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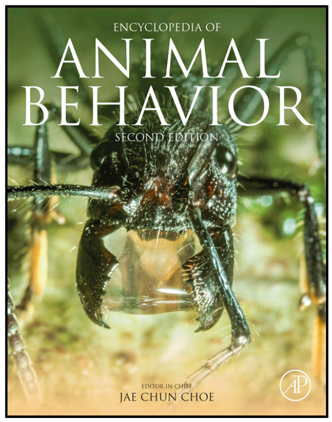

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Norway Rats☆

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Abstract

Norway rats served for decades as the main subject species in studies of behavior, its development and its neuroanatomical and hormonal substrates. Tens of thousands of research papers were and are still being published in which Norway rats serve as subjects. Here, we first, discuss some of the reasons for the rise and fall of Norway rats as a focus of behavioral research, then describe the origins of the domestic rat and the natural history of its wild forebear before reviewing a few of the plethora of research areas in which Norway rats have participated.

Keywords

Aggression; Audition; Cognition; Communication; Development; Domestication; Food choice; Learning; Neurological and psychiatric studies; Olfaction; Reproduction; Social learning; Taste; Thermoregulation; Vision

The Rise of Rats

Not all that many years ago, before biological approaches to the study of animal behavior came to the fore early in the 1970s, comparative and physiological psychologists conducted most behavioral research with animals. For the most part, these researchers were interested in exploring general laws of behavior, particularly those governing the formation of associations underlying learning. Because the focus was on elucidating general principles of behavior applicable to any species in any situation, convenience was a major determinant of the choice of species to study, and one species proved more convenient than any other. Indeed, in the 1930s and 1940s, more than 60% of all papers published in two of the leading animal-behavior journals of the time (the *Journal of Comparative and Physiological Psychology* and the *Journal of Animal Behavior*) were concerned with the behavior of a single organism, the Norway rat (*Rattus norvegicus*; Beach, 1950).

Given the focus on discovery of general behavioral principles that applied to all species, humans included, the Norway rat was not an altogether bad choice. Rats are members of the order Rodentia, the mammalian order with by far the greatest number of species (more than 2000), and of the genus *Rattus* (with more than 50 species), which is the most species rich of the murid family of rodents, the Muridae, that includes mice, gerbils, and hamsters.

Norway rats are about average size for a mammal (reports of Norway rats as big as cats are considerable exaggerations; a very large adult male rat weighs 500–600 g, making it a very small cat indeed) and a convenient size for laboratory work. Rats are neither so large as to make their maintenance in large numbers impractical nor so small as to make either direct observation of their behavior difficult or surgery particularly demanding. Domesticated rats are also easy to produce. They become sexually mature at 3 months of age, often have a dozen or more pups in a litter, can produce a litter every 21 days and breed all year round. Further, the ability of rats to thrive on relatively low-protein diets makes them inexpensive to feed, and unlike their often vicious and very timid wild forebears, rats of domesticated strains are easy to handle and will go about their business undisturbed even when nearby humans are watching their every move.

Important advantages accrued from having quite literally, hundreds of researchers working on various aspects of the behavior and physiology of a single species. Techniques developed, for example, to study rat learning were of use to those investigating the rat nervous system, and students of learning in rats benefited from information concerning rats' sensory systems. Further, the adequacy of the methods used in an experiment could be readily evaluated by others working with the same animal, so potentially important findings could be replicated (or not) almost immediately.

The Fall of Rats

The decline in the dominance of Norway rats as subjects in behavioral research had a number of causes. Perhaps foremost among these was a mid-twentieth century increased interest in the study of behavior among of a group of European biologists, the ethologists, whose study of any species began with construction of an ethogram, a complete description of the behavioral repertoire of a species observed unobtrusively in its natural habitat. Free living Norway rats are, unfortunately, most active in the dark and

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underground and are therefore difficult to observe. Even worse, humans have inadvertently transported Norway rats around the world, making identification of their place of origin, their natural habitat, all but impossible. Ethologists were particularly interested in interactions between animals and the environments in which they evolved. For example, the last of Tinbergen's four questions defining the field of ethology (Tinbergen, 1963), which came to serve as the main focus of research in ethology's descendant field, behavioral ecology, concerned the functions of behavior (i.e. the ways in which behavior increased survival and reproductive success in natural circumstances). Today, most free-living Norway rats live in man-made structures, feed on human. refuse or crops, and because of their close association with humans, are protected from many potential predators. Their current habitat is hardly natural. Consequently, the behavior of Norway rats in their natural habitat, wherever it may be, is simple not available for study. Further, ethologists were largely interested in species-typical behavior patterns (instincts believed to reflect fairly directly the action of natural selection on the genetic substrate of behavior), not in the behavioral flexibility that had captured the attention of comparative psychologists. Indeed, to comparative psychologists, one of the more appealing characteristics of rats was their lack of elaborate, heritable, species-typical behaviors that would interfere with studies of behavioral principles applicable to all species.

