# Testing the heat limitation hypothesis: Do lactating females make use of wind to increase their energy intake and reproductive performance under hot summer conditions?

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## Abstract

1. Global warming is rapidly emerging as a universal threat that could alter the distribution of many animal species and change their morphology, physiology, behavior and life history. The heat dissipation limitation (HDL) hypothesis proposes that females' reproductive performance is limited by their capacity to dissipate heat. Although exposure to wind is known to increase heat exchange, its effect on reproductive performance is unknown. 2. In this study, the effect of simulated wind on the energy budget and milk energy output of female striped hamsters (Cricetulus barabensis) was measured under cool (21°C) and hot (32.5°C) ambient temperatures and the preference of hamsters for windy conditions in lactating females was tested both in the laboratory and the wild. 3. Females lactating at 32.5°C significantly decreased their energy intake and milk output, and raised lighter offspring than those lactating at 21°C. Exposure to wind significantly increased both energy intake during lactation and heat loss at both temperatures. Females lactating at 32.5°C considerably increased their reproductive output when exposed to wind. Moreover, females kept at an ambient temperature of 21°C preferred sheltered conditions whereas those kept at 32.5°C preferred exposure to simulated wind. We captured significantly more lactating female hamsters on windy days in summer and on calm days in spring. Wrapping a glass vessel in the fresh pelt of a striped hamster significantly reduced the rate of both water loss and cooling. 4. These findings support the HDL hypothesis; high ambient temperatures do appear to limit the energy intake and reproductive output of lactating hamsters. Small mammals lactating under hot conditions may be able to utilize the cooling properties of wind to increase their energy intake and milk production, and thereby their reproductive output and fitness.


## Introduction

Global warming and increasing climatic variability could alter the distribution of animals and change their morphology, physiology, behavior and life history (Mifsud et al. 2011; IPCC Working Group 1 2014; Smith et al. 2014; Martin, Mead & Barboza 2018). High temperatures adversely impact small mammals by making it harder to dissipate heat, thereby increasing the risk of hyperthermia (Quiniou & Noble 1999). This risk is particularly high for lactating females because ingesting the additional food required to produce milk increases energy expenditure, and therefore heat production (Speakman & Król 2005). Therefore, the adverse effects of high temperature on small mammals are greatest during reproduction, and in particular, during lactation.

Exposure to high ambient temperatures has been widely reported to decrease food intake and milk yield in a variety of animals, including both small and large mammals (Cobble & Herman 1951; Morag, Kali & Furman 1969; Leon & Woodside 1983; Jansen & Binard 1991; Abdalla, Kotby& Johnson 1993; Black et al. 1993; Quiniou & Noblet 1999; Renaudeau & Noblet 2001; Król & Speakman 2003a; Król & Speakman

2003b; Renaudeau, Noblet & Dourmad 2003; Valencak, Hacklander & Ruf 2010; Valencak et al. 2013; Wu et al. 2009; Simons et al. 2011; Zhao 2011; Yang et al. 2013; Wen et al. 2017; Ohrnberger et al. 2018). Exposure to high temperatures typically reduces milk production, and thereby litter growth rate and other indicators of maternal reproductive performance (Król & Speakman 2003a; Król & Speakman 2003b; Wen et al. 2017). Król and Speakman (2003a, 2003b) advanced the heat dissipation limitation hypothesis (HDL) to explain the adverse effect of high temperatures on female reproductive performance. This proposes that ability to dissipate body heat limits a female's maximum rate of sustained energy intake and milk output. If this is true, female mammals lactating under hot conditions should compensate by either decreasing their milk production and extending the duration of lactation, or by decreasing their litter size or the size of their offspring. The latter two strategies should decrease the risk of hyperthermia, albeit at the cost of reduced reproductive performance and fitness. However, an alternate possibility is that females may attempt to maintain their reproductive performance under hot conditions by actively seeking out conditions that improve their ability to dissipate heat. This possibility is, to the best of our knowledge, so far untested.

Heat exchange between animals and the environment includes radiation, convection, conduction and evaporation, and the difficulty of dissipating heat under hot conditions is due, at least to some degree, by the low thermal conductance of the fur, which is important for insulation against cold. Wind increases heat exchange by increasing the effective thermal convection, conduction and evaporation (Porter & Gates 1969; Stevenson 1985). Many animal species frequently experience unpredictable changes in wind speed that can affect their activity and thermoregulation (Sun et al. 2001; Maia-Carneiro, Dorigo & Rocha 2012; Scheers & Van Damme 2002; Logan, Fernandez & Calsbeek 2015). Wind decreases the ambient air temperature thereby promoting heat loss by convection (Porter & Gates 1969; Kearney & Porter 2009; Ortega, Mencía & Pérez-Mellado 2017). In addition, wind increases water loss, which increases heat dissipation via convection and evaporation (Winne et al. 2001; Tracy & Christian 2005; Ortega, Mencía & Pérez-Mellado 2017). Migratory birds are known to select favorable wind conditions allowing faster, safer, and more direct, migration routes (Wiltschko & Wiltschk 2003; McLaren, Shamoun-Baranes & Bouten 2012; Vansteelant et al. 2015; Gutierrez et al. 2017). The flight of larger, soaring birds is particularly likely to be strongly affected by wind currents (Limiñana et al. 2013; Vidal-Mateo et al. 2016; Gutierrez et al. 2017; Vansteelant et al. 2017). For example, American white pelicans (*Pelecanus erythrorhynchos* ) adopt different flying strategies to cope with different wind conditions (Gutierrez et al. 2017). Changing wind conditions have been found to markedly affect the locomotion, foraging, activity levels and reproductive success of not only birds, but also insects and small mammals (Smith & Weston 1990; Hayes & Huntly 2005; Chapman et al. 2010; Cornioley et al. 2016; Miller et al. 2016). Although the effect of temperature on animals' physiology and behavior has been extensively studied, relatively is known about the effect of wind on the capacity to dissipate body heat and reproductive performance.

