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Heterozygosity and fitness in a California population of the labyrinth spider *Metepeira ventura* (Araneae, Araneidae)

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Abstract. The relationship between individual heterozygosity and characteristics likely to be associated with fitness was investigated in the labyrinth spider *Metepeira ventura*. Adult females and their egg sacs were collected at a coastal site in southern California, and three measures of bodily condition (carapace width, weight, residual index) and six measures of reproductive output (number of egg sacs, variation in egg number among sacs [coefficient of variation], total number of eggs, mean eggs/sac, mean eggs/sac divided by carapace width, mean eggs/sac divided by weight) were determined for each spider. The sample was polymorphic at three allozyme loci that were in Hardy–Weinberg equilibrium, and individual females were heterozygous at up to two of the three loci, forming three heterozygosity classes (0, 1, and 2). None of the bodily condition measures were significantly related to the number of heterozygous loci, while four of the reproductive output estimators (total number of eggs, mean eggs/sac, mean eggs/sac divided by carapace width, mean eggs/sac divided by weight) were significantly influenced by heterozygosity. In each significant case, values for class 2 females were less than those for class 0 and 1 females, whose values were usually more similar. Thus, while female bodily condition was comparable among classes, the most heterozygous females produced fewer total eggs and eggs per sac than their less heterozygous peers. The fact that females of *M. ventura* engage in a reproductive investment-number trade-off suggests that high-variability and low-variability females may be pursuing distinct reproductive strategies in the wild, with more heterozygous females being *K*-selected (smaller clutches, heavier eggs) and more homozygous females being *r*-selected (larger clutches, lighter eggs). Further investigation will be needed to assess more fully the fitness value of heterozygosity in *M. ventura*.

Additional key words: allozymes, spider reproduction

Considerable evidence from natural populations indicates that more heterozygous individuals are characterized by higher fitness than more homozygous individuals (Wang et al. 2002; Reed & Frankham 2003). Because measuring Darwinian fitness (lifetime reproductive success) in the wild is quite difficult (Endler 1986), correlates of fitness (e.g., growth rate, survival, fecundity) are more commonly esti-

mated in such studies (Slate & Pemberton 2002). The relationship between allozyme heterozygosity and one or more fitness estimators has often been the focus of investigation. The majority of these studies have shown that organisms that are heterozygous at several allozyme loci are larger, grow faster, live longer, and are more fecund than more homozygous conspecifics (e.g., Fitzsimmons et al. 1995; Hildner et al. 2003). While negative results are probably underreported in the literature (David 1998), meta-analysis has shown that positive associations between heterozygosity and fitness components are genuine and

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reasonably common (Britten 1996), although the genetic basis for these relationships remains unclear (Hansson & Westerberg 2002).

Spiders are perhaps the fifth largest animal order, with over 34,000 described species (Pechenik 2005), but have seldom been the subject of heterozygosity–fitness correlation studies. Among the cooperative spiders, species whose members share in nest building, prey capture, feeding, and brood care (Avilés 1997), *Agelena consociata* Denis 1965 (Agelenidae) has been found to have populations that contain remarkably few heterozygotes (mean $H_{OBS} = 1.8\%$), reflecting continual mating within colonies and limited inter-colony exchange (Riechert et al. 1986). Colonies of *A. consociata* are also minimally resistant to disease (Krafft 1970; Riechert & Roeloffs 1993). The extreme genetic homogeneity of such units likely increases their vulnerability to environmental challenges and, indeed, colony turnover in the wild is high (Riechert & Roeloffs 1993). Minimal heterozygosity and high colony turnover have also been reported for another cooperative spider, *Anelosimus eximius* Keyserling 1884 (Theridiidae) (Smith & Hagen 1996). Among the far more numerous non-social spiders, those that live as solitary individuals as adults, Ramirez & Saunders (1999) found that spiders from more heterozygous populations in two undescribed species of the coastal dune spider *Lutica* Marx 1891 (Zodariidae) were generally fatter than individuals from less heterozygous populations, presumably reflecting greater success in the acquisition and/or processing of dietary resources by more heterozygous individuals. While the results of these studies are all consistent with a positive relationship between heterozygosity and fitness, investigations of many more spider taxa will be needed to assess the potential generality of such a relationship for arachnids, given their immense biodiversity (Ramirez & Saunders 1999). In particular, studies that examine the relationship between individual heterozygosity (number of heterozygous loci per individual) and fitness measures would complement population-level studies such as those reviewed here and would likely lead to a better understanding of potential heterozygosity–fitness correlations (e.g., Wang et al. 2002).

