

Evolution of parental care in *Phodopus*: Conflict between adaptations for survival and adaptations for rapid reproduction¹

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SYNOPSIS. Two species of dwarf hamsters are used to develop a model of the proximate and ultimate selective forces leading to the evolution of parental care strategies. One species, *Phodopus campbelli*, has been studied extensively as a socially monogamous, biparental species; the other, *P. sungorus*, rears its young without male assistance.

The cold, arid habitat occupied by both species has selected for shape, insulation, and physiology that provide tolerance of extremely cold ambient temperatures and enhance survival when water availability is limited. At the same time, the small body size and highly seasonal environment have selected for rapid maturation and the most compressed reproductive cycle known in a mammal. Rapid reproduction increases water demands for milk production and further stresses water balance because maternal hyperthermia demands increased evaporative heat loss. Thus, in *Phodopus* habitat, rapid reproduction requires heat tolerance and water availability, which conflict with adaptations for survival.

In the habitat of *P. sungorus*, predictable rains allow a breeding season and females rear litters alone. In *P. campbelli*, water availability is insufficient for solitary reproduction. Instead, male presence alleviates thermoregulatory, and thus water balance, stresses on the female. The result is improved pup survival and growth. Therefore, an 'ultimate' reason for biparental care in *P. campbelli* is its harsh environment, and a 'proximate' reason is a need to reduce maternal water demand. Results confirm that independent physiological constraints, in addition to constraints on energy or time investment, can be essential selective pressures in the evolution of mammalian social organization and behavior.

INTRODUCTION

Charles Darwin, in both *The Origin of Species* (1859) and *The Descent of Man* (1871), explicitly recognized that sexual selection could favour character traits that decreased survival if their advantage in gaining mates and offspring compensated for that increased risk. Outside of sexual selection, potential conflicts between survival and reproduction are also easily recognized in trade-offs between investment in current reproduction/offspring and improved survival leading to future reproductive success. However, those trade-offs are assumed to occur in a currency, such as energy or time, which can be allocated by an individual.

Although clearly predicted on theoretical grounds, few practical examples illustrate direct conflict between adaptations for survival and adaptations for reproduction in terms of other physiological limitations.

Research reviewed in the following sections combines physiological, behavioral, and ecological approaches to develop such a model to explain the evolution of parental care strategies in two closely related dwarf hamsters in the genus *Phodopus*. One of the species, *P. campbelli*, has been studied extensively as a socially monogamous, biparental species, while the other, *P. sungorus*, rears its young without male assistance (e.g., Wynne-Edwards, 1995; Wynne-Edwards and Lisk, 1989). Results are used to argue that 1) relative to the Siberian hamster, *P. sungorus*, the colder, drier, more seasonal habitat occupied by the Djungarian hamster, *P. campbelli*, creates a more direct conflict between adaptations for survival (cold tolerance and water conservation),

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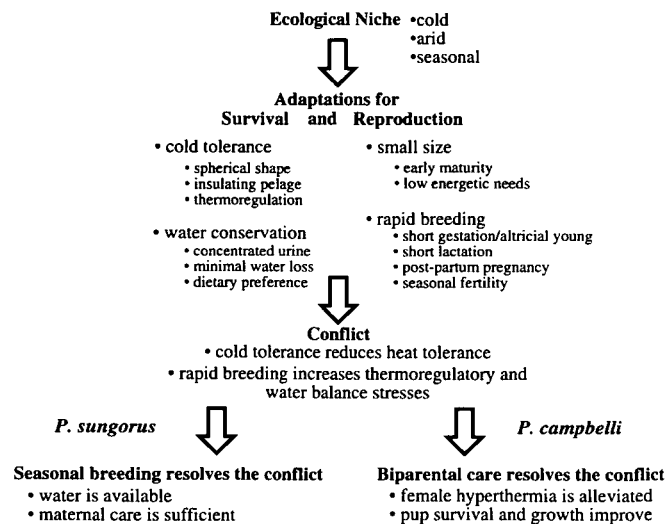


FIG. 1. Outline of the argument that a harsh ecological niche can create a direct conflict between adaptations for survival and adaptations for reproduction. In *P. sungorus*, seasonal rains resolve the conflict and allow females to rear litters without male assistance. In *P. campbelli*, biparental care relieves maternal hyperthermia and facilitates maternal care.

and adaptations for reproduction (small body size and rapid breeding); and 2) the conflict is resolved through social monogamy/biparental care which alleviates thermoregulatory and water balance stresses on the female, and improves pup survival and growth. Thus, the argument invokes direct conflict between adaptations for survival and adaptations for reproduction as an ultimate explanation for the evolution of biparental care (*sensu* Trivers, 1972; Clutton-Brock, 1991) in *P. campbelli*, but not *P. sungorus*. The key elements of this argument are outlined in Figure 1, and elaborated in detail in the sections that follow.

