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Phodopus campbelli. By Patricia D. Ross

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Phodopus campbelli (Thomas, 1905)

Djungarian Hamster

Cricetulus campbelli Thomas, 1905:322. Type locality “Shaborte, N.E. Mongolia (about 46°40'N, 114°E).” Corrected by Thomas, 1908:107; to “42°40'N, 116°20'E.” Allen (1940) gave coordinates of 42°40'N, 110°00'E.

Phodopus campbelli Hollister, 1912:3. Type locality “Chuisaya Stepppe (8 miles [13 km] south of Kosh-Agatch), Altai District, Siberia; 7300 ft [2225 m].”

P. (Cricetulus) campbelli, Hollister, 1912:3. First use of current name combination.

Cricetulus campbelli Thomas, 1917:703.


DIAGNOSIS. Phodopus campbelli (Fig. 1) is distinguished from the closely related striped hairy-footed hamster, P. songorus, by smaller ears, the lack of a dark patch on the crown of its head, and by the suffusion of yellow or buffy on the dividing line between the dorsal and ventral pelage (Hollister, 1912; Thomas, 1905). The mid-dorsal stripe of P. campbelli is narrower and more sharply defined. The fur on the underside of P. campbelli is slate gray basally, that of P. songorus white to the base (Allen, 1940). Unlike P. songorus, P. campbelli does not turn white in winter. The Chuisaya Stepppe population differs from the more eastern forms by its buffy tail, the shortness of its mid-dorsal stripe that ends about 2.5 cm above the root of the tail, slightly grayer coloration, and darker edges on the lateral margins of the dorsal pelage. The skull is smaller and more slender than that of P. songorus, with larger auditory bullae, and a greater interorbital breadth (Allen, 1940; Hollister, 1912).

GENERAL CHARACTERS. Phodopus campbelli is one of the dwarf hamsters. Ranges in external measurements (in mm) of eight specimens from Mongolia (Allen, 1940) and of one specimen from the Chuisaya Steppe (in parentheses; Hollister, 1912) are: length of head and body, 80–103 (102); length of hind foot, 12–18 (13.5); length of tail, 4–14; and length of ear, 13–15.

The lips and cheeks are creamy white. The rest of the face, head, and upperparts are gray-buff to grayish wood-brown tipped with black, the underfur slate gray. A well-defined mid-dorsal stripe runs from the nape of the neck to the base or up to 2.5 cm anterior to the base of the tail. The throat, underparts, and legs are creamy buff, the buff of the underparts extending upward to form three convex patches on the shoulders, sides, and hips. The upper surface of the hands and feet are silvery white. The palmar and plantar surfaces, with the exception of the interdigital, large hallucial, and small medial carpal pads on the forefoot, and the three small distal pads on the hind feet, are thickly furred (Thomas, 1905). Large internal cheek pouches extend back to the shoulders when full.

There are few available data on the body mass of this species in the wild. The average body mass of four males and one female captured near Manzhouli and Dalai Nor was 23.4 g (Zimmerman, 1964).

Ranges of cranial measurements (in mm) of 10 specimens from Mongolia (Allen, 1940) and one specimen from the Chuisaya Steppe (in parentheses; Hollister, 1912) are: greatest length of skull, 22.6–26.5 (27.0); nasal length, (11.1); interorbital breadth, (3.7); basal length, 19.2–22.7; condylobasal length, (25.0); palatal length, 10.8–12.9; zygomatic breadth, 11.8–14.3 (13.0); breadth across mastoids, 9.9–11.1; width across molars, 4.6–5.2; length of upper cheek teeth row, 3.2–3.9 (4.0); and length of lower cheek teeth row, 3.5–3.8.

DISTRIBUTION. Phodopus campbelli inhabits the steppes and semi-deserts of central Asia: the Altai Mountains, Tuvinian Autonomous Region (Tuva), Transbaikalia, Mongolia, NE Mongolia (Inner Mongolia), and the adjacent parts of Heilungkiang and Hebei provinces in northeastern China (Vorontsov et al., 1967; Zimmerman, 1964; Fig. 2). The northern boundary of the species in Tuva is the Khandagay-Samgaltay line (Yudin et al., 1979).