The striped hamster (*Cricetulus barabensis* ) is a common rodent in northern China, Russia, Mongolia and Korea (Zhang & Wang 1998). This species is nocturnal and granivorous, feeding mainly on the stems and leaves of plants during summer and seeds in the winter (Lu, Li & Zhang 1987; Zhang & Wang 1998; Song & Wang 2002, 2003; Zhao et al. 2010a; Zhao et al. 2010b). The striped hamster prefers sandy areas, as well as farmland and grassland. Breeding occurs from February to November, during which there are two reproductive peaks; one in spring and one in autumn (Xing, Feng & Lu 1991; Zhu & Qin 1991; Dong et al. 1993; Hou et al. 1993; Jiang et al. 1994; Bao et al. 2001; Wang et al. 2003; Zhao, Chi & Cao 2010c). The species experiences considerable seasonal fluctuations in both ambient temperature and wind speed, particularly in spring, autumn and winter. Although temperature is known to have a significant effect on the striped hamster's thermoregulation and reproduction, the effect of wind is unknown. This paper presents the results of four experiments designed to determine the effects of both temperature and wind on the maximum energy intake, reproductive output and thermal conductance, of lactating striped hamsters. We also examined the activity of wild hamsters on windy and calm days during both cool spring and hot summer conditions. We hypothesized that exposure to wind during hot weather may increase females' reproductive performance by improving their ability to dissipate body heat.

## Materials and methods

ANIMALS

Striped hamsters were obtained from the laboratory-breeding colony, the founders of which were captured in farmland at the center of Hebei province (115°13'E, 38deg12'S) on the North China Plain. The climate of this region is arid and characterized by warm, dry summers with a maximum temperature of 42degC, and cold winters in which the temperature can fall below -20degC (Zhao et al. 2010a; Zhao et al. 2010b). The animals were kept at 21+-1degC under a 12L:12D (light: dark, lights on at 0800h) photoperiod. Food (standard rodent chow, 17.6 kJ/g; Beijing Keao feed company, Beijing, China) and water were provided *ad libitum* .

Experiment 1 was designed to examine the effect of wind on the energy intake and reproductive performance of lactating female striped hamsters. Seventy 3 to 3.5-month-old, virgin, female hamsters were housed individually in plastic cages (29 x 18 x 16 cm) provided with sawdust bedding. Each female was paired with a male for two weeks after which the males were removed. Females that subsequently gave birth were allowed to raise their offspring for four days from parturition (day 1 to day 4 of the experiment), during which no measurements were made on either females or pups. On day 5 litter sizes were artificially adjusted so that each female had 8 pups which they were allowed to suckle for 16 days. Females were also randomly assigned to one of four treatment groups:

1. A 21degC group (21degC, n=9), in which females and pups were kept at an ambient temperature of 21 +- 1degC and not exposed to wind.
2. A 21degC plus wind group (21degC+W, n=9), in which females and pups were kept at an ambient temperature of 21 +- 1degC and exposed to simulated wind generated by an electric fan.
3. A 32.5degC group (32.5degC, n=18) in which females and pups were kept at an ambient temperature of 32.5 +- 1degC and not exposed to wind.
4. A 32.5degC plus wind group (32.5degC+W, n=18), in which females and pups were kept at an ambient temperature of 32.5 +- 1degC and exposed to simulated wind.

All treatments began on day 6 and continued until the end of the experiment on day 16. Wind was simulated using an electric fan (AUX FS1605, AUX Electrical Appliances Co., Ltd. China) to create a wind speed of 2m/s, ranging from 1.6 to 3.3m/s around inside the cages (Anemometer, Testo 405-V1, Testo Instruments International Trading Ltd. Germany).

BODY MASS AND FOOD INTAKE

The body mass and food intake of females were measured daily from day 5 to day 15. Food intake was calculated as the difference between the mass of the food provided and uneaten food on the following day, minus any food residue mixed with bedding material. Litter size and litter mass were also measured daily from day 5 to day 16.

ENERGY INTAKE AND DIGESTIBIITY

Gross energy intake (GEI) and digestibility were measured between days 13 and 14 of the experiment using the food balance method described previously (Grodzinski & Wunder 1975; Wen et al. 2018a; Wen et al. 2018b). In brief, a known quantity of food was provided, and any uneaten food and orts mixed with the bedding material were collected, together with feces, every 24h. Food and feces were separated manually after drying to constant mass at 60degC. The gross energy content of food and feces were then determined using an IKA C2000 oxygen bomb calorimeter (IKA, Germany). GEI, gross energy of feces (GEF), digestive energy intake (DEI) and digestibility were calculated using the following equations:

GEI (kJ/d) = [food provided (g/d) x dry matter content of food (%) – dry spillage of food and uneaten food] x gross energy content of food (kJ/g); GEF (kJ/d) =dry feces mass (g/d) x energy content of feces (kJ /g); DEI (kJ/d) =GEI–GEF; and digestibility (%) = DEI/GEI x 100%

MILK ENRGY OUTPUT

Milk energy output (MEO) during the peak of lactation (days 13-14) was assessed from the energy budget of litters, as described previously (Krol & Speakman 2003b). Pups obtain all their energy from their mother's milk, so total energy was calculated as the sum of the energy allocated for pups' daily energy expenditure (daily energy expenditure, DEE) and the growth of new tissue (Zhao et al. 2011). DEE was predicted from pup body mass on the basis of the relationship between the resting metabolic rate (RMR) and body mass, under the assumption that DEE = 1.4xRMR to take into account the energetic costs of pups' activity.

The equation used was (Krol & Speakman 2003b):

$$MEO = [(7.28+0.17xLM) \text{ x } CF + LM_{inc} \text{ x } GE_{pups}] \text{ x}100/d_{milk,}$$

where LM (g) is the litter mass on day 13; CF is the correction factor (CF=1.4, the mean ratio of DEE to RMR) and $GE_{pups}$ (kJ/g wet mass) is the gross energy content of the pups. The mean $GE_{pups}$ values used in this formula were determined using an IKA C2000 oxygen bomb calorimeter. $LM_{inc}$ (g/d) was the increase in litter mass between days 13 and 14, and $d_{milk}$ was the apparent digestibility of milk ($d_{milk}$-96%) (Krol & Speakman 2003b).

*Experiment 2* was designed to examine the effect of wind on the thermal conductance of fur and the rate of water evaporation at both a moderate (21degC) and high (32.5degC) temperature. Twelve female hamsters maintained individually at 21 +- 1degC were killed by $CO_2$ overdose as described previously (Zhao et al. 2013), and the entire pelage, except for the head, limbs and tail, immediately removed. Pelage from each hamster was then stitched around a 10mL (2cm diameter x 5.5cm long) glass vessel containing water. These pelage were randomly assigned to either a 21degC (21degC, $n$ =6) or a 32.5degC (32.5degC, n=6) treatment groups.