ADAPTATIONS FOR SURVIVAL

Phodopus sungorus and *P. campbelli* belong to the assemblage of five genera of dwarf hamsters native to the Palearctic (Flint, 1966). They share a recent common ancestry and are able to produce viable hybrid offspring in the laboratory (Iudin *et al.*, 1979). Wild caught *P. campbelli* and *P. sungorus* are the same size at adulthood (20–35 g), look very similar, and are clearly physically adapted for heat conservation at cold ambient temperatures. Their limbs are short, their tails rudimentary, and their surface area is minimal relative to body vol-

ume. In addition, and giving the genus its name, their insulating pelage extends to the soles of the feet and reduces heat loss through conduction to the substrate. Those adaptations improve survival in the cold, semi-arid steppes of Central Asia; metabolic heat production by *Phodopus* can maintain body temperature over several hours of exposure to temperatures as low as -40°C (Weiner and Heldmaier, 1987).

These adaptations to survival in a cold, dry environment render *Phodopus* vulnerable to elevated ambient temperatures (Heldmaier, 1975; Weiner and Heldmaier, 1987; Gordon, 1993). Superb insulation precludes exposed, well-vascularized, heat exchange surfaces. Thus, none of the long tail, large ears, and naked feet used to dissipate heat by desert rodents are available to *Phodopus*. In addition, the scarcity of water limits the utility of saliva spreading, and increased evaporative heat loss, as avenues for excess heat dissipation (Weiner and Heldmaier, 1987; Meschersky, 1993).

However, the two species are not sympatric, and the habitat of *P. campbelli* is drier, colder and more seasonal than that of *P. sungorus*. In typical *P. campbelli* habitat near Erzin (Tuva Autonomous Region, Russia 50.16°N , 95.14°E) mean monthly tem-

peratures never exceed 15°C, mean temperatures in January are well below -30°C, and more than half of the 210 mm of annual rainfall occurs in July and August (1980–88 weather records). No other habitat on any continent is an equivalent middle latitude desert experiencing the same combination of extreme seasonal variation in temperature and low, seasonal, rainfall. Although still as harsh as the badlands of Southern Alberta, the habitat of *P. sungorus* near Abakan (Hakasskaya region, Russia 53.43°N, 91.26°E) does not fall below a -20°C average in any month and receives 50% more rainfall (316 mm annually) spread over a five month season (1983–87 weather records).

The differences in habitat aridity translate into predictable differences in water conserving ability. While both species can survive on dietary water sources without drinking (Schierwater and Klingel, 1985; Trojan, 1977), kidney fresh weight is 15% heavier in *P. campbelli*, and less water is excreted as urine because urine osmolarity with *ad libitum* drinking water is 25% higher (Scribner, 1996). Drinking water in the form of dew is frequently available to *P. sungorus*, but rarely available to *P. campbelli* (unpublished data). Seeds are a major component of the diet and yield relatively little water upon oxidation, but both species supplement their diet with insects whenever possible, and *P. campbelli* digs for water-laden beetle larvae during the summer months (unpublished data).

Therefore, for both species, the harsh habitat has selected for adaptations that allow a small-bodied mammal to withstand extreme cold and survive with little water. However, water availability and cold stresses have been more severe in the evolution of adaptations for survival in *P. campbelli*.

ADAPTATIONS FOR RAPID REPRODUCTION

The extreme seasonality of the habitat, and the small body size of *Phodopus* adults, have also selected for the most compressed reproductive cycle known for any mammal (Newkirk *et al.*, 1997). Gestation is only 18 days in length and is followed by a postpartum mating that can result in the birth of a second litter without delayed implan-

tation. As a result, a first litter can gain independence, a second litter can be born, and a third litter can be conceived within 36 days of a first mating (Newkirk *et al.*, 1997; Parkening and Collins, 1991). In addition, as photoperiod is a reliable predictor of seasonal changes in climate in *Phodopus* habitat, photoperiod strongly influences reproduction and sexual maturation in *Phodopus* (Stetson *et al.*, 1989; Shaw and Goldman, 1995).