The small orb weaver *Metepeira* F.O.P.-Cambridge 1903 is a distinctly American spider, with a distribution extending from Alaska to Tierra del Fuego (Levi 1977; Piel 2001). This arachnid spins an orb-web in low vegetation, with an adjacent barrier web slightly to the side and above, wherein a cone-shaped retreat is placed. With adult females, egg sacs are placed within the retreat, which becomes progressively longer as egg sacs are added one by one

over time, with the most recent on the bottom (Comstock 1948; Piel 2001; unpubl. data). The preferred web site is typically unobstructed, rigid vegetation, such as dead or leafless branches, cactus, signposts, or fences (e.g., Uetz & Burgess 1979). Members of *Metepeira* have an annual life cycle; spiderlings emerge in spring and adults may be collected from summer to early fall (Levi 1977). In this study, we present the results of an analysis of the relationship between individual heterozygosity and characteristics likely to be associated with female fitness in *Metepeira ventura* Chamberlin & Ivie 1942, a species whose web sites are common on prickly-pear cacti (*Opuntia* Miller 1754 spp.) in southern California, especially near the coast (Ramirez & Fandino 1996; unpubl. data).

Methods

Sample collection

On September 1, 2003, we collected 84 adult females of *Metepeira ventura* and their egg sacs from a coastal hillside at Leo Carrillo State Park, Los Angeles County, California. The vegetation at this site consists of many small patches of *Opuntia*, intermixed with bushes and other vegetation. Web sites of *M. ventura* were primarily located in the cacti, consistent with prior observations (Ramirez & Fandino 1996). Individual females and their respective egg sacs were assigned unique identification numbers in the field, and the egg sacs were then preserved in alcohol pending subsequent examination. In the laboratory, carapace width (mm) and weight (mg) were determined for each live spider the day after collection, before storage at −85°C pending genetic analysis. Each spider's egg sacs were later opened, and the number of sacs and eggs per sac were recorded.

Fitness estimators

This study used a variety of fitness estimators. To assess a female's physiological state, three parameters of the female physique were measured—size (carapace width), weight, and body condition (residual index)—following the example of Danielson-François et al. (2002). Size and weight values were ln transformed, and the specific computational procedures of Jakob et al. (1996) were used to generate the residual index (residuals of body mass on body size), a non-destructive measure of body condition, for each spider. While the assessment of body condition (overall energy balance Speakman 2001) using the residual index has been a topic of considerable

debate (e.g., Jakob et al. 1996; Kotiaho 1999; Marshall et al. 1999; García-Berthou 2001; Green 2001; Schulte-Hostedde et al. 2001), Schulte-Hostedde et al. (2005) recently empirically re-validated the use of the residual index as a measure of body condition and found that it was superior to major alternatives that have been proposed.

To assess reproductive output, we determined six indices for each female collected with a multiple egg sac string ($n = 67$): number of egg sacs, variation in egg number among sacs (coefficient of variation), total number of eggs, mean number of eggs per sac, mean number of eggs per sac divided by female carapace width, and mean number of eggs per sac divided by female weight. These indices have been commonly used in studies of other orb weavers whose females produce multiple egg sacs, e.g., *Cyclosa turbinata* WALCKENAER 1842 (Spiller 1984); *Mecynogea lemniscata* WALCKENAER 1842 (Wise 1979); and *Philoponella oweni* CHAMBERLIN 1924 (Smith 1982, 1997), although their interpretation requires care. For example, Wise (1981) cautioned that number of egg sacs and total number of eggs may not always be reliable measures of reproductive output, as these parameters are directly related to a female's adult life span, which may not be uniform among individuals in a field-collected sample. Wise (1981) favored the use of mean number of eggs per sac and it has since become a prominent reproductive measure in many studies, as exemplified by its use in a population viability analysis of *M. datona* CHAMBERLIN & IVIE 1942 (Schoener et al. 2003). Mean number of eggs per sac normalized to a measure of female size (carapace width, weight), as we have done, has also been used (e.g., Suter 1990). On the other hand, as female spiders exhibit ever-smaller clutch sizes as they produce consecutive egg sacs (Marshall & Gittleman 1994), this will cause the mean number of eggs per sac to decline as more sacs are produced, potentially confounding comparisons between pairs of females or groups that differ in their egg sac production. In sum, while some of these indices are not without their limitations, it is clear that in comparisons of individuals or groups where sac production and variation in egg number among sacs are little different, they will likely function as reliable reproductive measures.

