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On the origin of domesticity: A test of Keeler's "black-gene" hypothesis

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In a classic set of papers on psychogenetics published in the 1940s, Clyde Keeler hypothesized that a single black recessive coat-color gene in Norway rats (*Rattus norvegicus*) was linked to docile, sluggish behavior as well as to reduced brain and adrenal gland size. Discovery of a possible "black-gene" rat in a large population of wild brown Norway rats prompted this test of Keeler's proposed genetic origin of domesticity. Comparisons included computer-monitored open-field activity, activity wheel performance, water consumption, and physiological measures. Contrary to Keeler's hypothesis, essentially no differences were found among wild black rats, their offspring, and brown rats on either the behavioral or the physiological measures. Our data would suggest that multigenic mechanisms of domestication, including selections and ontogenetic processes, seem to account best for the origin of domesticity.

The black rat is "sluggish" and "already tame by nature" (Keeler & King, 1942, p. 244). Further, this "laboratory mutant has so much of itself excised that it is really no longer a rat when compared with the unmutated members of its species" (Keeler, 1945, p. 38). These statements have been selected from a series of now classic papers on psychogenetics that link rat behavior and physiology to a single gene for coat color (see Robinson, 1965, for a review of Keeler's work). The study reported here is a direct test of Keeler's hypothesis, which predicts that any rat with the black phenotype, as well as the hooded and albino phenotypes (because these often mask the black gene), should exhibit docile and sluggish behavior as well as hypotrophy of the brain and adrenal tissue when compared with a brown counterpart. In fact, Keeler suggests that "it seems probable that the tame albino rat, at least the strain studied, was not domesticated by painstaking selection over long periods of time, but was modified in morphology principally by the introduction of three coat color genes, and in behavior particularly by the (non-agouti) black gene" (Keeler & King, 1942, p. 249).

METHOD

Subjects

Wild rats. Black (13 male and 4 female) and brown (10 male and 10 female) wild rats (*Rattus norvegicus*) were live-trapped in the city dump of Salem, Missouri, in the spring months of 1978. The nonbrown rats represented a very small portion of the total population (estimated less than 1% to 2%), and no albino rats were trapped or seen. The dump had more than 50 acres of open-surface garbage and had been in existence since the early 1920s. Shortly after the trapping was completed, the dump was closed, poisoned, and filled in by the city to comply with federal regulations.

One wild black female rat that had been trapped was bred to produce three litters by three different black male rats. All of the offspring of these matings were pure black, and a random selection of 10 male and 10 female offspring were laboratory reared in same-sex group housing until they were tested as adults.

Domestic rats. Experimentally naive albino rats (10 male and 10 female) were selected from our randomly bred colony of Sprague-Dawley rats. Ten male and 10 female hooded rats were obtained from a commercial supplier (Simonsen Laboratories, Inc.). Carl Hansen of the Veterinary Resources Branch, National Institutes of Health (NIH), generously supplied 9 male and 10 female black-gene rats.

Apparatus

Open field. The enclosed open field consists of 36 15.24-cm squares (6 by 6). Each square is independently suspended and designed so that the weight of an animal placed on any portion of the square activates a switch (Hughes, 1978). A cable connects the switches of the arena to a NOVA 3 minicomputer. A program, available from the authors, monitors the changes in the subject's position, traces the path taken by the animal, and records the totals of inner and outer square crossings minute by minute (see Figure 1).

Activity wheel. Each rat was monitored for 10 min in the open field (Run 1), weighed, and then placed in a Wahmann activity wheel for 6 days. Food and water was available ad lib. At the end of 6 days, each rat was removed from the activity wheel and again placed in the open field (Run 2). At the end of 10 min, a "stressor" was introduced into the arena (see Hughes, 1975) and a third 10-min recording of open-field activity was made (Run 3).

After the last open-field test, each rat was removed and given a lethal intracardiac injection of pentobarbital sodium, and physical measurements were taken.

RESULTS

Anatomical Measures

Tables 1 and 2 summarize the various means and standard errors of the mean for each group of rats for each physiological measure. The male rats were found to be heavier or larger in every physiological measure ($p < .01$); consequently, the sexes were treated separately for the purpose of making Tukey HSD mean comparisons ($\alpha = .1$).

