The precocial mouse, *Acomys cahirinus*

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Acomys cahirinus (the "spiny mouse") is a member of the same rodent subfamily as the laboratory rat and mouse. *Acomys* differs from the laboratory species in several ways, including the fact that it is adapted to a semiarid lifestyle and is born after a long gestation with functional sensory and motor systems. The existing, and quite dispersed, literature on the anatomy, physiology, and behavior of *Acomys* is briefly reviewed.

Acomys cahirinus (called the "spiny mouse" because of the bristly fur covering the rump area) has been used increasingly in psychobiological studies. *Acomys*, the laboratory rat (*Rattus norvegicus*), and mouse (*Mus musculus*) are all members of the same rodent subfamily (Murinae). However, the species have quite different adaptations, physiologies, and behaviors. Perhaps the most striking differences are in their early life histories. *Acomys*, a precocial mammal, is born after a relatively long gestation (39 days using the day after conception as Embryonic Day 1, or E1) with open ears and eyes and quite sophisticated sensory and motor capabilities. The rat and mouse are altricial species: they have shorter gestations (22 and 20 days, respectively), larger litter sizes, and are born considerably less mature (Figure 1). The result is an almost unique opportunity to compare developmental processes in phylogenetically related yet ontogenetically divergent species (see Dieterlen, 1963, for a discussion of uniformity in developmental patterns within the mammalian group). Comparative studies of the species might lead to a better understanding of the ways in which developmental patterns can be modified, and how the functional abilities of species change as a result. The following review briefly examines what is known about *Acomys* on evolutionary, ethological, neurological, and behavioral levels (Dieterlen, 1961; D'Udine & Alleva, 1988).

PHYLOGENY

Systematics

Little agreement exists on the exact number of species contained in the genus *Acomys*. While Dieterlen (1963) suggested there may be as many as 27 species, Corbet and Hill (1986) listed 9 (*A. cahirinus*, *A. cilicicus*, *A. louisae*, *A. minous*, *A. russatus*, *A. spinosissimus*, *A. sub-*

spinosus, *A. whitei*, and *A. wilsoni*), along with several races and strains. They also pointed out that several of the species are easily confused or have been included as strains of other species. Carleton and Musser (1984) also described nine species. On the other hand, Corbet (1978) claimed that only two species exist: *A. cahirinus* and *A. russatus*, suggesting that most other species are merely variants of *A. cahirinus*, some even with different numbers of chromosomes (Matthey, 1963; Matthey & Bacar, 1967; Petter & Roche, 1981).

Acomys is included within the order Rodentia, the infraorder Myomorpha, the superfamily Muroidea (mouse-like rodents), and the family Muridae, which contains over 100 genera (Carleton, 1984; Eisenberg, 1981). *Acomys*, along with the laboratory rat and mouse, is found within the largest subfamily of these, Murinae ("Old World rats and mice"). This fortunate occurrence allows *Acomys* to be compared with the most intensely studied altricial species available, allowing a wealth of information for comparative studies.

How Closely Related are *Acomys* and the Laboratory Rat and Mouse?

Determining exact phylogenetic relationships is a difficult task, especially in groups such as the rodents, which exhibit rapid evolutionary changes with tremendous amounts of convergence and parallelism. The oldest murid-like fossils (*Cricetodon*) come from the late Eocene in China (Carleton & Musser, 1984). Many reports suggest that murine rodents evolved from cricetid stock in the middle Miocene period (approximately 15 million years ago), although considerable differences of opinion appear to exist in the timing of the cricetid/murid separation. Simpson (1959) places the cricetid/murid separation at 10 million years ago. The oldest recognized murid genera, *Antemus*, was found in Pakistan (Jacobs, 1978). Jacobs suggested that two groups were derived from *Antemus*; one (*Progonomys*) gave rise to *Mus* and the mouse-like species, including *Acomys*. The other (*Karnimata*) gave rise to many other species, including *Rattus*. The first migration of the murids was toward Europe and North America as early as the Oligocene period. Murids appear to have invaded Africa later, in the Miocene era (Carleton & Musser, 1984; Eisenberg, 1981; Flynn, Jacobs, &

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Figure 1. Newborn *Acomys cahirinus* (left) and laboratory rat (*Rattus norvegicus*; right).

Lindsay, 1985; Hartenberger, 1985; Lavocat & Parent, 1985).

