

Extent of geographic range and magnitude of chromosomal evolution

LYNN W. ROBBINS, MICHAEL P. MOULTON* and ROBERT J. BAKER

Department of Biological Sciences, Texas Tech University, Lubbock, Texas, U.S.A.

ABSTRACT. A positive correlation between extent of geographic range and magnitude of chromosomal evolution was found in the rodent genera *Peromyscus* and *Onychomys*. It is postulated that the size of geographic range is positively correlated with the success of a species. These data can be interpreted as indicating that chromosomal evolution should be included among the genetic variables that may have adaptive value to a species.

Introduction

In 1859 Darwin stated that 'although small isolated areas have been in some respects highly favourable for the production of new species, yet that the course of modification will generally have been more rapid on large areas; and what is more important, that the new forms produced on large areas, which have been victorious over many competitors, will be those that will spread most widely, and will give rise to the greatest number of new varieties and species'.

Recently, Glazier (1980) hypothesized that a major pattern in *Peromyscus* evolution has been the proliferation of geographically restricted species from widespread species. He provided numerous ecological correlates to support his interpretation. Principally, he suggested that widespread species had evolved mechanisms to enhance colonization ability rather than specializations to specific ecological conditions.

In grasshopper mice (*Onychomys*) and in three species of the *Peromyscus maniculatus*-complex, it has been noted that the taxa with

the largest amount of chromosomal evolution also have the largest geographic range (Baker, Barnett & Greenbaum, 1979; Baker & Barnett, 1981); however, this relationship was not tested statistically. We define chromosomal evolution as the number of chromosomal rearrangements incorporated into the genome since divergence from a common ancestor.

A correlation between certain genetic factors (electrophoretic variability) and such ecological factors as environmental heterogeneity and niche width has been hypothesized (Levins, 1968). Are ecologically generalized species more variable genetically than ecologically specialized species? This has been tested, with little or no consensus. Powell (1971), Shugart & Blaylock (1973), Steiner (1977) and Mitter & Futuyma (1979) found a positive correlation between these factors, and McNaughton & Wolf (1970), Soule & Yang (1973), Sabath (1974), Selander (1976) and Valentine (1976) found no or negative correlation (for an overview, see Hedrick, Ginevan & Ewing, 1976). One study (Smith, 1981) using *Peromyscus* showed no positive correlation between niche width and levels of genic heterozygosity among combinations of up to four sympatric species. The overview of the results of these studies is that there is no clear delineation of

* Present address: Department of Zoology, University of Tennessee, Knoxville, Tennessee, U.S.A.

the relationship between genetic and ecological factors. However, understanding this relationship is critical to understanding the evolutionary process.

In this paper we ask if within a genus a correlation exists between some measure of success of the various species and their magnitude of chromosomal evolution? Our definition of a successful species is one that is more likely to persist through time. A critical assumption that we have made is that size of geographic range of a species is a measure of its likelihood to persist through time. Simply stated, species which occupy large ranges might also occupy many habitats, because larger area is strongly correlated with habitat diversity (MacArthur & Wilson, 1967, p. 17). Species with large geographic ranges might also have larger populations. It is possible that a species is widespread simply because the habitat it occupies is widespread. Such species would still be ecologically successful even if they were not ecologically generalized.

Both of these factors contribute to the evolutionary success of the species. Species that can live in many habitats will be more resilient to local extinction due to the effects of habitat alterations. Species with larger populations will be on the average more resilient to the effects of population perturbations such as localized outbreaks of disease, or changes in climate.

We test the null hypothesis that no relationship exists between size of the geographic range of species in the genera *Peromyscus* (seventeen species) and *Onychomys* (three species) and the amount of chromosomal change incorporated into the respective genomes of these species.

Materials and Methods

Chromosomal data

Robbins & Baker (1981), Baker *et al.* (1983a, b) and Greenbaum & Baker (1978) described the type and distribution of chromosomal rearrangements in seventeen species of *Peromyscus*. Baker, Barnett & Greenbaum (1979) and Baker & Barnett (1981) provide data for three species of *Onychomys*. These data are derived from the analysis of differentially stained chromosomes (G- and

C-bands). The results of these analyses are shown in Figs. 1 and 2. Species are grouped on the assumption that shared chromosomal rearrangements became established in a common ancestor and that the most parsimonious positioning of rearrangements would provide the most probable evolutionary tree for species thus far studied. The rearrangements considered unique to each species are depicted along the branch leading to that species. Pericentric inversions are noted by a Pi and heterochromatic additions by C+. An asterisk (*) indicates rearrangements that are polymorphic for a species but fixed within at least one population. The numbers correspond to the standard numbering system for *Peromyscus* chromosomes (Committee, 1977).

