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# METABOLISM AND THERMOREGULATION IN TWO RACES OF DJUNGARIAN HAMSTERS: *PHODOPUS SUNGORUS SUNGORUS* AND *P. S. CAMPBELLI*

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**Abstract**—1. Two races of Djungarian hamsters (*Phodopus sungorus sungorus* and *P. s. campbelli*) differ in their responses to low ambient temperatures.

2. The lowest temperature tolerated is 6–10°C higher in *P. s. campbelli* than in *P. s. sungorus*, both in summer and in winter, but the highest ($V_{O_2}$-max) and lowest (BMR) metabolic rates are similar in both subspecies.

3. Body temperature and overall conductance in the cold appear to be more variable in *P. s. campbelli* than in nominative sp.

## INTRODUCTION

The Djungarian hamsters occupy arid steppes and semideserts of central eastern Asia in low-dense, scattered populations. A number of subspecies have been distinguished, based mostly on morphological traits (Flint, 1966; Figala *et al.*, 1973; Meyer, 1967.

The two subspecies of *Phodopus sungorus*: *P. s. sungorus* Pallas, 1770, and *P. s. campbelli* Thomas, 1905, differ in many attributes: fur coloration (both in summer and winter), body size and the degree of sexual dimorphism, behaviour, and reproductive biology (Flint, 1966; Figala *et al.*, 1973; Meyer, 1967; Wynne-Edwards and Lisk, 1984 and personal observations). It is widely accepted, that these two forms represent subspecies (Bannikov, 1954; Bobrinskij *et al.*, 1965; Flint, 1966; Gromov and Baranova, 1981), differing in geographical distribution, with *P. s. campbelli* occupying easternmost part of the area of occurrance (Veselovský and Grundová, 1965; Flint, 1966). Some authors, however, grant the taxonomic rank of separate species to these forms (Yudin *et al.*, 1979; Yudin, 1980; Wynne-Edwards, personal communication).

The nominative form, *P. s. sungorus*, has become a popular laboratory animal and its physiology has been intensively studied (e.g. Figala *et al.*, 1973; Heldmaier, 1975; Heldmaier and Steinlechner, 1981; Heldmaier *et al.*, 1982; Steinlechner *et al.*, 1983 and others). On the other hand, until now not much has been known about the physiological traits of *P. s. campbelli*. The aim of this study was to compare the basic metabolic and thermoregulatory characteristics of the two forms.

## MATERIALS AND METHODS

The animals of both races were bred and raised in the laboratory, under natural photoperiod and at a constant room temperature of 23°C (see Heldmaier and Steinlechner, 1981 for the details). The measurements of oxygen consumption and $CO_2$ production at a wide range of ambient temperatures (from −53 to +37°C) were performed using an open respirometric system (Oxytest-S and Uras 2T, Hartmann and Braun), following the procedures described previously (Heldmaier, 1975; Heldmaier and Steinlechner, 1981). Winter measurements were carried out in January and the summer series in August 1985. Body temperatures ($T_b$) were taken at the beginning and at the end of each trial by the use of a rectal thermistor probe. In each experimental series eight individuals of *P. s. campbelli* and four of *P. s. sungorus* were used for comparison. Additionally, a series of measurements of $T_b$ alone in *P. s. campbelli* was made in summer, in animals exposed for 30 min to various ambient temperatures.

The cold limit is defined here as the ambient temperature below which the animals cannot maintain a positive heat balance; this is accompanied by a drop in $T_b$ and oxygen consumption. $V_{O_2}$-max is the highest rate of oxygen consumption achieved by the animals just above the cold limit. Regressions of oxygen consumption vs temperature were computed by the method of least squares using an iterative procedure, filtering out the uppermost outliers. The statistical significance of the differences between group means and regression coefficients were tested by ANOVA and, where appropriate, the *T*-method (Sokal and Rohlf, 1981).

## RESULTS

The hamsters of both races were significantly heavier in summer than in winter, with *P. s. campbelli* always being smaller than *P. s. sungorus* (Table 1). The basal metabolic rates (BMR), defined here as the minimum oxygen consumptions at thermoneutrality, were not statistically distinguishable, either between subspecies or between seasons ($P > 0.05$; Table 1). Initial body temperatures were slightly higher in winter than in summer; no subspecies-specific differences were observed (Table 1).