Morphological indexes of relatedness have placed *Acomys* well within the normal ranges of the murids; indeed, *Acomys* has been called simply a generalized mouse adapted to arid conditions (Kingdon, 1974). Nevertheless, molecular biological approaches to determining species relations (e.g., distance data from immunological, DNA annealing, or protein sequencing) have indicated that *A. cahirinus* is quite divergent from the remainder of the African murids. For example, an albumin immunological comparison suggests that *Acomys* and *Mus* are not closely related (Sarich, 1985), and starch gel electrophoresis of 11 protein loci suggests that although the remainder of the African murids may be monophyletic, *Acomys* diverges substantially (Bonhomme, Iskandar, Thaler, & Petter, 1985). Therefore, precise relationships between the species are difficult to judge.

GENERAL BIOLOGY

Distribution and Ecology

The genus *Acomys* inhabits western Asia to southern Africa, including the islands of Cyprus and Crete. *A. cahirinus* has the widest distribution in the range. *Acomys* are adapted for an arid lifestyle, living in rocky outcroppings (jebels) in desert regions (Delany & Happold, 1979; Petter, 1954). *A. cahirinus* subsists on a mixed diet, including insects, snails, and seeds, and is commensal with man (Vesey-Fitzgerald, 1966). Little is known about their social organization, although they have been reported to live in groups but to not build nests or burrows (Delany & Happold, 1979). Although commercial suppliers of the species are rare, it is usually not difficult to obtain breeding couples donated by researchers with existing laboratory colonies.

Special Adaptations

Because of their niche, *Acomys* have been studied often in order to understand strategies of temperature and water regulation (Borut, Horowitz, & Castel, 1972; Daily &

Haines, 1981; Haines & Schmidt-Nielsen, 1977; Horowitz & Borut, 1970; Shkolnik & Borut, 1969). They have several mechanisms for retaining water. For example, typical mammals living in nonarid areas obligate 30%–40% of total water turnover to evaporative water loss, whereas in *Acomys* the figure is closer to 14% (Daily & Haines, 1981). *Acomys* is also able to rapidly regulate its physiology in the face of dehydration. Urine formation may be reduced by 75% with 24 h of water deprivation; with extended deprivation, production can drop by more than 90%. Vascular permeability can be minimized through tight junctions, allowing water retention during dehydration (Borut et al., 1972). Species differences have also been reported within the *Acomys* genus. For example, *A. russatus* is better able than *A. cahirinus* to regulate its body temperature in response to heat stress, and is also better able to use salty solutions (Shkolnik & Borut, 1969). *Acomys* is reported to be in the middle of the expected range for small desert mammals, with other species whose diets are restricted mostly to seeds exhibiting even more extreme physiological regulation (Daily & Haines, 1981). Resting oxygen consumption is low, approximately 0.64 ml O₂/g/h, as compared with 1.27 ml in *Mus musculus* (Wise, 1977).

Reproduction

The male reproductive tract has been examined, with sperm first noted at Postnatal Days 35–45 (P35–45). Coagulation studies with seminal vesicle and coagulating gland extracts from laboratory rats, mice, hamsters, gerbils, and guinea pigs have indicated that substrates derived from *Acomys* are readily coagulated by the extracts from other species, whereas extract from *Acomys* coagulating glands is less effective when combined with substrates from the other species (Pietz, Foreman, & Schmitt, 1979).

A light microscopic study of the histology of the ovaries has been reported (Pietz, 1981), as well as an electron microscopic analysis of the cytology of the oocyte (Kang & Anderson, 1975). Both studies reported that *Acomys* is quite similar to most murine species. Estrous cycles

average 11 days (although considerable variability existed), and vaginal smears lack the clear-cut stages seen in rats (Pietz, 1981). The average age of vaginal opening is P45, when evidence of ovulation has also been observed. *Acomys* has an active luteal phase (Pietz, 1981). In the wild, *Acomys* preferentially breed after the start of rains, so that young are born during relatively lush seasons (Bodenheimer, 1949; Delany & Happold, 1979; Neal, 1983; Young, 1976). However, in the laboratory, females cycle year round. A postpartum estrous occurs (Dieterlen, 1961, 1962; Pietz, 1981), which is useful in determining times of conception (Brunjes, 1989). Although there has been informal speculation that the species might form pair bonds, our observations have suggested that this possibility is unlikely. Breeding pairs of *Acomys* left together can produce litters of pups consistently for several years.

Rhythmicity

A. cahirinus is a nocturnal species with quite regular circadian cycles. Weaver and Reppert (1987) have reported that robust rhythms in locomotor activity emerge as early as P5. Furthermore, these cycles are entrained by the mother before birth: cross fostering to mothers 180° out of phase at birth had no effect on subsequent cycles. Also indicative of prenatal entrainment is a correlation between maternal circadian cycles and patterns of 2-deoxyglucose uptake in the fetal suprachiasmatic nucleus. *A. russatus* has been reported to be active during the daytime (Shkolnik & Borut, 1969).