Three of the species of *Peromyscus* (*boylii*, *leucopus* and *maniculatus*) and one species of *Onychomys* (*torridus*) were polymorphic for some chromosomal rearrangements (Table 1). Thus, three counts of chromosomal rearrangements were analysed separately; minimum number, mean number and maximum number.

We estimate the size of the geographic ranges of sixteen species of *Peromyscus* and two species of *Onychomys* from Hall & Kelson (1959), *P. attwateri* from Schmidly (1974) and *O. arenicola* from Hinsley (1979).

Correlations between the size of geographic range and number of chromosomal rearrangements incorporated into the genome since divergence from a common ancestor with another species were calculated for both *Peromyscus* and *Onychomys*. An additional test of the correlation between the level of genic variability as measured by heterozygosity and the size of the geographic range was computed for the genus *Peromyscus*. Pearson product-moment correlations were used to test for all associations (Sokal & Rohlf, 1969). However, because of the highly skewed distributions of the number of chromosomal rearrangements for *Peromyscus*, Kendall's Tau and Spearman's rank correlations (Sokal & Rohlf, 1969) were also calculated to test this chromosomal and range association.

The species of *Peromyscus* and *Onychomys* that were included in this study are listed in Table 1. The chromosomal rearrangements

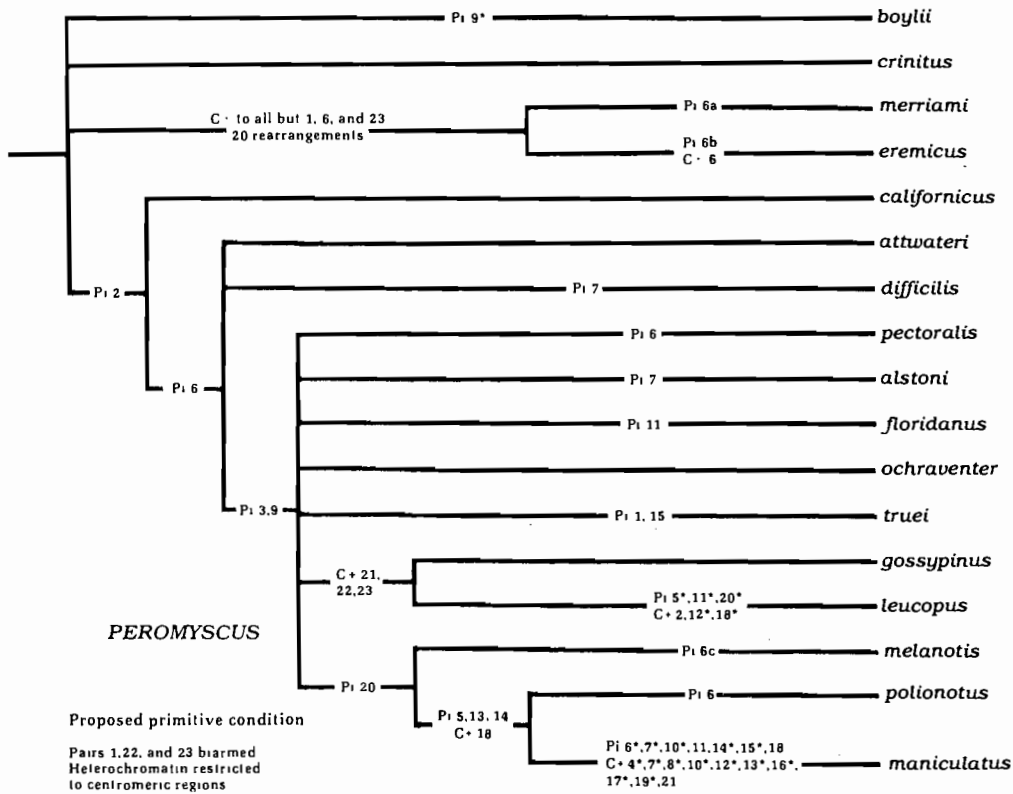


FIG. 1. Arrangement of seventeen species of *Peromyscus* derived from an analysis of chromosomal homology based on G- and C-bands. Pi = pericentric inversion and C+ = heterochromatic addition. An asterisk (*) indicates rearrangements that are polymorphic for a species but are fixed within at least one population. The numbers correspond to the standard numbering system for *Peromyscus* chromosomes (Committee, 1977).

