31 March 1967, Volume 155, Number 3770 **SCIENCE**

Behavior of Captive White-Footed Mice

Detailed studies of members of the genus *Peromyscus* have cast a number of old problems in new perspectives.

J. Lee Kavanau

White-footed mice, genus *Peromyscus*, are one of the most widespread, geographically variable groups of North American rodents (*1, 2*). Over 55 species are recognized (*2, 3*), more than in any other North American mammalian genus. Species occur from extreme northern Colombia northward to Alaska and Labrador. The animals are found in almost every habitat within their range and often are the most abundant mammals. Some species are found in low arid deserts, others in high tropical cloud forests. A few even inhabit barren arctic and alpine tundras.

Distinguishing characters of most species are long bicolored tails, large ears and eyes, and conspicuously darker and more richly colored fur on the upper parts of the body. When excited, many species thump rapidly with the forefeet, producing a drumming sound. White-footed mice are active at night throughout the year. "Subzero temperatures do not keep these graceful little creatures at home, and the snow-covered ground is covered with their dainty tracks during the coldest periods of mid-winter" (*4*). They spend the day in concealed nests of dry, unsoiled vegetation lined with plant down or shredded materials.

White-footed mice occasionally live in true pairs—a relatively rare occurrence among small mammals (*5*). Their home ranges usually encompass only 0.1 to 0.6 acre (*3*), and the ranges of individuals differing in sex, age, and species (*6*) may overlap considerably. There is evidence of pronounced homing ability (*7*). In the wild most individuals probably live less than 1 year. The diet is varied, including berries, fruits, greens, snails, beetles, crickets, and carrion. Large quantities of nuts, seeds, and pits are harvested for winter use. In turn, the mice are one of the main prey groups of many valuable game and fur-bearing animals.

The wide occurrence and extraordinary geographical variability of these mice make them particularly valuable for distributional, ecological, and evolutionary studies. Captive animals generally are docile, clean, odorless, and easily fed and cared for. They have a high rate of reproduction, often breeding throughout the year under suitable conditions.

For the past 6 years I have been investigating the behavior of two species of this interesting genus that are readily available locally, primarily from the point of view of its significance for survival, adaptation, and evolution. One of these species, *Peromyscus maniculatus* (the deer mouse), is the most widespread, varied, and adaptable species of the genus. The fact that over 60 subspecies have been recognized (*2*) testifies to its great plasticity. The other, *P. crinitus* (the canyon mouse), is confined to rocky habitats but ranges from hot deserts to cool heights.

By means of automatic, long-term surveillance of gross overt activities I am studying how behavior is distorted when animals are displaced from the stimulus- and structure-rich natural habitat to the relatively barren, highly restrictive laboratory enclosure; effects of compelling and attempting to compel animals to endure artificial nutritional, stimulus, and activity regimes; effects of allowing animals to control certain components of the environment; learning and memory capacity; social interactions; running in activity wheels; effects of simulated twilight transitions and nocturnal illumination; and individual behavior differences. The experimental approaches and some of the findings of these studies are presented in this article.

Control of Environment

Two important related factors that greatly influence the behavior of captive animals are "control of environment" and "compulsory regime" or compulsion (*8, 9*). Animals in the wild exercise a relatively high degree of control over the environment, for example, by selection of nest site, territory, food, and time and degree of activity and social contacts and by manipulation of many objects. But the activities of captive animals and their opportunities to interact with and modify the environment are restricted severely, with the consequence that their behavior becomes markedly distorted (*10*). A large amount of activity becomes channeled into "controlling the environment," that is, into manipulating, and altering relationships with, any susceptible environmental features. The most rewarding of several alternative outlets for activity (that is, the one engaged in most) presumably is the one that substitutes best for (or possibly even would be preferred to) the spectrum of activities in the wild (*11*). However, when outlets are highly restricted, as is usual, virtually any opportunity to modify environmental variables is exercised repeatedly, in little apparent relation to the appropriateness of the act as a substitute activity.

The author is associate professor of zoology at the University of California at Los Angeles.

Caged animals in my vivarium are given an 0.5-liter cardboard carton with a hole in its top and a small amount of sand and a cotton wad inside. In addition to providing a dark secluded nest, the carton furnishes a new channel for interaction with the environment. Thus, although some animals nest in the cartons without ever gnawing on them, others typically gnaw them into shreds and construct a nest. Nest construction apparently is only a secondary basis for this behavior, however. The modification of the environment accomplished by the gnawing seems to be the primary basis, for the animals continue to gnaw into shreds each new nest carton in turn until the cage is full of shredded material.

A second example of control of environment is provided by the activities of several mice in an enclosure containing a Plexiglas-wood nest and a wad of cotton. At the rear of the nest is a small crack through which the cotton can be grasped from outside. Animals of both sexes spend hours reeling the cotton wad out through this crack, compacting the fluffy, strung-out mass with their forelegs and teeth, stuffing the wad back into the entrance to the nest, and then repeating the entire sequence hundreds of times, day after day.

These simple examples illustrate the fact that confined animals are likely to modify or manipulate repeatedly, or to alter frequently their relationship with, any susceptible features of the environment. The repeated acts might take the form merely of running in a wheel, jumping on and off a platform, patrolling an enclosure, traversing mazes, or gnawing materials, or of turning on and off or otherwise modifying sound, illumination, a motor-driven activity wheel, intracranial stimulation, or other variables.

Compulsory Regime

An animal in the wild seldom is forced to endure conditions which it cannot escape or reduce in severity by appropriate behavior, for a relatively high level of control over the environment often permits the animal to escape noxious conditions and threats, and animals generally occupy niches in which "unexpected" events that have a critical significance for survival occur relatively infrequently. Much evidence suggests that animals tend to avoid situations which arise unnaturally or "unexpectedly." One might justifiably assert the existence of a tendency to seek stability of many variables of the *milieu extérieur*, that is, to seek a state of affairs in which conditions are highly predictable. But when an animal is displaced from the wild to the laboratory, it is compelled to exist in an environment which, though relatively fixed, is completely foreign and, from the animal's viewpoint, unpredictable. In these circumstances small mammals have a markedly conservative tendency to counteract or avoid unexpected and nonvolitional deviations from the status quo.

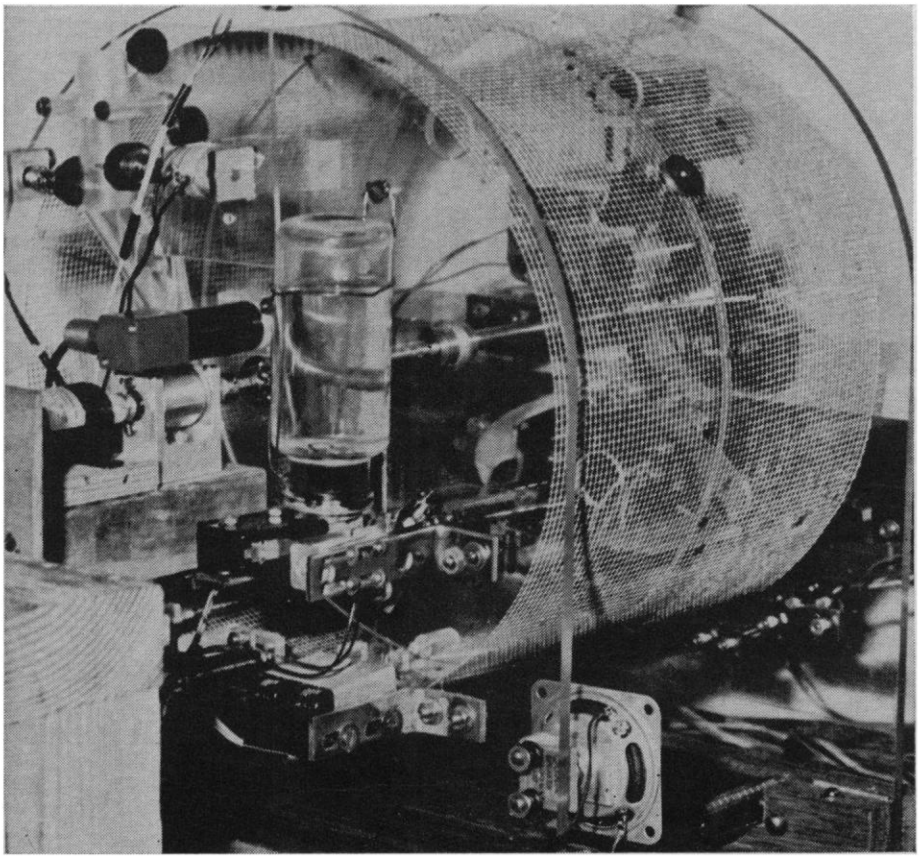


Fig. 1. The highly instrumented running-wheel enclosure used in some of the studies described here.

The failure to take into account the intrinsic tendencies of captive animals to modify environmental variables (almost independently of the nature of the variable) and to avoid or counteract unexpected and nonvolitional changes may be responsible for many conflicting findings (*8*). For example, taking these factors into account helps to resolve experiments in which rats rapidly learn a means of escape from electrical hypothalamic stimulation but do not "learn" a simple means of avoiding the same stimulus (*12*). Apparently hypothalamic stimulation is rewarding to the rats when its occurrence is expected, namely, shortly after the warning stimulus, but provokes aversion when it occurs unexpectedly.

Still better examples are provided by the so-called "paradoxical rewarding and aversive effects" of self-administered and non-self-administered electrical stimulation (*12*, *13*). When hypothalamic stimulation is applied by the experimenter, cats escape it by running a T-maze, but they themselves press levers that cause exactly the same stimulation to be applied. Rats repeatedly press a lever initiating hypothalamic stimulation and then rotate a wheel terminating it. In these cases one probably can regard the sensations produced by the stimuli as secondary and interpret the responses solely in relation to control of environment and response to compulsion. Thus, levers leading to the stimulation are pressed because it is rewarding to exercise control over the stimulus. Wheels are rotated turning off the stimulus for the same reason. Repeated turning on and off, like repeated cycling of cotton into and out of the nest, represents continued manipulation of the environment. On the other hand, cats run a T-maze and escape the stimulus because it occurs unexpectedly (*14*).

In principle, animals' repeatedly initiating and terminating a stimulus is analogous to children's repeatedly turning toys on and off. Similarly, terminating nonvolitional brain stimulation, but initiating the same stimulation volitionally, can be interpreted in the same way we view the act of a kitten or puppy refusing repeatedly to stay in a nest box when placed there but subsequently entering the box volitionally. Neither of these common examples is considered paradoxical (*15*).

Rationale of Animal Selection

For many physiological studies it is desirable to work with highly inbred animals. By this means individual differences in behavior, from the subcellular to the organismal level, are held to a minimum. One specific genetic pattern is selected from many possible ones. When highly inbred strains are used for behavior studies, the individual responses are likely to be much more uniform than those of wild animals, but the behavior may have only limited significance for the species as a whole and could even be quite misleading. When traits characteristic of wild individuals have been selected against, as is usual with domestic strains, the behavior is likely to have minimal ecological and evolutionary significance.

Experiments in my laboratory generally are carried out with wild-caught and first-generation captive-born animals. These usually are not selected for homogeneity, either of capture site, length of captivity, age, weight, sex, heredity, or experience. Since broad scope is given to the influences of individual and sex differences, the behavior of such heterogeneous stock tends to span a wide range of the response spectrum of the species. It thus provides a sound basis for interpretation and generalization. The greater the differences in the heredity and experience of the individuals, the greater the significance of similarities in their responses.

Detection, Recording, Data Reduction

The automatic, nonobtrusive detection and recording of overt activities of captive animals in my laboratory depend heavily on small, sensitive electromechanical and electromagnetic components, such as linear and rotary microswitches and solenoids, rotatable shutters, clutches, generators, and pressure transducers. Ferromagnetic conductance, capacitance, and reflective infrared sensors are employed for noncontact proximity sensing, and infrared and ultrasonic beams are used for line-of-sight sensing (*8, 9, 16–19*). Computer-type panels and standard hardware are used for programing and systems controls (*8, 9, 18, 20*). The programing system also functions as a real-time computer from which, by appropriate connections to digital printing timers and counters, all desired

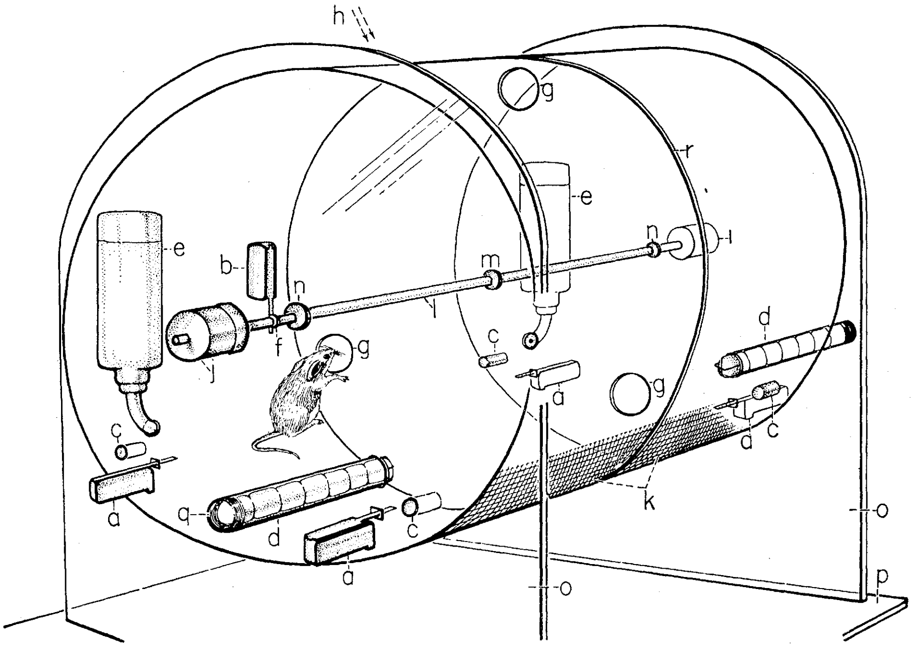


Fig. 2. Running-wheel enclosure for studies of control of illumination and effects of compulsion: *a*, control microswitches; *d*, food guns; *e*, water bottles; *g*, passageways in center pane; *h*, position of light source; *i*, tachometer generator; *o*, side panes; *r*, center pane; the motor is not shown.