THE EFFECT OF WIND ON WATER EVAPORATION

Vessels were warmed to 60degC and transferred to one of two temperature controlled rooms kept at either 21degC or 32.5degC, respectively. Water temperature was monitored using an encapsulated thermo-sensitive passive transponder (diameter 2 mm and length 14 mm; Destron Fearing, South St Paul, USA) in each vessel, and recorded on a Pocket Reader (Destron Fearing, South St Paul, USA) at one-minute intervals. Wind (2m/s) was simulated as in experiment 1. The temperature of glass vessels without pelage was also monitored under both temperatures to serve as a control.

THE EFFECT OF WIND ON WATER THERMOREGULATION

The rate of water evaporation was monitored using a glass plate (diameter, 10cm) filled with 40 g tap water at 37degC. This was placed on a balance in temperature controlled rooms at 21degC and 32.5degC. The simulated wind treatment at both temperatures was carried out as described above. The change in water weight was measured over 30 min at one-minute intervals.

Experiment 3 was designed to examine the effect of temperature on the preference of females for cages that were exposed to simulated wind or sheltered cages during the peak of lactation. Thirty lactating hamsters were organized as described in experiment 1. Females and their pups were housed in two plastic cages (29 x 18 x 16 cm) connected with a 15cm-long plastic tube of 5cm diameter that allowed females to move freely from one cage to the other. Females had free access to food and water in both cages. All females were kept at 21degC from days 0 to 5 until day 6 when they were randomly assigned to either a 21degC group ($n$ =15) or a 32.5degC group ($n$ =15). From day 10 till day 14, an electric fan was used to expose one of each pair of cages to an air speed of 1.6 – 3.3m/s. The preference of each female for the cage exposed to simulated wind or the sheltered cage was recorded by observing each female in succession for 40 s over a period of 10 min. The number of pups that stayed in the cage exposed to simulated wind or the sheltered cage was also recorded. Observations were carried out over 8 hours both day (8:00-10:00 and 18:00-20:00) and night (6:00-8:00 and 20:00-22:00). Observations during the night were made using a 30 W red light. The preference of females for the cages exposed to simulated wind or sheltered cages was assessed from the amount of time they spent each cage type and expressed as min/h.

Experiment 4 was designed to examine the preferences of wild female hamsters for windy vs calm days during spring and summer. This experiment was performed in late April and mid-July in a dry river bed in Shenze County, Hebei province (115deg13'E, 38deg12'S) on the North China Plain. A sparse growth of weeds covered the dry, sandy, river bed. The average daily maximum and minimum temperatures in late April were 27.2degC and 15.1degC, respectively, and 36.6degC and 27.1degC in mid-July. Windy days were defined as those on which the wind speed 20cm above the ground was more than 1.6 m/s during the night, and calm days were defined as those on which the wind speed was less than 1.6 m/s during the night. Wind speed was measured with an anemometer (Testo 405-V1, Testo Instruments International Trading Ltd. Germany). Hamsters were captured in 85 live-capture traps placed at 20 m intervals. The total number of adult females and the number of lactating females captured was recorded daily. Lactating females can be easily distinguished by their relatively large nipples. The percentage of lactating females was calculated as the number of lactating females divided by total number of adult females captured. All hamsters were released after their sex and lactation status had been recorded.

STATISTICS

Data were analyzed using SPSS statistical software (V 20.0). In Experiment 1, the effects of temperature and wind on body mass, food intake and the energy parameters of females, as well as on litter size and liter mass, were examined using a two-way ANOVA (temperature x wind), followed by Tukey's post hoc tests where required. Correlation coefficients between different variables were estimated using Pearson's correlation coefficient. In Experiment 2, the statistical significance of differences in water temperature and weight were analyzed using a two-way ANOVA (temperature x wind). In Experiment 3, the preference of females for cages exposed to simulated wind vs sheltered cages was assessed using a two-way ANOVA (temperature x wind). In Experiment 4, the statistical significance of differences in the total number of females and proportion of lactating females captured on calm and windy days in spring and summer was also assessed using a two-way ANOVA (season x wind). All data are presented as means +- SEM; $P$ -values <0.05 were considered statistically significant.

## Results

Experiment 1

BODY MASS

The body mass of the four treatment groups was not significantly different on day 5 prior to the commencement of the temperature and wind treatments (temperature, $F_{1,50}$=0.01,$P$ >0.05; wind, $F_{1,50}$=1.27,$P$ >0.05, Figure 1A). The body mass of females kept at an ambient temperature of 32.5degC subsequently became significantly lower than that of those kept at 21degC for the remainder of the experiment (day 6, $F_{1,50}$=13.37, $P$ <0.01). On the final day of the experiment (day 16), the body mass of hamsters kept at 32.5degC was 17.8% lower, on average, than that of those kept at 21degC (day 15, $F_{1,50}$=35.26, $P$ <0.01). Body mass was not, however, significantly affected by the simulated wind treatment (day 6, $F_{1,50}$=0.38,$P$ >0.05, day 15, $F_{1,50}$=0.27,$P$ >0.05).

FOOD INTAKE

Food intake did not differ significantly among the four treatment groups prior to commencement of the temperature and wind treatments (day 5, temperature, $F_{1,50}$=0.25,$P$ >0.05; wind, $F_{1,50}$=0.10,$P$ >0.05, Figure 1B). Females kept at an ambient temperature of 32.5degC subsequently consumed significantly less food than their counterparts kept at 21degC (day 6,$F_{1,50}$=64.79, $P$ <0.01). The food intake of females kept at 32.5degC was 51.1% lower, on average on day 14, than that of females kept at 21degC ($F_{1,50}$=69.67,$P$ <0.01). Wind also had a significant effect on food intake; females exposed to simulated wind consumed significantly more food at both 21degC and 32.5degC than those that were not (day 6,$F_{1,50}$=12.84, $P$ <0.05). The food intake of females exposed to simulated wind was 11.7% higher at 21degC, and 29.9% higher at 32.5degC, than that of females that were not exposed to simulated wind (day 14, $F_{1,50}$, =3.82,$P$ <0.05). Asymptotic food intake was significantly affected by both temperature ($F_{1,50}$=128.87,$P$ <0.01) and simulated wind ($F_{1,50}$=8.84, $P$ <0.01, Figure 2A). The asymptotic food intake of females kept at 32.5degC was 51.2% lower, on average (*post hoc* , $P$ <0.05) than that of those kept at 21degC. Exposure to simulated wind elevated asymptotic food intake by 17.1% at 21degC, and by 25.4% at 32.5degC (*post hoc* ,$P$ <0.05). Asymptotic food intake was also positively correlated with body mass (Figure 3A).

