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A STUDY OF RACIAL HYBRIDS IN THE DEER-MOUSE, *PEROMYSCUS MANICULATUS*

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THE present study is a preliminary attempt to determine the mode of inheritance of certain subspecific characters in the deer-mouse, *Peromyscus maniculatus*. The method employed was the hybridization of the two subspecies *rufinus* and *sonoriensis*. These two forms differ considerably in pelage color and to a lesser degree in certain body dimensions.

The stock of *sonoriensis* was presented by the Scripps Institution of the University of California through Dr. F. B. Sumner. The Carnegie Institution of Washington provided most of the field expenses for the expedition on which the stock of *rufinus* was secured. Funds for rearing the mice were provided by the Museum of Zoology and by grants from the Faculty Research Fund of the University of Michigan.

The stock of *sonoriensis*, from Victorville, California, was received in 1925. It was inbred when received and was further inbred in my laboratory. When prepared as specimens the mice of the 1-year age class averaged 47.5 (39–61) weeks old, and those of the 2-year class averaged 95.4 (79–115) weeks old.

The ancestral *rufinus* stock came from Buena Vista, Colorado. It was taken by myself, and its characters have been

reported upon previously (Dice, 1933, pp. 3–4). Most, but not all, of the *rufinus* used in making these crosses were descendants of a single pair of animals, whose offspring later were inbred and designated the E-line (Dice, 1933, p. 23). The E-line differs from the non-inbred Buena Vista stock only in a few characters, and I have here compared the hybrids with the average measurements of the non-inbred Buena Vista stock rather than with the averages of the inbred E-line.

When prepared as specimens the hybrid mice of the 1-year age class averaged for the F_1 generation 59.1 (45–67) weeks, for the F_2 generation 48.0 (43–55) weeks, and for the F_3 generation 49.1 (38–57) weeks of age. The 2-year age class is represented in the hybrids only in the F_1 generation, the mice of which averaged when prepared as specimens 83.8 (79–90) weeks of age.

Litter Size

The number of young per litter averaged $3.94 \pm .12$ in *Peromyscus m. rufinus* from Buena Vista and $3.86 \pm .18$ in the Ann Arbor-reared stock of *P. m. sonoriensis* from Victorville (Table I). No litter of either of these parent stocks contained at the time of weaning more than 6 young. Of 1567 broods of various forms of *Peromyscus* reared in California (Sumner, McDaniel, and Huestis, 1922, p. 140) one litter of 9 young and another litter of 8 young are reported; the average number of young per litter was 3.22.

In the first generation hybrids between *rufinus* and *sonoriensis,* the litters average $5.58 \pm .31$ young, which is considerably more young per litter than are produced by either parent subspecies; also, none of these hybrid litters contained less than 4 young, while some of the litters of each parent stock were made up of 3, 2, or even 1 young. Further, one hybrid litter contained 7 young, and another litter 10 young, both these being larger litters than produced by either parent stock. Ten young in a litter is a large number for these mice to rear, for there are only 6 mammae. That this number of young

TABLE I

LITTER SIZE. FREQUENCY OF LITTERS OF EACH NUMBER OF YOUNG

Peromyscus maniculatus rufinus and *P. m. sonoriensis*

Stock	Number of young per litter										Mean litter size
	1	2	3	4	5	6	7	8	9	10	
Rufinus, Buena Vista (not inbred)	4	7	10	18	18	7	–	–	–	–	3.94 ± .12
Sonoriensis (reared in Ann Arbor)	4	3	6	9	7	6	–	–	–	–	3.86 ± .18
Rufinus × *sonoriensis* F_1	–	–	–	3	4	3	1	–	–	1	5.58 ± .31
Rufinus × *sonoriensis* F_2	2	–	1	4	6	1	–	–	–	–	4.07 ± .26
Rufinus × *sonoriensis* F_2	4	2	7	–	1	–	–	–	–	–	3.43 ± .20

actually belonged to the one litter is certain, for a careful check was made at the time the record was taken.

The increase in litter size in the first hybrid generation between *rufinus* and *sonoriensis* is statistically significant, the differences between the F_1 hybrids and the *rufinus* parent stock being 5.0 times the probable error and between the hybrids and the *sonoriensis* parent stock 4.8 times the probable error. The increase of litter size in the first hybrid generation can probably be explained as due to hybrid vigor.

In the second hybrid generation of the *rufinus-sonoriensis* cross, the litter size is about the same as that of the two parent stocks, averaging 4.07 ± .26 young. In the third hybrid generation the litter size averages below that of either parent, being only 3.43 ± .20 young, but this decrease is not statistically significant.

