

DIFFERENCES IN ENDOGENOUS ACTIVITY WITHIN THE GENUS *PHODOPUS*

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Timing, distances, and durations of above-ground activity were monitored during three successive years in wild populations of dwarf hamsters (*Phodopus*). Both *P. campbelli* (Djungarian hamsters) and *P. sungorus* (Siberian hamsters) were nocturnal. However, *P. campbelli* arose earlier (before dark or soon after dark versus well after dark) and remained above ground 2.5 times longer than *P. sungorus*. Longer expeditions allowed female *P. campbelli* to travel farther than both sexes of *P. sungorus* at the same speed. In contrast, *P. campbelli* males were active for the same amount of time as females but travelled almost three times faster, covering much greater distances and larger areas. Patterns of wheel running by females in the laboratory confirmed the earlier onset and longer duration of activity in *P. campbelli*, demonstrating that differences between species in the wild were not simply responses to different environmental stimuli. Activity before and after dark and prolonged activity throughout the dark are interpreted as evidence that resource acquisition in the colder, drier, more seasonal habitat of *P. campbelli* requires more energy and time than resource acquisition in habitat of *P. sungorus*. As such, constraints on energy and time during the breeding season may have been important in the evolution of biparental care in *P. campbelli* but not *P. sungorus*.

Key words: *Phodopus*, Siberian hamster, Djungarian hamster, activity, wheel running

The Siberian hamster (*Phodopus sungorus*) and Djungarian hamster (*P. campbelli*) are native to the middle latitudes of continental Asia, are phenotypically similar, and were long considered subspecies (Honacki et al., 1982; Kartavtsev et al., 1984a, 1984b; Vorontsov et al., 1967). They share morphological and physiological adaptations to withstand extreme cold (superb insulation and spherical shape) and scarce water (highly concentrated urine, low evaporative water loss) and are the same body weight (20–35 g) in adulthood (Flint, 1966; Heldmaier, 1975; Meschersky, 1993; Scribner and Wynne-Edwards, 1994a; Trojan, 1977).

However, habitat of *P. campbelli* has 50% less rainfall, shorter seasonal rains, and colder mid-winter temperatures than habitat of *P. sungorus*. For *P. campbelli*, limited water availability combines with

limited maternal tolerance for elevated core body temperatures (a consequence of adaptations to withstand extreme cold) and constrains physiological responses of pregnant and lactating females to the thermoregulatory and water-balance stresses of reproduction (Newkirk et al., 1998; Scribner and Wynne-Edwards, 1994a, 1994b, 1994c). Continued male presence alleviates those maternal thermoregulatory stresses and improves maternal ability to care for the young (Walton and Wynne-Edwards, 1998). Thus, physiological constraints on maternal survival that conflicted with physiological demands of rapid reproduction in the cold, dry, seasonal habitat are considered the ultimate selective force that resulted in biparental care in *P. campbelli* but not *P. sungorus* (Wynne-Edwards, 1998).

Females also differ in their use of maternal energetic reserves during reproduction.

In contrast to female *P. sungorus*, which gain weight during gestation and lose it again during lactation, female *P. campbelli* lose weight and the majority of their white fat reserves by the time they wean a litter (Koteja et al., 1993; Stulberg and Wynne-Edwards, 1998). Likewise, survival of young declines more rapidly in *P. campbelli* than *P. sungorus* when environmental conditions are suboptimal (Newkirk et al., 1997; Scribner and Wynne-Edwards, 1994a; Wynne-Edwards and Lisk, 1989).

Different plant communities, which result from the differences in climate, may contribute to those differences in maternal energetics. *P. campbelli* is found in a semi-desert of stabilized sand dunes dominated by *Caragana* shrubs, and *P. sungorus* is found in ungrazed, short-grass steppe (Flint, 1966; Meyer, 1967; Wynne-Edwards et al., 1992). Resulting differences in resource (nutrient and water) availability (Weiner et al., 1982; Zvereva, 1982) may constrain patterns of foraging and limit energy availability in habitat of *P. campbelli* (Khokhlova et al., 1997).

If resource availability was more limiting in the semi-desert than in the short-grass steppe, we hypothesized that *P. campbelli* would be forced to travel farther from the burrow and spend more time above ground than *P. sungorus*. To test the hypothesis, we analyzed observations of each species in the wild over 3 successive years. To test the additional hypothesis that differences in activity were endogenous, we compared patterns of running wheel use in the laboratory where climate, photoperiod, food, and water were controlled.

MATERIALS AND METHODS

Hamsters were caught by live trapping or captured by hand. Captures by hand were made during behavioral interactions between hamsters active above-ground or by waiting at the entrance to a burrow for a hamster to emerge. In the latter case, scent-marking behavior by another hamster at the entrance to the burrow or sounds of interaction while another hamster was in the burrow

were used to identify appropriate locations to wait (Wynne-Edwards et al., 1992). Each hamster received an intraperitoneal radio-transmitter implant (L.L. Electronics, Urbana, IL) under Ketamine (75 mg/kg)-Acepromazine (7.5 mg/kg) anesthetic and was released within 2 h of the surgical procedure. Telemetry (Custom Electronics, Urbana, IL) was used to confirm the continued presence of a hamster in a burrow, identify other hamsters in the same burrow, and relocate hamsters temporarily lost from view in the vegetation. Otherwise, all data were collected by direct observation using battery-operated headlamps and hand-held flashlights.

