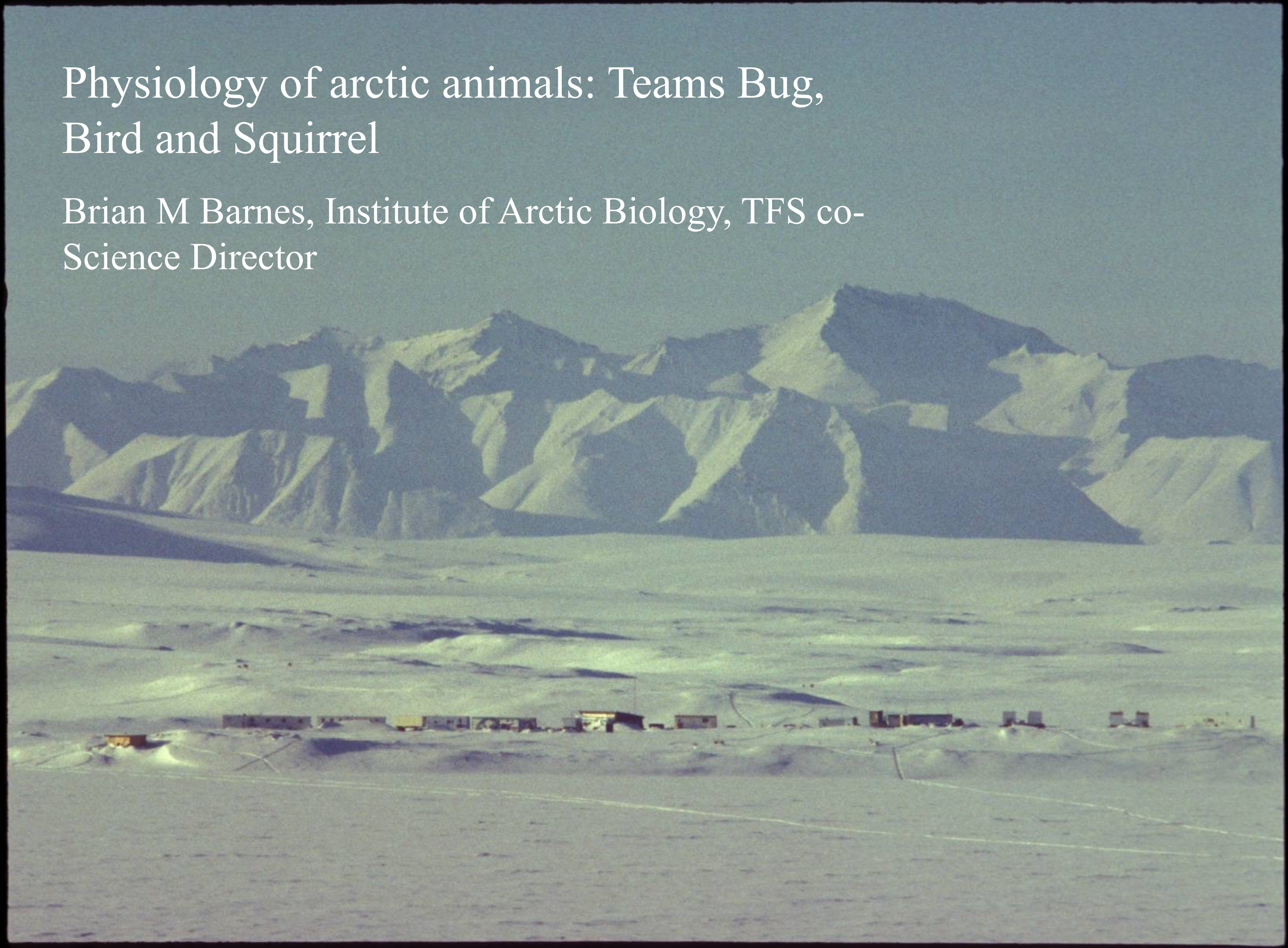
Physiology of arctic animals: Teams Bug, Bird and Squirrel

Brian M Barnes, Institute of Arctic Biology, TFS co-Science Director



Strategies for overwintering in the Arctic

- Stay active
- **Hibernate**
  - **remain at body temperatures > $0^{o}C$**
    - ❖ **endothermy**
    - ❖ **thermal refugia**
  - **cope with body temperatures < $0^{o}C$**
    - ❖ **freeze tolerance**
    - ❖ **freeze avoiding**
      - supercooling
      - antifreeze

Team Bug:

Team Bug

Jack Duman Valerie Bennett
Todd Sformo Kent Walters
Brian Barnes

Walters Jr, K, Sformo, T, Barnes, BM and Duman, JG, 2009. Freeze tolerance in an arctic Alaska stonefly. *Journal of Experimental Biology*, *212*(2), pp.305-312.
Duman JG, VA Bennett, R. Hochstrasser, T Sformo, BM Barnes (2004) Antifreeze proteins in Alaskan insects and spiders. *J Insect Physiol* 50:259-266.

Freeze and ice tolerant Stoneflies, *Nemoura arctica*

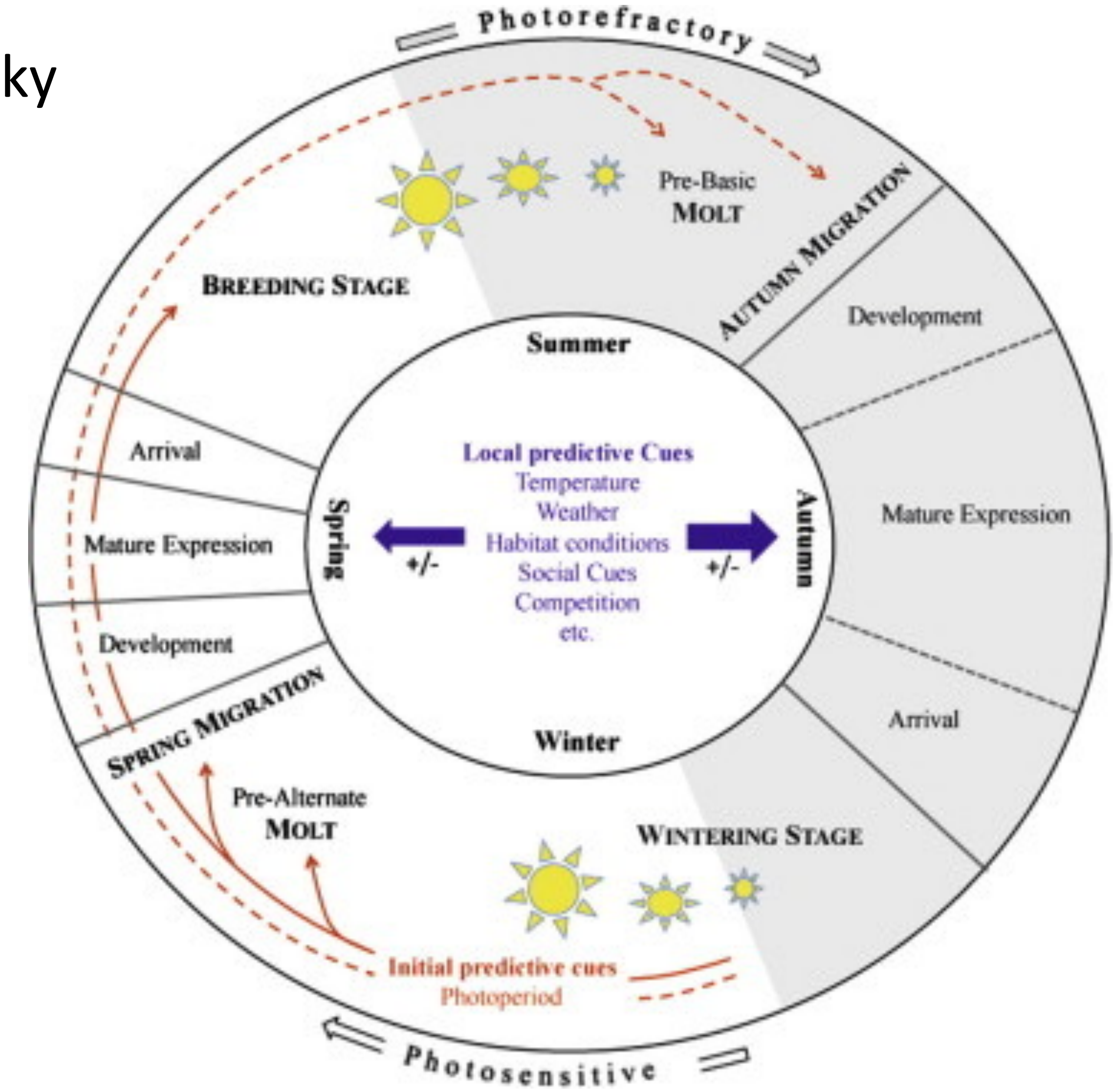
First report of freeze tolerance in aquatic invert. Last instar nymphs survive encased in ice to -15 C; thaw in spring, synchronized emergence as adults within one month.

Team Bird

John Wingfield

Marilyn Ramenofsky

JS Krause
HE Chmura
SL Meddle
KE Hunt
JH Perez
LM Romero
NT Ashley
LB Astheimer
WA Buttemer
Z Nemeth
S Bodine
SW Wood



Laura Gough
Natelie Boelman

JC Wingfield et al.

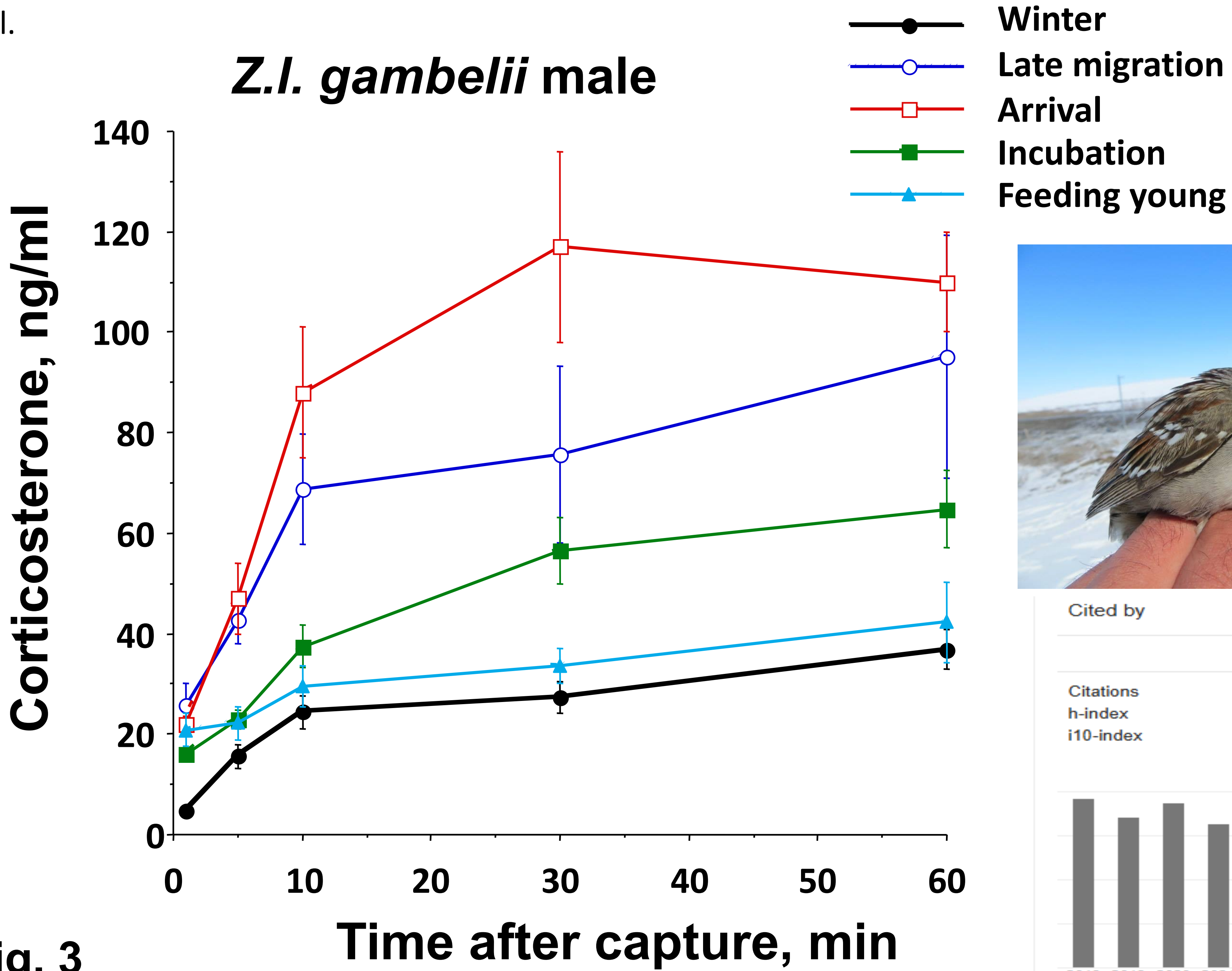
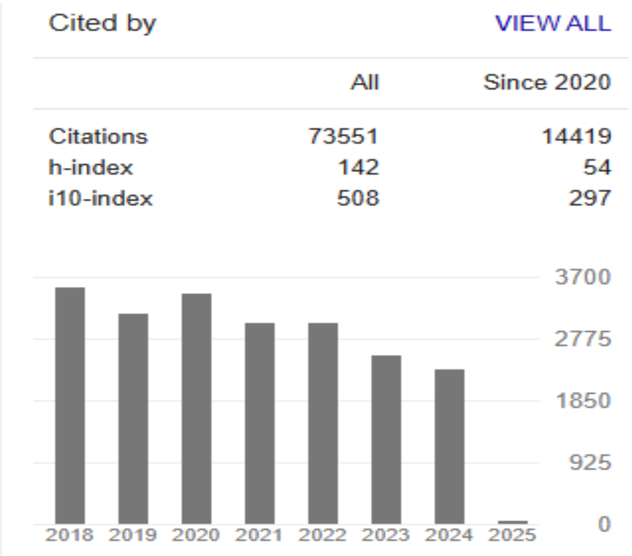