FOSSIL RECORDS. Fossils referred to the genus are known from the Pleistocene (Fint, 1966). Some Early Pleistocene fossils identified as Cricetulus from Somerset Cave in Britain and from other localities in Europe were assigned to Phodopus by Schaub (1930).

FORM AND FUNCTION. The skull is short, and the brain-case is proportionately large and rounded (Thomas, 1905). The incisive foramina are parallel sided, and the tympanic bullae are small and flattened, with funnel-like bony eustachian tubes (Fig. 3). The stapedial foramen is tiny, and the stapedial artery does not extend anterior to the bulb. The squamouspalatopharyngeal groove and the sphenomandibular foramen are absent (Carleton and Musser, 1984). In captivity under natural outdoor conditions, males began to become larger than females at 45 days of age, and had a statistically significant greater body mass by 145 days of age (Herberg et al., 1980). Under uniform laboratory conditions, males were significantly larger than females by 35 days of age (Sawrey et al., 1984).

Wild male and female hamsters use scent marks for home range delineation and conspecific communication. Both males and females use urine and feces, Harderian glands, skin glands behind the ears, and a mid-ventral sebaceous gland to scent mark (Wynee-Edwards et al., 1992).

At sexual maturity in both sexes, the mid-ventral gland consists of a large number of acini separated by connective tissue interlayers (Sokolov et al., 1988). The mid-ventral gland enlarges during the reproductive season (Vorontsov and Grutovoi, 1959), and is larger in males by 14 days of age (Sokolov et al., 1990b). In mature males

Fig. 1. Photograph of Phodopus campbelli from Erzin, Tuvinian Autonomous Republic, USSR, taken by K. E. Wynee-Edwards.
3–9 months of age maintained under a 14 L:10 D photoperiod, this gland averaged 4.1 mm long (anterior-posterior) and 3.5 mm wide. In mature females, the gland averaged 1.1 mm long and 1.0 mm wide, or less. The average mass of the gland in males 180 days old (n = 20) was 68.8 mg, in females of the same age (n = 20), less than 1.0 mg. In males, the mid-ventral gland has a posteriorly opening pocket of skin that contains sebaceous material. There is only a small area of sebaceous material on female glands (Reasner and Johnston, 1987). Cells of these glands respond to hormonal stimulation, and in males produce both progesterone and testosterone (Sokolov et al., 1992). Deposition of the mid-ventral gland’s secretion is facilitated by longitudinally grooved hairs with spatulate bases that grow on the periphery of the gland (Heisler, 1984).

In captive hamsters, the secretion does not seem to have a deterrent effect on conspecifics, but appears to be used for orientation (Müller-Subemer and Klingel, 1984). The secretion also contains a factor which accelerates the sexual maturation of female young and delays the sexual maturation of male young (Sokolov et al., 1990b).

In common with P. sungorus, but not P. roborovskii or other hamsters, the glandular field at the corner of the mouth surrounds the opening of a sac-like structure located between the skin of the cheek and the cheek pouch. The sacculus is formed during ontogenesis by a complex epidermal transformation of muscular and connective tissue and is completely developed by 20 days of life (Sokolov and Demina, 1992). The external wall of the sacculus is formed of two layers of fibrous elastic connective tissue separated by a thin layer of striated muscle fibers. The internal wall consists of a multilayered epithelium with an exfoliating lining. Dense sheets of dead cells are shed into the cavity of the sacculus and form part of the secretory substance, a whitish yellow substance with a sharp odor. The opening of the sacculus is surrounded by a ring of long strands of striated muscle fibers. The sacculi had an average mass of 7.5 and 8.4 mg and the contents of the sacculi weighed 4.1–20.5 and 5.7–10.1 mg in three males and three females, respectively. The contents of the sacculi may be used with the secretions of the sebaceous glands at the corners of the mouth to mark contents of cheek pouches or for defense (Sokolov et al., 1991).