The combination of open habitat and slow locomotion by the hamsters made it possible to maintain visual contact, usually <1 m from the hamster, throughout its above-ground activity (Wynne-Edwards et al., 1992). Behaviors, including the onset and termination of all above-ground activity, were recorded into a voice-activated Olympus Pearlorder[®] microcassette recorder equipped with an electronic time-date stamp. Spatial locations were determined by placing unique flags at known times linked to behavior and then mapping those flags during daylight.

Above-ground activity by each hamster was categorized as belonging to an expedition or a temporary emergence. An expedition was defined as any absence from a sleeping burrow with a duration of >5 min and a maximum distance of >1 m from the burrow entrance. Any time spent underground in a burrow other than a sleeping burrow was included within the expedition unless that burrow became a sleeping burrow during the next day. A sleeping burrow was any burrow that the hamster was last seen entering at the end of a night's observations and in which that hamster remained until first emergence the following evening. The first night after release was excluded from analyses in case the combination of anesthesia, handling, and observer presence had biased the activity of the hamster. Activity that did not meet the definition of an expedition (i.e., short appearances around the burrow entrance and movements within the burrow that approached the burrow opening) was considered a temporary emergence and was excluded from analyses.

We assumed that there was no above-ground activity during full daylight. During 215 h of daylight observations (1989 and 1990), only one

animal was active above ground. That female *P. campbelli* travelled 15 m to enter a second burrow. She had been implanted with a radiotransmitter the previous night and had not emerged since her release. Therefore, her behavior may have been an attempt to return to her preferred sleeping burrow. In all other cases, the last burrow entered in the morning was always the burrow in which that hamster was located the following evening.

Results for the onset of activity (start of the first expedition) were included only when the observations began ≥ 30 min before sunset and the hamster remained in the burrow for ≥ 30 min after the beginning of observations. Likewise, observations continued for ≥ 30 min after sunrise before the conclusion of activity (end of the last expedition) was used in analyses. The span of above-ground activity included only nights in which the animal was followed from before the start of the first expedition until after the end of the last expedition. We quantified the duration of above-ground activity only on those nights for which activity span was available and summed the number of minutes during which the hamster was active above-ground (as opposed to below-ground in the sleeping burrow). Distance travelled in a single night was estimated as the sum of the straight-line distances between successive flag locations. Because distance measures depended on the location of successive flags and did not include local activity in the region of any flag, all distances were minimum estimates of the actual distance travelled by the hamster. The maximum distance from the burrow during a night was the largest straight-line distance between any locator flag and the sleeping burrow. Speed of travel (m/min) was calculated on a nightly basis using distance travelled and duration of above-ground activity.

To test the hypothesis that species differences in activity were endogenous, running-wheel use in the laboratory, where climate ($18^{\circ}\text{C} \pm 1 \text{ SE}$) and photoperiod (14L:10D) were identical and both food (Purina Rodent Chow) and water were available ad lib., was compared. Adult females of each species that were neither pregnant nor lactating were acclimated (4 or 5 days) to modified aquaria equipped with nest boxes and running wheels. For 5 consecutive days, revolutions of the running wheel were summed to give a total for each hour of the 24 h day. Full details of the apparatus and data reduction are provided

in Scribner and Wynne-Edwards (1994b). Data were used to generate average light- and dark-phase values for running-wheel use in that study.

All times, including local sunset, dusk, dawn, and sunrise, were converted to decimal hours before analyses. We used JMP Version 3 running on a Power Macintosh (SAS Institute Inc., Cary, NC). Data were analyzed using two approaches. The first approach reduced all information for each hamster to single values representing the average of all measures for that animal (i.e., statistical independence was assumed at the level of individual hamsters). The second approach recognized the limited power of analyses based on a small number of hamsters to detect real differences (Thomas and Juanes, 1996) and considered each hamster-night to be an independent measure of activity. Assumptions of independence at the level of hamster-nights were statistically valid. Each night of observation was separated by a day without above-ground activity and, for the 13 hamsters with ≥ 7 nights of observations, coefficients of variation of each hamster were as large as coefficients of variation across hamsters. For example, standard deviations for the total distance travelled by a hamster over successive nights ranged from 31%–91% of its mean with a median of 66% while coefficients of variation for the same measure across hamsters of the same species and sex ranged from 37%–79% with a median of 52%. Thus, distances travelled over successive nights by one hamster were as variable as distances travelled by different hamsters of the same species and sex. Results were qualitatively similar for both statistical approaches. Parametric ANOVA followed by post-hoc testing with a critical alpha level of 0.05 was applied. Means $\pm 1 \text{ SE}$ are presented.

RESULTS

From 1988 to 1990, 24 *P. campbelli* and 11 *P. sungorus* were studied. Sample sizes for each sex, species, and year were small but included all animals in each local population followed for all nights after their initial capture (Table 1). The small local populations and highly social interactions between individuals complicated designations of independence for statistical analyses. Sample sizes had insufficient power to detect real differences (Thomas and Juanes,

TABLE 1.—Inclusive field observation dates, locations, and numbers of individuals studied for each of *Phodopus campbelli* and *P. sungorus* from 1988 to 1990. Because there was only one research team, observations for the two species were never synchronous. No reproductive adults have been seen in successive years, so there is no overlap in individuals across years. At the time of this work, study sites were within the U.S.S.R.; presently each study site falls within the current boundaries of Russia (Siberia), although Tuva is recognized as an independent region.

