Increased Capacity for Sustained Locomotion at Low Temperature in Parthenogenetic Geckos of Hybrid Origin

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ABSTRACT

The evolution of parthenogenesis is typically associated with hybridization and polyploidy. These correlates of parthenogenesis may have important physiological consequences that need be taken into account in understanding the relative merits of sexual and parthenogenetic reproduction. We compared the thermal sensitivity of aerobically sustained locomotion in hybrid/triploid parthenogenetic races of the gecko *Heteronotia binoei* and their diploid sexual progenitors. Endurance times at low temperature (10°, 12.5°, and 15°C, 0.05 km h^{-1}) were significantly greater in parthenogenetic females than in sexual females. Comparison of oxygen consumption rates during sustained locomotion at increasing speeds (0.05, 0.10, 0.15, 0.20, 0.25, and 0.30 km h^{-1}, 25°C) indicated that parthenogenetic lizards have higher maximum oxygen consumption rates and maximum aerobic speeds than do female sexual geckos. In addition, parthenogenetic geckos showed greater levels of voluntary activity at 15°C than did sexual geckos, although this pattern appears strongest in comparison to male sexual forms. Parthenogenetic lineages of *Heteronotia* thus have an advantage over sexual lineages in being capable of greater aerobic activity. This result is opposite of that found in prior studies of parthenogenetic teiid lizards (genus *Cnemidophorus*) and highlights the idiosyncratic nature of phenotypic evolution in parthenogens of hybrid origin.

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Introduction

If the study of parthenogenetic organisms is to provide insight into the relative merit of different genetic systems, including sexual reproduction, we must understand the consequences of parthenogenesis on organismal performance. A most striking pattern regarding the phenomenon of parthenogenesis is its frequent correlation with hybridity and polyploidy. There is evidence that hybridization plays an important role in the origin of parthenogenesis, particularly within the vertebrates (Wetherington et al. 1987; Moritz et al. 1989*a*). A recently formed parthenogenetic individual is also susceptible to increases in ploidy if it is mated by closely related males. Hybridization and polyploidy may also have important phenotypic consequences that could potentially affect the performance of a parthenogenetic organism and thus influence the persistence of a newly formed parthenogenetic lineage (Lynch 1984; Bierzychudek 1985; Arnold and Hodges 1995; Arnold 1997; Soltis and Soltis 2000).

The high heterozygosity of such organisms, for instance, may result in "hybrid vigour" (the "spontaneous heterosis hypothesis"; Lerner 1954; White 1970; Schultz 1971; Cole 1975; Wetherington et al. 1987; Hotz et al. 1999). This is suggested by the positive associations between allozyme heterozygosity and various fitness components in domestic and wild sexual organisms (e.g., Mitton and Grant 1984; Mitton 1993), by observations of increased thermal tolerance in unisexual Poeciliid fishes (Bulger and Schultz 1979), and by spontaneous heterosis in laboratory-synthesized hybridogenetic frogs (Hotz et al. 1999; but see Wetherington et al. 1987). Alternatively, incompatibilities among the newly combined genomes of hybrid parthenogens may lead to outbreeding depression and reduced performance. For instance, a study of five physiological performance variables in six lineages of parthenogenetic teiid lizards from the genus *Cnemidophorus* and their sexual progenitors revealed similar or lower performance in the parthenogens in comparison to sexual species (Cullum 1997).

In the latter study, locomotor endurance was the only trait to show a consistent pattern of reduced performance across all parthenogenetic lineages. To test the generality of this result, we compared parthenogenetic and sexual geckos of the *Heteronotia binoei* complex. In contrast to the condition in *Cnemidophorus*, we discovered that parthenogenetic *H. binoei* have an enhanced capacity for sustained locomotion relative to their sexual progenitors. The mechanistic basis for increased performance in parthenogenetic *H. binoei* appears to be an in-

creased maximum rate of oxygen consumption rather than a reduction in the minimum cost of transport.

Material and Methods

Study Species

Heteronotia are small (to 130 mm total length, 5 g), nocturnal lizards that are widely distributed throughout mainland Australia (Cogger 2000). The genetics and evolution of parthenogenesis in the *Heteronotia binoei* complex have been well studied (Moritz 1993 and references therein). Five distinct sexual taxa as well as triploid parthenogenetic races have been identified cytologically within the *H. binoei* complex. The parthenogenetic races originated through hybridization events between two of the sexual races (CA6 and SM6; Moritz 1983, 1984; Moritz et al. 1989*b*). Mitochondrial DNA analysis reveals two distinct maternal lineages: the 3N1 lineage, which has a CA6 maternal parent, and the 3N2 lineage, which has an SM6 maternal parent. Subsequent backcrossing within both of these maternal lineages of the original diploid hybrids with males of both progenitor species has produced two triploid races, one having a double dosage of the CA6 genome (form A: CA6/SM6/CA6) and the other having a double dosage of the SM6 genome (forms B and C, considered together in this article as form BC: CA6/SM6/SM6). In gross morphology, these two triploid forms resemble the sexual parental form for which they have a double genetic dosage, with form A having a banded back pattern like the CA6 sexual race and form BC having a speckled back pattern like the SM6 sexual race. We have thus used back pattern as a factor in our analyses to determine whether there are genome dosage effects on phenotypic traits independent of reproductive mode. Parthenogenesis in *H. binoei* is functionally apomictic since no recombination has been observed (Moritz 1984). The two parthenogenetic forms currently inhabit some of the driest regions of the Australian arid zone, where they are broadly sympatric with three of the sexual forms, including the two progenitor sexual races, CA6 and SM6.