Sex Ratio

Females average more numerous than males in both of the parent stocks of *rufinus* and *sonoriensis* used in producing these hybrids (Table II). The sex ratio is 92.6 ± 8.2 for the

TABLE II

Sex Ratios

Peromyscus maniculatus rufinus and *P. m. sonoriensis*

Stock	No. ♂	No. ♀	No. ♂ per 100 ♀
Rufinus, Buena Vista	113	122	92.6 ± 8.2
Sonoriensis, Victorville			
Reared at Ann Arbor	65	73	89.0 ± 10.2
Reared in California	350	373	93.8 ± 4.7
Rufinus × *sonoriensis*			
F_1	21	41	51.2 ± 9.3
F_2	24	33	72.7 ± 13.2
F_3	24	24	100.0 ± 19.5

stock of *rufinus* from Buena Vista. For the stock of *sonoriensis* from Victorville the sex ratios are low both for the animals reared in California by Sumner (Sumner, McDaniel, and Huestis, 1922, p. 146) and for those reared at Ann Arbor,

Michigan. For the *sonoriensis* reared in Ann Arbor the sex ratio is 89.0 ± 10.2. The probable errors of all these ratios are large, as calculated by the formula furnished by Pearl to Sumner, McDaniel, and Huestis (1922, p. 125), and none of the sex ratios differ from 100 by a statistically significant amount.

In the first generation hybrids between *rufinus* and *sonoriensis* the females are nearly twice as numerous as the males, the sex ratio being 51.2 ± 9.3. The sex ratio of the F_1 hybrids compared with that of the parent stocks differs from *rufinus* by 41.4 ± 12.3 and from *sonoriensis* (reared in California) by 42.6 ± 10.4. The differences are respectively 3.4 and 4.1 times their probable errors and are therefore of some statistical probability. The few hybrid individuals available for these comparisons, however, and the great variation in sex ratios in *Peromyscus* reported by Sumner, McDaniel, and Huestis and by Karol caution against concluding that the hybridization of *rufinus* and *sonoriensis* actually produced an increase in the proportion of females.

In hybrids of the second generation the proportion of males is greater than the first, but is still much less than in the parent stocks. Owing to the large probable errors the differences are of no statistical importance. In hybrids of the third generation the sexes are exactly equal in number.

The F_1 hybrids between various subspecies of the species *Peromyscus polionotus* were noted by Karol (1928, p. 160) to have a lower sex ratio than "pure" *polionotus,* but the difference is not statistically significant, and the author did not attach any importance to it.

The apparent decrease in the proportion of males in the F_1 generation of the cross between *rufinus* and *sonoriensis* does not agree with the findings of Sumner, McDaniel, and Huestis (1922, pp. 148–149), who found some indication that in hybrids in the genus *Peromyscus* the sex ratio was higher than in "pure" races. The differences described by these authors, however, are not of much statistical significance. The "hybrids" from Dr. Sumner's laboratory included animals of

the F_1, F_2, and later generations as well as animals from various back-crosses, so that Sumner's hybrids are not directly comparable with the various generations of the *rufinus-sonoriensis* cross.

Measurements of Body and Skeleton

The non-inbred stock of *rufinus* from Buena Vista averages smaller than Victorville *sonoriensis* in body length and in tail length, but larger in foot length and in ear length (Table III). The differences are all of statistical significance, being for the 1-year age class from 6.6 to 20.8 times their probable errors.

The F_1 hybrids average in body length smaller than either of the parent stocks, but the difference from *rufinus* is not significant. Compared with *sonoriensis* the hybrids of the 1-year class average 3.87 $\pm$ .75 mm. shorter, a significant difference 5.2 times its probable error, and the hybrids of the 2-year class average 3.39 $\pm$ 1.01 mm. shorter, a difference 3.4 times its probable error.

In tail length the F_1 hybrids are not significantly different from *sonoriensis,* but average longer than *rufinus.* The tails of the hybrids of the 1-year class average 5.09 $\pm$ .39 mm. longer than in *rufinus,* a difference 9.2 times its probable error, and those of the 2-year class average 1.41 $\pm$ .88 longer, a difference only 1.6 times its probable error. Owing to the small number of individuals in the 2-year class the probable error of this comparison is large, but the figures support the significant difference shown by the 1-year class.

