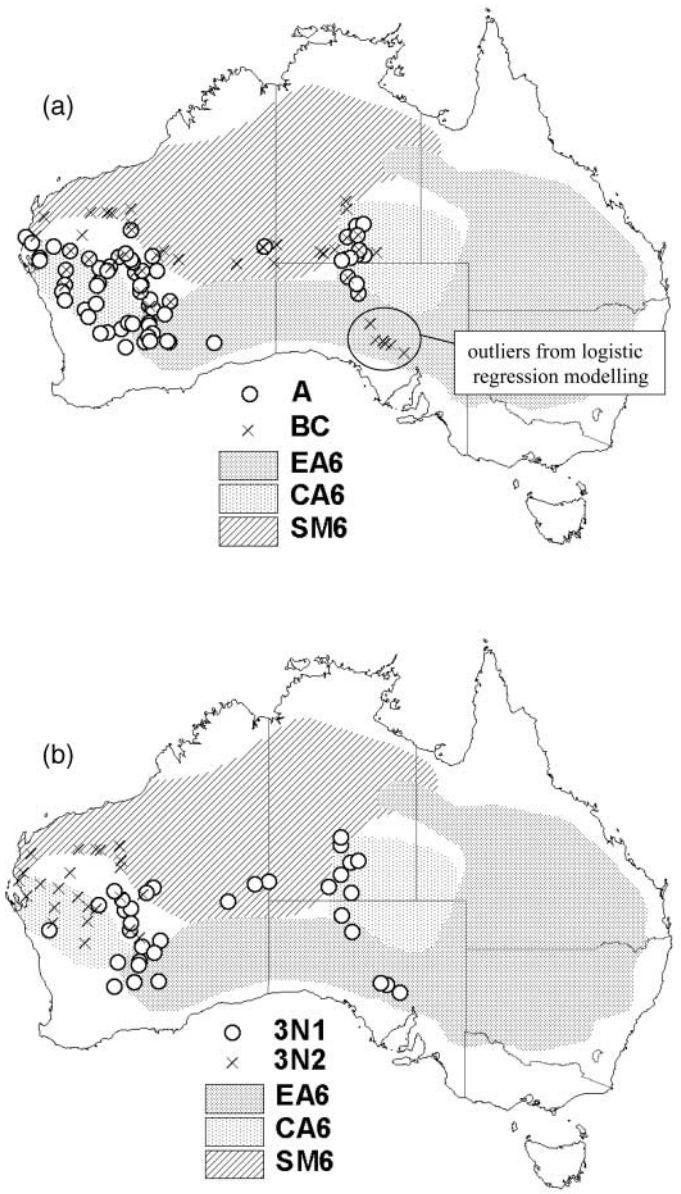

Fig. 2. Distribution of (a) chromosomal forms A and BC and (b) maternal lineages 3N1 and 3N2 of parthenogenetic *Heteronotia binoei* in relation to the CA6, SM6 and EA6 sexual races. Outlier BC populations that were excluded from the distributional modelling analyses are circled.

rainfall variability was calculated as the coefficient of variation of values between years. We initially based the rainfall variability surface on all 12 months of the year but found this to be strongly affected by patterns of rainfall during the dry season in parts of the northern half of Australia. This region experiences relatively high but seasonal rainfall, with an extremely low mean in the dry season during which occasional aseasonal rain strongly

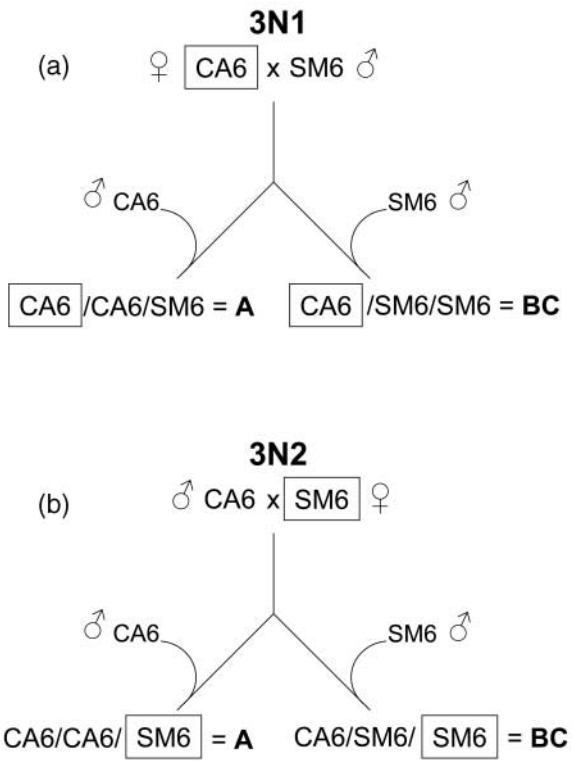

Fig. 3. Reciprocal hybrid origins of triploid parthenogenetic *Heteronotia binoei* from the CA6 and SM6 sexual races. 3N1 parthenogens have mtDNAs derived from CA6 sexual females and 3N2 parthenogens have mtDNAs derived from SM6 sexual females and are thought to represent independent origins. Backcrossing of the original parthenogenetic hybrids with males of the parental sexual races occurred in both directions and in both maternal lineages, with some triploids having a double dosage of the CA6 nuclear genome (designated form A) and others having a double dosage of the SM6 nuclear genome (designated form BC).

affects the annual coefficient of variation. However, since summer storms have the most biologically significant impact on the ecology of most of the arid zone (Stafford Smith and Morton, 1990), we restricted our analyses to summertime rainfall variability only.

Climatic analyses

Our analyses are based on samples of *H. binoei* from 160 localities around Australia (Figs 1, 2). Individuals from all of these sites were karyotyped and a subset were subject to mitochondrial analysis (see Moritz, 1993, and references therein for details). Sample sizes per taxon are provided in Table 1. We focus on the various parthenogenetic races and the two sexual races that gave rise to them, CA6 and SM6, with some consideration also given to the EA6 sexual race, since it is sympatric with the parthenogenetic races in some areas. For the logistic regression modelling of presence/absence (see below), we used additional records from the other sexual races within the *H. binoei* species complex as absence records

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

Reproductive mode	Race	Localities (*n*)
Sexuals	CA6	28
	SM6	37
	EA6	35
Parthenogens	A	66
	BC	46
	3N1_A	22
	3N1_BC	17
	3N2_A	17
	3N2_BC	13