ENER INTAKE AND DIGESTIBILITY

The GEI and DEI of females kept at an ambient temperature of 32.5degC was, on average, 54.9% and 55.2% lower, respectively, that that of females kept at 21degC (GEI, $F_{1,50}$=354.02,$P$ <0.01, Figure 2B; DEI,$F_{1,50}$=371.12, $P$ <0.01, Figure 2C). Maintaining females at an ambient temperature of 32.5degC also significantly affected GEF, and females kept at this temperature produced considerably less feces than those kept at 21degC ($F_{1,50}$=371.12, $P$ <0.01, Figure 2D). The GEI of females that were exposed to simulated wind, on average, 21.7% higher at 21degC and 28.8% higher at 32.5degC than that of females that were not exposed to simulated wind ($F_{1,50}$=28.30, $P$ <0.01). Irrespective of temperature, females exposed to simulated wind also had significantly higher DEI and produced more feces than those that were not exposed to simulated wind (DEI, $F_{1,50}$=28.85,$P$ <0.01; GEF, $F_{1,50}$=10.77,$P$ <0.01). Neither temperature or or exposure to simulated wind, significantly affected digestibility (temperature,$F_{1,50}$=1.83, $P$ >0.05; wind,$F_{1,50}$=0.01, $P$ >0.05, Figure 2E).

MEO

MEO was considerably affected by temperature; females kept at an ambient temperature of 32.5degC produced 58.1% less milk than those kept at 21degC ($F_{1,50}$=13.78, $P$ <0.01, Figure 2F). Although MEO was not significantly affected by exposure to simulated wind ($F_{1,50}$=0.01,$P$ >0.05), it was significantly affected by an interaction between temperature and simulated wind ($F_{1,50}$=9.42, $P$ <0.01). Furthermore, females exposed to simulated wind produced 25.6% less milk at an ambient temperature of 21degC (*post hoc* ,$P$ <0.05) but 64.2% more milk at 32.5degC (*post hoc* , $P$ <0.05). There was a significant correlation between MEO and asymptotic food intake; females that produced more milk seemed to consume more food (Figure 3B). MEO was also positively correlated with body mass (Figure 4A).

LITTER SIZE AND LITTER MASS

Litter size did not differ among the four treatment groups before treatments began (day 5, temperature, $F_{1,50}$=0.23,$P$ >0.05; wind, $F_{1,50}$=0.37,$P$ >0.05, Figure 5A). The litter size of females kept at an ambient temperature of 21degC did not change significantly during the experiment, whereas that of females kept at 32.5degC became significantly smaller from day 11 than that of females kept at 21degC (day 11, $F_{1,50}$, =4.68, $P$ <0.05). By the end of the experiment (day 16), the females kept at an ambient temperature of 32.5degC had raised, on average, 29.5% less pups than those kept at 21degC (day 15, $F_{1,50}$=9.72,$P$ <0.05). Litter size was also significantly affected by wind after day 13 (day 13, $F_{1,50}$=4.88,$P$ <0.05). On day 15, females that were exposed to wind raised 7.3% more pups at 21degC, and 56.0% more pups at 32.5degC ($F_{1,50}$=4.19, $P$ <0.05) than those that had not been exposed to wind (Figure 5A). There was a significant correlation between litter size and asymptotic food intake; females that raised more pups seemed to consume more food towards the end of the experiment at ambient temperatures of both 21degC and 32.5degC (Figure 3C). Litter size was also positively correlated with MEO; the more pups that females raised, the more milk they produced (Figure 4B).

Litter mass was not significantly different among the four treatment groups before the treatments began (day 5, temperature,$F_{1,50}$=0.02, $P$ >0.05; wind,$F_{1,50}$=0.11, $P$ >0.05, Figure 5B). The litter mass of females kept at an ambient temperature of 21degC was significantly higher than that of those kept at 32.5degC. From day 8 onwards, the litter mass of females kept at 32.5degC was significantly lower than that of those kept at 21degC (day 8,$F_{1,50}$=5.45, $P$ <0.01), and by the end of the experiment (day 16) the litter mass of females kept at 32.5degC was 38.6% lower, on average, than that of those kept at 21degC (day 15,$F_{1,50}$=20.51, $P$ <0.01). Although litter mass was not significantly affected by exposure simulated wind, it was by the interaction between temperature and simulated wind on day 14 and 15 (day 14, $F_{1,50}$=4.93,$P$ <0.05). At an ambient temperature of 21degC, the litter mass of females exposed to simulated wind was

12.6% lower than that of those that had not been exposed to simulated wind, whereas at 32.5degC the litter mass of females exposed to simulated wind was 47.7% higher than that of those which had not been exposed to simulated wind (*post hoc* , $P$ <0.05). Litter mass was positively correlated with asymptotic food intake; females that raised heavier offspring tended to consume more food in the second week of lactation at both 21degC and 32.5degC (Figure 3D). Litter mass was also positively correlated with MEO; females with heavier pups seemed to produce more milk at both 21degC and 32.5degC (Figure 4C).

Pup growth was significantly attenuated by temperature; the mean pup mass of females kept at an ambient temperature of 32.5degC was significantly lower from day 7 than that of those kept at 21degC (day 7, $F_{1,50}$=5.30, $P$ <0.01, Figure 5C). At the end of the experiment, the pups of females that had been kept at 32.5degC were 30.8% lighter, on average, than those that had been kept at 21degC (day 15, $F_{1,50}$=13.84, $P$ <0.01). Pup mass was not significantly affected by exposure to simulated wind (day 15, $F_{1,50}$=0.01, $P$> 0.05), but was by the interaction between temperature and simulated wind from day 7 to day 15 (day 7, $F_{1,50}$=4.91, $P$ <0.05). Pups raised by females that had been exposed to simulated wind were 18.8% lighter at 21degC, and 35.3% heavier at 32.5degC, than those raised by females that had not been exposed to simulated wind (day 15, $F_{1,50}$=5.46, $P$ <0.05, Figure 5C).