In foot length the F_1 hybrids average significantly larger than either parent stock. The difference from *rufinus* in the 1-year age class is for the females .327 $\pm$ .077 mm., which is 4.2 times its probable error, and for the males .360 $\pm$ .093 mm., which is 3.9 times the probable error. From *sonoriensis* the difference is for females .823 $\pm$ .080 mm., which is 10.3 times its probable error, and for the males 1.007 $\pm$ .110 mm., which is 9.2 times its probable error. The differences in the 2-year age class support the significance of these differences,

TABLE III

AVERAGE BODY MEASUREMENTS IN MILLIMETERS

Peromyscus maniculatus rufinus and *P. m. sonoriensis*

Stock	No.	Body length	Tail length	♀ Foot length	♂ Foot length	Ear length
Rufinus, Buena Vista						
1-year age class	161	85.72 ± .26	70.08 ± .23	19.738 ± .051	19.947 ± .044	17.935 ± .041
2-year age class	35	89.77 ± .53	70.94 ± .54	19.848 ± .105	20.121 ± .106	18.563 ± .109
Sonoriensis, Victorville						
1-year age class	65	88.81 ± .26	73.37 ± .32	19.242 ± .055	19.300 ± .073	16.686 ± .044
2-year age class	23	91.74 ± .58	74.00 ± .59	19.260 ± .112	19.630 ± .110	17.265 ± .137
Rufinus × *sonoriensis*						
F_1, 1-year age class:						
From *rufinus* mothers	23	81.87 ± .59	74.41 ± .49	.....	.....	17.500 ± .068
From *sonoriensis* mothers	10	92.00 ± .49	77.25 ± 1.13	.....	.....	17.933 ± .135
All 1-year age class	33	84.94 ± .70	75.17 ± .50	20.065 ± .058	20.307 ± .082	17.613 ± .065
F_1, 2-year age class	23	88.35 ± .83	72.35 ± .70	20.122 ± .074	20.160 ± .116	18.330 ± .065
F_2, 1-year age class	32	86.28 ± .47	67.00 ± .44	19.260 ± .105	19.933 ± .152	17.606 ± .072
F_3, 1-year age class	33	89.91 ± .37	67.64 ± .29	19.994 ± .063	19.827 ± .098	17.633 ± .088

though in each comparison the probable errors are greater and the individual comparisons therefore have somewhat less statistical significance.

In ear length the F_1 hybrids are intermediate between the two parent stocks, being significantly smaller than *rufinus* and larger than *sonoriensis*. Compared with *rufinus* the F_1 hybrids of the 1-year age class average .322 ± .077 mm. smaller, a difference 4.2 times its probable error, while the 2-year hybrids also are smaller, but not significantly so. Compared with *sonoriensis* the F_1 hybrids of the 1-year class average .927 ± .078 mm. longer in ear length, a difference which is 11.9 times its probable error, and the hybrids of the 2-year class average 1.065 ± .152 mm. longer, a difference 7.0 times its probable error.

It will be noted that the F_1 hybrids average in body length close to the measurements of *rufinus*, which is the smaller parent stock, while in tail length they average close to *sonoriensis*, the parent stock having the longer tail. In foot length the hybrids are significantly larger than either parent stock. In ear length the hybrids are intermediate. Only in foot length is there an indication of increased size which might be ascribed to heterosis. In the other body measurements the hybrids are intermediate or close to one or other parent stock. In body length indeed the hybrids average smaller than either parent stock, although the difference from *rufinus* is not significant.

The F_2 hybrids of the 1-year age class do not differ significantly from the F_1 hybrids in body length nor in ear length. In tail length the F_1 hybrids average 8.17 ± .67 mm. longer than the F_2 hybrids, a difference which is over 12 times its probable error. In foot length the F_1 females average .805 ± .120 mm. longer than the F_2 females, a difference which is 6.7 times its probable error, and therefore significant. The F_1 males average in foot length .374 ± .173 mm. longer than the F_2 males, a difference 2.2 times its probable error and not significant in itself, but which supports the presumption that the F_1 hybrids have on the average larger feet than the hybrids of the second hybrid generation.

The F_3 hybrids in body length average $3.63 \pm .60$ mm. longer than the F_2 hybrids, a difference 6.0 times its probable error, and therefore significant. There is no significant difference in tail length nor ear length between the F_2 and F_3 generations. In length of hind foot the F_3 females average $.734 \pm .122$ mm. longer than the F_2 females, a difference 6.0 times its probable error, and therefore significant, but the hind feet of the F_3 males are only slightly and not significantly shorter than those of the F_2 males.

It will be noted that there is no significant difference in ear length between the F_1, F_2, and F_3 hybrid generations. In body length the F_2 hybrids do not differ significantly from the F_1 hybrids, but the F_3 hybrids are significantly larger. In tail length the F_2 hybrids are considerably shorter than the F_1 hybrids, but the F_3 hybrids are nearly the same as the F_2 hybrids. In length of hind foot the males of the three hybrid generations are not significantly different, but the females of the second hybrid generation are distinctly smaller than those of the first generation, while the females of the third hybrid generation are much larger than those of the second generation, being about equal in this measurement to those of the first hybrid generation.