Collection and Maintenance of Animals

The animals used in this study were collected from the vicinity of Alice Springs and Ti Tree in the Northern Territory between August 22 and September 4, 2000 (late winter/early spring; see Kearney and Shine 2005 for more details). They included four individuals of each of two triploid races (A and BC) of the 3N1 maternal lineage of parthenogen as well as four female individuals of each of the sexual progenitor species (CA6 and SM6). Six additional male specimens were used in the study of voluntary activity levels (three CA6, three SM6). Specimens were identified (parthenogen vs. sexual) using a combination of microsatellite marker and mtDNA sequence analysis (Strasburg 2004; Strasburg and Kearney, forthcoming).

We transferred specimens to Lewis and Clark College in March 2002, where they were housed in a controlled-environment room. We maintained the geckos in plastic containers (22 cm × 13 cm × 8 cm) with plastic half-pipes for shelter and a 3-cm-deep substrate of sand. We kept room temperature at 25°C, and Flexwatt heat strips, located under each cage, provided a maximum substrate temperature of 35°C. This created a 10°C thermal gradient within the shelters provided, encompassing the geckos' mean preferred temperature (≈31°C; Kearney and Shine 2004). Photoperiod was matched to that of the central Australian township of Alice Springs (133.87°E, 23.71°S). We fed each gecko four crickets each, three times per week. Calcium (Repcal) and vitamin (Herptavite) supplements were provided once a week. Water was always available.

Endurance and Oxygen Consumption Measurements

We exercised the geckos on a custom miniature treadmill-respirometer after they were fasted for 2 d. For overall comparisons of endurance, we ran all 16 female geckos at 0.05 km h^{-1} (slow walking pace, chosen on the basis of observations of undisturbed, foraging animals) in a random order at three different temperatures: 10°, 12.5°, and 15°C. These temperatures are close to the lower limit that has been observed in *H. binoei* foraging in the wild (14.2°C; K. Henle, unpublished data) and led to fatigue at the chosen speed within a reasonable amount of time (<2 h). Our treadmill was designed to allow rapid changes (<30 min) in air temperature within the treadmill chamber, achieved by rapidly pumping water from a temperature-controlled water bath (VWR Scientific Products by Polyscience, model 1166) through the aluminium body of the treadmill and through a canopy covering the treadmill chamber. This facilitated a random assignment of temperature treatments to the geckos. Geckos were placed in the treadmill chamber for a 30-min equilibration period, which was sufficient for the lizards to settle and for their body temperature to reach equilibrium. A plastic bristle brush provided an adversive stimulus at the rear of the chamber, while a dark refuge at the front of the chamber provided a positive stimulus. Bright lights aimed at the sides of the chamber also encouraged the geckos to walk at a steady pace. Before measurement, we had each lizard do numerous practice trials on the treadmill. Endurance was measured as the amount of time a lizard could walk continuously on the treadmill at a given temperature, and trials were terminated once an animal repeatedly bumped against the brush, struggled, or refused to walk for more than 10 s.

We examined the relationship between oxygen consumption ($\dot{V}O_2$) and running speed for a subset of the individuals used in the endurance trials, following the procedures of Autumn et al. (1999). The geckos used included two individuals of each chromosome race of parthenogen (A and BC) as well as two individuals of each of the sexual progenitor species (CA6 and SM6). Fasted lizards were run as described above for the endurance trials, but air temperature was kept at 25°C, and lizards

were run at five different speeds (0.05, 0.10, 0.15, 0.20, 0.25, and 0.30 km h^{-1}). We chose 25°C for this study since this is close to the mean temperature at which *H. binoei* has been observed foraging in two independent studies (K. Henle, unpublished data: mean ± SE = 26.5 ± 0.632, $N = 53$, range = 14.2–36.5; E. Pianka, unpublished data: mean ± SE = 26.1 ± 1.060, $N = 24$, range = 18.4–35.0) and allowed sufficient deflections of O_2 concentration in the chamber. Outside air from a prefilled bladder was drawn into the chamber at 90 mL min^{-1} after passing through a filter composed of Drierite and Ascarite layers to remove H_2O and CO_2. The oxygen concentration was monitored by an Oxzilla Differential O_2 analyzer (Sable Systems) interfaced with a personal computer (PowerMac G3, Apple) and data acquisition hardware (NBMIO-16 Board, National Instruments) and software (LabVIEW version 5.1, National Instruments). The precision of the O_2 analyzer was ±0.0001%, whereas the deflections used for measurements were greater than 0.001%. The sample rate was 2 Hz. After obtaining an initial measurement of resting metabolic rate ($\dot{V}o_{2\,rest}$), which was recorded during the lizards' equilibration period in the chamber, we ran lizards at the speeds noted above and determined the steady state $\dot{V}o_2$ as the average of the final 3 min of at least 6 min of continuous locomotion. The first three speeds were usually included in the first trial, beginning at 0.05 km h^{-1} and gradually stepping up to 0.15 km h^{-1}. Lizards were tested at the highest three speeds (0.20, 0.25, and 0.30 km h^{-1}), one speed per trial, during subsequent trials. Each lizard was rested for at least a day between trials.