Genetics

As mentioned, the genetics of the genus *Acomys* is complex, especially in light of the uncertainty over the number of species and races. Zahavi and Wahrman (1956; Wahrman & Zahavi, 1953) reported that *A. cahirinus* has a diploid genome consisting of 38 chromosomes, whereas *A. russatus* has 66. However, the total amount of chromatin is quite similar in the two species (see also Matthey, 1963; Matthey & Baccar, 1967). A careful examination of the genome of *Acomys* from Israel (*A. cahirinus dimidiatus*) and Cyprus (*A. nesiotes*) indicated that although the number of chromosomes is the same, their morphology is quite different. Although *A. cahirinus* and the Cretan spiny mouse (*A. minous*) interbreed, their offspring are sterile, suggesting they too may be separate species (Eisenstraut & Dieterlen, 1969).

DEVELOPMENT

Prenatal

Perhaps the most intriguing aspect of the genus *Acomys* is their precocial birth. Their precocity is undoubtedly an adaptation to the hostile, arid environments in which they are found, allowing pups to attain early independence and perhaps helping them to escape predation. However, such a strategy is not the only successful one used in such environments. Gerbils, for example, fill a very similar niche

but are actually born slightly less mature than even the laboratory rat or mouse.

A tacit assumption in biological thinking has been that precocial and altricial species develop similarly, with the simple difference being the time of birth in the two species (Brunjes, 1988). The assumption is understandable; indeed, a superficial examination of *Acomys* and the rat would lead to the same conclusion. A newborn *Acomys* and a rat pup of the same postconception age (a P16–17 pup) exhibit striking similarities. Both have open ears and eyes, and both are motorically competent and fully furred. However, more detailed examinations, such as those outlined below, have demonstrated that the pups achieved this state by quite different routes.

Figure 2 depicts morphological development and growth curves in prenatal *Acomys*. Dieterlen (1963) was the first to publish an examination of prenatal changes in *Acomys*. In this thoughtful paper, Dieterlen compared external morphological development in the Sinai (*A. cahirinus dimidiatus*, 19 stages examined spanning E14–37) and Cretan (*A. minous*, three stages examined: E14, E22–25, and E31) spiny mice with the laboratory rat. Detailed descriptions of changes in body appearance (e.g., eyes, ears, olfactory organs, branchial arches, limb development) are presented, as well as lengths and numbers of somites. *A. minous* was reported to be born a bit less mature (and approximately 2 days earlier) than *A. cahirinus*, and to develop slightly more rapidly *in utero*.

Dieterlen (1963) reported that *A. cahirinus* develops much more slowly than the laboratory rat. At the earliest ages examined (approximately E14), *Acomys* is approximately 2 days less mature than the rat. By the time of birth in the rat (E22), *Acomys* is more than 5 days less mature. Four days later, the two species exhibit their greatest divergence, with *Acomys* being more than 7.5 days less mature than the rat.

A series of fascinating papers have been published by a Dutch group comparing the development of function in endodermally derived organs between *Acomys* and the laboratory rat (Lamers, Mooren, deGraaf, Markiewicz, & Charles, 1985; Lamers et al., 1982; Oosterhuis, Mooren, Charles, & Lamers, 1984). The comparisons were made in order to examine perinatal control of enzymatic activity, to determine, for example, whether developmental increases in enzymatic function may be coupled with specific developmental stages or events such as birth. One study (Oosterhuis et al., 1984) examined the development of two enzymes (phosphatidic acid phosphohydrolase and choline-phosphate cytidyltransferase) involved in the production of the lung surfactant phosphatidylcholine, which is central to pulmonary growth and differentiation. Although the shape of the developmental curves observed for the former enzyme were quite similar in the two species, the increase in *Acomys* occurred 16 days later. In the rat, two peaks of activity were found in choline-phosphate cytidyltransferase activity: one near the time of birth, presumably to ready the lung for postnatal life, and one approximately 2 weeks later in anticipation of

Figure 2. (A) and (B) Bouins-fixed *Acomys cahirinus* fetuses. (A) Left to right: Embryonic Days 16, 18 (with deformed cranium), 20, and 22. (B) Left to right: Embryonic Days 24, 26, 28, 30, and 34. Scale bar is in millimeters. (C) Developmental changes in crown-rump length (open circles) and body weight (filled circles). Bars = 1 SEM.

weaning. Only one peak was seen in *Acomys*, which occurred near the time of birth. Viewed in terms of time postconception, therefore, quite different patterns were seen in the two species. However, both species exhibited peaks in activity near the time of birth, suggesting a similar sort of developmental regulation.