In size of skull and skeleton the parent stock of *rufinus* averages larger than the stock of *sonoriensis* in all measurements (Table IV). The differences are, however, not of statistical significance for the condylo-zygomatic length of skull. For femur length and bullar width the differences are of statistical significance, being respectively 4.1 and 4.8 times their probable errors. For length of mandible and for condylo-premaxillary skull length the differences are of high significance, being respectively 14.5 and 8.6 times their probable errors.

The F_1 hybrids do not differ significantly from the *rufinus* parent stock in any skeletal measurement. Compared with the *sonoriensis* stock the hybrids are larger in every measurement, but the differences are not significant for femur length nor for condylo-zygomatic skull length.

TABLE IV

AVERAGE SKELETAL MEASUREMENTS IN MILLIMETERS; 1-YEAR AGE CLASS; BOTH SEXES
Peromyscus maniculatus rufinus and *P. m. sonoriensis*

Stock	No.	Femur	Mandible	Skull length	Condyle—zygoma	Bullar width
Rufinus, Buena Vista	149	15.980 ± .041	15.871 ± .026	24.006 ± .041	17.044 ± .027	10.655 ± .014
Sonoriensis, Victorville	50	15.692 ± .057	15.129 ± .044	23.378 ± .060	16.942 ± .042	10.520 ± .024
Rufinus × *sonoriensis*						
F_1 from *rufinus* mothers.....	21	15.638 ± .093	15.595 ± .061	23.662 ± .095	16.900 ± .065	10.600 ± .036
F_1 from *sonoriensis* mothers ..	11	16.436 ± .102	15.982 ± .084	24.545 ± .117	17.636 ± .075	10.927 ± .041
All F_1	32	15.912 ± .085	15.728 ± .054	23.966 ± .090	17.153 ± .065	10.716 ± .033
F_2	28	15.479 ± .072	15.596 ± .048	23.500 ± .925	16.721 ± .055	10.443 ± .033
F_3	19	15.879 ± .092	15.500 ± .079	23.737 ± .083	17.053 ± .055	10.572 ± .042

The F_2 hybrid generation averages smaller than the F_1 generation in all skeletal measurements. In femur length, condylo-zygomatic skull length, and bullar width, the differences between F_1 and F_2 are of statistical significance, being respectively 3.9, 5.1, and 5.9 times their probable errors. These F_2 hybrids are therefore nearest the *sonoriensis* parent in their skeletal dimensions.

The F_3 hybrid generation averages somewhat larger than the F_2 generation in femur length and condylo-zygomatic skull length, but does not differ significantly in the other skeletal measurements. Compared with the first hybrid generation the third averages smaller in all skeletal measurements, but none of the differences are of statistical importance.

No very important effect of heterosis upon body or skeletal size seems evident from the measurements of the hybrids. Only in foot length do the F_1 hybrids significantly exceed the measurements of both parent stocks. In all other measurements, both of the body and of the skull and skeleton, the hybrids are either close to one or other parent stock, or are intermediate between them. The hybrids of the second and third generations are different in certain measurements from the hybrids of the first generation, but in no measurement do these hybrids exceed the dimensions of the parent stocks to any important degree. It is interesting to note that ear length is intermediate between the two parent stocks in all three hybrid generations.

Pelage Color

In pelage color the two parent stocks differ greatly, *sonoriensis* being much paler than *rufinus* (Table V). The tint photometer readings of the dorsal stripe for red in *sonoriensis* from Victorville, average $13.02 \pm .29$ units more than in the non-inbred stock of *rufinus* from Buena Vista, and the darkest *sonoriensis* has about the same readings as the palest *rufinus*. In the color of the side the two parent stocks also differ greatly, though not quite so much as in the color of the dorsal stripe. In the reading for red of the side *sonoriensis* averages

10.34 ± .30 units more than *rufinus*. All the other color readings both of the dorsal stripe and of the side show similar striking differences between the two parent stocks.

The F_1 hybrids are nearly intermediate in color between the two parent stocks. This is true for all the colors and for both the dorsal stripe and the side. The differences in average tint photometer readings between the hybrids and either parent stock is of great statistical probability for every color comparison.

The hybrids of the second and third generations average slightly lower than the first generation hybrids in tint photometer readings of the dorsal stripe but for no color is the difference greater than twice its probable error, and therefore the lower readings are of no statistical importance. The colors of the dorsal stripe of the F_2 and F_3 generations are so nearly alike that they show no consistent nor significant difference from one another.