Fig. 3

High expression of heat shock protein in brain enhances stress response.



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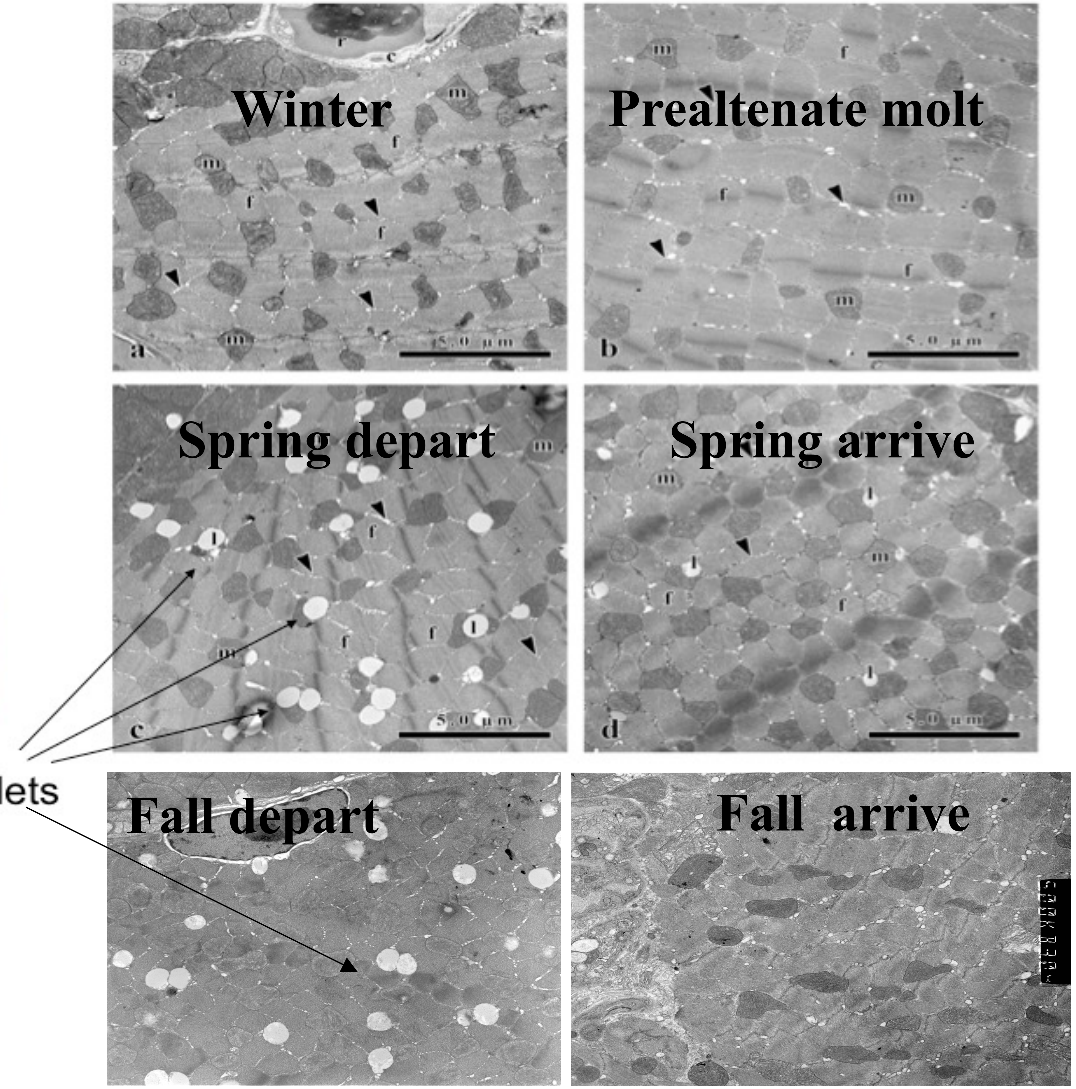
Citations	73551	14419
h-index	142	54
i10-index	508	297

Fat deposition by stage in flight muscle of migrant White-crowned Sparrow

Ramenofsky, M., Campion, A.W., Hwee, D.T., Wood, S.K., Krause, J.S., Németh, Z., Pérez, J.H. and Bodine, S., 2024. Comparison of the Phenotypic Flexibility of Muscle and Body Condition of Migrant and Resident White-Crowned Sparrows. *Ecological and Evolutionary Physiology*, *97*(1), pp.11-28.

Pectoral muscle histology



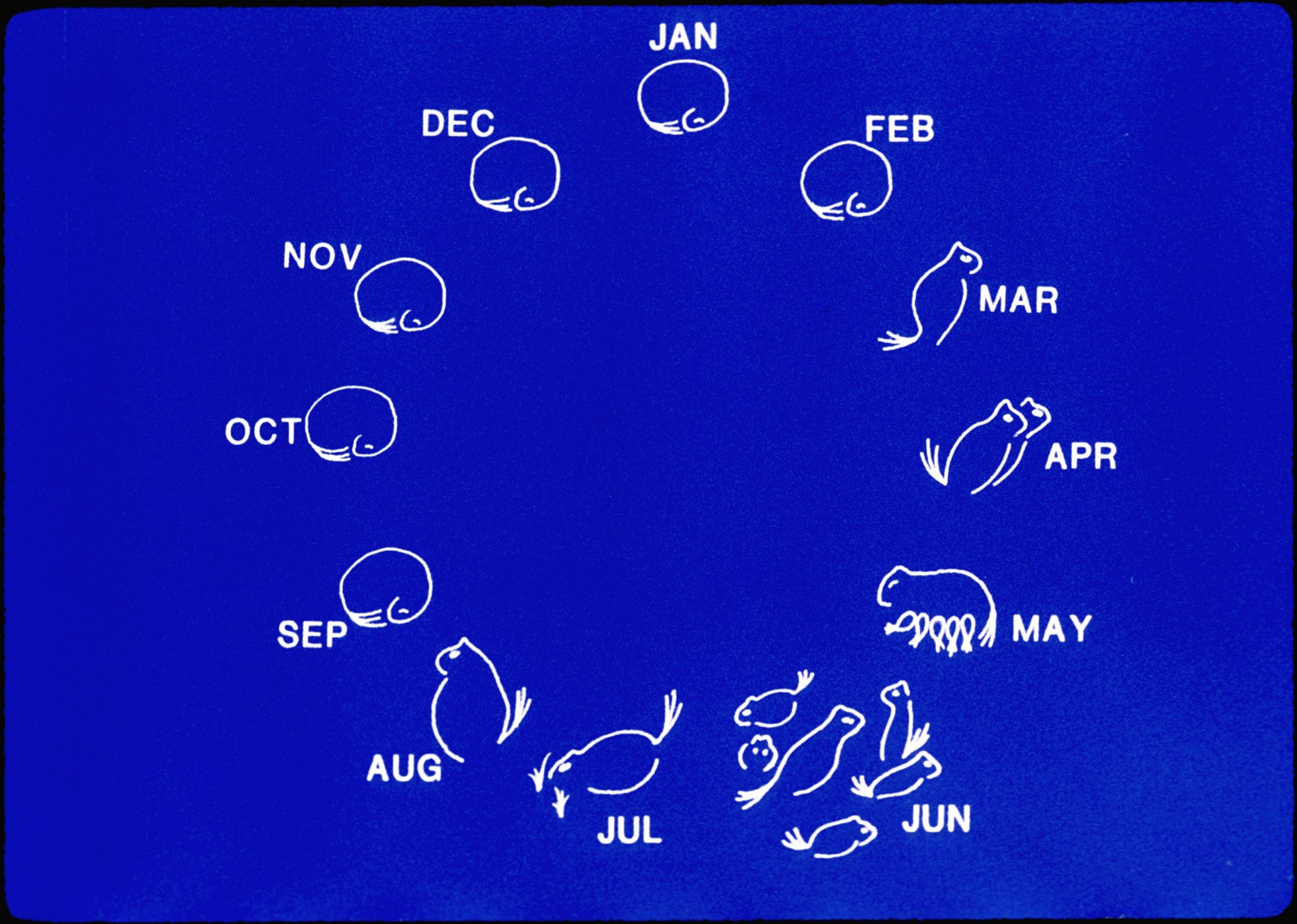
lipid droplets

Toolik Field Station

Institute of Arctic Biology

Team Squirrel:

