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Biosystematics and Life Histories of the PEROMYSCUS GUARDIA Group of Mice and PEROMYSCUS EREMICUS (Rodentia: Cricetidae)

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BIOSYSTEMATICS AND LIFE HISTORIES OF THE *PEROMYSCUS GUARDIA* GROUP OF MICE AND *PEROMYSCUS EREMICUS* (RODENTIA: CRICETIDAE)

by

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A Thesis in Partial Fulfillment

of the Requirements for the Degree

Master of Arts in the Field of Biology

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Each person whose signature appears below certifies that he has read this thesis and that in his opinion it is adequate, in scope and quality, as a thesis for the degree of Master of Arts.

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Dedicated to my Parents, Mr. and Mrs. George Brand,

whose encouragement and unselfish

generosity has made my education possible.

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CHAPTER I

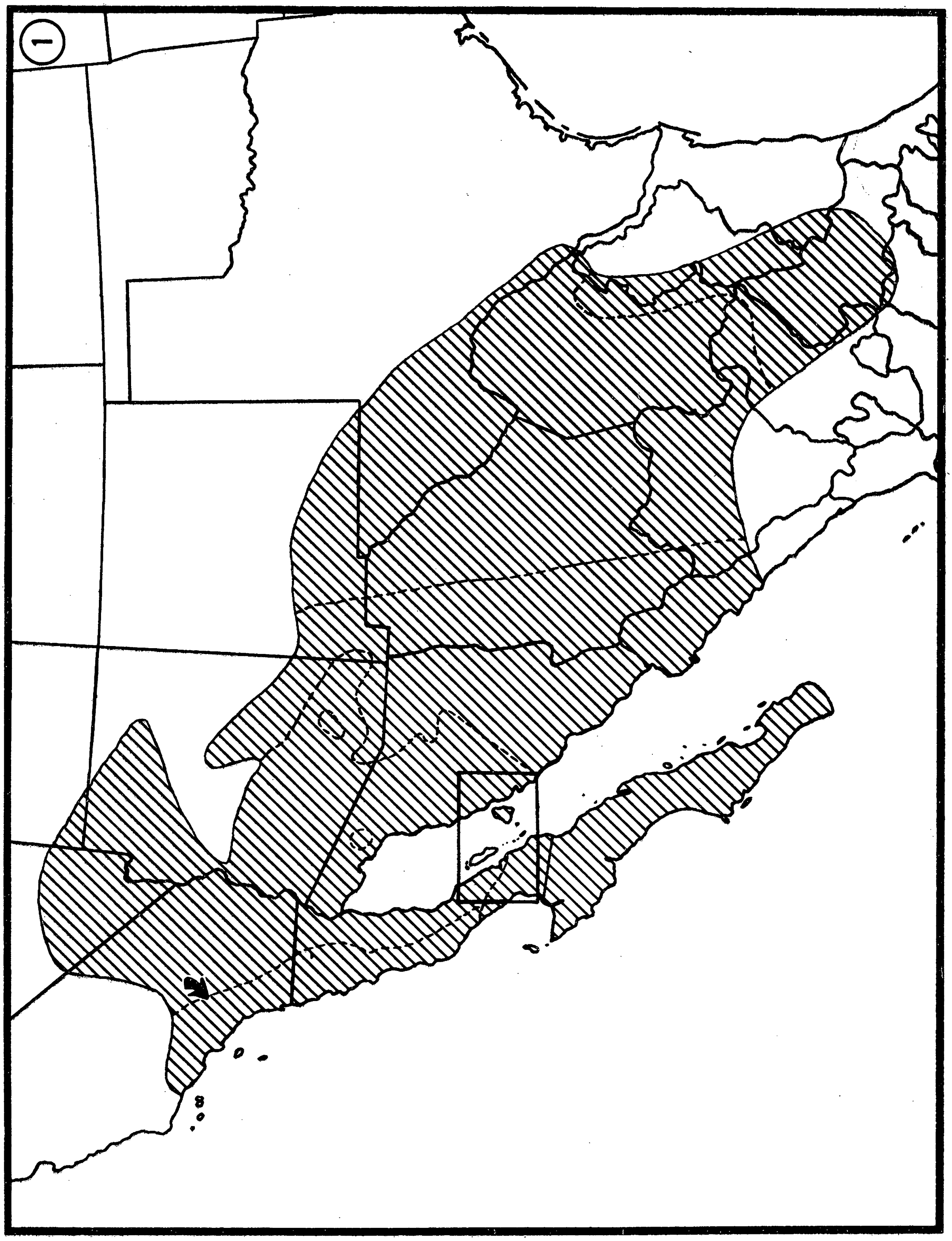
INTRODUCTION

The Gulf of California is a rectangular arm of the Pacific Ocean about 680 miles long, and from 60 to 120 miles wide, enclosed on its western side by the peninsula of Baja California and on its eastern side by the mainland of Mexico. A number of arid, rocky islands are located in this gulf, mostly along the western side (Fig. 1). Some of the islands are close to shore, in water less than 110 meters deep. The rest of the islands are in much deeper water, including a chain of islands in the vicinity of Bahia de los Angeles, Baja California, consisting of Islas Mejia, Granite, Angel de la Guarda, Partida Norte, Raza, Salsipuedes, San Lorenzo Norte, and San Lorenzo Sur (Soule, 1966) (Fig. 2).

Whitefooted mice of the genus *Peromyscus* are well represented on these islands. A total of 14 species of *Peromyscus* are found there, and 10 of these species are precinctive to the islands (Hall & Kelson, 1959; Huey, 1964; and Banks, in manuscript).

The cactus mouse, *P. eremicus* and the *P. guardia* group are in the subgenus *Haplomylomys*. *Peromyscus eremicus* is widely distributed in arid or semiarid areas in southwestern United States and

Figure 1. The range of *Peromyscus eremicus*. The arrow points to the approximate location where the specimens of *Peromyscus eremicus* used in this project were caught. The small rectangle indicates the area shown in Figure 2.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in Mexico, including Baja California and several islands in the gulf, where each precinctive island population is treated as a subspecies (Fig. 1).

The *P. guardia* group is found only on the previously mentioned chain of islands near Bahia de los Angeles (Fig. 2). *Peromyscus guardia* was first described by Townsend (1912) from Isla Angel de la Guarda. In 1932 Burt described two more subspecies, *P. guardia mejiae* Burt from Isla Mejia, and *P. guardia interparietalis* Burt from Isla San Lorenzo Sur. In 1962 R. E. Ryckman, while on a parasitology expedition in this region, caught a series of *Peromyscus* on Isla Salsipuedes (Ryckman & Ryckman, 1963). This was the first record of mice from Isla Salsipuedes. Since then, Richard C. Banks has collected *Peromyscus* on Isla San Lorenzo Norte, and Isla Granite; his revision of the taxonomy of this group is in manuscript. He has proposed that *P. guardia interparietalis* be raised to specific status, and has described 2 new subspecies of *interparietalis*: *P. interparietalis ryckmani* from Isla Salsipuedes, and *P. interparietalis lorenzi* from Isla San Lorenzo Norte; and 1 new subspecies of *guardia*: *P. guardia harbisoni* from Isla Granite.

The mice in this group resemble *P. eremicus*, but are larger, and have a characteristic skull shape, different from other members of the subgenus (Burt, 1932).

Figure 2. The range of the *Peromyscus guardia* group of mice.