Last, but not least, the domesticated rats that received so much attention from comparative psychologists had undergone several hundred generations of breeding in captivity. Exposure to artificial selection by humans breeding rats for both tameness and fertility in captivity ensured that the genetic substrate of domestic rats was not that of their wild forebears. Such artificial selection led some ethologists to assert that the behavior of laboratory rats was not 'natural,' and consequently, not worth studying.

As a practical matter, increasingly stringent regulations governing the breeding and maintenance of laboratory animals, made work with rats ever more expensive thus reducing the number of laboratories that could afford to use rats in experiments. Further, invention of procedures for generating genetically engineered strains of mice preceded by at least 14 years creation of analogous strains of rats. Burgeoning interest in exploring genetic substrates of behavior and utilizing genetic manipulations to analyze behavior made mice the species of choice for many scientists studying mechanisms of mammalian behavior, even if using mice as subjects meant repeating behavioral studies previously performed with rats. In sum, although work on the behavior of Norway rats and its mechanistic substrate continues today, the dominant position of the species in studies of behavior seems over.

What is the Origin of Laboratory Rats?

Norway rats, the forebears of all domesticated rat strains, are generally assumed to have originated somewhere in Asia, possibly in Northern China. It is known that sometime in mid-eighteenth century, Norway rats spread through Europe. The appellation Norway rat is believed to derive from the false, eighteenth-century presumption that the first of the species arrived in the United Kingdom on lumber ships coming from Norway, although there were probably no *Rattus norvegicus* in Norway when the species first invaded Britain. The black or roof rat (*Rattus rattus*), not the Norway rat, had been common in Europe before the larger and more aggressive Norway rat arrived and largely displaced them. Consequently, the black rat, not the Norway rat, was the principle vector in the recurring bouts of bubonic plague that killed 25% or more of the human population of Europe during the latter half of the fourteenth century. Norway rats arrived on the east coast of North America shortly after they arrived in Europe, and spread with the gold rush to California.

Today, Norway rats are to be found on every continent save Antarctica, from Nome, Alaska (64°N) to South Georgia Island (55°S), and in 1983 they crossed 'the final frontier,' travelling on the Soviet Union's unmanned Cosmos biosputnik satellites in studies of the effects of microgravity on pregnant rats. Norway rats went on to travel on NASA's space shuttle, participating in numerous investigations of the effects of space flight on, for example, vestibular function and development (Ronca and Alberts, 2000). Still, Norway rats do not thrive in areas with continental climates, such as Alberta, Canada, and northern Montana, USA, where winters are long and cold and human habitations are relatively sparse. Indeed, Norway rats are most successful in temperate climates. In the tropics, they are largely replaced by other species of their genus, for example, the more arboreal, lighter and longer-tailed *Rattus rattus* and *Rattus exulans* (the Polynesian rat).

Norway rats are the forebears of all domesticated rat strains whether albino, hooded, black or agouti colored. When, where, and how Norway rats were first domesticated is not known. In the nineteenth century, wild Norway rats served as prey in the brutal sport of rat baiting in which a dog was placed in a pit with large numbers of rats and bettors wagered on how many rats the dog would kill in a specified period. One story is that when rare albino wild Norway rats were trapped in the course of securing the large numbers of rats needed for rat baiting, the albinos were displayed in cages outside betting establishments and that these albino rats are the ancestors of at least some of today's domesticated strains. Whatever their source, domesticated albino rats were first used in the laboratory in 1895 at Clark University in Worcester, Massachusetts in studies of nutrition. Five years later, they were subjects in Willard Small's studies, also at Clark University, of the behavior of rats in mazes.