Species	Year	Nearest town	Latitude, Longitude	Inclusive dates	Number of males	Number of females	Number of hours observed	Number of minutes active
<i>P. campbelli</i>	1988	Erzin, Tuva	50.16N, 95.14E	23 Jul–19 Aug	5	6	280	4,830
	1989	Erzin, Tuva	50.16N, 95.14E	30 Jul–26 Aug	4	5	509	13,516
	1990	Erzin, Tuva	50.16N, 95.14E	24 Jul–9 Aug	2	2	365	5,452
<i>P. sungorus</i>	1988	Karasuk, Novosibirsk	53.44N, 78.02E	9–17 Sept	2	3	117	1,492
	1989	Beya, Hakasskaya	53.43N, 91.26E	8–17 Sept	2	2	288	2,353
	1990	Beya, Hakasskaya	53.43N, 91.26E	2–18 Jul	2	0	109	1,112

1996), animals could not be considered a random subset of a larger population because they encompassed the entire local population (Wynne-Edwards et al., 1992), observations were effectively continuous, and events such as mating were the focus of activity for most (or all) animals in the local population (K.E. Wynne-Edwards, in litt.). Intensity of observations also ranged from 2 nights to 19 nights/hamster so that statistical confidences in estimates for individuals were not the same for all hamsters.

Because these limitations were genuine constraints imposed by the social structure of the species, activity was analyzed by individual and on the basis of a hamster-night (59 male-nights and 77 female-nights for *P. campbelli*; 35 male-nights and 18 female-nights for *P. sungorus*). Results were similar with both approaches. Statistical analyses emphasize comparisons in which each hamster is represented only once by the average of all estimates for that individual. Illustrations assume independence between hamster-nights.

Duration of activity.—Individual *P. campbelli* often emerged before dark (27.2% of 122 nights) and remained above ground after dawn (29.3% of nights). No *P. sungorus* emerged before dark and few *P. sungorus* (11.3% of 53 nights) were active after dawn (Chi-squared with continuity correction = 15.9, *d.f.* = 1, $P < 0.0001$ for emergence; $\chi^2 = 5.7$, *d.f.* = 1, $P < 0.02$ for return to the burrow; Fig. 1). Thus, individual *P. campbelli* began above-ground activity significantly earlier relative to sunset (1.52 ± 0.20 versus 3.02 ± 0.30 h after sunset; $F = 18.2$; *d.f.* = 1, 29; $P < 0.0005$) and remained active significantly later relative to sunrise (1.86 ± 0.25 versus 3.86 ± 0.40 h before sunrise; $F = 19.3$; *d.f.* = 1, 29; $P < 0.0005$) compared with individual *P. sungorus*. Males and females did not differ in activity relative to the light-dark cycle ($P = 0.41$) and there was no interaction between species and sex ($P = 0.75$).

Activity span (5.69 ± 0.34 versus 3.51

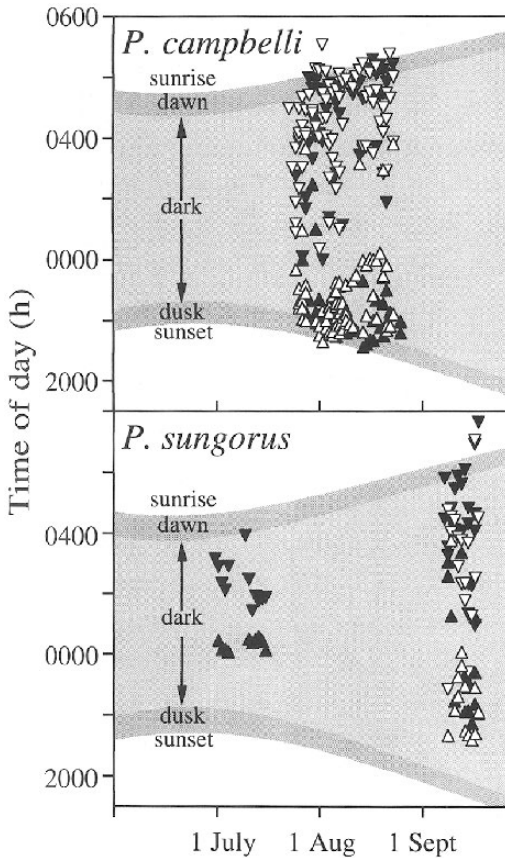


FIG. 1.—Time of day for the beginning of the first expedition (triangles pointing up) and the end of the last expedition (triangles pointing down) for male (black) and female (white) *P. campbelli* and *P. sungorus*. Local sunset, dusk, dark, dawn, and sunrise are shown for Erzincan (*P. campbelli*) and Beya (*P. sungorus*) sites.

± 0.52 h/night; $F = 12.63$; $d.f. = 1, 26$; $P < 0.002$) and duration of above-ground activity (222.0 ± 31.1 versus 83.4 ± 43.0 min per night; $F = 6.90$; $d.f. = 1, 16$; $P < 0.05$) confirmed that *P. campbelli* was active for a greater proportion of each night than *P. sungorus*. There was no evidence for a difference between sexes in either measure ($P = 0.89$, $P = 0.98$). Above-ground activity averaged 65% of the activity span of *P. campbelli* and 40% of *P. sungorus*. Results were similar when all nights of observation were considered with an effect of species ($F = 27.86$; $d.f. = 1, 112$; $P < 0.0001$) but

not sex ($F = 0.61$; $d.f. = 1, 112$; $P = 0.44$) on activity span. Activity spans of males and females were similar for *P. campbelli* (6.3 ± 0.5 h versus 5.6 ± 0.3 h; $t = 1.05$, $d.f. = 76$, $P = 0.30$) and *P. sungorus* (3.0 ± 0.5 versus 4.3 ± 0.5 h/night; $t = 1.74$, $d.f. = 33$, $P = 0.09$), although the direction of the differences between males and females differed, resulting in a significant interaction term ($P = 0.05$). Duration of above-ground activity was effected by species ($F = 34.39$; $d.f. = 1, 73$; $P < 0.0001$) but not sex ($F = 0.00$; $d.f. = 1, 73$; $P = 0.98$), and the interaction term was not significant ($P = 0.31$). Thus, *P. campbelli* emerged from the sleeping burrow earlier than *P. sungorus*, remained active longer into the morning, and spent >2.5 times as much time above ground each night.