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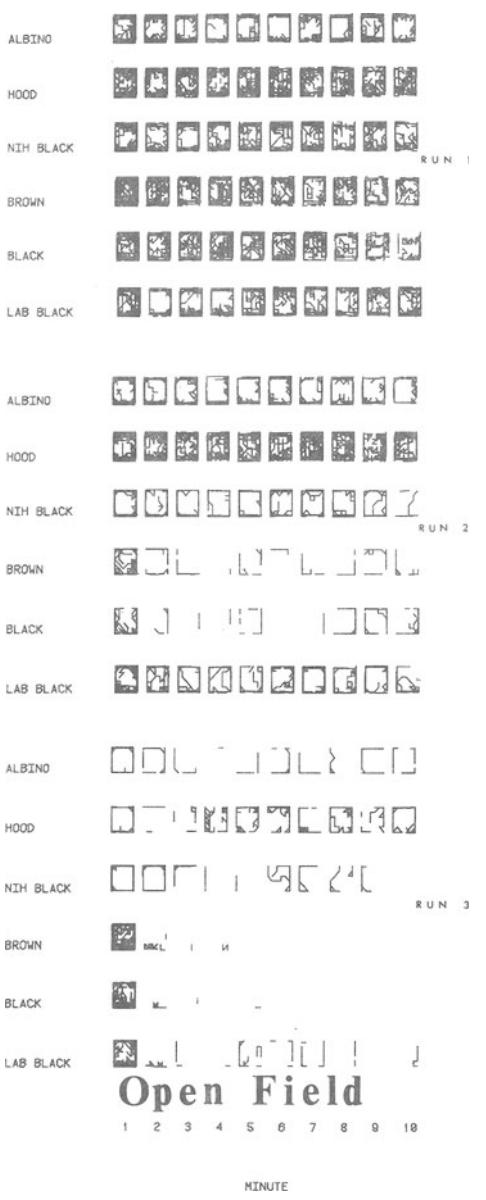

Figure 1. Open-field activity in which each pattern represents a computer graphic composite sequential tracing of the various groups' square crossings for each minute. All 36 of the squares of the computer-monitored open field are represented, with the darkest areas indicating the most frequent areas traversed.

Brain weight. The most important finding, contrary to Keeler's hypothesis, was that the brains of both genders of the wild black rats did not differ in size from those of the wild brown rats. Furthermore, the laboratory breeding and rearing of wild black rats did not significantly reduce the brain size. By contrast, with the exception of hooded male rats compared with brown rats, the brains of all the domestic male rats were smaller than those in all three groups of wild male rats [$F(2,108) = 77$, $p < .01$] (Table 1). Among the female rats, only the brains of the albino and NIH black-gene rats were smaller than those of the wild female rats (Table 2). Within groups of both sexes, the albino rats had smaller brains than the hooded rats [$F(2,108) = 11.7$, $p < .01$].

Adrenal weight. The results of the analysis of the adrenal gland weights closely paralleled those of the brain weights. Male and female groups of black-gene rats (wild and laboratory reared) did not differ from the wild brown groups (Tables 1 and 2); however, all of the domestic groups had smaller adrenal glands than the wild groups [$F(2,108) = 263$, $p < .01$]. Interestingly, the laboratory-reared black female rats had smaller adrenal glands than the brown female rats [$F(2,108) = 5.9$, $p < .01$], but the brains of the former were not smaller than those of the wild black rats that were trapped.

Humerus and femur lengths. Statistical analyses of the lengths of both humerus and femur indicated that domestication had minimal effect on their growth. Differences that were found for these measures [$Fs(2,108) = 10.9$ and 42, respectively; $ps < .01$] and the measures that are discussed below reflect the apparently younger age at testing of the NIH-derived domestic black rats and the laboratory-reared black rats. The wild black male rats that were trapped did not differ in size from their wild brown or domestic counterparts, with the exception of the younger NIH and laboratory-reared black rats. The four wild black female rats that were trapped were smaller than the other female rats.

Body length. As with bone lengths, the body lengths of the black male rats did not differ from those of the brown rats or domestic rats. Again, for both males and females, the younger NIH and laboratory-reared black rats were shorter than the others [$F(2,108) = 34$, $p < .01$]. The smaller black female rats were also shorter than their brown and albino female counterparts [$F(2,108) = 4.5$, $p < .01$].

Tail length. The tail lengths of black male and female rats did not differ from those of the other wild rat groups; however, the tails of the black male and brown rats were shorter than those of the hooded rats [$F(2,108) = 21$, $p < .01$]. The latter finding may reflect the greater likelihood of damage and loss of the tip of the tail in the natural environment. As in the other above measurements, the two younger groups of rats had shorter tails [$F(2,108) = 18.5$, $p < .01$].