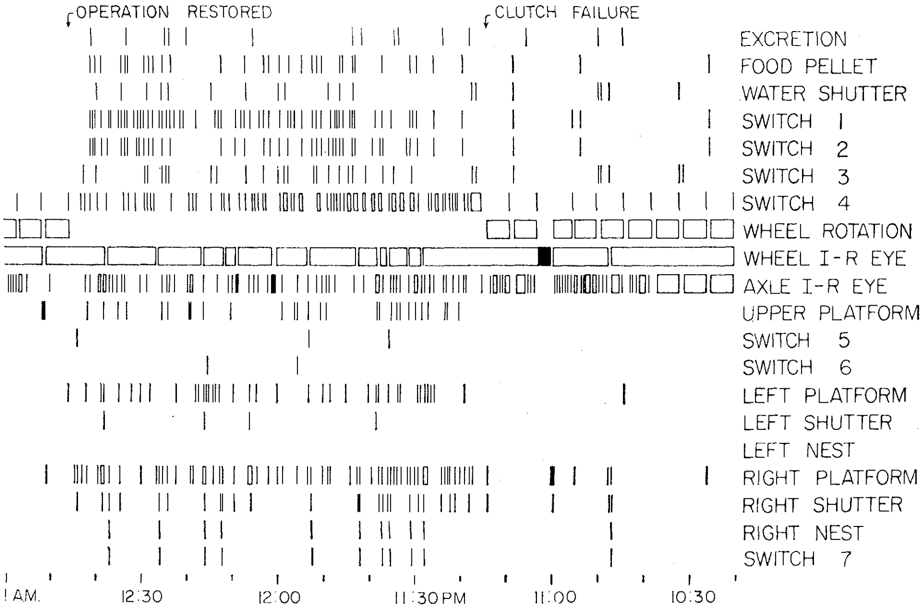


Fig. 3. Event record for deer mouse 1 during a night of the 15-percent ethanol regime, illustrating reactions to deprivation of wheel-running (beginning at the point marked "clutch failure"): open blocks, repetitive discharges; solid blocks, one continuous discharge; single lines, single discharges or a short repetitive burst. At the right are identified the channels indicating times of: eliminations; obtaining food pellets (after pressing the levers for switches 1 and 2 in sequence); unlocking the water shutter (switch 3); opening the water shutter; unlocking the wheel (switch 4); wheel rotations; interrupting the beams of electric eyes; presence on platforms; presence in the right nest; opening the nest shutters; and unlocking the right nest shutter from inside (switch 7). The left nest was closed off. Note that the time scale reads from right to left.

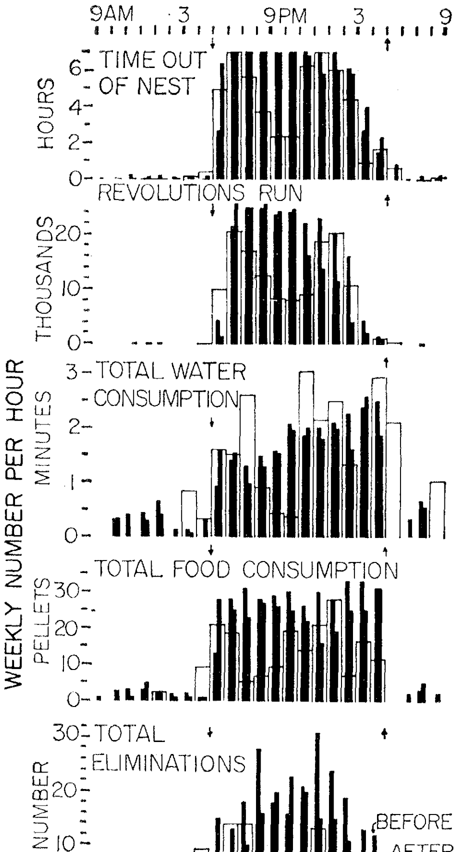
information is obtained (*9, 18*). Single and multipoint analog and event strip-chart recorders complete the recording ensemble.

Enclosures

The "running-wheel enclosure" (Fig. 1) is used primarily to obtain detailed activity profiles and to study learning. It consists of an activity wheel 30 centimeters in diameter mounted between transparent side-panes with attached nests, platforms, facilities for food and water, and programing, sensing, and control elements (*8, 9, 17, 18*). Wire grids beneath the wheel are shorted briefly by urine and droppings. A simplified enclosure of the same basic design (Fig. 2) is used to study control of environment and effects of compulsion (*8, 9, 17,* and below).

Social interactions are studied in the "social enclosure" (*19*). Individuals are identified at key locations by proximity sensing of small metal collars. The running-wheel and social enclosures lie at one extreme of design; only a relatively small amount of space is available, but this space is highly instrumented and several outlets for manipulating the environment are provided. Studies in these enclosures show that white-footed mice readily master complex relationships and characteristically exercise a high level of control over susceptible environmental variables (*8, 9, 17–19*).

In a third type of enclosure, the "extensive enclosure," space itself, that is, the size of the inhabited region, is the chief environmental variable controlled by the animal (*20*). Extensive enclosures contain hundreds of meters of linear runways and vertical, burrow-simulating mazes with hundreds of blind alleys.



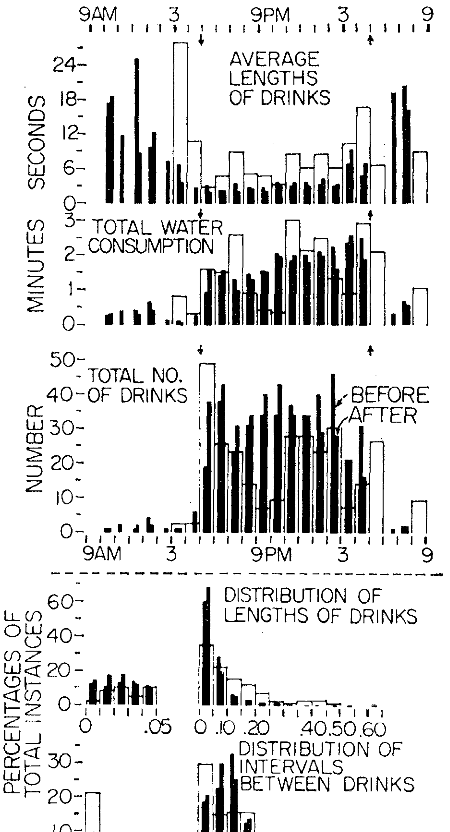


Fig. 4 (left). Activity profiles for deer mouse 1 for 1 prior week on water (first set of bars labeled "Before"), 3 days on 25 percent ethanol (open blocks), and 1 subsequent week on water (second set of bars labeled "After"). The quantities plotted represent the totals for each hour of the day for a 1-week period. The night period (dim light) begins at 5 p.m. (downward-pointing arrow) and ends at 5 a.m. (upward-pointing arrow). Fig. 5 (right). Drinking profiles and distributions for the regimes of Fig. 4.

Activity Profiles

White-footed mice learn complex experimental regimes with such facility that their learning capacity may have to be probed at the high levels employed with nonhuman primates. The program of the following study probably is the most complex experimental regime mastered by a nonprimate. To obtain a 97-milligram food pellet, the mice had to press two levers (of switches 1 and 2, Fig. 3) in correct sequence within 5 seconds. To obtain water, a third lever (of switch 3, Fig. 3) had to be pressed, unlocking a shutter which had to be brushed aside within 3 seconds. To leave the nest, a fourth lever (switch 7) had to be pressed, unlocking the nest shutter for 3 seconds so that the animal could brush it aside and go out; to run the activity wheel, a fifth lever (switch 4) had to be pressed, which unlocked the wheel for 5 minutes. This regime was learned readily with the aid of programed auditory cues, its complexity having been increased in single nightly steps (*18*). A 20-channel event record for male deer mouse 1 on this regime in the running-wheel enclosure is given in Fig. 3; two 1-week activity profiles are given by the sets of bars labeled "Before" and "After" in Figs. 4 through 6.

In brief synopsis, on an average day of the first 1-week regime the animal spent the daylight period resting in the nest, except for three brief excursions to the wheel during which it eliminated and often ate and drank (Figs. 4 and 5). During the nesting period it shifted its position 191 times. The nest was vacated 34 minutes after the bright (4 foot-candles, 42.5 lumens per square meter) day lights gave way to dim (0.0008 ft-c) night lights (downward-pointing arrows in Figs. 4 and 5). Departure was preceded by a "restless" period of 13 minutes during which body position was shifted 26 times. The animal spent the night running in the wheel (83 percent of the time; 33,000 revolutions), eating, drinking, exploring the enclosure, and so forth. It visited the nest briefly seven times. The nest was reoccupied 2 to 4 hours before the lights were brightened (upward-pointing arrows). However, the mouse left it again several times before "dawn" and ate, drank, and eliminated (Figs. 4 and 5). The animal ate 51 food pellets, took 57 drinks, averaging 3.6 seconds per drink, and eliminated 33 times per 24-hour period.

Correlations between eating, drinking, and eliminating are given by the first bars in each pair in Fig. 6. Each plot gives the distribution of time intervals (in percentage of the total number) between the beginning of an event and the next occurrence of the same or a different event. Eating and drinking tended to precede or follow elimination by less than 1 minute. Except for periods between daytime excursions, only infrequently did a period of greater than 15 minutes intervene between eating and the next drink; 69 percent of all instances occurred within 10 minutes.

Such activity profiles and correlations are useful for studying individual and species differences. They also pinpoint performances under precisely specified conditions, providing controls for studies of the effects of diet, drugs, diseased states, surgical intervention, and environmental changes. By way of illustration, some effects of modifying the liquid intake are given (Figs. 4–6). Following the regime described above, 15 percent ethanol was substituted for 1 week and 25 percent ethanol for an additional 3 days before water was restored. The second bar in each pair (Figs. 4–6) represents the same regime as the first bar, but for the week after 25 percent ethanol had been substituted (after 3 intervening days of adaptation). The open blocks are for the 3 days during which the mice were given 25 percent ethanol (expressed as 7 days to allow direct comparisons).

Behavior patterns changed markedly on 15 percent ethanol and more so on 25 percent ethanol. After return to water, the patterns (except for sleeping in the wheel) gradually returned to normal (Figs. 4–6). In general, ethanol produced an increasing lethargy and "attachment" to the nest. On 25 percent ethanol the animal spent 23 percent less time out of the nest at night than when on the water regime and made brief visits to the nest 120 percent more frequently. About ½ hour per night was spent resting in the wheel, a habit which developed on 15 percent ethanol. Running declined 33 percent, recorded eliminations 45 percent, and food consumption 37 percent. Total liquid consumption increased 40 percent, but water consumption was up only 5.5 percent. Although the number of drinks declined 21 percent, their average length doubled. Eating and eliminating less and taking fewer drinks resulted in a lengthening of most correlation intervals (Fig. 6; *21*).

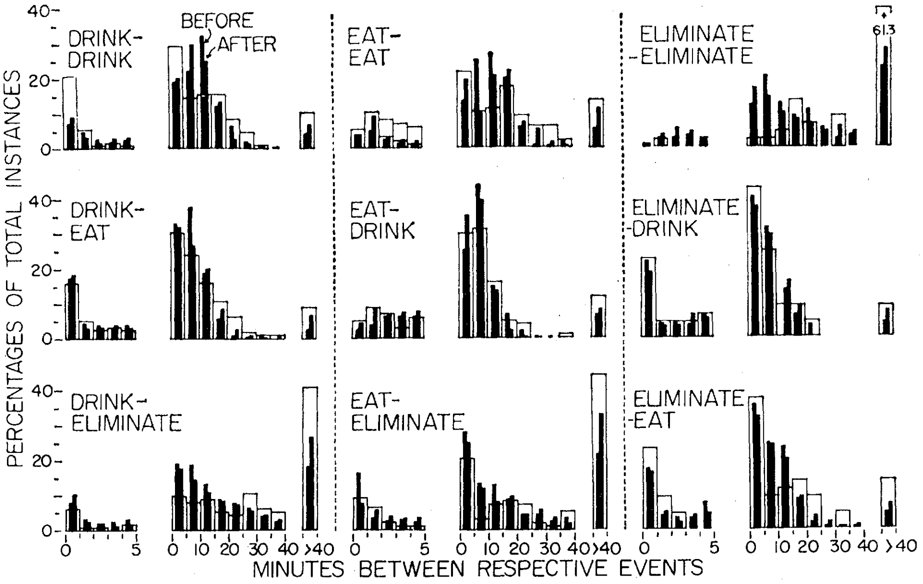


Fig. 6. Correlations between eating, drinking, and eliminating for the regimes of Figs. 4 and 5.