Experiment 2

THE EFFCT OF WIND ON WTER EVAPORATION AND THERMOREGULATION

We simulated the effect of wind on water loss and thermoregulation in hamsters by measuring the rate of evaporation and heat loss from a water filled glass vessel wrapped in the fresh pelt of a hamster under both simulated windy and calm conditions. The rate of water evaporation under simulated wind was significantly greater at 32.5degC than at 21degC after 27min (30min, $F_{1,8}$=6.03, P<0.05, Figure 6A). The slope of water evaporation was significantly increased by both temperature and exposure to simulated wind ($F_{1,8}$=21.98, P<0.01, Figure 6B). Exposure to simulated wind significantly decreased both the rate (3min, $F_{1,8}$=5.84, P<0.05, 30min, $F_{1,8}$=107.15, P<0.01, Figure 6A), and the slope ($F_{1,8}$=239.18, P<0.01, Figure 6B), of water evaporation.

The temperature of water filled glass vessels decreased more slowly at 32.5degC than at 21degC (1min, $F_{1,8}$=9.34, $P$ <0.01, 60min, $t_4$=219.28, $P$ <0.01, Figure 6C; slope, $F_{1,8}$=46.61, P<0.01, Figure 6D). Cooling was significantly affected by simulated wind; under simulated windy conditions the temperature fell by 47.8% at 21degC and by 25.2% at 32.5degC compared to vessels that were not exposed to simulated wind (1min, $F_{1,8}$=8.33, $P$ <0.01, 18min, $F_{1,8}$=406.67, P<0.01, Figure 6C). The difference in slope between simulated windy and calm conditions was 88.4% at 21degC and 70.3% at 32.5degC ($F_{1,8}$=410.02, $P$ <0.01, Figure 6D).

The cooling of water-filled glass vessels was significantly slower at 32.5degC than at 21degC (5min, $F_{1,8}$=5.49, $P$ <0.01, 30min, $F_{1,8}$=228.53, $P$ <0.01, Figure 6E) and the difference in the slope of temperature change was 19.98% less at 32.5degC than at 21degC ($F_{1,8}$=494.70, $P$ <0.01, Figure 6F). Wind significantly increased the rate of heat loss at both 21degC and 32.5degC (5min, $F_{1,8}$=6.74, $P$ <0.01, 30min, $F_{1,8}$=56.50, $P$ <0.01, Figure 6E), and also significantly increased the rate of temperature change ($F_{1,8}$=112.14, $P$ <0.01, Figure 6F).

Experiment 3

THE EFFCT OF TEMPERATURE ON THE PREFERENCE OF FEMALE HAMSTERS FOR WINDY OR CALM CONDITIONS DURING PEAK LACTATION

Significantly more pups were moved to sheltered cages at an ambient temperature of 21degC than at 32.5degC (6:00, $t_{28}$=20.39, $P$ <0.01, Figure 7A), and conversely, significantly more were moved to cages exposed to simulated wind at 32.5degC than at 21degC (21:50, $t_{28}$=15.81, $P$ <0.01, Figure 7B). Females clearly preferred to move their pups to sheltered cages at 21degC, whereas at 32.5degC this preference was less clear-cut (Supplementary materials, Figure S1A).

Temperature had a significantly effect on cage preference both during the day and night. Females kept at an ambient temperature of 32.5degC spent considerably less time in sheltered cages (6:00, $t_{28}$=4.78, P<0.01, Figure 7C) compared to those kept at 21degC (21:00, $t_{28}$=6.55, $P$ <0.01, Figure 7D). These results suggest that females during the peak of lactation preferred simulated windy conditions at 32.5degC and sheltered conditions at 21degC (Figure 7C, 7D, Figure S2).

Experiment 4

THE EFFCT OF WIND ON THE NUMBER OF WILD FEMALE HAMSTERS CAPTURED IN SPRING AND SUMMER

The number of wild female hamsters captured was significantly affected by wind, season ($F_{1,16}$=13.36,$P$ <0.01), wind ($F_{1,16}$=6.82,$P$ <0.01) and the interaction between these variables ($F_{1,16}$=25.49, $P$ <0.01, Figure 8A). In spring, 91.3% fewer lactating females were captured on windy days than on calm days, whereas in summer 5-times more lactating females were captured on windy days than on calm days (season,$F_{1,16}$=32.40, $P$ <0.01; wind,$F_{1,16}$=25.60, $P$ <0.01, interaction, $F_{1,16}$=67.60,$P$ <0.01, Figure 8B). The percentage of lactating females captured was significantly affected by season ($F_{1,16}$=7.70, $P$ <0.01), wind ($F_{1,16}$=4.98, $P$ <0.05) and the interaction between these ($F_{1,16}$=49.83,$P$ <0.01, Figure 8C).

**Discussion**

Striped hamsters suckling young at an ambient temperature of 32.5degC had a significantly lower sustained energy intake, produced less milk, and weaned lighter offspring, than those at 21degC. The temperature of a glass vessel wrapped in a fresh hamster pelt decreased at a significantly lower rate at 32.5degC than at 21degC, indicating that heat dissipation was considerably less at the higher temperature. This suggests that, consistent with the HDL hypothesis, the reduced capacity of female hamsters to dissipate heat at high temperatures may restrict their sustained energy intake and milk production. Females kept at an ambient temperature of 32.5degC that were exposed to simulated windy conditions increased their energy intake and milk production, which suggests that, by increasing the capacity to dissipate body heat, wind may allow an increase in milk production under hot conditions. More importantly, striped hamsters during the peak of lactation significantly preferred windy conditions at an ambient temperature of 32.5degC but not 21degC. Furthermore, the fact that significantly more lactating wild hamsters were captured on windy days than on calm days in summer, and on calm days than on windy days in spring, suggests that these are more active on windy days in summer and less active on windy days in spring. These findings support the hypothesis that wind increases female milk production by improving the capacity to dissipate body heat, thereby increasing reproductive performance and fitness under hot summer temperatures.