In winter, the nominative subspecies could tolerate low ambient temperatures below −50 C, while *P. s. campbelli* had already entered a negative energy balance at a temperature of −44.6°C on average (Table 1). However, both species reached quite simi-

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Table 1 Basic metabolic and thermoregulatory characteristics of two subspecies of Djungarian hamsters

| Item | Winter | | Summer | | |
|---|---|---|---|---|---|
| | *P. s. campbelli* | *P. s. sungorus* | *P. s. campbelli* | *P. s. sungorus* | *F* |
| Body weight (g) | 24.0 ± 5.11 | 27.4 ± 6.6 | 31.4 ± 5.8 | 35.9 ± 5.2 | 4.68* |
| BMR (ccm $O_2$/g per hr) | 1.63 ± 0.38 | 1.55 ± 0.24 | 1.88 ± 0.57 | 2.12 ± 0.16 | 1.75 |
| $T_b$ (°C) | 35.7 ± 1.3 | 36.5 ± 1.0 | 34.3 ± 0.8 | 34.5 ± 0.9 | 9.85† |
| Cold limit | −44.6 ± 2.0 | −51.3 ± 3.2 | −31.8 ± 4.6 | −42.4 ± 4.1 | 12.61† |
| $V_{O_2}$-max (ccm $O_2$/g per hr) | 14.56 ± 1.96 | 14.33 ± 2.53 | 12.93 ± 1.68 | 13.82 ± 1.17 | 1.14 |
| Conductance (mean of slopes) (ccm $O_2$/g per hr per degree) | 0.214 ± 0.035 | 0.174 ± 0.021 | 0.157 ± 0.018 | 0.135 ± 0.021 | 10.40† |
| Conductance (mean of slopes) (ccm $O_2$/animal per hr per degree) | 5.04 ± 0.94 | 4.67 ± 0.46 | 4.92 ± 0.95 | 4.87 ± 1.19 | 0.14 |
| Conductance (pooled regressions) (ccm $O_2$/g per hr per degree) | 0.191 $S_b$ = 0.005 | 0.179 $S_b$ = 0.007 | 0.159 $S_b$ = 0.003 | 0.132 $S_b$ = 0.005 | 31.09† |

(Averages ± S.D.: Statistical significations of differences: * − $P < 0.05$; − $P < 0.01$).

lar maximum $V_{O_2}$-max, averaging about 14.5 ccm $O_2$/g per hr. (Table 1). This corresponds to the rate of heat production of about 80 mW/g (Table 1).

In summer, the maximum rate of heat production of both hamster races were slightly lower than in winter (about 13.5 ccm $O_2$/g per hr on average, Table 1), but all the $V_{O_2}$-max values were not significantly different (Table 1). The cold limit is about 10°C higher in summer than in winter for both subspecies studied (Table 1).

Both races of hamsters also demonstrated different behavioural reactions when exposed to cold. The individuals of the nominative subspecies remained quiet during the whole trial, assuming a curled, heat-saving posture at lower ambient temperatures, with only short bursts of activity. In contrast, all the individuals of *P. s. campbelli* exercised vigorously and continuously attempted to get out of the chamber, except when exposed to extreme cold or warm temperatures. The peak metabolic rate during this activity reached the level of $V_{O_2}$-max during cold exposure (Fig. 1).

When taking into account only the minimum resting values of oxygen consumption at each ambient temperature, the two hamster races also differ with regard to the slope of their metabolic response. This was particularly striking in summer experiments. In *P. s. sungorus*, the metabolic rate increases linearly with falling ambient temperature, following the most typical pattern for homeothermic animals (Fig. 2). In contrast, in *P. s. campbelli*, the metabolic rate increases rapidly, reaching a near maximum level of $V_{O_2}$ at about −10°C in some individuals. At temperatures below −10°C there was either slight increase only, or