Electrophoresis

Horizontal starch gel electrophoresis was used to estimate the heterozygosity of each female. Electrophoretic procedures generally followed Ramirez (1990). Gels were 11.5% starch (StarchArt). Based on a survey of 19 enzymes, on up to two buffer systems, Ramirez & Fandino (1996) found five loci to be polymorphic in *M. ventura,* four of which yielded reliably scorable activity in this study: fumarase (FUM, E.C. 4.2.1.2), glucosephosphate isomerase (GPI, E.C. 5.3.1.9), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), and phosphoglucomutase (PGM, E.C. 2.7.5.1) (E.C. number denotes Enzyme Commission identification number, Commission on Biochemical Nomenclature 1979). With another araneid (*Argiope trifasciata* FORSKÅL 1775), Ramirez & Haakonsen (1999) found aspartate aminotransferase (AAT, E.C. 2.6.1.1) to be consistently scorable and polymorphic, as proved to be the case with *M. ventura* in this study. The recipes for AAT and PGM are based on Manchenko (1994), and those for the other enzyme stains follow references in Ramirez (1990). These five enzymes were resolved using three buffer systems: discontinuous tris-citrate I (Poulik 1957) (GPI); continuous tris-citrate I (Selander et al. 1971) (AAT, PGM); and tris-maleate (Selander et al. 1971) (FUM, IDH).

Data analysis

Agreement between observed genotypic proportions and Hardy–Weinberg expectations was evaluated for all females and for females with multiple egg sacs by calculation of exact significance probabilities (Haldane 1954) for each polymorphic locus. Females were assigned to heterozygosity classes as follows: class 0 = 0 loci heterozygous, class 1 = 1 locus heterozygous, etc., with each locus being treated equally, as is standard practice unless there are data to indicate otherwise (e.g., Gajardo & Beardmore 1989). One-way analysis of variance (ANOVA) was used to assess the association of the number of heterozygous loci per female with the nine fitness estimators. The ANOVA analyses of reproductive output were limited to females with multiple egg sacs ($n = 67$); ANOVA analyses of the physical parameters of this sample subset were also conducted. The remaining ANOVA analyses used the entire sample ($n = 84$). In cases where a significant difference was indicated by ANOVA, Fisher's protected least significant difference (PLSD) test (Saville 1990) was used to conduct *post hoc* pairwise comparisons among the means.

Results

Of the five loci screened, three (AAT, GPI, PGM) were polymorphic with four alleles each. Genotype frequencies at these three loci did not violate Hardy–Weinberg expectations for either all females or females with multiple egg sacs ($p > 0.05$). Hence, the

Table 1. Means ($\pm$ SE) of bodily characteristics of *Metepeira ventura* in three heterozygosity classes.

Bodily characteristics	Heterozygosity class			ANOVA	
	0	1	2	F	p
All females					
n	18	47	19		
Carapace width (mm)	2.238 (0.045)	2.211 (0.029)	2.171 (0.051)	0.515	0.600
Weight (mg)	36.839 (2.236)	38.315 (1.621)	36.268 (2.789)	0.278	0.758
Residual index	−0.045 (0.035)	0.016 (0.023)	0.003 (0.044)	0.929	0.399
Multiple-sac females					
n	17	38	12		
Carapace width (mm)	2.243 (0.047)	2.216 (0.032)	2.234 (0.056)	0.120	0.887
Weight (mg)	36.976 (2.367)	37.889 (1.874)	36.767 (3.245)	0.068	0.934
Residual index	−0.049 (0.037)	−0.004 (0.022)	−0.052 (0.045)	0.870	0.424

Data are presented for all females ($n = 84$) and for females with multiple egg sacs ($n = 67$). The results of one-way analysis of variance (ANOVA) tests for differences among the classes are also shown.

population of *Metepeira ventura* at Leo Carrillo was clearly in Hardy–Weinberg equilibrium, echoing the findings of Ramirez & Fandino (1996) for populations of *M. ventura* on Santa Catalina Island, California.