The decades of subsequent research on the behavior of Norway rats and its neural and hormonal substrates have led to publication of many tens of thousands of research articles. Obviously, it is not possible to thoroughly review so vast a literature here. In the following sections, we describe a cross section of the many areas in which studies of Norway rats have played an important role, and mention a scattering of findings that we find either intriguing or amusing. As discussed in Section '**Conclusion**' of the present article, a great deal more information concerning rats, both wild and domesticated, is available in the 'Further Reading.'

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Regulatory Systems

Some of the earliest studies of rat behavior were concerned with homeostasis, the maintenance of an internal environment within the boundaries compatible with life. The ability of rats to select items for ingestion, to regulate their intake so as to neither lose nor gain appreciable amounts of weight and to maintain a relatively constant body temperature each has an extensive literature (Rowland, 2002).

Selecting Foods

sults of experiments conducted in the 1940s and 1950s were interpreted by many as demonstrating that rats that had been deprived of a specific nutrient (e.g., thiamine) could select the food containing the missing nutrient from among a cafeteria of foods only one of which contained it. The results of these reports are responsible for the belief, widespread even today, that your body will lead you to seek out whatever foods you need to eat to remain healthy or to regain health should you become deficient in some nutrient. Unfortunately, the interpretation of this early research has proven exaggerated. Although rats that need sodium can identify sodium salts in foods or fluids, and thirsty rats will seek and ingest water (Rowland, 2002), rats fail miserably in selecting appropriate substances to ingest when in need of almost any other of the dozens of substances (vitamins and minerals) needed for health (Galef, 1991).

Controlling Body Temperature

Like other mammals, rats use both behavioral and physiological means to maintain an internal body temperature compatible with life. As the environmental temperature rises, rats seek cooler areas and should such behavioral response prove inadequate use evaporative cooling to reduce body temperature. Unlike humans (and horses), rats do not sweat. Instead, overheated rats spread saliva on their bodies (as do elephants). The rat's naked tail serves as a particularly effective window through which to release heat. Consequently, rats that have had their tails surgically removed have a markedly reduced ability to remain cool when exposed to elevated environmental temperatures. When the temperature falls, adult rats generate heat by shivering, and newborn rats, like newborn humans are largely dependent on brown fat thermogenesis to stay warm (Gordon, 1990; Terrien *et al.*, 2011).

Reproductive Behavior

Every aspect of reproduction from selection of a mate (Petrulis, 2013) to weaning of young (Fleming and Li, 2002) has been studied in Norway rats. There are, for example, detailed investigations of: (1) the cues that male rats use to determine if a female is in the receptive phase of her estrous cycle, (2) patterns of rat copulation and their effects on the impregnation of females, (3) the behavioral and sensory experiences of fetal rats and their effects on postnatal behavior, (4) the nest building that females engage in before parturition, (5) behaviors during parturition when dams lick their pups, gather them in the nest and assume a nursing posture over them, (6) the behavior of young both while seeking their mother's nipples and nursing and when the mother is absent from the nest, (7) mother's behavior toward her maturing young and her retrieval of pups that stray from the nest, (8) the gradual reduction in time a mother spends in contact with her offspring and changes in maternal delivery of milk as her young mature, (9) the increased aggression of mothers with young, and (10) the changes in pups behavior as they develop from ectothermic, blind, deaf and hairless eraser-sized newborns to independent juveniles (Alberts, 2008; Galef, 1981).

Perhaps surprisingly, the seemingly helpless blind and hairless pups huddled together in a nest can behaviorally regulate their temperature, spreading apart and increasing the surface area of the huddle to increase heat loss when the environmental temperature is high and forming a tight ball with a small surface area when the environmental temperature is low (Alberts, 1978). Equally surprising is the impact of prenatal life on later behavior. As first discovered in Norway rats, whether a fetal mammal is located in its mother's uterus adjacent to brothers or sisters (i.e., its intrauterine position) profoundly influences the amount of testosterone to which it is exposed before birth. As was subsequently established in studies with mice and gerbils, while an adult, much of an animal's hormonally influenced reproductive behavior is modified by intrauterine exposure to testosterone (Vom Saal, 1989). More generally, rats have been used in a variety of studies of the role of early experience in the development of behaviors (Alberts and Cramer, 1988; Smotherman and Robinson, 1995).