Loren Buck
Fran Kohl
Cory Williams
Shawna Karpovich
Michael Sheriff
Oivind Toien
Sarah Wilbur
Ryan Long
Jeanette Moore
Jun Yan
Andree Porchet
Alison York
Brian Barnes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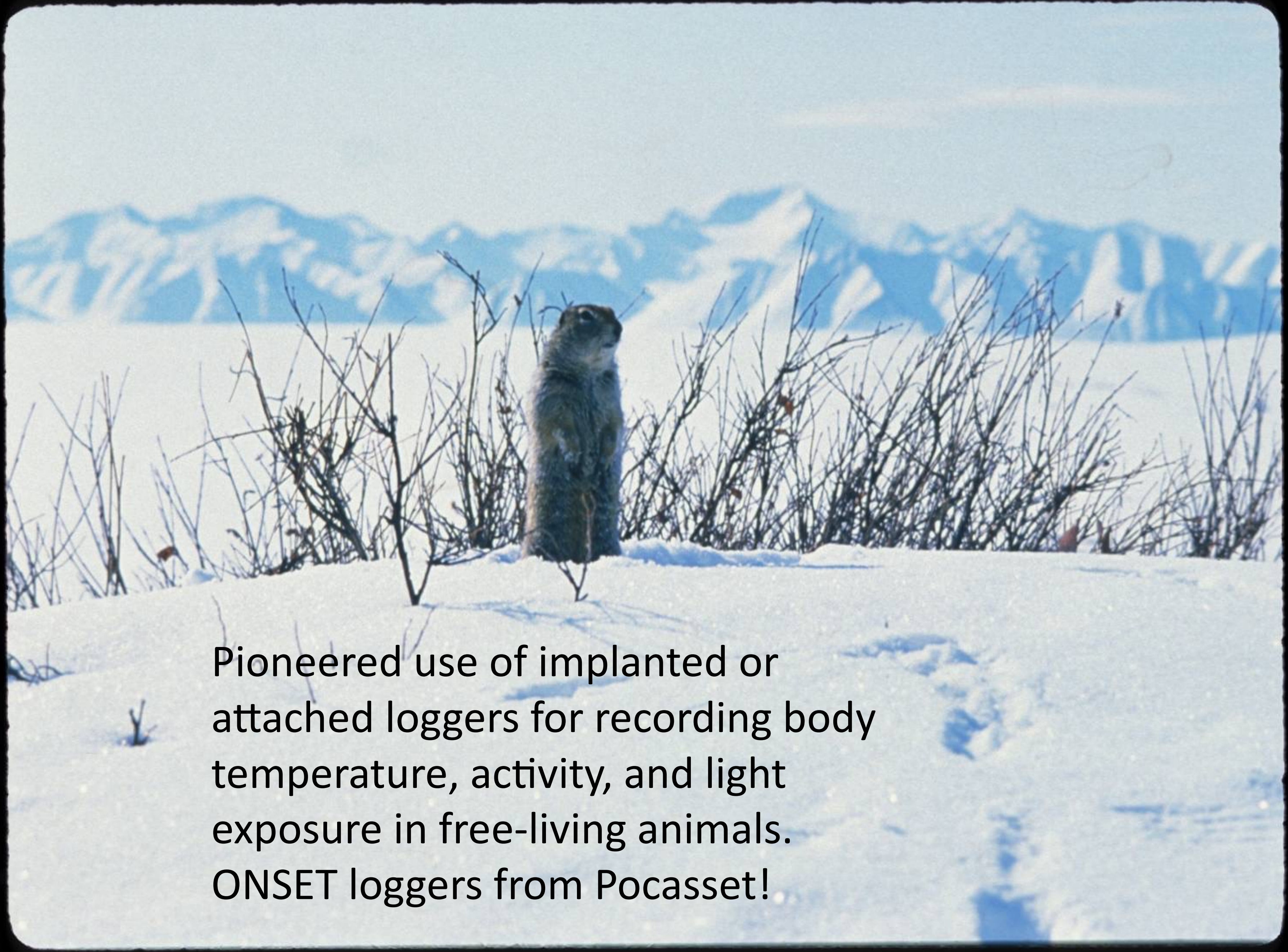
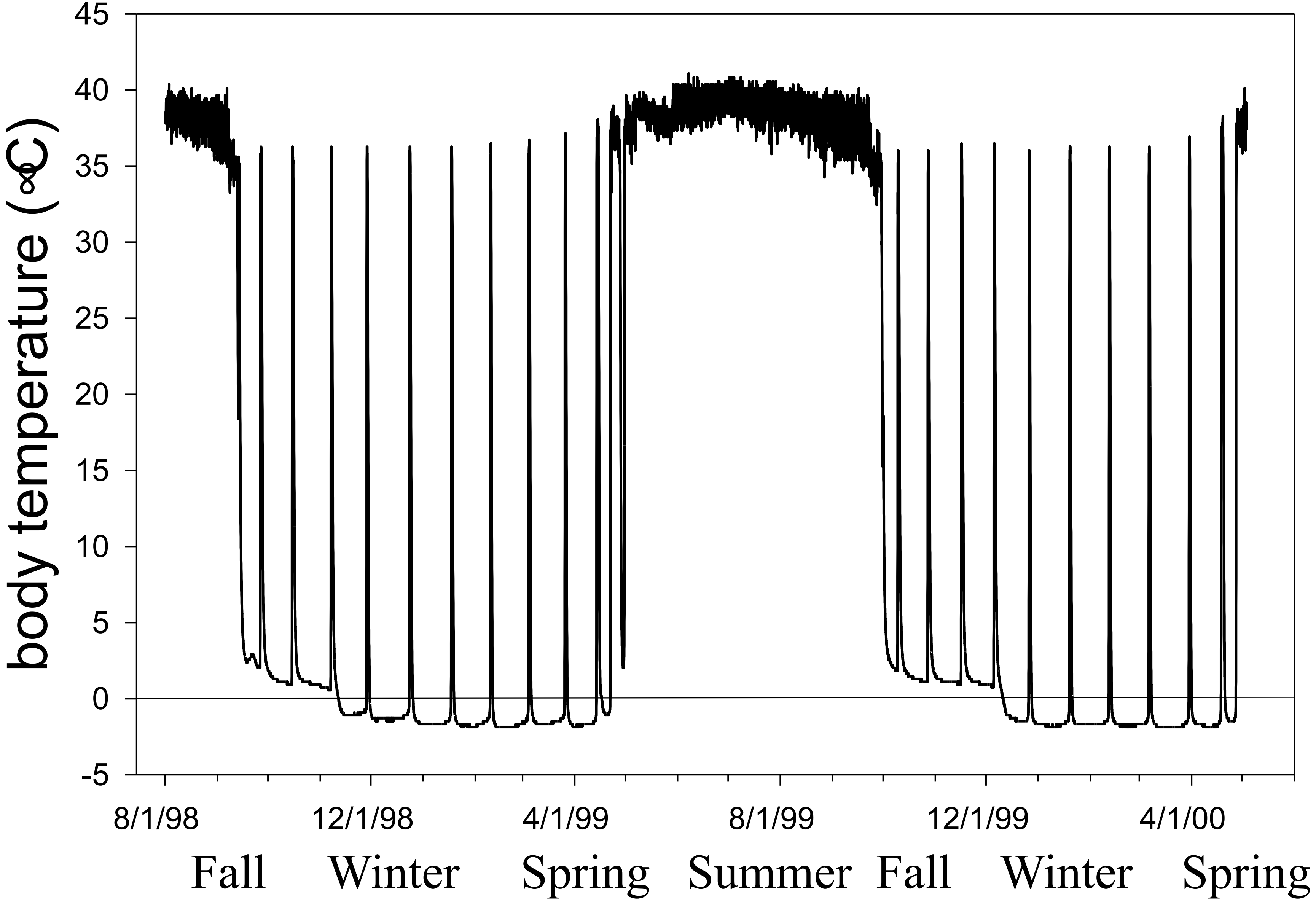
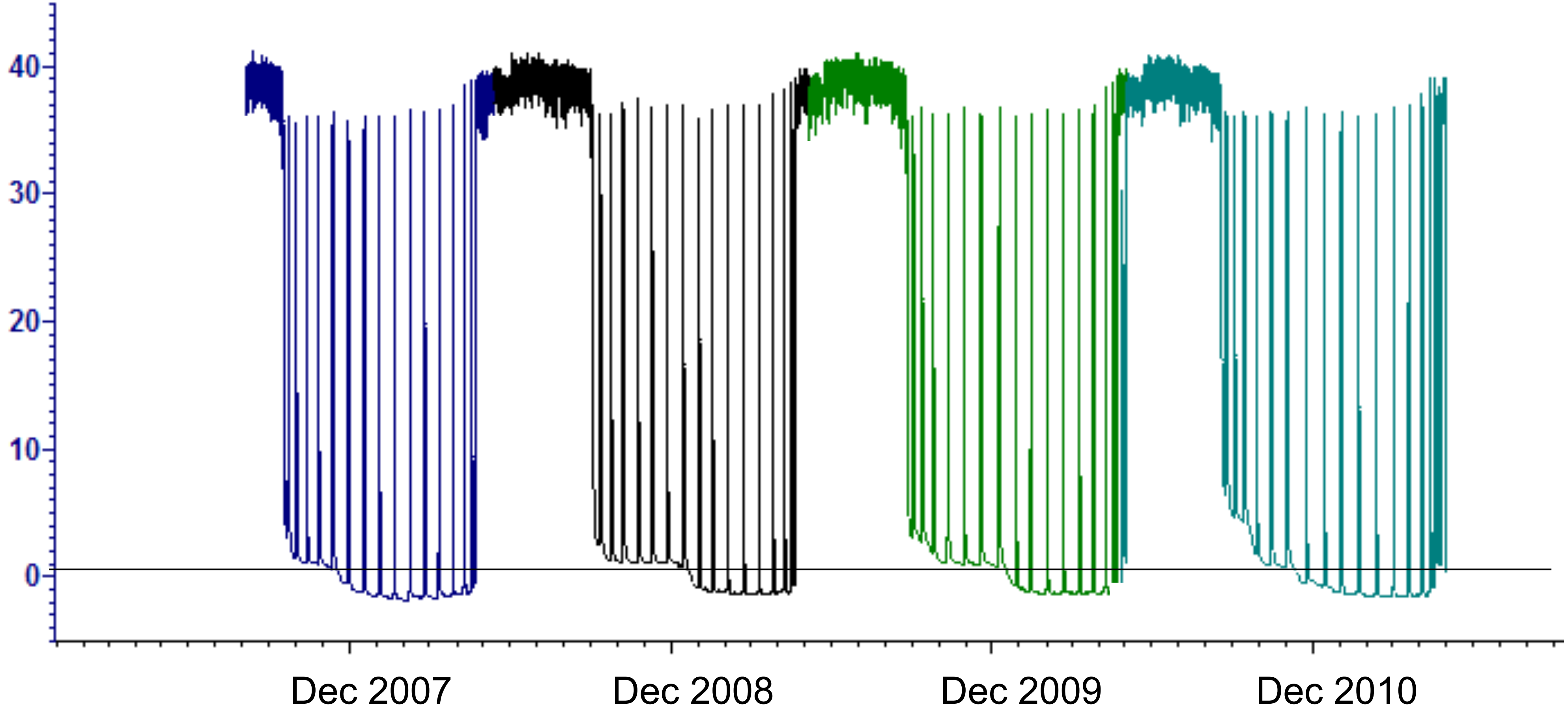

Pioneered use of implanted or
attached loggers for recording body
temperature, activity, and light
exposure in free-living animals.
ONSET loggers from Pocasset!

Two year record of body temperatures of a free-living arctic ground squirrel in northern Alaska

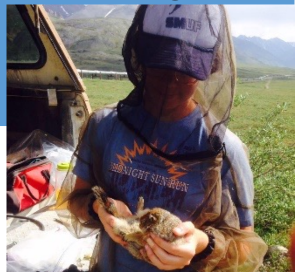


LIFE STORY OF FEMALE 627

>75% of life is spent underground; 25% at body temperatures lower than that of an ice cube



