

Genetic Control of Premating-Isolating Behavior: Kaneshiro's Hypothesis and Asymmetrical Sexual Selection in Pocket Gophers

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We studied 112 individuals from a zone of hybridization between two species of pocket gophers, *Geomys bursarius major* and *G. knoxjonesi*. Each individual was examined and assigned to a genotypic class based on diploid number, mitochondrial DNA, ribosomal DNA, and three allozymic systems, all of which were fixed for alternative conditions in pure parental populations. F_1 and F_1 -like individuals were found to possess only the mitochondrial DNA type of *G. knoxjonesi*, indicating that F_1 and " F_1 -like" individuals are the result of unidirectional mating between *G. knoxjonesi* females and *G. b. major* males. We find these data compatible with the predictions of the Kaneshiro hypothesis that asymmetrical sexual isolation involves the preferential mating of females of the derived species with males of the species that have retained primitive character states.

It is a widely accepted view that the first step in the speciation process is the appearance of some form of reproductive isolation between two conspecific populations (Chow et al. 1988; Dobzhansky 1940, 1970). Although reproductive isolation plays a critical role in speciation, its origin and evolution (particularly of ethological isolation) is still largely controversial and in most cases unknown (Arnold et al. 1987; Coyne et al. 1988; Heth and Nevo 1981; Mayr 1970).

Of the two types of reproductive isolating mechanisms (Dobzhansky 1970; Mayr 1970), premating mechanisms are the most difficult to identify as they involve behavior, courtship, and/or copulatory incompatibilities. Postmating mechanisms, however, are generally easier to detect, in that no viable offspring may be produced, a reduced number of viable offspring may be produced, or dysgenic traits may be present in the offspring. Premating isolating mechanisms are often asymmetric, and Kaneshiro (1976, 1980, 1983, 1987, 1989, 1990) noted that nonreciprocal isolation between ancestral (primitive) and derived species of Hawaiian *Drosophila* followed a consistent pattern. The model proposed by Kaneshiro assumes that during founder events and the subsequent explosive colonization the "elements of behavior" are changed because of severe genetic drift and relaxed sexual selection. This allows females of the derived species to accept the courtship overtures of males of the

founder species (primitive) as well as males of the derived species.

However, because some elements of the courtship behavior have been changed in the derived species, females of the founder or primitive species only mate with conspecific males because they alone possess a complete courtship ritual. Females of the founder species discriminate against males of the newly derived species with their incomplete or changed courtship ritual. A critical component of Kaneshiro's predictions is a genetic basis for the behavioral elements in the courtship repertoire. A change in these elements may result from the loss or fixation of genetic elements in the newly derived population. The power of the Kaneshiro model is that, under appropriate conditions, it allows inferences to be made about the direction of evolution.

The Kaneshiro model has been widely examined, and several conditions have been identified that are necessary for the model to be valid (DeSalle and Templeton 1987; Giddings and Templeton 1983). First, the ancestral population should give rise to the derived population through a founder event followed by a rapid increase in population size. Second, the ancestral population should not have undergone any serious bottlenecks since the founding event. Finally, there should have been very little or no gene flow between the two populations after the founding event. As noted by Ehrman and Wasserman (1987) and

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DeSalle and Templeton (1987), there is more than one mechanism that can yield asymmetrical isolation, and the existence of asymmetry alone cannot be used to infer the direction of evolution, unless the conditions exist for the Kaneshiro model to be valid.

Although Kaneshiro's hypothesis was developed from analyses of *Drosophila*, Giddings and Templeton (1983) suggested that fossorial rodents may lend themselves well to testing this model. Fossorial rodents of the genus *Geomys* would appear to be particularly appropriate, as two species, *G. bursarius major* and *G. knoxjonesi* hybridize in a narrow hybrid zone in eastern New Mexico (Baker et al. 1989; Pembleton and Baker 1978). An extensive study by Baker et al. (1989) showed that *G. b. major* and *G. knoxjonesi* differed in diploid number, mitochondrial DNA (mtDNA), and ribosomal DNA (rDNA) haplotypes, and exhibited fixed differences at three allozymic systems: alcohol dehydrogenase (Adh), lactate dehydrogenase (Ldh-1), and peptidase (Pep-B-1). The combination of these six independent genetic markers permitted unequivocal identification of parental types, as well as F_1 and F_1 -like individuals and six genotypic classes representing backcross individuals. The results indicated that hybridization was occurring over a distance of 3 km (20/80 criterion of Hafner 1982) and that the structure and maintenance of the zone was most compatible with the predictions of the "dynamic equilibrium model" (Moore 1977) in that gene flow into the hybrid zone from parental types was balanced by selection against hybrid individuals. From these data, Baker et al. (1989) concluded that *G. b. major* and *G. knoxjonesi* were behaving as biological species with the integrity of their respective gene pools being maintained.