Peromyscus guardia guardia
Isla Angel de la Guarda

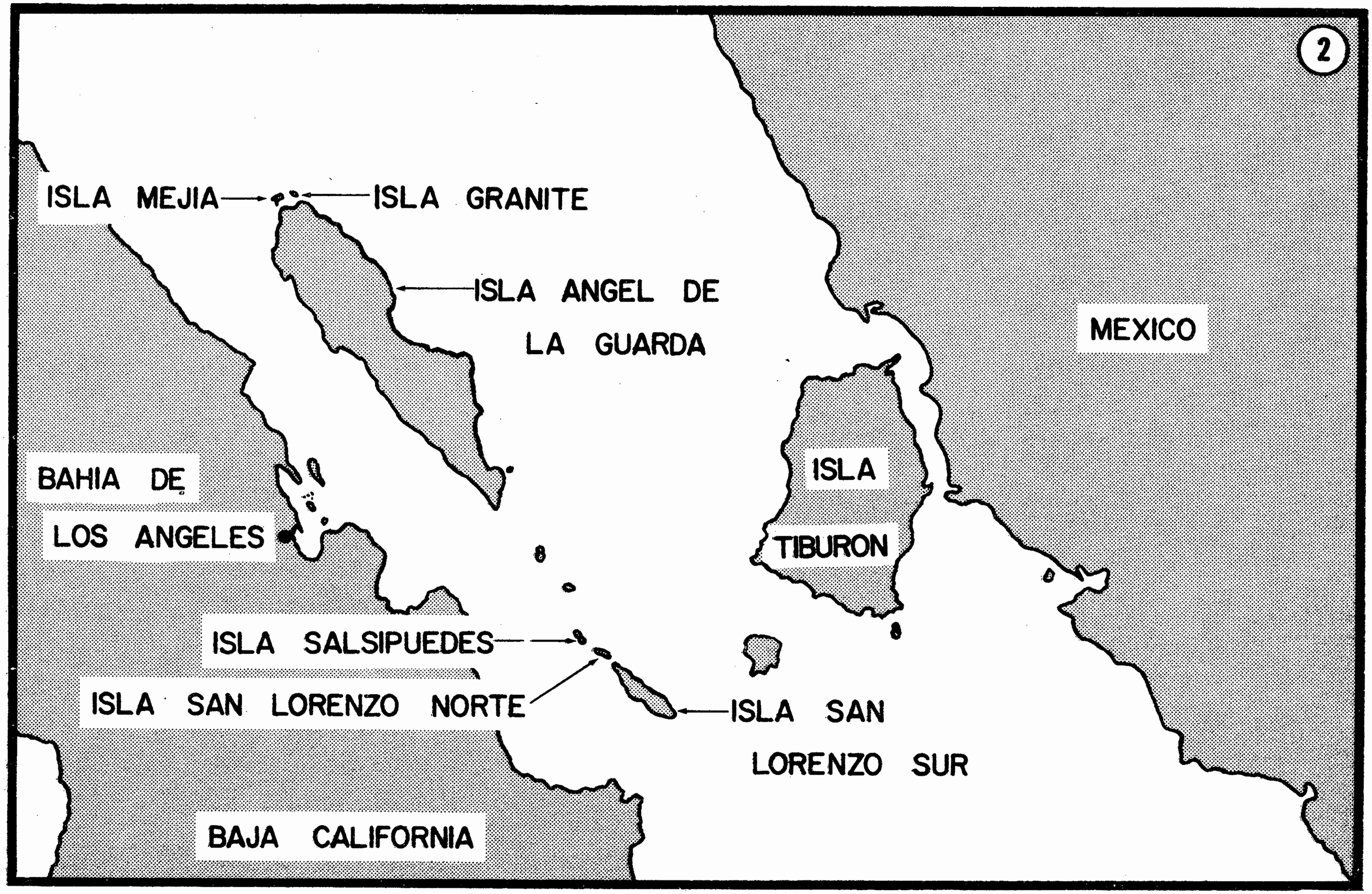
Peromyscus guardia mejiae
Isla Mejia

Peromyscus guardia harbisoni
Isla Granite

Peromyscus interparietalis interparietalis
Isla San Lorenzo Sur

Peromyscus interparietalis lorenzi
Isla San Lorenzo Norte

Peromyscus interparietalis ryckmani
Isla Salsipuedes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ISLA MEJIA
ISLA GRANITE
ISLA ANGEL DE
LA GUARDA
MEXICO
BAHIA DE
LOS ANGELES
ISLA
TIBURON
ISLA SALSIPUEDES
ISLA SAN LORENZO NORTE
ISLA SAN
LORENZO SUR
BAJA CALIFORNIA

The purpose of this study was to investigate the relationship of P. eremicus (Baird) to the P. guardia group. The methods used were hybridization to determine the possible degree of interfertility, comparison of blood proteins by serum electrophoresis, and morphological studies. Laboratory observations were also made on the life histories of P. eremicus and P. interparietalis Burt.

A number of workers have studied speciation in Peromyscus (Dice, 1933, 1937, 1940; Dice & Liebe, 1937; Sumner, 1923; and Watson, 1942); these studies have demonstrated that in the laboratory the subspecies within a species are interfertile, and the species within a species group may be completely or partially interfertile (Dice, 1940), even though there is no evidence of hybridization in nature. Peromyscus leucopus (Rafinesque) and P. gossypinus (Le Conte) are completely interfertile in the laboratory (Dice, 1937), and their ranges overlap widely across the southern states, yet they remain distinct, and only 4 specimens have been reported which may be natural hybrids (McCarley, 1954). Species in different species groups or subgenera have all been intersterile (Dice, 1940).

Because it has been demonstrated that valid, sympatric species of Peromyscus may be interfertile in the laboratory, hybridization of allopatric populations in the laboratory doesn't prove them to be conspecific. There may be mechanisms of reproductive isolation which would keep the groups distinct if their ranges became connected naturally. As stated by Blair (1951), "It seems to be generally true that diverging populations of animals usually acquire mechanisms of reproductive isolation before they have diverged genetically to the point of intersterility." Sexual isolation seems to be of special importance in Peromyscus (Dice, 1940). However, hybridization data is useful in determining how far a population has gone in the process of speciation.

Taxonomy of geographically isolated populations is especially difficult, since it is usually impossible to determine for sure if they would be reproductively isolated if they should come together in nature. Mayr, Linsley, & Usinger (1953:103-104) recommend that the taxonomic status of isolated populations be decided by inference. If the degree of differentiation of the isolated population from its relatives is as great as the amount of difference that commonly separates valid sympatric species in that genus, then it could be classed as a species.

The feasibility of using serum proteins, as revealed by electrophoresis, as a taxonomic character has been investigated by Johnson & Wicks (1959). They compared the electrophoretic patterns of a number of small mammal genera, including Peromyscus, and found that there is individual variation, but that each species has a characteristic pattern. These patterns, with some exceptions, tend to verify present taxonomic relationships at the generic and specific level (Johnson & Wicks, 1959). Thus it appears that serum proteins have some value as a taxonomic character. It is interesting to note that Johnson & Wicks found the electrophoretic pattern of P. crinitus (Merriam) to be more like that of P. maniculatus (Wagner) than like the subgenus Haplomylomys, where it has been customarily placed. This agrees with the conclusion of Hooper & Musser (1964), (based on a study of phalli), that P. crinitus should be in the subgenus Peromyscus rather than Haplomylomys.

CHAPTER II

HYBRIDIZATION

Methods and Materials

All mice were kept in metal cages 8 x 14 x 6 inches, with wire mesh or perforated metal tops. They were provided with cotton for nest material and sand or wood shavings for floor material. Their diet was mouse pellets, with fresh lettuce daily and horsemeat once a week. They were kept in a room which was lighted through two skylights in the roof. There was no temperature control in this room, but due to the structure of the building, the animals were protected from extremes of temperature. The cages were checked daily, and data on each new litter was recorded.

The stocks used in the hybridization experiments were as follows:

Peromyscus eremicus (Baird): These mice were all caught in Reche Canyon, 3 miles north of Sunnymead, Riverside Co., California, in the spring of 1965. According to Osgood (1909), individuals from this locality are intergrades between the subspecies *eremicus* and *fraturculus* (Miller).

Peromyscus interparietalis ryckmani Banks: The individuals used in this study were all descendants from 18 mice caught on Isla Salsipuedes in 1962 by R. E. Ryckman.

Peromyscus interparietalis: In June, 1965, 13 individuals of P. interparietalis interparietalis Burt were collected by the author on Isla San Lorenzo Sur, and 12 individuals of a newly described subspecies, P. interparietalis lorenzi Banks (Banks, in manuscript) were caught on Isla San Lorenzo Norte. By accident these two stocks became mixed; this mixed group will subsequently be referred to as the Islas San Lorenzo population.

Peromyscus guardia guardia Townsend: These mice were collected in June, 1965, by the author, at Puerto Refugio, at the north end of Isla Angel de la Guarda, and near the south end of the same island, in the vicinity of Isla Pond.

Peromyscus guardia mejiae Burt: All of the specimens were collected in June, 1965, by the author, on Isla Mejia.

Five to 10 pairs each of P. eremicus and P. interparietalis ryckmani and 5 pairs of P. guardia guardia were maintained to provide information on reproduction and development of the young, and as control groups for the hybrid crosses. In all cases the males and females were kept together except when attempts were made to determine the gestation time. The following matings were attempted: 5

pairs of eremicus ♀♀ X interparietalis ryckmani ♂♂, and 5 pairs of the reciprocal were maintained for 16 months. Two pairs of interparietalis ryckmani ♀♀ X guardia guardia ♂♂, and 5 pairs of the reciprocal; 5 pairs of eremicus ♀♀ X guardia guardia ♂♂, and 2 pairs of the reciprocal; 3 pairs of interparietalis ryckmani ♀♀ X guardia mejiae ♂♂; and 3 pairs of guardia mejiae ♀♀ X eremicus ♂♂ were maintained for 9 months.

Results

Both P. interparietalis ryckmani and P. eremicus bred readily in the laboratory, but interparietalis ryckmani females were more prolific than eremicus. These populations also hybridized successfully in the laboratory. The females seemed to produce young at about the same rate whether their mates were conspecific or of the other species. Thus the cross interparietalis ryckmani ♀♀ X eremicus ♂♂ was more prolific, with 17 young, than the reciprocal cross, eremicus ♀♀ X interparietalis ryckmani ♂♂, with 9 young.

Fifteen litters of interparietalis ryckmani X eremicus hybrids were born within a year, but 3 of these litters and 1 individual from a fourth litter were killed by their parents soon after birth. This problem was not encountered in the control populations. All of the hybrids which were not killed by the parents matured normally.

The hybrid sex ratio was abnormal. Eleven hybrid litters contained 19 males and 7 females. The cross interparietalis ryckmani ♀♀ X eremicus ♂♂ produced 11 males and 6 females, and the cross eremicus ♀♀ X interparietalis ryckmani ♂♂ produced 8 males and 1 female.

The F_1 hybrid females were mated with F_1 hybrid males, and both sexes proved to be fertile. Six litters of F_2 hybrids were born. Two litters were killed by the parents, but the other four matured normally.

No progeny were obtained in matings between the following: 2 pairs of interparietalis ryckmani ♀♀ X guardia guardia ♂♂, and 5 pairs of the reciprocal; 5 pairs of eremicus ♀♀ X guardia guardia ♂♂, and 2 pairs of the reciprocal; 3 pairs of interparietalis ryckmani ♀♀ X guardia mejiae ♂♂; and 3 pairs of guardia mejiae ♀♀ X eremicus ♂♂. The above cannot be interpreted as indicating that these populations are or are not reproductively isolated because no reproduction occurred in the control colonies of P. guardia guardia.

CHAPTER III

MORPHOLOGY

Methods and Materials

At the completion of the hybridization study 43 Peromyscus eremicus, 38 P. interparietalis ryckmani, and 15 F_1 hybrids were preserved as study skins and skulls. The skulls were measured, and the skull and body measurements were analyzed statistically.

The measurements taken were the total length, tail length, head and body length, length of hind foot, height of ear from notch, greatest length of skull, zygomatic breadth, width of interorbital constriction, length and width of interparietal, nasal length, shelf of bony palate, alveolar length of maxillary tooth row, diastema, alveolar width of incisors, width of rostrum, and rostral-incisor height (Fig. 3).

The body measurements were recorded to the nearest millimeter. The length of the skull and the zygomatic breadth were measured with a vernier caliper accurate to 0.1 mm, and the other skull dimensions were measured with a microscope grid accurate to 0.05 mm.

