APPARENT CHROMOSOMAL HETEROSIS IN A FOSSORIAL MAMMAL

For the past decade numerous investigators have attempted to explain the plethora of genetic polymorphisms found in nature (see Ayala 1976). However, few researchers have been able to document how polymorphisms have been maintained, whether the polymorphisms were genic or chromosomal. Our investigations into the maintenance of a Robertsonian chromosomal polymorphism in the plains pocket gopher, *Geomys bursarius major*, has revealed evidence that this polymorphism is maintained by differential viabilities of the three chromosomal morphs, with the heterozygote being favored.

Data were obtained from specimens collected during the spring of 1973 and the spring of 1975. Samples were taken at a time when the population consisted of distinct adult and subadult components. All specimens analyzed were karyotyped by standard bone marrow techniques (Baker 1970). Animals possessing 70 chromosomes with 68 acrocentric chromosomes and 2 biarmed chromosomes were designated morph *AA*. Animals possessing 71 chromosomes with 70 acrocentric chromosomes and 1 biarmed chromosome were designated morph *Aa* (fig. 1). Animals possessing 72 acrocentric chromosomes were designated morph *aa*. Specimens were aged according to whether or not fusion was complete between the basioccipital and basisphenoid bones (Russell 1968; Hendrickson 1975). Table 1 shows the distribution of animals with respect to age and chromosomal morph. The population sampled inhabited the soils along a railroad right-of-way from 6.4 km east of Idalou, Lubbock County, Texas, to Ralls, Crosby County, Texas, a distance of roughly 20 km. A contingency χ^2 test was used to compare morph frequencies in subadults and adults. As Hardy-Weinberg statistics are not really adapted to deal with linear populations, it is important to question whether or not this population is functioning as a panmictic unit. Because we found no evidence of clinal variation of chromosomal frequency, we have no reason to believe the population is not functioning as a panmictic unit.

Only one adult and one subadult of homozygous morph *AA* was observed, so all homozygous morphs were lumped for the contingency χ^2. The χ^2 was 3.6, with an associated probability of .06. The frequencies of heterozygotes and homozygotes appear to be different in subadults and adults, and the most likely cause of this difference is selection by differential viability.

The test indicated a tendency toward an excess of heterozygosity. This finding was unexpected for an animal whose entire natural history strategy, small population size, territoriality, low vagility and, in this instance, linear population, would predict instead a deficiency of heterozygous individuals. The method of maximum likelihood was used to estimate the viability of the homozygous morphs relative to that of the heterozygotes. This relative viability is given by $\hat{v} = (x_2 y_1)/(x_1 y_2)$, or if a correction for bias is applied,

$$vv = \frac{(x_2 + ½)(y_1 + ½)}{(x_1 + ½)(y_2 + ½)},$$

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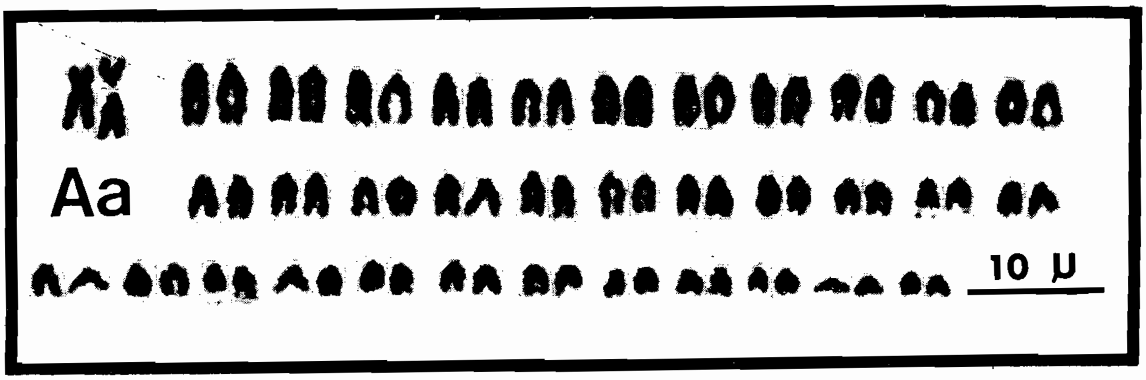

FIG. 1.—Karyotype of a female *Geomys bursarius major* with the heterozygous $2n = 71$ karyotype. The large biarmed chromosome is designated *A* and two acrocentrics which are believed to represent the homologous arms to the biarmed chromosome are designated *a*.

