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A Comparison of the Physical Development and Ontogeny of Behaviour in the Djungarian Hamster and the Desert Hamster

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Physical and behavioural development during the first four weeks after birth were investigated in five litters each of two closely related species of dwarf hamster, the Mongolian form of the Djungarian hamster, *Phodopus campbelli*, and the desert hamster, *Phodopus roborovskii*. Both species showed the most rapid growth rate just after birth. With the exception of tail length, *P. campbelli* maintained the highest growth rate for the first two weeks after birth. The earliest morphological and behavioural development in all categories investigated was seen in *P. campbelli*. Behavioural profiles showed significant interspecific differences in the distribution of social, locomotory, ingestive, and digging behaviours, but no significant differences in grooming and investigatory behaviours over the 28 day sampling period. Behavioural differences were more reflective of adaptive responses to environmental conditions than they were of phylogenetic relationships.

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1. INTRODUCTION

The Mongolian form of the Djungarian hamster *Phodopus campbelli* Thomas, 1905, and the desert hamster *Phodopus roborovskii* Satunin, 1902 are considered to be distinct but closely related species (Corbet, 1978; 1984). They differ, however, in both morphology and habitat requirements.

Phodopus campbelli is found in a variety of habitats throughout most of Mongolia and the adjacent parts of the USSR (Corbet, 1978). Adults weigh 32 g on average, and attain a total length ranging from 90 to 100 mm. The dorsal pelage is grey tinged with brown, with a well defined black mid-dorsal stripe. Whitish fur with a dark grey base covers the undersides and patches on the shoulders and hips.

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Adult *P. roborovskii* weigh approximately 18 g, with a body length ranging between 68 and 92 mm. The dorsal pelage is beige and grey, and the venter, limbs, tail, mystacial pads, and a patch above each eye are pure white. Their habitat is restricted to shifting sand dunes in the deserts of western and southern Mongolia, Inner Mongolia, and the adjacent parts of the U.S.S.R. and the People's Republic of China (Corbet, 1978).

Some aspects of the postnatal development and the ontongeny of behaviour of *P. campbelli* have been discussed by Flint (1966), Meyer (1967), and Daly (1976). The physical development and the mean body mass for the first 30 days post partum of *P. roborovskii* have been given by Flint (1966). Hamann (1987) briefly compared aspects of the behaviour of young *P. campbelli* and *P. roborovskii.*

The obejctives of this study were to obtain a qualitative and quantitative description of the behaviour and physical development of each species, and to examine behavioural similarities and differences which might be indicative of phylogenetic affinity on the one hand, but reflect respective adaptations to somewhat different ecological circumstances on the other.

2. METHODS

2.1. Subjects

Qualitative and descriptive data were obtained from the first and second generation offspring of fifteen mated pairs of *P. roborovskii* obtained on loan from the Metropolitan Toronto Zoo, and twelve pairs of *P. campbelli* donated by Dr. P. Crowcroft.

Breeding pairs of both species were housed in 25×50×30 cm aquaria in a temperature controlled animal room (21°C). Cage floors were covered with Beta-chip hardwood bedding, and shredded paper towels were provided for nest material.

The diet for both species consisted of a mixture of Purina rabbit chow and wild birdseed supplemented with carrots, lettuce, and alfalfa sprouts. Water was freely available.

A reverse 15L:9D light schedule facilitated observation and assured the manitenance of reproductive condition. Illumination during the dark period was supplied by a bank of four 25 watt red light bulbs.

Five litters of each species (minimum litter size=3) were sampled to determine the ontogeny of adult behaviour. This sample size was dictated by the small number of litters born to *P. roborovskii* during the 14 months of the study. Of the nine litters born to this species, only five had three or more young which survived to maturity. In contrast, 19 litters of three or more young survived to adulthood out of the 26 litters born to *P. campbelli* during the same period.

2.2. Procedure

As soon as pregnancy was apparent, males were removed. Pregnant females were observed frequently to determine the exact time of parturition (day 0). All behavioural observations were begun 30 minutes after lights out: the observed time of greatest activity for both species. Sampling began after the mother was removed from the cage, and the young had been given a five minute period of time to acclimatize to her absence. Five minute continuous behavioural sequences (Altmann, 1974) were recorded on tape daily for each of three young selected at random from each litter from day 1 to day 28 giving a total sample of 75 minutes per day for each species. Elements of adult behaviour in both species were determined from observation of both breeding stocks. By the age of 28 days, adult behaviours, with the exception of sexual behaviour, were fully developed. After the behavioural sampling for each litter was completed, all young were individually weighed to the nearest 0.01 g, and standard measurements were taken of total body, hind foot, tail and ear lengths. The young and their mother were then returned to the cage. Additional morphological data obtained from two litters of *P. roborovskii* during a preliminary study were included in the analyses.