Much time was spent in the nest between 7 p.m. and midnight (Fig. 4), a habit which is reflected in the profiles for other activities (Figs. 4 and 5). Part of the decrease in recorded eliminations resulted because the animal began to foul the nest, in sharp contrast to its normal habits.

Social Interactions

Effects of social interactions are illustrated by studies of two mature female deer mice in the social enclosure (*19*). Each animal was studied alone for 7 days, then both together for 7 days, and then each separately again for a like period. Living alone, each had a distinctive behavior pattern; mouse 2 spent most of the night running the wheel, whereas mouse 8 was relatively inactive and spent most of the night in the nest. In consort the animals' activities changed markedly, with the pattern of each changing in the direction of the other's. For example, mouse 2 now spent 47 percent less time out of the nest at night, whereas mouse 8 spent 19 percent more time out. The mice had a strong tendency to remain in each other's company. Mouse 8 followed mouse 2 to and from the nest and through a passage between compartments on 52 percent of all possible occasions—31 percent of the time within 1 minute and 70 percent within 5 minutes. On 63 percent of the occasions when mouse 8 left the company of mouse 2 (without being followed) it returned within 2 minutes. When returned to a solitary existence each animal resumed its previous pattern of behavior.

The most complex extensive enclosure contains 427 meters of linear runways. The shortest one-way path through its vertical maze system is 96 meters long, has 1205 90-degree turns, 48 meters of vertical passageways, and opens into 445 blind alleys, the latter occupying 53 percent of the total space. White-footed mice explore and learn to traverse this complex maze system in as few as 2 or 3 days without extrinsic reward or prior deprivation (*20*). Even though this maze is vastly more complex than the ones employed in studies with domestic rodents, there is no reason to believe that the limits of the learning capacity of white-footed mice have been approached.

Maze-learning much resembles the learning of serialized activities by human beings, as when one learns a piano piece from memory (*22*). In the case of the mice, however, the mazes must be learned both forward and backward, since there is but one point of access and exit. Once learned, mazes can be negotiated with remarkable speed and agility. Animals usually explore one maze completely and retraverse it several times before beginning to explore another. Sometimes they fail to return to explored regions, just as portions of the habitat are abandoned in the wild. Return trips usually are much faster than outward ones, for there is a much greater tendency to "re-explore" blind alleys on outward trips. Active animals tend to avoid a dark maze; this suggests that dim light is preferred to darkness (see also below).

Patterns of spontaneous movement in extensive enclosures are similar to known patterns in the wild (*20*). Because the patterns are established and followed without extrinsic reward, these activities appear to be the expression of inherited tendencies to explore and to develop wide-ranging locomotor activity. This interpretation is in conflict with the generally accepted postulate that hunger and thirst play leading roles in motivating wide-ranging locomotor movements. Accordingly, studies of learning in simple mazes with deprived domestic animals and extrinsic rewards may have but limited significance for understanding the behavior of wild and relatively unconfined animals.

The fact that experimental animals frequently make supernumerary instrumental responses after delivery or onset of rewards is well known but has been little understood. Several factors undoubtedly are involved, of which neither control of environment nor the adaptive value of the behavior has been given adequate attention. It is unrealistic to expect animals to cease pressing levers immediately after onset or delivery of a reward, for "rewards" in the wild often are proportional to the degree of repetition of responses. Wild animals infrequently encounter situations, identical in all discernible ways, in which the same response that leads to a reward at one instant does not do so a moment later.

The significance of post-reward lever pressing is elucidated by studies in which: (i) different rewards are obtained by pressing different levers; (ii) levers have more than one function; (iii) sequential lever pressing brings about step-by-step changes; and (iv) lever functions are altered in different phases. Some of these studies and their bearing on this problem are treated below. In general my findings are consistent with anthropomorphic interpretations. Excluding accidental immediate supernumerary presses occurring in cases of sequential stepwise control, the animals appear to be seeking either immediate further reward or alteration of the environment, prolongation or accumulation of reward, or some other previously programed or unknown reward. Post-reward lever pressing rarely occurs when a second press withdraws the reward (*8*).

"Incorrect" Responses

"Incorrect" responses are closely related to post-reward lever pressing. Investigators sometimes are puzzled by the fact that once an animal has learned a discrimination well, it nonetheless still makes some "incorrect" responses. Actually, these responses are incorrect only from the point of view of the investigator's rigidly prescribed program, not from that of the animal. The basis for these responses is that the animal has a certain degree of variability built into many of its behavior patterns. This variability is adaptive to conditions in the wild, where there are many relationships that are not rigidly prescribed.

The marked variability of certain responses of white-footed mice is illustrated by food-pellet procural on the regimes of Figs. 4 through 6. Deer mouse 1 did not always approach the levers directly and press them in correct sequence, despite long practice (*18*). Often it investigated the food tray first. On a typical night on the water regime it obtained 50 pellets using the correct sequence but failed 23 times using incorrect lever-pressing patterns. This behavior is adaptive to variable conditions. Thus, when there is a pellet in the tray, lever pressing is skipped; when the sequence is changed, or a single or double pressing of either lever suffices, this is discovered quickly. The habit of deviating fairly frequently from stereotyped "correct" responses, together with a high level of spontaneous activity, underlie the remarkable facility with which white-footed mice can be taught to cope with complex contingencies.

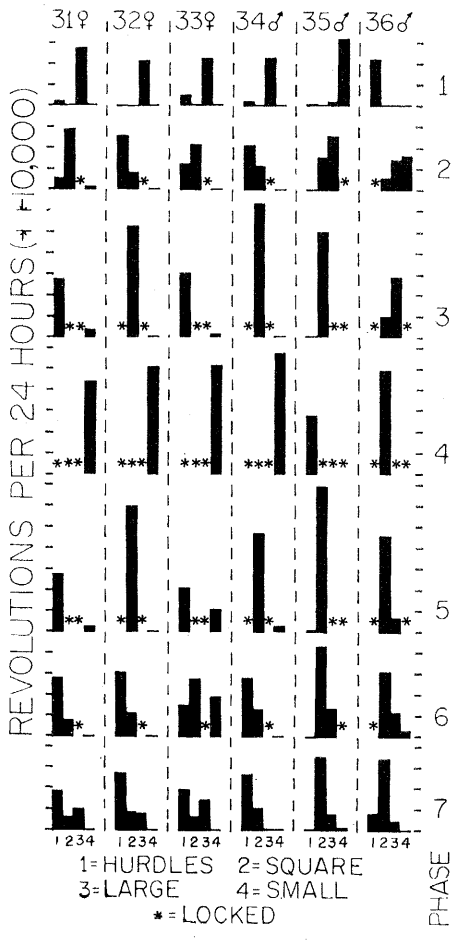


Fig. 7. Wheel-running preferences of six deer mice.

Lever pressing becomes highly selective on complex regimes. A striking illustration is the reaction of deer mouse 1 when its pressing of the switch-4 lever failed to unlock the wheel (*18*). The animal customarily unlocked the wheel every 5 or 6 minutes at night and ran until the wheel relocked 5 minutes later. When the wheel failed to unlock ("clutch failure," Fig. 3), the behavior of the "frustrated" animal changed markedly. It became intensely active, eliminating often and visiting all parts of the enclosure frequently, including areas otherwise visited infrequently (Fig. 3). The animal pressed the switch-4 lever 110 times in the next 90 minutes in unsuccessful attempts to unlock the wheel, and pressed all other levers that were functional in the program 131 times. But even during this period of excitement it was highly selective, for it largely ignored switches 5 and 6 (only 5 presses), which never had been functional and normally were pressed only rarely. As soon as the clutch was repaired (Fig. 3, 12:45 a.m.) the normal routine was resumed.

Wheel-Running

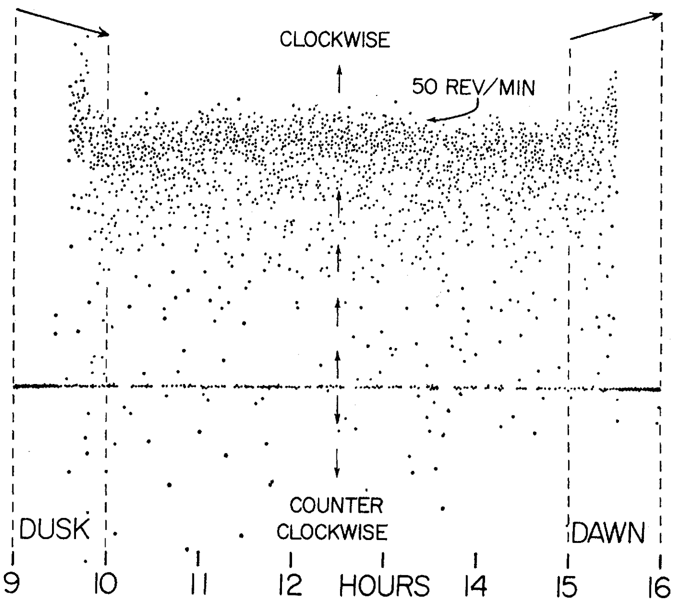
When fully adapted to the running-wheel enclosure on a bright-dim light regime, white-footed mice typically spend most of the dim-light phase (up to 89 percent of the time) running the wheels. Similar but less striking behavior is well known for small mammals on bright-dark regimes (bright light, then darkness, then bright light, and so on). It is important to elucidate the causal factors underlying wheel-running, for in small enclosures this activity is, perhaps, the best substitute for the spectrum of activities in the wild, and is used extensively as a quantitative measure of activity and rhythmicity.

Running a wheel provides a means of sustained vigorous exercise otherwise difficult to achieve for closely confined animals. Since vigorous activity keeps muscles in optimum condition, this aspect of wheel-running can be regarded as adaptive. However, the opportunity for vigorous exercise can explain the appeal only partly, for in enclosures which provide ample space for sustained vigorous running and jumping, mice frequently spend much time running a wheel (*20*). Furthermore, rodents that have escaped or been released enter and run accessible activity wheels (*23*). Accordingly, other rewarding features of the act must be sought. One such feature is the manipulation of the wheel (accelerating, decelerating, and so on). Another is the acrobatics performed in large wheels, such as jumping onto and over the axle and across it along a diameter, as well as darting back and forth through passageways in the center pane (Figs. 1 and 2).

Another clue was provided by some preliminary studies (*24*) in which canyon mice obtained experience running several different coaxially mounted "wheels." In a free-choice situation, animals experienced with and proficient in running all the wheels tended to prefer a square "wheel" to a round one. Starting, stopping, and running in the square wheel require jumping at the corners at rates up to 15 times per second. Accordingly, this preference suggested that exercise in which quick reflex actions and split-second timing and coordination of movements play a large role is preferred to exercise in which vigorous muscular activity is the primary requirement. To test this hypothesis, additional studies employing a round wheel with hurdles have been carried out (*25*). I reasoned that if split-second timing and coordination and quick reflex actions are important, a round wheel with hurdles probably would be even more suitable than a square wheel, for an animal actually must jump upward to clear the hurdles, whereas an animal running in the proper rhythm in a square wheel merely has to jump across to the approaching sides as the corners pass beneath.

The four wheels used were: two round wheels 15 and 25 centimeters in diameter, a round wheel 25 centimeters in diameter with four 1.9-centimeter-high hurdles, and an 18-centimeter square wheel. Three captive-born female littermates and three wild-caught male deer mice were studied individually. As in the preliminary study, all four wheels were available to the inexperienced animals in phase 1, until a constant pattern of running was established and maintained for 2 to 4 days. The preferred wheel then was locked and the experiment continued with the partially experienced animals until a new constant pattern was established and maintained (phase 2). The favored wheel of the remaining three then was locked (phase 3) and, afterward, the favored wheel of the remaining two (phase 4). After the animals had learned to run the last wheel, the wheels were unlocked in the reverse order (phases 5 and 6) until all four wheels were available to the fully experienced animals (phase 7). The running patterns in each phase are plotted in Fig. 7.

In phase 1, four animals (including the three littermates) preferred the



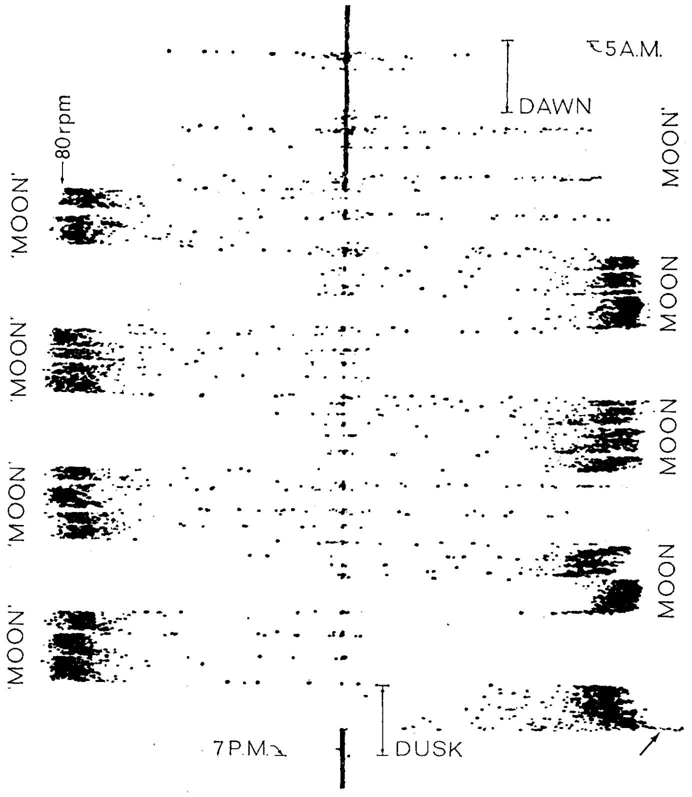


Fig. 8 (left). Speedomax G running record for deer mouse 2 during a night on a 16-hour periodicity employing twilight transitions of varying color temperature. Each dot gives the instantaneous speed (linear scale) and direction of running at 4-second intervals. The dim-light source was in the clockwise direction in all phases. This running record (and that of Fig. 14) was drawn from a more complex multicolor record for more than one variable, whereas the record of Fig. 9 was photographed directly from the original unicolor record for running only.