Within each night, activity was organized into expeditions. Expeditions were longer in *P. campbelli* than *P. sungorus* (51.2 ± 5.6 versus 32.9 ± 3.8 min; $F = 4.94$; $d.f. = 1, 30$; $P < 0.05$), with no effect of sex ($P = 0.35$) and no interaction term ($P = 0.70$). Results were similar when all expeditions were considered. Expeditions were more than twice as long for *P. campbelli* than *P. sungorus*, and no differences between male (= 174) and female (= 257) *P. campbelli* or male (= 89) and female (= 54) *P. sungorus* expedition durations were found (Fig. 2).

Distance travelled.—The difference in time budget between species translated to differences in distances travelled. In a night, *P. campbelli* travelled farther than *P. sungorus* ($1,167 \pm 203$ versus 267 ± 31 m/night; $F = 14.94$; $d.f. = 1, 29$; $P < 0.001$) with male *P. campbelli* travelling farther than female *P. campbelli* ($1,641 \pm 348$ versus 822 ± 195 ; $t = 2.19$, $d.f. = 17$, $P < 0.05$) but no difference between male and female *P. sungorus* (254 ± 38 and 283 ± 56 ; $t = 0.44$, $d.f. = 9$, $P = 0.67$). Greater distances travelled by *P. campbelli* included travel that ranged farther from the sleeping burrow than *P. sungorus* (232 ± 48 versus 68 ± 9 m; $F = 11.46$; $d.f. = 1, 29$; $P <$

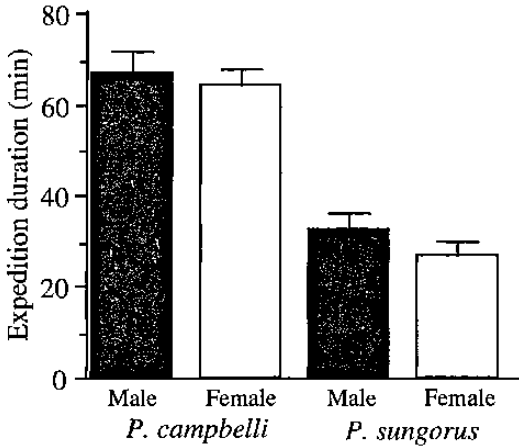


FIG. 2.—Mean (\pm SE) duration of above-ground expeditions for male and female hamsters of each species. A total of 174 male and 257 female expeditions was included for *P. campbelli*. For *P. sungorus*, 89 male and 54 female expeditions were included.

0.005) and did not differ between males and females. Male *P. campbelli* reached distances three times farther from the burrow than female *P. campbelli* (370 ± 92 versus 131 ± 19 m; $t = 2.95$, $d.f. = 17$, $P < 0.01$) while male and female *P. sungorus* did not differ (71 ± 13 and 64 ± 12 m; $t = 0.41$, $d.f. = 9$, $P = 0.69$).

Results were similar when all nights were considered independent estimates of activity with *P. campbelli* travelling significantly farther ($F = 38.86$; $d.f. = 1, 188$; $P < 0.0001$) and reaching greater distances from the sleeping burrow ($F = 36.48$; $d.f. = 1, 188$; $P < 0.0001$) than *P. sungorus*. Likewise, male and female *P. campbelli* differed in total distance travelled per night and maximum distance from the burrow whereas male and female *P. sungorus* did not (Fig. 3).

Speed of travel.—The interaction of time above ground and distance travelled was represented as travelling speed (m/min; Fig. 3). As in the measures that define speed, there was a significant difference between the species with *P. campbelli* travelling faster than *P. sungorus* ($F = 35.30$; $d.f. = 1, 23$; $P < 0.0001$). However, there also