From these data the discriminant functions were computed, and a canonical scattergram was plotted. The scattergram was based on a

Figure 3. A skull of *Peromyscus* showing measurements used in this study.

A. Greatest length of skull
B. Zygomatic breadth
C. Interorbital constriction
D. Interparietal length
E. Interparietal width
F. Nasal length
G. Shelf of bony palate
H. Maxillary tooth row
J. Diastema
K. Width of incisors
L. Width of rostrum
M. Rostral-incisor height

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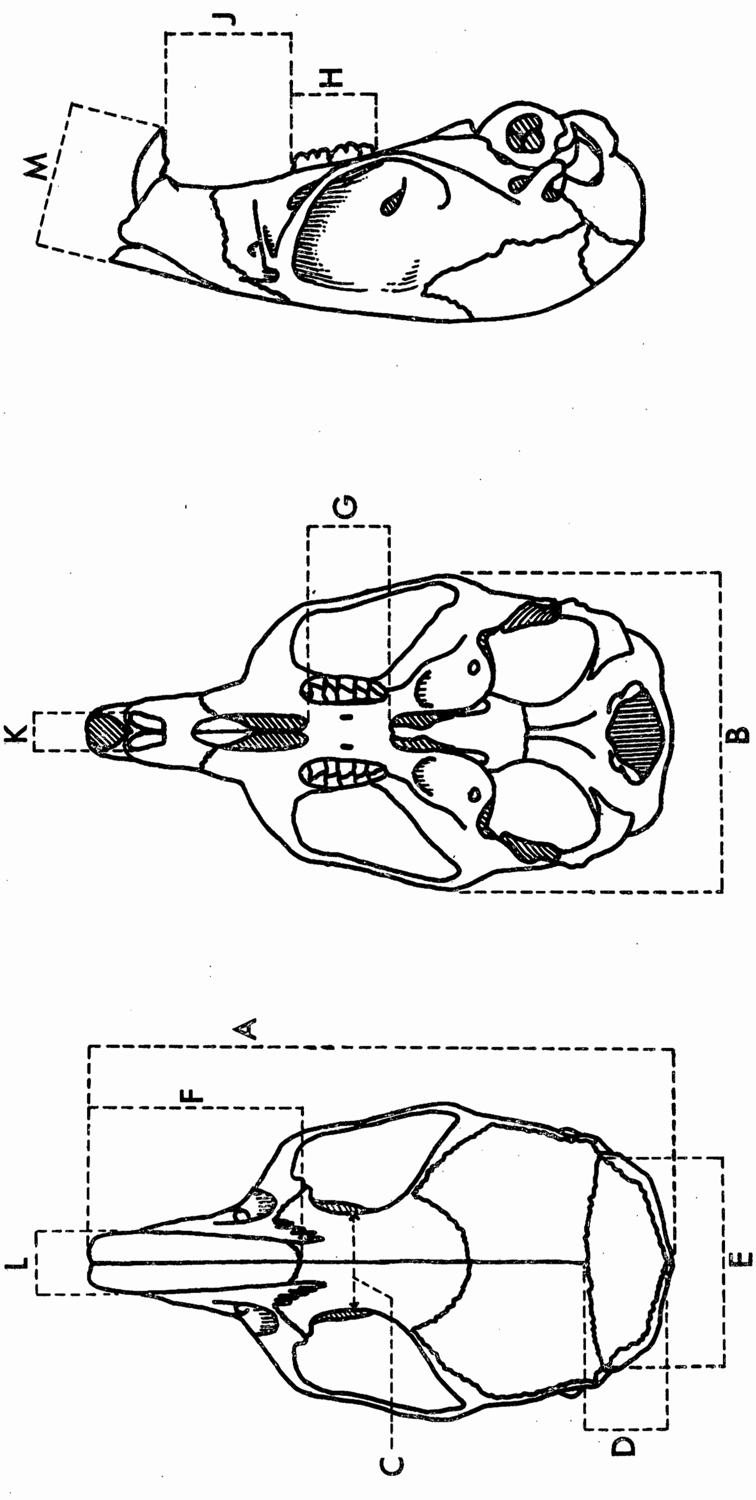


series of canonical variables computed from the original series of measurements. The two canonical variables which were most significant in distinguishing between the populations were treated as the X and Y coordinates on the scattergram (Fig. 4), and the point of intersection was plotted for each individual.

The distinctness of the populations was further tested by feeding the original data back through the computer as measurements of unknown animals, and the computer was programmed to attempt to identify the populations by comparison with the discriminant functions.

These statistical programs were developed at the University of California at Los Angeles under the supervision of W. J. Dixon (1965), and have been used extensively in biomedical applications.

Results

The measurements which on the basis of the discriminant functions most clearly show the differences between the populations are given in table 1. All the measurements shown except the width of the interparietals indicate differences between *P. eremicus* and *P. interparietalis ryckmani* which are significant at the 99% level. These populations are quite distinct. The most obvious difference is in the size of the rostrum and the incisors, which is reflected in the measurements of the width of the incisors, width of the rostrum, and the rostral-incisor height. The total length of *P. eremicus* is greater

Table I. Morphological measurements (in mm) of 4 populations of *Peromyscus*.

	P. eremicus				*P. interparietalis ryckmani*				*P. erem.* ♀ X *P. inter.* ♂				*P. inter.* ♀ X *P. erem.* ♂			
	N	M	SE	R	N	M	SE	R	N	M	SE	R	N	M	SE	R
Total length	41	189.02	1.34	171.00-211.00	38	182.63	1.23	173.00-204.00	5	200.00	5.48	189.00-215.00	10	203.00	3.35	197.00-225.00
Tail length	41	103.51	1.02	96.00-120.00	38	94.89	.73	87.00-109.00	5	110.00	3.16	106.00-121.00	10	108.00	2.00	103.00-122.00
Head and Body length	41	85.12	.73	72.00- 96.00	38	92.55	.51	86.00- 99.00	5	89.80	2.56	83.00- 97.00	10	95.60	1.33	93.00-103.00
Skull length	34	24.24	.09	23.70- 25.90	38	24.71	.09	24.30- 26.20	5	24.60	.24	24.90- 25.70	10	26.40	.37	25.70- 27.30
Zygomatic breadth	38	12.03	.05	11.80- 13.50	38	13.03	.06	12.80- 14.10	5	12.82	.24	12.40- 13.30	10	13.91	.17	13.40- 14.20
Interparietal length	40	3.38	.04	2.90- 4.00	38	2.78	.04	2.00- 3.10	5	2.92	.09	2.75- 3.25	10	3.05	.06	2.60- 3.25
Interparietal width	39	9.35	.04	8.85- 10.00	38	9.27	.04	8.90- 9.75	5	9.56	.14	9.10- 10.00	10	9.85	.04	9.75- 10.40
Nasal length	43	9.15	.05	8.40- 9.95	38	9.74	.04	9.30- 10.40	5	9.78	.07	9.55- 9.95	10	10.38	.06	10.20- 10.80
Maxillary tooth row	43	3.73	.02	3.50- 4.00	38	3.89	.02	3.70- 4.20	5	4.00	.03	3.90- 4.15	10	3.99	.03	3.85- 4.25
Incisor width	43	2.04	.01	1.90- 2.25	36	2.61	.01	2.45- 2.75	5	2.30	.03	2.20- 2.40	8	2.51	.07	2.25- 2.90
Rostral width	43	2.47	.02	2.30- 2.75	38	2.66	.02	2.45- 3.00	5	2.60	.03	2.50- 2.70	10	2.76	.04	2.65- 3.00
Rostral-incisor height	43	6.14	.04	5.35- 6.80	38	6.50	.03	6.10- 6.80	5	6.54	.07	6.30- 6.75	10	6.88	.09	6.45- 7.30

N, Sample size; M, Mean; SE, Standard error of the mean; R, Range than _interparietalis_ _ryckmani_. This is due to the longer tail length of _P._ _eremicus_, because _interparietalis_ _ryckmani_ is larger in head and body length.