2.3. Analyses

2.3.1. Growth

Instantaneous growth rates (IGR) for each external measurement were calculated using the formula of Lackey (1967): $[\ln(m2)-\ln(m1)](d2-d1)$, where ln m2 and ln m1 represented the natural logs of measurements taken on days d2 and d1. The time period d2 — d1 was four days. The data were plotted on semi-log paper, and the growth rates were read from the curves. This provided a basis for interspecific comparisons which were not apparent from the raw data. Standards for adult weight, total body length, hind foot, ear, and tail lengths used to calculate the percentage of growth attained by the young at the end of the 28 day sampling period were based on those of 35 adult *P. campbelli* and 29 adult *P. roborovskii*.

2.3.2. Behaviour

Because there was no information available concerning the behaviour of *P. roborovskii*, and only brief descriptions of some behavioural elements in *P. campbelli* (Daly, 1976), it was necessary to construct ethograms for both species. Each behavioural element was placed into one of eight major categories for analysis: Social, Grooming, Investigatory, Locomotive, Ingestive, Digging, Lateral Forepaw Push, and Other (Table 1). The category Other contained all those behaviours, mostly neonatal, that were not assigned to the first seven categories.

The first day of appearance of each element of adult behaviour was noted for each young. A 28 day behavioural profile was constructed for the young of each species by dividing the daily total number of behavioural elements in each major behavioural category by the daily total of all behavioural elements observed.

Table 1

Behavioural categories and elements used to determine: (1) the first day of occurrence of behaviours and (2) the daily frequencies of behaviours in the young of *P. campbelli* and *P. roborovskii*.

Behaviour	Description
Other	Forepaw paddle; hindleg paddle; squirm; fall over; right; motionless; sleep; change sleep position; yawn; limb quiver; body quiver; nest build.
Social	Climb over other young; push between other young; push; push under other young; watch other young; approach; avoid; present side or back; sniff — naso--nasal; sniff — other part of body; allogroom; forepaw box/strike; forepaw push; nuzzle; flee; follow; chase: freeze; attack; bite; fight — wrestle; mount; steal; roll on back (submit).
Investigatory	Sniff substrate; sniff object; head raise — sniff; head raise — one forepaw raise — sniff; rear (upright).
Dig	Forepaw dig; forepaw dig — hind leg kicks; forepaw dig — anterior torso twist.
Maintenance	Lick forepaws; forepaw wash; snout wash — one or both forepaws; face wash — one or both forepaws; overhead wash — one or both forepaws. Hindfoot scratch (nose, side of head, top of head, ear, neck, shoulder, forelimb, under arm, side, abdomen, back); lick — nibble (forepaws, forearm, flank, hind leg, hind foot, abdomen, anogential area, back); urinate; defecate; back wriggle; head shake; body shake.
Locomotion	Crawl; walk; run; climb (objects); pivot; rear-hop.
Ingestive	Pick up food (forepaws, incisors); gnaw; chew; push food into pouch; push food out of pouch; drop food; manipulate food; carry food; spit out food; drink water.
Lateral Forepaw Push	Push aside Beta-chips; cover self; manipulate nest material; pivot.

3. RESULTS

3.1. Growth and Physical Development

In our study, all *P. campbelli* females had a gestation period of between 18 and 19 days. In contrast, the gestation period of three consecutive litters born to the same *P. roborovskii* female, timed from the first post-ejaculatory lock to the birth of the first young were 22.5, 20.5, and 19.2 days, respecitvely.

The young of each species were dark red and hairless at birth. Claws and incisors were present, and the ear pinnae, eyes, and digits were sealed. Cranial sutures and viscera were visible beneath the skin.