The relationship between aerobically submaximal $\dot{V}o_2$ and running speed is typically described by a linear equation (Bennett 1982; Gatten et al. 1992),

$$\dot{V}o_2 = y_0 + C_{min} \times \text{speed},$$

where y_0 is the y-intercept of the $\dot{V}o_2$ versus speed curve, or idling cost, and C_{min} is the slope. C_{min} is defined as the amount of energy necessary to move 1 g of body mass a distance of 1 km, and it represents the fuel economy of an animal. We defined the maximum rate of oxygen consumption ($\dot{V}o_{2\,max}$) for each individual as the mean $\dot{V}o_2$ attained when an increase in speed resulted in no significant increase in $\dot{V}o_2$. The speed at which $\dot{V}o_{2\,max}$ is attained is the maximum aerobic speed (MAS). To determine the MAS for each individual, we calculated linear regressions of $\dot{V}o_2$ versus speed for the three lowest speeds and then compared the fit of the regression as we sequentially included the higher speeds. We selected MAS as the speed above which the fit of the regression (r^2) decreased.

Measurement of Voluntary Activity Levels

To determine whether parthenogenetic geckos were capable of greater levels of voluntary activity at low temperature, as suggested by our results on endurance and energetics, we recorded activity levels of parthenogenetic and sexual lizards in a laboratory setting. For this experiment, we used six parthenogenetic (three form A, three form BC) and six sexual female lizards (three CA6, three SM6) from the endurance study described above and an additional six male sexual lizards (three CA6, three SM6). The experimental arena consisted of a 300 × 210 × 180-mm open plastic container with a sand substrate and a plastic half-pipe placed at one end of the container as a retreat site. The container was placed in a temperature-controlled cabinet set at 15°C with fluorescent lighting set to a 12L : 12D photoperiod. A motion-sensitive video camera (Irez USB KritterCam, GlobalMedia Group, Scottsdale, AZ) was mounted above the container and was controlled by a PC computer using motion detection software (iVISTA VideoWebPage 3.1, San Diego, CA). Since *H. binoei* is nocturnal, it was necessary to devise a means of recording activity at low light levels. One hour before laboratory nighttime, we dusted individual lizards with fluorescent pigment (on the anterior portion of the head and the dorsal surface and tail) before placing them into the arena. An ultraviolet light provided dim illumination during the nighttime and caused the powder on the lizard to fluoresce brightly, thus enabling the video camera to detect the motion of the lizard despite the low light level. If motion was detected, the motion detection software executed a custom-written visual basic program that recorded the date and time. If the lizard was moving continuously, the software registered motion at approximately 15-s intervals. We used the number of such motion events as an index of activity level. We directly observed the behaviour for the first half of each night to ensure that the motion detection system was accurately recording activity.

Results

Treadmill Endurance

We analyzed treadmill endurance data using repeated-measures ANCOVA, with body mass as a covariate, reproductive mode and back pattern as factors, and body temperature (10°, 12.5°, or 15°C) as the repeated measure (Table 1). Endurance and mass were log transformed before analysis to improve the normality of the data. This analysis revealed significant effects of reproductive mode and body temperature, with no interactions between any of the factors and body mass as a significant (negative) covariate (Table 1). Endurance increased with temperature, ranging from between 0.5 and 7 min at 10°C to between 11 and 84 min at 15°C (Fig. 1). Moreover, at each temperature, the parthenogenetic individuals exhibited consistently greater endurance than sexuals, with a mean difference in running time of up to 16 min at 15°C (Fig. 1).

Table 1: Results of repeated-measures ANCOVA on endurance, with reproductive mode and back pattern as factors, natural log-transformed body mass as a covariate, and temperature as the repeated measure

Source	df	MS	*F*	*P*	*G-G*	*H-F*
Between subjects:						
Reproductive mode	1	.573	7.637	.018		
Back pattern	1	.023	.309	.590		
Reproductive mode × back pattern	1	.009	.119	.737		
Log mass	1	.420	5.594	.038		
Error	11	.075				
Within subjects:						
Temperature	2	.163	4.391	.025	.042	.025
Temperature × reproductive mode	2	.014	.373	.693	.620	.693
Temperature × back pattern	2	.047	1.259	.304	.297	.304
Temperature × reproductive mode × back pattern	2	.050	1.352	.279	.277	.279
Temperature × log mass	2	.045	1.227	.313	.304	.313
Error	22	.037				

Note. Greenhouse-Geisser $\epsilon = 0.697$; Huynh-Feldt $\epsilon = 1.000$.