To test the Kaneshiro hypothesis it is critical to document derived versus primitive taxa. Evidence that *G. knoxjonesi* is derived and *G. b. major* is primitive comes from phylogenetic studies of the genus *Geomys* (Davis 1986). Cladistic studies of mtDNA and rDNA by Davis (1986) demonstrated that *G. knoxjonesi* represents a highly derived lineage of a *G. bursarius* complex and that *G. b. major* represents a central lineage typical of the complex. *G. knoxjonesi* is a peripheral isolate of the *G. bursarius* complex and ecologically is a derived specialist, restricted to deep, sandy, aeolian soils. The *G. bursarius* complex as a whole and *G. b. major* in particular are generalists and occupy various soil types

within their range, including endurete soils as well as deep, sandy soils. We propose that if *G. knoxjonesi* were not present in the deep, sandy, aeolian soils, these areas would be invaded by *G. b. major*, but if *G. b. major* did not occupy the endurete soils then *G. knoxjonesi* would not be able to invade areas that are not sandy in composition.

In this article we examine the data generated by Baker et al. (1989) plus data from an additional 37 individuals from the same hybrid zone. The additional specimens were collected in the summer of 1988 and were analyzed using the same methods and systems used by Baker et al. (1989) both to increase the sample size of the initial study and to estimate the magnitude of variation in the dynamics and structure of the hybrid zone between samples. Baker et al. (1989) demonstrated significant asymmetry in the production of F_1 and F_1 -like individuals, and data from the hybrid zone were also used to examine the Kaneshiro model (Kaneshiro 1976, 1980, 1983, 1987, 1989, 1990) by comparing the direction of the observed asymmetry with that predicted by the model. If F_1 individuals are produced as a result of asymmetric matings, and if these matings involve the females of the derived type (*G. knoxjonesi*) and males of the generalist type (*G. b. major*), we would accept this as support of the Kaneshiro model.

Materials and Methods

We collected 75 individuals in 1986 and 37 individuals in 1988, during the summer of both years, from a naturally occurring hybrid zone, along a 6-km north-south transect along the DeBaca-Roosevelt county line, 15.5 miles S and 3.0 miles E of Taiban, New Mexico. See Pembleton and Baker (1978) and Baker et al. (1989) for a detailed description of this hybrid zone. We trapped animals using live traps (Baker and Williams 1972) and transported them to the laboratory at Texas Tech University for analyses. Animals were karyotyped using the yeast-stress in vivo method of Lee and Elder (1980) and samples of heart, liver, kidney, and muscle were collected and stored at -80°C until allozymic, mtDNA, and rDNA studies could be conducted. We prepared voucher specimens as skins and skeletons and deposited them in The Museum, Texas Tech University. Methods for preparing, identifying, and scoring the above systems are listed in Baker et al. (1989).

Results

We scored all individuals for diploid number, rDNA, mtDNA, Adh, Ldh-1, and Pep-B-1 following Baker et al. (1989) and Davis (1986). Of the 112 individuals examined, 25 had genotypes characteristic of *G. knoxjonesi*, 29 had genotypes characteristic of *G. b. major*, and 58 had a combination of *G. b. major* and *G. knoxjonesi* characteristics. We conclude that these individuals with combination genotypes had a hybrid ancestry (Table 1 and Baker et al. 1989). Following Baker et al. (1989) an F_1 individual would have the following characteristics: $2n = 71$, heterozygous at Ldh-1, Adh, and Pep-B-1, and 40%–60% *G. b. major* rDNA. Although 50% rDNA is the logical choice for an F_1 individual, the 40%–60% range was necessary to correct for copy-number variation in the rDNA repeat between the two species (Baker et al. 1989). Additionally, Baker et al. (1989) categorized individuals with $2n = 71$, heterozygous for the three allozyme systems, and with rDNA compositions outside the range of 40%–60% *G. b. major* as F_1 -like individuals. Using the above criteria, 52% of the specimens (58 out of 112) were of hybrid origin; of these, six fit the criteria for F_1 individuals, of which all six had the mtDNA of *G. knoxjonesi*. The F_1 -like category included 16 individuals, of which 13 possessed the mtDNA of *G. knoxjonesi* and three possessed the mtDNA of *G. b. major*.