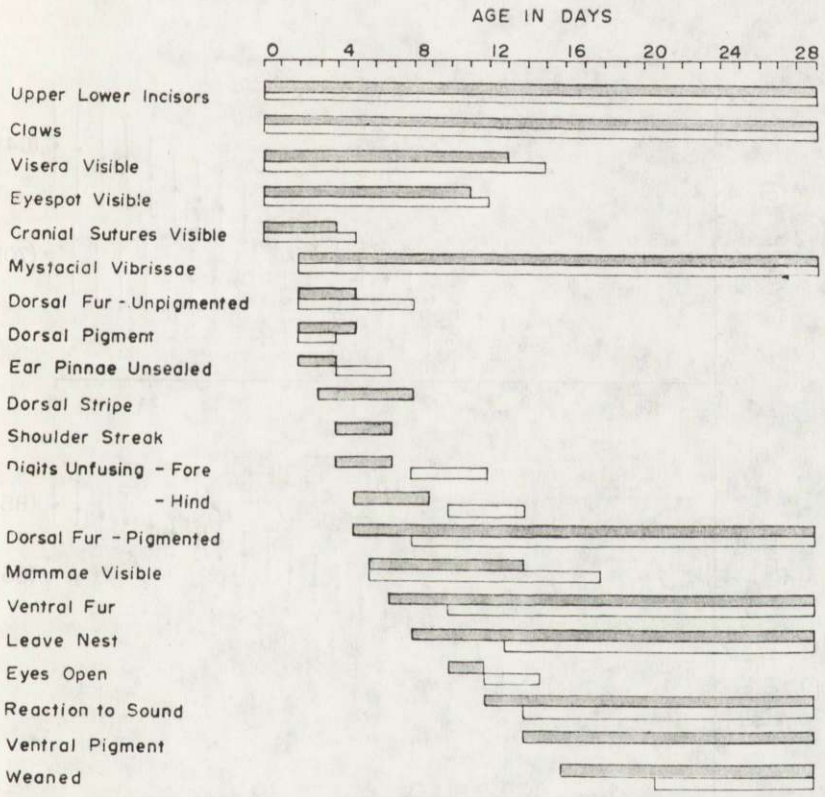

Fig. 1. First day and subsequent appearance of morphological characteristics during physical development. Hatched bars=*P. campbelli;* open bars=*P. roborovskii.*

Mystacial vibrissae, faint dorsal pigment across the scapular and hip region, and fine unpigmented fur were evident in both species by day 2. After this time, with the exception of the appearance of mammae on the females of each species on day 6, *P. campbelli* showed the most rapid physical development (Fig. 1).

Mean values of weight, total length, and hind foot, tail, and ear lengths are given in Fig. 2. Tail and ear lengths were the most difficult to measure accurately, particularly after the eyes had opened. The young would contract, or move their tails to the side, or move their heads and put their ears back as soon as the ruler came into contact. *P. roborovskii* would also try to escape by twisting, digging, and after 21 days of age, by biting. On day 28 there were no significant inter-

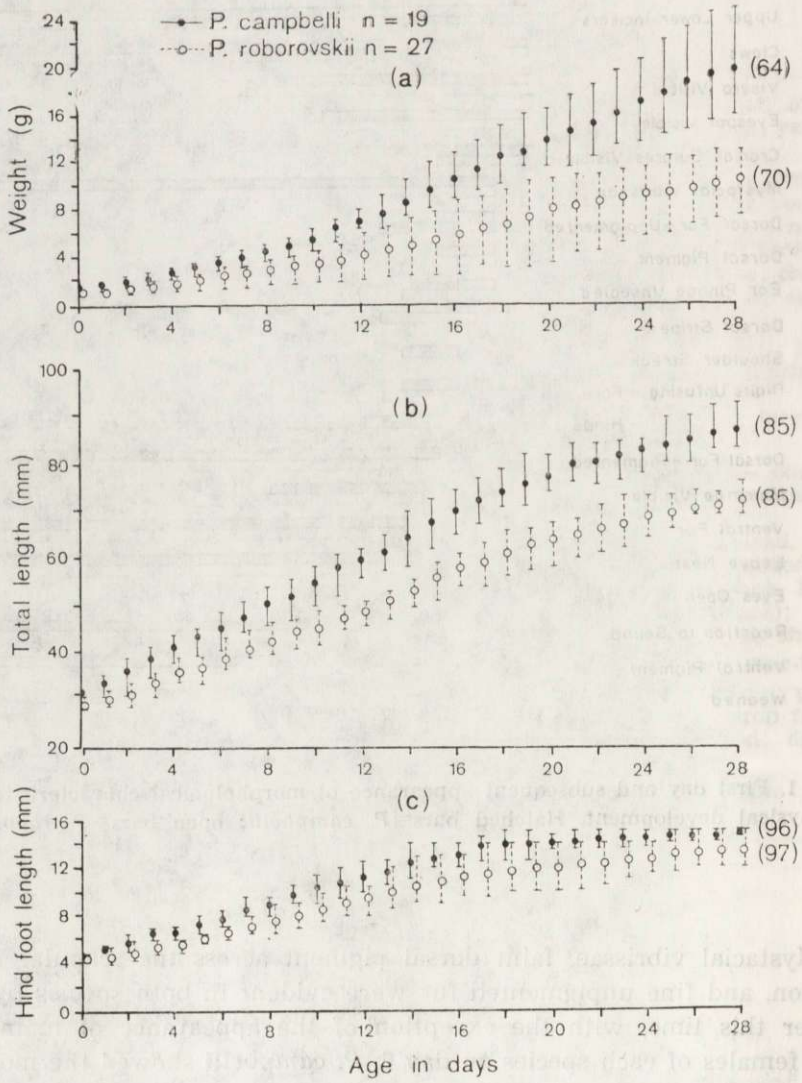

Fig. 2. Absolute growth data for the young of *P. campbelli* and *P. roborovskii* for days 0 to 28: (a) weight, (b) total length, (c) ear length, (d) tail length and (e) kind foot length. Circles represent mean values; vertical lines represent ranges; standard errors were too small to be shown at this resolution. $n=19$ (*P. campbelli*); $n=27$ (*P. roborovskii*). Numbers in brackets at day 28 represent percentage of adult growth attained.