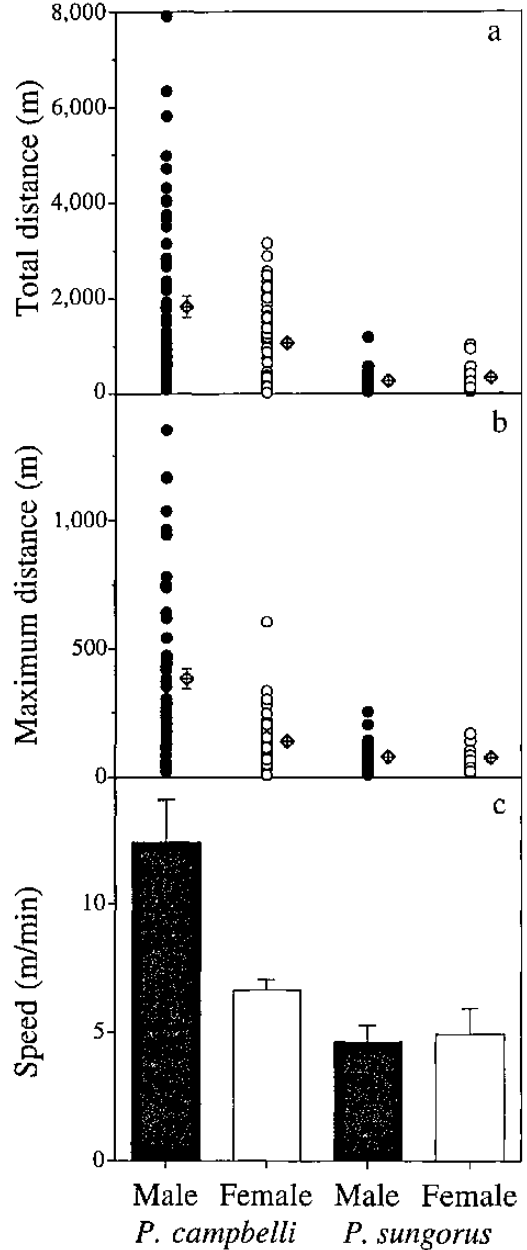


FIG. 3.—Mean (\pm SE) and underlying distributions for a) the total distance travelled by individuals of each species and sex during a night of activity, b) the maximum distance the trajectory took the animal from its sleeping burrow, and c) the mean (\pm SE) speed travelled.

was an effect of sex ($F = 11.82$; $d.f. = 1, 23$; $P < 0.005$) and an interaction between species and sex ($P < 0.005$). Male and female *P. sungorus* travelled the same speed (4.1 ± 0.8 and 4.1 ± 1.0 m/min; $t = 0.01$, $d.f. = 9$, $P = 0.99$), and that speed did not differ from *P. campbelli* females (6.1 ± 0.7 ; $t = 1.61$, $d.f. = 10$, $P = 0.14$), so that the longer time spent active above ground explained the greater total distance travelled by *P. campbelli* females relative to *P. sungorus* females. In contrast, the average speed travelled by male *P. campbelli* was twice as fast as female *P. campbelli* (11.4 ± 0.6 ; $t = 5.65$, $d.f. = 11$, $P < 0.0001$) and almost three times as fast as *P. sungorus* of either sex. Thus, male *P. campbelli* did not spend more time active than females, but they travelled much faster and covered greater total distances each night.

Annual variability.—Although the absence of females from the 1990 sample, use of two locales, and separation of Julian dates in different years of *P. sungorus* observations would have precluded meaningful interpretation of activity differences between years, there was no evidence for changes in distance travelled per night ($F = 0.33$; $d.f. = 2, 52$; $P = 0.72$), duration of above-ground activity per night ($P = 0.63$) or speed of travel ($P = 0.92$) across years in *P. sungorus*.

In contrast, there was an effect of year on the distance travelled by *P. campbelli* ($F = 17.64$; $d.f. = 2, 135$; $P < 0.0001$). However, the basis for that difference was not shared by male and female *P. campbelli* (effect of sex, $F = 7.66$; $d.f. = 1, 135$; $P < 0.01$; interaction between year and sex, $F = 6.86$; $d.f. = 1, 135$; $P < 0.005$) because males travelled significantly farther in 1989 ($2,863 \pm 386$ m) than either 1988 (926 ± 127 m) or 1990 ($1,191 \pm 164$ m) while females travelled farthest in 1990 ($1,628 \pm 172$ m), less distance in 1989 ($1,258 \pm 111$ m), and very little distance in 1988 (263 ± 41 m). Results for maximum distance from the burrow were similar except that there was no effect of year on female *P. camp-*

belli. The annual changes in distance did not affect speed of travel for male ($P = 0.90$) or female ($P = 0.91$) *P. campbelli*.

Use of running wheel.—Laboratory measures of wheel-running activity confirmed differences between species seen in the wild (Fig. 4). In both species, wheel use was linked to photoperiod. However, *P. campbelli* was more likely to begin running before lights-off than *P. sungorus* ($\chi^2 = 50.2$, $d.f. = 1$, $P < 0.0001$). Wheel running always began before lights-off in *P. campbelli* (7 females over 5 days) while wheel running began after lights-off 90% of the time in *P. sungorus* (6 females over 5 days). Peak wheel running was similar for *P. campbelli* and *P. sungorus* females ($5,412 \pm 260$ and $5,206 \pm 213$ revolutions/h). During a 24 h period, wheel revolutions by *P. campbelli* were 42% higher than wheel revolutions by *P. sungorus* ($t = 11.3$, $d.f. = 12$, $P < 0.0001$). The difference in wheel running in the laboratory between species was smaller than the 2.5 fold difference in the duration of above-ground activity each night or the almost three fold difference in the distance travelled by females measured in the field but supported those results. Thus, under controlled conditions, *P. campbelli* began running earlier, remained running longer, and had run farther by the end of a day.

DISCUSSION

Our prediction that the harsher, less productive, drier habitat of *P. campbelli* would increase the time spent in above-ground activities relative to *P. sungorus* was supported by these results. *P. campbelli* arose earlier, remained above-ground longer, spent more time away from the burrow on each expedition, and returned to the burrow later than *P. sungorus*. Within each sex, males and females were similar in each of the above measures. Thus, *P. campbelli* was active above ground for a larger percentage of a longer activity span, resulting in >2.5 fold more time exposed on the surface during a night.