Social Behavior

Free-living wild rats are intensely social beings and live in colonies consisting of from a few to several hundred individuals. Colony members share a burrow system and paths through the environment that they defend against intrusions by unfamiliar conspecifics (others of the same species). Their social life involves numerous forms of stereotypical interaction: sniffing investigations, allogrooming (the grooming of conspecifics), play and dominance relations among others.

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Communication

Such social life requires communication, and Norway rats communicate in a variety of interesting ways. They mark their environments with both urine and sebaceous secretions that allow individual identification and create trails that guide movement of conspecifics through the environment. Rats vocalize during social and sexual interactions and in response to the presence of potential predators, and much of their vocalization is ultrasonic (i.e., in a frequency range too high for humans to hear (Potfors, 2007).

Aggression

The aggressive behavior of rats has been used to explore: the stimuli that elicit, direct, and terminate aggressive interactions, the neural and endocrine substrates of aggression, and rats' postures and movements while interacting aggressively or stealing food from one another (Lore *et al.*, 1984). Intruders into the territory of a colony of wild rats are vigorously attacked, and even brief attacks on intruders that do not produce detectable wounds can have fatal consequences, though the causes of such death are not well understood. In recent decades, ethical concerns have led to a marked decrease in research on aggressive behavior in mammals.

Predation

Laboratory rats' predatory behavior toward mice and the response of rats to cats and other potential predators were also studied for many years. Again, ethical concerns have largely ended experiments involving direct interaction of predators with mammalian prey.

Social Learning

Life in socially tolerant groups provides rats with opportunities to both observe and learn from the behavior of others of their species. Numerous papers have been published concerned with the finding that after a naïve 'observer' rat interacts for a few minutes with a 'demonstrator' rat that has recently eaten a distinctively flavored food, the observer rat shows a substantial increase in its liking for whatever food its demonstrator ate. Rats have also been shown to learn to dig for buried food by watching other rats do so. After learning socially either to eat a particular food or to dig for food, an observer rat can act as a demonstrator for new, naïve observers, and such chaining can be sustained for several 'generations' thus producing rat 'traditions' (Galef, 2003).

Sensory Systems

Rats are sensitive to a broad range of stimuli; visual, auditory, olfactory, tactile, thermal, gustatory and vestibular. Many of the rat's sensory systems have been fully explored, and have their own voluminous literature.

Vision

In nature, Norway rats are most active at dusk and dawn, and possibly as a result, they are less dependent on vision than other well-studied mammals such as cats and ferrets. The visual, acuity, even of wild rats is quite poor, and domesticated rats have about half the visual acuity of their wild brethren, with albino strains of rat suffering from particularly poor vision. All strains of Norway rat lack both color vision and a fovea (small rodless area of the retina with greatest acuity), and their visual cortex is less clearly functionally differentiated than that of some other mammals (Prusky *et al.*, 2002).

Olfaction

Like many other animals, rats have two independent, but complementary systems for dealing with chemical stimuli, one the olfactory system and the other an auxiliary olfactory sense organ, the vomeronasal organ, that may primarily handle chemicals important in social interactions, the pheromones (chemicals that carry messages between members of the same species). The receptors in the vomeronasal system are separate from those in the main olfactory system and project to separate loci in the central nervous system. Rats have a keen sense of smell, and throughout life, depend heavily on olfactory stimuli in their day-to-day functioning. Prenatal exposure to odorants can have lasting effects on rats' postnatal behavior. Infants quickly learn to identify the odor of their mother and home nest and use olfactory cues to find their mother's nipples to nurse. Adult rats deposit scent marks in the environment that allow others to identify their age, sex, reproductive state, and dominance status and provide scent trails that conspecifics follow when foraging (Brown and Mcdonald, 1985; Liberles, 2014).

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Taste

The taste perceptions of rats and humans are surprisingly similar. Members of the two phylogenetically quite distant mammals almost always find the same flavors attractive or repulsive. Consequently, Norway rats have served as models for understanding human taste perception (Norgren, 1995). Like humans, rats display different facial expressions when experiencing pleasant and unpleasant flavors. However, there is no evidence that the disgust faces of rats dissuade other rats from eating the food that a grimacing animal has found distasteful. Also like humans, rats find it particularly easy to associate experience of an unfamiliar flavor, but not an unfamiliar noise or visual cue, with later gastrointestinal upset. After a single experience, both rats and humans learn to avoid a novel flavor to which they were exposed hours before becoming ill.