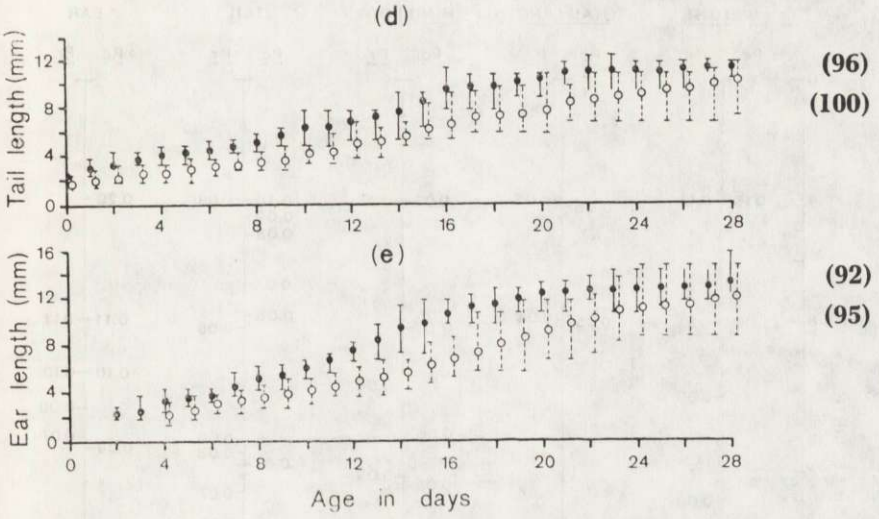

Fig. 2. Concluded.

specific differences in the percentage of adult growth attained in the five characters measured.

Instantaneous growth rates (IGR) (Fig. 3) show that growth was most rapid in both species just after birth. With the exception of tail length, *P. campbelli* maintained the highest growth rate during the first two weeks after birth.

3.2. Behaviour

3.2.1. Social

The social behaviours of the young prior to eye opening consisted of pushing against, crawling over, pushing between, and burrowing under siblings. These behaviours were observed throughout the 28 day sampling period. *P. campbelli* young directly approached and sniffed each other on day 10. These behaviours did not occur in *P. roborovskii* until day 13, the day after eye opening in this species. All social behaviours were expressed at an earlier age in *P. campbelli* (Fig. 4).

3.2.2. Grooming

P. roborovskii young were capable of scratching their elbows and shoulders with contact between the hind foot and body by day 2 (Fig. 5). With the exception of scratching and forepaw licking, which was observed in both species on day 8, all grooming behaviours were seen first in *P. campbelli.*

