Adaptive nature of chromosomal rearrangement: differential fitness in pocket gophers

R. J. Baker, R. K. Chesser, B. F. Koop & R. A. Hoyt*
The Museum and Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA

Abstract

A chromosomal centric fusion polymorphism in populations of the plains pocket gopher, *Geomys bursarius*, was studied to determine the relative fitness associated with the karyotypic phenotypes. There was a greater number of heterozygous individuals than expected ($\chi_1^2 = 8.58$, $P = 0.001$). Calculations indicate that the viabilities of the two chromosomal homozygotes were only 35 and 76 percent or that of the heterozygote. Differences in fitness values for the chromosomal morphs for *Geomys* strongly emphasize the possible adaptive nature of the karyotype and provides a primary mechanism for chromosomal evolution, even in species composed of demes of relatively large size. This is the first case of positive chromosomal heterosis in vertebrates. The plains pocket gopher can now be added to the few empirically documented samples of balanced polymorphism.

Introduction

The forces responsible for chromosomal evolution in natural populations have been the subject of considerable debate in recent years (Atchley & Woodruff, 1981; Templeton, 1981). Because chromosomal rearrangements often result in meiotic problems in the heterozygous individuals which reduce fertility (Lande, 1979) and chromosomal rearrangements are not generally accepted as having a positive phenotypic effect in the heterozygote (John, 1981), it has been concluded that inbreeding and genetic drift are requisites to most chromosomal evolution (Lande, 1979; Wilson *et al.*, 1975; Bush *et al.*, 1977; White, 1978). It has been proposed that such deleterious chromosomal types must become established when populations are small, thereby resulting from sampling error which overrides the reduced fitness of the heterozygote. However, examples where the fitness values of a chromosomal heterozygote are greater than either homozygote (positive heterosis) would document that meiotic problems could be compensated for by a phenotypic advantage and that in some cases, differential selective values for chromosomal phenotypes must be considered as a tangible force in karyotypic evolution. An example of such is described below for a population of the plains pocket gopher, *Geomys bursarius.*

The population under study consists of individuals with three chromosomal phenotypes representing a centric fusion-fission rearrangement; AA with a $2N = 70$, two large biarmed autosomes; Aa with a $2N = 71$, one large biarmed autosome; and aa with a $2N = 72$ with all autosomes acrocentric (Patton *et al.*, 1980). Patton *et al.* suggested two possible features to explain the maintenance of the chromosomal polymorphism in the population. First, they hypothesized that the fitness value for the heterozygote was greater than that for either homozygote (their probability value that the variation in fre-

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* Present address: Central Texas Zoo, Route 10, Box 173E, Waco, TX 76708, USA.

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quency of individuals with different karyotypic phenotypes were not the result of random error was not statistically significant, P = 0.06). Second, they hypothesized that the positive heterosis was primarily expressed in differential survival in the subadult age group as compared to the juvenile and adult age groups (Patton *et al.*, 1980). Additionally, Lewontin (1974) has cautioned that when examining fitness values involving heterosis, samples from a single point in time can result in a statistical bias. However, if genotypic frequencies do not significantly vary between samples collected at different time periods, the probability that the samples accurately reflect heterotic values becomes greatly enhanced. Our additional 98 specimens from this population allows us to test Patton *et al.* (1980) hypotheses and to heed Lewontin's caveat.

Material and methods

We obtained standard karyotypes from 98 specimens of *Geomys bursarius major* collected along the railroad-highway right-of-way from 6.4 km east of Idalou, Lubbock Co. to 3.2 km east of Lorenzo, Crosby Co., Texas (a distance of 16 km). The standard karyotypes were obtained using the procedure of Baker (1967). All specimens were then determined to be either subadult or adult by examination of the degree of ossification of cranial surfaces (Patton *et al.*, 1980).

Areas adjacent to the railroad-highway right-of-way were cotton fields which were void of pocket gopher populations. Contact with other *Geomys* populations was restricted to highway right-of-ways. Limited samples of *Geomys* from other West Texas areas indicate that the polymorphism is present over a wide geographic area and that the 2N = 72 condition is the most common homozygous type. *Geomys bursarius* is a highly fossorial mammal which lives virtually its entire life below ground. Individuals are highly territorial with only solitary gophers inhabiting any particular burrow system, except for times of mating and for the couple of months in which the young live in the maternal burrow (Patton *et al.*, 1980).

Results and discussion

The frequencies of the chromosomal morphs for the animals we collected in the spring of 1979 were virtually identical to those for samples collected by Patton *et al.* (1980) from this same population in the spring of 1973 and of 1975. Data for the two studies were, therefore, combined (Table 1). The number of different cytotypes in Patton *et al.* was AA = 2, Aa = 45, and aa = 48, whereas, in our sample the numbers were AA = 4, Aa = 47, and aa = 47.