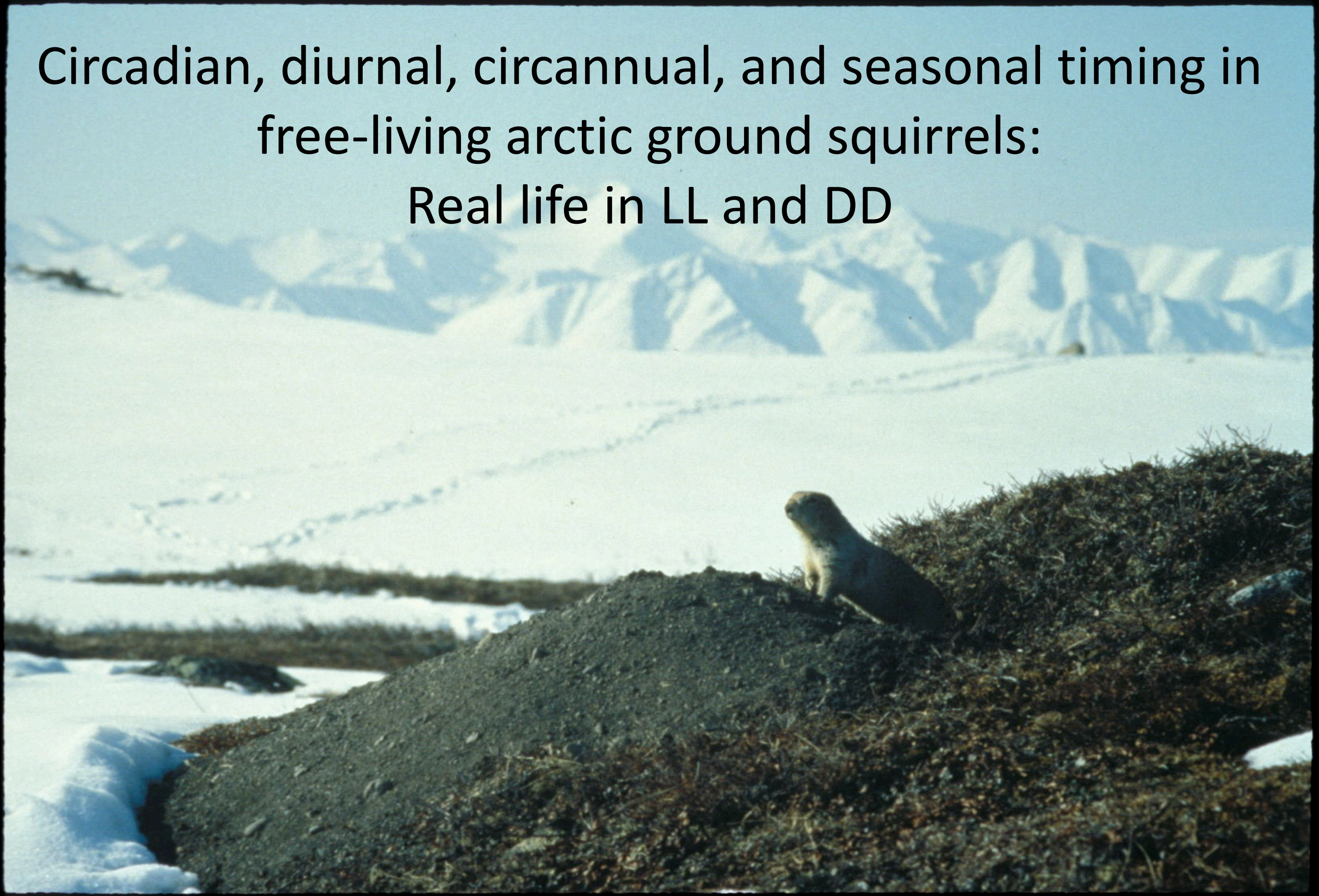
Wilbur Sarah, Deane Cody…Barnes BM et al. "Survival estimates of free-living arctic ground squirrels (*Urocitellus parryii*): effects of sex and biologging." *Canadian Journal of Zoology* 100.4 (2022): 251-260.



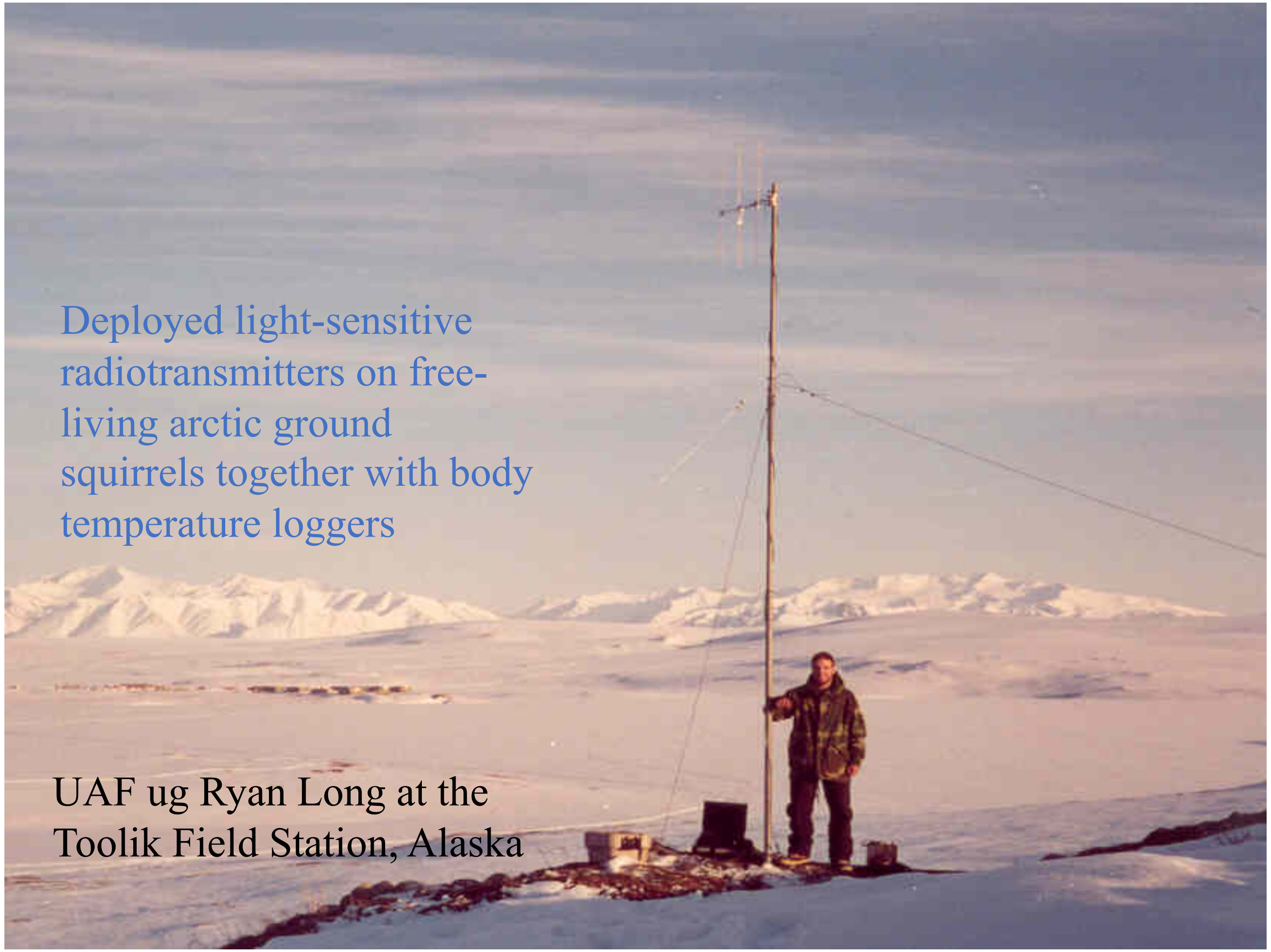
Arctic ground squirrels decrease core body temperature to -3.0 °C.

Barnes BM (1989) Freeze avoidance in mammals: Body temperatures below 0°C in an arctic hibernator. *Science* 244:1593-1595

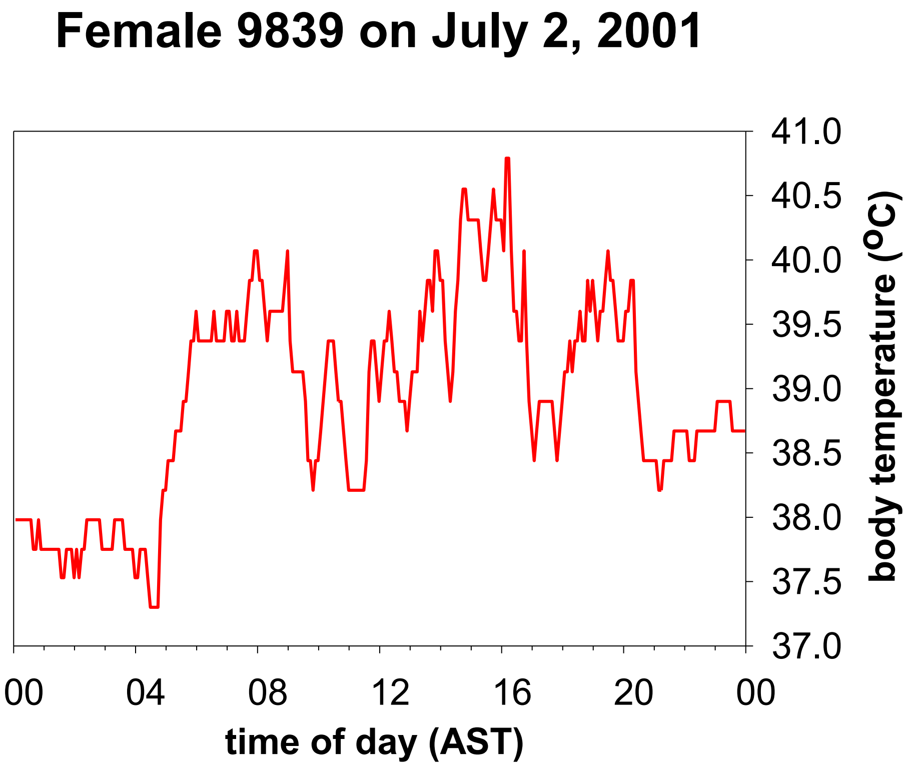
Circadian, diurnal, circannual, and seasonal timing in free-living arctic ground squirrels: Real life in LL and DD



arctic ground squirrel, *Urocitellus parryii*


Deployed light-sensitive radiotransmitters on free-living arctic ground squirrels together with body temperature loggers
UAF ug Ryan Long at the Toolik Field Station, Alaska