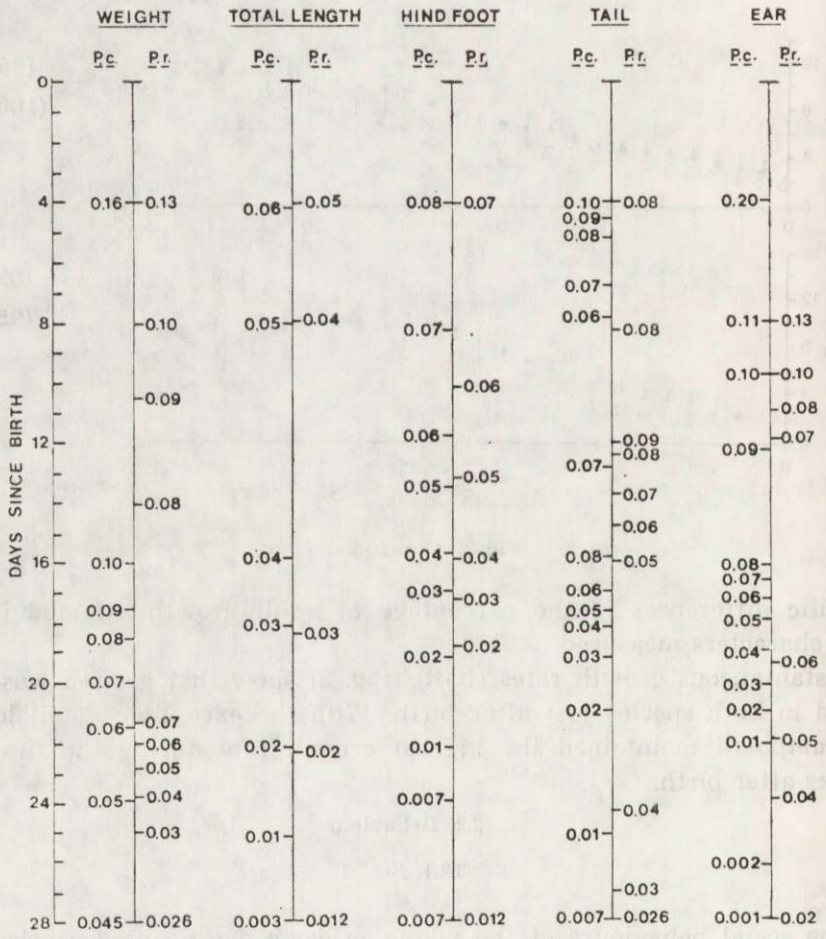

Fig. 3. Instantaneous growth rates for *P. campbelli* and *P. roborovskii* from day 0 to day 28.

3.2.3. Locomotion

Neonates of both species would move about the nest by wriggling the body, or by pulling themselves over littermates by using their forepaws. *P. campbelli* young began to crawl between days 4 and 6, whereas *P. roborovskii* did not crawl until days 7 to 9. *P. campbelli* young left the nest for the first time using plantigrade locomotion on days 7 and 9, two days prior to eye opening. *P. roborovskii* young did not leave their nests until their eyes had opened, and by this time locomotion was fully

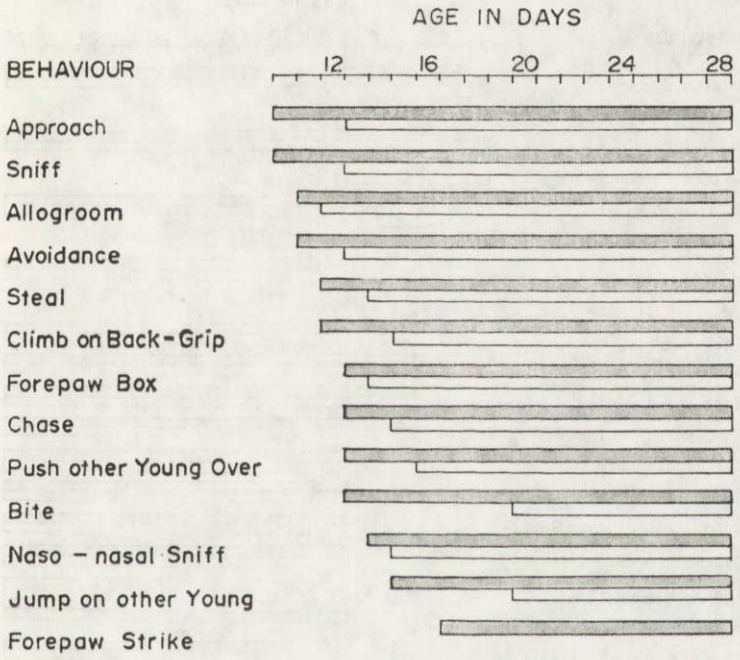

Fig. 4. First day and subsequent appearance of selected elements of social behaviour. Hatched bars=*P. campbelli;* open bars=*P. roborovskii.*

digitigrade, and movement more rapid than observed in *P. campbelli.* As the young matured this rapid movement became pronouncedly more brisk, in contrast to the more phlegmatic *P. campbelli.*

Rear-hopping, which was seen first on days 17 and 18 in *P. campbelli,* was never observed in *P. roborovskii.* By day 20, the young *P. campbelli* could hop a distance of 10 to 12 cm.

3.2.4. Ingestion

The first evidence of adult ingestive behaviour in *P. campbelli* was a flurry of activity in the nest and the sound of seed coats cracking on days 7 and 8. The young would crawl over, push under or between each other, then paw and sniff the sides of the nest with their hind ends oriented towards the ceiling. The young would frequently flip over their heads onto their backs, then right themselves and continue to search for seeds. The first seeds eaten were relatively small millet seeds.