Fig. 9 (right). Photograph of a Speedomax G running record (points at 4-second intervals) for a captive-born canyon mouse on a night during which the direction of the "moon" was changed every hour. The unlabeled arrow at the lower right indicates the early burst of high-speed running (very brief for this animal); dots to the right of the center line represent running in one direction, to the left, in the other; the positions of the "moon," dawn, and dusk markers indicate the directions of the artificial moon and twilight sun with respect to the direction of running.

large round wheel, one the small round wheel, and one the hurdles. The small round wheel was the last choice of the same four animals in phase 4, whereas the hurdle wheel and the square wheel were the last choices of the other two, respectively. However, the fully experienced animals with the full range of choice in phase 7 showed a large preference for either the hurdles or the square wheel. The same group of four animals preferred the hurdle wheel, the other two the square wheel (Fig. 7). Thus, the wheel preferred by fully experienced animals turned out to be only the second choice (twice), third choice (thrice), or the last choice (once) of the inexperienced animals of phase 1—never the first choice.

These results confirm the thesis that one of the rewarding aspects of wheel-running for wild rodents is its requirement for split-second timing and coordination of movements and quick reflex actions. The results also point up a significant fact for the design of laboratory studies, namely that results obtained in free-choice experiments with inexperienced animals may be completely misleading, even after long experimental periods. This comes about because, as mentioned above, some behavior of animals tends to be quite conservative. In this case, the first one or two wheels run may monopolize subsequent running (*25*).

The same conservatism is seen in selection between sources of food and water. For example, in the enclosure of Fig. 2, paired food guns (*d*) and water bottles (*e*) are available. Although some variability is exhibited (as with other categories of behavior), typically only one food source is used. The other often is left untouched until the first is exhausted. If the first source is replenished periodically, the second may remain untouched. Conservatism also tends to apply to the use of water sources. To a degree, such conservatism has survival value; animals that tend to confine their movements to well-worn beaten tracks within the home range (compare conservatism in wheel-running) and to eat and drink only at familiar sites (when alternate sources are available) are the ones most likely to survive.

Another approach to the significance of wheel-running utilizes motor-driven wheels. White-footed mice engage repeatedly in motor-driven running (MDR) if they themselves start the rotation of the wheel (*8*). Accordingly, one can make direct comparisons of the reward value of running free and motor-driven wheels. Two wild-caught male canyon mice (Nos. 20 and 25) were studied on a regime in which pressing either of two levers unlocked the wheel for 2 minutes, making free running possible, and pressing either of two other levers started rotation of the wheel for 2 minutes at 33 revolutions per minute. On this program, sessions of running the free wheel occurred over three times as frequently as those of MDR (*8*). These findings reinforce views on the importance of vigorous exercise, manipulation, timing, and so forth, in wheel-running, because running the free wheel allows much manipulation and acrobatics, and can occur at high speeds, whereas manipulation is more limited in MDR and the speed must be kept comparatively low (for purposes of safety).

In another experiment with the same animals, pressing any lever started rotation (at 25 revolutions per minute) of the stationary locked wheel but stopped rotation and locked the wheel if it already was rotating (*8*). On this program (see also the treatment below) the animals ran less than 40 percent as much as they did with free wheels, a result which substantiates the existence of a preference for free running.

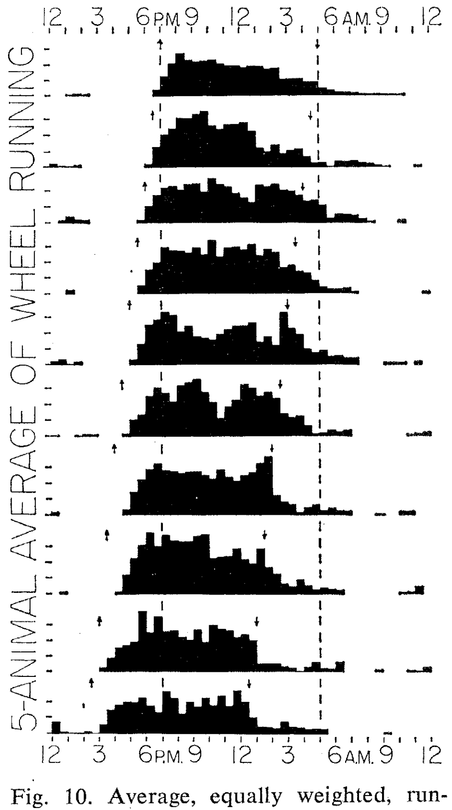


Fig. 10. Average, equally weighted, running patterns (½-hour grid) for four deer mice and one canyon mouse during a dark-dim (0.0008 foot-candle) light regime for 7 days (averaged at top) on a 24-hour rhythmicity and 9 subsequent days on a 23½-hour rhythmicity.

Responses to Light

A significant feature of the sustained wheel-running of white-footed mice is that most individuals run almost entirely (up to 99.99 percent) in one direction (*8, 18, 27*). The position of the dim-light source is the chief factor determining running direction, although other features of the enclosure also can play a role. If the light source is mounted in alignment with the wheel (Fig. 2, *h*), most animals consistently run either toward or away from it (*26*). On the other hand, in darkness —on the commonly employed bright-dark regime—running direction tends to be haphazard.

Artificial twilight transitions about 1 hour long have been simulated by two methods: (i) in the varying-color-temperature method, the potential applied to a cluster of four miniature lamps is varied continuously between 1 and 6.5 volts; (ii) in the constant-color-temperature method, 92 bulbs of 15 different intensities are turned on or off progressively in a sequence of 52 steps (*27*). Both types of light transition elicit several additional responses. Whereas animals that begin to run in light of constant intensity—whether bright, dim, or dark—usually warm up to top speed gradually, over a period of 1 to 3 hours (*8, 18, 27*), animals that begin during a dusk usually run in a brief burst at high speed during the first 5 to 15 minutes (Fig. 8; Fig. 9, small arrow). An analogous brief burst of running at high speed also occurs if the animal is running sustainedly at the time of the dawn transition, just before running ceases (Fig. 8), whereas no characteristic pattern emerges when the phase of sustained running ceases before dawn (Fig. 9) or under other constant conditions of illumination. The onset and cutoff intensities for twilight running usually range from 1 to 10 times that of the full moon (FM = 0.012 to 0.023 foot-candle).

The middle to late phase of dusk and the early phase of dawn have a great activity-stimulating effect upon white-footed mice, whereas the middle to late phase of dawn has a strong inhibitory effect (*27*). One of the most striking ways to show these strong influences is to present a series of alternate dusk and dawn transitions in immediate succession through the normal activity period. Of two male canyon mice tested on this regime, one responded to almost every transition (*27*). It began running in a high-speed burst, as usual, in the first dusk, and ceased in a high-speed burst and retired to its nest during the first dawn. The same responses occurred during the second dusk and dawn. The animal "overslept" the middle phase of the third dusk but began running in the late phase (warming up rather than beginning at high speed). It ceased in a high-speed burst and retired to its nest a third time during the third dawn. The fourth dusk also was overslept, the animal once again warming up rather than beginning to run at high speed. Sustained running ceased, as usual, before the final dawn, which began at its usual time, 2 hours after the end of the fourth dusk. Both animals always ceased running promptly in response to dawn. Failure to respond promptly at mid-phase of every dusk apparently is a consequence of the strong activity-inhibiting effect of the immediately preceding dawn. These twilight responses show clearly that if approximately natural stimuli are presented to captive animals, even on a thoroughly unnatural time schedule, the animals can be "forced" to respond in an approximately natural way, almost at the will of the investigator.

A significant feature of twilight running is that a given animal consistently runs with the same orientation to the setting and rising "sun" as to the "moon." In early studies there was only a single fixed light source. Thus, in running in one direction all night (Fig. 8) the mice might have been orienting relative to any one of the three dim-light phases (setting "sun," rising "sun," or "moon") and ignoring the other two, or they simply could have been orienting relative to any dim light. The use of independent light sources mounted opposite one another reveals a strong orienting effect of any dim light on the running direction of the mice.

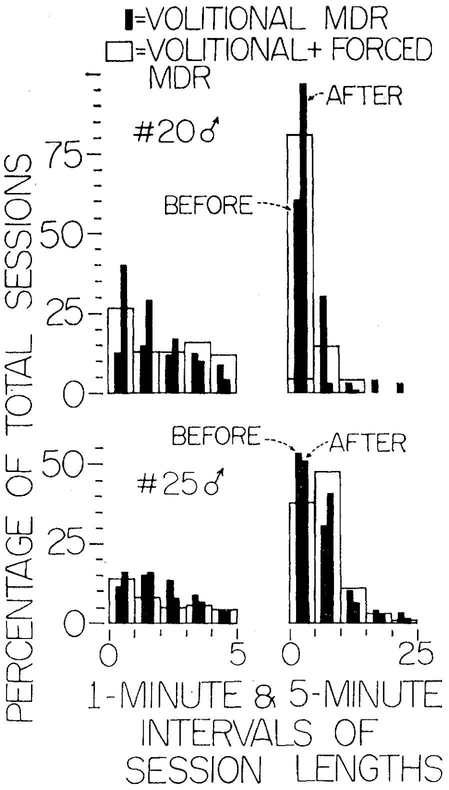


Fig. 11. Distributions of session lengths of volitional motor-driven running (MDR) on two programs for canyon mice 20 and 25. The first set of bars is for MDR before, and the second set for MDR after the program of volitional plus forced MDR. The volitional MDR on the latter program is shown by the open blocks. The periodic forced MDR on this program was negligible and is not depicted.

Most animals run almost exclusively toward or away from constant dim light and the artificial twilight sun at low intensities, regardless of the direction in which the lights are presented. When the "moon" and the twilight "sun" are present concurrently, the animals orient with respect to the "sun" (that is, to the source of changing intensity). If the "moon" is omitted or cut off temporarily, running remains predominantly unidirectional, with the direction determined by the position of the last light source seen. These findings suggest that white-footed mice use the twilight sun and moon (and possibly other celestial light sources and prominent topographical features) as navigational references.

The consistency of the dim-light orientation is shown strikingly by the running record of Fig. 9 for a male canyon mouse. The animal was on an imposed 24-hour light cycle (14 hours of bright light), with the "sun" setting and rising in the same direction (*28*). The "moon" appeared opposite the "sun" at the end of dusk (8 p.m.) and its longitude was shifted 180 degrees every hour during the night. The animal consistently (98.7 percent) ran toward the source of dim light, changing direction every time the source changed.

If deer mice are given complete control over the intensity of ambient illumination (*9*, and below), they select dim light during active periods and very dim light during inactive periods. This finding emphasizes the unsuitability of the abrupt bright-dark laboratory regimes that are employed customarily with nocturnal animals. In the wild, nocturnal mice generally are in very dim light or darkness during the day, not bright light. During the night they generally are in dim light, not darkness. Laboratory bright light is appropriate during the day only if a dark nesting area is provided. The unnatural bright-dark regime of the laboratory succeeds because active nocturnal animals avoid bright light much more than darkness. In fact, on abrupt dark-dim regimes, mice are active in the dim light, not darkness. In other words, the preference of the active animal for dim light (over darkness) exceeds that of the inactive animal.

In the experiment just referred to, six deer mice and two canyon mice (four males, four females), all wild-caught, were exposed to a 24-hour dark-dim (14:10) regime for 7 days, beginning with a dim phase at normal nighttime. Four deer mice and one canyon mouse ran vigorously during the dim-light phase (Fig. 10, top); the other three animals scarcely ran at all and virtually ignored the light regime (*29*). To show that the five animals actually were following the light regime, rather than simply maintaining an endogenous 24-hour rhythm in synchrony with it, a 23.5-hour light cycle was instituted for 9 subsequent days. All five animals entrained to the shortened rhythmicity (Fig. 10, beginning second from top).

Compulsion and Nest Occupancy

When mice in experimental enclosures are disturbed during the day, they often leave the nest. Sometimes they reenter almost immediately; at others they wait until the disturbance is over. But if they are placed back in the nest by hand, they leave it again immediately (as do kittens and puppies). They persist in leaving, no matter how many times they are put back. In this relatively clear-cut case, an act or situation which is rewarding when carried out volitionally is avoided when initiated by force—the animal responds by doing the opposite.

Compulsion and Wheel-Running

An equivalent response is elicited when one attempts to force mice to run a motor-driven wheel. If the experimenter starts the wheel rotating, and the mice are able to stop it (by pressing levers), they do so within seconds (*8, 17*). No matter at what time, at what rate or direction of rotation, or how experienced the animals are at MDR (motor-driven running), they turn off the rotating wheel promptly. MDR is rewarding only when it is initiated volitionally.