Lactation is the most energetically demanding part of the life cycle of small, female mammals and the increased food intake needed to meet the energy requirements of offspring frequently reaches a ceiling during the peak of lactation known as the limitation on sustained energy intake (Thompson 1992; Thompson & Nicol 2002). We found that the food intake of female striped hamsters increased during lactation and was significantly affected by temperature. The asymptotic food intake and gross energy intake of females lactating at an ambient temperature of 32.5degC were 51.2% and 54.9% less, respectively, than those of females lactating at 21degC. Adverse effects of high temperature on lactation have been observed in a variety of animals, including laboratory mice (*Mus musculus,* Krol & Speakman 2003a; Krol & Speakman 2003b; Wen et al. 2017), rats (*Rattus norvegicus,* Morag, Kali & Furman 1969; Leon & Woodside 1983; Jansen & Binard 1991), Brandt's voles (*Lasiopodomys brandtii,* Wu et al. 2009), common voles (*Microtus arvalis* , Simons et al. 2011), Mongolian gerbils (*Meriones unguiculatus,* Yang et al. 2013), golden hamsters (*Mesocricetus auratus* , Ohrnberger et al. 2018), European brown hares (*Lepus europaeus* , Valencak, Hacklander & Ruf 2010), sheep (*Ovis aries* , Abdalla, Kotby& Johnson 1993), pigs (*Sus scrofa* , Black et al. 1993; Quiniou & Noblet 1999; Renaudeau & Noblet 2001; Renaudeau, Noblet & Dourmad 2003) and dairy cattle (*Bos taurus* ) (Cobble & Herman 1951). Collectively, these results suggest that the height of the food intake ceiling during peak lactation is lowered by high temperatures. As this ceiling defines the envelope within which all competing biological functions are constrained (Speakman & Krol 2005), its reduction by high temperatures could adversely affect many aspects of physiology and behavior, in particular reproductive performance.

We found that the asymptotic food intake and gross energy intake of female hamsters during peak lactation were significantly affected by exposure to wind. The asymptotic food intake of hamsters lactating under simulated windy conditions at 21degC and 32.5degC were 17.1% and 25.4% higher, respectively, than those lactating under sheltered conditions. The gross energy intake of females kept at both 21degC at 32.5degC under simulated windy conditions was 21.7% and 28.8% higher, respectively, than that of females that were not exposed to simulated wind. This suggests that the response of female hamsters to wind is temperature dependent. The main energy output during lactation is meeting the energy requirements of offspring (Hammond & Diamond 1992; Hammond & Diamond 1997; Krol & Speakman 2003a; Krol & Speakman 2003b; Speakman & Krol 2005; Valencak, Hacklander & Ruf 2010; Valencak et al. 2013). The marked increase in energy intake under windy conditions should therefore enhance milk production.

As expected, female hamsters lactating at an ambient temperature of 32.5degC had worse reproductive performance than those lactating at 21degC. Females lactating at 32.5degC produced, on average, 58.1% less milk, raised 29.5% fewer pups and had litters weighing 38.6% less, than those at 21degC. High temperatures have been found to reduce milk output in a variety of animal species (Cobble & Herman 1951; Morag, Kali & Furman 1969; Leon & Woodside 1983; Jansen & Binard 1991; Abdalla, Kotby& Johnson 1993; Black et al. 1993; Quiniou & Noblet 1999; Renaudeau & Noblet 2001; Krol & Speakman 2003a; Krol & Speakman 2003b; Renaudeau, Noblet & Dourmad 2003; Wu et al. 2009; Valencak, Hacklander & Ruf 2010; Simons et al. 2011; Zhao 2011; Valencak et al. 2013; Yang et al. 2013; Wen et al. 2017; Ohrnberger et al. 2018). These findings suggest that global warming could negatively affect the reproductive performance and fitness of many mammals. The HDL hypothesis predicts that the increased difficulty of dissipating body heat at higher temperatures limits both energy intake and milk production (Krol & Speakman 2003a; Speakman & Krol 2003b; Speakman & Krol 2005; Wen et al. 2017). We found that the temperature of a water filled vessel wrapped in a fresh hamster pelt decreased at a significantly slower rate at 32.5degC than at 21degC, indicating that the thermal exchange of fur might be much less at 32.5degC than at 21degC. This is consistent with the HDL hypothesis' prediction that the capacity of the body to dissipate heat could limit both maximum energy intake and milk production.

If the HDL is true, then any improvement in the capacity to dissipate body heat could increase milk production and thereby potentially increase fitness (Krol & Speakman 2003a; Speakman & Krol 2003b; Speakman & Krol 2005). We found that exposure to simulated wind significantly increased both the evaporation and cooling rate of a fur-wrapped vessel at either 21degC or 32.5degC. This suggests that wind can considerably increase heat dissipation under both cool and hot conditions. Consistent with this prediction of the HDL hypothesis, exposure to simulated wind significantly increased the milk production of females at an ambient temperature of 32.5degC, but not at 21degC. An alternative hypothesis, the peripheral limitation hypothesis (PLH), proposes that the mammary glands reach the maximum extent of their capacity during peak lactation, thereby limiting both sustained energy intake and reproductive output (Hammond et al. 1994; Hammond, Lloyd & Diamond 1996; Hammond & Kristan 2000; Zhao & Cao, 2009 Zhao, Chi & Cao 2010c). The increased food intake we observed under simulated windy condition at 21degC could possibly be caused by the thermoregulatory demands of other tissues, such as the liver, skeletal muscle and brown adipose tissue, rather than that of offspring. Although this finding supports the peripheral limitation hypothesis, it does not refute the HDL hypothesis. The HDL and PLH are both likely to be valid under different conditions (Speakman & Krol 2010; Speakman & Krol 2011) i.e., reproductive performance could be limited both by the capacity of the mammary glands to produce milk and that of the body to dissipate heat; in other words, the PLH could be more applicable at room temperature and the HDL at higher temperatures (Wen et al. 2017). Reducing heat stress in lactating dairy cows is a major issue in the dairy industry where reduced milk production and increased mortality during heat waves cost many millions of dollars (Speakman & Krol 2010; Speakman & Krol 2011). We found that simulated wind significantly increased the thermal conductance and capacity to dissipate heat of striped hamsters at a relatively high ambient temperature, thereby increasing their milk energy output and reproductive performance. Exposure to wind during hot conditions could therefore reduce heat stress and improve the reproductive value and fitness of both wild animals and livestock.