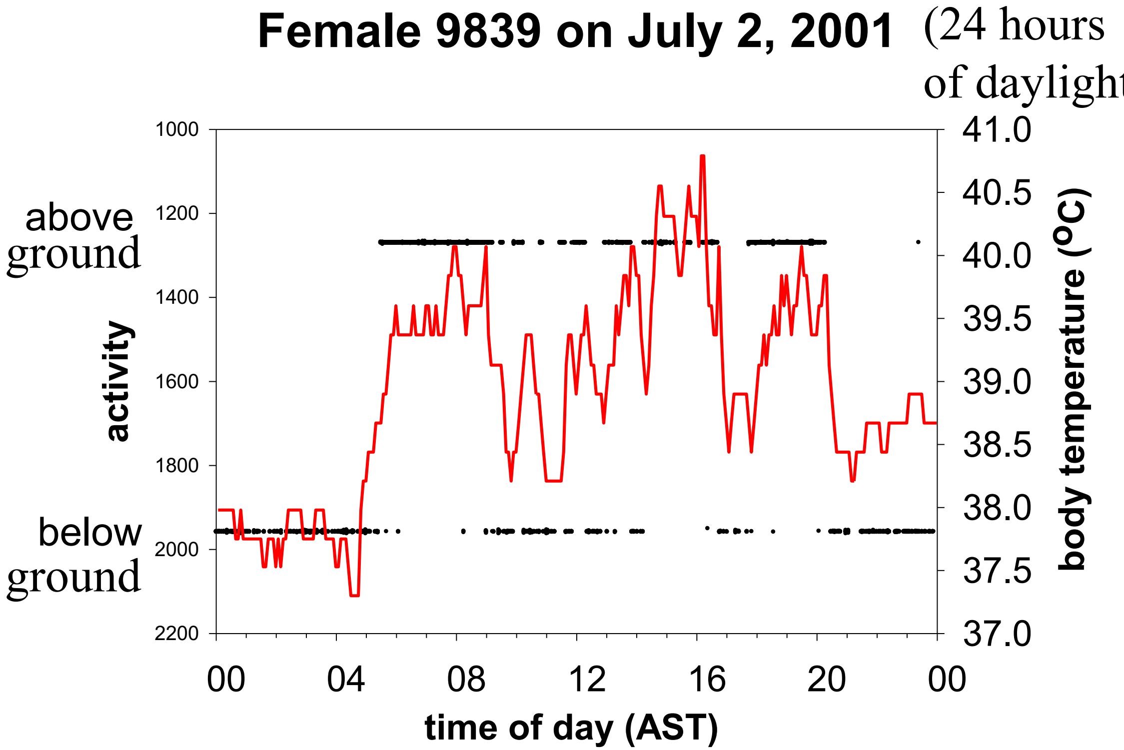
Te>38^{o}C



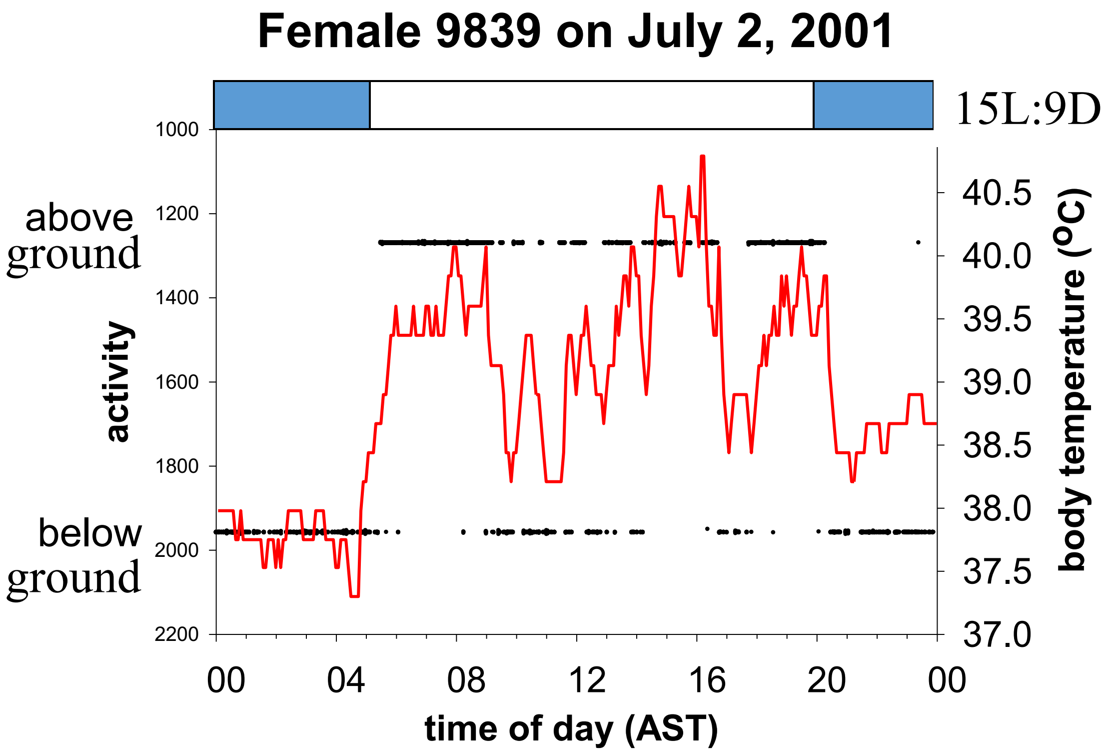
Female 9839 on July 2, 2001
41.0
40.5
40.0
39.5
39.0
38.5
38.0
37.5
37.0
body temperature (^{o}C)
00
04
08
12
16
20
00
time of day (AST)

Te>38^{o}C

(24 hours of daylight)

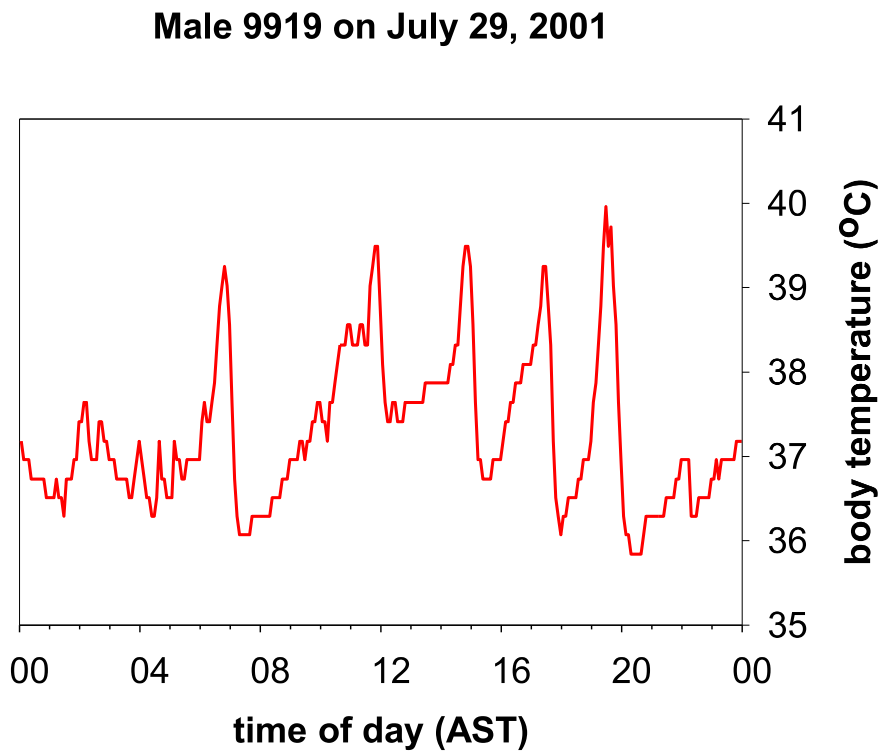


Te>38°C

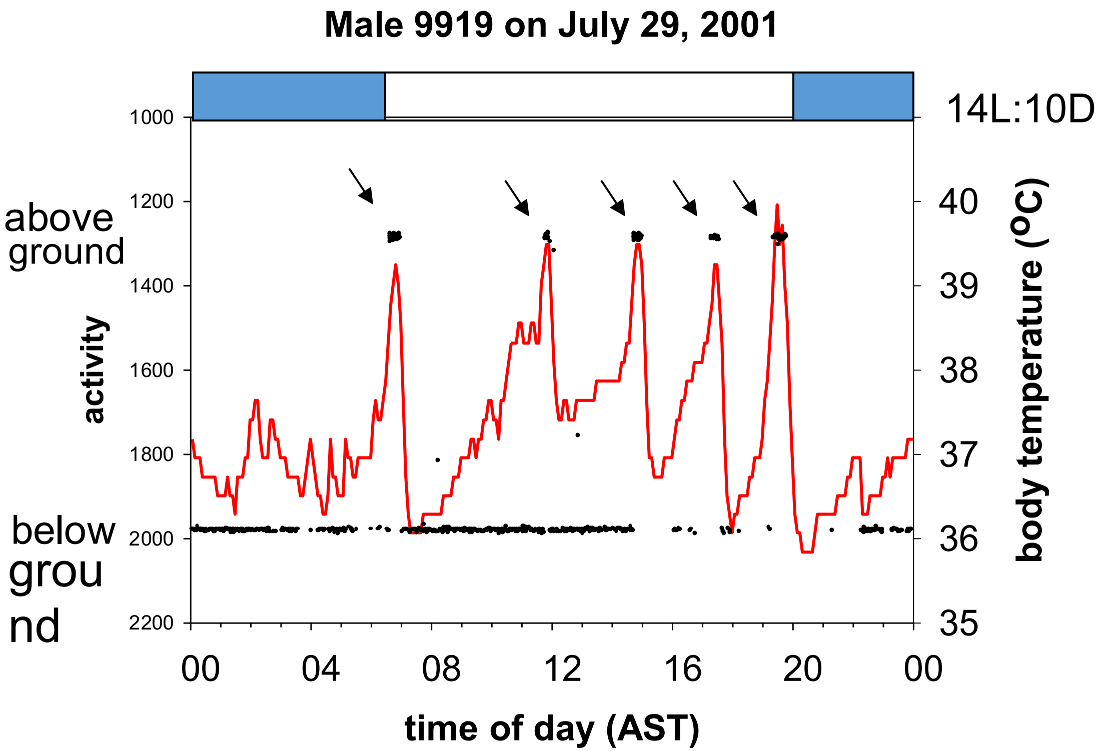


Female 9839 on July 2, 2001
15L:9D
above ground
below ground
activity
1000
1200
1400
1600
1800
2000
2200
body temperature (°C)
40.5
40.0
39.5
39.0
38.5
38.0
37.5
37.0
00
04
08
12
16
20
00
time of day (AST)

Te<10^{o}C


Male 9919 on July 29, 2001
41
40
39
38
37
36
35
body temperature (^{o}C)
00
04
08
12
16
20
00
time of day (AST)

Te<10^{o}C

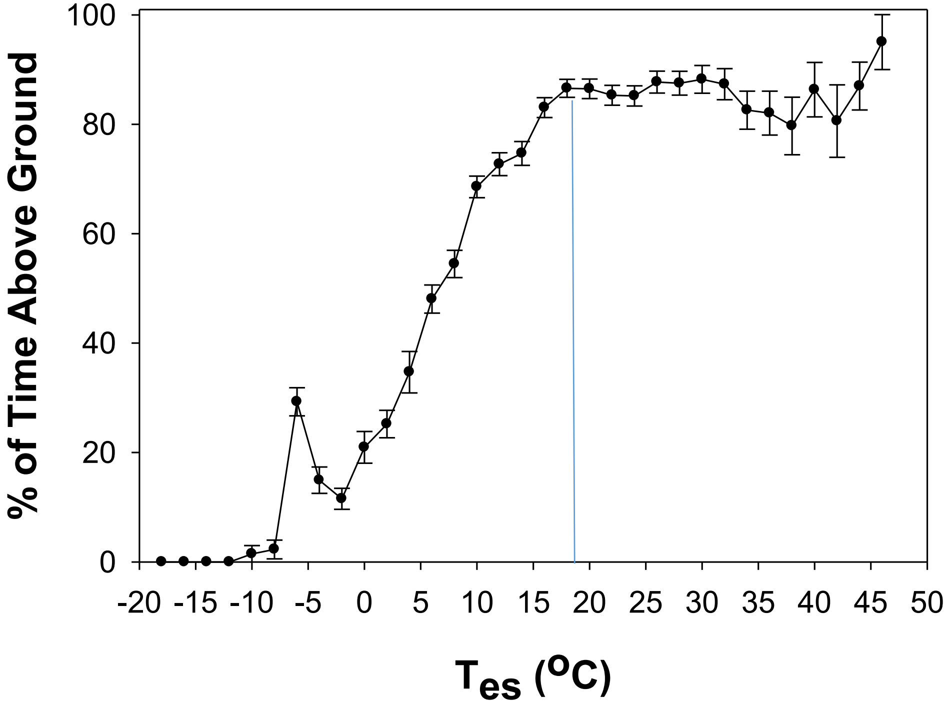


Arctic ground squirrels elevate their body temperature prior to emerging to the surface. Why?

The above-ground thermal environment influences time spent above ground by arctic ground squirrels.