For the color of the side there is no important difference between the hybrids of the F_1, F_2, and F_3 generations for the readings for red and for yellow. In the colors green, peacock, and blue-violet, the F_1 generation averages slightly lighter than F_2 or F_3, as shown by higher tint photometer readings. The amount of difference does not exceed 1.22 ± .28 units for any color, and the differences are in general of slight statistical probability, ranging between 3 and 4 times their probable errors. The F_2 and F_3 generations average almost the same in the color of the side.

The tint photometer averages show that all the hybrids, both of the first, second, and third generations are intermediate in color between the parent stocks. There is no certain indication of any change in color between the F_1 hybrids and those of later generations.

The colors of these hybrids appear to be a blend of the colors of the parent races, and there is no indication of a segregation of the parental color either in the second or in the third hybrid generations.

TABLE V

AVERAGE TINT PHOTOMETER READINGS, BOTH SEXES, 1-YEAR AND 2-YEAR AGE CLASSES COMBINED

Pelage color of *Peromyscus maniculatus rufinus* and *P. m. sonoriensis*

Dorsal Stripe	No.	Red	Yellow	Green	Peacock blue	Blue-violet
Rufinus, Buena Vista	196	9.28 ± .09	7.93 ± .07	6.54 ± .05	5.84 ± .05	5.15 ± .04
Sonoriensis, Victorville	85	22.30 ± .27	18.93 ± .26	15.58 ± .23	13.23 ± .21	12.17 ± .19
Rufinus × *sonoriensis*						
F_1 from *rufinus* mothers	37	15.24 ± .26	12.78 ± .24	10.05 ± .19	8.62 ± .18	7.68 ± .13
F_1 from *sonoriensis* mothers	19	15.58 ± .49	12.95 ± .43	11.26 ± .32	9.68 ± .28	8.95 ± .28
All F_1	56	15.36 ± .24	12.84 ± .22	10.46 ± .17	8.98 ± .16	8.11 ± .14
F_2	41	14.98 ± .21	12.46 ± .18	10.24 ± .13	8.61 ± .10	7.93 ± .10
F_3	33	14.85 ± .23	12.30 ± .20	10.30 ± .14	8.58 ± .14	7.97 ± .11
Side						
Rufinus, Buena Vista	196	23.81 ± .13	20.45 ± .11	15.58 ± .09	13.10 ± .08	11.60 ± .07
Sonoriensis, Victorville	85	34.15 ± .27	29.42 ± .23	23.13 ± .20	20.02 ± .18	18.10 ± .17
Rufinus × *sonoriensis*						
F_1 from *rufinus* mothers	37	25.32 ± .30	20.68 ± .23	16.03 ± .22	13.84 ± .22	12.24 ± .19
F_1 from *sonoriensis* mothers	19	28.74 ± .43	24.16 ± .38	19.79 ± .32	17.37 ± .27	15.47 ± .27
All F_1	56	26.48 ± .29	21.86 ± .25	17.30 ± .24	15.04 ± .23	13.34 ± .21
F_2	41	26.27 ± .32	21.51 ± .33	16.27 ± .24	14.10 ± .19	12.12 ± .19
F_3	33	26.39 ± .29	21.67 ± .28	16.39 ± .25	14.06 ± .25	12.21 ± .22

Variability

The characters of size and color distinguishing the subspecies *rufinus* and *sonoriensis* are shown above to be inherited in a blending manner. According to the theory of multiple factors without dominance, which is currently held by many geneticists to account for inheritance of the blending type, the F_2 hybrid generation should be more variable than F_1 and also more variable than either parent. I have therefore calculated the coefficients of variation for the measurements and tint photometer readings of the parent stocks *rufinus* and *sonoriensis,* and of the first, second, and third hybrid generations.

In body and skeletal measurements, the parent *sonoriensis* stock has, in general, smaller coefficients of variation than the parent *rufinus* stock (Table VI). This probably indicates the greater amount of inbreeding to which the *sonoriensis* stock had previously been subjected.

The F_1 hybrids do not differ greatly from their parent stocks in the variability of body dimensions. Only in body length is there a significant increase in variability in F_1. The coefficient of variation of body length is $1.97 \pm .61$ per cent greater in the hybrids than in the parent *rufinus* stock and $3.50 \pm .62$ per cent greater than in the parent *sonoriensis* stock. The differences are respectively 3.2 and 5.7 times their probable errors. In foot length both sexes of the F_1 hybrids have smaller coefficients of variation than the parent stocks, but only in the comparison of the female F_1 mice with the parent *rufinus* stock is the difference of importance, $1.51 \pm .27$ per cent, a difference which is 5.5 times its probable error. In ear length the F_1 hybrids have smaller coefficients of variation than either parent stock, but only in the comparison with *rufinus* is the difference of possible significance, being $1.19 \pm .31$ per cent, a difference 3.8 times its probable error.