Discussion

The genetic control of mate choice is apparent in a comparison of true F_1 s and F_1 -like individuals with other hybrid individuals (Table 2). We tested the null hypothesis that the F_1 s are equally likely to possess *G. knoxjonesi* or *G. b. major* mtDNA by using the binomial probability test $(0.5)^N$ where N is the number of individuals with *G. knoxjonesi* mtDNA. For F_1 individuals, the probability of sampling six individuals and getting only *G. knoxjonesi* mtDNA is 0.0156 under the null hypothesis that such an individual is equally likely to have *G. knoxjonesi* or *G. b. major* mtDNA. For F_1 -like individuals, the probability of getting three or fewer *G. b. major* mtDNA genomes in a sample of 16 individuals given an equal probability of *G. knoxjonesi* and *G. b. major* mtDNA is 0.0192. Overall, the probability of drawing three or fewer *G. b. major* mtDNA genomes out of a sample of 22 individuals that are F_1 hybrids at allozymic and chromosomal markers is

Table 1. Genotypes^a of individuals based on diploid number (2n), mitochondrial DNA (mtDNA), ribosomal DNA (rDNA), and three allozymes

ID no.	Sex	2n	mtDNA	rDNA ^b	Allozyme			Proportion genome of <i>G. b. major</i> ^c
					Adh	Ldh	Pep	
30751	M	70	K	0	K	K	K	K 0/8
30752	F	70	K	0	K	H	K	H 1/8
30753	F	70	K	0	K	K	K	K 0/8
30754	F	71	K	90.6	H	H	H	H 4/8
30755	F	71	K	26.1	H	H	H	H 4/8
30756	M	71	M	22.9	H	H	M	H 5/8
30757	M	70	K	0	K	K	K	K 0/8
30758	F	71	M	100	M	H	M	H 6/8
30759	M	70	K	0	K	K	K	K 0/8
30760	F	70	K	0	K	K	K	K 0/8
30761	F	72	M	100	M	M	M	M 8/8
30762	F	72	M	97.8	M	M	M	H 8/8
30763	M	72	M	100	M	M	M	M 8/8
30764	—	—	K	91.3	M	M	M	H 6/6
30765	—	—	K	76.5	—	M	H	H 3/4
30766	F	70	K	0	K	K	K	K 0/8
30770	F	71	K	0	K	K	K	H 1/8
30777	M	71	M	100	H	—	M	H 4/6
30778	F	70	K	0	K	K	K	K 0/8
30779	F	72	K	100	K	H	K	H 3/8
30780	M	70	K	0	K	K	K	K 0/8
30781	F	71	M	79.2	H	H	H	H 4/8
30782	F	71	K	92.2	H	H	H	H 4/8
30783	F	70	K	0	K	K	K	K 0/8
30784	F	72	M	97.1	M	M	H	H 7/8
30785	M	72	M	100	M	M	H	H 7/8
30786	F	72	M	100	M	M	M	M 8/8
30787	M	72	M	100	M	M	M	M 8/8
30788	M	72	M	100	M	M	M	M 8/8
30789	M	70	K	0	K	K	K	K 0/8
30790	M	71	M	100	H	H	M	H 5/8
30791	F	70	K	0	K	K	K	K 0/8
30792	F	70	K	93.8	H	H	H	H 3/8
30793	F	72	M	100	M	M	M	M 8/8
30794	F	72	M	100	M	M	M	M 8/8
30795	F	72	M	100	H	M	M	H 7/8
30796	F	72	M	100	M	M	M	M 8/8

Dashes indicate missing values.

^a Genotype designations: H = heterozygote, K = *G. knoxjonesi*, and M = *G. b. major*.

^b rDNA values expressed as the percentage of *G. b. major*.