The large cheek pouches, like those of other hamsters, are an extension of the adoral cavity (Verontsov, 1967). Food and other substances enter the cheek pouch from a hole in the diastema. The size of the pouch opening in P. campbelli is controlled anteriorly by the buccinatorius pars orbicularis oris muscle and posteriorly by a combination of the buccinatorius pars internamaxillaris, buccinatorius pars mandibularis anterior and other buccinatorius muscles. The cheek pouch retractor muscle, derived from a slip of the trapezius muscle, originates from the spines and humboldorsal fascia of the lumbar vertebrae and inserts into the medial and lateral walls of the posterior one-fourth of the pouch. The pouch epithelium consists of a highly keratinized 30 µm-thick stratum corneum and a well-developed stratum granulosum, four to five cells thick. The internal wall of the pouch consists of folds and numerous cone-like dermal papillae. A peninsula of highly folded tissue extends into the empty pouch, and becomes part of the wall structure when the pouch is full (Ryan, 1986). By 11 days of age the cheek pouches are big.
enough to contain a sunflower seed (Ross and Cameron, 1989). Food is collected in one pouch at a time and, when full, the pouches extend forward past the shoulder and the shoulder blade (Vorontsov, 1967).

The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16. The size of the molars decreases posteriorly such that each molar is only two-thirds as long as the preceding tooth (Vinogradov and Argiropulo, 1941). The first, second, and third upper cheek teeth occupy approximately 45, 30, and 25% of the upper toothrow, and the three lower molars occupy approximately 40, 31, and 29% of the lower toothrow, respectively (Wahlert, 1894; Fig. 3).

The islets of Langerhans in healthy pancreatic tissue are few, small, and scattered. Most are innervated by unmyelinated nerve fibers which terminate on all three major cell types, a central mass of insulin producing B-cells surrounded by a rim of A and D cells that produce glucagon and somatostatin, respectively. In P. cambelli that develop hyperglycemia, pancreatic cells become degranulated and glycogen is deposited only in the Golgi complexes and nuclei are free (Herberg et al., 1980; Voss et al., 1978). The stomach, like that of all true hams, is two chambered, with a cornaceous stomach and a glandular stomach (Vorontsov, 1957).

Phodopus campbelli, like P. sungorus and P. roborovskii, has a highly effective renal mechanism for conserving water, is capable of excreting concentrated urine, but has no unique mechanisms for the excretion of excess salts. In an ambient temperature of 18°–20°C and a relative humidity of about 60% with water freely available, the mean osmotic urinary concentration was 2.627 mOsm (n = 20). Urea was withheld, urine was excreted freely during continual water loading (30 ml/g). P. cambelli had excreted more of the load (70%) than P. roborovskii (43%) and less of the load than P. sungorus (87%). Approximately 80% of excess potassium chloride and salt were excreted after salt loading, almost twice as much as in P. roborovskii (45%—Mescherski and Khsikin, 1990).

The efferent ducts of male P. cambelli are made up of three functionally different types of cells. The most frequent, as in most mammals, are principal or nonciliated cells. The apical cytoplasm of these cells contains coated vesicles, pits, and several classes of tubular profiles. The apices are covered with dense fields of microvilli. The lateral plasma and basal membranes are elaborately interdigitated, and dense populations of mitochondria and fenestrated capillaries adjacent to the basal interdigitations suggest intercellular transport. Nonciliated cells, like those of the rat (Rattus norvegicus), are involved in fluid-phase and absorptive endocytosis. The number of lysosomes in the cytoplasm, however, are far fewer than in the rat. Two types of columnar cells extend from the basal lamina to the lumen. The first has many microvilli and few cilias, the second has many cilia and few microvilli. The latter cell type contains more mitochondria, lysosomes, and mucous granules. Neither cell type has tubular complexes (Nagy, 1990).