The F_2 hybrids show no significant difference in variability from the F_1 generation in most measurements of the body and skeleton. Only in length of hind foot is there a possible significant increase in the coefficients of variation, which are

TABLE VI

AVERAGE COEFFICIENTS OF VARIATION IN PER CENT; 1-YEAR AGE CLASS

Variability in dimensions of *Peromyscus maniculatus rufinus* and *P. m. sonoriensis*

Stock	Body length	Tail length	♀ Foot length	♂ Foot length	Ear length
Rufinus, Buena Vista	5.05 ± .19	6.02 ± .23	3.43 ± .18	2.92 ± .15	4.29 ± .16
Sonoriensis, Victorville	3.51 ± .21	5.15 ± .31	2.59 ± .20	2.93 ± .27	3.24 ± .19
Rufinus × *sonoriensis*					
F_1	7.02 ± .58	5.36 ± .47	1.92 ± .20	2.23 ± .28	3.10 ± .26
F_2	4.61 ± .39	5.33 ± .46	3.62 ± .38	3.91 ± .54	3.41 ± .29
F_3	3.51 ± .29	3.71 ± .31	1.97 ± .22	2.84 ± .35	4.27 ± .35
	Femur	Mandible	Skull length	Condyle—zygoma	Bullar width
Rufinus, Buena Vista	4.58 ± .18	3.01 ± .12	2.93 ± .12	2.71 ± .11	2.12 ± .09
Sonoriensis, Victorville	3.75 ± .26	2.99 ± .20	2.70 ± .18	2.63 ± .18	2.35 ± .16
Rufinus × *sonoriensis*					
F_1	4.47 ± .38	2.87 ± .24	3.14 ± .27	3.20 ± .27	2.54 ± .22
F_2	3.65 ± .33	2.40 ± .22	3.09 ± .28	2.60 ± .23	2.48 ± .22
F_3	3.75 ± .41	3.23 ± .36	2.25 ± .25	2.09 ± .23	2.48 ± .25

1.70 ± .44 per cent greater in F_2 for the females and 1.68 ± .61 per cent greater for males, the differences being respectively 3.9 and 2.8 times their probable errors. The coefficient of variation of the body length measurement is 2.40 ± .70 per cent *less* in F_2 than in F_1, the difference being 3.4 times its probable error, and possibly significant. Compared with the parent stocks the F_2 hybrids are not significantly more variable in any measurement.

The F_3 hybrids do not differ significantly from F_2 in the variability of any measurement of the body or skeleton. Compared with the F_1 generation the F_3 is significantly more variable in body length, the difference in coefficients of variation being 3.50 ± .65 per cent, a difference 5.3 times its probable error. In foot length, however, in which F_2 was indicated to be possibly more variable than F_1, F_3 is not significantly different in variability from F_1.

For pelage color the variability, as shown by the coefficients of variation of the tint photometer readings (Table VII), is nearly the same, both for dorsal stripe and side color, in the two parent stocks, *rufinus* and *sonoriensis*.

The F_1 hybrids do not differ significantly in the variability of the color of the dorsal stripe from either parent stock. The coefficients of variation of the tint photometer readings for the several color screens are slightly less in the F_1 hybrids than in either parent stock, and in no comparison are the differences significant. The side color of the F_1 hybrids is somewhat more variable than of either parent stock. The coefficients of variation of the tint photometer readings for red, however, do not differ significantly between the F_1 hybrids and either parent stock. For the other colors the coefficients of variation of the F_1 hybrids exceed those of the parent stocks by amounts ranging from 3.4 to 4.0 times their probable errors.

The F_2 hybrids are *less* variable in the color of the dorsal stripe than the F_1 hybrids. The difference between the F_2 and F_1 hybrids in the coefficients of variation of the tint photometer readings is not significant for the readings for red,