^c The proportion of the genome that is *G. b. major*.

$$\sum_{x=0}^3 (x^{22})(0.5)^{22} = 0.0023$$

All tests were significant at the 5% level for both the F₁ and F₁-like classes, resulting in rejection of the null hypothesis. We interpret these data to indicate that successful crosses of *G. knoxjonesi* females with *G. b. major* males occur at a higher frequency than would be expected if mating between the two species occurred at random. Additionally, 23 of 36 non-F₁ hy-

Table 2. Frequency of F₁, F₁-like, and other hybrid individuals based on mtDNA type

	mtDNA of <i>G. knoxjonesi</i>	mtDNA of <i>G. b. major</i>
F ₁	6	0
F ₁ -like	13	3
Other hybrids	23	13
Total	42	16

brids had a *G. knoxjonesi* mtDNA haplotype.

Although it initially appears that there is an abundance of non-F₁ hybrid individuals with *G. knoxjonesi* mtDNA (23 out of 36), there are five ways to generate a non-F₁ hybrid individual with *G. knoxjonesi* mtDNA and three ways to generate a non-F₁ hybrid with *G. b. major* mtDNA (Appendix). We use the term non-F₁ hybrid to denote individuals that are a result of backcrosses to either parental type and of hybrid-by-hybrid crosses (F₂). We cannot distinguish F₂ individuals as their genotypes could resemble either a reconstituted parental type or any of the possible genotypes representing backcross individuals. The only exception occurs when individuals are fixed for alternative alleles; however, this condition is present in only one of 112 individuals from the contact zone. Our data suggest that all F₁ individuals have the mtDNA of *G. knoxjonesi*, and this limits the means by which non-F₁ hy-

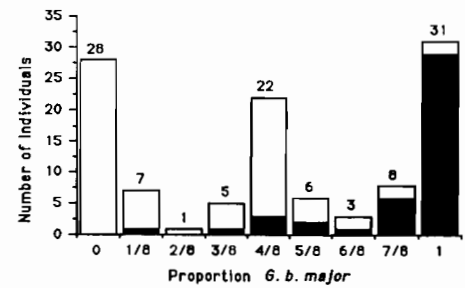


Figure 1. Histogram depicting the frequency of 111 individuals with proportions of the genome characteristic of *G. b. major* calculated from diploid number, and the three allozymic systems. One individual (TK 30777) not shown as a genotype was 4/6 *G. b. major*. The solid portion of each bar represents the individuals with the mtDNA type of *G. b. major*; the open bar represents individuals with *G. knoxjonesi* mtDNA. Number above each bar indicates the number of individuals represented.

brid individuals are produced with the mtDNA of *G. b. major*. Additionally, Baker et al. (1989) concluded that these pocket gophers are an example of Haldane's Rule (Haldane 1922) and that male hybrids experience greater infertility than female hybrids. If Haldane's Rule is operative, it would make the production of a non-F₁ hybrid individual with *G. b. major* mtDNA even less probable.

Baker et al. (1989) used the four markers that behave like single loci (diploid number, Adh, Ldh-1, and Pep-B-1) to develop a classification scheme that involves nine classes of genotypes to depict the distribution of hybrid genotypes. In this classification, where genotypes are based on the proportion of the genome identified as being *G. b. major*, an individual that is heterozygous at all four loci would fall into the 4/8 class, whereas an individual having seven alleles identifiable as *G. b. major* alleles would be classified in the 7/8 class. If F₁ individuals are backcrossing to both parental types at the same probability, then a frequency of 1:4:6:4:2:4:6:4:1 would be expected across the nine genotypic classes (0/8 to 8/8). Baker et al. (1989) found a paucity of individuals in the 2/8 and 6/8 classes where the largest frequency of individuals would be expected from backcrosses. In fact, all classes had a reduction in the number of expected hybrid individuals, with the exception of the F₁ and F₁-like class. Using the same criteria as Baker et al. (1989) to generate the nine genotypic classes, we found a similar scarcity of hybrids in the non-F₁ classes relative to the number of F₁ and F₁-like individuals (Figure 1). The distribution of individuals among the genotypic classes in this study was not different from that described by

Baker et al. (1989) based on a chi-square goodness of fit contingency table test ($\chi^2 = 0.43$, $df = 8$, $P < .05$). This suggests that successful backcrossing to parental types occurs at a lower frequency than expected.