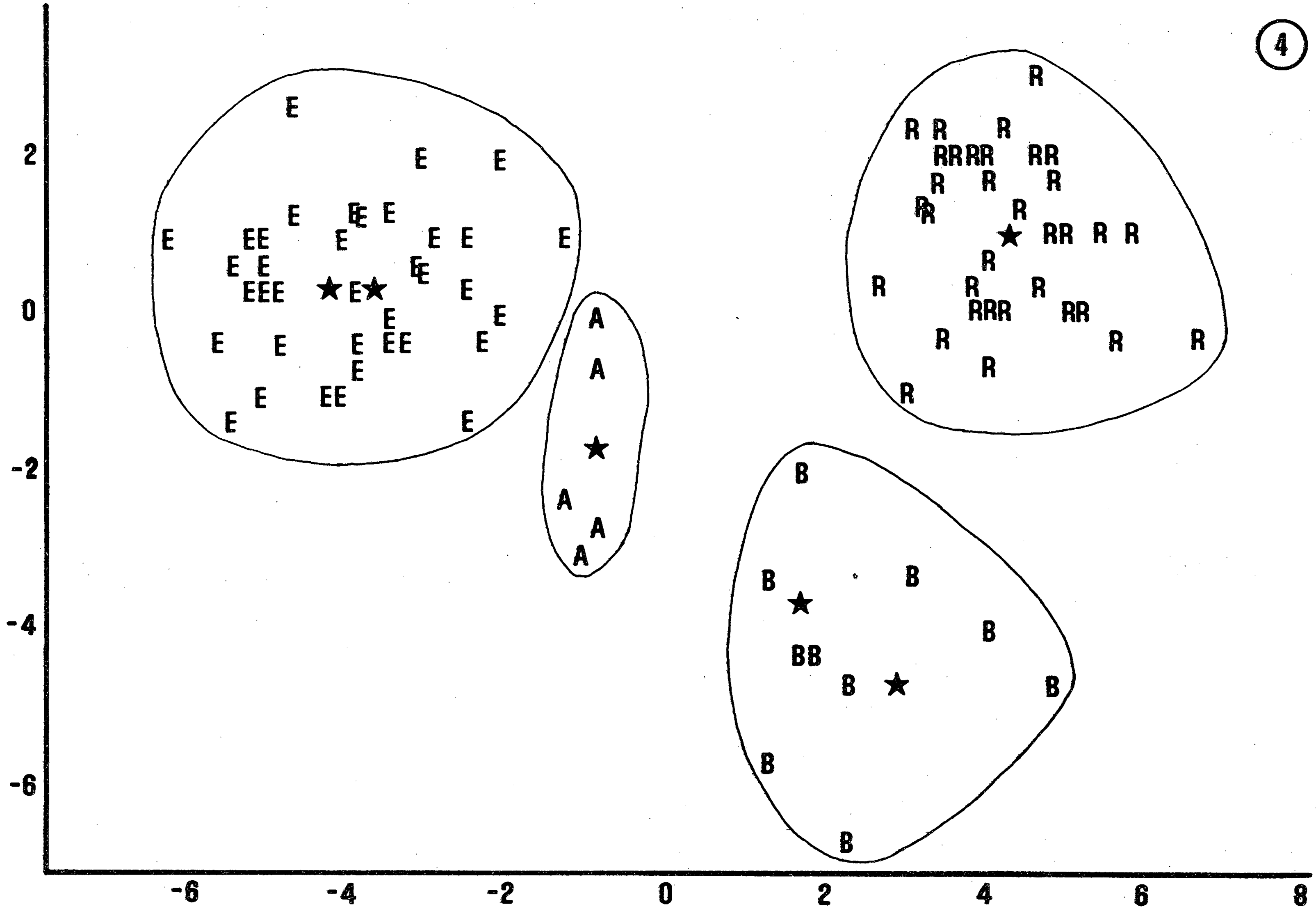
The hybrids are recognizably different from both parental populations. They are intermediate between the parents in width of the incisors and length of the interparietals, but in all other measurements the hybrids are larger than either parental population.

The scattergram (Fig. 4), based on all the measurements taken reveals the morphological relationships more clearly. There is a wide gap between _P._ _eremicus_ and _P._ _interparietalis_ _ryckmani_. The hybrids are between the parents on the graph, but are also below them, reflecting the fact that the hybrids are intermediate in some respects, but in other ways are different from either parental population. Also, the scattergram shows that each hybrid is more like its maternal progenitor than its paternal progenitor.

When the original data were run through the computer as unknowns, every individual was identified to the correct population.

Figure 4. A scattergram from *Peromyscus* morphological data, based on the canonical variables. Stars (★) indicate group means. Two stars in a group indicate the means for the males and females.

E = *Peromyscus eremicus*
R = *Peromyscus interparietalis ryckmani*
A = *Peromyscus eremicus* ♀ X *Peromyscus interparietalis* ♂ hybrid
B = *Peromyscus interparietalis* ♀ X *Peromyscus eremicus* ♂ hybrid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CHAPTER IV

SERUM PROTEIN ELECTROPHORESIS

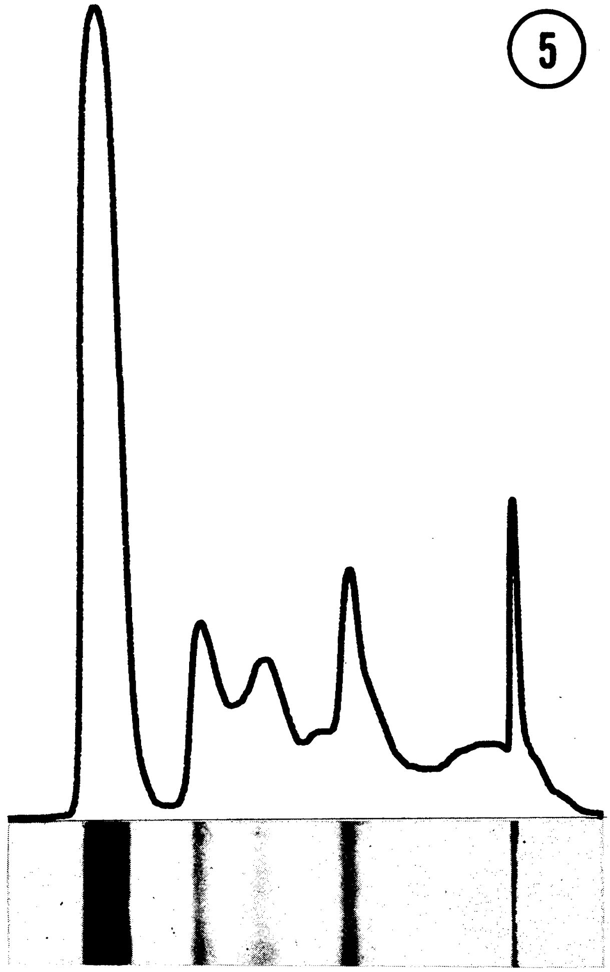
Methods and Materials

The blood serum proteins of the 5 populations described in Chapter 2 and the *P. eremicus* X *P. interparietalis ryckmani* hybrids were compared by cellulose acetate strip electrophoresis.

Blood was taken from the tails of the mice, drawn into capillary tubes, and centrifuged. The serum was then applied to Sepraphore III cellulose acetate strips with a Gelman applicator, and the strips were then placed in an electrophoresis cell. The cell contained 500 ml. of cold (6-10^{o} C.) Gelman high resolution buffer, at a pH of 8.8. Electrical current was run through the cell for one hour. Current strength was maintained at 1.5 ma/strip, between 200 and 300 volts, by a Spinco Duostat regulated D. C. power supply. The strips were then stained with Ponceau S stain, and cleared in a mixture of methyl alcohol and acetic acid. (More detailed instructions may be found in Manual No. 70176-A from the Gelman Instrument Co., Ann Arbor, Michigan.)

The finished strips were then scanned with a Densicord Recording Electrophoresis Densitometer, and the resultant tracings (Fig. 5) were

Figure 5. A finished cellulose acetate strip showing the protein bands and the tracing made by the densitometer. The black line at the right is the point of application of the serum.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used in a statistical analysis of the protein patterns. For each tracing, the height of the curve above the base line was measured at 30 equally spaced intervals. For these series of measurements the discriminant functions were computed and a scattergram was plotted by the same procedure as described above in the section on morphology.

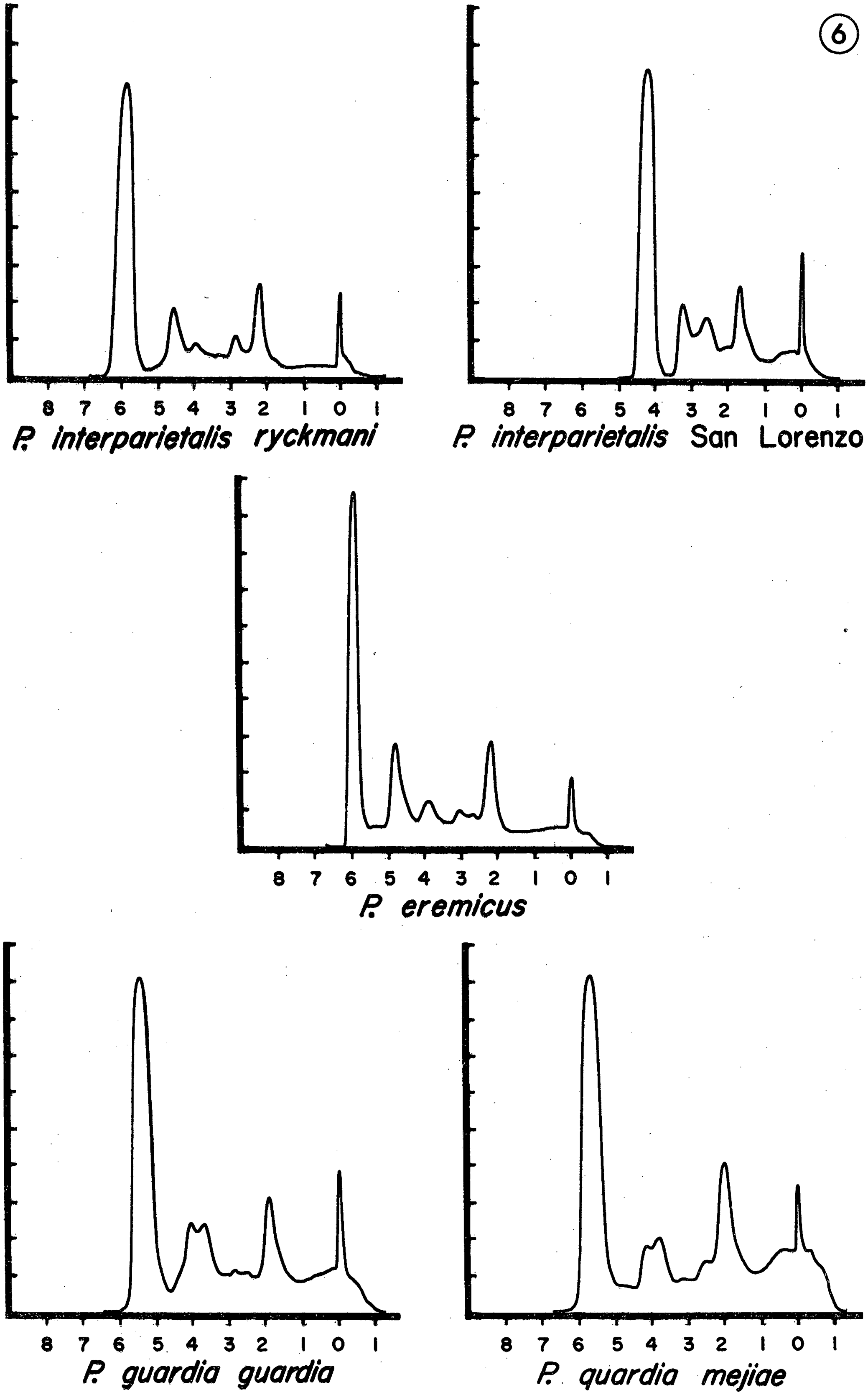
Results

Within groups there was some individual variation, but each group had a characteristic pattern.