Voluntary Activity Levels at Low Temperature

Upon introducing lizards into the experimental arena where we measured voluntary activity levels, all lizards immediately took shelter in the retreat site and emerged only once the bright fluorescent lights had switched off. All lizards ceased activity once the lights switched back on again at the end of the night. Two-factor ANOVA of natural log-transformed activity levels of lizards, as recorded by the motion detection software, with sex (i.e., sexual male, sexual female, or parthenogenetic female) and back pattern as factors, revealed a significant effect of sex only (sex effect: $F_{2,12} = 4.602$, $P = 0.033$; back pattern effect: $F_{1,12} = 2.182$, $P = 0.165$; interaction: $F_{2,12} = 1.808$, $P = 0.206$). Post hoc pairwise comparisons within sex were ambiguous, with a significant difference only between sexual males and parthenogenetic females (sexual male × parthenogen: $P = 0.026$; sexual male × sexual female: $P = 0.291$; sexual female × parthenogen: $P = 0.347$). When male and female sexual lizards (which did not differ significantly from each other) were pooled and compared with the parthenogens, there was a significant effect of reproductive mode ($F_{1,14} = 5.352$, $P = 0.036$), with parthenogens showing a higher level of activity than sexuals (means ± SE for untransformed data: sexuals = 113.08 ± 41.78, range = 12–484; parthenogens = 288.0 ± 108.56, range = 82–766). There was no effect, however, of back pattern ($F_{1,14} = 1.034$, $P = 0.326$), nor was there an interaction between back pattern and reproductive mode ($F_{1,14} = 0.466$, $P = 0.506$).

Energetics of Locomotion

The results of our analyses on the energetics of locomotion in *Heteronotia binoei* are summarised in Table 2. The C_{min} falls within the range of values previously calculated for geckos (Autumn et al. 1999) and was not significantly different between parthenogenetic and sexual lizards ($F_{1,5} = 0.133$, $P = 0.723$, with body mass included as a covariate). (In addition, there were no differences in $\dot{V}O_{2\,rest}$ [$F_{1,5} = 0.128$, $P = 0.735$] or y_0 [$F_{1,5} = 0.046$, $P = 0.838$].) The $\dot{V}O_{2\,max}$ was 17% higher in parthenogenetic than sexual *H. binoei* ($F_{1,5} = 4.649$, one-tailed $P = 0.042$; Table 2; Fig. 2*a*). This was a one-tailed test, given our prior knowledge that endurance was higher in the parthenogens than in the sexuals. In the latter analysis, mass was included as a covariate but was not statistically significant ($P = 0.656$). When the analysis was rerun without mass as a covariate, the effect of reproductive mode was strengthened ($F_{1,6} = 7.056$, one-tailed $P = 0.019$). For sexual lizards, $\dot{V}O_{2\,max}$ was attained at speeds of approximately 0.15 km h^{-1}, while for parthenogens, $\dot{V}O_{2\,max}$ was attained at speeds of approximately 0.23 km h^{-1} (Fig. 2*a*). At speeds faster than the MAS determined for each group, the lizards fatigued in fewer than 8 min (Fig. 2*b*). Indeed, parthenogenetic lizards ran significantly longer than sexuals at 0.25 km h^{-1} (ANCOVA: reproductive mode: $F_{1,5} = 8.020$, $P = 0.037$; body mass: $F_{1,5} = 3.110$, $P = 0.138$; Fig. 2*b*).

Discussion

The major finding of our study was an enhanced capacity for sustained locomotion in parthenogenetic lineages of *Heteronotia binoei* compared with that of the sexual races that gave rise to them, at least in the lineages we have sampled. This result was apparent in two respects. First, parthenogenetic *H. binoei* exhibit greater treadmill endurance capacity. Parthenogenetic *H. binoei* can sustain locomotion on a treadmill for

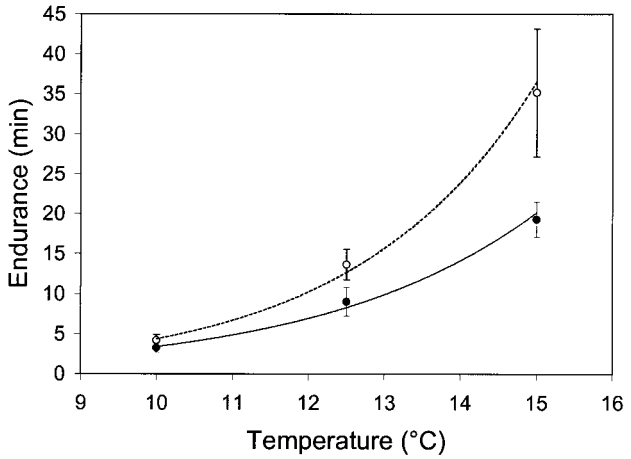

Figure 1. Mean (±SE) locomotor endurance at low speed (0.05 km h^{-1}) and low temperature (10°, 12.5°, and 15°C) for sexual (*filled circles*) and parthenogenetic (*open circles*) forms of *Heteronotia binoei*.

approximately 1.5 times as long as their sexual progenitors over a range of low temperatures. Second, parthenogenetic *H. binoei* appear to be more active at low temperature than the sexual forms (males in particular), suggesting that enhanced endurance capacity may be utilized voluntarily by the geckos.