(Fig. 1). Additional absence points were randomly allocated in the extreme southeast and southwest of the continent, where *Heteronotia* is know to be absent (Cogger, 2000). We queried the six climate surfaces with the GIS program ArcView to obtain point estimates of climatic conditions at localities where *H. binoei* 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 generally, to test for genome dosage effects in the parthenogens resulting from the reciprocal origins of triploidy and to compare among groups of clones with independent origins (3N1 *vs* 3N2). Second, we used discriminant function analysis to determine how well the various taxa can 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 for three sexual races – CA6, SM6 and EA6 – and the two chromosome races of parthenogen A and BC, based on the six climatic covariates. For logistic regression, we also fitted a model for the two parthenogenetic races combined, A + BC, and each maternal lineage, 3N1 and 3N2. All-subset fitting, in conjunction with Akaike's information criterion (AIC) model averaging, was used both to determine the relative importance (AIC weights) for each of the six climatic variables and to develop a predictive model; this is an information-theoretic approach to model selection detailed by Burnham and Anderson (1998). Thus model selection uncertainty was implicit in coefficient estimation, model prediction and associated standard errors. Both linear and quadratic polynomial terms were considered in constructing all possible combinations of the six covariates. We used AICc because the ratio of survey sites ($n = 177$) to parameters in the global model ($K = 14$) was <40 (as advocated by Burnham and Anderson, 1998). The difference (Δ_i) between the AIC values of each model and that of the Kullback-Leibler information best model was then calculated and the AICc weight derived for each model. Model-averaged coefficient estimates, point estimation (predictions) and respective standard errors were calculated from a reduced candidate model set whereby only models with $\Delta_i < 4$ were considered. Accordingly, weights were normalized to sum to 1 for this reduced candidate set. Note that in calculating model-

averaged coefficients, weighted coefficients were summed up across all models in the reduced candidate set (i.e. where $\Delta_i < 4$), not just those models containing the covariate of interest. An outline of this 'full model-averaged estimator' is given in Burnham and Anderson (1998), specifically formula (5.8). Using this approach, model-averaged coefficients are derived for all covariates and not just those found in the AICc best model. Accordingly, a modified estimator of standard error was used (Burnham and Anderson, 1998).

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

Comparisons of mean environments

All six climatic variables were significantly different among the CA6, SM6, EA6, A and BC races of *Heteronotia binoei* (ANOVA: all $P < 0.0001$, Fig. 4). Tukey-adjusted multiple comparisons indicated that the two parental sexual races differed for all climatic variables (Fig. 4a–f). The two parthenogenetic chromosome races differed only for temperature and humidity, with A occurring in cooler, more humid environments than BC – that is, they differed in the same manner as CA6 differed from SM6 (Fig. 4a–f). The two parthenogenetic chromosome races did not differ from each other for temperature seasonality or rainfall seasonality, but they were both significantly different from the parental sexual races to which their genomes were biased (Fig. 4d,e). Parthenogens were intermediate to the parental sexuals for rainfall variability (Fig. 4f). There were no differences between CA6 and form A parthenogens for temperature, although form BC parthenogens occurred in cooler environments than SM6 parthenogens (Fig. 4a). Neither were there differences between form A and BC parthenogens and CA6 sexuals for rainfall, although all three exist in a significantly drier environment than the SM6 race (Fig. 4b). The parthenogens occupied environments of similar humidity to the parental forms to which their genomes were biased (Fig. 4c). Finally, the EA6 race differed significantly from all other taxa for temperature and rainfall seasonality, occurred in similar temperature seasonality and rainfall variability environments to the parthenogenetic taxa, had similar rainfall to all taxa but SM6, and similar humidity to the CA6 sexual race and the form A parthenogens (Fig. 4).

The dual, reciprocal origins of the two triploid parthenogenetic races allows a robust comparison between them in the form of a two-factor ANOVA, with chromosome race crossed with maternal lineage (Table 2, Fig. 5). Significant differences were detected between chromosome forms A and BC for temperature, humidity, rainfall seasonality and rainfall variability (Fig. 5a,c,e,f). Again, these differences were in the same direction as occurred between the CA6 and SM6 sexual races (Fig. 4a,c,e,f). These patterns were consistent between groups of clones with independent origins in that there were few interactions between chromosome and maternal lineages. The only exception was a significant interaction for mean rainfall with form A occurring in drier environments than form BC only for the 3N2 maternal lineage, with no difference between these chromosome lineages in the 3N1

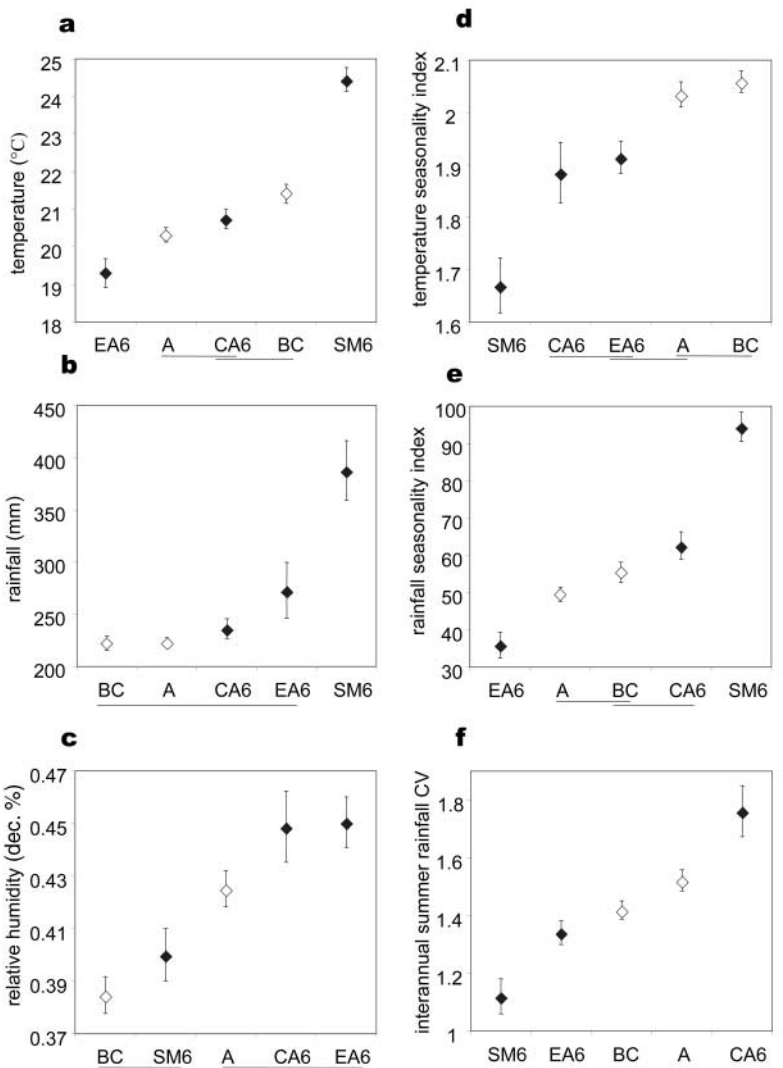

Fig. 4. Mean values (± standard error) of (a) annual temperature, (b) annual rainfall, (c) annual relative humidity, (d) seasonality of temperature, (e) seasonality of rainfall and (f) inter-annual variation in summer rainfall for the CA6, SM6 and EA6 sexual races (solid symbols) and the form A and BC parthenogenetic races (open symbols) of *Heteronotia binoei*. 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.