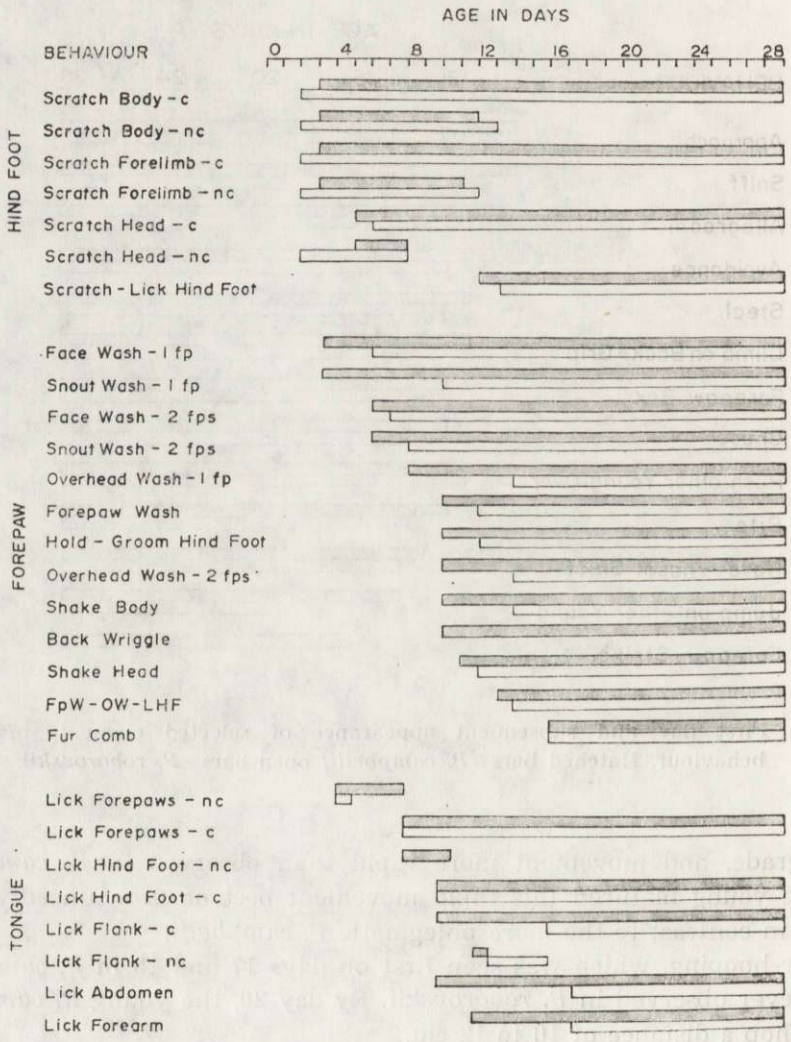

Fig. 5. First day and subsequent appearance of grooming behaviour. c=contact between hind foot and the body; nc=no contact between the hind foot and the body; fp=one forepaw; fps=two forepaws; sequence FpW — OW — LHF= forepaw wash — overhead wash — lick hind foot. Hatched bars=*P. campbelli;* open bars=*P. roborovskii.*

By day 11, the cheek pouches were large enough to contain a sunflower seed.

Most elements of adult ingestive behaviour were seen first in *P. campbelli,* and all ingestive behaviours were fully developed in this species by day 12 (Fig. 6).

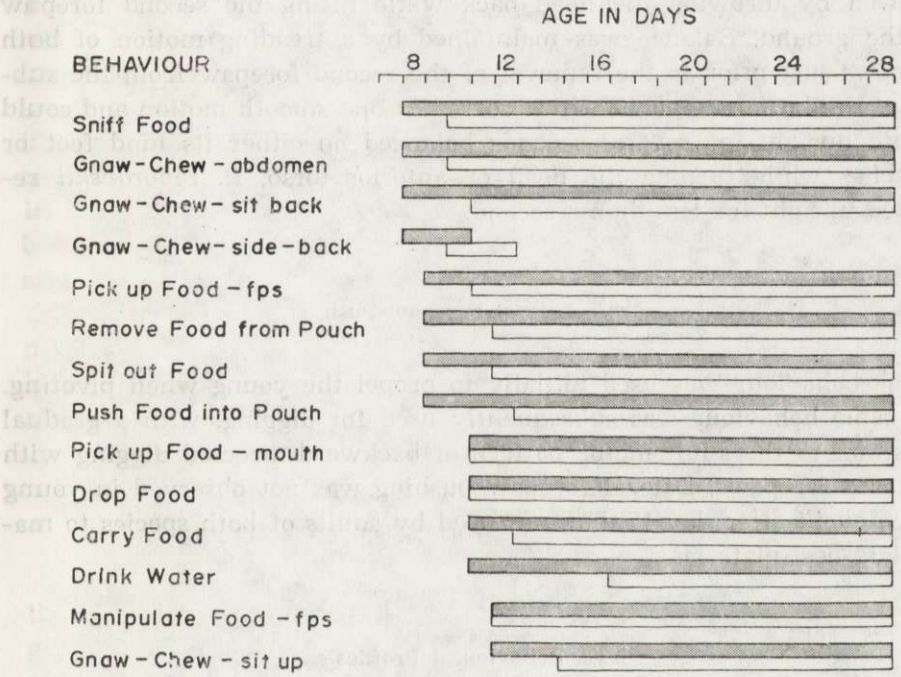

Fig. 6 First day and subsequent appearance of element of ingestive behaviour. fps=two forepaws. Hatched bars=*P. campbelli;* open bars=*P. roborovskii.*