Individual females were heterozygous at up to two of the three polymorphic loci, collectively forming three heterozygosity classes (0/3, 1/3, 2/3), hereafter referred to as classes 0, 1, and 2. Bodily characteristics for the three heterozygosity classes, using all females and only females with multiple egg sacs, are summarized in Table 1. With both groups, the mean values for carapace width and weight are virtually the same among the classes, while the residual index values are close to zero and display no obvious pattern. None of these measures are related to the number of heterozygous loci for either group (ANOVA tests, Table 1).

Measures of reproductive output for females with multiple egg sacs are shown in Table 2. Sac number

and variation in egg number among sacs (coefficient of variation) differ little among classes and such differences are non-significant (ANOVA tests, Table 2). In contrast, mean values for total egg number vary by ~ 20 from class to class, with class 1 showing the highest mean and class 2 showing the lowest mean (Table 2). Mean number of eggs per sac, as both an absolute value and relative to carapace width and weight, is up to 26% less for class 2 females compared with values for class 0 and 1 females, which are much more similar. For these latter four measures, differences in reproductive output by heterozygosity class are significant (ANOVA tests, Table 2). In addition, pairwise PLSD testing for these four measures indicates that differences between class 1 and 2 females are always significant ($p < 0.02$), while differences between class 0 and 2 females are often significant or nearly so (p-values: 0.272, total egg number; 0.073, eggs/sac; 0.038, eggs/sac divided by carapace width; 0.056, eggs/sac divided by weight); class 0 and 1

Table 2. Means ($\pm$ SE) of reproductive output measures for *Metepeira ventura* in three heterozygosity classes.

Reproductive output	Heterozygosity class			ANOVA	
	0	1	2	F	p
n	17	38	12		
Sac number	2.882 (0.256)	3.158 (0.175)	2.833 (0.297)	0.643	0.529
Coefficient of variation (inter-sac for egg #)	0.242 (0.033)	0.258 (0.026)	0.303 (0.040)	0.595	0.555
Egg number (total for all sacs)	97.941 (10.797)	119.053 (9.060)	76.833 (11.010)	3.489	0.037*
Mean eggs/sac	33.941 (2.807)	36.583 (1.671)	26.817 (2.491)	4.046	0.022*
Mean eggs/sac//carapace width	15.023 (1.059)	16.283 (0.575)	12.010 (1.029)	5.886	0.005**
Mean eggs/sac//weight	0.940 (0.061)	0.986 (0.029)	0.779 (0.082)	4.044	0.022*

// denotes division by. Data are presented for females with multiple egg sacs ($n = 67$). The results of one-way analysis of variance (ANOVA) tests for differences among the classes are also shown. *$p < 0.05$; **$p < 0.01$.

females do not differ significantly for any measure (p > 0.05). Overall, these results indicate that while females in these classes were comparable in terms of physical parameters, the most heterozygous females generally underperformed their less heterozygous peers in terms of reproductive output.

Discussion

In contrast with the usual pattern for genetic variation in mainland and island populations (Frankham 1997), the Leo Carrillo population of *Metepeira ventura* proved to be less polymorphic than the Santa Catalina Island populations studied by Ramirez & Fandino (1996), resulting in a limited number of heterozygosity classes in the present study. Nonetheless, the reproductive performance of these classes was clearly not uniform, providing the first evidence for a potential relationship between individual heterozygosity and fitness parameters for an arachnid.

As our Leo Carrillo sample was field collected, we could not control for many conditions likely to influence reproductive parameters, such as female age and foraging history. In spite of these potentially confounding factors, the most heterozygous females produced the fewest total eggs and eggs per sac (in both absolute and size-specific terms). While a reduction in total eggs and mean eggs per sac might indicate that the females producing them are physically smaller, given that clutch size and female size are positively correlated in spiders (references in Brown et al. 2003), this was not the case in this study, as the class 2 females were not significantly smaller than their class 0 and 1 counterparts (Table 1).