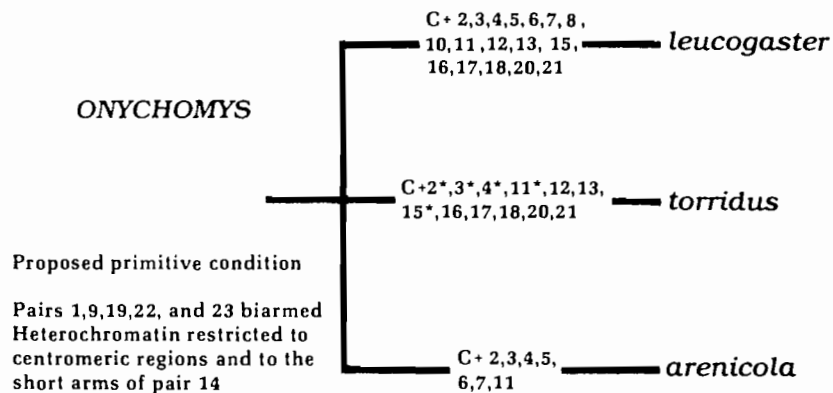


FIG. 2. Arrangement of three species of *Onychomys* derived from an analysis of chromosomal homology based on G- and C-bands. C+ = heterochromatic additions. An asterisk (*) indicates rearrangements that are polymorphic for a species but are fixed within at least one population. The numbers correspond to the standard numbering system for *Peromyscus* chromosomes (Committee, 1977).

TABLE 1. Number of chromosomal rearrangements, since divergence from the hypothesized ancestor for a genus (Figs. 1 and 2); minimum, maximum and mean genic heterozygosity; and geographic range of species of the genera *Peromyscus* and *Onychomys*. References for genic data are: (1) Avise *et al.* (1979); (2) Avise *et al.* (1974a); (3) Avise *et al.* (1974b); (4) Smith *et al.* (1973); and (5) Price & Kennedy (1980).

	Chromosomal rearrangements	\bar{H}	Genic (min-max)	Range (10^6 km ²)	References
<i>Peromyscus</i>					
<i>alstoni</i>	1			0.04	
<i>attwateri</i>	0	0.0	(0.0)	0.39	(2)
<i>boylli</i>	0-1	1.9	(0.08-3.1)	1.80	(2)
<i>californicus</i>	0	6.5	(2.9-10.6)	0.12	(3)
<i>crinitus</i>	0	-	-	0.60	
<i>difficilis</i>	1	0.7	(0.0-0.8)	1.02	(1)
<i>eremicus</i>	2	3.5	(0.4-7.9)	1.18	(3)
<i>floridanus</i>	1	5.3	(4.6-6.4)	0.08	(4)
<i>gossypinus</i>	0	2.9	(0.0-7.7)	0.75	(5)
<i>leucopus</i>	4-5	4.3	(0.0-13.5)	4.66	(5)
<i>maniculatus</i>	5-10	9.1	(5.4-12.4)	8.38	(1)
<i>melanotis</i>	0	2.6	(0.0-3.2)	0.40	(1)
<i>merriami</i>	1	1.6	(1.6)	0.18	(3)
<i>ochraverter</i>	0	-	-	0.002	
<i>pectoralis</i>	1	2.0	(1.2-3.1)	0.66	(2)
<i>polionotus</i>	0	6.1	(5.1-8.1)	0.23	(4)
<i>truei</i>	2	3.8	(3.0-4.8)	1.22	(1)
<i>Onychomys</i>					
<i>arenicola</i>	7	-	-	0.09	
<i>leucogaster</i>	17	-	-	2.50	
<i>torridus</i>	8-11	-	-	0.87	

were derived from Figs. 1 and 2, whereas mean individual heterozygosity (H) and the minimum and maximum values for the popu-

lations studied were taken from the published literature.

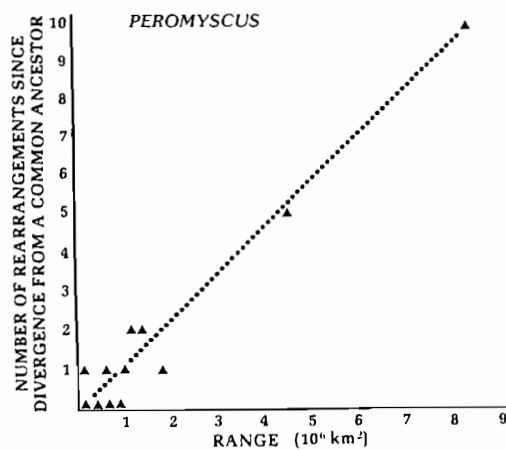


FIG. 3. Correlation between number of chromosomal rearrangements since divergence from a common ancestor and geographic range for seventeen species of *Peromyscus* ($r = 0.970$; $P < 0.0001$). In five cases a single triangle represents more than one species (see Table 1).