In summer, the average basal metabolic rate (±SE) is 1.88 ± 0.57 cmO2·g⁻¹·h⁻¹ and the rectal temperature is 34.3 ± 1.7°C. In winter, the average basal metabolic rate falls to 1.63 ± 0.38 cmO2·g⁻¹·h⁻¹ and the rectal temperature is 35.7 ± 1.3°C. Maximum oxygen consumption in winter (1.45 ± 1.96 cmO2·g⁻¹·h⁻¹) is higher than in the summer (12.93 ± 1.68 cmO2·g⁻¹·h⁻¹—Weiner and Heldmaier, 1987).

Phodopus campbelli is less well adapted to cold temperatures than P. sungorus. The lowest ambient temperatures tolerated in summer and winter, measured by maximum rates of oxygen consumption, are −31.8°C and −44.6°C, respectively, 6–10°C higher than in P. sungorus. Thermogenic response to cold is not linear, as in P. sungorus. As the ambient temperature is lowered, the basal metabolic rate increases rapidly and, at −10°C, the body temperature shows a sudden drop to 23.7°C (Weiner and Heldmaier, 1987). Pup survival is high (95%, n = 107) in litters (n = 19) raised by both parents at an ambient temperature of 21°C, but drops significantly (52%, n = 78) in litters (n = 16) raised by both parents at 4°C (Wyne-Edwards and Lisk, 1969).

Phodopus campbelli is prone to genetically determined abnormalities in the metabolism of carbohydrates and lipids (Herberg et al., 1980; Voss et al., 1978). P. campbelli has a tendency to develop spontaneous tumors of the mammary glands, squamous cell skin cancers, lungs, uterus, ovary, and reticulum tissue. Tumors can also be induced by exposure to chemical carcinogens (7,12-dimethylbenz[a]anthracene, 3-methylcholanthrene, diethylnitrosamine, and methylhydrolsourea) and oncogenic viruses (Rous sarcoma virus, simian adenovirus, and human adenovirus). P. campbelli is resistant to urethan and, in common with the Chinese hamster, Cricetulus griseus, but not the Syrian hamster, M. auratus, simian virus 40 (Pogoszian, 1975). Structural changes in the X chromosome and autosomes have been demonstrated in the karyotypes of cells from chemically induced tumors (Sokova and Pogoszian, 1989). For these reasons and because of small size and the ease with which it can be maintained, P. campbelli has been used as a useful subject for cancer and cytogenetic studies (Cantrell and Padovan, 1987; Pogoszian and Sokova, 1977; Sokova and Pogoszian, 1989). Captive hamsters are susceptible to obesity and ringworm, Trichophyton mentagrophytes (Pogoszian, 1975; Young, 1974). Slow locomotion is a lack of noticeable responses to bright lights and human observers, open habitat, and low population densities enable field studies of entire populations. Individual hamsters were tracked using interperitoneal implants (Wyne-Edwards et al., 1992).

ONTOGNY AND REPRODUCTION. The breeding season in Tuva begins in the middle of April (Flint and Golovkin, 1961), in Mongolia at the end of April or the beginning of May (Bannikov, 1954), and in Transbaikalia at the end of April or the beginning of May (Nekepirov, 1960). It ends in September or early October throughout the range (Meyer, 1967). Captive animals breed throughout the year (Flint, 1966; Meyer, 1967), but a greater number of offspring are born during the summer (Jordan, 1971; Pogoszian, 1975). In Transbaikalia, females that are capable of reproducing weigh at least 14 g, and spermatogenesis in males from this locality is evident in males weighing less than 25 g during the summer. Female offspring of breeding stock captured in this locality had their first litters at about 48 days of age (Meyer, 1967). In contrast, females descended from a Tuva population had their first litters at 35 days of age.