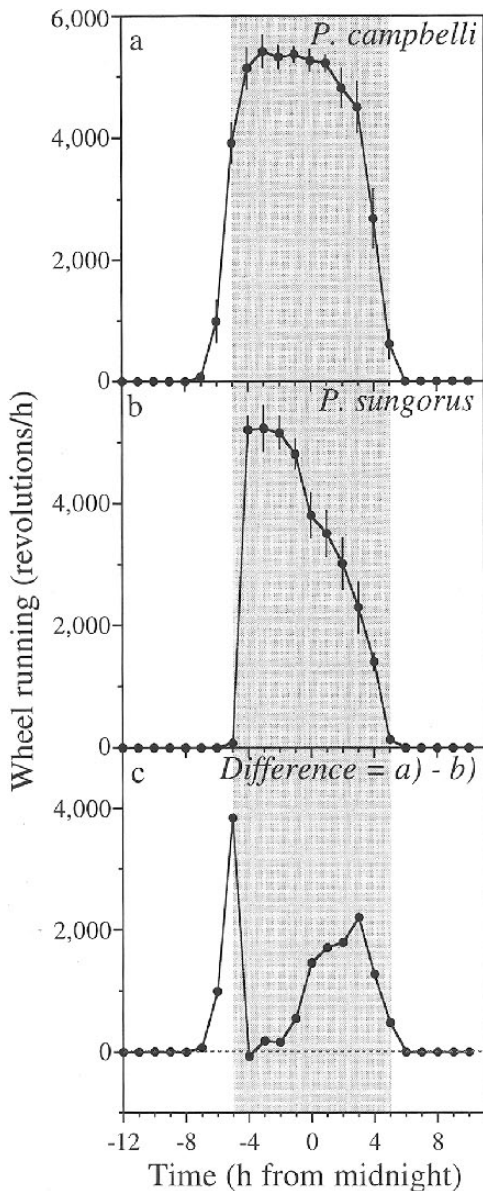


FIG. 4.—Hourly mean (\pm SE) wheel-running activity for a) 7 adult female *P. campbelli* and b) 6 adult female *P. sungorus* that were neither pregnant nor lactating. Data were collected as revolutions per minute over 5 days, then collapsed to revolutions per hour for each female before this analysis. Thus, error bars represent only the variation among females. Panel c) shows the difference between *P. campbelli* and *P. sungorus* with earlier and later activity in *P. campbelli*. Shading indicates the 10-h dark phase of the 14L:10D photoperiod.

During that longer exposure on the surface, *P. campbelli* also travelled farther each night and reached greater distances from the burrow than *P. sungorus*. Within each species, neither the number of expeditions nor their duration differed for males and females. However, male *P. campbelli* travelled farthest in a night and reached the greatest distances from the burrow. That was achieved by tripling the average speed of travel relative to female *P. campbelli* and both sexes of *P. sungorus*. Thus, although male and female *P. sungorus* appeared to use space and time in similar ways, male and female *P. campbelli* clearly differed in the use of space despite their similar time budgets.

For females of the two species, more time spent above ground equated with more distance travelled at the same speed. Therefore, earlier activity, greater time above ground each night, longer duration of each expedition, and greater distances from the burrow in the course of each expedition could each be interpreted as evidence that resource acquisition required larger home ranges and more foraging effort in *P. campbelli*.

Results for male *P. campbelli* were more complex. Although male and female *P. sungorus* were similar in all measures of activity, male *P. campbelli* differed from females in the speed of travel, reaching greater distances from the burrow each night, and travelling farther. Therefore, behaviors other than foraging and maintenance activities were probably important determinants of the activity patterns of male *P. campbelli*. The most obvious candidate for this sex difference would be increased time allocated to social interactions and searching for mates. Scent-marking ranges of female *P. campbelli* were non-overlapping and much smaller than the extensive areas visited by males (Wynne-Edwards et al., 1992). That larger area included the sleeping burrows of several females, and encroached on the scent-marking ranges of other males (Wynne-Edwards et al., 1992).

Therefore, greater distances and faster speeds of male *P. campbelli* than females probably involved increased time allocation to social interactions rather than increased effort for individual maintenance.

Several cues might have been involved in the difference in the timing of first activity between species. For example, the two species could differ in their responses to photoperiod. Photoperiod is a strong seasonal and laboratory entraining signal for activity in *P. sungorus* (Hamann, 1987). For that reason, activity data were analyzed as differences from local sunset and sunrise. However, temperature cycles also can entrain circadian wheel-running activity in *P. sungorus* (Tokura and Oishi, 1985) and entrain seasonal activity in many species (Hamann, 1987; Randall and Theissen, 1980; Rowsemitt, 1991). The large circadian temperature change typical of continental climates could provide a strong entraining rhythm, particularly because the high air temperatures typical of mid-day are lethal to dwarf hamsters (Heldmaier, 1975). Thus, although burrow temperatures are stable (Walton and Wynne-Edwards, 1998), local differences in absolute temperature at sunset, the rate of cooling after sunset, or the minimum temperature reached during a night may explain some of the variation between species.

Avoidance of aggressive social interactions (Janson, 1990), including temporal niche segregation from other syntopic species (Bruseo and Barry, 1995), also can influence patterns of activity and may have contributed to differences between species. At each field site, there were other similarly sized, nocturnally active rodents present at >50 times the population density of these hamsters (*P. campbelli* with *Cricetulus barabensis* and *P. sungorus* with *Lagurus lagurus*) and larger-bodied rodent species. Competition with those species may have influenced activity in either habitat.