Results

In *Peromyscus* there was a significant positive correlation ($r = 0.969$) between the maximum number of chromosomal rearrangements and size of geographic range (Fig. 3, Table 2). The significance of this relationship was not altered by considering either the minimum or mean number of rearrangements. In *Onychomys* we found a significant positive correlation ($r = 0.996$) between size of range and magnitude of chromosomal evolution (Fig. 4, Table 2).

Discussion

Our data show that species in the genera *Peromyscus* and *Onychomys* which currently have a widespread geographic distribution have incorporated more chromosomal re-

TABLE 2. Correlations between the number of chromosomal rearrangements since divergence from a common ancestor and geographic range, and genic heterozygosity versus geographic range for species within *Peromyscus* and *Onychomys*. Results of Pearson's product-moment correlation, and Spearman's and Kendall's Tau ranked correlations are presented.

Genus	Chromosomal rearrangements			Genus heterozygosity
	Minimum	Mean	Maximum	
<i>Peromyscus</i>				
Pearson	$r = 0.877$ $P < 0.0001$	$r = 0.947$ $P < 0.0001$	$r = 0.969$ $P < 0.0001$	$r = 0.549$ $P < 0.05$
Spearman	$r = 0.488$ $P < 0.05$	$r = 0.555$ $P < 0.05$	$r = 0.617$ $P < 0.01$	$r = 0.042$ $P < 0.887$
Kendall	$r = 0.409$ $P < 0.05$	$r = 0.454$ $P < 0.05$	$r = 0.508$ $P < 0.01$	$r = 0.099$ $P < 0.622$
<i>Onychomys</i>				
Pearson	$r = 0.973$ $P < 0.5$	$r = 0.997$ $P < 0.1$	$r = 0.996$ $P < 0.1$	—
Spearman	$r = 1.00$ $P < 0.0001$	$r = 1.00$ $P < 0.0001$	$r = 1.00$ $P < 0.0001$	—
Kendall	$r = 1.00$ $P < 0.0001$	$r = 1.00$ $P < 0.0001$	$r = 1.00$ $P < 0.0001$	—

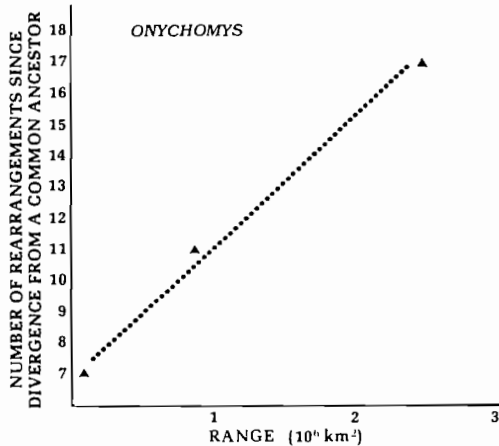


FIG. 4. Correlation between number of chromosomal rearrangements since divergence from a common ancestor and geographic range for three species of *Onychomys* ($r = 0.996$; $P < 0.05$).

arrangements into their genome than have geographically restricted species. As previously stated, widespread species might either occupy several habitats or a single widespread habitat. In the genus *Peromyscus*, the most widespread species (*maniculatus* and *leucopus*) occupy many habitats (Baker, 1968). The other species in this genus occupy much smaller ranges (Table 1). However, of

these remaining species, those with the most chromosomal rearrangements (*eremicus* and *truei*), generally occupy more widespread habitats (Baker, 1968).

Glazier's (1980) hypothesis is that a widespread, ecologically generalized species of *Peromyscus* gave rise to ecologically specialized species with restricted geographic ranges. Our results reveal that there is a differential rate of chromosomal evolution which is correlated with extent of current geographic range.

It is logical to predict that present-day widespread species of these genera are more likely to give rise to new species than are species with restricted ranges. Is there any genetic basis to support this prediction?

In the genus *Peromyscus* we found a highly significant correlation between magnitude of chromosomal evolution and size of geographic range, and genic (electrophoretic) data (Table 1) show that the most widespread species (*leucopus* and *maniculatus*) have the highest heterozygosity values known in the genus. Size of geographic range and mean heterozygosity values were also significantly correlated ($r = 0.55$). Clearly, the widespread species in this genus are the species with the greatest rate of chromosomal evolution, and the greatest pool of genetic variability.

These are exactly the species one would predict that would give rise to new species (Darwin, 1859; Glazier, 1980). Thus, the chromosomal and genic data support Glazier's and Darwin's hypothesis. In *Onychomys*, there are only three recognized species, which are too few taxa to test for this pattern.