maternal lineage (Fig. 5b). Significant differences existed between the maternal lineages for temperature, rainfall seasonality and rainfall variability (Fig. 5a,e,f). There were no differences between maternal lineages for humidity and temperature seasonality, nor were there differences between chromosome races for temperature seasonality (Fig. 5c,d).

Table 2. *F*-statistics and *P*-values of two-factor analyses of variance comparing the effect of chromosome race (either form A or form BC) and maternal race (either 3N1 or 3N2) for the six climatic variables

Climatic variable	Chromosome race (C)	Maternal race (M)	C × M
Temperature			
$F_{1,65}$	13.685	57.397	1.386
P	*0.001*	*< 0.001*	0.244
Rainfall			
$F_{1,65}$	3.259	0.072	5.678
P	0.076	0.789	*0.020*
Humidity			
$F_{1,65}$	6.833	0.090	0.121
P	*0.011*	0.765	0.729
Temperature seasonality			
$F_{1,65}$	0.562	1.914	1.116
P	0.456	0.171	0.295
Rainfall seasonality			
$F_{1,65}$	7.831	51.718	3.408
P	*0.007*	*< 0.0001*	0.069
Rainfall variability			
$F_{1,65}$	4.093	6.292	1.013
P	*0.047*	*0.015*	0.318

Multidimensional comparisons

The first discriminant analysis contrasted the three sexual races, CA6, SM6 and EA6. The two discriminant functions calculated for this comparison significantly discriminated among the taxa based on the six climatic variables (Wilks' $\lambda_{6,2,97} = 0.205$, $F_{18,184} = 18.540$, $P < 0.0001$). Mean annual temperature and rainfall seasonality correlated positively and most strongly with discriminant function one (DF1), while rainfall variability correlated strongly and negatively with discriminant function two (DF2) (Table 3). A scatter plot of the scores for the two discriminant functions demonstrates clear separation between the three sexual races (Fig. 6a), which is reiterated by the success of the discriminant function in classifying these taxa (classification success: EA6 = 79%, CA6 = 77%, SM6 = 84%).

The second discriminant analysis contrasted the two chromosome races of parthenogen (A and BC), pooling over maternal lineage, with the two parental sexual races (CA6 and SM6). The combination of the three discriminant functions calculated for this comparison resulted in significant discrimination among taxa (Wilks' $\lambda_{6,3,173} = 0.268$, $F_{18,475} = 15.664$, $P < 0.0001$). Tests of residual roots indicated that all three discriminant functions were statistically significant (all $P < 0.05$); however, the third discriminant function was relatively uninformative, as indicated by its low eigenvalue and canonical correlation coefficient

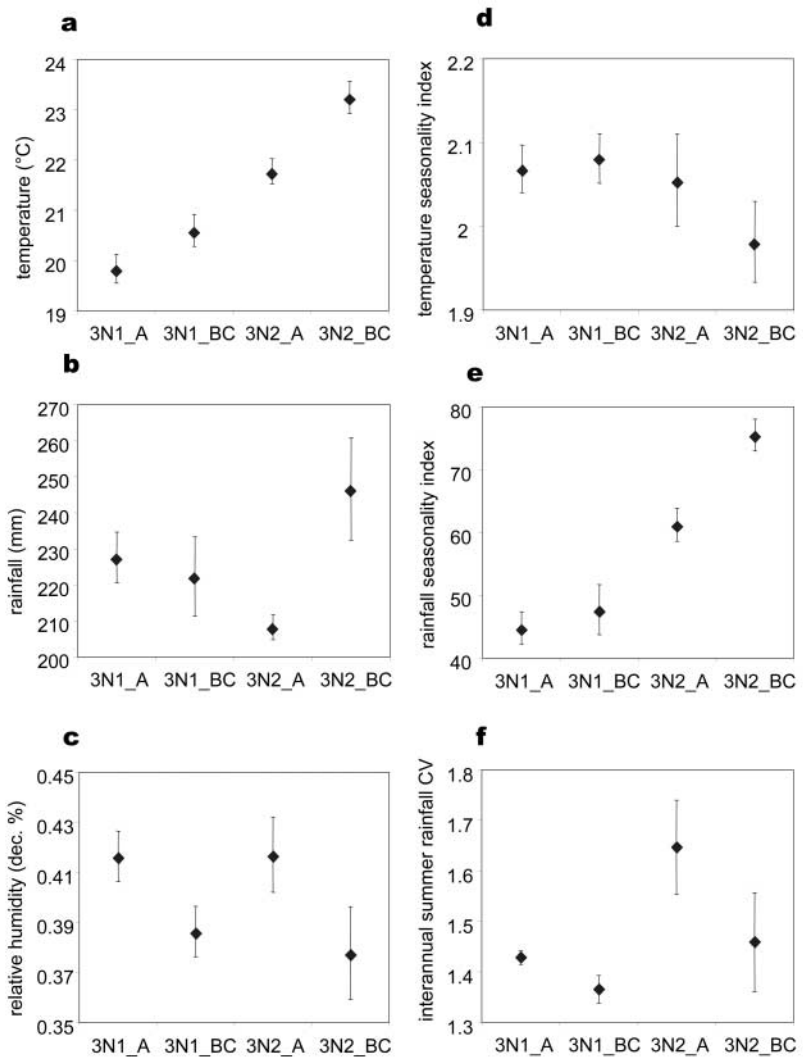

Fig. 5. Mean values (± standard error) of (a) annual temperature, (b) annual rainfall, (c) annual relative humidity, (d) seasonality of temperature, (e) seasonality of rainfall and (f) inter-annual variation in summer rainfall for the two chromosomal races (form A and form BC) of the two maternal lineages (3N1 and 3N2) of parthenogenetic *Heteronotia binoei*.