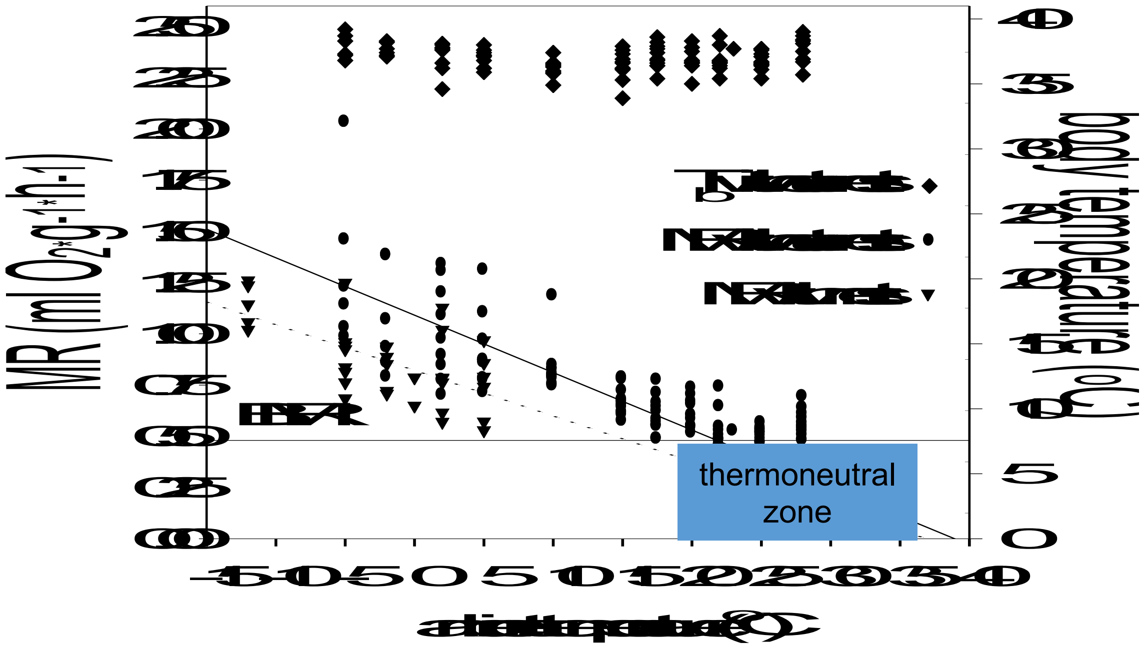
5am-10pm

May-Aug

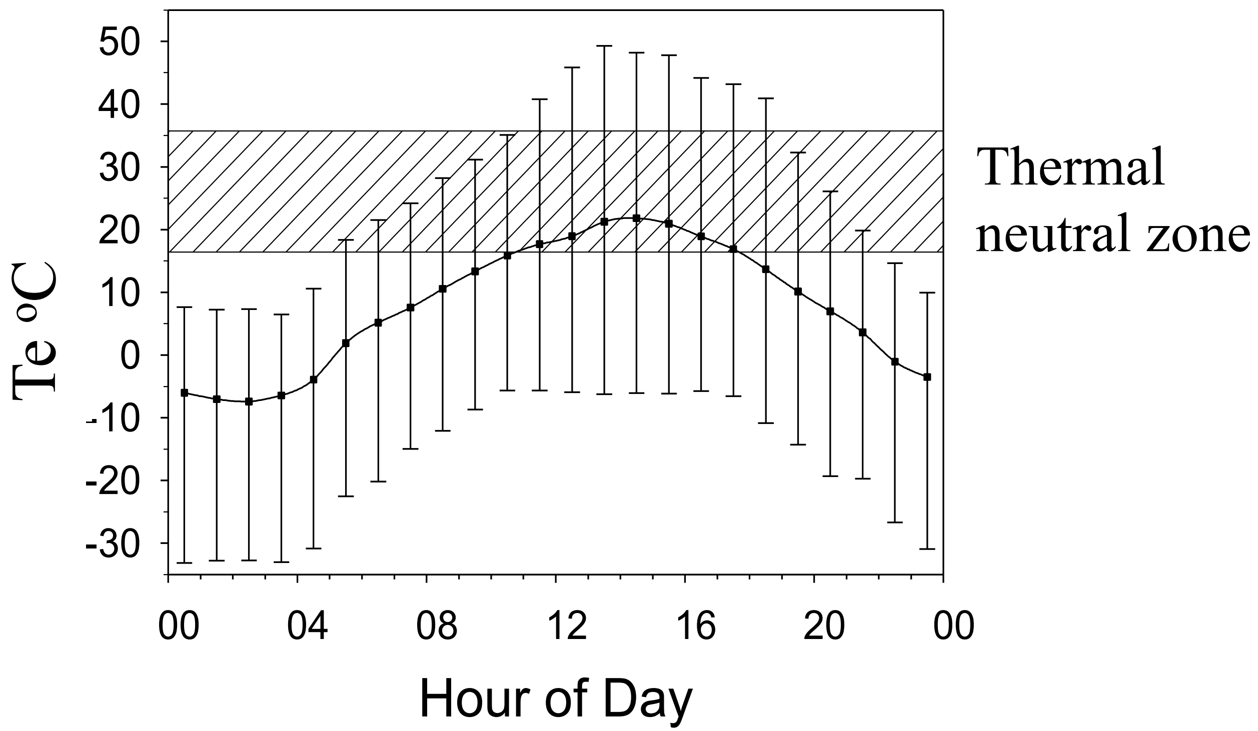


R Long, T Martin, BM Barnes, *J. Mammal* (2006)

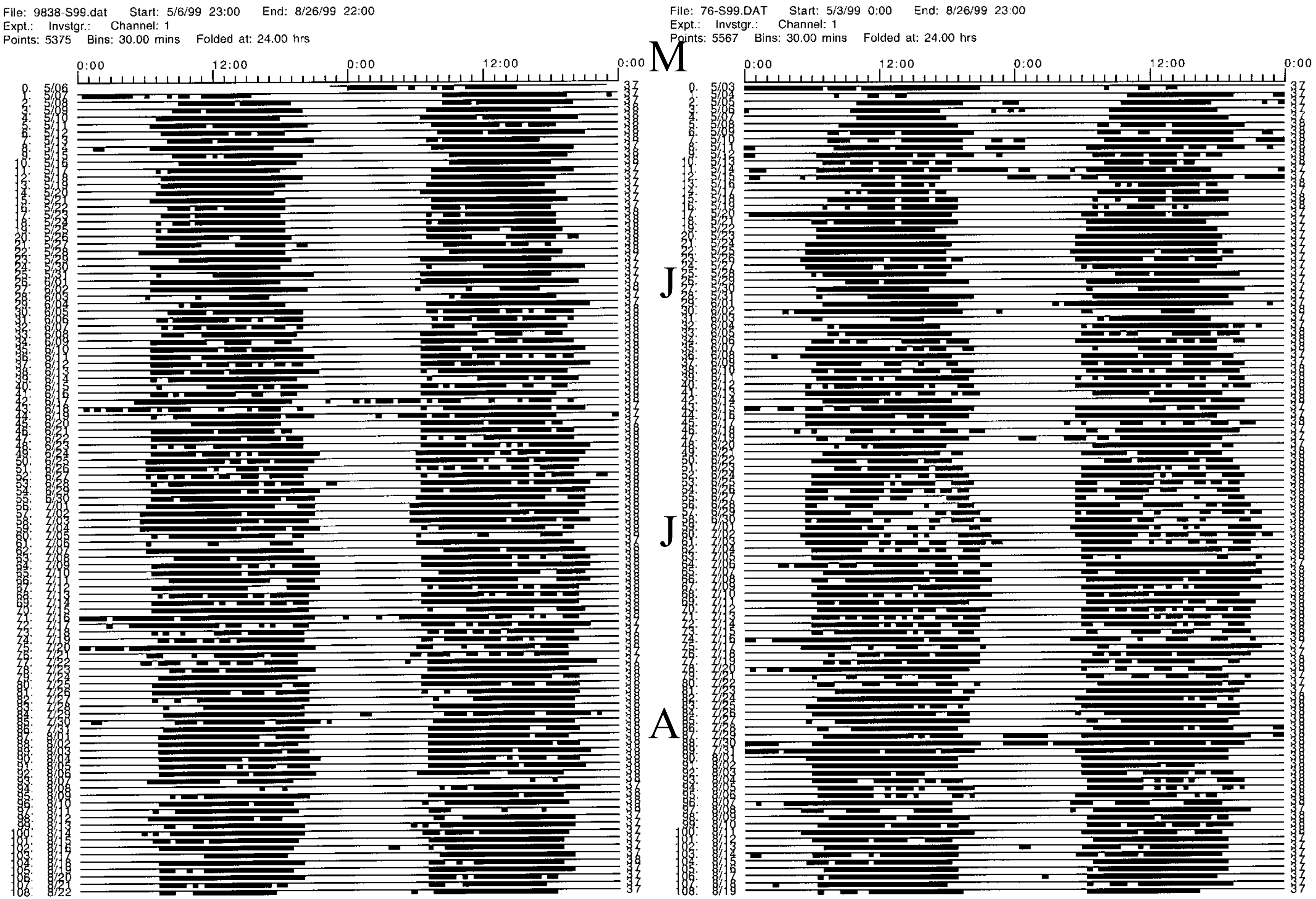
Metabolic Rate (MR) versus ambient temperature (Scholander curve) in arctic ground squirrels.



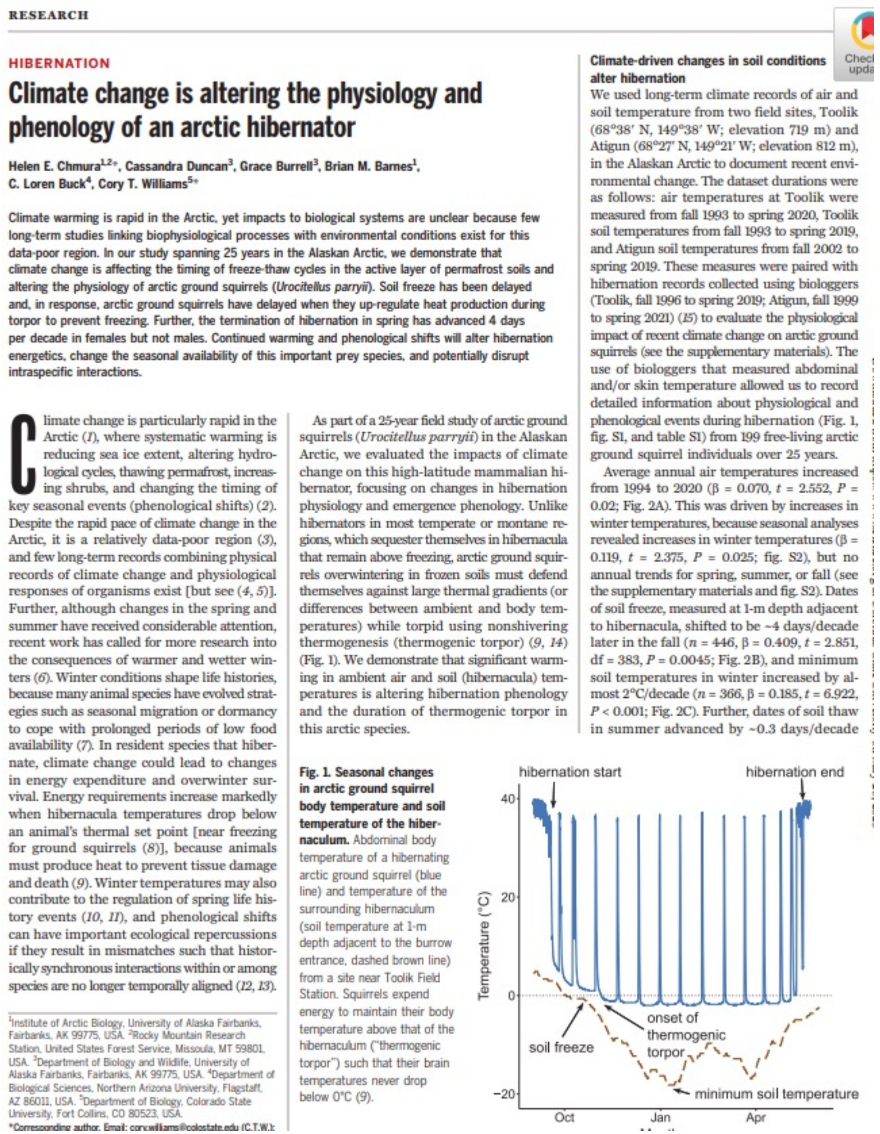
Distribution of environmental temperatures throughout the 24-h cycle.



arctic ground squirrels – timing of body temperature peaks May-Aug



Climate change is altering the physiology and phenology of an arctic hibernator.



RESEARCH

HIBERNATION

Climate change is altering the physiology and phenology of an arctic hibernator

Helen E. Chmura[1,2*], Cassandra Duncan[3], Grace Burrell[3], Brian M. Barnes[1], C. Loren Buck[4], Cory T. Williams[5*]

Climate warming is rapid in the Arctic, yet impacts to biological systems are unclear because few long-term studies linking biophysiological processes with environmental conditions exist for this data-poor region. In our study spanning 25 years in the Alaskan Arctic, we demonstrate that climate change is affecting the timing of freeze-thaw cycles in the active layer of permafrost soils and altering the physiology of arctic ground squirrels (*Urocitellus parryii*). Soil freeze has been delayed and, in response, arctic ground squirrels have delayed when they up-regulate heat production during torpor to prevent freezing. Further, the termination of hibernation in spring has advanced 4 days per decade in females but not males. Continued warming and phenological shifts will alter hibernation energetics, change the seasonal availability of this important prey species, and potentially disrupt intraspecific interactions.