This extremely rapid reproduction exacerbates the thermal and water balance problems imposed by the harsh habitat. To reproduce successfully, females must provide not only food and water (in the form of milk) but also the body contact (heat) needed for growth of altricial pups (Jans and Woodside, 1990). Lactation increases the water needs of a female (Baverstock and Watts, 1975; Oswald *et al.*, 1993), increases her evaporative water loss (Knecht *et al.*, 1980) and elevates her average daily energy requirements (Thompson, 1992) which, in turn, contributes to maternal hyperthermia (Leon *et al.*, 1978; Knecht *et al.*, 1980; Kittrell and Satinoff, 1988). At the same time, dissipation of excess body heat is hindered by pup contact that occludes and insulates the female's ventral surface (Jans and Leon, 1983). These increases in maternal body temperature directly limit mother-pup contact (Woodside *et al.*, 1980; Scribner and Wynne-Edwards, 1994b) and reduce circadian rhythmicity in body temperature by elevating body temperatures during the resting phase of the day-night cycle (Scribner and Wynne-Edwards, 1994c; Walton and Wynne-Edwards, 1998).

In response to the increased thermal stresses and water requirements of reproduction, *Phodopus* might have been expected to evolve prolonged maternal investment. Instead, litters are born after just 18 days of gestation and rapidly change from naked, poikilothermic neonates with unfavourable (high) surface area to volume ratios, into independently thermoregulating, well-insulated versions of the adult (Newkirk *et al.*, 1995; Newkirk *et al.*, 1998). Pup thermogenesis begins within a week after birth and pup thermoregulation begins as a threshold weight for BAT (brown adipose

tissue) thermogenesis is achieved, usually before the end of the second week (Newkirk *et al.*, 1995).

At various times of year, the majority of habitats colonized by small mammals have similar conflicts between adaptations for survival and adaptations for rapid reproduction. Species typically respond to the conflict by restricting the breeding season to the most favorable time of year. Although its habitat is harsher than most, *P. sungorus* appear to respond in the same way by restricting breeding to the May to September season when rainfall is reliable. However, the habitat of *P. campbelli* is sufficiently colder, drier, and more seasonal to have resulted in a conflict between adaptations for survival and adaptations for rapid reproduction, which is not resolved even during the most favourable breeding season of the year. This habitat difference between *P. sungorus* and *P. campbelli* has been an ultimate selective force that has influenced all aspects of their biology, including maternal strategies, maternal physiology and social organization.

MATERNAL INVESTMENT AND PUP GROWTH

Although non-reproductive female *P. sungorus* and *P. campbelli* have the same initial weight and consume the same quantity of chow from an *ad libitum* supply, maternal reserves are used differently during reproduction in each species. *Phodopus sungorus* increase fat reserves during gestation (Koteja *et al.*, 1993) and finish lactation at their pre-reproductive weight with about 50% of fat reserves remaining, whereas *P. campbelli* lose weight over gestation and lactation (for a total loss of over 20% of body weight; Scribner, 1996) and finish lactation with minimal fat reserves (unpublished data).

Strategies for heat transfer to pups also differ in the two species. Although the ventral temperature maintained by two non-breeding adults in a nest box is the same in each species, and average maternal core temperatures are similar throughout reproduction (although see below for species differences in temperature distributions during a day), nest temperatures during body con-

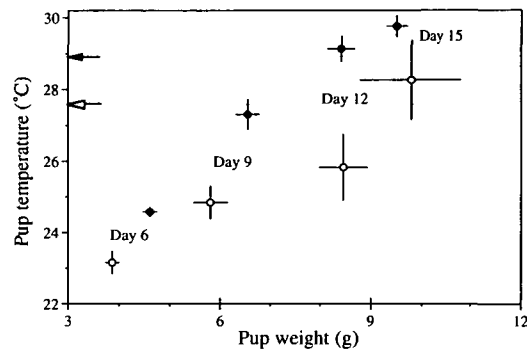


FIG. 2. Illustration of the complex relationship between pup age, pup weight, initial huddle temperature, and the temperature of isolated pups 15 min after separation from the parents. Data are presented for *P. sungorus* (filled symbols) and *P. campbelli* (open symbols) on days 6, 9, 12 and 15 after birth. The standard error bar in the y-dimension illustrates the variance in final temperature of pups at that age while the error bar in the x-dimension illustrates the variance in weight for the same pups at that age. Pups began the cooling trial at the average huddle temperature indicated by the filled (*P. sungorus*) and open (*P. campbelli*) arrows against the y-axis. Reproduced from Newkirk *et al.* (1998).

tact with pups are a full degree warmer in *P. sungorus* than *P. campbelli* (Fig. 2).