The *P. eremicus* pattern was similar to the *P. interparietalis ryckmani* pattern, and *P. guardia guardia* closely resembled *P. guardia mejiae*. *Peromyscus guardia* could be readily separated from the other populations, and the Islas San Lorenzo group also seemed distinct from its relatives. The hybrid patterns did not closely resemble either parental population. A representative tracing from each population is shown in Figs. 6 and 7. Figure 7 also includes patterns of *P. crinitus*, *P. boylii*, and *P. californicus* for comparison.

The results of the statistical analysis are shown in the scattergram, Figure 8. The males and females are grouped separately, so there are two group means for each population, except for hybrid population A, which consisted of only males. The scattergram reveals the relationships clearer than a visual examination of the tracings. Each population falls into a distinct group, with a small amount of

Figure 6. Representative tracings of serum electrophoresis patterns for Peromyscus eremicus and the Peromyscus guardia group. The sharp peak above the zero point is the result of an ink line at the point of application.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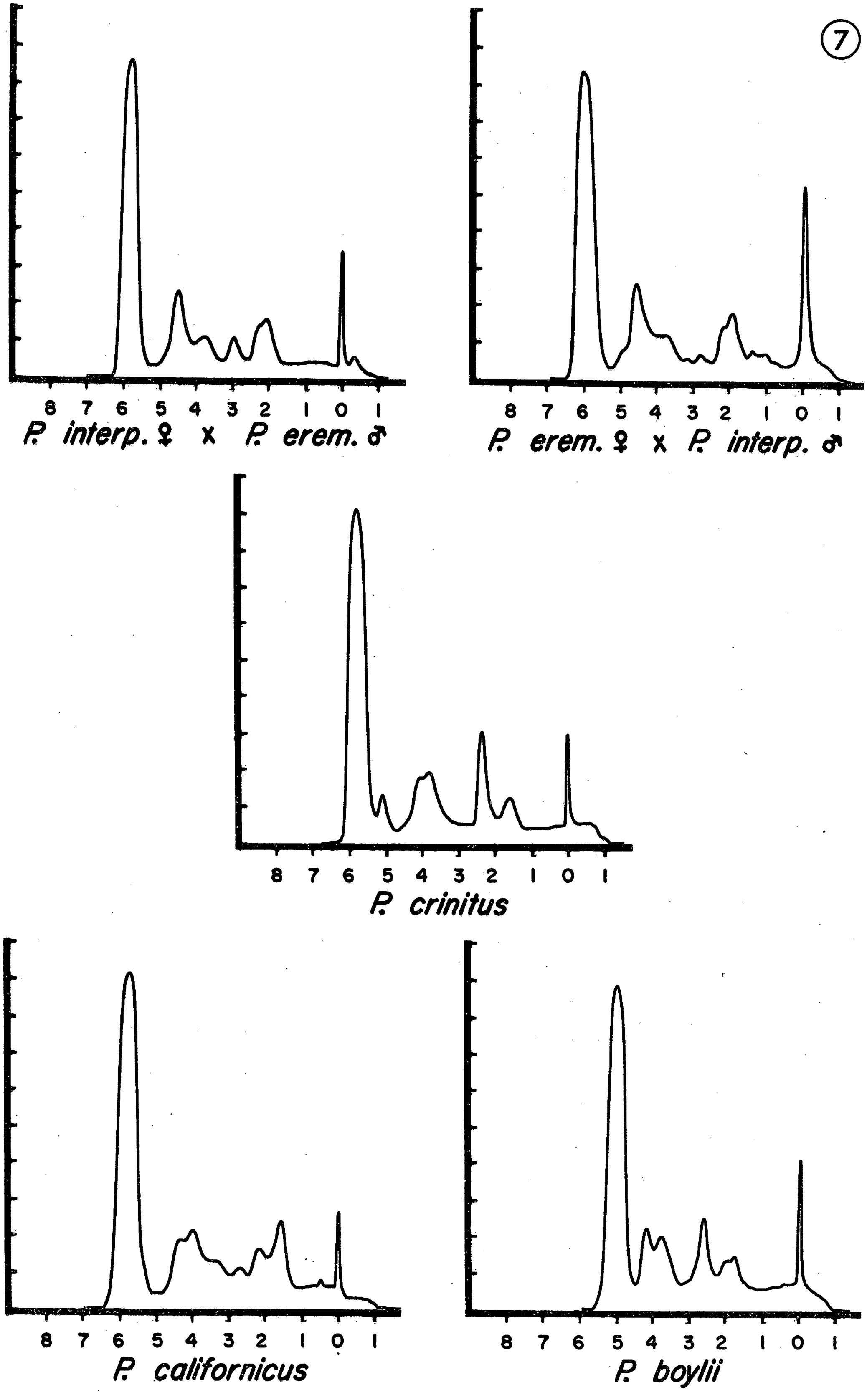
8 7 6 5 4 3 2 1 0 1
P. interparietalis ryckmani
8 7 6 5 4 3 2 1 0 1
P. interparietalis San Lorenzo
8 7 6 5 4 3 2 1 0 1
P. eremicus
8 7 6 5 4 3 2 1 0 1
P. guardia guardia
8 7 6 5 4 3 2 1 0 1
P. quardia mejiae

Figure 7. Representative tracings of serum electrophoresis patterns for the *Peromyscus interparietalis* X *Peromyscus eremicus* hybrids and for three other species of *Peromyscus*. The sharp peak above the zero point is the result of an ink line at the point of application.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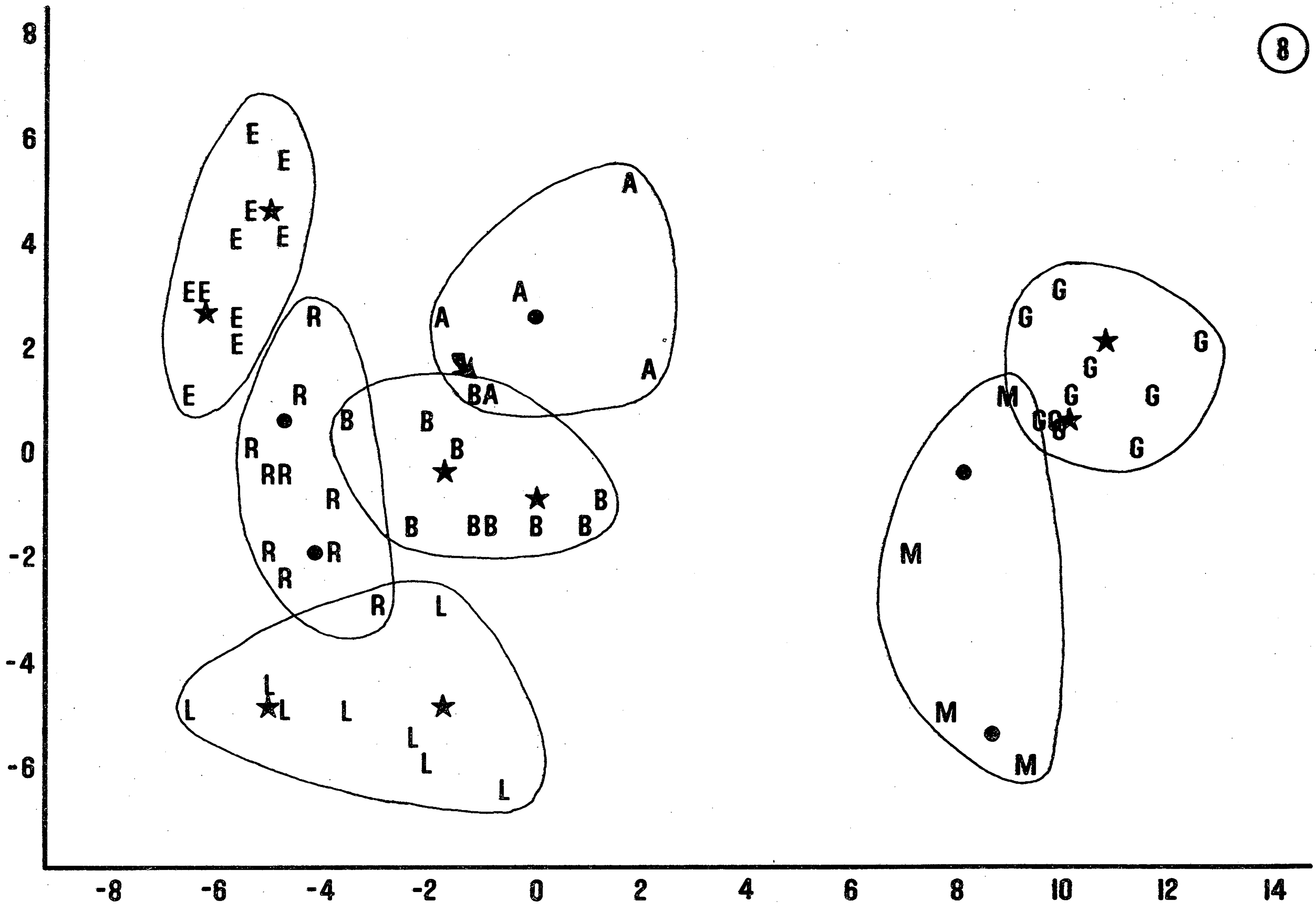
8 7 6 5 4 3 2 1 0 1
P. interp. ♀ x P. erem. ♂
8 7 6 5 4 3 2 1 0 1
P. erem. ♀ x P. interp. ♂
8 7 6 5 4 3 2 1 0 1
P. crinitus
8 7 6 5 4 3 2 1 0 1
P. californicus
8 7 6 5 4 3 2 1 0 1
P. boylii

Figure 8. A scattergram from Peromyscus electrophoretic patterns, based on the canonical variables. Stars (★) and closed circles (●) indicate group means. Two symbols in a group indicate the means for the males and females. The arrow indicates the 2 hybrid individuals which were incorrectly identified by the computer.