Climate change is particularly rapid in the Arctic (*1*), where systematic warming is reducing sea ice extent, altering hydrological cycles, thawing permafrost, increasing shrubs, and changing the timing of key seasonal events (phenological shifts) (*2*). Despite the rapid pace of climate change in the Arctic, it is a relatively data-poor region (*3*), and few long-term records combining physical records of climate change and physiological responses of organisms exist [but see (*4*, *5*)]. Further, although changes in the spring and summer have received considerable attention, recent work has called for more research into the consequences of warmer and wetter winters (*6*). Winter conditions shape life histories, because many animal species have evolved strategies such as seasonal migration or dormancy to cope with prolonged periods of low food availability (*7*). In resident species that hibernate, climate change could lead to changes in energy expenditure and overwinter survival. Energy requirements increase markedly when hibernacula temperatures drop below an animal's thermal set point [near freezing for ground squirrels (*8*)], because animals must produce heat to prevent tissue damage and death (*9*). Winter temperatures may also contribute to the regulation of spring life history events (*10*, *11*), and phenological shifts can have important ecological repercussions if they result in mismatches such that historically synchronous interactions within or among species are no longer temporally aligned (*12*, *13*).

As part of a 25-year field study of arctic ground squirrels (*Urocitellus parryii*) in the Alaskan Arctic, we evaluated the impacts of climate change on this high-latitude mammalian hibernator, focusing on changes in hibernation physiology and emergence phenology. Unlike hibernators in most temperate or montane regions, which sequester themselves in hibernacula that remain above freezing, arctic ground squirrels overwintering in frozen soils must defend themselves against large thermal gradients (or differences between ambient and body temperatures) while torpid using nonshivering thermogenesis (thermogenic torpor) (*9*, *14*) (Fig. 1). We demonstrate that significant warming in ambient air and soil (hibernacula) temperatures is altering hibernation phenology and the duration of thermogenic torpor in this arctic species.

Fig. 1. Seasonal changes in arctic ground squirrel body temperature and soil temperature of the hibernaculum. Abdominal body temperature of a hibernating arctic ground squirrel (blue line) and temperature of the surrounding hibernaculum (soil temperature at 1-m depth adjacent to the burrow entrance, dashed brown line) from a site near Toolik Field Station. Squirrels expend energy to maintain their body temperature above that of the hibernaculum ("thermogenic torpor") such that their brain temperatures never drop below 0°C (*9*).

Climate-driven changes in soil conditions alter hibernation

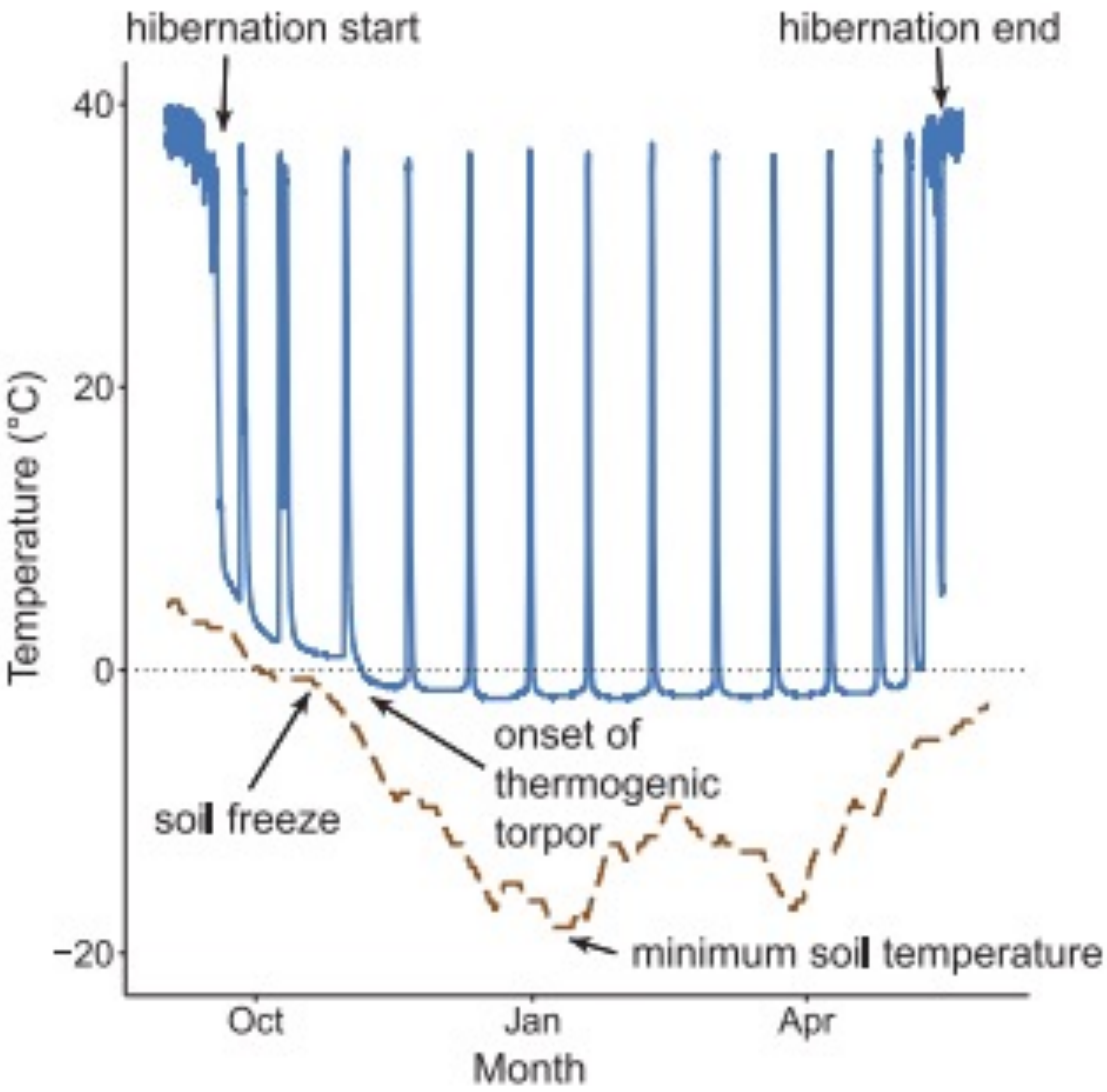
We used long-term climate records of air and soil temperature from two field sites, Toolik (68°38′ N, 149°38′ W; elevation 719 m) and Atigun (68°27′ N, 149°21′ W; elevation 812 m), in the Alaskan Arctic to document recent environmental change. The dataset durations were as follows: air temperatures at Toolik were measured from fall 1993 to spring 2020, Toolik soil temperatures from fall 1993 to spring 2019, and Atigun soil temperatures from fall 2002 to spring 2019. These measures were paired with hibernation records collected using biologgers (Toolik, fall 1996 to spring 2019; Atigun, fall 1999 to spring 2021) (*15*) to evaluate the physiological impact of recent climate change on arctic ground squirrels (see the supplementary materials). The use of biologgers that measured abdominal and/or skin temperature allowed us to record detailed information about physiological and phenological events during hibernation (Fig. 1, fig. S1, and table S1) from 199 free-living arctic ground squirrel individuals over 25 years.

Average annual air temperatures increased from 1994 to 2020 ($\beta = 0.070$, $t = 2.552$, $P = 0.02$; Fig. 2A). This was driven by increases in winter temperatures, because seasonal analyses revealed increases in winter temperatures ($\beta = 0.119$, $t = 2.375$, $P = 0.025$; fig. S2), but no annual trends for spring, summer, or fall (see the supplementary materials and fig. S2). Dates of soil freeze, measured at 1-m depth adjacent to hibernacula, shifted to be ~4 days/decade later in the fall ($n = 446$, $\beta = 0.409$, $t = 2.851$, df = 383, $P = 0.0045$; Fig. 2B), and minimum soil temperatures in winter increased by almost 2°C/decade ($n = 366$, $\beta = 0.185$, $t = 6.922$, $P < 0.001$; Fig. 2C). Further, dates of soil thaw in summer advanced by ~0.3 days/decade

[1]Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA. [2]Rocky Mountain Research Station, United States Forest Service, Missoula, MT 59801, USA. [3]Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA. [4]Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA. [5]Department of Biology, Colorado State University, Fort Collins, CO 80523, USA.
*Corresponding author. Email: cory.williams@colostate.edu (C.T.W.);

Science 380:846-849 May 2023

Arctic ground squirrel burrow #22, Toolik Lake Alaska. Soil temperature loggers.