Hearing

Relative to humans, hearing in rats is shifted toward higher frequencies, and rats can detect sounds with frequencies as high as 80 kHz. Rats produce a number of auditory signals both audible to humans and in the ultrasonic range. Relatively little work has been done on audible rat vocalizations, possibly because of their great variability. However, rats' more stereotyped ultrasonic vocalizations and the responses to them have received considerable attention (Potfors, 2007).

Ultrasounds (40–50 kHz) are emitted by infant rats when they cool. Adult rats emit a 22 kHz 'long-call' in aversive situations (e.g., after losing a fight or detecting a cat) and, perhaps surprisingly, after ejaculating. Rats also emit a 50 kHz 'chirp' that may be associated with pleasant events (e.g., playing or being tickled) that has been described as a form of laughter, although it also occurs in some unpleasant circumstances, for example, during aggression or in response to some types of pain.

All these ultrasonic vocalizations can affect the behavior of rats that hear them. Mother rats are attracted to the ultrasonic vocalizations of pups, and there is some evidence that exposure to 22 kHz long calls increases the wariness of rats hearing them. Although rats can use their ultrasonic vocalizations to detect objects at a distance, they are far less sophisticated in their use of ultrasound for echolocation (the use of reflected sound waves to detect objects) than are bats.

Somatosensation

The sense of touch plays in important role in rats' movements about their environment. Rats are 'thigmotactic'; they are biased toward remaining in physical contact with vertical surfaces, presumably to protect against predation. Rats' vibrissae, the whiskers around their noses, are extremely sensitive to tactile stimuli, and have been compared with human fingertips. Rats can move their vibrissae independently across surfaces, allowing them to discriminate among objects of different size, texture and shape (Michenson *et al.*, 2011).

Learning and Cognition

In the decades when rats were the predominant species in behavioral studies, they most often served as subjects in investigations of learning (Domjan, 2015). At first, such studies took place in complex mazes with many choice points that were believed to mirror the complex burrow systems in which wild rats live. When behavior in such complex environments proved intractable to analysis, experimenters shifted to simple T-mazes with only a single choice point. Finally, rats were studied in highly automated Skinner boxes, where subjects were rewarded for pressing levers with food delivered on various schedules.

Most recently, studies of the ability of rats to solve cognitively demanding tasks have been in vogue. In the Morris water maze, rats are placed, on successive trials, in random locations in a small circular tank filled with water. To escape from the water, which the rats find mildly aversive, they have to learn the location of a platform hidden just beneath the water's surface. In different version of the task, the rats can use visual cues in the surrounding room, a beacon directly indicating the location of the platform, or information concerning the distance of the platform from the wall of the test chamber to find it. Solution of the task using cues outside the pool itself can require the rat to form a 'cognitive map' of the relationship between cues in the room and the location of the platform.

Perhaps the most challenging task with which rats have been presented is the multiarm maze. Here, as the name of the apparatus implies, a rat is placed on the central platform of a maze with several arms (8 is the most common number) and a small piece of food is placed at the end of each arm farthest from the central platform. The rat is free to explore the maze until it has recovered food from the end of each arm. Greatest efficiency requires that a rat enter each arm of the maze only once, a performance that requires the subject to remember which arms it has previously entered. Rats are extraordinarily good at this task, and make relatively few errors, rarely reentering a previously visited arm of the maze.

Rats as Neurological and Psychiatric Models

No review of the role of Norway rats in psychological research would be complete if it did not at least mention the important role of the Norway rat as a model system in biomedical research, making invaluable contributions to basic and applied/clinical studies,

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exploring the causes, treatment and, hopefully, cure of a wide range of disease states. Brain lesioned rats have served as models for human focal stroke and human cerebral injury and rats injected with neurotoxin to produce dopamine depletion have served in studies of Parkinson's disease (Boulton *et al.*, 1992). A variety of techniques have been used to produce symptomologies in rats associated with seizure disorders seen in humans. Both aged and lesioned rats are used in the attempt to understand the cognitive impairments associated with Alzheimer's disease. Rats have also served as model systems in which to study behavioral disorders such as anxiety, obsessive-compulsive disorder, autism, addiction and depression (McKinney, 1988; Geyer and Markou, 1995). Research on the "stress axis" involving the interaction of hypothalmus, and pituitary and adrenal glands started with early studies of social and environmental stresses on rats experiencing overcrowding as a result of population growth. Indeed, the confluence of information concerning the social, cognitive and emotional behaviors of rats together with information on their neuroanatomical, genetic and hormonal substrates continues to make Norway rats important subjects in the investigation of disease states.