The average number of offspring per litter in females from Transbaikalia was 8.2 (Meyer, 1967). One gravid female captured near Manzhoubi in Inner Mongolia had nine embryos (Zimmerman, 1964). Females in laboratory colonies have from 1 to 18 litters with 1–9 offspring per litter (Pogoszian, 1975).

Parturition is followed immediately by a fertile post-partum estrus (Wyne-Edwards and Lisk, 1984). The gestation period of captive females has been reported as 17.5–18.5 days (Daly, 1976), 18–19 days (Ross and Cameron, 1989), and as 20–22 days (Flint, 1966; Flint and Golovkin, 1961; Meyer, 1967). The minimal gestation period in captive females was 13 days (Herberg et al., 1980).

At birth (day 1), young are hairless and have a body mass of approximately 1.5 g. Incisors and claws are present, but the digits, eyes, and ear pinnae are sealed. Rates of morphological development differ by about a day in different parts of the species’ range. Ear pinnae on young from Tuva begin to separate from the head on day 1 and separation is complete by day 7. The eyes are completely open on day 4, while incisors from Transbaikalia occurs on days 2 to 4. Fur first appears on the head, then the back, sides and abdomen. Young from Tuva and Transbaikalia are completely furred by day 7. Digits on the forefoot of most young from Tuva are completely separate on day 5, but not until a day later on young from Transbaikalia. The eyes of most young from Tuva are open by day 9, and those of young from Transbaikalia, by day 10 (Meyer, 1967).

Increase in the mass of young born in captivity, and the growth rates of the length of head and body, length of tail, length of hind foot, and length of the ear were most rapid just after birth. By 28 days of age young attained 63.5% of their adult mass of 32.1 g, 85% of their adult (102.1 mm) total length, 96% of adult (15.3 mm) hind foot and tail (11.8 mm) lengths, and 92% of their adult (14.8 mm) ear length. These young were weaned by 17 days of age (Ross and Cameron, 1989).

Captive females become sexually mature at about 2 months of age. Vesicular follicles form at least 16 days prior to the first spontaneous ovulation. Weaning female P. campbelli exposed for 10 days to male or to androgenic androgens in male urine have larger uteri, ovaries, adrenals glands and testes. Female are younger at first ovulation than those housed alone or with sisters (Gudernacht et al., 1992; Reaser and Johnston, 1988). In captivity, most (85–88%) sexually mature females show regular 4-day estrous cycles; the ones that remain have 5-day or a mix of 4- and 5-day cycles (Wyne-Edwards and Elders, 1987).

The time of behavioral receptivity of captive females at the beginning of the dark phase of the light cycle, and the time of ovulation, a little after the mid point of the dark phase, are consistent.
with those observed in the golden hamster, Mesocricetus auratus. The 17 β-estradiol concentration rises from a baseline of 54 pg/ml on the morning of estrus over the first 48 h after ovulation to a high of 187 pg/ml about 12 h before ovulation, then falls rapidly to the baseline concentration. Unlike in M. auratus, progesterone plays no part in the behavioral receptivity of the female. The level of serum progesterone peaks during the early afternoon of diestrous day 2 at 8.0 pg/ml and is only present in a concentration of 2.504 pg/ml at the time of peak receptivity. Primary follicles measure, on average, 83 (n = 32; range, 39–123) μm in diameter, pre-ovulatory, or Graafian follicles, 455 (n = 35; range, 257–658) μm in diameter. Fewer than 100 follicles are in the ovary, and the ovulation follicle (primary or secondary) are usually filled. At ovulation, 3–8 ova are shed (Wyne-Edwards et al., 1987a).

ECOLOGY. The burrow consists of four to six vertical and horizontal tunnels. The tunnel leading to the nest chamber can be as deep as 1 m below the surface of the ground, but most are only 25–30 cm deep (Flint, 1966; Veselovsky and Grundova, 1964). The nest is built of dry grass (Flint, 1966) and sheep's wool (Yudin et al., 1979).