E = Peromyscus eremicus
R = Peromyscus interparietalis ryckmani
L = Peromyscus interparietalis subspp., Islas San Lorenzo
G = Peromyscus guardia guardia
M = Peromyscus guardia mejiae
A = Peromyscus eremicus ♀ X Peromyscus interparietalis ♂ hybrid
B = Peromyscus interparietalis ♀ X Peromyscus eremicus ♂ hybrid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overlap between groups; Peromyscus guardia guardia and P. guardia mejiae are close together and are distinctly separate from the other populations. Peromyscus interparietalis from Isla Salsipuedes and from Islas San Lorenzo are also close together and are more like P. eremicus than P. guardia (Fig. 2). The relationship between the hybrids and their parents as shown by the serum proteins is similar to that shown by morphology (Fig. 4).

When the original data were treated as unknowns the computer correctly identified every individual except 2. The 2 misidentified individuals were reciprocal F_1 hybrids as indicated in Fig. 8 by an arrow; their identity was reversed. All of the other 55 mice studied were correctly identified to population and sex.

CHAPTER V

LIFE HISTORIES AND ECOLOGY

The life cycle of *Peromyscus eremicus* has been studied very little, and the *P. guardia* group has not previously been reared in the laboratory. The breeding colonies which were maintained for biosystematic studies provided an opportunity to study the life histories of these species.

Methods and Materials

Two populations were studied; *P. eremicus* from Reche Canyon, Riverside Co., California, and *P. interparietalis ryckmani* from Isla Salsipuedes. The Salsipuedes mice were all from the laboratory colony originally collected in 1962, and the *P. eremicus* were field collected or first generation laboratory bred individuals. The data on growth and development were based on the offspring of 6 pairs of *P. eremicus* and 10 pairs of *P. interparietalis.*

The density of the mice in various habitats on the islands was measured by computing the number of mice caught/number of trap nights for each habitat.

The laboratory environment of these animals is discussed above, in the section on hybridization. Each pair was usually kept together at all times. In order to determine the gestation period, some of the males were removed from their cage within 24 hours after the birth of a litter, and were not replaced until the birth of the next litter, or until it was obvious that the female was not pregnant.

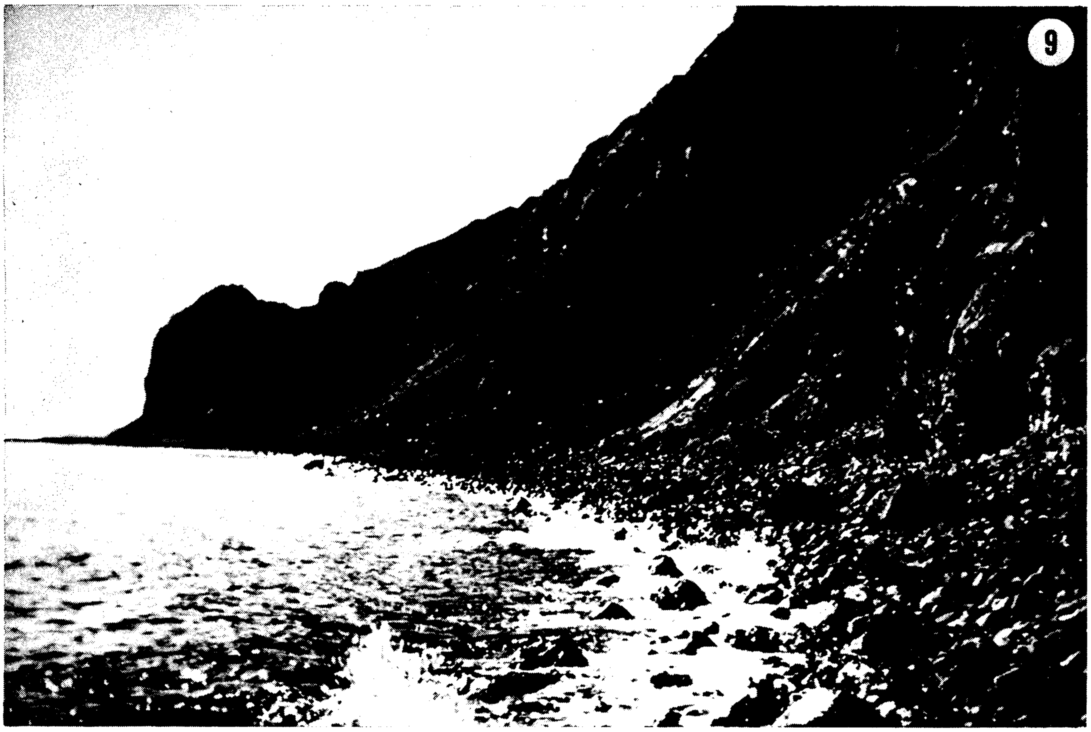
At least once each day the mice were checked for new litters, and observations were made concerning the development of the young. The young mice were weighed twice a week on a triple beam balance.

Ecology

The islands inhabited by the P. guardia group are arid and very rocky, with little vegetation. Banks (in manuscript) states that these mice seem to be equally abundant in all microhabitats. Our trapping indicated that they are in many parts of the islands, but are concentrated along the rocky beaches. In 1962, on Isla Salsipuedes, R. E. Ryckman set 18 live traps along the rocky beach and caught 18 Peromyscus. In June, 1965, the author made additional collections on Isla Mejia, Isla Angel de la Guarda, and Islas San Lorenzo. A total of 340 trap nights in rocky canyons and brushy, sandy flats yielded 7 Peromyscus (2.1% catch), while 218 trap nights along rocky beaches yielded 63 Peromyscus (29% catch). The population density appeared to be low in the interior but much higher on the rocky beaches. Figures 9 and 10 illustrate two areas that yielded a 25% catch of Peromyscus. The mice appear to prefer beaches with rather large

Figure 9. The habitat of Peromyscus interparietalis interparietalis along the west coast of Isla San Lorenzo Sur. The mice were quite numerous along the rocky beach in the foreground.

Figure 10. The habitat of Peromyscus guardia guardia along the southeast coast of Isla Angel de la Guarda. The author is shown setting traps in the foreground; mice were most numerous just above the tide zone.


9


10

rocks; this permits the mice to move between and under the rocks. They are apparently not dependent on terrestrial plants for food, because a number of them were caught at the foot of high, sheer cliffs, with no vegetation near by. In this situation, whatever they had eaten must have come from the sea.

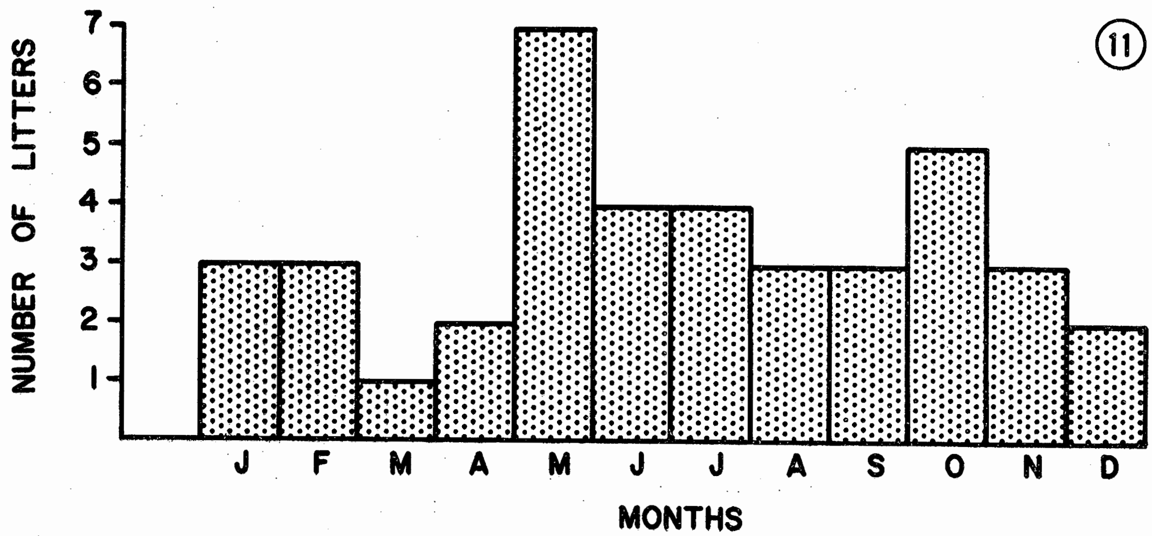
There is an indication that P. eremicus will also live in this habitat. Two specimens of P. eremicus were trapped near Puertocitos, Baja California, on a rocky beach similar to those on the islands.

Breeding Habits

The few field observations that are available suggest that the peak of breeding activity of the P. guardia group is in early spring (Banks, in manuscript). In June, 1965, of 13 females trapped for this study, on Isla Angel de la Guarda, 2 were pregnant; a litter of 3 was born of July 4, and another litter of 3 on July 10. Of 3 females from Isla Mejia and 6 females from Islas San Lorenzo, none were pregnant.

In the laboratory studies, mice of the Salsipuedes population bore litters every month of the year, with the largest number of litters in May (Fig. 11). The apparent reduction in breeding in March and April is probably due to the small sample size (40 litters for the entire year), but it is evident that they will breed throughout the year. The

Figure 11. *Peromyscus interparietalis ryckmani* born in captivity during a one year period; the distribution of birth dates of 40 litters is shown by month.


NUMBER OF LITTERS
7
6
5
4
3
2
1
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS
11

birth dates of 8 litters of _P. eremicus_ born in the laboratory were also distributed throughout the year.

Peromyscus interparietalis ryckmani is much more prolific in the laboratory than _P. eremicus_. Several pairs of _P. eremicus_ never produced young, and the others bore from 1 to 5 litters in a year. All pairs of _P. interparietalis ryckmani_ bred successfully, with most females producing from 2 to 6 litters in a year. Two especially prolific females produced 9 and 10 litters, respectively, in a year.