Conclusion

In this brief article, we have just begun to scratch the surface of research on the behavior of rats. Many topics that have been the focus of extensive research programs have not even been mentioned, among them: play, circadian rhythms in activity, locomotion, grooming, exploratory behavior, motivation, schedules of reinforcement, memory, the immune system, foraging and response to pain. This list could be lengthened considerably without difficulty. Many other topics, although mentioned, (e.g., vestibular sensation, process of domestication, etc.) have been discussed only superficially.

'Further Reading' provides both greater depth and greater breadth of coverage than this brief article of the role of rats in both science and everyday life. Barnett's *The Rat: A Study in Behavior*, although somewhat dated, provides classic descriptions of the behavioral repertoires of wild rats and discussion of some laboratory work with domesticated rats. Meehan's *Rats and Mice: Their Biology and Control* provides an introduction to the extensive literature on the control of pest populations of rats. Both Telle's and Calhoun's classic articles are difficult to find today, but provide some of the best descriptions available of the social behavior of wild rats. Munn's *Handbook of Psychological Research on the Rat* and *Stevens' Handbook of Experimental Psychology* provide summaries of research with laboratory rats in its heyday. Other recommendations provide introductions to specific topics covered here. Most important among these is Wishaw and Kolb's recent, 500-page edited volume *The Behavior of the Laboratory Rat* that provides a compact and up-to-date review of much of the experimental work with domesticated rats.

Several publications about Norway rats intended for lay audiences appeared during the last decade. S.A. Barnett's '*The Story of Rats*' and Lore & Flannelly's '*Rat societies*' are trustworthy.

See also: **Learning and Teaching:** Mammalian Social Learning: Non-Primates.

References

Alberts, J.R., 1978. Huddling by rat pups: Group behavioral mechanisms of temperature regulation and energy conservation. Journal of Comparative and Physiological Psychology 92, 231–245.
Alberts, J.R., 2008. The nature of nurturant niches in ontogeny. Philosophical Psychology 21, 295–303.
Alberts, J.R., Cramer, C.P., 1988. Ecology and experience; Sources of means and meaning of developmental change. In: Blass, E.M. (Ed.), Handbook of Behavioral Neurobiology, Vol. 9: Behavioral Ecology and Developmental Psychobiology. Plenum Press, New York, pp. 1–39.
Beach, F.A., 1950. The snark was a boojum. American Psychologist 5, 115–124.
Boulton, A.A., Baker, G.B., Butterworth, R., 1992. Animal Models of Neurological Disease 1: Neurogenerative Diseases. Humana Press, New York.
Brown, R.E., Mcdonald, D.W., 1985. Social Odors in Mammals. Oxford University Press, Oxford.
Domjan, M., 2015. The Principles of Learning. Cengage Press, Stamford, CT.
Fleming, A.S., Li, M., 2002. Psychobiology of maternal behavior and its early determinants in nonhuman mammals. In: Bornstein, M.H. (Ed.), Handbook of Parenting: Biology and Ecology, vol. 2. Lawrence Earlbaum Associates, Mahwah, N.J., pp. 61–99
Galef Jr., B.G., 1981. The ecology of weaning: Parasitism and the achievement of independence by altricial mammals. In: Gubernick, D.J., Klopfeer, P.H. (Eds.), Parental Care. Plenum Press, New York, pp. 211–241.
Galef Jr., B.G., 1991. A contrarian view of the wisdom of the body as it relates to dietary selfselection. Psychological Review 98, 218–223.
Galef Jr., B.G., 2003. "Traditional" foraging behaviors of brown and black rats (*Rattus norvegicus* and *Rattus rattus*). In: Fragaszy, D.M., Perry, S. (Eds.), The Biology of Traditions. Cambridge University Press, Cambridge, U. K., pp. 159–186
Geyer, M.A., Markou, A., 1995. Animal models of psychiatric disorders. In: Bloom, F.E., Kupfer, D.J. (Eds.), Psychopharmacology: the Fourth Generation. Raven Press, New York, pp. 787–798.
Gordon, J.C., 1990. Thermal biology of the laboratory rat. Physiology & Behavior 47, 963–991.
Liberles, S.D., 2014. Mammalian pheromones. Annual Review of Physiology 76, 151–175.
Lore, R., Nikoletseas, M., Takahashi, L., 1984. Colony aggression in laboratory rats: A review and some recommendations. Aggressive Behavior 10, 59–71.
McKinney, W.T., 1988. Models of Mental Disorders: a New Comparative Psychiatry. Plenum, New York.
Michenson, B., Grant, R.A., Arkley, K., et al., 2011. Active vibrissal sensing in rodents and marsupials. Philosophical Transactions of the Royal Society 366, 3037–3048.
Norgren, R., 1995. Gustatory system. In: Paxinos, G. (Ed.), The Rat Nervous System. Academic Press, Sydney, pp. 751–771.
Petrulis, A., 2013. Chemosignals, hormones and mammalian reproduction. Hormones and Behavior 63, 723–741.
Potfors, C.V., 2007. Types and functions of ultrasonic vocalizations in rats and mice. Journal of the American Association for Laboratory Animal Sciences 46, 28–34.