Studies of urea cycle enzymes from the liver have revealed still different patterns. In the rat, carbamoylphosphate synthetase, arginase, and ornithine trans-

carbamoylase activity increases just before birth, remains elevated for the first 5 postnatal days, and then exhibits a slow increase to adult levels. In *Acomys*, a quite different pattern has been noted, with steady increases occurring throughout the pre- and postnatal periods (Lamers et al., 1985). The results have been interpreted to indicate that the delayed birth in *Acomys* results in a merging of perinatal and weanling peaks in enzyme activities in the species (Lamers et al., 1985). The fact that the emer-

gence of the enzymes occurs with a different timetable both within and between species suggests that they are independently regulated.

Lamers et al. (1985) reported that the timetable of prenatal development of choline acetyltransferase activity in the central nervous system is almost identical in *Acomys* and the rat (however, see below). Two other studies have examined prenatal brain development, and found substantial differences between the species. The first was an examination of Nissl-stained tissue from the developing visual cortex, hippocampus, and olfactory bulb (Brunjes, 1989). Rat and spiny mouse fetuses were collected approximately every other day throughout gestation, beginning at E14 and ending at E34 (approximately 5 days before birth in *Acomys*, and P12 in the rat). Large differences in the rate of development were observed, substantiating the results of Dieterlen (1963). By E14, *Acomys* is almost 2 days less mature than the same postconception-aged rat. For example, the E14 *Acomys* telencephalic region is simply a pseudostratified neuroepithelium with few postmitotic neurons, and the optic vesicle is still broadly continuous with the lumen of the neural tube, characteristics seen 2 days earlier in the rat. Differences between the species continue to increase: by birth in the rat, *Acomys* was found to be approximately 4 days less mature (see Figure 3). The largest differences between the species were observed at E28, when *Acomys* was found to strongly resemble the newborn (E22) rat (e.g., the olfactory ventricle is closed throughout most of the olfactory bulb, the dentate gyrus has formed its characteristic V shape, and the cortical plate is confined to the superficial cortical laminae). By the time of birth in *Acomys*, the brains of the two species appear grossly similar, although considerable differences in subsequent development have also been reported (see below). In comparison to the rat, therefore, *Acomys* exhibits considerably slower growth during midgestation, allowing more resolution into early brain development.

A second study examined the generation of the major cell classes in the telencephalon with tritiated thymidine techniques (Brunjes, Korol, & Stern, 1989). Although in general, cell production begins later and lasts longer in *Acomys* than in the rat, no simple relationship was found between times of proliferation of the major cell classes in the two species. This finding suggests that there must be regional controls that can be modified both between species (e.g., the general late beginning of cell production seen in *Acomys*) and within areas. A similar sort of heterochrony has been observed in postnatal brain development, described below.

Little is known about prenatal behavioral development in *Acomys*. Dieterlen (1962, 1963) reported that most newborns he examined exhibited twisted umbilical cords, leading him to the conclusion that considerable movement does take place. Movements resembling respiration were first observed after E26, whereas limb movements were not observed until E32.

Birth occurs approximately 39 days after conception. In a beautiful paper describing the birthing process, Dieterlen (1962) indicated that *Acomys* exhibit a form of "midwifery." Indeed, female and male *Acomys* have been observed to actively engage themselves in helping to coax young out of the birth canal, fighting over afterbirths, and so forth. However, Young (1976) housed *Acomys* females in group and single situations and found that infant mortality was similar between groups, suggesting that this behavior has little effect on the probability of viable births.

Postnatal

Newborn *Acomys* pups are covered with a soft gray fur, and their eyes open within several hours after birth. After weaning, a second growth of stiffer brown fur emerges over the lower back area, and later covers most of the dorsum (Strasser, 1968). Growth curves for this period are depicted in Figure 4.

Neural growth. Several studies have examined facets of central nervous system development. In general, these studies have demonstrated that postnatal growth is also different between *Acomys* and the laboratory rat and mouse. For example, *Acomys* exhibits more rapid volumetric growth in the hippocampal formation (Brunjes, 1984) and olfactory bulb (Brunjes, 1983) and development of myelin staining (Tessitore & Brunjes, 1988) than would be expected when compared with same postconception-aged rats and mice. However, not all regions exhibit this effect. Developmental changes in the density of cells in the visual neocortex, for example, are quite similar between *Acomys* and *Mus* (Brunjes, 1985).