The steps also shares the paths, tunnels, and burrows of Ochotona daurica in the high steppes and semi-deserts of the Barga Upland in northern Manchuria, and the burrows of O. manchurica in the rocks and cliffs of the Great Khingan Range (Louchakshin, 1940). On the Mongolian Plateau about 100 miles north of Kalgan (Zhangiaqiao), P. campbelli shares the burrows of Meriones in preference to its own (Allen, 1940; Thomas, 1908).

Population densities are low and stable. In various habitats in Transbaikalia, P. campbelli accounted for only 0.01–0.60% of the rodents captured during yearly rodent censuses from 1944 to 1958. These were caught in traps baited with bread soaked in vegetable oil (Flint, 1966). In Tuva, P. campbelli made up 0.2–4.5% of the small rodents captured in various habitats during 1958 and 1959; the highest numbers were trapped on Potentilla- Artemisia (cinquefoil-wormwood) and grass-wormwood steps (Flint and Golovkin, 1961). The habitat by Lake Tere Xol on the Mongolian border is characterized by open sand dunes and Artemisia and Potentilla steppe with Caragana bushes 0.2–3.0 m in diameter. Here, each female hamster's 3–5-ha home range contains just over 1,000 bushes (Wyne-Edwards et al., 1992).

Pholopus campbelli was common along the caravan route from Kalgan to Tashul (Thomas, 1908). Nine specimens of P. campbelli were collected during six expeditions to Mongolia between 1963 and 1968: a male on an open Caragana steppe (1,400 m), a male on an Artemisia steppe (600 m), a female on a mountain steppe partially covered with stone and rock near a marmot burrow (1,100 m), two males and one female on a gravel steppe with sandy, gravel, and grassy areas (Topal, 1973). In Manchuria, P. campbelli is found in association with Pitymys brandti, Microrus gregalis, Cricetulus barbatus, and Allactaga sibirica (Louchakshin, 1940). P. campbelli also inhabits areas of human habitation, and is found in Mongolian yurts, and more substantial buildings, particularly during the winter (Flint, 1966). In the northwestern part of its range, P. campbelli is found in association with four other species of hamsters, P. roborovskii, Cricetulus barbatus, C. curatus, and C. longicaudatus. The diets of the four hamster species are sufficiently different to avoid competition (Flint and Golovkin, 1961). Although the range of P. campbelli shows a considerable overlap with that of P. roborovskii (Flint, 1966), the two species do not come into direct contact (Verontsov, 1967). P. campbelli occupies stable ground (Verontsov, 1960), or clay areas that are avoided by the desert hamster (Flint, 1966), and is found in desert and steppe areas, as well as the periodically dry mud flats of Mongolia (Argyropulu, 1933; Flint, 1966; Hamann, 1987; Schmidt et al., 1986).

The diet of P. campbelli varies among different parts of its range. Fifty-one species of plants have been identified in the diet of the Tuva population, the most important being Stipa capillata, Allium, Iris ruthenica, and L. flavus. In contrast, only 10 species of plants have been identified in the diet of the Tuva population. Two of the most important are Potentilla and Aneurolepidium (Flint, 1966). The cheek pouches of a male P. campbelli captured in Tuva contained 12 P. capillata and the protein of a beetle (Pectophorus umbratus; Zimmerman, 1964). In captivity, these hamsters eat wheat grain, sunflower seeds, dandelions, locusts, and citrus fruit (Jordan, 1971; Yudin et al., 1979).

Predators include the eagle owl (Bubo babo), the steppe eagle (Aquila nipalensis), the kestrel (Falco tinnunculus), the saker falcon (F. cherrug), and the Corsac fox (Vulpes corsac) (Brom, 1932; Lipiyan and Tatarsov, 1952; Peshkov, 1957). In southeastern Transbaikalia, P. campbelli remains accounted for 7.7% of the stomach contents of 52 steppe foxes during the summer, and 2.6% of the stomach contents of 38 steppe foxes during the winter (Heptner and Naumov, 1974).