3.2.5. Digging

P. campbelli were capable of digging using alternate forepaws by day 11, *P. roborovskii* by day 10. After day 18, digging became an increasingly important part of the behavioural repertoire of *P. roborovskii.* All the young would dig together in one corner, one climbing on top of the other, pushing the hamster on the bottom of the group away from the glass. This animal would then climb on top of the group and the process would be repeated. Up to 30 minutes at a time would be sent in this activity. *P. campbelli,* in contrast, dug infrequently.

3.2.6. Investigation

The first directed sniffing of an object was observed in *P. campbelli* on day 7, one day prior to *P. roborovskii.* A *P. roborovskii* seldom sniffed while in an upright position, but would stop, raise its head and one forepaw, and sniff, with vibrissae twitching. This was accompanied or

followed by throwing the head back while lifting the second forepaw off the ground. Balance was maintained by a treading motion of both forepaws just prior to the removal of the second forepaw from the substrate. Unlike *P. campbelli* which reared in one smooth motion and could remain upright for several seconds balanced on either its hind feet or haunches while turning the head or anterior torso, *P. roborovskii* remained upright for less than a second.

3.2.7. Lateral Forepaw Push

This behaviour was used initially to propel the young when pivoting. The same behaviour was subsequently used for digging, with a gradual transition to the adult motor pattern of backward directed digging with alternate forepaws. Lateral forepaw pushing was not observed in young *P. campbelli* after day 17, but was used by adults of both species to manipulate nest material.

3.2.8. Behavioural Profiles

The behavioural profiles for each species (Fig. 7) show the daily frequencies of elements of behaviour in each major category as a percentage of the total number of behavioural elements observed daily in each species.

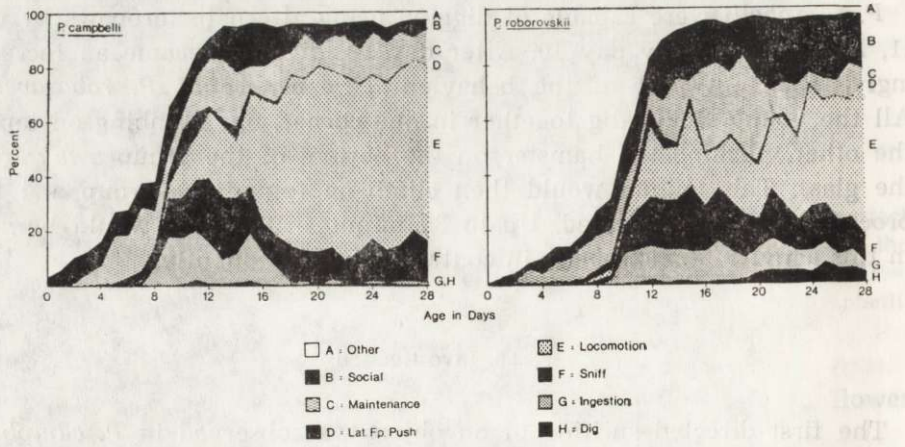

Fig. 7. Behavioural profiles for young *P. campbelli* and *P. roborovskii*. The ordinate represents the percentage of elements of behaviour observed daily in each major behavioural category.

The daily frequencies of neonatal and other behaviours which were not assigned to a particular category declined rapidly in both species from day 1 to day 12. The earlier appearance of behavioural elements in *P. camapbelli* is evident by day 8. The decline in the percentage of ingestive, social, grooming, and investigatory, and the increase in locomotory behaviours which is evident in *P. campbelli* during days 15 and 16 was not seen in *P. roborovskii*. Although the percentage of locomotory behaviours increased in *P. roborovskii* after day 21, social behaviour and digging remained important.

The Kolmogorov-Smirnov 2-Sample Test showed that there were significant interspecific differences ($p<0.05$) in the distribution of social, locomotory, ingestive, and digging behaviours during the first 28 days after birth.

4. DISCUSSION

The close agreement of our morphological data on *P. campbelli* with those of Meyer (1967) suggests that laboratory maintenance over several generations did not affect the temporal pattern of development in our experimental stock, and that the emergance of behaviour dependent on physical development in this species is similar to that observed in nature.

While the interspecific differences in the rate of physical and behavioural development shown here do not reflect unequivocal phylogenetic relationships, we believe they are indicative of adaptive responses to different ecological circumstances. The rates of development shown by *P. campbelli* and *P. roborovski* do not differ greatly from the hamsters *Cricetus cricetus* (Eibl-Eibesfeld, 1953). *Cricetulus griseus* (Daly, 1976; Stolba & Kummer, 1972), *Cricetulus barabensis*, and *Cricetulus curtatus* (Flint, 1966).