Growth of pups reared by each species also reflect different strategies for maternal investment (Fig. 2). *Phodopus sungorus* pups grow faster than *P. campbelli* pups early in lactation and attain both independent thermoregulation and nutritional independence earlier (Scribner and Wynne-Edwards, 1994b; Newkirk *et al.*, 1995, 1998). Both the higher nest temperature and the greater maternal fat reserves in *P. sungorus* probably contribute to the faster early pup growth. However, early independence decreases the subsequent growth rate of *P. sungorus* pups relative to *P. campbelli* pups, so that the day 18 weight of the largest pup in each species is similar (Newkirk *et al.*, 1998). Day 18 weights correspond to the earliest date on which a second litter conceived during a postpartum estrus could be born (Newkirk *et al.*, 1997) and correlate well with weights of dispersing pups caught in the wild (Wynne-Edwards, 1987).

The species also differ in within-litter patterns of pup growth, as *P. campbelli* females rear litters with larger within-litter

variance in pup weight than *P. sungorus* (Fig. 2). In *P. campbelli* pup mortality occurs throughout lactation and litters typically contain at least one pup weighing more than 11.5 g on day 18 (a viable dispersal weight; Wynne-Edwards, 1987), although other pups in the same litter may weigh less than half that amount at the same age. In contrast, *P. sungorus* pups rarely die during lactation and tend to be similar in weight at weaning (Newkirk *et al.*, 1998). As a result, when conditions are good *P. campbelli* typically increase the proportion of pups in their litter which are going to reach a heavy dispersal weight, whereas *P. sungorus* typically increase the litter size they are rearing.

These patterns of maternal investment are finely tuned on a day-to-day basis in *Phodopus*. In addition to the ability to delay implantation of a second litter conceived during a post-partum estrus (to extend the interval of maternal investment in a primary litter), there is strong evidence that *Phodopus* females can adjust the development rate (date of birth) of a late-term, *in utero*, litter in response to the growth performance of the nursing litter (Newkirk *et al.*, 1997). Thus, females can commit to an immediate second reproductive effort without risking loss of that investment because the energetic demands of the nursing litter continue for longer than 18 days.

These species differences in maternal strategies and pup growth are most easily detected when ambient temperatures are over 21°C and *P. campbelli* have poorer reproductive success than *P. sungorus* (Wynne-Edwards and Lisk, 1989; Walton and Wynne-Edwards, 1998). Such ambient temperatures would not occur in the underground burrows of either species ($18 \pm 1^\circ\text{C}$ during the breeding season), but increase maternal thermoregulatory stresses in the same way that water scarcity would increase thermoregulatory stresses in the natural environment. When these thermoregulatory stresses are removed, pup growth and weaning weight are the same in both species. However, even reducing ambient temperature to 18°C and providing food and water *ad libitum* do not completely elimi-

nate the species differences in reproductive success.

MALE PRESENCE AND REPRODUCTIVE SUCCESS

The continued presence of the male parent, which has a neutral (or slightly negative) impact on pup survival and growth in *P. sungorus*, is essential for high pup survival and rapid pup growth in *P. campbelli* (Wynne-Edwards, 1987; Wynne-Edwards and Lisk, 1989; Scribner and Wynne-Edwards, 1994a; Walton and Wynne-Edwards, 1998; Newkirk *et al.*, 1997, 1998). An essential role in offspring survival is accepted as the primary selective force in the evolution of monogamy and paternal care (Clutton-Brock, 1991).

Low population densities can also be a selective force in the evolution of monogamy because long distances between potential mates decrease opportunities for additional matings (Kleiman, 1981). Population densities in *P. campbelli* are extremely low for a small mammal (Flint, 1966; Wynne-Edwards *et al.*, 1992) and lower than population densities for *P. sungorus* (unpublished data). However, the presence of multiple males outside the burrow of a receptive *P. campbelli* female (Wynne-Edwards, 1995), and the long distances (several kilometers) travelled by individual *P. campbelli* males in a single night (Wynne-Edwards *et al.*, 1992), both suggest that the low population density does not effectively limit contact with conspecifics. In addition, paternal care that evolved because access to other potential mates was severely limited might be expected to enhance offspring survival or growth rate, but would not predict failure of reproductive effort when females attempt to rear a litter without the male present.

Phodopus sungorus and *P. campbelli* are also behaviorally distinct in several ways. *Phodopus sungorus* establish stable intra-sexual dominance hierarchies (Wynne-Edwards and Lisk, 1987, 1988), and females can both dominate males and successfully mate with multiple males (Wynne-Edwards and Lisk, 1988). *Phodopus campbelli* differ from *P. sungorus* in each of these measures. They fail to establish stable intra-sexual dominance hierarchies, so that intra-sexual

aggression can quickly result in death (Wynne-Edwards and Lisk, 1984, 1987). Males are dominant over females (Wynne-Edwards and Lisk, 1988), and females fail to successfully implant pregnancies following matings with multiple males (Wynne-Edwards and Lisk, 1984), even in the wild (unpublished data). Since *P. campbelli* pregnancies also fail when prior familiarity with the male is low, or when the male deserts soon after mating (Wynne-Edwards *et al.*, 1987; unless his odour persists; Johnson, 1992), the pregnancy blocking response in *P. campbelli* functions as an adaptive response to terminate investment in a litter that has a low probability of receiving paternal care. Thus, differences in social structure, and pregnancy failure in the absence of paternal care, each confirm observed differences in social structure in the wild and support the conclusion that biparental care is common in *P. campbelli* but not in *P. sungorus*.