TABLE 1

FREQUENCY OF DIFFERENT CHROMOSOMAL MORPHS OF *Geomys bursarius major**

	CHROMOSOMAL MORPH		
	AA	*Aa*	*aa*
Adults	1	19	11
Subadults	1	26	37
Total	2	45	48

* Illustrating chromosome frequencies of $2n = 70(AA)$, $71(Aa)$, and $72(aa)$ of adults, subadults, and total population.

where x_1 is the number of subadult homozygotes and x_2 that of subadult heterozygotes and the number of adult homozygotes and heterzygotes are y_1 and y_2. More useful is $v' = \ln vv$, whose variance is approximately var $v' = 1/(x_1 + 1) + 1/(x_2 + 1) + 1/(y_1 + 1) + 1(y_2 + 1)$ (Haldane 1956). Confidence limits for v' can be transformed into confidence limits for vv. Calculations with our data give $vv = 0.44$. This viability is significantly different from 1, the value expected if there is no selection, at a level just beyond the conventional 5% level. This result is, of course, expected to be nearly the same as that obtained from the contingency χ^2 test on the data.

We feel a probability of .06 indicates a biologically real effect; that is, the maintenance of the observed chromosomal polymorphism in *Geomys bursarius major* must be due to greater viability of animals possessing the heterozygous karyotype (heterosis). This conclusion is even more significant when one considers that most features of the population biology of the plains pocket gopher would generally promote homozygosity.

Geomys bursarius is a highly fossorial mammal which lives virtually its entire life below ground. The animals 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. There are no data which suggest that these animals disperse to seek specific mates during the breeding season, but it appears that they mate with other animals living in close proximity. Finally, pocket gophers in west Texas are seldom found in populations of more than a few hundred individuals, with populations often being isolated by many kilometers of unfavorable habitat. Numerous searches for the tell-tale mounds made by this species failed to produce evidence of emigration from this population or immigration into this population from any surrounding population. On theoretical grounds one would therefore predict a high degree of monomorphism for animals utilizing this fossorial habitus. These theoretical expectations appear to be born out by electropheretic data presented by Penny and Zimmerman (1976). Twelve populations of *Geomys bursarius* were analyzed at five polymorphic loci. These populations were characterized by apparent random fixation or near fixation for alternative alleles at all five loci. In contrast, Baker et al. (1973) found this chromosomal polymorphism in every population of *Geomys bursarius major* examined.

Most discussions (White 1968; Patton 1969; Key 1968; Bush 1975) of the events and mechanisms of establishment of a chromosomal aberration in a population infer that small population size is needed to overcome the disadvantage of meiotic problems in the heterozygote. The example reported here suggests that in some cases the fitness in a heterozygote may outweigh meiotic problems. If, however, the heterozygote were fitter than the old homozygote (resulting in the survival of the new chromosomal morph) but less fit than the new homozygote, then the new chromosomal rearrangement could become rapidly fixed even in large populations. The implication of these data is that the heterozygote meiotic bottleneck may not invariably be the deterrent to chromosomal evolution that prior discussions have suggested.

Bickham and Baker (1979) have described a canalization model of chromosomal evolution that emphasizes the importance of the adaptive nature of the karyotype. The fact that the polymorphism in the plains pocket gopher offers a selective advantage great enough to ensure its survival despite any meiotic problem and inbreeding is additional proof of the adaptive nature of the karyotype. Therefore, we feel these data support the theory that the maintenance of this chromosomal polymorphism is due to heterosis whose advantages outweigh the effects of small population size and high potential of inbreeding. These data represent the first evidence from mammals of natural selection favoring a particular chromosomal morph and, to our knowledge, represent the first indication of heterosis of a Robertsonian type chromosomal polymorphism.

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