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Prusky, G.T., Harker, K.T., Douglas, R.M., 2002. Variation in visual acuity within pigmented and between pigmented and albino rat strains. Behavioral Brain Research 136, 339–348.
Ronca, A.E., Alberts, J.R., 2000. Effects of spaceflight on vestibular responses in neonatal rats. Journal of Applied Physiology 89, 2318–2324.
Rowland, N.E., 2002. Thirst and sodium appetite. In: Stevens, S.S., Pushler, H., Gallistel, C.R. (Eds.), Handbook of Experimental Psychology, vol. 3. Wiley, New York, pp. 669–707.
Smotherman, W.P., Robinson, S.R., 1995. Tracing developmental trajectories into the prenatal period. In: Lecanaut, W.P., Fifer, N.A., Krasnegor, W.P., Smotherman, W.P. (Eds.), Fetal Development: a Psychobiological Perspective. Lawrence Earlbaum, Hillsdale, pp. 15–32.
Terrien, J., Perret, M., Aujard, F., 2011. Behavioral thermoregulation in mammals. Frontiers in Bioscience 16, 1428–1444.
Tinbergen, N., 1963. On the aims and methods of ethology. Zeitschrift Fur Tierpsychologie 20, 410–433.
Vom Saal, F.S., 1989. Sexual differentiation in litter-bearing mammals: Influence of adjacent fetuses in utero. Journal of Animal Science 67, 1824–1840.

Further Reading

Barnett, S.A., 1975. The Rat: A Study in Behavior. University of Chicago Press, Chicago, IL.
Barnett, S.A., 2001. The Story of Rats. Allen & Unwin Crow's Nest, New South Wales.
Burn, C.C., 2008. What is it like to be a rat? Sensory perception and its implications for experimental design and rat welfare. Applied Animal Behaviour Science 122, 1–32.
Calhoun, J.B., 1963. The Ecology and Sociology of the Norway Rat. Public Health Service Publication No. 1008. U.S. Department of Health. Bethesda, MD.
Gallistel, R., Pashler, H., 2002. Stevens' Handbook of Experimental Psychology. Learning, Motivation and Emotion, , third ed.vol. 3. Wiley, New York.
Lore, R., Flannelly, K., 1977. Rat societies. Scientific American 236, 106–115.
Meehan, A.P., 1984. Rats and Mice: Their Biology and Control. Rentokil Ltd East Grinstead, UK.
Munn, N.L., 1950. Handbook of Psychological Research on the Rat: An Introduction to Animal Psychology. Riverside Press Cambridge, Massachusetts.
Shair, H.N., Barr, G.A., Hofer, M.A., 1991. Developmental Psychobiology: New Methods and Changing Concepts. Oxford University Press, Oxford.
Shettleworth, S.J., 1998. Cognition, Evolution and Behavior. Oxford University Press, Oxford.
Stricker, E.M., 1990. Neurobiology of Food and Fluid Intake. Plenum Press, New York.
Telle, H.J., 1966. Beitrag zur Kenntnis der Verhaltensweise von Ratten, vergleichend dargestellt bei Rattus rattus und Rattus norvegicus. Zeitschrift Fur Angewandte Zoologie 53, 129–196.
Whishaw, I.Q., Kolb, B., 2005. The Behavior of the Laboratory Rat: A Handbook with Tests. Oxford University Press, Oxford.