Ectoparasites include Amphiphiysylla linguispina, A. aniceps, A. schelkovskii, Paradoxopilosus naryni, Wagneria tecta, W. schelkovskii, and Neopsylla, none of which are exclusive to P. campbelli (Flint, 1966). No internal parasites have been reported. In a captive breeding colony, P. campbelli lived in mated pairs with their current litter and displayed a well-defined dominance hierarchy. Each pregnant female built a new nest with the help of the male prior to parturition. Siblings and offspring were driven off. The α-male of the litter remained in the nest to mate with an immigrant female, and the other young dispensed. Strange conspecifics were attacked by both dominant males and females. Immature males were bitten, injured, and occasionally castrated or killed. Young animals remained sexually inactive, and sexual development in young males was retarded (Müller-Sutmeyer and Klinge, 1984).

Support for obligate monogamy in captive P. campbelli is given by Wyne-Edwards (1987) who found that mated pairs raised litters more successfully than did lone females or pairs of sibling females in spite of the fact that the female was lactating and gestating her next litter. Females did not become pregnant if mated in the presence of two or more males (Wyne-Edwards and Lisk, 1984), and showed pregnancy block if housed with an unfamiliar male or abandoned by their mate at a critical period after mating and before implantation (Wyne-Edwards et al., 1987).

In all natural populations, females are more numerous than males. Males are at higher risk due to their greater mobility (Meyer, 1971). In Tuva, the home ranges of females do not overlap and an area may be visited by more than one male (Wyne-Edwards et al., 1992). Males may visit one or more females to mate (Meyer, 1967; Wyne-Edwards et al., 1992).

The average life span of P. campbelli in captivity was 278 days for nine males, and 356 days for six females. The oldest male lived 654 days and the oldest female 618 days (Herberg et al., 1980). Captive Djungarian hamsters born in late summer or early autumn survived through the following two winters, living an average of 2–2.5 years (Hamann, 1987).

BEHAVIOR. The Djungarian hamster is crepuscular and nocturnal, and is active throughout the year (Flint, 1966). Its locomotion is slow and sluggish (Hamann, 1987) with a maximum running speed of approximately 6.5 km/h (Wyne-Edwards et al., 1992).

The first day of appearance (day 0 = day of birth), and the mean day of appearance (in parentheses) of grooming, feeding, and digging behavior in eight litters of P. campbelli reared under laboratory conditions was as follows: scratching with contact, 5 (5.5); gnawing, 5 (7); overhead grooming, 7 (9); scratching with foot-ticks, 9 (12.5); body grooming, 11 (12.5); shaking, 13 (17); mouthing food, 7 (8); eating, 8 (8); eating sitting up, 12 (12); carrying food to nest, 13 (16); forepaw digging, 9 (10); and complete digging, 13 (7.5–12) (Wyne-Edwards et al., 1992).

The home-cage activity of 12 adult males in an air-conditioned room under a reversed 16 L:8 D photoperiod over a 24 h period was acyclic. Percentages of time spent in four categories of behavior during the light phase and the dark phase (in parentheses) were: sleep, 71% (66%); groom, 10% (14%); eat, 9% (11%); and locomotion, 6% (4%); the overall temporal pattern of wheel running of adult males over 29 consecutive days was nocturnal although the temporal patterns of some hamsters were acyclic (Sawrey et al., 1984).

Under natural conditions, captive P. campbelli showed both a daily and seasonal periodicity in behavior. The greatest number of nest exits was recorded just after 1800 h, the least at 0230 h. Peak yearly activity (6.5 h/day) was observed during February, the time of least activity (< 15 min/day) observed in the sympatric desert hamster, P. roborovskii. Several hours of wheel running by individual hamsters on more nights would be followed by nights of reduced running, or by no running at all (Hamann, 1987).