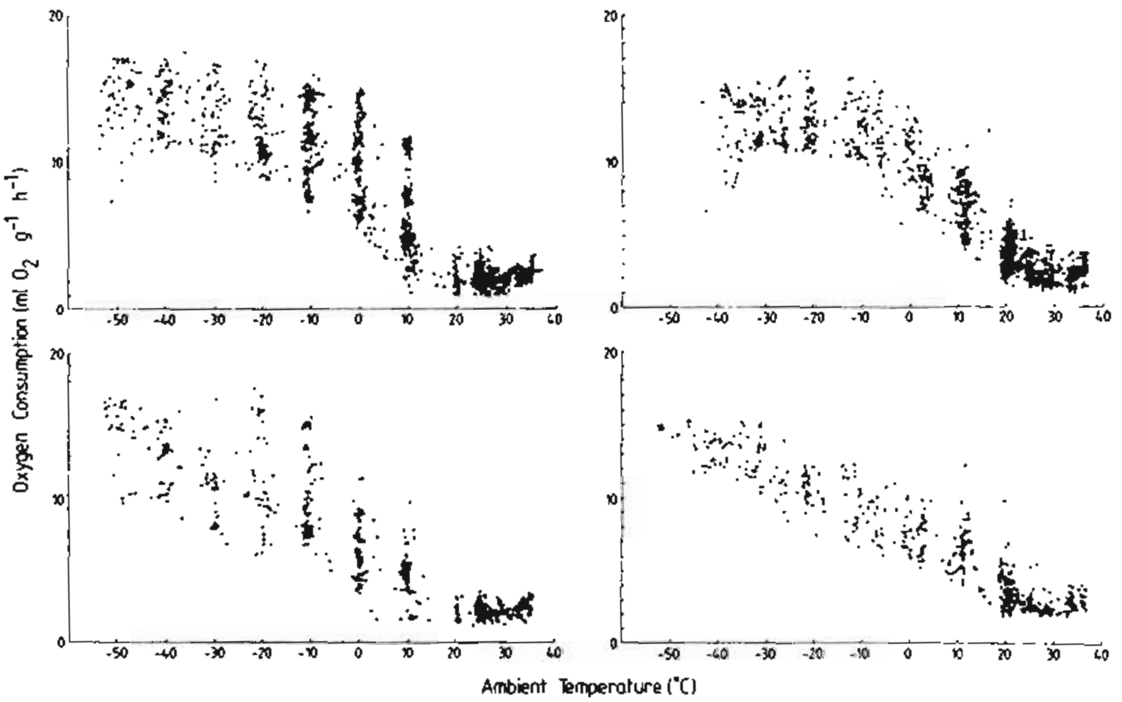


Fig. 1. All records of metabolic rates of Djungarian hamsters at various ambient temperatures. Top: *P. s. campbelli*: C, D (left = winter; right = summer). Bottom: *P. s. sungorus* (left = winter; right = summer).

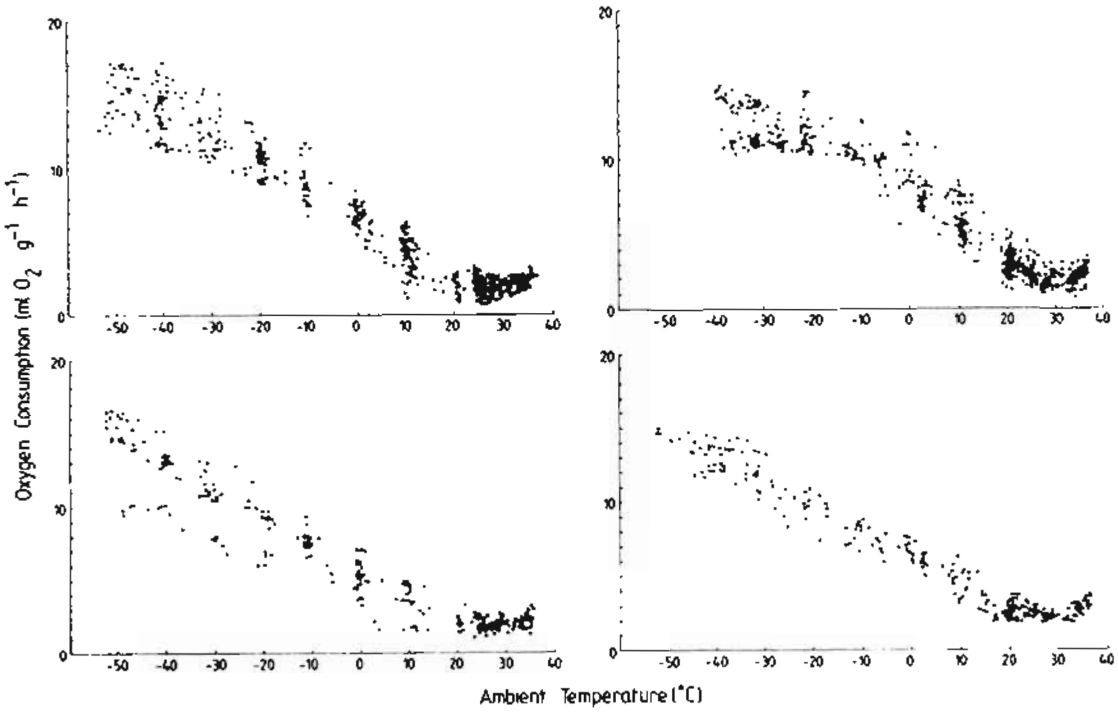


Fig. 2. Resting metabolic rates of Djungarian hamsters at various ambient temperatures. Top: *P. s. campbelli*; C, D (left = winter; right = summer). Bottom: *P. s. sungorus* (left = winter; right = summer).