In addition to differences between species, interesting variations have also been found within *Acomys*. Different rates of growth (volumetric expansion) have been noted in several structures. For example, at birth, the olfactory bulb is approximately 50% of the size attained by P60, and growth is rapid, with the structure achieving 90% of its adult volume in the first 10 postnatal days. The hippocampal formation is also 50% of its adult size at birth, but exhibits more gradual development, achieving only 70% of its adult size by P20. The cerebral cortex is much larger at birth (70% of its adult size) and exhibits rapid growth during the first 10 postnatal days. The differential growth seen both within and between species suggests that there must be independent control of maturation in the various areas. Differential controls of development such as these might be just the kind of factors that are altered during the divergence of a species from a stem stock. Thus, comparative studies such as these may be a key to understanding the process of evolution (Brunjes, 1985).

It appears that the brain of *Acomys* is also quantitatively different from that of the rat. For example, D'Udine and Gozzo (1983) have indicated that the hippocampus is larger in *Acomys* than in the rat. The relative size of the olfactory bulb granule cell zone appears to be smaller in *Acomys* than in the rat (Brunjes, 1989).

Figure 3. Photomicrographs taken from an Embryonic Day 22 *Acomys* embryo (left panels) and a same postconception-aged (newborn) rat. (A) and (D). Transverse sections through caudal telencephalon. Scale bars = 0.25mm. (B) and (E). Higher magnification view of the developing hippocampal region. In the rat (E), the dentate gyrus has formed as a cloud of cells capping the developing pyramidal cell zone. (C) and (F). Higher magnification pictures of developing dorsal (visual) cortex. The cortical plate has almost disappeared in the rat, whereas only a few cells can be seen at the ventral margin in the *Acomys*. Scale bars for Panels B, C, E, and F = 0.05 mm.

Figure 4. Age-related changes in postnatal body weight for male (open circles) and female (closed circles) *Acomys cahirinus*. Bars = 1 SEM.

Postnatal development of the cholinergic system (choline acetyltransferase and acetylcholinesterase activity, muscarinic receptor binding sites) has also been reported to differ between *Acomys* and the rat. As expected due to their longer gestation, *Acomys* has much higher levels of cholinergic function at birth and a less steep postnatal developmental curve than the rat (Pintor, Alleva, & Michalek, 1986).

Olfactory bulb maturation has received substantial attention in *Acomys* (Brunjes, 1983, 1988; Leon, Cooper-smith, Ulibarri, Porter, & Powers, 1984). The rat and mouse bulb have been demonstrated to exhibit considerable postnatal neural plasticity (Brunjes & Frazier, 1986). For example, closure of a single external naris at birth, thereby blocking airflow on one side of the nasal cavity and depriving receptors of normal stimulation, resulted in a 25% decrease in the size of the ipsilateral olfactory bulb by P30 (Brunjes & Frazier, 1986). Brunjes (1988) found that *Acomys* deprived in a similar way exhibited more dramatic changes than those seen in the altricial animals: the "deprived" olfactory bulbs were 40% smaller than normal bulbs. Furthermore, in the rat, there is a "sensitive period" for the effects of such deprivation: naris closure after P10, followed by a survival period of 30 days, has relatively little effect on bulb size. However, unilateral deprivation in *Acomys* as late as P30 still resulted in a greater than 20% reduction in the size of the olfactory bulb. Therefore, *Acomys* actually appears to be more affected by alterations in levels of environmental stimulation than does the rat or mouse, and as such is an excellent species for examinations of neural plasticity.

Behavioral. A large number of studies examining early behavioral development in *A. cahirinus* have been reported, primarily by R. H. Porter and his colleagues (Porter, 1986, 1987, 1989). Although these studies are of a diverse nature and overlap both technically and conceptually, they have been broken down into three categories (see also the section on parental behavior).

1. *Early odor preferences.* Some of the first behavioral studies reported in *Acomys* examined "olfactory imprint-

ing." *Acomys* pups were given 1 h of exposure to either cumin or cinnamon on the day of birth. Twenty-four hours later, they were given a two-choice preference test and were found to prefer the odor to which they had been previously exposed (Porter & Etscorn, 1974). Like avian imprinting, the odor preferences exhibited somewhat of a primacy effect: the first odor experienced was preferred over a second as long as exposure times were kept equal (Porter & Etscorn, 1975). Furthermore, a sensitive period appeared to exist, with odor exposure on P1-3 being most effective in inducing preferences (Porter & Etscorn, 1976). Janus (1988, 1989) has recently extended these findings by using naturally occurring odors, more complex testing situations, and longitudinal designs. As a result, the phenomena look less like classical imprinting; for example, reliable preferences could be demonstrated with exposure as late as P16.