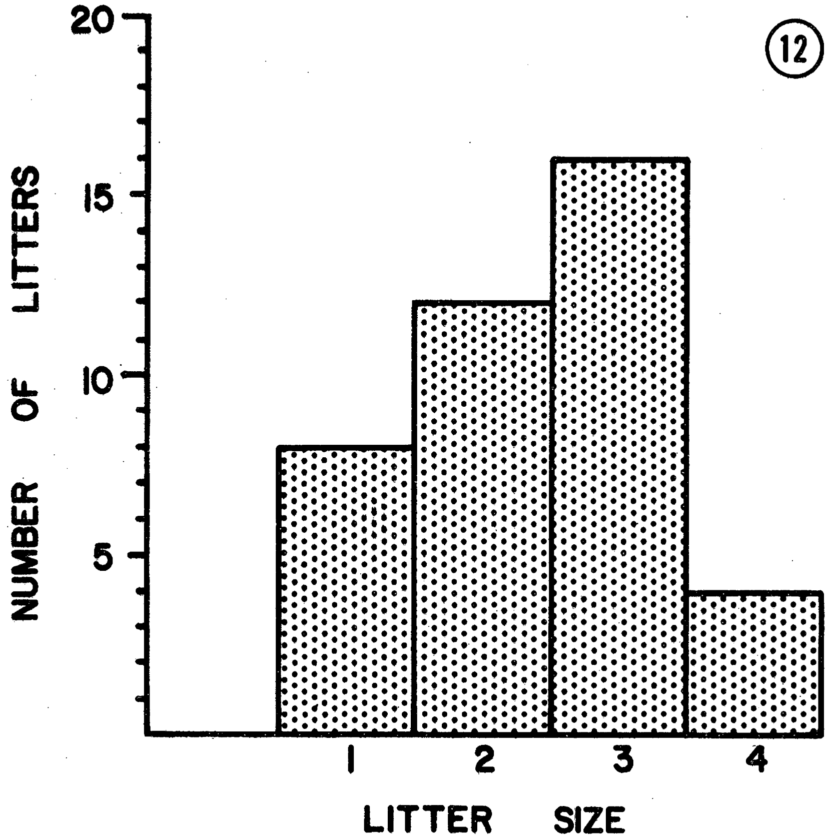
The mean litter size of _P. interparietalis ryckmani_ was similar to _P. eremicus_. Svihla (1932) found the mean litter size of 5 litters of _P. eremicus_ to be 2.60/litter. Davis and Davis (1947) found the mean of 404 litters of _P. eremicus_ to be 2.42/litter. In this study the litter size for _P. interparietalis ryckmani_ ranged from 1 to 4, averaging 2.4 (40 litters) (Fig. 12), while the maximum litter size for _P. eremicus_ was 3, with an average of 2.22 (14 litters) (Fig. 13).

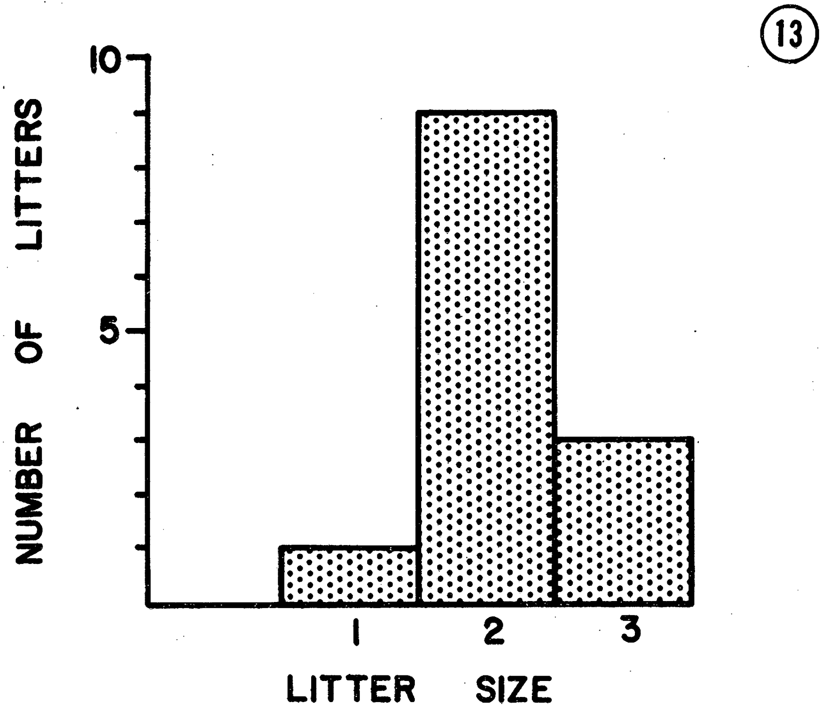
In the study by Davis and Davis (1947), the sex ratio for _P. eremicus_ was 64 males to 57 females, or 112 males to 100 females. The sex ratio of _P. interparietalis ryckmani_ was very close to that, with 52 males and 46 females, or 113 males to 100 females (43 litters).

Svihla (1932) found the gestation period of one non-lactating _P. eremicus_ to be 21 days. In another case (Davis and Davis, 1947), the individual females had litters at intervals of 28 to 30 days. In the

Figure 12. Litter size frequency of 40 litters of *Peromyscus interparietalis ryckmani* born in captivity.

Figure 13. Litter size frequency of 14 litters of *Peromyscus eremicus* born in captivity.


12
NUMBER OF LITTERS
20
15
10
5
1
2
3
4
LITTER SIZE


13
NUMBER OF LITTERS
10
5
1
2
3
LITTER SIZE

present study, there were 25 instances in which a female P. interparietalis bore litters in consecutive months, with the interval between litters ranging from 27 to 37 days, and averaging 31.9 days. All other litters were at least 2 months apart. According to Svihla (1932), females of most species of Peromyscus are in estrus immediately following parturition, but females of the subgenus Haplomylomys are not. Of Haplomylomys, Svihla was studying only P. eremicus and P. californicus. Apparently P. interparietalis is in estrus following parturition. Several attempts were made to determine the gestation period by removing the male within 24 hours after parturition. In 3 cases this was successful, and yielded gestation periods of 32, 35, and 32 days, respectively, for lactating females. Since they do seem to be in estrus immediately following parturition, the time between consecutive litters may approximate the gestation period, with an average of 31.9 days for lactating females. If this is correct, the non-lactating gestation may be similar to that of P. crinitus (Egoscue, 1964), because lactation is known to lengthen gestation by 2 to 7 days (Svihla, 1932). The condition of the young at birth is also similar to P. crinitus.

Attempts to determine the precise gestation period for eremicus were unsuccessful. Two females had litters in consecutive months at intervals of 35 days in each instance.

Growth and Development

The pattern of development is similar in these 2 species. At birth they are naked, the dorsal surface is pigmented, vibrissae are present, and the ears are folded. On almost all individuals, the pinna unfold within 24 hours or soon thereafter. Hair appears on the dorsal surface by the 2nd day and on the ventral surface on the 5th or 6th day; by this time the thick, black hair is obvious on the dorsal surface. The eyes usually open sooner in P. interparietalis than in P. eremicus (Table 2). The young remain attached to their mother most of the time until they are weaned. This seems to be a gradual process, and begins on the 20th to the 22nd day for P. eremicus, and from the 16th day to the 21st day for P. interparietalis. After this they still receive part of their nourishment from the mother, but by the 25th day of age they all appear to be weaned. One individual of P. interparietalis was seen eating lettuce on his 16th day. This was the earliest age at which the young were observed eating solid food.

In P. eremicus the post-juvenile molt begins on the 34th to the 37th day. In P. interparietalis it is quite variable, with the molt beginning on the 35th to the 55th day, but with the majority starting on the 38th to the 43rd day. Other aspects of development are covered in Table 2.

Table II. Comparative development of 2 species of Peromyscus

	P. interparietalis ryckmani	P. eremicus
Weight at birth	2.55-3.0 gm. Mean = 2.74	1.85-2.60 gm. Mean = 2.23
Pinna erect	Most within 24 hours All within 48 hours	Most within 24 hours All within 48 hours
Righting response	24-48 hours	24-48 hours
Incisors erupt	Lower incisors - 3rd to 6th day. Usually on 4th or 5th day. Upper incisors 1 or 2 days later.	Two litters - 3rd day. One litter - 2nd day.
Auditory meatus opens	8th to 11th day. Usually on 10th day.	9th to 11th day. Usually on 10th or 11th day.
Eyes open	11th to 14th day. Usually on 11th or 12th day.	11th to 15th day. Usually on 13th to 15th day.

Peromyscus interparietalis is heavier than P. eremicus at birth, and throughout its development. Fig. 14 illustrates the average growth curves for both species up to 60 days of age.

The pattern of the post-juvenal molt is similar in both species. The molt begins in the middle of the ventral surface, and moves forward and to the sides. The molt proceeds to the gray dorsal area around the front legs and in the middle of the sides. These areas join along the side, and move up along the length of each side, moving faster in the center, and finally meet across the middle of the back. By this time the ventral side has completed its molt, including the ventral surface of the head. On the back it moves simultaneously toward the head and the tail. The top of the head is the last area to molt, finishing on the forehead between the ears.