Analysis indicated significantly greater number of heterozygous individuals than expected ($\chi_1^2 = 8.58$, $P = 0.001$). The fitness of each homozygous chromosomal morph relative to that of the heterozygote was calculated by dividing the observed-to-expected ratio of each homozygote type by that for the heterozygote (Wilson & Bossert, 1971). These calculations indicated that the viabilities of the AA and aa chromosomal morphs were only 35 and 76 percent respectively of that for the heterozygote. These data are clearly indicative of positive heterosis associated with a chromosomal condition.

The highly significant excess of heterozygosity in a population of pocket gophers is rather surprising because the low vagility, small population sizes, and territoriality, associated with fossorial species should promote homozygosity (Selander *et al.*, 1974; Penney & Zimmerman, 1976; Zimmerman & Gayden, 1981). Electrophoretic data confirm that low genetic polymorphism and random fixation for alternative alleles in different populations are typical for this and similar species (Selander *et al.*, 1974; Penney & Zimmerman, 1976; Zimmerman & Gayden, 1981). However, the high selective advantage of heterozygotes for this chromosomal rearrangement results in a balanced polymorphism. Our additional data did not provide statistical confirmation of Patton *et al.*'s second hypothesis that differential survival was primarily expressed in the subadult age group. Relative to the exophenotypic

Table 1. Observed and expected frequencies of different chromosomal morphs for a population of *Geomys bursarius*. Fitness values and selection coefficients are calculated relative to those for the heterozygous type.

	AA (2N = 70)	Aa (2N = 71)	aa (2N = 72)
Observed	6	92	95
Expected	14.01	75.98	103.01
Relative fitness	0.354	1.0	0.762
Selection coefficient	0.646	0.0	0.238

(Bush, 1981) and endophenotypic (John, 1981) debate alluded to by Templeton (1981), differential survival in the plains pocket gopher is an example of exophenotypic selection. However, we hasten to note that this single example does not rule out the possibility that endophenotypic consequences are also viable forces in chromosomal evolution (Templeton, 1981).

The plains pocket gopher provides an ideal model for investigating the significance of chromosomal evolution in small, isolated populations (Wilson *et al.*, 1975; Bush *et al.*, 1977; White, 1978). Gopher populations have presumably undergone numerous bottlenecks in various parts of their range by way of founder events and habitat restrictions. Perhaps most important, the high frequency of heterozygous chromosomal morphs should insure that individuals possessing the 'mutant' chromosomal type will be included in many, if not most, of the bottlenecked populations. Using current models of chromosomal evolution (Lande, 1979; Templeton, 1980) one would predict that random drift would override the selective differentials leading to fixation of one of the chromosomal morphs in some populations.

Studies of isolated inbreeding populations of *Periplaneta americana* and *Blaberus discoidalis* have shown that translocation heterozygotes can be selected for to offset inbreeding depression (John & Lewis, 1957, 1958, 1959; Lewis & John, 1957). It has also been shown that in *Drosophila* and the onion fly (Dobzhansky, 1970; Vosselman and Van Heemert, 1980), inversions can be associated with a positive heterotic effect. Our data on the plains pocket gopher provide the first example of positive chromosomal heterosis for higher vertebrates (Bengtsson & Bodmer, 1976). Additionally, it should be noted that the relative fitness values reported here are of greater magnitude than those associated with any other chromosomal rearrangements thus far studied. Data presented here document that at least in some cases, the superior viability of heterozygotes for a chromosomal rearrangement may override potential loss of fitness due to meiotic problems (in this example there may or may not be meiotic problems in the heterozygote).

Although balanced polymorphism resulting from heterozygote superiority is a well accepted genetic phenomenon, it has been empirically documented in a relatively few cases. This example of the plains pocket gopher can now be added to that list.

In some models of chromosomal evolution meiotic problems in the heterozygote are thought to be compensated for by higher fitness values resulting from the chromosomal rearrangement (Bickham & Baker, 1979). The differences in fitness values for the chromosomal morphs for *Geomys bursarius* strongly emphasize the possible adaptive nature of the karyotype (Bickham & Baker, 1979; Bush, 1981; John, 1981) providing a primary mechanism for chromosomal evolution, even in species composed of demes of relatively large size. In this case, heterosis has apparently been of sufficient magnitude to prevent fixation of alternative chromosomal morphs in a species which has been characterized as having fixation of numerous electrophoretic alleles (Selander *et al.*, 1974; Penney & Zimmerman, 1976; Zimmerman & Gayden, 1981). These data clearly provide empirical evidence that positive chromosomal heterosis can be associated with a chromosomal mutation. As has been pointed out by John (1981), such empirical data have been woefully lacking.

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