2. *Maternal pheromones.* A long series of studies performed by Leon and his collaborators (e.g., Leon, 1974; Leon & Behse, 1977) examined the attraction of young rat pups to a diet-specific odor of dams. Preferences of a similar sort have been demonstrated in *Acomys*. *Acomys* pups were given a series of two-choice preference tests for bedding from a number of different sources. Lactating females produce an attractant that is emitted for at least 35-38 days if lactation is maintained (Porter & Doane, 1976; Porter, Doane, & Cavallaro, 1978). The preference appears to be experience-dependent: *Acomys* pups prefer bedding from lactating females eating a diet similar to the maternal one over that from mothers eating novel food (Doane & Porter, 1978; Porter & Doane, 1976). *Acomys* pups will also be attracted to bedding from lactating *Acomys* females over lactating *Mus* females, although early cross-fostering reverses these preferences (Porter, Deni, & Doane, 1977). Given the choice between bedding from a lactating *Acomys* female on a diet different from the maternal one, and bedding from a lactating *Mus* female on a diet similar to that in the home nest, *Acomys* pups chose on the basis of diet rather than species. Therefore, dietary cues appear to be more salient, although pups can discriminate on the basis of species cues as well (Porter & Doane, 1977). Preferences for bedding from lactating females appear to wane around P25, when pups begin to prefer bedding from nonlactating females (Porter, Doane, & Cavallaro, 1978).

3. *Development of social preferences.* Like rats (see Alberts, 1981), young *Acomys* pups huddle vigorously. Newborns spend large amounts of time in contact with each other and their parents (Deni, Wilson, & Reisert, 1983). An age-related decrease in the time spent engaged in this important behavior is apparent. For example, from P14 to P22, the mean time spent in contact with siblings decreased from 43% to 4.4% of an observational period. Once again, experience seems to direct the behavior: pups raised with littermates spend more time huddling than do pups reared alone (Porter, Cernoch, & Matochik, 1983; Porter, Tepper, Baumeister, Cernoch, & Matochik, 1982). Preferences for associating with siblings emerge as early as P14-16 (Porter & Wyrick, 1979).

Considerable attention has been given to examining social preferences of weanling (P25–30) *Acomys*. Pups at this age preferentially huddle with littermates (Porter, Wyrick, & Pankey, 1978). Experience seems to be important in regulating the preferences. Previous exposure to strange weanlings increases their attractiveness, whereas individual isolation for 8 days diminishes preferences for siblings (Porter & Wyrick, 1979; Porter, Wyrick, & Pankey, 1978). Pups cross-fostered between *Acomys* mothers at P10 or P20 prefer to associate with foster pups rather than with siblings. The effect is at least partially due to the effects of maternal cues. For example, siblings separated but suckled by the same mother prefer to associate, whereas siblings nursed by separate dams do not (Porter, Tepper, & White, 1981; see also Porter, Matochik, & Makin, 1984), which suggests that olfactory cues may be significant. Indeed, pups made anosmic with zinc sulfate infusions have reduced preferences for siblings, and odorizing pups can decrease their preferences for siblings and increase the attractiveness of strangers (Porter, Matochik, & Makin, 1983; Porter, McFadyen-Ketchum, & King, 1989). *Acomys* pups can discriminate between littermates and nonlittermates when the diet of both groups are held constant. This preference disappears when pups are rendered anosmic (Porter, 1988).

Other studies. Ingestive behavior has also been examined in young *Acomys*. Solid food consumption occurs initially about P4–6 (Dieterlen, 1963; D'Udine, Gerosa, & Drewett, 1980; Porter, Cavallaro, & Moore, 1980). Estimates of when weaning occurs in *Acomys* vary widely. Young (1976), for example, claims that pups usually are weaned by P28 but can successfully be weaned as early as P18. Pups born more or less than 1 standard deviation away from mean body weight tend to retain their standing throughout the first 4 weeks of life. Both the maternal environment and the ability of pups to orient to lactating females may play a role in the maintenance of these differences (Porter, Makin, & Matochik, 1986).

OTHER STUDIES OF *ACOMYS*

A number of other topics have been examined in *Acomys* in varying detail. Several of these are mentioned below.

Aggressive behavior. Adult female *Acomys* are more aggressive than males (Andres & Deni, 1982; Moore, McRaney, & Hicks, 1981; Porter, 1976). Porter (1976) has offered a lengthy description of aggressive behavior observed between triads of all combinations of sexes. He reported that chasing, not fighting, appears to be the primary aggressive behavior, that there are apparently few appeasement gestures, and that environmental stimuli (e.g., home vs. strange cages) affect levels of aggression. Moore et al. (1981) reported that REM sleep deprivation resulted in temporary elevations in aggression in females. Females are more likely to treat sexually inexperienced males as intruders than males with previous breeding experience (Andres & Deni, 1982).