Body weight. Both sexes of the black rats did not differ from those of the brown rats in body weight (Tables 1 and 2), except that the younger NIH and laboratory-reared black rats were lighter [$F(2,108) = 11.7$, $p < .01$].

Activity Wheel

In contrast to Keeler's hypothesis that black rats are sluggish, the activity wheel scores indicated that the behavior of black rats is similar to that of brown rats. Statistically, no differences were noted on any of the days. Further, the daily activity of both sexes of black rats was more than double that of all three domestic rat groups [$F(10,540) = 5.1$, $p < .01$].

Table 1
Mean Values of Various Physiological Measurements for Male Wild and Domestic *Rattus Norvegicus*

		Domestic						Wild					
		Albino		Hooded		NIH Black		Brown		Black		Lab Black	
	F(5,54)	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Brain Weight (in Milligrams)	12.2	778.0	14.0	854.0	22.0	834.0	17.0	909.0	16.0	936.0	24.0	930.0	12.0
Adrenal Weight (in Milligrams)	17.8	198.0	12.0	208.0	11.0	184.0	5.0	438.0	33.0	448.0	53.0	404.0	39.0
Humerus (in Millimeters)	8.8	30.8	.4	29.6	.2	26.6	.5	29.9	.5	29.6	.9	28.8	.3
Femur (in Millimeters)	9.3	40.2	.5	38.7	.4	35.4	.3	38.7	.5	38.5	.7	37.2	.5
Body (in Centimeters)	8.2	24.8	.4	24.1	.3	21.3	.1	23.7	.5	23.1	.8	22.0	.3
Tail (in Centimeters)	10.7	20.9	.4	21.7	.3	18.0	.1	19.3	.7	19.0	.5	20.0	.3
Body Weight (in Grams)	10.1	461.0	22.0	465.0	14.0	291.0	7.0	418.0	29.0	379.0	26.0	354.0	21.0

Note–Brain weight values represent brain weight/body length × 10^4*; adrenal weight values represent adrenal weight/body length* × 10^6*. All F values (p < .01) represent a one-way analysis of variance (see text for detailed analyses and mean comparisons).*

Table 2
Mean Values of Various Physiological Measurements for Female Wild and Domestic *Rattus Norvegicus*

		Domestic						Wild					
		Albino		Hooded		NIH Black		Brown		Black		Lab Black	
	F(5,48)	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Brain Weight (in Milligrams)	10.2	827.0	13.0	920.0	12.0	874.0	15.0	923.0	12.0	944.0	8.0	932.0	21.0
Adrenal Weight (in Milligrams)	51.4	293.0	10.0	376.0	31.0	284.0	9.0	633.0	26.0	589.0	16.0	505.0	24.0
Humerus (in Millimeters)	14.7	28.0	.4	27.5	.2	25.0	.1	27.7	.4	26.4	.7	26.2	.3
Femur (in Millimeters)	10.1	36.3	.5	35.4	.2	32.7	.3	36.6	.5	36.9	1.7	33.7	.4
Body (in Centimeters)	9.6	21.8	.3	21.3	.2	19.8	.2	21.8	.4	20.3	.4	20.2	.3
Tail (in Centimeters)	7.6	19.2	.3	20.0	.2	17.2	.2	19.3	.5	18.6	1.1	18.1	.3
Body Weight (in Grams)	12.0	294.0	11.0	303.0	8.0	215.0	5.0	302.0	16.0	249.0	24.0	230.0	11.0

Note–Brain weight values represent brain weight/body length × 10^4*; adrenal weight values represent adrenal weight/body length* × 10^6*. All F values (p < .01) represent a one-way analysis of variance (see text for detailed analyses and mean comparisons).*

Water Consumption

Analysis of the total daily water consumption while in the activity wheel indicated that in no case did the water consumption of the wild black rats differ from that of the brown rats. Black and brown male rats consistently consumed more water than the males of the other groups on Days 2-6 [$F(5,540) = 3.9$, $p < .01$].

Open Field

An analysis of variance indicated a four-way interaction of Runs by Domestication by Groups by Minutes [$F(36,1944) = 2.8$, $p < .01$]. This was plotted with a computer graphics terminal (Figure 1). Each rat's path overlapped and was offset slightly from the previous path, resulting in a visual average of each group's activity. This showed that the ambulatory activity decreased with each additional exposure to the open field; this was more evident for the wild than for the domestic rats. Also, there was more activity in the first few minutes than later. This was particularly noted in Run 3, in which the "stressor" was introduced at the beginning of the run. All of the wild rats showed an extremely active response to the noxious stimulus but were inactive afterward. Contrary to what Keeler's hypothesis would predict, it is clear from Figure 1 that the "black-gene" rats responded to all phases of the open-field test situation in the same manner as the brown rats did. The wild rat behavioral response to the open-field sharply contrasts with that of the domestic rats, whereas the laboratory-reared black rats demonstrated features common to both.