The idea that the more widespread species would be most likely to give rise to new species is consistent with Brown's (1957) model of centrifugal speciation. There are also chromosomal data from *Peromyscus* (Greenbaum *et al.*, 1978; Robbins & Baker, 1981; Baker *et al.*, 1983a, b) that show that (1) the peripherally isolated species of *P. melanotis* and *P. polionotus* were derived from a *P. maniculatus*-like ancestor; (2) *P. gossypinus* was derived from a common ancestor with *P. leucopus*; and (3) *P. maniculatus* and *P. leucopus* have undergone many chromosomal changes, whereas the geographically isolated species that shared a common ancestor with the wide-ranging species have maintained the more primitive condition (Fig. 1).

There are three possible explanations for this evolutionary pattern. First, it is possible that a large geographic range allows for a higher probability of fixation for any chromosomal rearrangement. Second, a chromosomal rearrangement might impart some phenotypic advantage that enables the species to increase or at least maintain its geographic range. Third, it is possible that both size of geographic range and number of chromosomal rearrangements are affected simultaneously by unknown factors.

In our analysis we tested for positive correlations between number of chromosomal rearrangements and size of geographic range. Correlation analysis is concerned with how two or more variables vary together. Thus we tested the third explanation listed above. The first two possible explanations imply that one of these variables is dependent on the other, and it is not obvious which, if either, depends upon the other.

In one primary aspect, chromosomes are viewed as evolving under a unique selective regime. Because the heterozygote for a chromosomal mutation can produce inviable gametes due to meiotic problems, it is generally believed that the chromosomal

heterozygote is less fit than either the old or the new homozygote. Consequently, it has been argued that the heterozygous stage in chromosomal evolution is relatively short-lived with most chromosomal rearrangement mutations being eliminated. Fixation of a new chromosomal rearrangement is generally viewed as occurring only under special conditions (Lande, 1979).

In this study we have identified only two types of chromosomal rearrangements, pericentric inversions, and heterochromatic short arm additions. It is doubtful that heterochromatic additions result in meiotic problems in these genera because of the high level intraspecific variation in some species (Baker & Barnett, 1981; Baker *et al.*, 1983b). The above discussion concerning the unique nature of the selective regime for chromosomal evolution may not be applicable to these changes. On the other hand, pericentric inversions are thought to cause serious meiotic problems (Lande, 1979) and therefore any increase in the rate of incorporation of pericentric inversions requires some compensating special circumstances to account for loss of fitness in the heterozygote due to meiotic malassortment.

Four factors (Bickham & Baker, 1980) are viewed as influencing the rate of chromosomal evolution: (1) variation in mutation rate (McClintock, 1978; Lande, 1979); (2) variation in deme size and breeding structure (White, 1968; Arnason, 1972; Bush, 1975; Bush *et al.*, 1977; Wilson *et al.*, 1975; Lande, 1979); (3) presence or absence of mechanisms which reduce meiotic malassortment in the heterozygote (White, 1973); and (4) chromosomal rearrangements which increase the fitness of both the heterozygote's and new homozygote's phenotype sufficiently to outweigh the reduced fitness resulting from meiotic problems in the heterozygote (Dobzhansky, 1970; Vosselman & Heemert, 1980; Bengtsson & Bodmer, 1976; Bickham & Baker, 1979; Patton, Baker & Genoways, 1980). Would one predict that any or all of the four factors recognized as important in rate of chromosomal evolution are associated with size of the geographic range in these two genera?

(1) *Mutation rate.* Thompson & Woodruff (1980) have presented data which suggest that

the mutation rate is greater in situations where two differentiated groups interbreed. In some ways, such a system is compatible with Brown's (1957) explanation of why the central species is evolving more rapidly than the peripheral isolates. However, the effect noted by Thompson & Woodruff (1980) have not been shown to be associated with extent of geographic range and empirical data are clearly needed to evaluate its role in *Peromyscus* and *Onychomys* chromosomal evolution.

(2) *Variation in deme size and breeding structure.* It is theoretically well documented (Wright, 1941; Bengtsson & Bodmer, 1976; Lande, 1979) that in intensely inbred populations, a new chromosomal mutation can be fixed due to sampling error, even if the individual with the new mutation is less fit than individuals with the original homozygous condition. The question is then, do species with the larger geographic range have such highly inbred demes that inbreeding could account for such a magnitude of chromosomal evolution? We do not think this probable for the following reason.