Diabetes. A number of studies have examined strains of *A. cahirinus* which exhibit obesity, glycosuria, and hypertrophy of the islets of Langerhans. In most adult animals, approximately 1% of the endocrine pancreas is occupied by islets. Gonet, Stauffacher, Pictet, and Renold (1965; see also Pictet, Orci, Gonet, Rouiller, & Renold, 1967) calculated that in diabetic *Acomys*, the ratio is closer to 15%, although the insulin content of the islets does not differ (Nesher, Abramovitch, & Cerasi, 1985). Insulin release is defective when the mice are confronted with a number of challenges (Cameron, Stauffacher, Orci, Amherdt, & Renold, 1972; Gutzeit et al., 1974; Nesher et al., 1985; Rabinovitch, Gutzeit, Grill, Kikuchi, Renold, & Cerasi, 1975; Rabinovitch, Gutzeit, Kikuchi, Cerasi, & Renold, 1975; Rabinovitch, Gutzeit, Renold, & Cerasi, 1975). *Acomys* does not exhibit a rapid peak in insulin secretion to a glucose challenge, and pancreatic responsiveness is quite delayed, perhaps due to deficits in B-cell adenylate cyclase/cyclic AMP responses (Rabinovitch, Gutzeit, Kikuchi, Cerasi, & Renold, 1975). Morphological studies have failed to find the innervation seen in the normal pancreas. Electrical stimulation of the vagus does result in increased plasma insulin levels in *Acomys*, but the response is not blocked by several cholinergic muscarinic antagonists, including atropine methylnitrate and carbachol (Ionescu & Jeanrenaud, 1988). However, liver glucose production may be more sensitive to insulin in *Acomys* than in other rodents, limiting the consequences of decreased insulin output (Cerasi & Jeanrenaud, 1979). Evidence exists that the diabetes seen in *Acomys* may be a result of obesity due to diets containing high percentages of fats coupled with a normally low insulin response (Gutzeit, Renold, Cerasi, & Shafrir, 1979). As a result, the species has been suggested as a good animal model for chemical or latent diabetes (Gutzeit et al., 1979; Nesher et al., 1985).

Studies of metabolic activity prompted by the work with diabetes have indicated that compared with laboratory rodents, *Acomys* has (1) a relatively small liver (3.6% of body weight, compared to 6.1% in albino mice and 4.2% in rats); (2) lower activity of several enzymes of glycolytic pathways, including glucokinase, pyruvate kinase, aldolase, glucose-6-phosphate dehydrogenase, and 6-phosphogluconate dehydrogenase; (3) increased activity in several enzymes involved in gluconeogenesis (e.g., glucose-6-phosphatase, pyruvate carboxylase); (4) relatively similar levels of enzymes involved in amino acid metabolism (e.g., aminotransferases); and (5) differential liver responsiveness to starvation, including a different threshold of diet carbohydrate, which triggers changes in liver enzyme activity (Gutman, Hasin, & Shafrir, 1972).

Exploratory behavior. Birke, D'Udine, and Albonetti (1981) demonstrated that *Acomys* and the laboratory mouse exhibit quite different behaviors when placed in a strange environment. Adults were placed in a small box that opened into an adjacent arena. Mice exhibited quite cautious behavior, making only short forays into the open field. *Acomys*, however, moved quickly into the area and made rapid dashes around the perimeter. *Acomys* also

spent more time investigating objects placed in the open field. For example, a large piece of pipe was explored by *Acomys*, but was used as a refuge by *Mus*. When frightened, *Mus* tended to use the pipe as a haven, whereas *Acomys* simply fled. Male *Acomys* appear to be more cautious than females (Birke & Sadler, 1986a).

Species differences in distractibility have also been examined (Birke & Sadler, 1986b). Male and female *Acomys* and *Mus* were trained to exhibit stable performance in a runway situation. When novel stimuli were added, the performance of male *Acomys* was much more affected than that of male *Mus*. The opposite relationship was encountered for females of the two species.

Feeding. Naloxone attenuates both food and water intake in *Acomys* (as it does in the rat but not in the hamster), indicating an opioid-sensitive feeding mechanism (Czech, 1987). Feeding in *Acomys* is not stimulated by 2-deoxyglucose, although it does cause hyperglycemia. Insulin injections will induce moderate feeding bouts (Czech, 1988). Food sharing has also been examined in young *Acomys* (Porter, Moore, & White, 1981).