DISCUSSION

"The most important contribution of the present study is its proof that temperament and behavior are inherited in gene controlled parcels [identified by coat color] and that personality may be synthesized by combining various modifying genes" (Keeler & King, 1942, p. 249). By contrast, we found that live-trapped black-gene rats did not differ from wild brown rats on a number of behavioral and physiological measures. Further, essentially the same was true for the laboratory-reared offspring of the black rats. Wild rats in almost all respects differed from domestic rats in activity measures and brain and adrenal gland sizes. Hence, Keeler's hypothesis of a black gene for domesticity based on these measures is not supported by the present investigation. Domestication and all of its ramifications (Boice, 1973, 1980), not "black genes," appear to account for the data.

An important question, of course, is whether the black gene of this study was the same one that Keeler tested. Keeler (1942) stated that his black rats were derived from segregants from a cross of three Wistar albino females with a brown Norway rat. There is no indication of whether the brown Norway male was recently trapped or an inbred laboratory variety left from King's (1939) work. If the male was a laboratory variety, King first reported black mutants in the 12th to the 14th generations of laboratory rearing. Robinson (1965) stated that Keeler's black rats were a substrain of King's (1939) rats. In any case, the

female albino rats would have contributed 50% of the domestic genes to the offspring, and this could have accounted for a substantial portion of the domestic characteristics that Keeler (1942) reported, in spite of the effects of 12-14 generations of laboratory rearing.

By contrast, the black rats used in the present study were live-trapped in a natural environment, and the laboratory-reared black rats were first-generation products of wild black rats. The live-trapped black rats may have been either products of a spontaneous mutation or offspring of domestic albino or hooded rat pets released into the population, which, in turn, mated with the wild brown population. It was noted earlier that no albino rats were seen or trapped, although this would not have precluded their existence. The trapping of a small number of brown-and-white and black-and-white rats would suggest the release of someone's pet at some point in time. There is no way to establish for certain the origin of the live-trapped black rats of this study. However, we can state that the black rats of this study were defined environmentally, physiologically, and behaviorally as wild rats and offered a simple test of black vs. brown genes unconfounded by laboratory rearing.

The wild black rats contrasted starkly with the inbred NIH domestic black rats, which were, for the most part, indistinguishable from the domestic albino rats. Clearly, the black gene was represented in two very distinct phenotypes, with domestication as the only apparent variable.

Ultimately, how does one account for the differences between the findings of this study and those of Keeler (1942)? The origin of the "gene pool" for each study cannot be determined. However, methodological considerations may account for some of the differences. Many of Keeler's assertions were based on anecdotal reports (Keeler & King, 1942) or very subjective measures of emotionality, such as puffing cigar smoke into the cage (Keeler, 1942). A partial resolution to this problem is to use less subjective measures, such as water consumption, activity wheel performance, and the open field, to test for "sluggishness" and "emotionality." The critical question of whether black rats differed from brown rats was answered, at least for this study, without introducing subjective arbitrary notions of emotionality.

The physiological measures Keeler (1947a) reported may also have limitations. For example, it is not clear if body weight or length ratios were used by Keeler to calculate the values for brain and adrenal weights. Without this control, differences occasioned by age or seasonal nutritional availability can be substantial. The black rats of Keeler's were "all descended from coat-character mutants appearing in an inbred stock of gray animals originally caught in the wild" (Keeler, 1947b, p. 204). It is unclear whether these are the same black rats on which the behavioral work was done (Keeler & King, 1942) and/or whether they are all from the same litter (Hughes, 1979).

In conclusion, the present research supports contemporary efforts, which emphasize the polygenic process of domestication (Boice, 1973, 1980), rather than the simple notion of a single recessive gene for domesticity. Clearly, many factors are involved in complex behavioral organisms (Boice, 1980), and the powerful effects of environment can reverse domestication influences on behavior (Boice, 1977; Hughes, 1975). Further, if the black rats of this study were the offspring of feralized domestic rats, then reversal of physiological as well as behavioral domestication changes have also now been demonstrated.

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