A striking example of avoidance of nonvolitional MDR is the behavior of deer mice in two isolated running-wheel enclosures when the wheel in each enclosure is programed to start rotating when the rotation of the other wheel is stopped (by pressing any of the four levers). Confronted with this program, a pair of mice engages for hours in a tenacious alternating lever pressing "tug-of-war." Each animal repeatedly—usually within seconds—turns its motor off, and thereby turns on the other's (*8*).

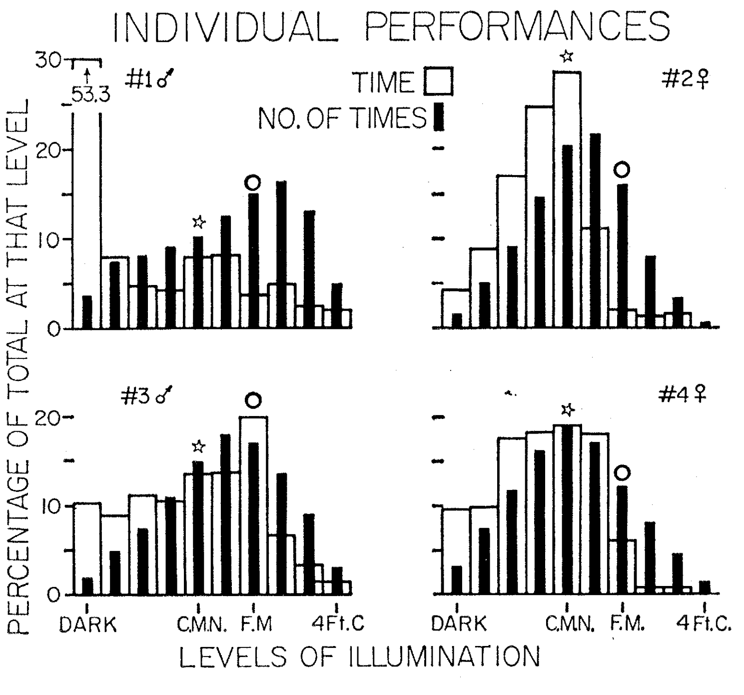
When an animal starts and runs a motor-driven wheel volitionally, there is also a strong tendency to restart the wheel promptly after it is stopped by the experimenter. Thus, canyon mice repeatedly turn the wheels back on within seconds after they go off automatically after 15- or 30-second sessions (*8*). These results make a strong case for avoidance of actions or events instituted nonvolitionally, regardless of whether the animal is being forced to initiate or cease an activity. However, the case to this point is not conclusive. One could argue that the animals are not responding conservatively but merely are exercising control over the wheel, that is, that since they find it rewarding to be able to start and stop the rotation of the wheel, they do so at every opportunity.

The first thesis—of response to compulsion—is supported by experiments in which animals both start and stop the rotation of the wheel volitionally. Under these conditions they start and stop the wheels only 20 to 50 times per night. But when they are able only to start or stop the wheel, after it is either stopped or started automatically, they do so hundreds of times. More support comes from experiments in which the motor was started periodically during a regime in which canyon mice 20 and 25 were engaged in volitional MDR, that is, were both starting and stopping the wheels (*8*). First there were 8 days of volitional MDR (Fig. 11, bars labeled "Before"). The volitional MDR was continued for the next 12 days but, in addition, the motor was turned on automatically every 60, 30, and 15 minutes during consecutive 4-day periods. The responses were clear cut. Both animals turned off the motor within seconds of the 672 automatic starts.

Session-length distributions for the concurrent volitional MDR are given by the open blocks in Fig. 11. The amount of volitional MDR of mouse 25 did not change but the average session-length increased somewhat. However, the superimposed forced schedule markedly reduced mouse 20's volitional MDR, which practically ceased after the 6th day. In the last 6 days, No. 20 turned off the motor 478 times and turned it on only 12 times. Considering that the same levers turned the motor on and off, this behavior was remarkably selective and goal directed.

These results show that the response to nonvolitional MDR is primarily one of avoidance or conservatism rather than a manifestation of control of environment—otherwise the mice would not stop the wheel promptly after each automatic start (*30*). The results also show that attempts to compel animals to engage in an otherwise rewarding activity may make even the volitional performance nonrewarding. When the animals were returned to a purely volitional regime (Fig. 11, second set of bars labeled "After"), mouse 20 showed a dramatic resumption of MDR. Both animals now found it more rewarding to start and stop the wheels, for the daily number of sessions (but not revolutions) increased markedly over that for any of the previous 20 days (*8*).

These results emphasize one of the hazards of using relatively uniformly responding strains for behavior studies. Findings on MDR based upon the behavior of an inbred strain responding as did mouse 20 would support a theory incompatible with an equally com-



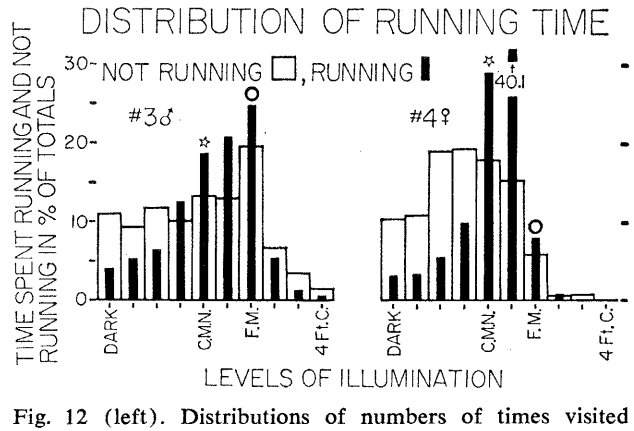


Fig. 12 (left). Distributions of numbers of times visited (bars) and total time spent (blocks) at various intensity levels (*32*) by four deer mice having bidirectional control (by pressing levers) over the intensity of illumination (see text); open circles, intensity of full moon; open stars, intensity on clear moonless night. Fig. 13 (above). The total time (open blocks of Fig. 11) subdivided into distributions of the time spent running (bars) and not running (open blocks) at the various light intensities (*32*) for deer mice 3 and 4 on the regime of Fig. 12 (data not obtained for mice 1 and 2).

pelling theory based upon the uniform behavior of an inbred strain responding in mouse 25's fashion. By giving rein to the marked individual differences existing in populations of wild animals, one obtains the added perspective needed to interpret many aspects of behavior.

Compulsion and Control of Light

In studies of control of ambient illumination, the interaction of at least three factors influences responses: the conservative tendency to counteract promptly any nonvolitional change in intensity (response to compulsion); the tendency to alter the intensity of illumination frequently (control of environment); and the tendency to spend more time at certain intensities than others (selectivity). Each factor may vary with the phase of the activity cycle, the type of previous experience and degree of adaptation to the regime, and the type of regime (*9, 31*). Accordingly, interpretation of responses is far more difficult than for nest occupancy and wheel-running studies. However, the experiments give greater insight into the interaction of behavioral variables, have greater ecological significance, and allow greater scope for the expression of individual and species differences. For these reasons I treat the following findings in considerable detail.

Complete control. The studies of control of illumination proceeded through nine phases spanning 15 to 20 weeks. Space permits treating only the first two and last phases. In the last phase, four fully adapted wild-caught deer mice (2 males, 2 females) were studied individually for 2 to 4 weeks in the isolated running-wheel enclosures of Fig. 2 (*9*). The animals had bidirectional instrumental control over the light intensity in 10 steps (*32*). Each press of either of two levers (Fig. 2, *a*) on one side of the enclosure stepped the intensity one level higher, on the other side, one level lower.

Although no external time cues were given, the mice maintained 23-to-25-hour rhythms and established characteristic patterns of controlling the illumination (Figs. 12 and 13). Selected intensities were roughly the same as those experienced at corresponding phases of activity in the wild, with a lower average level being maintained during rest and sleep than during activity (Fig. 13). The animals exercised a high level of control over light intensity during active periods, frequently running back and forth, stepping the light intensity up and down (Fig. 14).

Table 1. Figures for the performance of mice Nos. 1 through 4 in the study of compulsion and control of illumination.

Phase	Percent of possible times the mice stepped at least one level				Percent of the responses in which the mice stepped all nine levels				Average number of level changes per 24-hour period				Minutes to the first step off or on during active periods								Minutes taken to attain level 10 after the first level change							
													<9 steps				9 steps				During active periods				Beginning active periods			
	#1	#2	#3	#4	#1	#2	#3	#4	#1	#2	#3	#4	#1	#2	#3	#4	#1	#2	#3	#4	#1	#2	#3	#4	#1	#2	#3	#4
1	55	84	55	74	65	99	29	36	210	360	82	119	2.7		3.2	2.0	2.8	2.2	3.1	0.91	8.2	1.1	36	24	2.7	1.3	23	18
2	58	31	49	66	41	52	59	78	174	92	83	124	2.6	4.1	3.5	3.6	2.3	3.8	3.1	2.4	12	11	24	13	4.4	13	17	11
1*			62	87			47	38			108	138			1.9	1.8			1.3	1.2			32	19			22	13

* Second week of phase 1.

Exposure to the brightest level (4 foot-candles) was infrequent and typically very brief. Periods in darkness also were infrequent but lasted longer and seldom occurred during activity. Mice 2 through 4 spent 77 percent of the time in the range of one-half starlight to full moon (FM = open circles in Figs. 12–15), 8 percent in darkness, and only 0.5 percent at 4 foot-candles. However, mouse 1 spent 53 percent of the time in darkness, for it usually turned the lights off at the beginning of inactive periods.

These results on complete control are the simplest to interpret, for the animals were fully adapted to controlling illumination and compulsion was absent (*9*). The findings provide controls and baselines for other phases of the study. First, they show which intensity ranges are preferred during different phases of activity; second, they show that fully adapted animals continue to alter the intensity of illumination frequently, months after the novelty has worn off; and third, they give values for the frequency of these alterations (*33*) by fully adapted animals exhibiting a high degree of selectivity.

Phase 1. In phase 1 of the same study, the lights were turned fully on every half hour for mice 1 and 2 and every hour for mice 3 and 4. Each press on any lever stepped the intensity down one level. The levels for mice 3 and 4 were the 10 used on the regime of complete control (*32*). For mice 1 and 2 the levels were brighter (*34*), with none between those of darkness and a clear moonless night (open stars in Figs. 12–15). Program details were the same in phase 2 except that the lights then were turned off periodically and could be stepped back on. The following results (*35*) are for 7 days of each phase (after 2 to 4 days of adaptation).

When the lights were turned on periodically, the animals responded (Table 1) by stepping the intensity down at least one level 67 percent of the occasions possible, and fully off after 56 percent of the responses (unless otherwise indicated, figures given in the text are equally weighted averages for two or four animals; individual figures are given in the tables). The behavior of mouse 2 was striking, for

Table 2. Data on "false presses" (continuation of lever pressing after lights had been turned on or off) by mice Nos. 1 through 4 in the study of compulsion and control of illumination.

Phase or transition period	Percent of occasions off or on that false presses occurred				False presses per period off or on (No.)				False presses per hour off or on (No.)				Minutes to first false press after off or on			
	#1	#2	#3	#4	#1	#2	#3	#4	#1	#2	#3	#4	#1	#2	#3	#4
1	73	33	59	69	11	5.0	3.1	4.6	28	4.1	6.0	6.0	2.0	5.4	4.1	4.5
1–2	100	100	93	100	44	54	14	47	86	240	34	82	0.42	1.0	3.1	1.2
2	89	93	75	99	15	24	19	58	54	120	34	75	2.0	1.2	4.6	2.7
2–1			81	92			19	19			91	23			2.3	2.7
1*			72	78			6.7	9.6			11	2.0			4.0	6.0

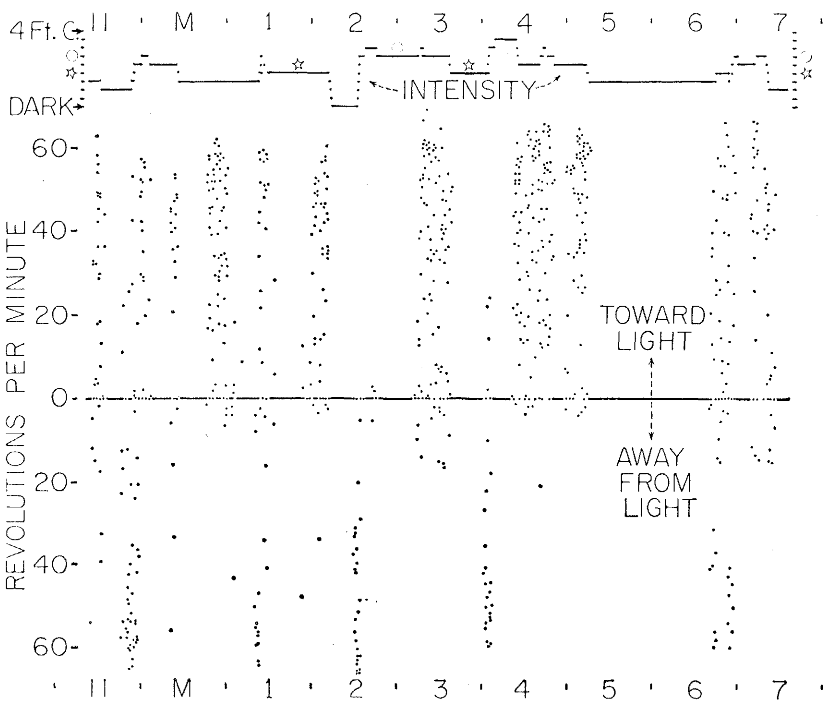
* Second week of phase 1.

it stepped the lights fully off 279 times (of 336 possible). It was in the process of stepping the lights off two other times but was interrupted by their going on automatically.