The significant underperformance in reproductive parameters by the most heterozygous individuals of *M. ventura* was unexpected because, as noted earlier, positive relationships between individual heterozygosity and fitness correlates are much more common (Wang et al. 2002; Reed & Frankham 2003). While prior spider studies have similarly reported positive relationships between heterozygosity and fitness (Riechert & Roeloffs 1993; Smith & Hagen 1996; Ramirez & Saunders 1999), these were all population-level studies and hence differed significantly from our individual-level study of *M. ventura,* which suggests a negative relationship. As detailed demographic and ecological data for *M. ventura* do not exist, as is true of most non-social *Metepeira* species (Levi 1977; Piel 2001), it is difficult to completely assess the significance of the reproductive differences between the more heterozygous and less heterozygous females in this study. However, one element of

the available evidence suggests that the most heterozygous females may not be at a reproductive disadvantage, as outlined below.

A recent study of the relationship between clutch size and offspring mass in *M. ventura* at Leo Carrillo State Park has shown that egg mass in this population responds to clutch size in a classic reproductive investment-number trade-off (Smith & Fretwell 1974) for both single-sac and multiple-sac females (M.G. Ramirez, unpubl. data). That is, larger clutches are composed of lighter eggs, while smaller clutches have heavier eggs. In the context of the present study, this suggests that the females of *M. ventura* that produced the fewest total eggs and mean eggs per sac (class 2 spiders) had more massive eggs on average than their peers. As spider offspring that are larger/heavier are generally superior in terms of survival and fitness (e.g., Tanaka 1992, 1995; Walker et al. 2003), this would imply that the spiderlings of the most heterozygous females experience greater fitness. Of course, an explicit study of the relative performance of the offspring of less heterozygous and more heterozygous females of *M. ventura* will be needed to confirm such a prediction.

Given their potential to produce more massive eggs, it is possible that the most heterozygous females are at a selective advantage over their more homozygous peers. If this were true, then a heterozygote excess in our Leo Carrillo sample might be expected at polymorphic loci due to overdominance (selection favoring heterozygotes; Mitton 1989) or associative overdominance (the heterozygote excess at non-selected loci that results from linkage to loci showing overdominance; Nei 1987). The fact that heterozygote excesses were not present at any of the polymorphic loci, as genotype frequencies were in conformance with Hardy–Weinberg expectations, suggests that more homozygous and more heterozygous females may both do well in natural settings. With reference to the *r*- and *K*-life history continuum (Pianka 1970), more homozygous females appear to be reproductive *r* strategists (larger clutches, lighter eggs), whereas more heterozygous females seem to be *K* strategists (smaller clutches, heavier eggs).

As Tanaka (1995) has shown for a single population of the funnel-web spider *Agelena limbata* THORELL 1897 (Agelenidae), both strategies can be successful over the long term. Specifically, he found that some females produced many spiderlings that were smaller, while others produced fewer spiderlings that were larger. He also found that under poor food conditions, larger spiderlings were superior in terms of survival. This led him to observe that if prey abundance in the wild is variable from year to year, then a

mixture of females producing variably sized offspring would be advantageous. That is, when prey was scarce, larger spiderlings would be favored, conferring greater fitness on females who produced small broods of larger offspring; however, when prey was abundant, both large and small spiderlings would likely do well, potentially conferring greater fitness on females who produced larger broods of smaller offspring. Similarly, more homozygous and more heterozygous females of *M. ventura* may be differentially successful reproductively, given environmental conditions that vary spatially and temporally, and may be fit in complementary ways. The latter is the case in the white-tailed deer *Odocoileus virginianus* Zimmerman 1780; highly heterozygous females are in better condition at conception and are more likely to have twin fetuses, while more homozygous females mature earlier and are more likely to have single fetuses, which grow faster than twin fetuses (Chesser & Smith 1987). Clearly, detailed ecological and genetic studies (*sensu* Ramirez & Saunders 1999) will be needed to elucidate more clearly the fitness value of heterozygosity in *M. ventura*.

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