This paternal care could increase reproductive success in *P. campbelli* through one or several proximate mechanisms. For example, males could improve pup growth and survival in *P. campbelli* by acting as a heat source for the pups when the female is away from the nest. There is evidence in support of that behavioral hypothesis (Wynne-Edwards, 1995). When the male parent is present, pups are rarely left alone for more than three minutes (significant cooling of the huddle; Newkirk *et al.*, 1995), so that the warm temperature needed for pup growth (Hill, 1972) is stably maintained. In contrast, solitary females often leave the nest for the extended periods of time (Wynne-Edwards, 1995; Walton and Wynne-Edwards, 1998) needed to dissipate the excess heat burden of pup contact (Scribner and Wynne-Edwards, 1994b).

However, paternal nest attendance does not have the predicted effect of allowing the female to increase the duration of her absences from the nest (and thus behaviorally reduce her maternal hyperthermia). Unlike *P. sungorus* females, paired *P. campbelli* females spend more, not less, time in contact with their young litter (Wynne-Edwards, 1995).

In addition, although it is clear that *P.*

campbelli females cannot rear a litter without the male present, whereas *P. sungorus* females can, an explanation is also needed for why the species differ. In other words, a description of paternal nest attendance in *P. campbelli* is not sufficient to explain the evolution of biparental care unless it can also explain "why" similar paternal behavior is not seen in *P. sungorus*. In *Phodopus*, the "why" is intimately linked to temperature and water regulation in the two species.

MATERNAL HYPERTHERMIA IN *PHODOPUS*

As has been described in detail for the laboratory rat (Jans and Leon, 1983; Kittrell and Satinoff, 1988), both *P. sungorus* and *P. campbelli* experience a disruption in body temperature during lactation (Fig. 3). It is similar in magnitude in each species (about 1.0°C) and restricted primarily to an increase in daylight body temperatures. Thus, it has the effect of almost eliminating the endogenous circadian rhythmicity in body temperature typical of non-reproductive females of each species (Scribner and Wynne-Edwards, 1994c). However, although the disruption in average body temperatures is similar in each species, the underlying distributions giving rise to the average temperature are not the same (Scribner and Wynne-Edwards, 1994b).

The distribution of core body temperatures for solitary females, as measured by telemetry once per minute, 24 hr per day, during late gestation (G16 = two days before parturition) and early (L3), mid (L9), and late (L15) lactation (birth = L0), are shown in Figure 4. The two species are similar in late gestation and after pups achieve independent thermoregulation in late lactation. However, during early and mid lactation, solitary *P. campbelli* spend over 25% of their daylight time at temperatures more than 1.0°C warmer than their mean temperature when not lactating, as compared to only 10% of time for solitary *P. sungorus*. Thus, solitary *P. sungorus* not only maintain higher nest temperatures for pup growth, they also regulate maternal body temperature within narrower limits that minimize time at the hottest core temperatures. When the same measures were re-