The evolution of enhanced endurance may provide a strong selective advantage to organisms employing a widely foraging strategy as opposed to a sit-and-wait strategy when searching for food (or mates; Pianka 1966; Huey and Pianka 1981). Moreover, there may be direct trade-offs between these two strategies (Huey and Pianka 1981). Field observations of *H. binoei* indicate that individuals of this species forage widely (Henle 1990); thus, there is good reason to expect that enhanced endurance capacity would be advantageous. The enhanced endurance of parthenogenetic *H. binoei* would allow a greater distance to be covered at a given temperature and would also enable activity at lower body temperatures than otherwise possible. This suggests that the activity patterns and times of parthenogenetic and sexual *H. binoei* may differ, reducing the extent of niche overlap and thus competition between them. However, the voluntary lower limit chosen in a thermal gradient by parthenogenetic *H. binoei* is similar to females of the SM6 race and higher than females of the CA6 race (Kearney and Shine 2004), suggesting other factors may influence the lower thermal limit to foraging. The remainder of our discussion focuses on possible proximate physiological and genetic bases for enhanced endurance in parthenogenetic *H. binoei*.

Physiological Basis for Enhanced Endurance in Parthenogenetic H. binoei

Endurance capacity (time to fatigue at a steady speed) in ectothermic vertebrates has been well studied from an energetic perspective in both diurnal and nocturnal species (e.g., Bennett 1982; Gatten et al. 1992 and references therein; Autumn et al. 1999). This provides a mechanistic basis from which to interpret the patterns we observed in *H. binoei*. Endurance capacity is dependent on temperature and body size (Bennett 1982), but at a given body size and temperature, the MAS (Gatten et al. 1992) is the principle determinant of endurance. The MAS is the slowest speed at which the maximum rate of aerobic metabolism (as measured by the maximum rate of oxygen consumption $\dot{V}O_{2\,max}$) is attained. At speeds below the MAS, locomotion is fueled primarily by aerobic metabolism and can be sustained for long periods of time (minutes to hours). At speeds above the MAS, locomotion is fueled primarily by accelerated glycolysis, and fatigue occurs rapidly (seconds to minutes). The MAS is a linear function of both the $\dot{V}O_{2\,max}$ and fuel economy (the minimum cost of locomotion, C_{min}). Thus, parthenogenetic *H. binoei* may achieve an increase in MAS, and hence endurance, through an increase in $\dot{V}O_{2\,max}$, a decrease in C_{min}, or both.

Because $\dot{V}O_{2\,max}$ is highly temperature sensitive, a nocturnal lizard such as *H. binoei* faces a considerable thermal handicap to its capacity for sustained locomotion (Autumn et al. 1999). For example, field-active *H. binoei* have body temperatures as low as 14.2°C (K. Henle, unpublished data), which is well below their own preferred body temperature (≈31°C; M. Kearney, unpublished data) and the thermal physiological optima of most diurnal and nocturnal lizards (≈35°C or greater; Huey et al. 1989; Autumn et al. 1994, 1997, 1999; Autumn and Denardo 1995). As a group, nocturnal geckos generally have a reduced C_{min} in comparison to diurnal lizards, which partially offsets the thermal handicap imposed by nocturnal activity (Autumn et al. 1994, 1997, 1999). In the case of *H. binoei*, our energetics data suggest that there is no difference in C_{min} between parthenogenetic and sexual lineages but that parthenogens have an elevated maximum aerobic capacity ($\dot{V}O_{2\,max}$), leading to a 50% increase in MAS. Thus, the mechanistic basis for increased endurance in the parthenogenetic lineages of *H. binoei* over the sexual lineages appears to be an elevated maximum aerobic capacity.

Genetic Basis for Enhanced Endurance in Parthenogenetic H. binoei

What kind of genetic changes associated with the origin of parthenogenesis in *H. binoei* are likely to have led to the concurrent evolution of an enhanced $\dot{V}O_{2\,max}$ and consequent increased capacity for sustained locomotion? Since parthenogenetic *H. binoei* are of hybrid origin and are triploid, their enhanced endurance may be a direct reflection of either of these genetic phenomena. We discuss each of these possibilities in turn.