Likewise, risk of predation could have influenced patterns of above-ground activity. Longer exposures above ground and

greater distances from the home burrow were expected to increase predation risk in *P. campbelli* when compared with *P. sungorus* (Brillhart and Kaufman, 1991; Daly et al., 1992). However, that increased risk could have been offset if the predator density or predation intensity were less in habitat of *P. campbelli* (Brown et al., 1988). Unfortunately, quantitative assessment of risk of predation was not possible because population densities were extremely low and continuous observer presence effectively deterred potential predators. Steppe eagles (*Aquila rapax*) were active at dusk and dawn in both habitats, a short-eared owl (*Asio flammeus*) was nocturnally active in the habitat of *P. sungorus*, and small mustelid (*Martes* and *Mustela*) carnivores had the potential to locally devastate populations of *Phodopus* but were transient. Therefore, predation was certainly a risk in each habitat, but it was not possible to estimate a comparative risk of predation for each habitat or year.

Although local environmental cues may have influenced activity at different sites, those cues were not sufficient to explain the earlier onset of above-ground activity in *P. campbelli* because endogenous differences persisted under constant conditions. In the laboratory with ad lib. food and water, tightly controlled ambient temperature, and invariant light cycles without dusk or dawn, *P. campbelli* began running on the wheel earlier (before lights off) and sustained wheel running longer than *P. sungorus*. Because the difference between species was still expressed under constant conditions, it must have a genetic basis and be the result of divergent evolution during the time since hamsters shared a common ancestor. Thus, the interaction of circadian pacemaker(s), melatonin signals, and behavior would be expected to differ at a neuroendocrine level in the two species (Bernard et al., 1997; McArthur et al., 1997).

Limited resource availability may have selected directly for paternal behavior in *P. campbelli*. In the laboratory, the positive

impact of paternal presence on care of young is not the direct result of paternal behavior directed towards young; it is primarily the indirect result of alleviation of maternal thermoregulatory and water-balance stresses (Walton and Wynne-Edwards, 1998; Wynne-Edwards, 1998). In the wild, a male *P. campbelli* spends time alone with a litter when the female is absent and provisions weaned pups in the natal burrow (Wynne-Edwards, 1995). Therefore, direct paternal care for young and paternal resource acquisition to nourish young may contribute directly to survival of young in the wild. Female activity already spans the majority of the time from dusk until dawn in *P. campbelli*, and a second adult may be needed to acquire sufficient nutrients and water from a harsh environment (Khokhlova et al., 1997) to raise a litter successfully.

As predicted by the relative harshness of the two habitats, *P. campbelli* was active longer each night and travelled farther from the burrow than *P. sungorus*. Differences between species were so extensive that, even in the peak breeding season of July and August, the ability of female *P. campbelli* to acquire resources may have been limited by the length of the night. Thus, divergent evolution in activity patterns joins evidence of divergent evolution in male and female behavioral endocrinology between *P. campbelli* and *P. sungorus* (McMillan and Wynne-Edwards, 1998; Reburn and Wynne-Edwards, 1999) and supports the hypothesis that physical features of the environment (temperature, aridity, and seasonality) ultimately were responsible for divergence of social systems between *P. campbelli* and *P. sungorus* (Wynne-Edwards, 1998).

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LITERATURE CITED

- BERNARD, D. J., S. LOSEE-OLSON, AND F. W. TUREK. 1997. Age-related changes in the photoperiodic response of Siberian hamsters. *Biology of Reproduction*, 57:172-177.
- BRILLHART, D. B., AND D. W. KAUFMAN. 1991. Influence of illumination and surface structure on space use by prairie deer mice (*Peromyscus maniculatus bairdii*). *Journal of Mammalogy*, 72:764-768.
- BROWN, J. S., B. P. KOTLER, R. J. SMITH, AND W. O. WIRTZ. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia*, 76:408-415.
- BRUSEO, J. A., AND R. E. BARRY, JR. 1995. Temporal activity of syntopic *Peromyscus* in the central Appalachians. *Journal of Mammalogy*, 76:78-82.
- DALY, M., P. R. BEHREND, M. I. WILSON, AND L. F. JACOBS. 1992. Behavioral modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour*, 44:1-10.
- FLINT, W. E. 1966. Die zwerghamster der paläarktischen fauna. A. Ziemsen Verlag, Wittenberg Lutherstadt, Germany.
- HAMANN, U. 1987. Zu aktivität und verhalten von drei taxa der zwerghamster der gattung *Phodopus* Miller, 1910. *Psychopharmacology Bulletin*, 52:65-76.
- HELDMAIER, G. 1975. Metabolic and thermoregulatory responses to heat and cold in the Djungarian hamster, *Phodopus sungorus*. *Journal of Comparative Physiology*, 102:115-122.
- HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPL (EDS.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc., and the Association of Systematic Collections, Lawrence, Kansas.
- JANSON, C. H. 1990. Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 40:922-934.
- KARTAVTSEV, Y. F., I. V. KARTAVTSEVA, AND N. N. VORONTOV. 1984a. Population genetics and genogeography of wild mammals. Part IV. Level of heterozygosity in five species of palearctic hamsters (Mammalia, Cricetini). *Genetika*, 20:954-960.
- . 1984b. Population genetics and genogeography of wild mammals. Part V. Genetic distances between representatives of different genera of palearctic hamsters (Rodentia, Cricetini). *Genetika*, 20:961-966.
- KHOKHLOVA, I. S., M. KAM, AND A. A. DEGEN. 1997.