$V_{O_2}$ remained constant (Fig. 2). At the end of each trial the body temperature was only slightly lower than normal in *P. s. sungorus* (31.8 ± 0.92°C), while in *P. s. campbelli* it dropped dramatically (23.7 ± 1.75°C), even though the experiment was always interrupted immediately after the drop in oxygen consumption was noticed. In *P. s. campbelli* which were exposed to various ambient temperatures for about 30 min each time, a distinct drop in body temperature was observed at about −10°C (Fig. 3). A similar, though less obvious tendency to a non-linear metabolic response to low ambient temperature could also be observed in the winter series (Fig. 2).

Due to the lack of the continuous measurement of body temperature during metabolic measurements, the overall conductance could only be estimated as a slope coefficient of linear regression forced through the resting metabolism data vs temperature. The group averages estimated as arithmetic means of individual slope coefficients do not differ numerically and in the pattern of variation from the slope coefficients of pooled regressions (Table 1). In *P. s. campbelli* the overall conductance was always greater than in the nominative form (Table 1), as well as the weight-specific conductances in winter were always greater than in summer (differences highly significant, Table 1). However, when calculated per individual, the overall conductances are virtually identical in both seasons (Table 1).

At high ambient temperatures the metabolic rate tends to increase at about 32°C in all experimental groups (Fig. 2). After exposure to high ambient temperatures, the $T_b$ of both subspecies increased uniformly by approx. 3–4°C in summer and by approx. 2°C in winter.

## DISCUSSION

Some interesting ecophysiological differences between the two forms can be demonstrated. The most obvious one concerns the metabolic response to cold. Both subspecies of hamsters reached similar maximum rates of oxygen consumption, but in *P. s. campbelli* this level was achieved at ambient temperatures up to 10°C higher than in *P. s. sungorus* (Table 1), indicating a less well developed cold tolerance in *P. s. campbelli*. Taking into account the similar body temperatures and basal metabolic rates of both races, only different heat transfer coefficients could be responsible for this effect. Indeed, the approximate estimates of overall conductance are higher for *P. s. campbelli* than for *P. s. sungorus* in

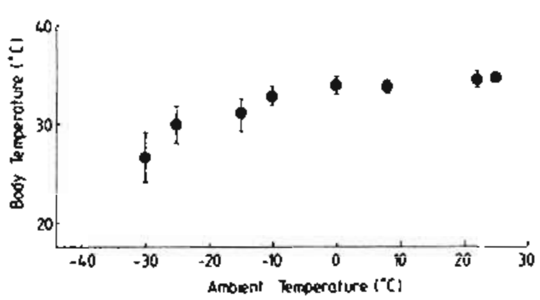


Fig. 3. Rectal temperatures of *P. s. campbelli* after exposition to various ambient temperatures (mean ± 2 SE).

both seasons. Paradoxically, the weight-specific values of conductance tended to be higher in winter than in summer. This, however, can be fully explained by the great difference between summer and winter body weights, the effect has been thoroughly discussed previously (Heldmaier and Steinlechner, 1981).

On the other hand, the pattern of thermogenic response to cold of *P. s. campbelli* seems to deviate from the most commonly accepted linear model (Fig. 2). An exaggerated increase in oxygen consumption can be observed in moderately cold temperatures, while a near maximum level of metabolism is maintained over an extended range of low ambient temperatures. This effect could be explained by substantial changes in conductance below thermoneutrality. Such a phenomenon has already been reported for other rodents (e.g. *Dipodomys deserti*, McNab, 1980); also, Heldmaier (1975) demonstrated a similar, though less dramatic pattern in *P. s. sungorus* in the spring. The procedure used to fit a single linear equation ignores the apparent non-linearity in the data, and thus the slope coefficients approximate to the minimum values of conductance. The striking difference in behavioural reaction suggests that the thermoregulatory strategy of *P. s. campbelli* in the cold is dominated by a behavioural response to escape to a refuge, despite the high energetic cost of such an activity, while *P. s. sungorus* relies upon its body insulation and heat-generating capabilities.

In general, these findings seem to support the view that the two hamsters deserve the taxonomic status of separate species. The higher conductance and higher critical temperatures of *P. s. campbelli* suggest that this form is adapted to less harsh environmental conditions than the nominative one. The geographical distribution of *P. s. campbelli* is poorly known (Yudin *et al.*, 1979). According to several authors, the specimens of this form were collected in Mongolia, Tuva, China and southern Trans-Baikal region (Bannikov, 1954; Bobrinskij *et al.*, 1965; Gromov and Baranova, 1981). On the other hand, the individuals studied in east-central Mongolia (Weiner and Górecki, 1981) belonged to the nominative subspecies. It is possible, that the area of distribution of *P. s. campbelli* extends to that region of eastern Asia, where the continental climate is tempered by the influence of the Pacific Ocean.

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