TABLE VII

AVERAGE COEFFICIENTS OF VARIATION IN PER CENT FOR TINT PHOTOMETER READINGS; 1-YEAR AND 2-YEAR AGE CLASSES

Variability in color of *Peromyscus maniculatus rufinus* and *P. m. sonoriensis*

Dorsal stripe	Red	Yellow	Green	Peacock blue	Blue-violet
Rufinus, Buena Vista	19.07 ± .65	18.16 ± .62	16.51 ± .56	16.44 ± .56	16.50 ± .56
Sonoriensis, Victorville	16.38 ± .85	19.07 ± .99	20.22 ± 1.04	21.24 ± 1.10	21.61 ± 1.12
Rufinus × *sonoriensis*					
F_1	17.32 ± 1.10	18.69 ± 1.19	18.45 ± 1.17	19.49 ± 1.24	19.36 ± 1.23
F_2	13.15 ± .98	13.40 ± 1.00	11.62 ± .86	11.50 ± .86	12.23 ± .91
F_3	13.06 ± 1.08	13.66 ± 1.13	11.84 ± .98	13.75 ± 1.14	11.79 ± .98
Side					
Rufinus, Buena Vista	11.51 ± .39	11.10 ± .38	11.55 ± .39	12.14 ± .41	13.19 ± .45
Sonoriensis, Victorville	10.63 ± .55	10.84 ± .56	11.54 ± .60	12.14 ± .63	12.49 ± .64
Rufinus × *sonoriensis*					
F_1	11.97 ± .76	14.50 ± .92	15.55 ± 1.00	16.69 ± 1.06	17.24 ± 1.10
F_2	11.46 ± .85	14.41 ± 1.07	13.83 ± 1.03	12.91 ± .96	14.85 ± 1.11
F_3	9.43 ± .78	10.89 ± .90	13.18 ± 1.09	15.15 ± 1.26	15.56 ± 1.29

and for yellow the difference between the two generations is only 5.29 ± 1.55 per cent, which is 3.4 times its probable error. For the readings of green, peacock blue, and blue-violet the differences are respectively, 4.7, 5.3, and 4.6 times their probable errors and therefore are of considerable significance. The F_2 hybrids do not differ significantly from the F_1 mice in the amount of variability in the color of the side. This is true for all of the 5 color screens for which tint photometer readings were made. The coefficients of variation for each color screen are actually somewhat less in the F_2 hybrids than in the F_1, but the differences are not statistically significant.

The F_3 hybrids do not differ significantly from the F_2 in the variability of pelage color either of the dorsal stripe or side.

My data fail to show any important increase of variability in the F_2 generation, as required by the theory of multiple factors. There is, it is true, an apparently slight increase of variability in foot length in F_2 as compared to F_1, but the variability of body length is less in F_2 than in F_1 by a possibly significant amount. For no other measurement is there a significant difference in variability between the F_2 hybrids and the F_1 hybrids or the parent stocks.

For pelage color also the F_2 hybrids fail to show an increase in variability. On the contrary the tint photometer readings have smaller coefficients of variation in F_2 than in F_1, and for certain color screens in the dorsal stripe readings the decrease in variability is of considerable statistical significance.

Differences Between Reciprocal Crosses

The possibility that some characters may be inherited through the cytoplasm rather than through the chromosomes has been suggested by Castle (1933, pp. 1011–1015). To test this possibility in the hybrids between *rufinus* and *sonoriensis* I have, for the 1-year age class, calculated separately the measurements of the F_1 hybrids borne by *rufinus* mothers from those borne by *sonoriensis* mothers. Unfortunately, the number of specimens of the F_1 generation available is too few for fully dependable comparisons to be made.

In body length the F_1 hybrids from *sonoriensis* mothers average 10.13 ± .76 mm. longer (see Table III) than those from *rufinus* mothers, a difference 13.3 times its probable error and certainly significant for the specimens at hand. It should be noted that the hybrids from *sonoriensis* mothers average larger in this measurement than the *sonoriensis* parent stock, which is the larger of the two stocks hybridized, and that the hybrids borne by *rufinus* mothers average smaller than the parent *rufinus* stock. In body length the hybrids therefore resemble their mothers rather than their fathers.

In tail length and in ear length the F_1 hybrids borne by *sonoriensis* mothers average larger than those borne by *rufinus* mothers, but in neither measurement is the difference of statistical importance. No attempt has been made to calculate the differences between the reciprocal crosses for foot length nor for weight, for on account of the considerable sexual differences in these characters the number of individuals in each class are too few for satisfactory comparisons.

In all skeletal measurements the F_1 hybrids borne by *sonoriensis* mothers exceed those borne by *rufinus* mothers (Table IV). The least significant difference is that for length of mandible, which is .387 ± .104 mm. longer in the offspring from *sonoriensis* mothers, a difference of 3.7 times its probable error and therefore possibly significant. The most significant difference, .736 ± .099 mm., is that of the condylo-zygomatic skull length, in which the difference is 7.4 times its probable error. For femur length the difference is .798 ± .138 mm., a difference 5.8 times its probable error. As the *rufinus* parent stock averages larger for these skeletal measurements than the *sonoriensis* stock, the hybrids resemble their fathers in skeletal dimensions rather than their mothers.