(Table 3). Temperature, rainfall seasonality and rainfall correlated positively and most strongly with DF1, while temperature seasonality and rainfall variability were moderately negatively correlated with this axis (Table 3). Humidity, temperature seasonality and rainfall variability were most strongly correlated with DF2, with temperature seasonality being positively correlated and humidity and rainfall variability being negatively correlated (Table 3). As in the first analysis, there is clear separation between the two parental races, CA6 and SM6, based on DF1 (Fig. 6b); however, there is poor discrimination among the CA6 sexual

Table 3. Predictor variable loadings, canonical *R*-values and eigenvalues for discriminant function analyses comparing various combinations of the CA6, SM6 and EA6 sexual races and A and BC parthenogenetic races

		Correlations of predictor variables with discriminant functions		
Comparison	Predictor variable	1	2	3
CA6, SM6, EA6	Temperature	**0.955**	−0.037	n/a
	Humidity	−0.444	−0.070	n/a
	Rainfall	0.470	0.276	n/a
	Temperature seasonality	−0.476	−0.246	n/a
	Rainfall seasonality	**0.924**	−0.107	n/a
	Rainfall variability	−0.441	**−0.712**	n/a
	Canonical *R*	0.801	0.654	n/a
	Eigenvalue	1.790	0.749	n/a
CA6, SM6, A, BC	Temperature	**0.851**	−0.025	−0.208
	Humidity	−0.187	**−0.674**	**0.569**
	Rainfall	**0.742**	−0.248	0.374
	Temperature seasonality	**−0.592**	**0.632**	−0.211
	Rainfall seasonality	**0.817**	−0.452	−0.051
	Rainfall variability	**−0.573**	**−0.591**	−0.239
	Canonical *R*	0.812	0.401	0.256
	Eigenvalue	1.929	0.192	0.070
CA6, SM6, 3N1_A, 3N1_BC	Temperature	**0.937**	−0.180	0.047
	Humidity	−0.210	**−0.579**	−0.580
	Rainfall	**0.691**	−0.101	−0.404
	Temperature seasonality	**−0.595**	**0.521**	0.280
	Rainfall seasonality	**0.851**	−0.480	−0.184
	Rainfall variability	**−0.606**	**−0.666**	0.185
	Canonical *R*	0.836	0.506	0.179
	Eigenvalue	2.316	0.344	0.033
CA6, SM6, 3N2_A, 3N2_BC	Temperature	**0.899**	0.270	0.017
	Humidity	−0.301	−0.457	0.362
	Rainfall	**0.697**	−0.264	0.246
	Temperature seasonality	−0.499	0.490	−0.077
	Rainfall seasonality	**0.813**	−0.134	−0.052
	Rainfall variability	**−0.727**	−0.134	−0.217
	Canonical *R*	0.801	0.584	0.209
	Eigenvalue	1.791	0.518	0.046

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

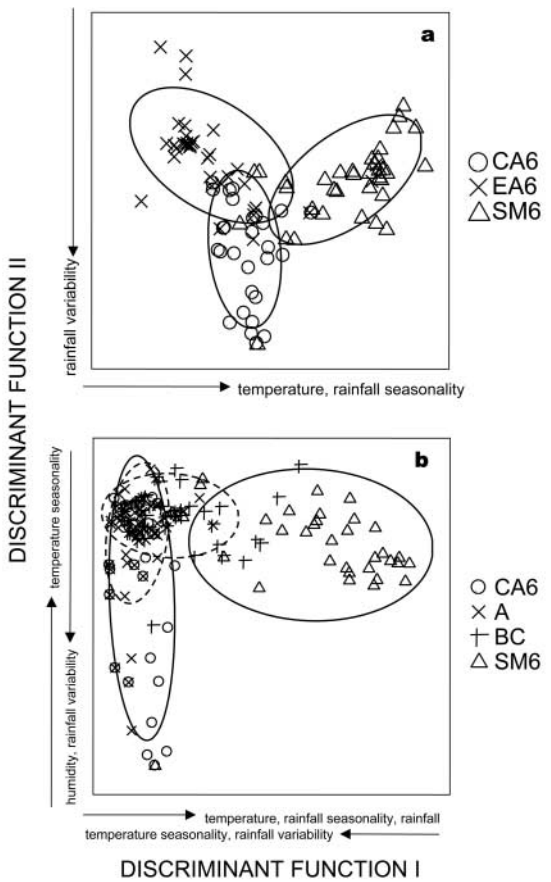

Fig. 6. Scores from discriminant function analyses plotted against discriminant function 1 and 2 for (a) the three sexual races (CA6, SM6 and EA6) of *Heteronotia binoei* and (b) the two parental sexual races, CA6 and SM6, and the two chromosome races of parthenogens, A and BC. Arrows indicate direction 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.

race and the A and BC parthenogenetic races (classification success: CA6 = 43%, SM6 = 80%, A = 55%, BC = 54%). The two parthenogenetic chromosome races are clearly biased towards the climatic environment of the CA6 sexual race, although within this they are biased towards the less humid, more thermally seasonal part of the CA6 environment where rainfall is less variable (Fig. 6b). Nevertheless, there is some correspondence between the parthenogenetic chromosome races and the sexual races to which their genomes are biased, as indicated by the orientation of the confidence ellipses in the scatter plot (Fig. 6b) and by the manner in which they were misclassified by the discriminant function. That is, chromosome form A was more often misclassified as CA6 than SM6 (6 misclassified as CA6, 0 as SM6) and chromosome form BC was more often misclassified as SM6 than CA6 (5 misclassified as SM6, 1 as CA6). Based on the confidence ellipses, the parthenogenetic races appear to occupy a narrower range of climatic environments – that is, to have a narrower environmental niche – than the sexual lineages (Fig. 6b).