Two female hamsters observed in the field (Wyne-Edwards et al., 1992) were active above ground for an average of 4.1 h on
15, and 2.6 h on eight consecutive nights, respectively, between dusk and dawn. Each female spent approximately 40% of this time traveling, 12% resting, and 12% feeding. Most ventral gland, vaginal, rolling, and urine scent marking occurred early in the evening during the first and second expeditions from the burrow. Both females distributed over 50% of their scent marks under bushes and tussock grass. Marks were also placed on sandy and open grass substrates and by burrows, but the two females differed significantly in their choice of substrates. Scent marking by males in the same area was restricted to each male’s own home range, with the largest concentration at the periphery. Males sometimes marked near the burrow of a female during mating (Wynne-Edwards et al., 1992). Captive males direct their scent marks at both male and female conspecifics, discriminate between male and female odors, and investigate areas marked by males and females in a different manner (Reasner and Johnston, 1987).

The basic pattern of copulatory behavior consists of one to several discrete series of mounts, each series terminated by a brief ejaculatory lock (Wynne-Edwards and Lisk, 1984), or no lock (Sawrey et al., 1984), and separated from the next series of mounts by a refractory period. Several intermissions occur before each ejaculation (Sawrey et al., 1984; Wynne-Edwards and Lisk, 1984), at which time the male and female both fall onto their sides, the male grasping the female with his forepaws so that she is unable to escape for approximately 9 s (Sawrey et al., 1984). Intermount pursuit is slow, and lordosis is brief. Repeated thrusting is observed only as the male tires. Unreceptive females will strike a male with a snapping motion of one or both forepaws while in an upright posture (Dake, 1976). Mating may take from 4 to 6 h, and can extend on average, six complete ejaculatory series (Wynne-Edwards and Lisk, 1984). A copulatory plug is deposited after ejaculation (Sawrey et al., 1984). The measures of copulatory behavior obtained in pairs where estrus was induced by injecting the females with estradiol benzoate are not comparable to those obtained from pairs where females were in natural estrus (Sawrey et al., 1984).

In 10 min agonistic interactions with like-sexed conspecifics, dominant male P. campbelli were more aggressive than dominant female P. campbelli. The frequencies of attacks,ashes, bites, and boxes during same-sex male interactions were all significantly higher than those of same-sex female interactions. Dominant males could inflict serious physical injury or death by biting the head and neck of their opponent. This behavior was not observed in P. campbelli females or during similar interactions between same-sexed P. sungorus males and females. P. campbelli females display less aggression towards conspecific males than P. sungorus females (Wynne-Edwards and Lisk, 1987).

Phodopus campbelli reacts to cold exposure by exercising vigorously, and trying to escape to shelter instead of resting in a curled posture and relying on its capacity for heat production and behavioral thermoregulation (Dake, 1976). Mating may take from 4 to 6 h, and can extend on average, six complete ejaculatory series (Wynne-Edwards and Lisk, 1984). A copulatory plug is deposited after ejaculation (Sawrey et al., 1984). The measures of copulatory behavior obtained in pairs where estrus was induced by injecting the females with estradiol benzoate are not comparable to those obtained from pairs where females were in natural estrus (Sawrey et al., 1984).

GENETICS. The diploid number of chromosomes (2n) is 28 (Matthey, 1960) and the fundamental number is 51 (Schmid et al., 1986). Of the autosomes, 18 are metacentric, 4 are submetacentric, and 4 are acrocentric (Spyropoulos et al., 1982). The X chromosome is polymorphic (Vorontsov et al., 1967) and the Y chromosome is acrocentric. The X chromosome is about 15 μm in length and the Y chromosome is 6.0 μm, consisting of 7.3 and 2.9% of the total synaptonephal karyotype length of 205.2 μm (Spyropoulos et al., 1982). With the exceptions of the 12th and 13th pairs which are acrocentric in P. campbelli and submetacentric in P. sungorus, the autosome complement is the same in both species (Bigger and Savage, 1976). This suggests that P. campbelli seeks refuge from extreme cold despite the energetic cost of such activity (Weiner and Heldmaier, 1987).

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