First, the extremely high heterozygosity (H) of parthenogenetic *H. binoei* ($H = 0.32$; Moritz et al. 1989*b*), which stems

Table 2: Summary statistics of energetics data per individual lizard tested

Animal No.	Reproductive Mode	Back Pattern	Mass (g)	$\dot{V}o_{2\,rest}$ (mL O_2 g^{-1} h^{-1})	y_0 (mL O_2 g^{-1} h^{-1})	C_{min} (mL O_2 g^{-1} km^{-1})	r^2	$\frac{y_0}{\dot{V}o_{2\,rest}}$	$\dot{V}o_{2\,max}$ (mL O_2 g^{-1} h^{-1})	$\frac{\dot{V}o_{2\,max}}{\dot{V}o_{2\,rest}}$	$\dot{V}o_{2\,max} - \dot{V}o_{2\,rest}$ (mL O_2 g^{-1} h^{-1})	Maximum Aerobic Speed (km h^{-1})
1	Sexual	Banded	2.04	.122	.121	1.180	.927	.988	.289	2.364	.167	.15
2	Sexual	Banded	2.59	.071	.179	1.349	.993	2.526	.384	5.430	.313	.15
3	Sexual	Speckled	3.27	.076	.152	1.179	.997	1.991	.327	4.292	.251	.15
4	Sexual	Speckled	2.69	.049	.142	1.217	.982	2.933	.331	6.834	.283	.15
Mean			2.65	.079	.148	1.231	.975	2.110	.333	4.730	.253	.15
5	Parthenogen	Banded	3.21	.077	.122	1.187	.949	1.595	.407	5.315	.330	.25
6	Parthenogen	Banded	2.35	.067	.081	1.628	.999	1.209	.406	6.042	.339	.20
7	Parthenogen	Speckled	3.40	.176	.282	.501	.935	1.604	.386	2.196	.210	.20
8	Parthenogen	Speckled	2.87	.068	.168	.760	.974	2.480	.366	5.387	.298	.25
Mean			2.96	.097	.163	1.019	.964	1.722	.391	4.735	.294	.23

Note. See text for definitions of terms.

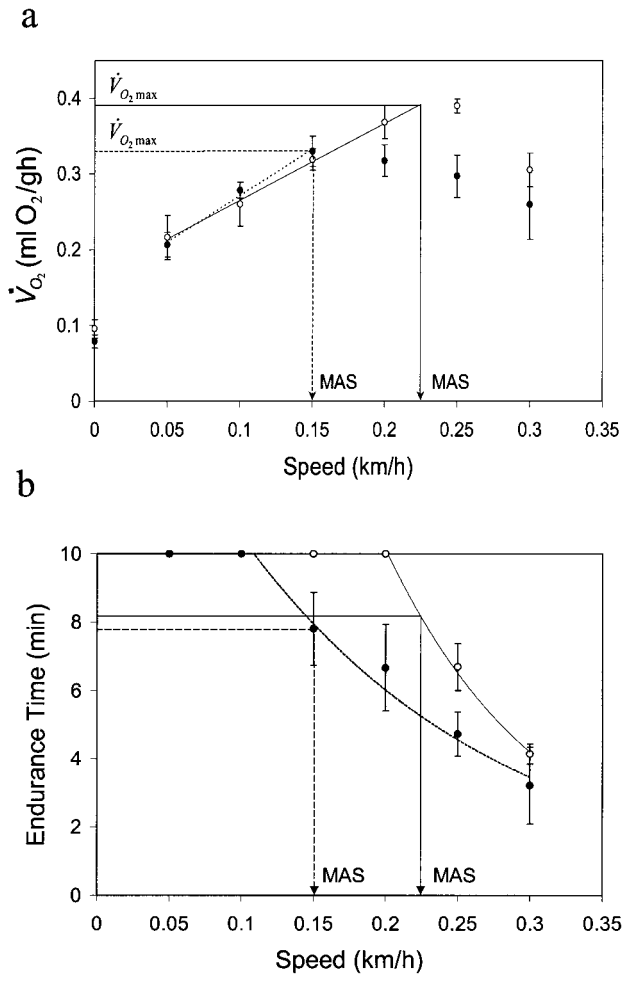

Figure 2. Relationship between running speed and (*a*) steady state oxygen consumption rate ($\dot{V}O_2$) and (*b*) endurance for sexual (*filled circles*) and parthenogenetic (*open circles*) forms of *Heteronotia binoei*. Maximum oxygen consumption rate ($\dot{V}O_{2\,max}$) and maximum aerobic speed (*MAS*) are indicated.

from their hybrid origin, may confer a degree of heterosis, or hybrid vigor (White 1970; Schultz 1971; Cole 1975; Mitton and Grant 1984; Wetherington et al. 1987). This may be true of *H. binoei* with respect to endurance. However, it is clearly not the case for parthenogenetic organisms in general; the same trait shows the opposite pattern in six independently derived hybrid lineages of parthenogenetic teiid lizards of the genus *Cnemidophorus* (Cullum 1997). Sexual hybrids of *Cnemidophorus* also show a weak trend for reduced endurance capacity (Dohm et al. 1998), which suggests that it is hybridization per se that leads to reduced endurance in the parthenogenetic forms. The different patterns with respect to endurance in *Cnemidophorus* and *Heteronotia* cannot be explained through different foraging strategies since *Cnemidophorus* (also known as racerunners) are well known to be extremely active foragers (Pianka 1966).