It has been previously reported that wind has extensive effects on the behavior of animals, particularly birds (Smith & Weston 1990; Hayes & Huntly 2005; Chapman et al. 2010; Cornioley et al. 2016; Miller et al. 2016). For example, American white pelicans adopt different flying strategies in response to changes in wind conditions (Gutierrez et al. 2017). We found that female hamsters lactating at an ambient temperature of 21degC spent most of the day sheltering from simulated wind, whereas those lactating at 32.5degC spent significantly more time in simulated windy conditions. This indicates that lactating female hamsters prefer windy conditions when it is hot, but not when it is cool. As previously mentioned, wind increases heat exchange between the body and the environment (Porter & Gates 1969; Stevenson 1985). Heat loss under cool conditions is significantly exacerbated by wind (Porter and Gates 1969; Winne et al. 2001; Tracy & Christian 2005; Kearney & Porter 2009; Ortega, Mencia & Perez-Mellado 2017). This suggests that under cool conditions animals exposed to wind increase their food intake to meet the increased energy demands of thermoregulation. Conversely, under hot conditions wind could improve the capacity to dissipate body heat, thereby increasing milk production and reproductive output. We caught more wild, lactating female hamsters on calm than on windy days in spring, which suggests that these are less active on windy days. However, in summer the reverse was true; we caught 5-times more lactating females on windy days than on calm days. Collectively, our results suggest that the effect of wind on the behavior of lactating females is temperature dependent. Birds are known to vary their migration routes and flight strategies according to the wind conditions (Wiltschko & Wiltschk 2003; McLaren, Shamoun-Baranes & Bouten 2012; Liminana et al. 2013; Vansteelant et al. 2015; Vidal-Mateo et al. 2016; Gutierrez et al. 2017; Vansteelant et al. 2017). Female mammals may have a strong preference for windy conditions in the heat of summer because wind makes it easier to dissipate heat and thereby increase milk production and fitness.

**In conclusion**

Lactating female striped hamsters kept at a relatively hot ambient temperature significantly decreased their energy intake and milk output during the peak of lactation, and raised significantly lighter offspring than those kept at a cooler temperature. Exposure to simulated wind significantly increased the energy intake and thermal conductance of hamsters lactating at a cooler temperature, but had no effect on milk output; results that support the PLH. However, consistent with the HDL hypothesis, the energy intake, milk output and capacity to dissipate heat of females at an ambient temperature of 32.5degC were all significantly increased by exposure to simulated wind. Moreover, lactating females kept at an ambient temperature of 21degC displayed a strong preference for sheltered conditions, whereas those kept at 32.5degC preferred simulated windy conditions. Wild, lactating female hamsters also appear to be more active on windy days in summer but on calm days in spring. Collectively, our results not only demonstrate the negative effects of high temperature on the maximum rate of energy intake and reproductive output, but also provide evidence that exposure to wind may improve milk production, and thereby the productivity and fitness, of small mammals during hot summer conditions.

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**Figure legends**

**Figure 1.** The effect of ambient temperature (21degC and 32.5degC) and simulated wind on the body mass (A) and food intake (B) of lactating, female striped hamsters (*Cricetulus barabensis* ). Females were housed at either 21degC or 32.5degC from Day 5 of the experiment and exposed to simulated wind from Day 6; NW = no wind, W = simulated wind. Data are means +- s.e. $P_{\mathrm{tem}}$ indicates the period in which there was a significant temperature effect and $P_{\mathrm{w}}$ the period in which there was a significant wind effect; *$P <0.05$, **$P <0.01$.

**Figure 2.** The effect of ambient temperature (21degC and 32.5degC) and wind on the asymptotic food intake (A), gross energy intake (GEI, B), digestive energy intake (DEI, C), gross fecal energy (GEF, D), digestibility (E) and milk energy output (MEO, F), of lactating, female striped hamsters (*Cricetulus barabensis* ) between day 13-14 of lactation. Females were housed at either 21degC or 32.5degC from Day 5 of the experiment

and exposed to simulated wind from Day 6; NW = no wind, W = simulated wind. Data are means +- s.e. $P_{\text{tem}}$ indicates a significant temperature effect and $P_{\text{w}}$ a significant wind effect; **$P$ <0.01.

**Figure 3.** Effect of ambient temperature (21degC and 32.5degC) and wind on the relationship between asymptotic food intake and the body mass (A), milk energy output (MEO, B), litter size (C) and litter mass (D), of lactating, female striped hamsters (*Cricetulus barabensis* ). Females were housed at either 21degC or 32.5degC from Day 5 of the experiment and exposed to simulated wind from Day 6; NW = no wind, W = simulated wind. ** $P$ <0.01.

**Figure 4.** Effect of ambient temperature (21degC and 32.5degC) and wind on the relationship between milk energy output (MEO) and the body mass (A), litter size (B) and litter mass (C), of lactating, female striped hamsters (*Cricetulus barabensis* ). Females were housed at either 21degC or 32.5degC from Day 5 of the experiment and exposed to simulated wind from Day 6; NW = no wind, W = simulated wind. **$P$ <0.01.

**Figure 5** The effect of ambient temperature (21degC and 32.5degC) and wind on the litter size (A), litter mass (B) and pup mass (C), of lactating, female striped hamsters (*Cricetulus barabensis* ). Females were housed at either 21degC or 32.5degC from Day 5 of the experiment and exposed to simulated wind from Day 6. NW = no wind; W = simulated wind. Data are means +- s.e. $P_{\text{tem}}$ indicates the period in which there was a significant temperature effect and $P_{\text{w}}$ the period in which there was a significant wind effect; *$P$ <0.05, **$P$ <0.01.

**Figure 6** The effect of temperature and wind on the water loss (A, B) and cooling rate of a plain glass vessel (C, D) and the cooling rate of a glass vessel wrapped in the fresh pelt (E, F) of a striped hamster (*Cricetulus barabensis* ). NW = no wind; W = simulated wind. Data are means +- s.e. $P_{\text{tem}}$ indicates the period in which there was a significant temperature effect and $P_{\text{w}}$ the period in which there was a significant wind effect; *, $P$ <0.05, **, $P$ <0.01.

**Figure 7.** Effect of ambient temperature (21degC or 32.5degC) on the number of pups moved by female striped hamsters (*Cricetulus barabensis* ) to sheltered cages (A) vs cages exposed to simulated wind (B), and the amount of time females spent in sheltered cages (C) vs cages exposed to simulated wind (D). Data are means +- s.e.

**Figure 8.** Effect of wind on the number of wild, lactating, female striped hamsters (*Cricetulus barabensis* ) captured in live traps on windy and calm days in spring and summer. (A) total number of females captured, (B) number of lactating females captured, and (C) percentage lactating females captured. Data are means +- s.e..$P_{\text{s}}$ indicates significant seasonal effects and $P_{\text{w}}$ significant wind effects; *$P$ <0.05, **$P$ <0.01.