In pelage color there is an indication that the mother may have more influence than the father. As shown by Table V the F_1 hybrids from *sonoriensis* mothers average lighter in color than the mice of the reciprocal cross from *rufinus* mothers. In every color and for both dorsal stripe and side the tint photometer readings average higher in the F_1 hybrids

borne by *sonoriensis* mothers. The differences are most pronounced in the readings for the color of the side, where the differences in the several color comparisons range between 3 and 4 tint photometer units, and with probable errors 6.6 to 10.4 times their probable errors. The color of the dorsal stripe does not differ so greatly between these reciprocal crosses, though in every color comparison the descendants from the *sonoriensis* mothers average slightly the lighter colored. The differences in tint photometer readings for the red and for the yellow are not significant, being less than the probable errors. For the other colors, however, the differences may be of possible significance, being from 3.2 to 4.1 times their probable errors. The indication from the small amount of data is that in pelage color the F_1 hybrids tend to resemble their mothers rather than their fathers.

The tendencies shown by the F_1 hybrids in these reciprocal crosses are apparently somewhat contradictory. Thus in body length the hybrids tend to resemble their mothers, while in measurements of the femur and skull they tend to resemble their fathers. In color the hybrids tend to resemble their mothers, but the small number of specimens available makes hazardous the drawing of any positive conclusions.

Discussion

The subspecies of *Peromyscus* differ from one another in general body size, in the proportional size of certain parts of the body, in pelage color, in the distribution of color over the body, or in combinations of these characters. Previous studies of other kinds of mammals by many investigators have shown that the characters of size, color, and color pattern (spotting) seldom are inherited in a simple Mendelian manner, but usually as a blend of the parental characters.

The characters distinguishing the subspecies *rufinus* and *sonoriensis* are shown by this study to be inherited in a blending manner and agree with previous studies of *Peromyscus* by Sumner (1932, 39–51).

As reported above, the hybrids between the subspecies

rufinus and *sonoriensis* are not more variable in most body dimensions or in pelage color in the second than in the first hybrid generation. There is also a tendency for the F_1 hybrids to resemble in certain characters either their mothers or their fathers. These evidences might be considered to support the suggestion of Castle, cited above, that the theory of multiple factors does not adequately explain blending inheritance.

The failure of the F_2 hybrid generation to be more variable than F_1, however, does not agree with the results obtained by Sumner (1932, 39–51) and his associate Huestis who found generally in hybrids between various races of *Peromyscus* that there was some increase in variability in F_2. The parent stocks employed by all of us have been variable, and much more certain results could be obtained by crossing mice from two inbred lines. The F_2 and F_3 generations in my studies were both produced by a considerable amount of brother-sister matings, and this close inbreeding would be expected to decrease the variability of the offspring. I suspect that this may explain the difference between my results and those of Sumner; but even with inbreeding in F_1 there should be an increase of variability in F_2 under the theory of multiple factors.

It should be pointed out also that the number of specimens of the F_1 and F_2 hybrid generations available are too few for fully satisfactory statistical calculations, and this is particularly true of the comparisons of the first generation hybrids obtained from the reciprocal crosses. Furthermore, the F_1 hybrids resemble their mother subspecies in some characters and their father subspecies in other characters, so the results of the reciprocal crosses are apparently not consistent.

Nevertheless the failure of these preliminary studies to support the multiple factor hypothesis of blending inheritance justifies further extensive experiments, which are planned for the immediate future.

Summary

Hybrids between the two subspecies, *Peromyscus maniculatus rufinus,* from Buena Vista, Colorado, and *P. m. sonori-*

ensis, from Victorville, California, were reared for the first, second, and third hybrid generations.

In all body and skeletal measurements the hybrids average near one or other parent stock or are intermediate between them, except in hind-foot length, in which the F_1 hybrids average larger than either parent subspecies.

In pelage color, both of the dorsal stripe and of the side, all generations of the hybrids are intermediate between the two parent stocks.

The F_2 and F_3 hybrid generations show no important increase in variability over the F_1 hybrids or the parent stocks, either in body or skeletal measurements or in tint photometer readings of pelage color. On the contrary, body length and certain readings of dorsal stripe color are both somewhat less variable in F_2 than in F_1. There is a possible slight increase of variability of foot length in F_2 over F_1.

As shown by reciprocal crosses, the F_1 hybrids tend to resemble their mothers in body length and in pelage color, while in skeletal measurements they tend to resemble their fathers.

The results in this case of blending inheritance are not those expected under the theory of multiple factors without dominance, but the data are insufficient for a critical test of the theory.

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