Second, polyploidy often leads to an increase in cell size (Stebbins 1950; Szarski 1970). This may have implications for metabolic processes, although it has been suggested that polyploidy would lead to a reduction, rather than an increase, in metabolic rates (Szarski 1983). In *Cnemidophorus*, three of the six parthenogenetic lineages examined were triploid while the other three were diploid, but all showed a tendency for reduced locomotor endurance (Cullum 1997). Moreover, studies of metabolic rates in diploid and tetraploid frogs, both at rest and during forced locomotion, showed no detectable differences between ploidy levels (Kamel et al. 1985). Thus, it appears unlikely that hybridization or polyploidy lead to enhanced locomotor endurance in general. Instead, the exact nature of the effects may vary on a case-by-case basis, depending on the idiosyncratic interactions between the newly combined genomes. Recent experimental results on allopolyploid plants support this contention, at least with respect to gene expression (Adams et al. 2003; Otto 2003).

Parthenogenetic *H. binoei* evolved through repetitive hybridization events that generated a diverse array of clones (Moritz et al. 1989*b*). Thus, an alternative explanation to the spontaneous evolution of high endurance in parthenogenetic *H. binoei* through hybridization or polyploidy is that selection favoured only those clones with high endurance, despite an originally diverse range of endurance capacities in the original clones. High endurance appears to have evolved in this manner in clones of the gynogenetic fish *Poeciliopsis* 2 *monacha-lucida*; the two clones examined had greater swimming endurance than the maternal sexual progenitor *P. monacha*, although one clone had better endurance than the other clone (Vrijenhoek and Pfeiler 1997). This hypothesis could be tested directly in *H. binoei* if it proves possible to create synthetic parthenogenetic hybrids in the laboratory, as has been achieved in unisexual fish (Wetherington et al. 1987), frogs (Hotz et al. 1999), and grasshoppers (White et al. 1977).

Conclusion

The evolution of parthenogenesis in vertebrates does not take place through a simple transition of the genetic system from sexual to asexual. Instead, it arises in association with hybridization, and very often with polyploidy, and significant phenotypic effects. Our study highlights the idiosyncratic nature of these phenotypic effects among disparate vertebrate taxa and even among families of the same order. In contrast to the association between the evolution of parthenogenesis and reduced locomotor endurance in teiid lizards of the genus *Cnemidophorus* (Cullum 1997), our study on gekkonid lizards of the genus *Heteronotia* shows an association between parthenogenesis and increased locomotor endurance that appeared to result from an increased maximum oxygen consumption rate. This casts doubt on the hypothesis that there is a general advantage or disadvantage incurred by hybridity or polyploidy

in the evolution of parthenogenesis. However, in both *Heteronotia* and *Cnemidophorus*, the result was novel phenotype with respect to the sexual progenitors. Such patterns emphasize the opportunity for the creation of genetic and ecological novelty that a hybrid origin of parthenogenesis presents. Such novelty may be a key contributor to the ecological success of parthenogenetic lineages derived via hybridization, at least in the short term.

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Literature Cited

Adams K.L., R. Cronn, R. Percifield, and J. Wendel. 2003. Genes duplicated by polyploidy show unequal contributions to the transcriptome and organ-specific reciprocal silencing. Proc Natl Acad Sci USA 100:4649–4654.

Arnold M.J. 1997. Natural Hybridization and Evolution. Oxford University Press, New York.

Arnold M.J. and S.A. Hodges. 1995. Are natural hybrids fit or unfit relative to their parents? Trends Ecol Evol 10:67–71.

Autumn K. and D.F. Denardo. 1995. Behavioral thermoregulation increases growth rate in a nocturnal lizard. J Herpetol 29:157–162.

Autumn K., C.T. Farley, M. Emshwiller, and R.J. Full. 1997. Low cost of locomotion in the banded gecko: a test of the nocturnality hypothesis. Physiol Zool 70:660–669.

Autumn K., D. Jindrich, D. Denardo, and R. Mueller. 1999. Locomotor performance at low temperature and the evolution of nocturnality in geckos. Evolution 53:580–599.

Autumn K., R.B. Weinstein, and R.J. Full. 1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. Physiol Zool 67:238–262.

Bennett A.F. 1982. The energetics of reptilian activity. Pp. 155–199 in C. Gans and F.H. Pough, eds. Biology of the Reptilia. Vol. 13. Academic Press, New York.

Bierzychudek P. 1985. Patterns in plant parthenogenesis. Experentia 41:1255–1264.

Bulger A.J. and R.J. Schultz. 1979. Heterosis and interclonal variation in thermal tolerance in unisexual fishes. Evolution 33:848–859.

Cogger H.G. 2000. Reptiles and Amphibians of Australia. 5th ed. Reed Books, Sydney.

Cole C.J. 1975. Evolution of parthenogenetic species of reptile. Pp. 340–355 in R. Reinboth, ed. Intersexuality in the Animal Kingdom. Springer, New York.