Finally, we repeated the initial discriminant analysis comparing the two chromosome races of parthenogen with the two parental sexual races as before, but analysing the two maternal parthenogenetic lineages separately (Table 3, Fig. 7). Both analyses significantly discriminated among the taxa (3N1 comparison: Wilks' $\lambda_{6,3,100} = 0.217$, $F_{18,269} = 10.702$, $P < 0.0001$; 3N2 comparison: Wilks' $\lambda_{6,3,91} = 0.226$, $F_{18,243} = 9.348$, $P < 0.0001$) and in both cases the third discriminant function was uninformative in classification (3N1 comparison: $\chi^2_4 = 3.373$, $P = 0.4974$; 3N2 comparison: $\chi^2_4 = 4.484$, $P = 0.345$). The manner in which the climatic variables correlated with the discriminant functions was very similar to the initial analysis in which maternal lineage was pooled, being identical for the 3N1 lineage, but with temperature seasonality dropping out on DF1 and rainfall variability dropping out on DF2 for the 3N2 maternal lineage (Table 3, Fig. 7). However, there was a difference in the extent of overlap, and the relative environmental breadths, of the parthenogens compared with the

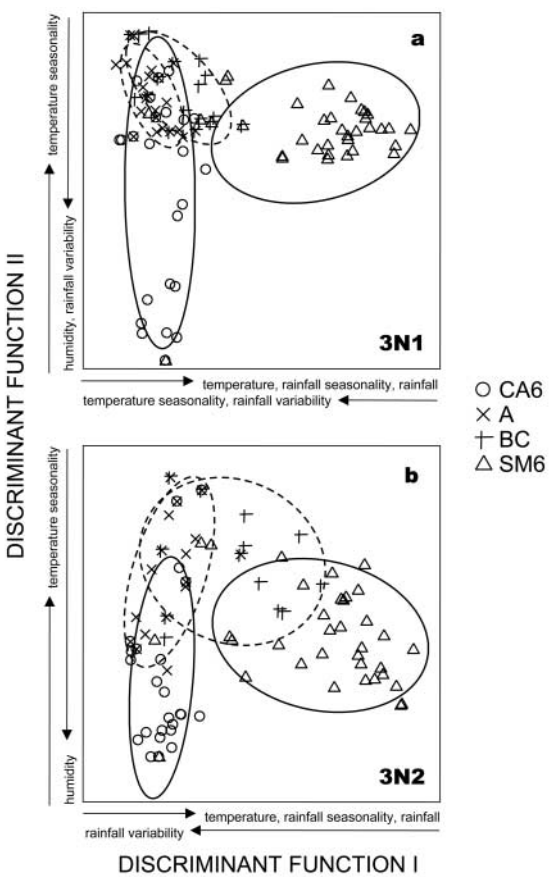

Fig. 7. Scores from discriminant function analyses plotted against discriminant function 1 and 2 for analyses of *Heteronotia binoei* contrasting the two parental sexual races, CA6 and SM6, with the two chromosome races of parthenogen, forms A and BC, separately for (a) the 3N1 maternal lineage and (b) the 3N2 maternal lineage of parthenogen. 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.

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 as a function of the six climatic covariates

Taxon	χ^2	d.f.	*P*	R^2
ABC	2.005	6	0.919	0.58–0.62
A	2.049	6	0.915	0.59–0.62
EA6	3.071	8	0.930	0.43–0.51
CA6	3.228	6	0.780	0.47–0.53
3N1	5.701	6	0.458	0.34–0.40
BC (without outliers)	5.720	6	0.455	0.48–0.53
SM6	6.978	7	0.431	0.58–0.63
BC (with outliers)	12.529	6	0.084	0.36–0.40
3N2	10.834	5	0.055	0.51–0.61

Note: Taxa are ranked in decreasing order of *P*-values.

sexuals, as indicated by the scatter plots (Fig. 7). Specifically, the 3N1 parthenogens were biased towards the climatic environment of the CA6 sexual race and had a much narrower envelope (Fig. 7a), whereas the 3N2 parthenogens overlapped more with the sexual races and had similar environmental breadths (Fig. 7b).

Climate correlates of spatial distribution

The models fitted to the spatial distribution of the different races of *H. binoei* based on the six climatic covariates provided a good fit to the observed distribution points for all taxa except the 3N2 and BC parthenogenetic lineages (Table 4). In the latter case, we found the extreme southeastern populations (Fig. 2a) to be strong outliers. The fit of the model was markedly improved after removing these points and we only present results for this second model. The AIC weightings of the model-averaged coefficients provide an indication of the relative importance of the different covariates in predicting distribution (Fig. 8; see Table 5 for estimated coefficients and standard errors). In many cases, the best model included a quadratic term and for these we examined plots of the profiles of these relationships to assess whether the response was best described as a positive or negative relationship, or as an intermediate optimum. In general, rainfall-related covariates were important in modelling distribution. For example, all three sexual races were strongly associated with rainfall seasonality, SM6 and CA6 being positively, and EA6 being negatively, associated. For models of the parthenogenetic races, rainfall seasonality was not important but there was a very tight quadratic relationship with mean rainfall for every lineage except 3N2. The only sexual race for which mean rainfall was important was SM6, which showed a negative relationship. Rainfall variability was important for the CA6 and EA6 sexual races and the form A parthenogens, with quadratic, negative and positive associations, respectively. Humidity was also important in modelling distribution, being strongly weighted in all models except that for CA6; however, the form of the association also varied among taxa, being negative for SM6 and form BC and 3N1 parthenogens, positive for form A and 3N2 parthenogens, and quadratic for EA6 and form A+BC parthenogens. Seasonality of

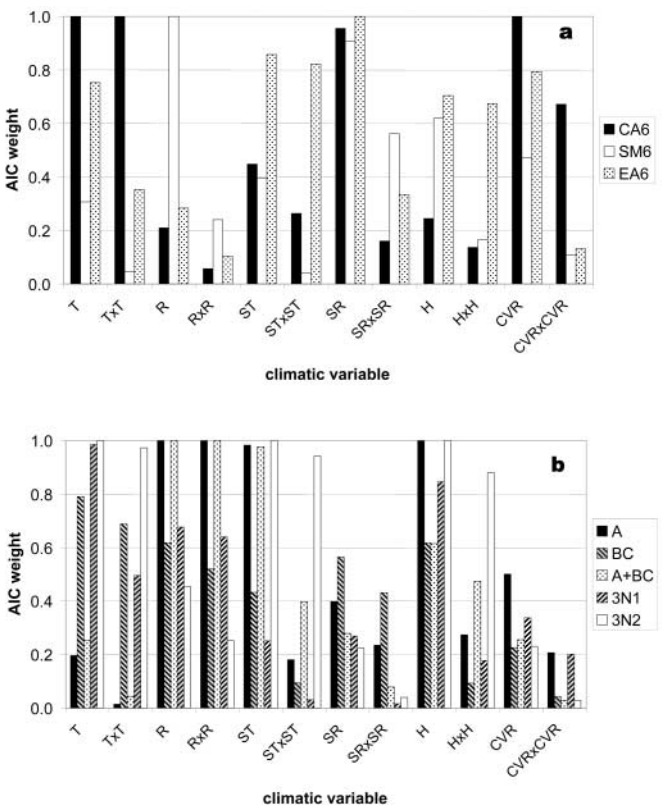

Fig. 8. Model-averaged AICc weightings of the coefficients estimated for the six climatic variables (as linear and quadratic terms) in logistic regression modelling of the distribution of (a) the sexual races CA6, SM6 and EA6 and (b) the parthenogenetic races A, BC, A+BC, 3N1 and 3N2 of *Heteronotia binoei*. T = temperature, R = rainfall, ST = temperature seasonality, SR = rainfall seasonality, H = humidity, CVR = rainfall variability.

temperature was important for the EA6, A and A+BC models, showing a quadratic relationship in the former and a positive relationship in the latter two. Finally, mean temperature was important in models for the EA6 and CA6 sexual races and the 3N1, 3N2 and BC parthenogens, showing a quadratic relationship in the former taxon and a positive relationship in the latter four taxa. Prediction of spatial distributions from the fitted models generally provided good correspondence with the current distributions, although the parthenogenetic races are predicted to occur further to the east than their present distribution (Fig. 9). This suggests that the geographic ranges of these recently derived parthenogenetic lineages are not yet at equilibrium, at least with respect to the abiotic factors considered here.