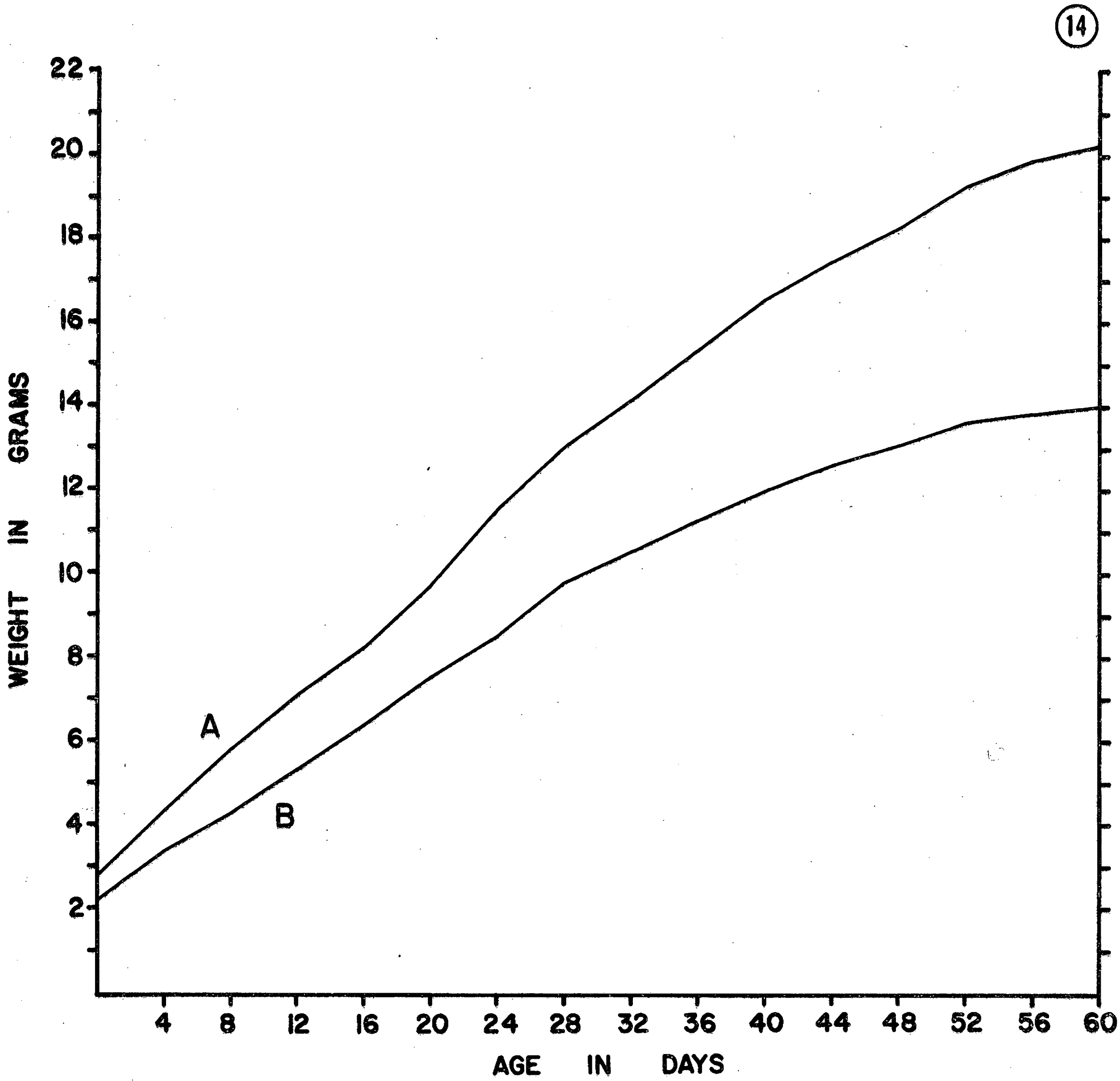
Temperament and Behavior

There is an obvious temperament difference between P. eremicus and P. interparietalis ryckmani. Peromyscus eremicus is excitable and shy, and seldom attempts to bite when handled. Peromyscus interparietalis is less excitable and is quite aggressive. They will bite readily when disturbed, especially if there are young in the nest.

In both species, when a male is placed with a female, they may be compatible right away, or they may fight for a short time. Thereafter

Figure 14. Mean growth curves, based on weight.

A = _Peromyscus interparietalis ryckmani_ (7 litters)
B = _Peromyscus eremicus_ (6 litters)


14
22
20
18
16
14
12
10
8
6
4
2
WEIGHT IN GRAMS
A
B
4 8 12 16 20 24 28 32 36 40 44 48 52 56 60
AGE IN DAYS

they share the same nest, even when there are newborn young in the nest.

Both species built fluffy, globular cotton nests in the laboratory.

CHAPTER VI

DISCUSSION

Peromyscus interparietalis ryckmani is distinct from *P. eremicus* in morphology, blood proteins, and certain aspects of development, but they have not yet diverged far enough to have developed mechanisms of intersterility; they interbreed freely in the laboratory. Except for the unusual sex ratio, the hybrids appear to be normal, and they are fully fertile. The sex ratio may reflect the genetic divergence of the 2 populations, however with a larger number of litters the difference might diminish.

The hybrids are intermediate between the parents in some respects, however they exhibit the condition of heterosis, and are different from either parent in some characters. They are significantly larger than either parent in many body and skull dimensions. The laboratory reared controls and their progenitors were of equivalent size but the laboratory hybrids were larger than their progenitors.

The F_1 hybrid specimens were readily distinguished from their parental progenitors on the basis of morphology and the composition of their blood proteins.

As Johnson and Wicks (1959) found to be true in the mammals they worked with, the serum electrophoretic patterns of the mice in this study differed between populations, and reflected taxonomic relationships. If it can be assumed that the distance between populations on the scattergram indicates the amount of genetic separation, the picture given by serum protein composition agrees with the current understanding of relationships within this group, based on morphology (Banks, in manuscript; and Burt, 1960) and hybridization. This supports the use of serum proteins as a taxonomic character in mammals.

The condition of the young at birth and the patterns of early development are similar in P. interparietalis and P. eremicus, and are similar to P. crinitus and P. californicus. At birth and during early development these 4 species are several days more advanced than the young of the subgenus Peromyscus of the same age (Egoscue, 1964; McCabe and Blanchard, 1950; and Svihla, 1932).

Banks (in manuscript) discusses the possible history of the P. guardia group. The submarine topography of the Gulf of California is of little help in determining the derivation of the island populations. The whole island chain is separated from the peninsula of Baja California by the Salsipuedes Basin, which is over 800 fathoms deep. There has been extensive fault activity in the Gulf of California, and there is some evidence that the Salsipuedes Basin may be of recent origin (Rusnak, Fisher, and Shepard, 1964; and Shepard, 1950).

SUMMARY

The Peromyscus guardia group of mice, inhabiting islands in the Gulf of California, have previously been studied very little. This study was undertaken to investigate the taxonomic relationship of this group to P. eremicus and to study certain aspects of the biology of both groups.

Hybridization experiments were conducted between P. eremicus from Riverside Co., California, and P. interparietalis ryckmani from Isla Salsipuedes, in the Gulf of California, Mexico. These crosses produced fertile hybrids, indicating that these two species are closely related and have not yet developed mechanisms of intersterility. P. guardia did not breed in the laboratory under the conditions used in this study.

A morphological study was made of P. eremicus, P. interparietalis ryckmani and their F_1 hybrids. From the skin and skull measurements the discriminant functions were computed and a canonical scattergram plotted. Peromyscus interparietalis ryckmani is quite distinct morphologically from P. eremicus. The hybrids were larger than either parent, and resembled their maternal progenitor more than their paternal progenitor.

The blood proteins of _P. eremicus_, two subspecies of _P. interparietalis_, the hybrids mentioned above, and two subspecies of _P. guardia_ were compared by serum electrophoresis. In this study and in previous work with mammals the protein patterns reflected taxonomic relationships at the generic and specific levels. In this study the protein patterns were analyzed by use of the discriminant functions and a canonical scattergram. The picture given by this procedure agreed closely with current understanding of the systematics of this group. The electrophoretic pattern for _P. guardia guardia_ is similar to _P. guardia mejiae_; and the pattern for _P. interparietalis ryckmani_ and _P. interparietalis_ subspp. from Islas San Lorenzo are similar to each other. _Peromyscus interparietalis_ is similar to _P. eremicus_, but _P. guardia_ is quite different from _P. eremicus_ and _P. interparietalis_. Serum proteins appear to be a useful taxonomic character.

The _P. guardia_ group of mice inhabit arid, rocky islands. The population density appears to be low in the interior of the islands but much higher on the rocky beaches.

The pattern of growth and development is similar in _P. eremicus_ and _P. interparietalis_, but there are a few consistent differences. The pattern of development in these species is similar to the other members of the subgenus _Haplomylomys_; i. e., they are born in a more advanced state than members of the subgenus _Peromyscus_.

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LOMA LINDA UNIVERSITY

Graduate School

BIOSYSTEMATICS AND LIFE HISTORIES OF THE *PEROMYSCUS GUARDIA* GROUP OF MICE AND *PEROMYSCUS EREMICUS* (RODENTIA: CRICETIDAE)

by

Leonard R. Brand

An Abstract of

a Thesis in Partial Fulfillment

of the Requirements for the Degree

Master of Arts in the Field of Biology

June 1966

ABSTRACT

The purpose of this project was to investigate the taxonomic relationship and the biology of Peromyscus eremicus, and the Peromyscus guardia group of mice from islands in the Gulf of California.

Hybridization experiments were conducted between P. eremicus and P. interparietalis ryckmani. They were interfertile and produced fertile hybrids. Peromyscus guardia did not breed in the laboratory.

Body and skull measurements for P. eremicus, P. interparietalis ryckmani, and their F_1 hybrids were analyzed by computing the discriminant functions and plotting a canonical scattergram. Peromyscus interparietalis ryckmani is quite distinct from P. eremicus. The hybrids were larger than either parent and resembled their maternal progenitor more than their paternal progenitor.

Blood proteins of P. eremicus, P. interparietalis, and P. guardia were compared by serum electrophoresis, and from the protein patterns the discriminant functions were computed and a canonical scattergram plotted. Peromyscus interparietalis is similar to P. eremicus, and P. guardia is quite different from both of them. Within a species, the subspecies showed similar patterns. Serum proteins appear to be a useful taxonomic character.

The pattern of growth and development is similar in P. eremicus and P. interparietalis with a few consistent differences.