Learning. Although it has been reported that desert species have difficulties learning illness-induced fluid aversions, this does not seem to be the case for *Acomys* (Etscorn, 1977). Deni (1977) has reported that *Acomys* has a difficult time inhibiting a previously learned response.

Parental behavior. With the large body of literature examining early behavioral development in *Acomys*, one would expect a substantial interest in the role of the parents. Indeed, beginning with Dieterlen's (1962) fascinating early account of midwifing (see above), there has been quite a bit of interest in the respective roles of both parents (D'Udine et al., 1980; Makin & Porter, 1984; Porter et al., 1980; Porter & Doane, 1978; Szijarto et al., 1985). *Acomys*, as mentioned, tend to live in colonies without nests. Newly parturient mother will nurse any pup. By P8, mothers prefer to nurse their own offspring, but will still suckle others. Dominant mothers may claim all pups and exclude other mothers (Porter & Doane, 1978; Porter et al., 1980). Time spent nursing declines throughout the first 4 postnatal weeks, with little apparent after P26–30 (Porter et al., 1980). Female spiny mice assume a nursing posture similar to that seen in rats, and a typical stretch reflex is observed in pups with milk letdowns (D'Udine et al., 1980). In a similar fashion, newly parturient females will retrieve any pup, but with age begin to retrieve their own pups first (Porter & Doane, 1978). Retrieval rates decrease as pups age, as a result of both changes in the stimulus characteristics of the pup and the state of the mother (Porter et al., 1980).

Although pups spend time huddling with both parents (indeed, they may spend much more time with the father than the mother; Makin & Porter, 1984; Szijarto et al., 1985), a considerable amount of time is spent with all family members huddling together. However, in a two-choice situation, fathers will spend more time in contact with unfamiliar pups than with their own, with the age of the unfamiliar pups apparently making little difference. Ex-

perienced fathers appear to treat pups differently than do those with no previous pup contact (Makin & Porter, 1984).

Sensory capabilities. Langley (1988) examined the role of audition, vision, and olfaction in prey (cricket) catching in *Acomys*. Olfaction and audition appeared to be the most important modalities, but, reinforcing their classification as a nonspecialized omnivore, they could easily shift dominant modalities when needed. Greenberg (1986) reported that *Acomys* has good depth perception and that they rely more heavily on visual cues than do gerbil species. Several studies examining social behavior in *Acomys* have indicated that the olfactory system plays a dominant role in the species (see the section on prenatal behavior; Matochik, 1988; Porter & Doane, 1979; Porter, Matochik, & Makin, 1986; Porter & Ruttle, 1975; Porter, Sentell, & Makin, 1987; Porter & Treadway, 1974).

Taste preferences. Harriman (1980) investigated taste preferences of adult *Acomys* in a series of two-choice drinking tests. Sugars (fructose, glucose, lactose, maltose, and sucrose) were approached, whereas salts (MgSO_4 , KCL, NaCl) and acids (HCl and citric) were treated indifferently or avoided. *Acomys* rejected or treated hypotonic NaCl solutions indifferently.

CONCLUSIONS

Why are *Acomys* precocial? This question has been grappled with before (Dieterlen, 1963), with few apparent answers. Dieterlen (1963) and Gould (1977) have argued that precocity is a derived state. Evolutionary theory would suggest that the move toward precocial offspring occurs in order to aid survival—that demands made by particular niches are most easily met by producing young that are relatively mature. The most obvious quality of *Acomys*' niche is its harshness, which suggests that this might be the factor that favors the production of competent young. But, as mentioned previously, precocial young are not necessary to survive in an arid niche; quite altricial animals, such as gerbils, flourish in similar environments.

Dieterlen (1963), reviewing a large body of literature, found three rodent species with unusually long gestations: *Acomys*, *Sigmodon*, and *Nyctomys*. All live in widely different habitats, have large variations in social organization, and are subjected to varying degrees of predation. Although that study indicates that precocial young have independently evolved several times, it leaves explanations of the factors directing evolution towards precocial young difficult to formulate. Dieterlen's study also emphasized the fact that rodent species have been quite successful in populating almost every area through the use of a multitude of strategies.

Nevertheless, the present review indicates that large differences in brain growth, physiology, and behavior exist between the laboratory rat and mouse and *Acomys*. As a result, they afford uniquely suitable species for interspecific comparisons, perhaps allowing insight into the

mechanisms that regulate development (Gould, 1977; Bonner, 1982; Raff & Kaufmann, 1983), and thus greater understanding of both ontogeny and phylogeny.

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