The earlier physical and behavioural development of *P. campbelli* may reflect the adaptation of this species to open steppe habitats where the nests and mobile young are likely subject to intense levels of predation. Loukashkin (1940) found this hamster sharing the paths, tunnels, and burrows of two species of *Ochotona*, and Allen (1940) reported it occupying the burrows of *Meriones*. *P. campbelli* remains have been found in eagle owl, steppe eagle, kestrel, and shrike pellets, as well as steppe fox droppings (Flint, 1966). The same predator-prey relationship exists between the above predators and *Cricetulus barabensis* (Flint, 1966), a species which also inhabits open steppes, and whose young are even more precocial than *P. campbelli*. Several behaviours seen during general observations of *P. campbelli* support the above hypothesis. Shortly after

the young were capable of hearing (day 14), they reacted to a sharp sound by freezing and remaining motionless for several seconds to minutes. Eventually, one young would move and sniff its siblings, in turn. At this point, all the young would resume their normal activity. This phenomenon was observed in all litters until days 20—24, after which the response could not be elicited. Freezing involved a catatonic condition in which the young would remain rigid even when picked up and handled. Rigid young were also found on top of newborn litters, buried under nesting material, while the mother was absent from the nest. Freezing during this particular stage of development in *P. campbelli* would aid the survival of both subadults that are just gaining their independence, and younger siblings, whose mothers have left the nest. Furthermore, the tendency of *P. campbelli* mothers to attack strange objects immediately in defense of their newborn young also suggests that the nest may be vulnerable to predation.

No information is available on the predators of *P. roborovskii*. The openings to the burrows of this species are hidden by shifting sand shortly after the animal has passed through (Allen, 1940), which might protect the nest against predation to some degree. The young studied, in contrast to those of *P. campbelli*, did not leave the nest until after their eyes had opened and they were capable of rapid digitigrade locomotion. The tendency of *P. roborovskii* mothers to flee when confronted with a strange object, deserting their young, indicates that this species may not be under the same selective pressure to protect their offspring in the wild. The young showed no tendency to freeze when confronted with a sudden noise, but instead fled, or dug under the nest material. The appearance of rapid locomotion after the eyes had opened and the young being capable of leaving the nest may reflect the necessity of being able to move swiftly from cover to cover in an arid sandy habitat. It was noted, however, that adult *P. roborovskii* which were housed in large arenas would freeze when confronted with a strange conspecific. Freezing in adult *P. roborovskii* was noted also by Hamann (1987).

The magnitude of developmental differences in *P. campbelli* and *P. roborovskii* was no greater than that observed among species of *Peromyscus* (King, 1958; Layne, 1966). In *Peromyscus*, however, the observation that the earliest physical and behavioural development was shown by the most timid and nervous species led King to believe that "tameness" was highly correlated with long development. This phenomenon was also observed in *Microtus* (Frank, 1954). The converse was observed in *P. campbelli* and *P. roborovskii*, where *P. campbelli*, the most aggressive of the two species, showed the earliest overall develop-

ment, reaching sexual maturity by two to two and one half months of age, at least two months earlier than *P. roborovskii*. *P. roborovskii* never became "tame", and always attempted to escape or bite when picked up, even if handled daily after birth, particularly after 21 days of age. Unlike *P. campbelli*, *P. roborovskii*, in nature, avoids areas of human habitation (Flint, 1966).

The difficulty in breeding *P. roborovskii* may be a reflection of the stress imposed on this animal under laboratory conditions, and may account for the paucity of information which was available to us prior to this study.

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PORÓWNANIE ROZWOJU FIZYCZNEGO I ZACHOWANIA U CHOMIKA DŻUNGARSKIEGO I CHOMIKA ROBOROWSKIEGO

Streszczenie

Badano rozwój fizyczny i zachowanie dwóch blisko spokrewnionych gatunków chomików *(Phodopus campbelli* i *P. roborovskii)* w czasie 4 pierwszych tygodni życia (Tabela 1). Najintensywniejszy wzrost stwierdzono u obydwu gatunków zaraz po urodzeniu. *P. campbelli* wykazywał szybszy wzrost przez pierwsze 2 tygodnie życia, jak również szybszy rozwój morfologiczny i behawioralny (Ryc. 1, 2, 3). Stwierdzono znaczne różnice międzygatunkowe w zachowaniach socjalnych, poruszaniu się i grzebaniu nor, a brak różnic w zachowaniach eksploracyjnych i pielęgnacyjnych (Ryc. 4, 5, 6, 7).