A general impression of the individual performances, which differed greatly, can be gained from the upper graphs in each set in Fig. 16. The elapsed time from the lights' going on to the first step down is plotted against the time taken to step from level 2 to the last level visited during each half-hour or hour period. Performances are far more selective than might appear at first sight, since both scales are partially logarithmic.

Responding occurred mostly during periods of running. The condition of the lights was not altered during long intervals of rest and sleep (*36*). Mouse 2 (and to some extent mouse 4) was exceptional in that, contrary to its normal habits, it became active much of the time; its longest period of inactivity was only 3.5 hours. All four animals maintained 23- to 25-hour rhythms.

One can divide the responses roughly into two groups—those that occur during active periods and those that occur at the beginning of active periods (and during inactive periods)—by taking responses that occur within 10 minutes of the lights' going on as opposed to those that occur after 10 minutes. By this criterion, the first press after "lights on" during active periods occurred after 2.4 minutes. The sooner the first step down occurred, the more likely it was that the animal would step the lights all the way off (Table 1). Thus, elapsed times to the first step generally were less for nine-step cases than for cases of fewer than nine steps. This suggests that the motivation to



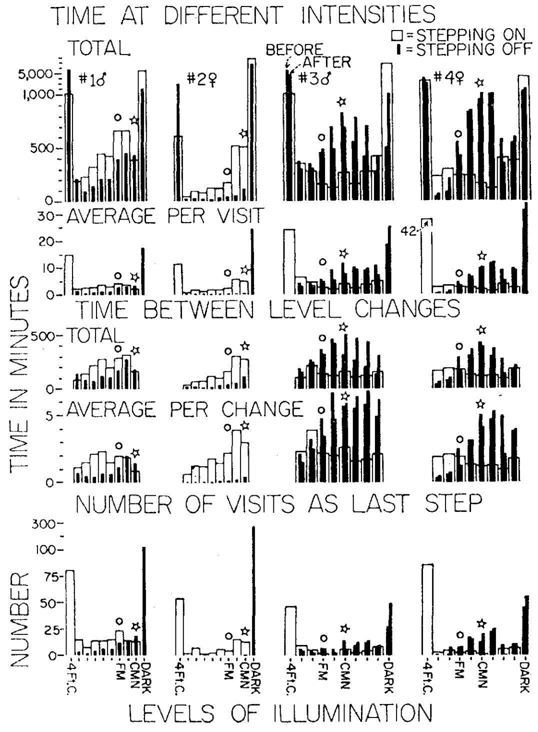


Fig. 14 (left). Reconstruction of Speedomax G record of the speed and direction of wheel-running and the concurrent levels of illumination for deer mouse 4 during a typical period of activity on the regime of Figs. 12 and 13 (complete control). Direction of running was predominantly toward the light and the animal made most alterations of the level of illumination while it was running. The amount of running, compared to that in Figs. 8 and 9, was more than is indicated by the record, for points were recorded only at 8-second intervals. The record of levels of illumination, although overlapping the running record in the original (in ink of different color) has been condensed and displaced to the top of the record. Fig. 15 (right). Overall total and average times, total and average times between level changes (dwelling times), and number of visits as last step at the various levels of illumination (text, *32, 34*) during phases 1 (bars) and 2 (open blocks) of the control of illumination study for deer mice 1 through 4. For animals 3 and 4 both the first and second weeks (bars labeled "Before" and "After") of phase 1 are plotted. Ordinates of the top and bottom plots are partially logarithmic.

respond was stronger, the sooner the first response occurred after the lights went on (*37*).

The time taken to step the lights fully off after the first step (Table 1) was 34 percent less at the beginning of active periods than during active periods (except for mouse 2 whose time of only 1.1 minute could scarcely be improved upon). Hence, once the resting animal was aroused to respond, it stepped the lights fully off much more quickly than it did when it was already active. It is significant that mice 1 and 2 stepped the lights fully off much more rapidly and much more frequently than did mice 3 and 4.

Lever pressing did not cease after the lights were fully off. On 59 percent of these occasions the mice continued to press the levers in darkness ("false offs"). There were six presses per period off, amounting to 11 presses per hour off, with the first false off occurring after 4 minutes (Table 2). The occurrence of these frequent (but not prompt) false offs suggests strongly that the mice were seeking further control over the intensity of illumination—perhaps trying to regain dim levels.

The performance of mouse 2 was most clear cut (Figs. 15–17). Its rapid stepping of the lights fully off almost every time was not because of a preference for darkness, for with complete control it spent only 4.3 percent of the time in darkness (Fig. 12). Moreover, the plots in Fig. 15 (bars) show only weak selectivity from level to level. Either mouse 2 was responding vigorously to compulsion or it was seeking control over the lights to the greatest degree. The latter explanation is unlikely, since mouse 2's false offs were the least for the group (Table 2). Nor did mouse 2 show the greatest tendency to control the lights during the regime of complete control (*33*). Accordingly, it can be concluded that mouse 2 responded vigorously to compulsion but exercised only moderate environmental control characterized by weak selectivity.

Mouse 1 showed greater selectivity (Fig. 15, bars); in stepping the light down, it tended to dwell ("average per change") longest at the lower intensities, and often left the lights at dim levels. It is unlikely that the frequent false offs by mouse 1 were due to a strong tendency to seek dim light and avoid darkness, for with complete control (Fig. 12) this mouse spent 53 percent of the time in darkness. Hence the most frequent, soonest, and highest rate and number of false offs by mouse 1 (Table 2) probably should be interpreted as mainly a seeking of further control of the lights. This interpretation is consistent with the fact that mouse 1 altered the intensity most frequently on the regime of complete control (*33*).

Mice 3 and 4 were highly selective, as is shown clearly in Fig. 15 (first set of bars). Much time was spent at intermediate dim levels. In fact, the intensity distributions for these mice, even in this first phase, begin to resemble those exhibited months later on complete control (Figs. 12 and 13). On 67 percent of responses they left the lights at dim levels (*38*).

Transition to phase 2. Dramatic reactions occurred during the 2-day transition to phase 2. Now that lever pressing stepped the lights on instead of off, the mice pressed more and more quickly as the lights brightened, and often in a fast staccato after the lights were

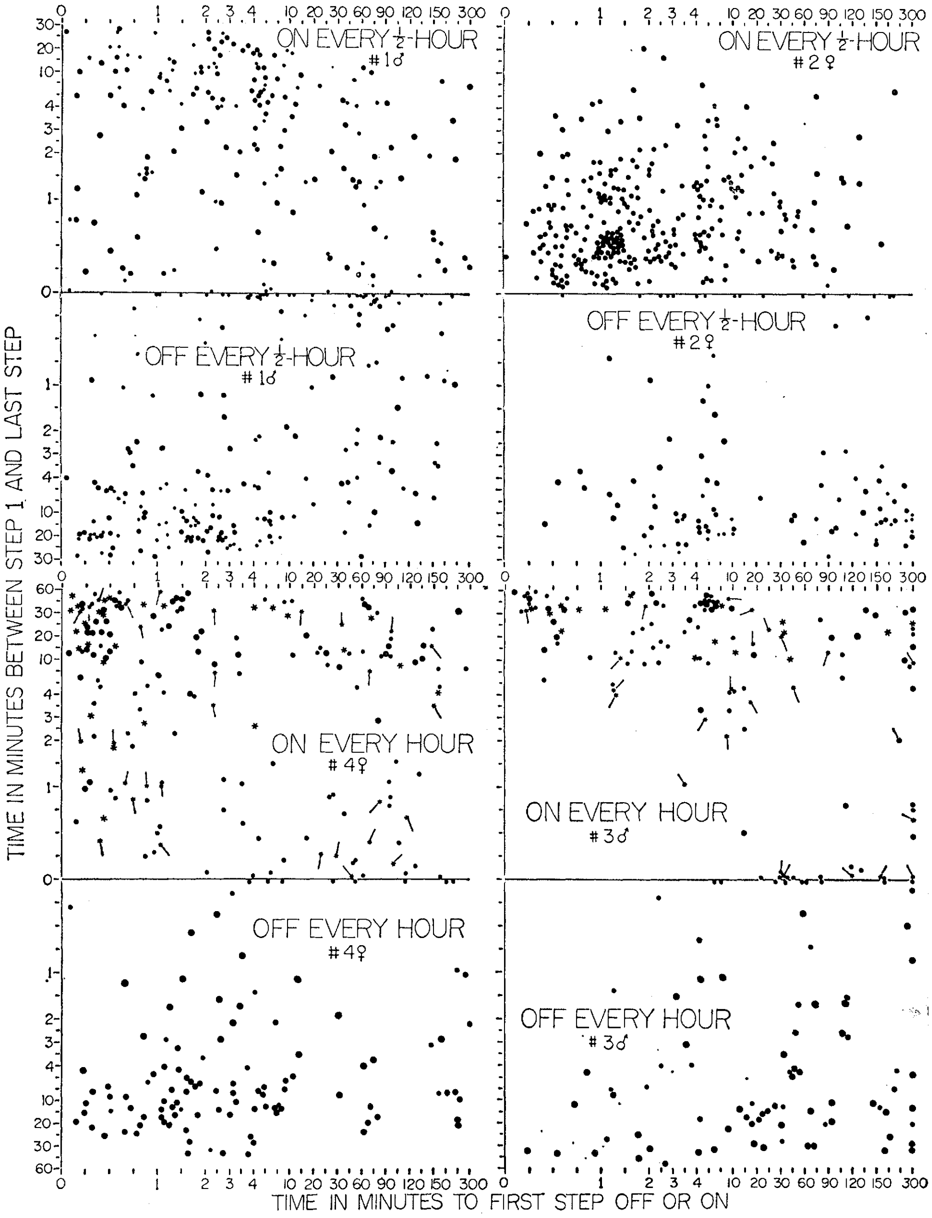


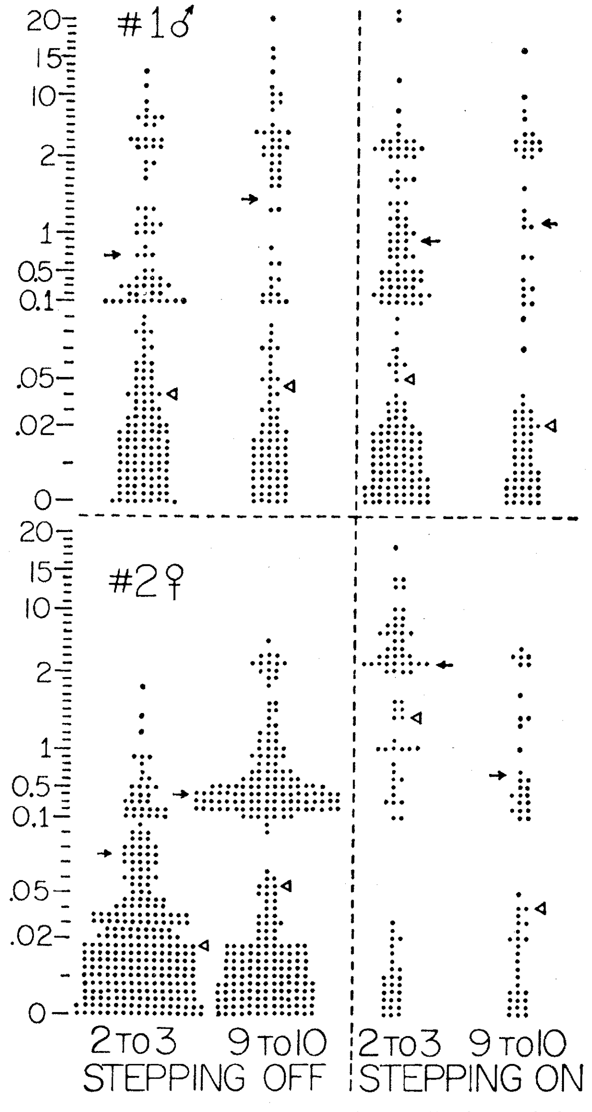
Fig. 16. Partially logarithmic plots of elapsed time to taking the first step versus elapsed time from the first step to the last step taken for deer mice 1 through 4 during phases 1 (on periodically) and 2 (off periodically) of the control of illumination study. Large dots are for cases in which the lights were stepped fully off or fully on (nine steps); small dots are for fewer than nine steps; small dots lying very close to the abscissae generally are for only one or two steps. The large stars and small stars with tails have the same significance as the large and small dots, except that they are for the 3-day extension of phase 1 (for mice 3 and 4) in which sound was presented hourly (see *36*).

fully on and further presses were without effect. "False ons" occurred on virtually every occasion the lights were fully on (Table 2). There were 40 presses per occasion on, amounting to 110 presses per hour on, with the first false on occurring after 3.3 minutes. These figures are remarkably different from those of phase 1.

It appears that the strong tendencies to modify the level of illumination repeatedly and respond conservatively to nonvolitional alterations led the animals to step the lights fully on over and over again, even though this entailed passing beyond the preferred dim range to the level avoided most on complete control. It is difficult to avoid the anthropomorphic interpretation that the rapid and frequent false ons were attempts to turn the lights back off or to lower intensities, especially since such behavior at the "on" switches did not occur during the program of complete control, when "off" switches also were present (*39*). Both the tendency to avoid bright light and a vigorous reaction to the loss of the step-down control of intensity of phase 1 underlie this response (*40*).