If a population was finely subdivided to a point where random genetic drift could increase the probability of fixing a chromosomal mutation (Lande, 1979), it should also favour fixation of genic differences (Wright, 1965). In *P. maniculatus* there are twelve chromosomal mutations (five inversions and seven heterochromatic additions) which have alternative morphs fixed in different populations (Baker *et al.*, 1983b). Genic data from *P. maniculatus* indicate a high level of polymorphic loci (average 23%) yet examination of specimens from seventeen locations failed to provide a single case where alternative alleles were fixed on samples from different locations (Avisé, Smith & Selander, 1979). We do not interpret these genic data as being consistent with the hypothesis that populations of *maniculatus* are highly inbred.

The requirements for social structure as envisaged by Lande (1979) do not fit the pattern seen in either *P. leucopus* (Metzgar, 1971) or *P. maniculatus* (Metzgar, 1979). High population turnover rates and complex environments make maintenance of discrete social units difficult and of low adaptive value (Metzgar, 1979).

It is possible that *P. maniculatus*

underwent considerable chromosomal evolution at some point in its evolutionary past. At that time, this species might have existed in small, highly inbred demes. Once the mutations were fixed, the population could have expanded and invaded the majority of the North American continent. But, if this scenario was true, we should not expect a high level of chromosomal polymorphism within and between populations. In *P. maniculatus*, chromosomal polymorphism is more common than in any other studied species of *Peromyscus* (Baker *et al.*, 1983b).

Finally, the data now suggest that two chromosomally distinct populations of *P. leucopus* (Baker *et al.*, 1983a) which differ by three pericentric inversions produce viable hybrids and backcross individuals in the zone of contact. Moreover, the chromosomally distinct races of *P. maniculatus* (Baker *et al.*, 1983b) are genetically identical, although highly polymorphic. Data in Avisé *et al.* (1979) suggest that these rearrangements are no barrier to gene flow. We find no data which support the hypothesis that differential rates of chromosomal evolution in *Peromyscus* and *Onychomys* are the result of differential deme sizes (or social structuring) in geographically widespread species as opposed to less widespread species.

(3) *Presence or absence of mechanisms which reduce meiotic problems in the heterozygote.* There are no empirical data which are available to determine if the extent of meiotic problems resulting from a given type of chromosomal rearrangement is associated with extent of geographic distribution of a species. At this time, it would be extremely difficult, if not impossible, to collect empirical data to test such a relationship.

(4) *Chromosomal rearrangements increase fitness and are adaptive.* A species with a phenotype advantage resulting from a new chromosomal rearrangement should expand its range to a greater extent than a species without such chromosomal evolution. If there is a low mutation rate for chromosomal mutations which impart a positive phenotypic effect, then it is easy to envisage that a species composed of many individuals has a greater chance of having such a mutation than would a species composed of fewer individuals. If rate of chromosomal rearrange-

ment incorporation is strictly a function of number of mutations which impart a positive phenotypic effect in both the heterozygote and new homozygote, then a species with ten times as many individuals as another species, should have an evolutionary rate ten times greater. However, as noted by John (1981) and Lande (1979), there are no empirical data documenting such phenotypic advantages resulting from chromosomal mutations. Nonetheless, the possibility of such a cause and effect relationship to explain the observed pattern in these two genera cannot be discounted at this time.

Finally, we note that the probability of the correlation being due to chance is low both because of the statistical values ($P < 0.0001$ in *Peromyscus* and $P < 0.055$ for *Onychomys*) and because the pattern is evident in two different genera. Nonetheless, we hasten to note that the pattern does not hold in some other genera (for example, *Reithrodontomys*, *Oryzomys* and *Sigmodon*).

Again, Darwin's (1859) thoughts seem appropriate. 'Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare and, as I believe, the future success and modification of every inhabitant of this world.' Organisms potentially have a variety of genetic variables available to maximize success. Our data suggest that chromosomal evolution should be included among the genetic variables that are at times critically associated with some measures of success. No genetic variable will likely always be positively correlated with success. Yet, studies which reveal the extent to which any given variable is correlated with measures of success may shed some light on the role each plays in the evolutionary process.

Acknowledgments

We wish to thank C. S. Hood, B. F. Koope, J. L. Patton, S. L. Pimm and F. B. Stangl, Jr, for helpful comments on earlier versions of this manuscript, and R. K. Chesser for his help with the statistical analyses. This work was supported in part by NSF Grant

No. DEB-80-04293 to R.J.B. and by the Institute for Museum Research, Texas Tech University.