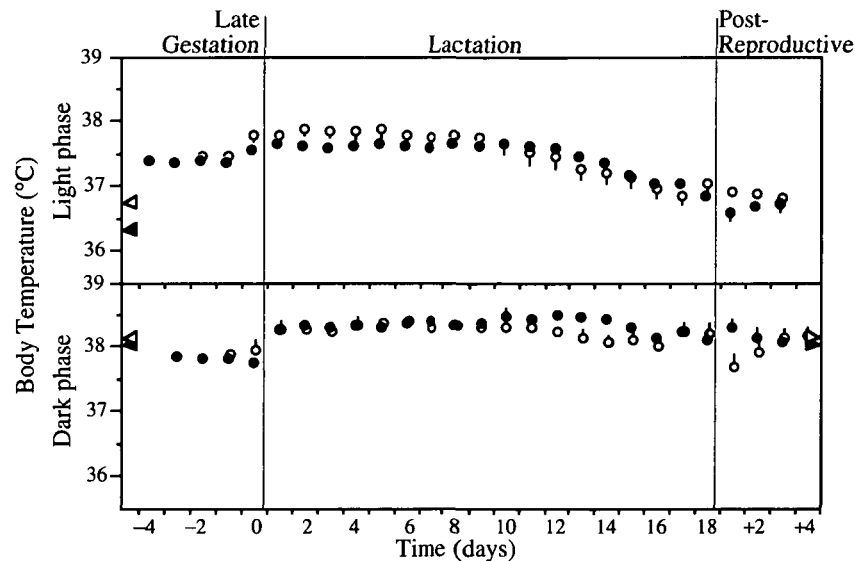


FIG. 3. Mean (\pm SE) core body temperature during the 14 hr light and 10 hr dark phases for solitary female *P. sungorus* (filled circles) and *P. campbelli* (open circles) throughout reproduction. Error bars reflect the number of females per species. Arrows on the y-axis indicate the comparable values for non-reproductive adults. Pups were removed on day 18 after birth. Composite redrawn from Scribner and Wynne-Edwards (1994c).

corded from solitary *P. campbelli* females at 23°C (Walton and Wynne-Edwards, 1998), temperature distributions had the same shape, and the same proportion of time spent at the highest temperatures (Fig. 5).

Even when ambient temperature is decreased to 18°C, solitary *P. campbelli* females are experiencing prolonged exposure to the hottest maternal temperatures. Therefore, although pups survive better at the reduced ambient temperature, the thermal burden tolerated by the female is the same at either ambient temperature. Such similarity between the body temperature distributions at the two ambient temperatures suggests that solitary *P. campbelli* females are adjusting their behavior to achieve that distribution.

As the 5°C reduction in ambient temperature increases the differential between maternal core temperature and ambient temperature, passive loss of excess maternal heat to the atmosphere (along the heat gradient) is faster at the lower ambient temperature. Therefore, shorter maternal nest absences at the lower ambient temperature (Walton and Wynne-Edwards, 1998) are

probably the result of faster heat loss to the environment that allows a female to adjust her (hyperthermic) core body temperature without prolonged absences from the nest. In that light, solitary *P. campbelli* females attempting to breed at 18°C, while successful at rearing pups, are clearly experiencing a major, and probably a physiologically costly, thermoregulatory stress. At the higher ambient temperature, maintenance of a tolerable maternal core body temperature distribution constrains the ability of a solitary *P. campbelli* female to contact her pups (and may limit water available for milk), resulting in poor reproductive success.

MALE PRESENCE ALLEVIATES MATERNAL HYPERTHERMIA IN *P. CAMPBELLII*

Male presence dramatically shifts the core body temperature distributions for *P. campbelli* females (Fig. 5). When *P. campbelli* females are paired with males, their body temperature distribution is narrower, involves only rare exposure to the hottest temperatures (3–6% of a day), and is similar in all respects to the temperature distributions of solitary *P. sungorus* females (Walton and Wynne-Edwards, 1998). This

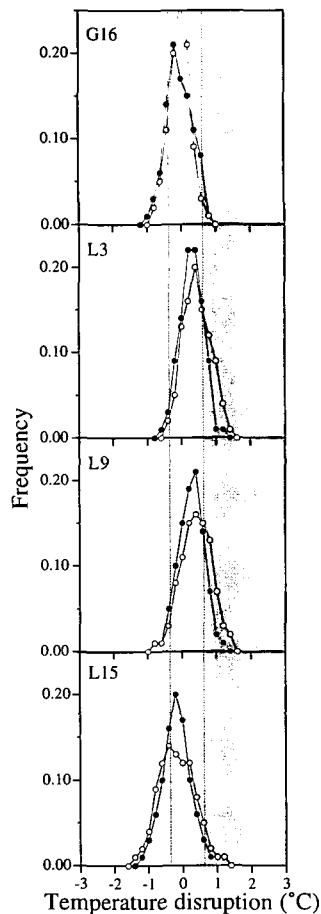


FIG. 4. Frequency distributions of maternal body temperatures for solitary *P. sungorus* (filled circles) and *P. campbelli* (open circles) during the 14 hr light phase of late gestation (G16), early lactation (L3), mid lactation (L9) and late lactation (L15). Ambient temperature was maintained at $18 \pm 1^\circ\text{C}$. Birth occurred on G18 = L0. Pups were removed on L18. Data are recalculated from Scribner and Wynne-Edwards (1994c) with temperatures expressed as deviations from the average temperature of that female when not reproductive (post-separation day 2). The vertical line through a temperature disruption of -0.4°C indicates the adjusted mean daily temperature for those females if running wheels had not been used at night (Scribner, 1996; Saunders, 1994). The area underneath the distribution curve beyond $+0.6^\circ\text{C}$ (shaded) represents the proportion of daylight time during which female core temperatures were more than 1.0°C higher than the daily average.