The influence of withdrawal of environmental control also is shown by the following experiment. On return to a second week of phase 1 (Figs. 15, 18, and 19) after phase 2, similar vigorous prompt "false pressings" by mice 3 and 4 occurred in the transition period (Table 2), even though the levers then were being pressed when the lights were fully off. Thus, responses to withdrawal of environmental control occur regardless of whether it is the ability to step the lights on or off that is withdrawn, and even when other environmental control is substituted. As noted above (see Fig. 3), when control over the environment is withdrawn without substitute, the mouse reacts with astonishing vigor.

Phase 2. The mice responded to the lights going off periodically by stepping the intensity up at least one level on 51 percent of the occasions possible, and fully on after 58 percent of these responses (Fig. 16, lower graphs in each set). While the percentage of nine-step responses (that is, to lights fully on) declined markedly for mice 1 and 2, it increased markedly for mice 3 and 4 (Table 1). Once again, the sooner the first step occurred, the more likely it was that the light intensity would be altered the full nine steps (*37*). Com-



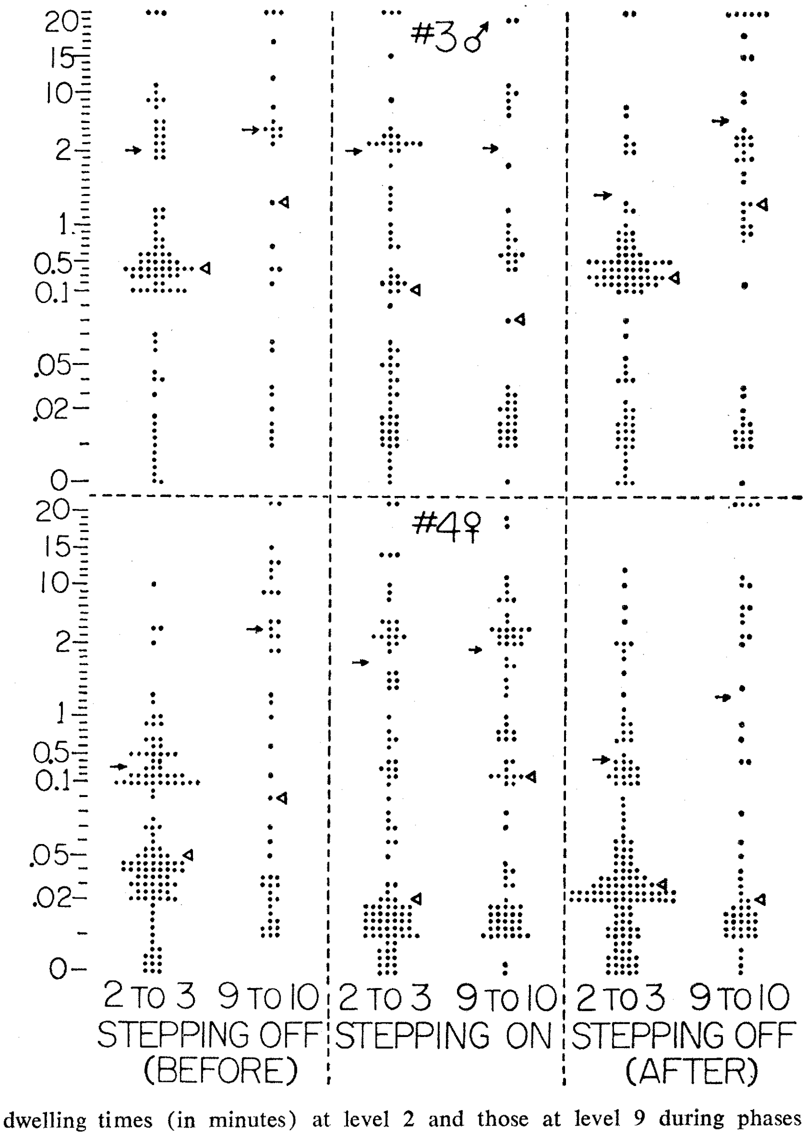


Fig. 17 (left) Partially logarithmic distributions of the dwelling times (in minutes) at level 2 and those at level 9 during phases 1 (stepping off) and 2 (stepping on) for deer mice 1 and 2 in the control-of-illumination study. Level 2, stepping off, is the same intensity as level 9, stepping on, and level 9, stepping off, is the same as level 2, stepping on. Fig. 18 (right). Partially logarithmic distributions of the dwelling times (see Fig. 17) for deer mice 3 and 4. The stepping-off sections labeled "Before" and "After" are for the first and second weeks of phase 1.

pared to phase 1, the times taken to go from level 2 to level 10 (fully on) during active periods are markedly greater for mice 1 and 2 but markedly less for mice 3 and 4. False-on performances were "toned down" considerably from the transition period, but they still greatly exceeded the negligible false ons on the program of complete control (*39*).

Mouse 2 showed definite signs of selectivity for the lower intensities (Fig. 15, blocks versus bars). It waited much longer than in phase 1 before the first step (Fig. 16) and stepped nine levels (fully on) much less quickly and much less frequently. In brief, response to compulsion (that is, conservative responses to nonvolitional level changes) now played a much smaller role for mouse 2 and selectivity a much greater role. Selectivity also played a greater role for mouse 1 (Fig. 15), but a glance at Fig. 16 reveals that its performances in the two phases were not radically different (*41*).

Mice 3 and 4 responded fewer times than in phase 1 but they stepped the full nine steps almost twice as often (Table 1), despite the fact that they avoided bright light much more than darkness on complete control (Figs. 12 and 13). For both mice the amount of selectivity, although considerable, declined markedly from phase 1 (Fig. 15, open blocks versus first set of bars). Both the average dwelling times and the last-step visits at intermediate levels declined extensively.

Phase 1 versus phase 2. The distributions of dwelling times are a valuable comparative performance index. As an example, the time spent at level 2 on the way to level 3 is compared with the time at level 9 on the way to level 10 (Figs. 17 and 18). It is important to consider both distributions and averages, because a very few long visits change the average markedly when most visits are very short. Both the averages (arrows) and the median values (triangles) are indicated in the figures. These data must be interpreted in terms of the finding that on complete control, the high light intensities of level 2–1 (level 2, phase 1) and level 9–2 were avoided relative to the low ones of level 9–1 and level 2–2 (*32, 34*).

The differences in the distributions of Figs. 17 and 18 indicate that, insofar as levels 2 and 9 are concerned, mouse 1 showed more dwelling-time selectivity in phase 1 than in phase 2, mouse 2 showed considerable dwelling-time selectivity in phase 1 (*42*) and a greater amount in phase 2, and selectivity played an important role for mice 3 and 4 in phase 1. The phase 2 distributions are inconclusive for mouse 3. For mouse 4 they definitely do not suggest the showing of a preference for the dim light of level 2 over the bright light of level 9. The latter results are consistent with the conclusion that selectivity of mice 3 and 4 decreased markedly in phase 2 (*43*).

Perhaps the best indicator of selectivity is the concomitant wheel-running. During phase 1, mice 3 and 4 averaged 16 revolutions in bright light before pressing a lever. But during phase 2, in darkness, they averaged 93 revolutions before the first press (*44*). These data suggest that active animals avoid bright light much more than darkness, in agreement with the definitive results on complete control (Figs. 12 and 13). Moreover, in bright light the animals altered the intensity much more frequently before beginning to run than they did in darkness (*45*).

To attempt a definitive interpretation of these findings would be premature, since the results of phases 3 through 8 are pertinent but cannot be treated here. However, the basis for the

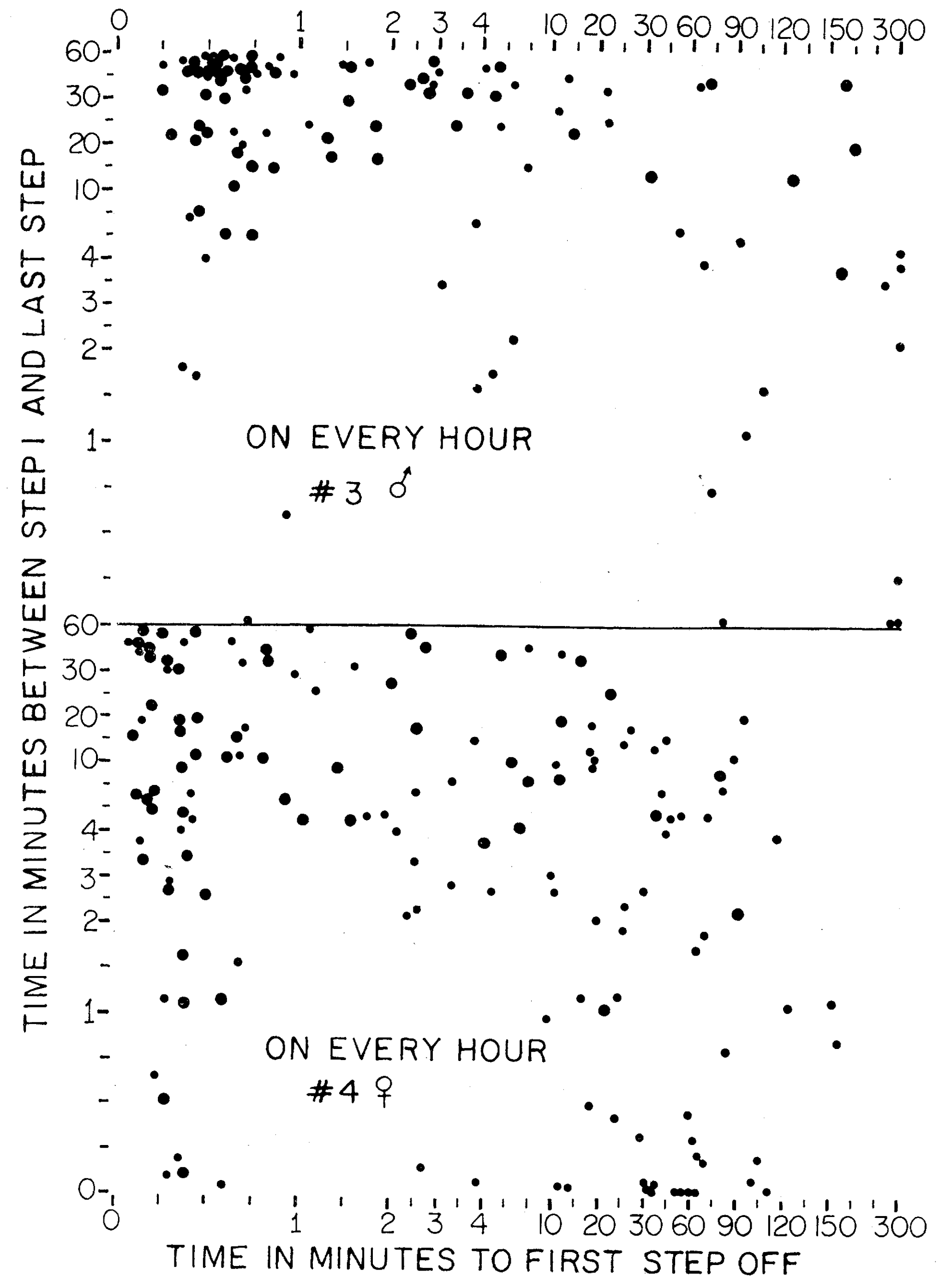


Fig. 19. Partially logarithmic plots of elapsed time to taking the first step versus elapsed time from the first step to the last step taken (see Fig. 16) for deer mice 3 and 4 during the second week on phase 1.

quantitatively different behavior of the two pairs of deer mice between the two phases may be sought among three factors. First, mice 1 and 2 had long prior experience with other instrumental control (see above), whereas mice 3 and 4 were inexperienced. Second, mice 3 and 4 were subjected to much less compulsion and had twice as much time to step the lights off and on, since their lights were turned on and off hourly rather than half-hourly. Third, there were six dim levels of full-moon intensity and below for them, but only three for mice 1 and 2.

One of the reasons for repeating phase 1 with mice 3 and 4 was to test whether prior experience with instrumental control would affect their performances. Although the false off performances (Table 2) were somewhat more vigorous than during the first week of phase 1, these do not supply a valid criterion for comparison, since they were strongly influenced by withdrawal of the environmental control of the preceding phase 2. On the other hand, in the second week of phase 1, increases occurred in all frequency-of-response categories and decreases in most response-time categories (Table 1; see also Fig. 15, second set of bars versus first set; Fig. 18, right versus left; Fig. 19 versus Fig. 16). Accordingly, the long prior experience of mice 1 and 2 with instrumental control probably was partly responsible for the quantitative performance differences between the two pairs of animals.

But the chief basis for the differences in results probably lies in the differences in the regimes. If all else were equal, mice 3 and 4 would be much more likely to reach level 10 than would mice 1 and 2, since they had twice as much time in which to do so. Although mice 3 and 4 did, indeed, step the lights fully on a larger fraction of the times, they stepped them fully off a smaller fraction (Table 1). In fact, for mice 3 and 4 these fractions almost doubled from phase 1 to phase 2, while at the same time declining 43 percent for mice 1 and 2. This consideration leads us to look at the averages of the dwelling times (Fig. 15, "average per change"), since in any given hour or half-hour period, the sum of the dwelling times at levels 2 to 9 is the time taken to step from level 2 to level 10. One finds that the average dwelling times decreased greatly in phase 2 for mice 3 and 4 but increased greatly for mice 1 and 2 (*46*). These changes, of course, mean that the probability that an animal would step fully on in phase 2 was greatly increased for mice 3 and 4 but greatly decreased for mice 1 and 2. But recounting these facts is simply another way of asserting the differences and changes in selectivity that were found.