- A small gerbil that maximizes intake of energy from low-energy food. *Journal of Mammalogy*, 78:158–162.
- KOTIJA, P., E. KROL, J. STALINSKI, AND J. WEINER. 1993. Energetic cost of reproduction in altricial and precocial rodents. *Mesogee*, 53:7–12.
- MCCARTHR, A. J., A. E. HUNT, AND M. U. GILLETTE. 1997. Melatonin action and signal transduction in the rat suprachiasmatic circadian clock: activation of protein kinase C at dusk and dawn. *Endocrinology*, 138:627–634.
- MCMILLAN, H. J., AND K. E. WYNNE-EDWARDS. 1998. Evolutionary change in the endocrinology of behavioral receptivity: divergent roles for progesterone and prolactin within the genus *Phodopus*. *Biology of Reproduction*, 59:30–38.
- MESCHERSKY, I. G. 1993. On the difference in thermoregulation in two species of hamsters of the genus *Phodopus*. *Zoologicheskii Zhurnal*, 72:146–151.
- MEYER, M. N. 1967. Peculiarities of the reproduction and development of *Phodopus sungorus* (Pallas) of different geographical populations. *Zoologicheskii Zhurnal*, 46:604–614.
- NEWKIRK, K. D., H. J. MCMILLAN, AND K. E. WYNNE-EDWARDS. 1997. Length of delay to birth of a second litter in dwarf hamsters (*Phodopus*): evidence for post-implantation embryonic diapause. *The Journal of Experimental Zoology*, 278:106–114.
- NEWKIRK, K. D., B. L. W. CHEUNG, S. J. SCRIBNER, AND K. E. WYNNE-EDWARDS. 1998. Earlier thermoregulation and consequences for pup growth in the Siberian versus Djungarian dwarf hamster (*Phodopus*). *Physiology and Behavior*, 63:435–443.
- RANDALL, J. A., AND D. D. THEISSEN. 1980. Seasonal activity and thermoregulation in *Meriones unguiculatus*: a gerbil's choice. *Behavioral Ecology and Sociobiology*, 7:267–272.
- REBURN, C. J., AND K. E. WYNNE-EDWARDS. 1999. Hormonal changes in males of a naturally biparental and a uniparental mammal. *Hormones and Behavior*, 35:163–176.
- ROWSEMITT, C. N. 1991. Activity rhythms in female montane voles (*Microtus montanus*). *Canadian Journal of Zoology*, 69:1071–1075.
- SCRIBNER, S. J., AND K. E. WYNNE-EDWARDS. 1994a. Moderate water restriction differentially constrains reproduction in two species of dwarf hamster (*Phodopus*). *Canadian Journal of Zoology*, 72:1589–1596.
- . 1994b. Disruption of body temperature and behavior rhythms during reproduction in dwarf hamsters (*Phodopus*). *Physiology and Behavior*, 55:361–369.
- . 1994c. Thermal constraints on maternal behavior during reproduction in dwarf hamsters (*Phodopus*). *Physiology and Behavior*, 55:897–903.
- STULBERG, S. E., AND K. E. WYNNE-EDWARDS. 1998. Maternal and pup contributions to different patterns of pup growth in *Phodopus* species. *Physiology and Behavior*, 64:715–722.
- THOMAS, L., AND JUANES, F. 1996. The importance of statistical power analysis: an example from *Animal Behaviour*. *Animal Behaviour*, 52:856–859.
- TOKURA, H., AND T. OISHI. 1985. Circadian locomotor activity rhythm under the influences of temperature cycle in the Djungarian hamster, *Phodopus sungorus*, entrained by 12 hour light–12 hour dark cycle. *Comparative Biochemistry and Physiology, A. Comparative Physiology*, 81:271–275.
- TROJAN, M. 1977. Water balance and renal adaptations in four palaeartic hamsters. *Naturwissenschaften*, 64:591–592.
- VORONTOV, N. N., S. I. RADZHABLI, AND K. L. LYAPUNOVA. 1967. Karyological differentiation of allopatric forms of hamsters of the superspecies *Phodopus sungorus* and heteromorphism of the sex chromosomes in the females. *Doklady Biological Sciences*, 172:55–58.
- WALTON, J. M., AND K. E. WYNNE-EDWARDS. 1998. Paternal care reduces maternal hyperthermia in Djungarian hamsters (*Phodopus campbelli*). *Physiology and Behavior*, 63:41–47.
- WEINER, J., W. GRODZINSKI, A. GORECKI, AND K. PERZANOWSKI. 1982. Standing crop and above-ground production of vegetation in arid Mongolian steppe with *Caragana*. *Polish Ecological Studies*, 8:23–39.
- WYNNE-EDWARDS, K. E. 1995. Biparental care in Djungarian but not Siberian dwarf hamsters (*Phodopus*). *Animal Behaviour*, 50:1571–1585.
- . 1998. Evolution of parental care in *Phodopus*: conflict between adaptations for survival and adaptations for rapid reproduction. *American Zoologist*, 38:238–250.
- WYNNE-EDWARDS, K. E., AND R. D. LISK. 1989. Differential effects of paternal presence on pup survival in two species of dwarf hamster (*Phodopus sungorus* and *P. campbelli*). *Physiology and Behavior*, 45:465–469.
- WYNNE-EDWARDS, K. E., A. V. SUROV, AND A. YU. TELITZINA. 1992. Field studies of chemical signaling: direct observations of dwarf hamsters (*Phodopus*) in Soviet Asia. Pp. 485–491, in *Chemical signals in vertebrates VI*. (R. L. Doty and D. Müller-Schwarze, eds.). Sixth ed. Plenum Publishing Corporation, New York.
- ZVEREVA, G. A. 1982. Seasonal aspects of steppe communities in central Tuva. *Ekologiya*, 2:18–25.

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