response to pairing (narrowed distribution, reduced average maternal temperature and rare high maternal temperatures) also occurs at an ambient temperature of 18°C

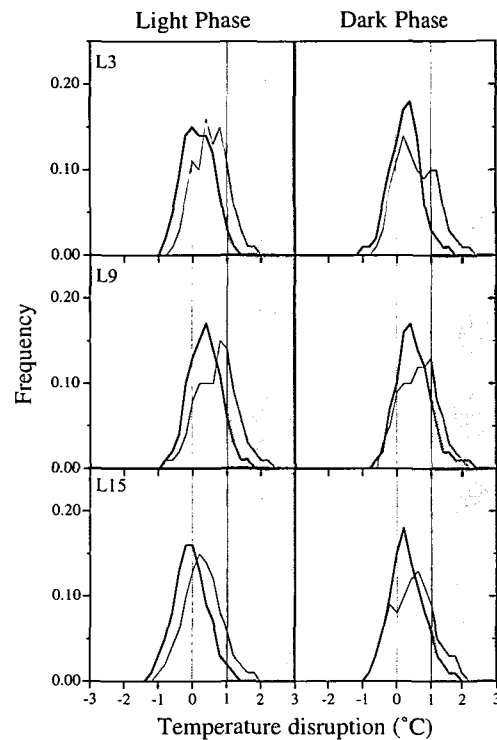


FIG. 5. Frequency distributions of maternal body temperatures for solitary (thin line) and paired (thick line) *P. campbelli* during the 14 hr light and 10 hr dark phases of early lactation (L3), mid lactation (L9) and late lactation (L15). Ambient temperature was maintained at $23 \pm 1^\circ\text{C}$. Data are redrawn from Walton and Wynne-Edwards (1998) and are expressed as deviations from the non-reproductive temperature. As for Figure 4, the vertical line through a temperature disruption of 0°C indicates the mean daily temperature and the shaded area beyond $+1.0^\circ\text{C}$ provides a visual indication of the proportion of that light or dark phase during which female temperatures were more than 1.0°C higher than their daily average.

(Scribner, 1996). Thus, biparental care virtually eliminates high maternal body temperatures in *P. campbelli* and converts maternal temperature distributions to the pattern typical of *P. sungorus*.

Male presence therefore improves female reproductive success through elimination of maternal exposure to high body temperatures (Walton and Wynne-Edwards, 1998). This change in maternal body temperature is not caused by a behavioral shift towards longer maternal absences for cooling (Wynne-Edwards, 1998). Instead, male presence prevents the establishment of any signifi-

TABLE 1. Similarities and differences between *P. campbelli* and *P. sungorus*.

i) Similarities		Reference(s)*
Body size	Females 18–30 g, males 25–35 g	Ludin <i>et al.</i> , 1979
Phenotype	Spherical shape, short limbs, rudimentary tail Dense pelage extending to cover the soles of the feet	Flint, 1966
Reproductive cycles	Estrus cycle 4 (or 5) days Gestation 18 days, post-partum gestation ≥ 18 days (no obligatory delay of implantation)	Parkening and Collins, 1991; Newkirk <i>et al.</i> , 1997
Litter size and growth	Average 5–6 pups, range 1–9; birth weight approx. 1.7 g Day 18 weight under ideal conditions 12–16 g	Newkirk <i>et al.</i> , 1998
ii) Differences		Reference(s)*
a) Habitat	<i>P. campbelli</i>	
Rainfall	210 mm/yr July–August peak	This paper
Temperature	Low $\leq -30^{\circ}\text{C}$ in January High $\leq 15^{\circ}\text{C}$ in July–August	This paper
Vegetation	Stabilized sand dunes and <i>Caragana</i> shrubs	Flint, 1966; Wynne-Edwards <i>et al.</i> , 1992
b) Social Structure	<i>P. sungorus</i>	
Parental strategy	Biparental care Variable pup size within litters so that one or more pups often grow slowly	Wynne-Edwards, 1995; Newkirk <i>et al.</i> , 1998
Social dominance	Male-male aggression can lead to death	Wynne-Edwards and Lisk, 1987a, b
Pup independence	Independent thermoregulation by pups only late in lactation	Newkirk <i>et al.</i> , 1998
Adult distribution	Very low densities Home ranges of one male and one female overlap	Wynne-Edwards <i>et al.</i> , 1992; Wynne-Edwards, 1995
c) Physiology		
Heat tolerance	Water balance fails above 31°C	Heldmaier, 1975; Meschersky, 1993
Urine concentration	As high as any desert rodent known (3.3 ± 0.1 Osm/kg) Small urine volume and large kidney size	Trojan, 1977; Scribner, 1996
	Water loss increased, but manageable, at 36°C Only 80% of the <i>P. campbelli</i> value (2.6 ± 0.1 Osm/kg) Larger urine volume and smaller kidney size	