**Figure S1** The effect of ambient temperature (21degC or 32.5degC) on the amount of time striped hamster (*Cricetulus barabensis* ) pups spent in cages that were exposed to simulated wind (green rectangles) or sheltered cages (brown rectangles), or both (grey rectangles). Each rectangle represents 10 min.

**Figure S2** The effect of ambient temperature (21degC or 32.5degC) on the amount of time that lactating, female striped hamsters (*Cricetulus barabensis* ) spent in cages that were exposed to simulated wind (green rectangles) or sheltered cages (brown rectangles). Each rectangle represents 10 min.

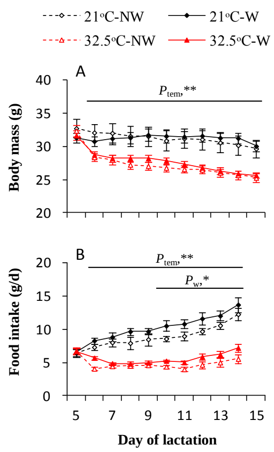


**Figure 1**

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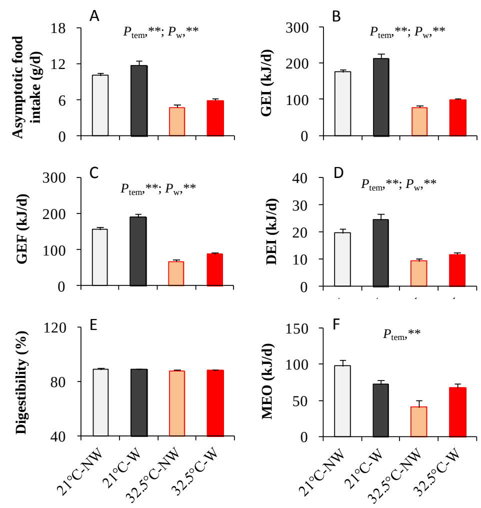


Figure 2

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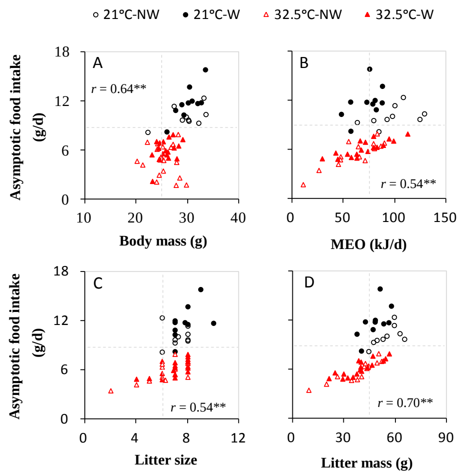


Figure 3

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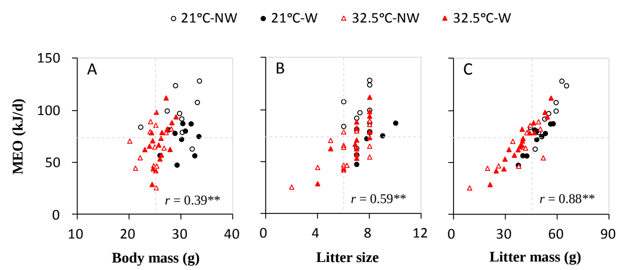


Figure 4

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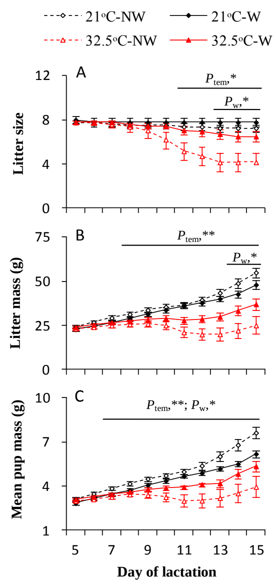


**Figure 5**

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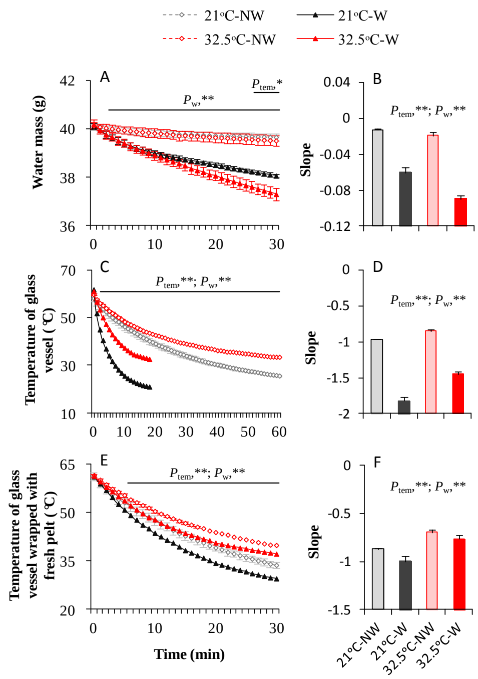


**Figure 6**

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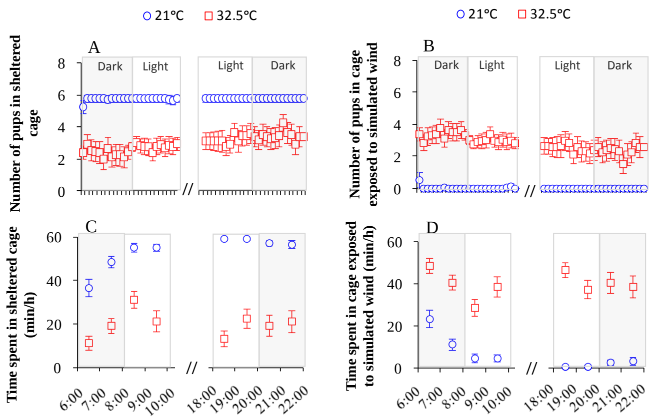


Figure 7

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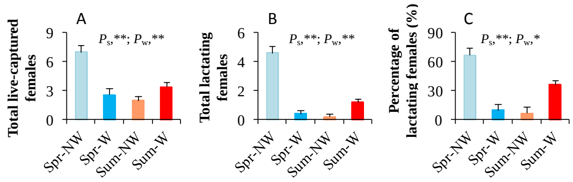


**Figure 8**

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