DISCUSSION

An understanding of the environmental associations of the parental sexual taxa is an important starting point for interpreting those of the parthenogenetic races. These sexual

Table 5. 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 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
CA6	43	β	−170.417	**1.273**	**−0.003**	0.003	0.000	0.124	0.000	**0.080**	0.000	20.637	−24.585	**35.356**	**−14.302**
		SE	65.239	**0.529**	**0.001**	0.006	0.000	0.168	0.000	**0.049**	0.000	24.470	25.275	**24.348**	**8.118**
SM6	32	β	−4.569	**0.061**	0.000	**−0.009**	0.000	−0.015	0.000	**−0.029**	**0.001**	**12.278**	−25.688	−2.857	0.307
		SE	19.954	**0.075**	0.000	**0.009**	0.000	0.020	0.000	**0.099**	**0.001**	**31.546**	26.470	2.827	0.628
EA6	25	β	−63.990	**0.136**	0.000	0.001	0.000	**0.350**	**−0.001**	**−0.127**	0.000	**121.013**	**−136.191**	**−8.864**	0.814
		SE	30.283	**0.133**	0.000	0.002	0.000	**0.176**	**0.001**	**0.055**	0.000	**45.832**	**53.227**	**5.465**	1.679
A	27	β	−52.752	−0.013	0.000	**0.179**	**0.000**	**0.099**	0.000	0.072	−0.001	**−5.387**	39.055	**13.817**	−5.157
		SE	17.101	0.021	0.000	**0.056**	**0.000**	**0.069**	0.000	0.067	0.001	**55.916**	40.315	**13.918**	4.822
BC	35	β	−98.092	**0.733**	**−0.002**	**0.063**	**0.000**	0.059	0.000	0.094	−0.001	**−11.912**	3.291	0.003	−0.058
		SE	73.533	**0.437**	**0.001**	**0.041**	**0.000**	0.067	0.000	0.092	0.001	**11.778**	8.861	0.771	0.115
A+BC	7	β	−27.869	0.010	0.000	**0.106**	**0.000**	**0.287**	**−0.001**	0.007	0.000	**−94.011**	**119.757**	0.394	0.019
		SE	19.993	0.018	0.000	**0.033**	**0.000**	**0.253**	**0.000**	0.009	0.000	**60.963**	**62.956**	0.981	0.179
3N1	35	β	−21.520	**0.197**	**−0.001**	**0.059**	**0.000**	0.015	0.000	0.008	0.000	**−9.986**	−10.077	11.715	−6.541
		SE	42.061	**0.376**	**0.001**	**0.044**	**0.000**	0.021	0.000	0.013	0.000	**25.987**	18.904	14.824	7.048
3N2	29	β	−290.728	**1.597**	**−0.003**	0.013	0.000	**0.841**	**−0.002**	0.009	0.000	**−85.285**	**166.483**	0.682	−0.099
		SE	103.241	**0.692**	**0.001**	0.023	0.000	**0.434**	**0.001**	0.018	0.000	**87.446**	**89.817**	1.707	0.384

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.

taxa occupy geographically discrete distributions that correspond to a basic climatic subdivision of the Australian arid zone. The SM6 race occurs in the warmer northern half of the arid zone (Fig. 1) that is predominantly under the influence of the tropical monsoon system of northern Australia. This region is characterized by reliable but sporadic summer rainfall and a distinct dry season in the cooler months, and distributional modelling of SM6 indicates a tight correspondence with rainfall seasonality and mean rainfall (Table 5, Fig. 8a). In contrast, the CA6 race has a disjunct distribution occupying the cooler southern half of the arid zone (Fig. 1) that is characterized by lower, less seasonal and less reliable rainfall. Accordingly, the distribution of this taxon is associated with temperature and is positively associated with rainfall variability (Table 5, Fig. 8a). The CA6 race is also positively associated with rainfall seasonality (Table 5), although unlike SM6 it corresponds more with winter rainfall, especially on the west coast. Finally, the EA6 sexual race, which occurs sympatrically with the parthenogens in some regions, but was not involved in their hybrid origin, also occupies a climatically distinct environment characterized by low temperature and low rainfall seasonality and variability (Figs 4, 6a). The distribution of this taxon is also strongly associated with rainfall seasonality as well as rainfall variability, humidity and temperature seasonality (Table 5, Fig. 8a). In multidimensional space, these three taxa separate very strongly according to the six climatic variables we considered (Figs 6, 7) with only a small percentage being misclassified by the discriminant functions. The distinctiveness of the climatic environments occupied by the sexual taxa and the good correspondence of their distribution with climate implies significant differences in their physiology and life history. It also supports the hypothesis that range shifts associated with climatic oscillations during the late Pleistocene or Holocene were important in driving hybridization events between the parental taxa (Moritz *et al.*, 1989).

Since parthenogenetnic *H. binoei* are hybrids between the CA6 and SM6 sexual races, we might expect them to have an intermediate phenotype and hence occupy intermediate environments to those of their sexual progenitors (Moore, 1977). However, in this particular case we might also expect some degree of bias caused by genome dosage differences, since there are two triploid forms of parthenogen. In particular, the environment of form A parthenogens could be biased towards that of CA6 and the environment of form BC parthenogens could be biased towards that of SM6. Such partial or complete recovery of the parental niches could be especially advantageous if an intermediate niche is limited or non-existent. The univariate and multivariate comparisons provide strong evidence for such genome dosage effects. In all cases where there are differences between form A and form BC parthenogens in their climatic environments, they differ in the same manner that CA6 sexuals differ from SM6 sexuals (Figs 4, 5). Most convincingly, this pattern is borne out in both maternal lineages of parthenogens, which represent independent origins of the two triploid forms (Table 2, Fig. 5). The pattern is also apparent in the relative alignment of confidence ellipses in the scatter plots of the discriminant function scores (Figs 6a, 7) and in the patterns of misclassification by the discriminant functions. A broad north/south division is also apparent in the distribution of form A and BC parthenogens, although some of the most southerly populations of parthenogen are form BC (Fig. 2a).