TABLE 1. Continued

ii) Differences	Reference(s)*	
	<i>P. campbelli</i>	<i>P. sungorus</i>
Maternal thermoregulation	Acutely hyperthermic 25% of daytime Male presence reduces this to 5% Most litters, but only 50% of pups, survive All measures improve when the male is present	Acutely hyperthermic 10% of daytime Excellent pup survival and growth No change when male is present
Breeding at $\geq 21^{\circ}\text{C}$		Walton and Wynne-Edwards, 1998; Scribner and Wynne-Edwards, 1994c Wynne-Edwards, 1987; Wynne-Edwards and Lisk, 1989

* References listed are examples only. See text for details and additional citation.

cant hyperthermia relative to non-reproductive core body temperatures (Walton and Wynne-Edwards, 1998). Thus, maternal hyperthermia in *P. campbelli* appears to be a facultative (and costly) response to pup needs for exogenous heat, rather than a natural consequence of the metabolic demands (Thompson, 1992) and endocrine changes (Woodside *et al.*, 1981) associated with lactation.

Therefore, in *P. campbelli*, male presence does not improve reproductive success solely through direct paternal behavior. The indirect effect of paternal presence—reduced maternal hyperthermia—is probably the most important for pup survival and growth. In effect, paternal presence in *P. campbelli* resolves the conflict between adaptations for survival and adaptations for rapid reproduction. Reduced maternal hyperthermia improves mother-pup contact and reduces thermoregulatory water demand. Maternal ability to invest in reproduction is then increased so that rapid reproduction is possible in spite of the low water availability and the need to maintain excellent insulation. Male presence in *P. campbelli* compensates for the extra 85 mm of summer rainfall and the extra three months of reliable rainfall that are available in the habitat of *P. sungorus*.

CONCLUSION

The phenotypic similarities and close relatedness of *P. campbelli* and *P. sungorus*, when combined with the clear differences between the two species in habitat, social structure, and physiology (summarized in Table 1), have resulted in an integrated model proposing both proximate and ultimate causal explanations for the evolution of different parental strategies in the two species.

There is little doubt that biparental care is important to *P. campbelli* in the wild. Improved reproductive success in *P. campbelli* when males are present has been demonstrated repeatedly in the laboratory (Wynne-Edwards, 1987; Wynne-Edwards and Lisk, 1988; Scribner and Wynne-Edwards, 1994a; Walton and Wynne-Edwards, 1998). Staged laboratory encounters have confirmed patterns of social tolerance (Wynne-

Edwards and Lisk, 1984, 1987, 1988). Field studies have provided behavioral observations of mating exclusivity, and direct paternal care, in the wild (Wynne-Edwards *et al.*, 1992; Wynne-Edwards, 1995; unpublished observations). In each case, the comparable evidence for *P. sungorus* has suggested that social tolerance may increase seasonally (Wynne-Edwards, 1995), but that solitary maternal care of young is typical.

This model proposes that the 'ultimate' selection pressure that resulted in the evolution of biparental care in *P. campbelli*, but not *P. sungorus*, was the physical environment. *Phodopus campbelli* habitat is sufficiently colder, drier, and more seasonal than *P. sungorus* habitat, that conflicts between essential adaptations for survival and rapid reproduction are not resolved by favorable environmental conditions during any season of the year (Fig. 1). The 'proximate' selection pressure resulting in the 'need' for biparental care in *P. campbelli* was a limited tolerance for elevated maternal body temperatures. In *P. campbelli*, high maternal body temperatures become a physiological constraint limiting mother-pup contact, and thus the reproductive success, of solitary *P. campbelli* females attempting to rear a litter. Further support for this 'proximate' explanation of the 'need' for biparental care is found in the alleviation of maternal hyperthermia, and an increase in mother-pup contact, when males are present. Thus, both direct and indirect benefits of paternal presence are implicated as mechanisms responsible for the improvement in pup survival and growth when males remain with the female and litter.

The clear evolutionary advantage to male mammals of concentrating their effort on mating while leaving all of the parental effort to females (Trivers, 1972), the comparative rarity of paternal care in mammalian species (Kleiman, 1977), and the small range of species typically used in physiological research have precluded the development of other integrated models of the role that physiological constraints, resulting from selection for adaptations not directly linked to reproduction, may play in the evolution of mammalian social organization

and behavior. However, this single example from the genus *Phodopus* confirms that independent physiological constraints on breeding adults, in addition to constraints on energy or time investment, can be essential to the evolution of parental care strategies.

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