Cullum A. 1997. Comparisons of physiological performance in sexual and asexual whiptail lizards (genus *Cnemidophorus*): implications for the role of heterozygosity. Am Nat 150:24–47.

Dohm M.R., T.G.J. Garland, C.J. Cole, and C.R. Townsend. 1998. Physiological variation and allometry in western whiptail lizards (*Cnemidophours tigris*) from a transect across a persistent hybrid zone. Copeia 1998:1–13.

Gatten R.E., K. Miller, and R.J. Full. 1992. Energetics at rest and during locomotion. Pp. 314–377 in M.E. Feder and W.W. Burggren, eds. Environmental Physiology of the Amphibians. University of Chicago Press, Chicago.

Henle K. 1990. Population ecology and life history of three terrestrial geckos in arid Australia. Copeia 1990:759–781.

Hotz H., R.D. Semlitsch, E. Gutmann, G.-D. Guex, and P. Beerli. 1999. Spontaneous heterosis in larval life-history traits of hemiclonal frog hybrids. Proc Natl Acad Sci USA 96:2171–2176.

Huey R.B., P.H. Niewiarowski, J. Kaufmann, and J.C. Herron. 1989. Thermal biology of nocturnal ectotherms: is sprint performance of geckos maximal at low body temperatures? Physiol Zool 62:488–504.

Huey R.B. and E.R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.

Kamel S., J.E. Marsden, and F.H. Pough. 1985. Diploid and tetraploid grey treefrogs (*Hyla chrysoscelis* and *Hyla versicolor*) have similar metabolic rates. Comp Biochem Physiol 82A:217–220.

Kearney M. and R. Shine. 2004. Morphological and physiological correlates of hybrid parthenogenesis. Am Nat 164: 803–813.

———. 2005. Lower fecundity in parthenogenetic geckos than sexual relatives in the Australian arid zone. J Evol Biol 18: 609–618.

Lerner I.M. 1954. Genetic homeostasis. Olilver & Boyd, London.

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

Mitton J.B. 1993. Enzyme heterozygosity, metabolism, and developmental stability. Genetica 89:47–65.

Mitton J.B. and M.C. Grant. 1984. Associations among protein

heterozygosity, growth rate, and developmental homeostasis. Annu Rev Ecol Syst 15:479–499.

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

———. 1984. The origin and evolution of parthenogenesis in *Heteronotia binoei* (Gekkonidae) I. Chromosome banding studies. Chromosoma 89:151–162.

———. 1993. The origin and evolution of parthenogenesis in the *Heteronotia binoei* complex: synthesis. Genetica 90:269–280.

Moritz C., W.M. Brown, L.D. Densmore, J.W. Wright, D. Vyas, S. Donnellan, M. Adams, and P. Baverstock. 1989*a*. Genetic diversity and the dynamics of hybrid parthenogenesis in *Cnemidophorus* (Teiidae) and *Heteronotia* (Gekkonidae). Pp. 87–112 in R.M. Dawley and J.P. Bogart, eds. Evolution and Ecology of Unisexual Vertebrates. New York State Museum, Albany.

Moritz C., S. Donnellan, M. Adams, and P.R. Baverstock. 1989*b*. The origin and evolution of parthenogenesis in *Heteronotia binoei* (Gekkonidae): extensive genotypic diversity among parthenogens. Evolution 43:994–1003.

Otto S.P. 2003. In polyploids, one plus one does not equal two. Trends Ecol Evol 18:431–433.

Pianka E.R. 1966. Convexity, desert lizards, and spatial heterogeneity. Ecology 47:1055–1059.

Schultz R.J. 1971. Special adaptive problems associated with unisexual fishes. Am Zool 11:351–360.

Soltis P.S. and D.E. Soltis. 2000. The role of genetic and genomic attributes in the success of polyploids. Proc Natl Acad Sci USA 97:7051–7057.

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

Strasburg J.L. 2004. Eight highly polymorphic microsatellite loci for the Australian gecko *Heteronotia binoei*. Mol Ecol Notes 4:456–458.

Strasburg J.L. and M. Kearney. Forthcoming. Phylogeography of sexual *Heteronotia binoei* (Gekkonidae) in the Australian arid zone: climatic cycling and repetitive hybridization. Mol Ecol.

Szarski H. 1970. Changes in the amount of DNA in cell nuclei during vertebrate evolution. Nature 226:651–652.

———. 1983. Cell size and the concept of wasteful and frugal evolutionary strategies. J Theor Biol 105:201–209.

Vrijenhoek R.C. and E. Pfeiler. 1997. Differential survival of sexual and asexual *Poeciliopsis* during environmental stress. Evolution 51:1593–1600.

Wetherington J.D., K.E. Kotora, and R.C. Vrijenhoek. 1987. A test of the spontaneous heterosis hypothesis for unisexual vertebrates. Evolution 41:721–731.

White M.J.D. 1970. Heterozygosity and genetic polymorphism in parthenogenetic animals. Pp. 237–262 in M.K. Hecht and W.C. Steere, eds. Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky. Elsevier North-Holland, Amsterdam.

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