Mitochondrial DNA analyses indicate that the origins of the parthenogenetic races were spatially and temporally restricted (Moritz, 1991; Moritz and Heideman, 1993). Thus, there appears to have been differential selection on the A and BC parthenogenetic forms as they spread to occupy their current geographic range. This implies that there are phenotypic differences between the two chromosome forms that mirror those of the parental taxa. This

is certainly true for at least one aspect of their morphology: the CA6 sexuals and form A parthenogens tend to have a more banded back pattern, whereas SM6 and form BC are more speckled in appearance. A detailed comparison of ecophysiological traits is currently underway and preliminary results also support this notion (M. Kearney, unpublished). These patterns of ecological differentiation among distinct clonal races are consistent with predictions of the frozen-niche variation hypothesis. The reciprocal formation of these allotriploids may thus have increased their combined environmental envelope over that of the original allodiploids, contributing to their broad geographic distribution.

The broad geographic distribution of parthenogenetic *H. binoei* is not unusual among parthenogenetic organisms. Such patterns have been used in support of the 'general purpose genotype' hypothesis, which argues that the transition to parthenogenesis should be accompanied by selection for highly generalized phenotypes that maximize geometric mean fitness (Baker, 1965; Parker *et al.*, 1977; Templeton, 1982; Lynch, 1984; Schlosser *et al.*, 1998). Indeed, in the case of parthenogenetic *H. binoei* it has been suggested that 'the niche of this taxon appears to be broader than that of its bisexual progenitors' (Suomalainen *et al.*, 1987, p. 94). However, broad geographic distributions are not necessarily indicative of a broad environmental niche; they may represent the occupation of a narrow but widely available niche (Vrijenhoek, 1998; James and Shine, 2000). In the case of *H. binoei*, the existence of a general purpose genotype would be supported if their broad geographic distribution corresponded to their occupation of an equivalently broad range of climatic conditions – the 'environmental niche' (Austin *et al.*, 1990; Peterson *et al.*, 1999). In fact, the degree of scatter in the discriminant function plots, a representation of environmental breadth (Green, 1971), suggests the opposite (Figs 6b, 7). The two parental sexual taxa have similar sized environmental niches despite their different geographic ranges (Fig. 6b). In contrast, parthenogenetic *H. binoei* generally have a narrower envelope than the sexuals (Fig. 6b), although this varies with maternal lineage; the envelope of the 3N2 lineage is similar in size to that of the sexuals (Fig. 7b), whereas that of the 3N1 lineage is much narrower (Fig. 7a). The latter result is unexpected, since the 3N1 lineage has by far the broader geographic range of the two maternal lineages (Fig. 2b). These patterns weaken the case that parthenogenetic *H. binoei* have general purpose genotypes in comparison to their sexual progenitors.

Genetic evidence (Moritz, 1991; Moritz and Heideman, 1993) indicates that parthenogenetic lineages of *H. binoei* originated recently in western Australia. It is therefore important to consider the possibility that they are still expanding their range. The predicted spatial distributions from the logistic regression analyses (Fig. 9) encompass the current distribution of the sexual races but suggest the occurrence of environments suitable for parthenogenetic forms further to the east. Subsequent to these predictions, extensive searching in the eastern region predicted as suitable for parthenogens has revealed only sexual forms (CA6 and EA6), thus further eastward expansion of parthenogenetic forms may be possible if there are no geographic barriers to dispersal. In this context, it is possible that the 'channel country' – grassland-dominated drainages from southwestern Queensland to the Lake Eyre basin in northeast South Australia – together with the arid Simpson Desert in southeast Northern Territory, represents such a barrier, at least for the 3N1 and A clones (Figs 9 and 10). If eastward expansion does continue, it will be interesting to observe the fate of the eastern populations of the CA6 race, since it is possible that the disjunct distribution of this sexual race has resulted from displacement by parthenogenetic forms (Fig. 1).

Since parthenogenetic *H. binoei* must have arisen at the contact between the SM6 and CA6 sexual races, most likely in western Australia, it is striking how little, if any, northward