Testing the null hypothesis that there is an equal probability of generating non- F_1 hybrid individuals with *G. knoxjonesi* or *G. b. major* mtDNA using a chi-square goodness of fit test contingency table, the observed data differed significantly ($\chi^2 = 40.96$, $df = 1$, $P > .05$) from the expected. Because these individuals must be generated by crosses between one parental type and a hybrid, or by two hybrids, it is apparent that mechanisms that regulate the crosses for generating F_1 and F_1 -like individuals have changed sufficiently to allow a parental female with *G. b. major* mtDNA to mate with a hybrid male. This also provides evidence that there is no fertility barrier to the production of offspring by this mating.

The resolution provided when data are available to document both (1) the maternal inheritance and frequency of the reciprocal crosses and (2) the extent of reconstituted parental genomes and nuclear gene flow permits the statistical examination of some of the alternative models that have been proposed for speciation. For example, several models have hypothesized that a single founder-flush event (i.e., genetic revolution of Mayr 1954, 1976; genetic transience of Templeton 1981, 1982; and Kaneshiro 1976, 1980, 1989) may be the primary event in establishing an isolating mechanism. An extension of such a hypothesis would predict that all populations generated from this "flush" event would be expected to inherit such a genetic isolating mechanism (Templeton 1981, 1982). We cannot prove that a founder-flush event was involved in the differentiation of *G. knoxjonesi* and *G. b. major*, although it is an assumption of the Kaneshiro model; we do know that *G. b. major* is associated with the central stock of the *G. bursarius* complex and that *G. knoxjonesi* appears to be a derived member of this complex, both genetically and ecologically (Davis 1986; Baker et al. 1989).

The data herein are supportive of the Kaneshiro model (1976, 1980, 1983, 1987, 1989, 1990) that asymmetrical sexual isolation is unidirectional with the derived-type females of *G. knoxjonesi* mating preferentially with the more primitive males of *G. b. major*. However, some mechanism or mechanisms are present that allow the reciprocal cross (female *G. b. major* \times male *G. knoxjonesi*) to occur between highly

heterozygous individuals or between a highly heterozygous individual and a parental type. This is evident as 16 out of 59 hybrid individuals in this study possessed *G. b. major* mtDNA.

If examination of other hybrid zones between *G. b. major* and *G. knoxjonesi* reveals a similar degree of isolation between *G. b. major* females and *G. knoxjonesi* males, then this would be compatible with the hypothesis that a founder-flush event established such a mechanism. If the degree and/or direction of such an isolating mechanism varies between geographic localities, then other alternative explanations must be invoked (i.e., rejection of the hypothesis that the isolation mechanisms were established in a single founder-flush event or require additional evolution to modify the isolating mechanism subsequent to its establishment). The exciting aspect is that some of the newer DNA techniques used in combination with the more classical methods could provide sufficient resolution of a hybrid zone to allow some ideas about speciation events to be tested under natural conditions.

Before the availability of a maternally inherited marker, such as mtDNA, this intermediate state of speciation involving sexual selection could not be well documented. We think that this state of partial isolation through sexual selection may prove common in higher vertebrate taxa that have incomplete isolating mechanisms. As such, data from stickleback fish (McPhail 1969), mole rats (Heth and Nevo 1981), and pocket gophers (this study) may prove that the prediction of the Kaneshiro hypothesis is more applicable to vertebrates than previously thought. In light of the difficulty in testing this type of hypothesis in the past (Giddings and Templeton 1983), this is a welcome observation.

Appendix

The five possible means to generate non- F_1 hybrid individuals with *G. knoxjonesi* mtDNA and the three means to generate non- F_1 hybrid individuals with *G. b. major* mtDNA: Non- F_1 hybrid individuals with *G. knoxjonesi* mtDNA: hybrid female with *G. knoxjonesi* mtDNA \times parental male with *G. b. major* mtDNA, hybrid female with *G. knoxjonesi* mtDNA \times parental male with *G. knoxjonesi* mtDNA, hybrid male with *G. knoxjonesi* mtDNA \times parental female with *G. knoxjonesi* mtDNA, hybrid female with *G. knoxjonesi* mtDNA \times hybrid male with

G. b. major mtDNA, and two hybrids—both with *G. knoxjonesi* mtDNA; Non- F_1 hybrid individuals with *G. b. major* mtDNA: hybrid male with *G. knoxjonesi* mtDNA \times parental female with *G. b. major* mtDNA, hybrid male with *G. knoxjonesi* mtDNA \times hybrid female with *G. b. major* mtDNA, and two hybrids—both with *G. b. major* mtDNA.

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