The analysis, then, hinges upon the bases for the greater selectivity of mice 3 and 4 in phase 1 and for the marked decreases in their selectivity in phase 2. As a working hypothesis, one can suggest that the chief basis for the first difference is that mice 3 and 4 had six non-avoided dim levels (FM and below) to select among, whereas mice 1 and 2 had only three. Thus, putting the matter simply, since mice 3 and 4 had a much greater opportunity for selecting, they selected to a much greater degree.

The great drop in selectivity of mice 3 and 4 in phase 2 seems to have been largely a consequence of a much greater competition in phase 2 between the tendencies to alter the level of illumination repeatedly and to react to compulsion on the one hand, and selectivity on the other. The propensities to modify the environment repeatedly and react to compulsion probably are strongest at the moment lever pressing in response to the changed level of illumination begins, and lessen progressively in a sequence of repeated presses. Accordingly, competition between these acts and level selecting would be greatest for mice 3 and 4 in phase 2, when the non-avoided dim intensities were attained in the first few responses, and least in phase 1 when they were attained in the last few. Although similar considerations would hold for mice 1 and 2, their opportunity to select between dim-light intensities was so much less that the effect of competition on the overall response pattern probably was much less.

Summary

Detailed studies of the behavior of captive white-footed mice have cast a number of old problems in new perspectives. Many responses of small captive mammals cannot be interpreted at face value because of severe distortions of behavior that are caused by depriving the wild animal of natural outlets for activity. Confined animals are likely to seize upon and repeatedly exercise virtually any opportunities to modify (and alter their relationships with) their surroundings. In addition they have a strong tendency to counteract nonvolitional and "unexpected" deviations from the status quo. As a result, their responses do not bear an immutable relationship to the nature of the stimulus or other variable being modified; stimuli and activities that are rewarding in certain circumstances are avoided in others. These aspects of behavior have been illustrated by studies of nest occupancy, running in motor-driven wheels, and control of intensity of illumination. The results of the control-of-illumination studies suggest the complex interplay of tendencies to modify features of the environment, to avoid conditions imposed compulsorily, and to select preferred levels of illumination.

The importance of split-second timing, coordination, and quick reflex actions in the running of activity wheels is indicated by the fact that experienced white-footed mice prefer running in square "wheels" and wheels with hurdles to running in plain round wheels. The relatively conservative behavior of these mice in selecting between multiple sources of food and water and different types of activity wheels suggests the need for careful experimental design in free-choice studies with inexperienced animals. The tendency of trained animals to give some so-called "incorrect" responses even after long experience can be interpreted most reasonably in terms of the adaptive value of a certain degree of variability of behavior in the wild.

White-footed mice readily master complex regimes in which several different levers and shutters must be pressed or rotated in certain sequences within seconds for different rewards. They quickly learn to traverse mazes containing hundreds of blind alleys and do so frequently without extrinsic reward. It is unlikely that these remarkable learning performances even begin to approach the capacities of the animals.

When two female mice having markedly different solitary behavior patterns were placed in consort, the behavior of each changed, becoming more like that of the other, and the animals showed a strong tendency to remain in each other's company. The behavior of mice in enclosures of great extent casts doubt upon the postulate that hunger and thirst play leading roles in the motivation of wide-ranging locomo-

tor movements. Accordingly, studies of deprived domestic animals in simple mazes may have but limited significance for understanding the behavior of wild and relatively unconfined animals.

The existence of marked individual differences between mice selected at random from wild populations sounds the need for a cautious approach in the interpretation of results obtained with highly inbred domestic animals. The relatively uniform behavior of inbred strains represents only a small fragment of the total response spectrum for the species and probably has minimal significance for adaptation and evolution in the wild.

When allowed to control the intensity of illumination by operating a series of switches, white-footed mice establish a roughly 24-hour regime consistent with that experienced in the wild, namely dim light during periods of activity and very dim light during periods of inactivity. Consistent with this finding, when exposed to a dim-dark light cycle, the mice are active during the dim phase, not in darkness. Artificial twilight transitions of both constant and varying color temperature have several marked effects upon the activity of white-footed mice. The existence of a strong orienting influence of dim light on the direction of wheel-running suggests that mice in the wild use the twilight sun and the moon (and possibly other celestial light sources) as navigational references.

References and Notes

1. The name "white-footed mouse" is in common use for the species *Peromyscus leucopus*. Here, following Hall and Kelson (*2*), I shall use this common name to refer to the genus *Peromyscus* in general.
2. E. R. Hall and K. R. Kelson, *The Mammals of North America* (Ronald, New York, 1959), pp. 600–58.
3. E. P. Walker, *Mammals of the World* (Johns Hopkins Press, Baltimore, 1964), vol. 2, p. 776.
4. W. J. Hamilton, *American Mammals* (McGraw-Hill, New York, 1939).
5. L. R. Dice, *Cranbrook Inst. Sci. Bull.* **2**, 1 (1932); W. E. Howard, *Contrib. Lab. Vertebrate Biol. Univ. Mich.* **43**, 1 (1949); F. W. Blair, *Ecology* **39**, 113 (1958).
6. F. W. Blair, *J. Mammal.* **23**, 27 (1942).
7. O. J. Murie and A. Murie, *ibid.* **12**, 200 (1931); M. Murie, *ibid.* **44**, 338 (1963).
8. J. L. Kavanau, *Behaviour* **20**, 251 (1963).
9. ———, in *Systems Analysis in Ecology*, K. E. F. Watt, Ed. (Academic Press, New York, 1966), pp. 99–146.
10. An important factor contributing to behavioral distortion is the fact that the captive animal is freed from the need to escape enemies and search for food, activities which occupy a large fraction of a mouse's time in the wild. The severe limitations imposed upon captive animals and the consequent distortions of their behavior are well known to directors of zoological gardens. This topic has been discussed in detail by H. Hediger in *Wild Animals in Captivity* (Dover, New York, 1964).
11. In the category of "rewarding acts" I include any acts (except those of avoidance) that captive animals engage in repeatedly without extrinsic reward (such as food, water, social contacts, a nest). For practical purposes the use of the word "rewarding" in the text sometimes is redundant.
12. W. W. Roberts, *J. Comp. Physiol. Psychol.* **51**, 391 (1958).
13. N. E. Miller, *Science* **126**, 1271 (1957); G. W. Brown and B. D. Cohen, *Am. J. Psychol.* **197**, 153 (1959).
14. Of course, turning off an unexpected stimulus also is an act of controlling the environment.
15. I do not deny the importance of specific stimulus sensations, but only wish to emphasize that the nature of the stimulus often may be secondary to other considerations.
16. J. L. Kavanau and K. S. Norris, *Science* **134**, 730 (1961); J. L. Kavanau, *J. Mammal.* **43**, 345 (1962).
17. J. L. Kavanau, *Ecology* **43**, 161 (1962).
18. ———, *ibid.* **44**, 95 (1963).
19. ———, *Science* **134**, 1694 (1961); *Anim. Behaviour* **11**, 263 (1963).
20. D. H. Brant and J. L. Kavanau, *Nature* **204**, 267 (1964); *Ecology* **46**, 452 (1965); other papers in preparation.
21. The unlengthened correlations are noteworthy; drinks were clustered together much more frequently within 1 minute, and the habits of frequently eating food pellets within 5 minutes of each other, and of drinking and eating within 5 minutes after eliminating, were maintained. The 0-to-3-minute eliminate-eat correlation increased markedly, mostly at the expense of the 3-to-5-minute one.
22. In fact, animals that pause to groom or sleep often appear to be lost upon resuming movement. They then make slow progress and many mistakes before resuming rapid passage along the direct route, much as the beginning pianist playing from memory has difficulty resuming after an interruption.
23. Personal communications from J. Aschoff, J. A. King, and K. Lorenz.
24. J. L. Kavanau and D. H. Brant, *Nature* **208**, 597 (1965).
25. J. L. Kavanau, *Z. Tierpsychol.*, in press.
26. At the time of writing the count is seven animals toward the light, two animals away from the light, and one animal oriented with respect to other features of the enclosure. The time taken for these consistent orientations to become established corresponds roughly to the time taken for sustained running to develop, namely, anywhere from several days to several weeks.
27. J. L. Kavanau, *Nature* **194**, 1293 (1962); *Experientia* **18**, 382 (1962); other papers in preparation.
28. Note that on this light cycle canyon mice cease sustained running 30 to 120 minutes before the beginning of 'dawn' and run only sporadically without orientation thereafter (Fig. 9).
29. Of the other three animals, one followed an endogenous 24.5-hour rhythmicity and one a 24-hour rhythmicity in phase with its prior activity cycle. The second canyon mouse was erratic at first but eventually (last 9 days) followed a 24-hour rhythmicity with activity from 10 p.m. to 7 a.m.
30. The responses after the motor started automatically (at least during active periods) would be expected to be the same as those following volitional starts if the mice were exercising nothing more than environmental control in both cases.
31. On a program of complete control, minimum environmental control with maximum selectivity would be the selection of a certain preferred dim level during activity, and the same or some other dim level during inactivity, with the intensity altered at most twice a day. Maximum environmental control with minimum selectivity would be the repeated scanning of intensity levels during activity, with equal time being spent at all levels during both active and inactive periods.
32. Levels of illumination for all animals on complete control and for mice 3 and 4 in phases 1 and 2 were: darkness, 0.000038, 0.00011, 0.00029 (roughly one-half starlight), 0.0008 (roughly clear moonless night), 0.003, 0.018 (roughly full moon = FM), 0.094, 0.62, and 4.0 foot-candles (*9*).
33. Average numbers of level changes per day on complete control were 172, 123, 101, and 137 for deer mice 1, 2, 3, and 4, respectively. For comparison, when mice 3 and 4 were inexperienced and the levers were functionless, rates of lever pressing were only 9.0 and 9.4 per day (*9*).
34. Levels of illumination for mice 1 and 2 in phases 1 and 2 were: darkness, 0.0008, 0.0059, 0.025 (roughly FM), 0.094, 0.25, 0.62, 1.0, 2.2, and 4.0 foot-candles.
35. J. L. Kavanau, unpublished.
36. One is tempted to conclude that the mice were not aware of the condition of the lights while asleep. However, white-footed mice are usually very alert to their surroundings when inactive. In fact, when mice 3 and 4 were awakened periodically by sound, they did not step the intensity down more frequently or behave differently in other respects. This is shown in Fig. 16, where the large solid stars and small stars with tails are for a 3-day continuation of phase 1 with sound presented hourly for 1 minute. Hence, inactive mice often may be aware of the bright light being turned on but may be too drowsy or insufficiently motivated to respond.
37. The data of Table 1 suggest that these differences can be attributed only partly to the fact that the sooner the first step was taken, the more time there was available (before the next automatic alteration) to step the full nine steps.
38. It cannot be argued that mice 3 and 4 frequently left the lights at dim levels because they could not see at these low levels and "thought the lights were off." The resuts of other phases of the study, in which some intensity levels were omitted, as well as the results on the phase of complete control, show that the mice select levels by means of the actual intensity or color temperature of the light (color temperature varied with intensity in these studies), not by counting the number of steps.
39. Average number of false ons per occasion fully on during the regime of complete control were only 2.2, 1.2, 1.0, and 0.50 for animals 1, 2, 3, and 4, respectively. The lights were turned fully on 119, 11, 83, and 50 times, for an average visit length of 3.4 1.1, 6.8, and 0.33 minutes. On this regime false ons were almost all immediate supernumerary presses, whereas in the transition to phase 2 and during phase 2 false ons occurred mostly during repeated subsequent returns to the switches.
40. Such withdrawal is a form of compulsion, since the animals are forced to exchange the control of illumination of phase 1 for that of phase 2.
41. Ordinates of Fig. 16 are reflected about the abscissae to facilitate comparisons; if the patterns were mirror images, the role of selectivity could be presumed to be relatively small. The patterns of deer mouse 1 are most like mirror images.
42. A complete analysis based upon these distributions would, of course, have to include those of levels 3 through 8. Accordingly, a great deal of weight cannot be attached to discrepancies between this incomplete analysis and conclusions based upon more complete data. Even complete dwelling time distributions do not take into account the times of visits that are the last step in a sequence.
43. The interactions determining dwelling times at different levels are complex. However, if selectivity operates at all, the ratio of the average time at level 2 to the average time at level 9 should increase from phase 1 to phase 2, since this ratio is for avoided to non-avoided intensities for phase 1 but for non-avoided to avoided intensities for phase 2. The ratios do, in fact, increase, by factors of 1.6, 2.3, 2.1, and 11 for mice 1, 2, 3, and 4, respectively.
44. These data were not obtained for deer mice 1 and 2.
45. In bright light the intensity was altered before running on 11 and 17 percent of occasions, in darkness on only 1.2 and 6.4 percent of occasions.
46. For deer mice 1 and 2 the average dwelling times (averaged over each of the eight intermediate levels) increased from 0.88 and 0.14 to 1.7 and 2.1 minutes; for mice 3 and 4 they decreased from 4.6 and 2.6 to 2.3 and 1.5 minutes.
47. Supported by NSF grant GB 3959. I thank Drs. S. A. Barnett, D. H. Brant, J. T. Enright, R. H. Glaser, A. D. Grinnell, J. A. King, F. B. Turner, and B. W. Walker for many helpful comments and suggestions concerning the rough draft of the manuscript.