References

- Arnason, U. (1972) The role of chromosomal rearrangement in mammalian speciation with special reference to Cetacea and Pinnipedia. *Hereditas*, 70, 113–118.
- Avise, J.C., Smith, M.H. & Selander, R.K. (1974a) Biochemical polymorphism and systematics in the genus *Peromyscus*. VI. The *Boyllii* species group. *J. Mamm.* 55, 751–763.
- Avise, J.C., Smith, M.H., Selander, R.D., Lawlor, T.E. & Ramsey, P.R. (1974b) Biochemical polymorphism and systematics in the genus *Peromyscus*. V. Insular and mainland species of the subgenus *Haplomyiomys*. *Syst. Zool.* 23, 226–238.
- Avise, J.C., Smith, M.H. & Selander, R.K. (1979) Biochemical polymorphism and systematics in the genus *Peromyscus*. VI. The *boyllii* species differentiation in members of the *truei* and *maniculatus* species groups. *J. Mamm.* 60, 177–192.
- Baker, R.H. (1968) Habitats and distribution. *Biology of Peromyscus (Rodentia)* (ed. by J. A. King), pp. 98–126. American Society of Mammalogists Publ. No. 2. 64, 356–359.
- Baker, R.J. & Barnett, R.K. (1981) Karyotypic orthoselection for additions of heterochromatic short arms in grasshopper mice (*Onychomys*: Cricetidae). *Southwestern Nat.* 26, 125–131.
- Baker, R.J., Barnett, R.K. & Greenbaum, I.F. (1979) Chromosomal evolution in grasshopper mice (*Onychomys*: Cricetidae). *J. Mamm.* 60, 297–306.
- Baker, R.J., Robbins, L.W., Stangl, F.B., Jr & Birney, E.C. (1983a) Chromosomal evidence for a major subdivision in *Peromyscus leucopus*. *J. Mamm.* 64, 356–359.
- Baker, R.J., Robbins, L.W., Greenbaum, I.F. & Parker, L.E. (1983b) Patterns and relative rates of chromosomal evolution in the *Peromyscus maniculatus* complex. *Evolution*, (in press).
- Bengtsson, B.O. & Bodmer, W.F. (1976) On the increase of chromosome mutations under random mating. *Theoret. Pop. Biol.* 9, 260–281.
- Bickham, J.W. & Baker, R.J. (1979) Canalization model of chromosomal evolution. *Bull. Carnegie Mus. nat. Hist.* 13, 70–84.
- Bickham, J.W. & Baker, R.J. (1980) Reassessment of the nature of chromosomal evolution in *Mus musculus*. *Syst. Zool.* 29, 159–162.
- Brown, W.L. (1957) Centrifugal speciation. *Q. Rev. Biol.* 32, 247–277.
- Bush, G.L. (1975) Modes of animal speciation. *Ann. Rev. Ecol. Syst.* 6, 339–364.
- Bush, G.L., Case, S.M., Wilson, A.C. & Patton, J.L. (1977) Rapid speciation and chromosomal evolution in mammals. *Proc. nat. Acad. Sci. U.S.A.* 74, 3942–3946.
- Committee for Standardization of Chromosomes of *Peromyscus* (1977) Standardized karyotype of