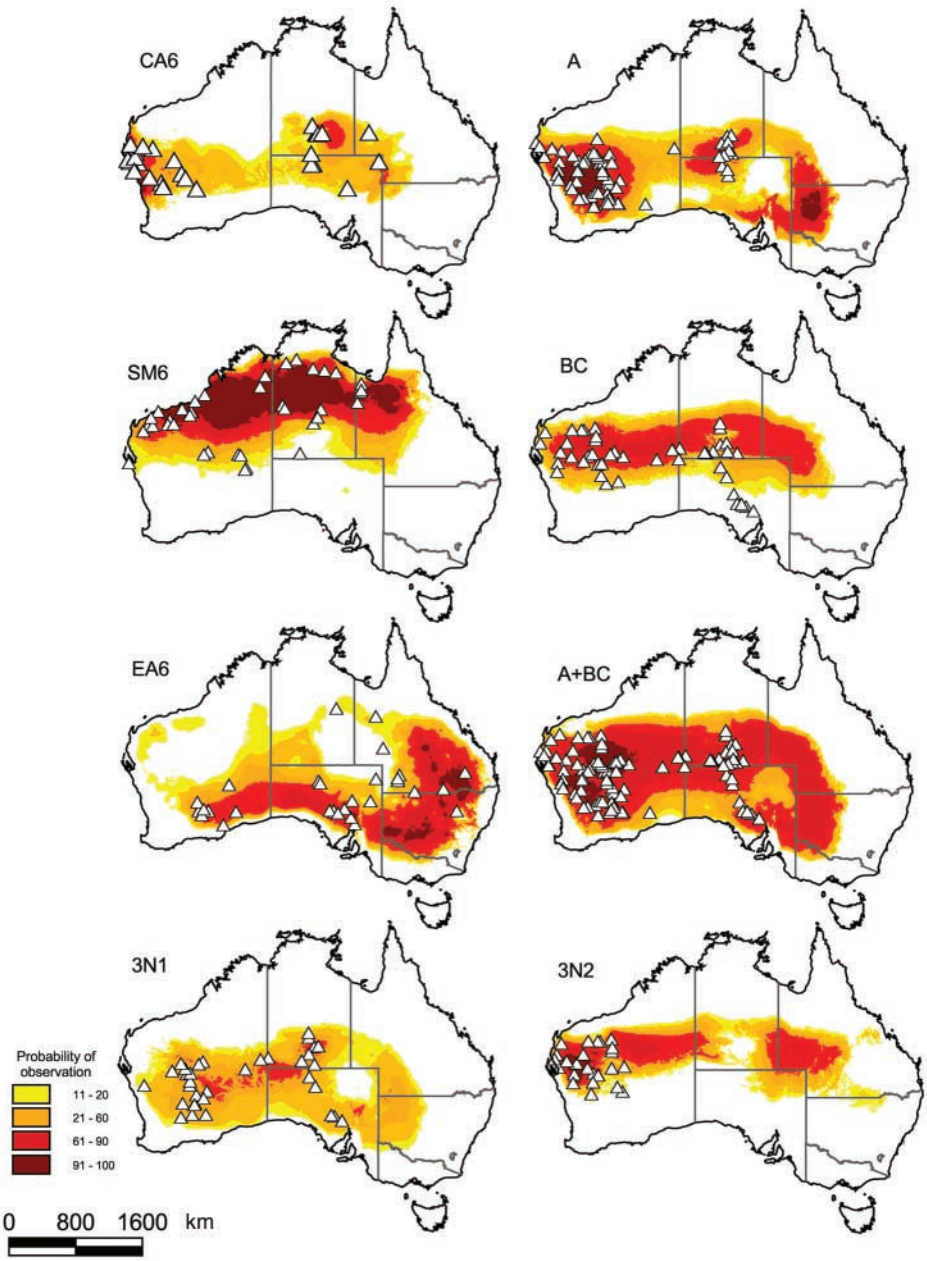

Fig. 9. Predicted distributions of the various sexual and parthenogenetic forms of *Heteronotia binoei* based on logistic regression models of probability of occurrence as a function of six climatic variables: annual temperature, annual rainfall, annual relative humidity, seasonality of temperature, 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.

spread has occurred despite considerable eastward and southward spread (Fig. 2). Very little northward expansion was predicted for parthenogenetic *H. binoei* by the distributional modelling (Fig. 9). Moreover, despite the tendency described above for parthenogenetic *H. binoei* to be biased in their environmental niches towards those sexual taxa to which their nuclear genomes are biased, overall they are biased towards the climatic environment of the CA6 sexual race. This is apparent in multidimensional space (Figs 6b, 7) as well as in their actual (Figs 1, 2) and predicted (Fig. 9) spatial distributions. There are several possible reasons for this pattern, including direct interactions with the SM6 sexual race such as destabilizing hybridization (Lynch, 1984). Sperm have been found in the oviducts of wild-caught parthenogenetic females from regions of overlap with the EA6 and CA6 sexual races (Whittier *et al.*, 1994) and there are occasional cases of apparently sterile tetraploid parthenogens resulting from matings with CA6, SM6 and possibly also EA6 males (Moritz, 1984).

Alternatively, the distribution of parthenogenetic *H. binoei* may be limited by more indirect processes associated with general environmental transitions. For instance, the northern boundary of the parthenogenetic *H. binoei* roughly corresponds to a habitat transition from mulga (*Acacia aneura*) dominated woodland to spinifex (*Triodia* spp.) sand plains and semi-arid woodland (Fig. 10). In fact, there is good correspondence generally between the distribution of mulga woodland and the distributions of parthenogenetic *H. binoei* together with the EA6 and CA6 sexual races (Fig. 10). Nix and Austin (1973) noted that mulga predominates where rainfall is low and aseasonal and in this study we have shown that the distributions of *H. binoei* are also strongly associated with rainfall patterns,

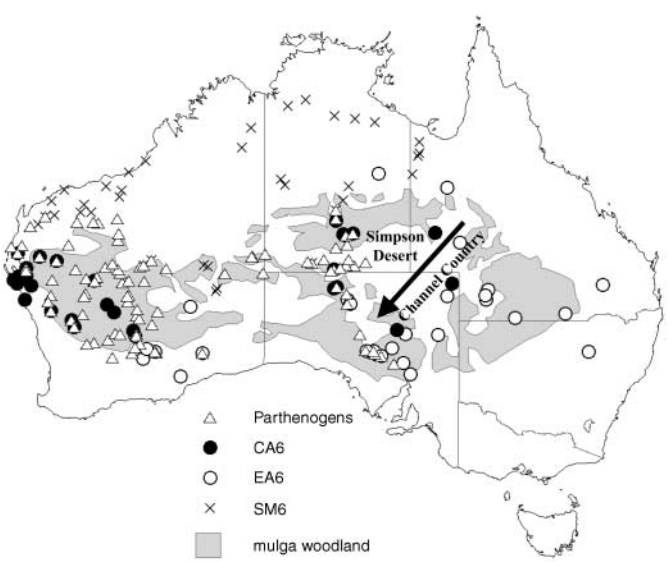

Fig. 10. Distributions of sexual and parthenogenetic *H. binoei* in relation to the distribution of mulga woodlands (mulga distribution based on Nix and Austin, 1973). The location of the Simpson Desert and the Channel Country, two potential barriers to the eastward spread of the parthenogens, are also indicated.

with the parthenogens occupying environments with the lowest rainfall and where rainfall is least seasonal and of relatively low annual variability (Fig. 4). Such predictably unfavourable environments have been called adversity selected (A-selected), as opposed to r-selected (unpredictable) or K-selected (predictably favourable) environments (Greenslade, 1982, 1983). The reduced importance of biotic interactions in such A-selected environments may reduce the hypothesized advantages of sexual reproduction (Glesener and Tilman, 1978; Hamilton *et al.*, 1990) while at the same time favour the fixed genotypes and enhanced ability to survive at low density conferred by parthenogenesis (Gerritson, 1980; Greenslade, 1982, 1983).

In summary, we have shown that the parthenogenetic races of *H. binoei*, although widespread, occupy a relatively restricted environmental niche characterized by persistently low rainfall. This is more consistent with explanations of geographic parthenogenesis that focus on the advantages of all-female reproduction rather than the existence of intermediate or general purpose genotypes. However, we also find evidence that the evolution of triploidy through backcrossing with the parental sexual forms has biased the environmental associations of the parthenogenetic forms towards those of the sexual races to which their genomes are biased and produced evidence consistent with the frozen-niche variation hypothesis. An important focus for future investigations is to assess the potential roles of destabilizing hybridization and climatic transitions as factors limiting the distribution of parthenogenetic forms in the northern part of their range.

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