- deer mice, *Peromyscus* (Rodentia). *Cytogenet. Cell Genet.* 19, 38–43.
- Darwin, C.R. (1859) *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. John Murray, London.
- Dobzhansky, T. (1970) *Genetics of the evolutionary process*. Columbia University Press.
- Glazier, D.S. (1980) Ecological shifts and the evolution of geographically restricted species of North American *Peromyscus* (mice). *J. Biogeogr.* 7, 63–83.
- Greenbaum, I.F. & Baker, R.J. (1978) Determination of the primitive karyotype for *Peromyscus*. *J. Mamm.* 59, 820–834.
- Greenbaum, I.F., Baker, R.J. & Ramsey, P.R. (1978) Chromosomal evolution and its implications concerning the mode of speciation in three species of deer mice of the genus *Peromyscus*. *Evolution*, 32, 646–654.
- Hall, E.R. & Kelson, K.R. (1959) *The mammals of North America*, Vol. II, pp. 547–1083. Ronald Press, New York.
- Hedrick, P.W., Ginevan, M.E. & Ewing, E.P. (1976) Genetic polymorphism in heterogeneous environments. *Ann. Rev. Ecol. Syst.* 7, 1–32.
- Hinesley, L.L. (1979) Systematics and distribution of two chromosome forms in the southern grasshopper mouse, genus *Onychomys*. *J. Mamm.* 60, 119–128.
- John, B. (1981) Chromosomal change and evolutionary change: a critique. *Evolution and speciation* (ed. by W. R. Atchley and D. S. Woodruff), pp. 23–51. Cambridge University Press.
- Lande, R. (1979) Effective deme size during long-term evolution estimated from rates of chromosomal evolution. *Evolution*, 33, 234–251.
- Levins, R. (1968) *Evolution in changing environments*. Monogr. Pop. Biol., Princeton University Press.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press.
- McClintock, B. (1978) Mechanisms that rapidly reorganize the genome. *Stadler Symp., Univ. Missouri*, 10, 25–47.
- McNaughton, S.J. & Wolf, L.L. (1970) Dominance and the niche in ecological systems. *Science*, 167, 131–139.
- Metzgar, L.H. (1971) Behavioral population regulation in the woodmouse, *Peromyscus leucopus*. *Amer. Midl. Nat.* 86, 434–448.
- Metzgar, L.H. (1979) Dispersion patterns in a *Peromyscus* population. *J. Mamm.* 60, 129–145.
- Mitter, C. & Futuyma, D.J. (1979) Population genetics consequences of feeding habits in some forest Lepidoptera. *Genetics*, 92, 1005–1021.
- Patton, J.C., Baker, R.J. & Genoways, H.H. (1980) Apparent chromosomal heterosis in a fossorial mammal. *Amer. Nat.* 116, 143–146.
- Powell, J.R. (1971) Genetic polymorphisms in varied environments. *Science*, 174, 1035–1036.
- Price, P.K. & Kennedy, M.L. (1980) Genic relationships in the white-footed mouse, *Peromyscus leucopus*, and the cotton mouse, *Peromyscus gossypinus*. *Amer. Midl. Nat.* 103, 73–82.
- Robbins, L.W. & Baker, R.J. (1981) An assessment of the nature of chromosomal rearrangements in 18 species of *Peromyscus* (Rodentia: Cricetidae). *Cytogenet. Cell Genet.* 31, 194–202.
- Sabath, M.D. (1974) Niche breadth and genetic variability in sympatric natural populations of *Drosophila* flies. *Amer. Natur.* 108, 533–540.
- Schmidly, D.J. (1974) *Peromyscus attwateri*. Mammalian Species No. 48, 1–3. American Society of Mammalogists.
- Selander, R.K. (1976) Genic variation in natural populations. *Molecular evolution* (ed. by F. J. Ayala), pp. 21–45. Sinauer Sunderland, Massachusetts.
- Shugart, H.H. & Blaylock, G.B. (1973) The niche-variation hypothesis: An experimental study with *Drosophila* populations. *Amer. Natur.* 107, 575–579.
- Smith, M.H., Selander, R.K. & Johnson, W.E. (1973) Biochemical polymorphism and systematics in the genus *Peromyscus*. III. Variation in the Florida deer mouse (*Peromyscus floridanus*). A Pleistocene relict. *J. Mamm.* 54, 1–13.
- Smith, M.F. (1981) Relationships between genic variability and niche dimensions among co-existing species of *Peromyscus*. *J. Mamm.* 62, 273–285.
- Sokal, R.R. & Rohlf, R.J. (1969) *Biometry. The principles and practice of statistics in biological research*. W. H. Freeman & Co., San Francisco.
- Soule, M. & Yang, S.Y. (1973) Genetic variation in side-blotched lizards on islands in the Gulf of California. *Evolution*, 27, 593–600.
- Steiner, W.W.M. (1977) Niche width and genetic variation in Hawaiian *Drosophila*. *Amer. Natur.* 111, 1037–1045.
- Thompson, J.N., Jr & Woodruff, R.C. (1980) Increased mutation in crosses between geographically separated strains of *Drosophila melanogaster*. *Proc. nat. Acad. Sci. U.S.A.* 77, 1059–1062.
- Valentine, J.W. (1976) Genetic strategies of adaptation. *Molecular evolution* (ed. by F. J. Ayala), pp. 78–94. Sinauer Sunderland, Massachusetts.
- Vosselman, L. & Heemert, C. van (1980) Meiotic disjunction and embryonic lethality in sex-linked double-translocation heterozygous males of the onion fly, *Hylemya antiqua* (Meigen). *J. theoret. Genet.* 58, 161–167.
- White, M.J.D. (1968) Models of speciation. *Science*, 159, 1065–1070.
- White, M.J.D. (1973) *Animal cytology and evolution*. William Clowes and Sons, London.
- Wilson, A.C., Bush, G.L., Case, S.M. & King, M.C. (1975) Social structuring of mammalian populations and rates of chromosomal evolution. *Proc. nat. Acad. Sci. U.S.A.* 72, 5061–5065.
- Wright, S. (1941) On the probability of fixation of reciprocal translocations. *Amer. Natur.* 75, 513–522.
- Wright, S. (1965) The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution*, 19, 395–420.