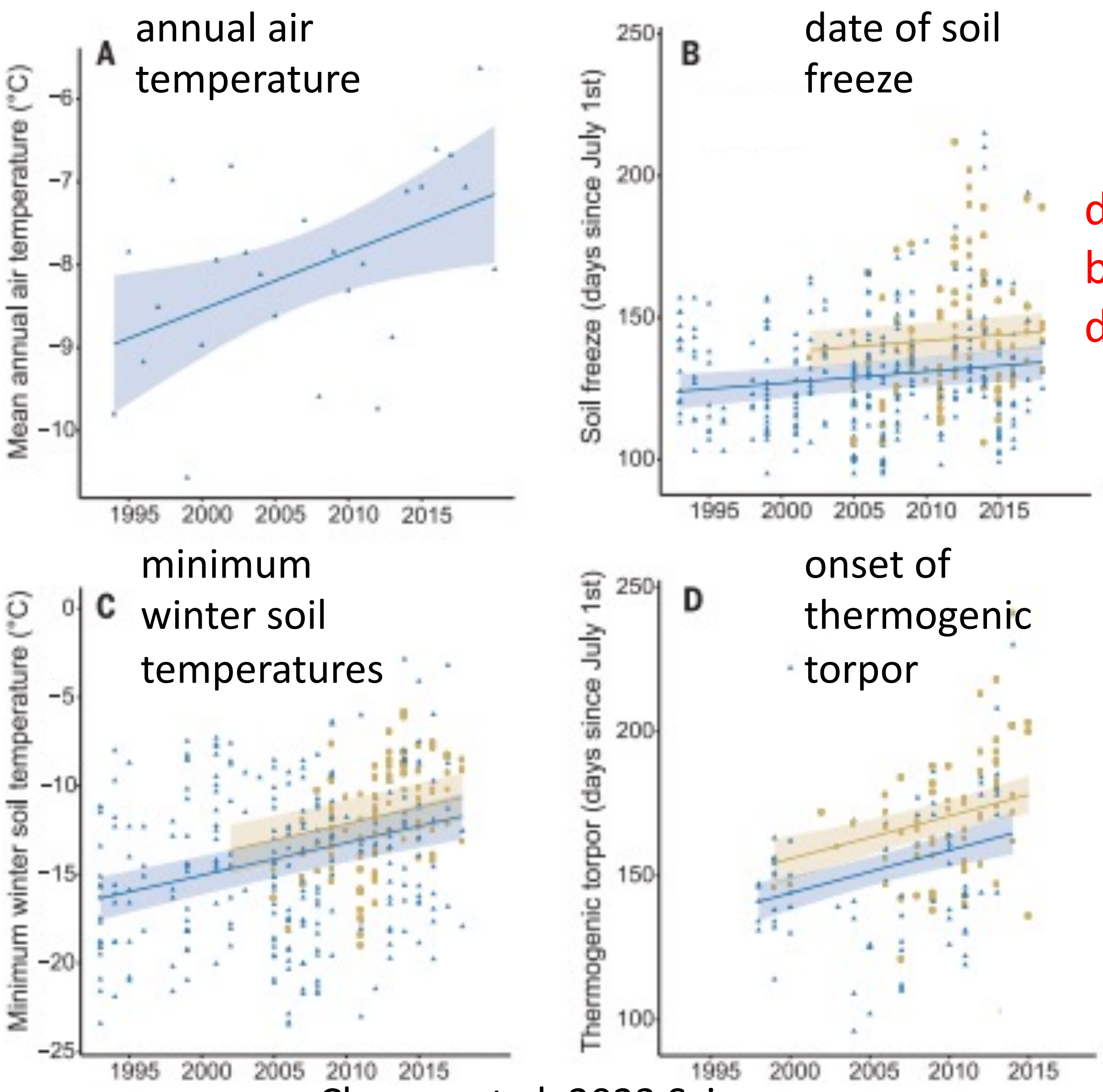


Chmura et al. *Science* 380:846-849 26 May 2023

Climate change over 25 years at the Toolik Field Station in northern Alaska

+ 1.5°C due to winter and fall only

+ 5°C



delayed by 10 days

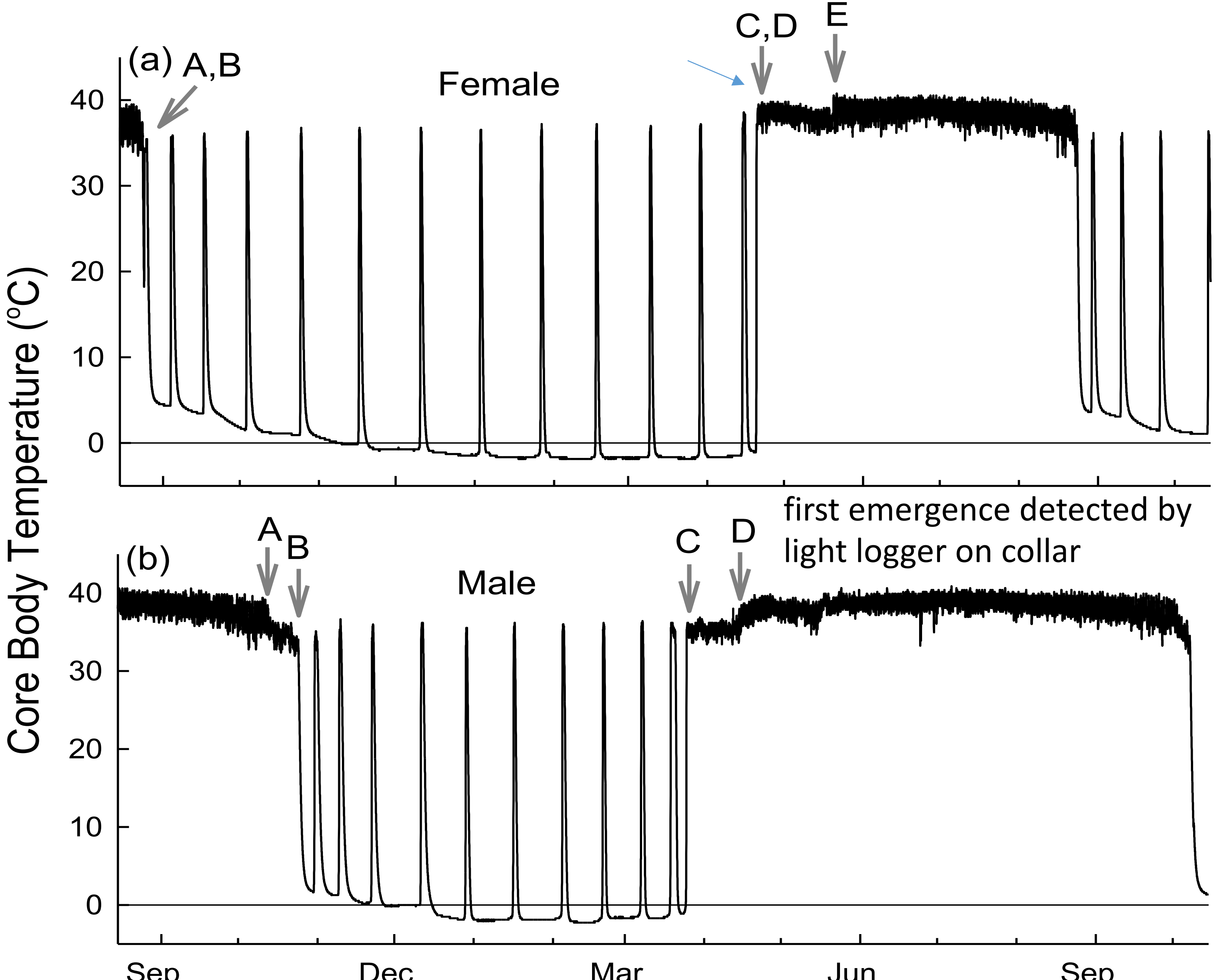
delayed by 35 days

Chmura et al. 2023 Science

Sex differences in hibernation phenology

A = entry

B =start of heterothermy

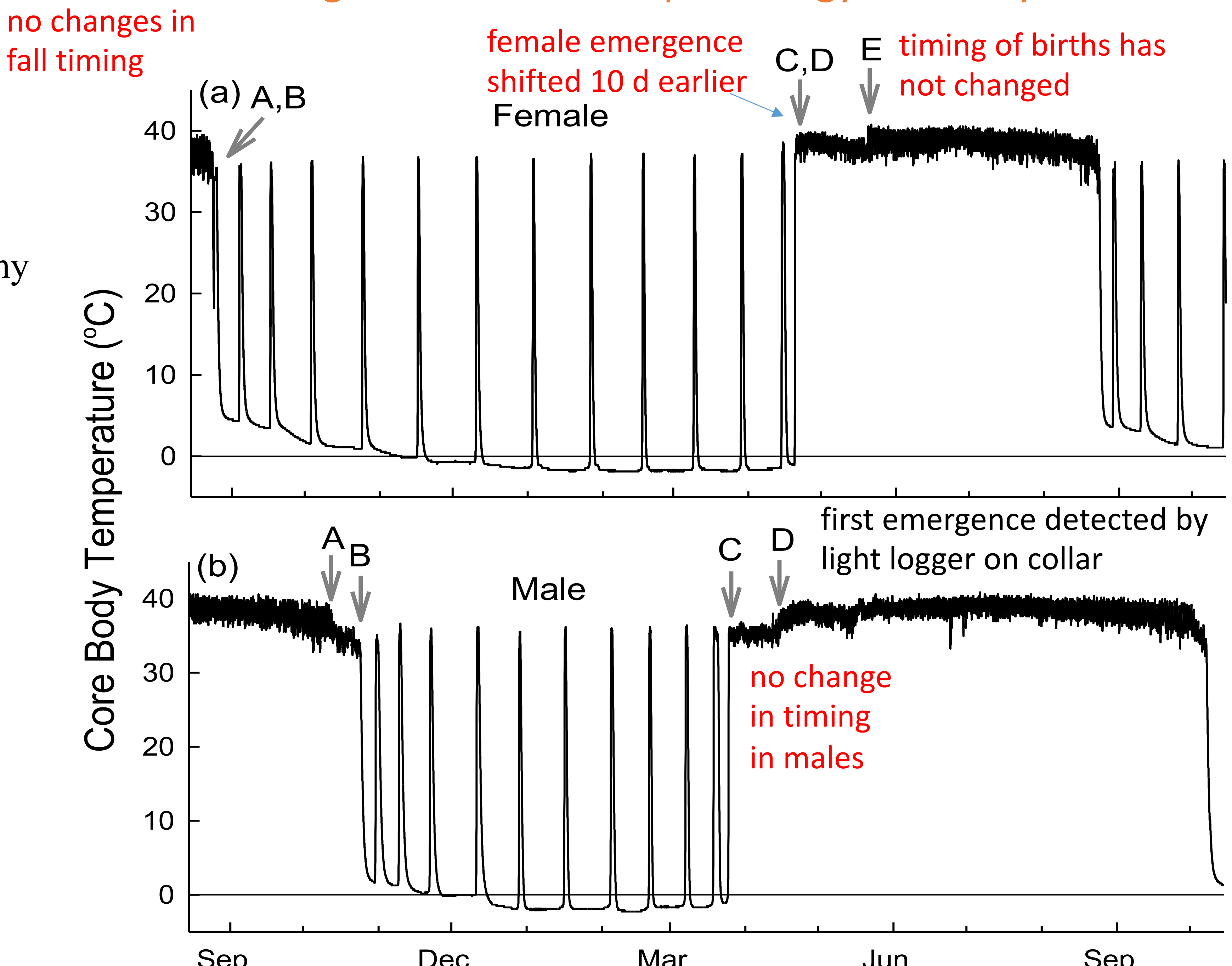


C = end of heterothermy

D = emergence

E = parturition

changes in hibernation phenology over 25 years



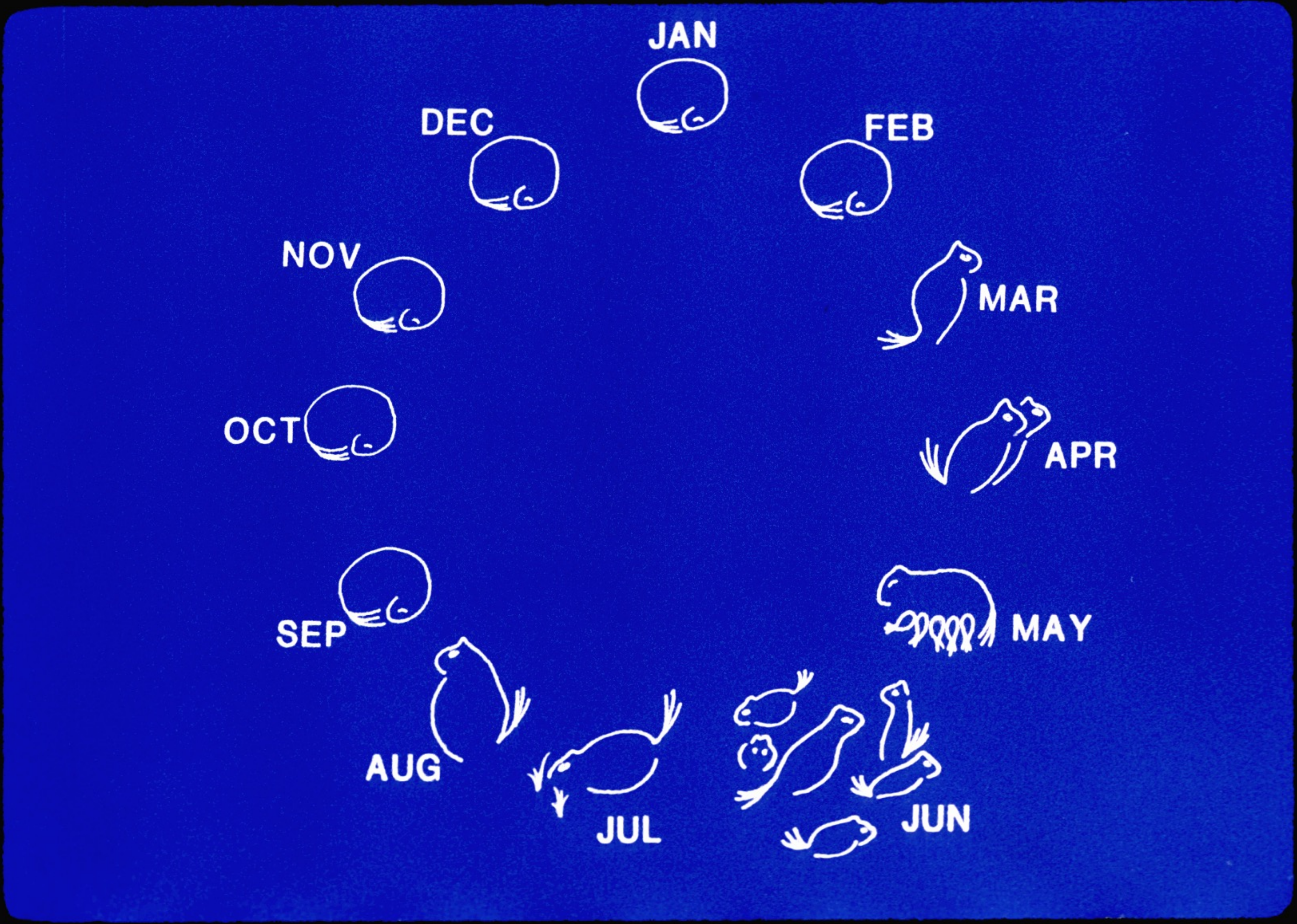
A = entry

B =start of heterothermy

C = end of heterothermy

D = emergence

E = parturition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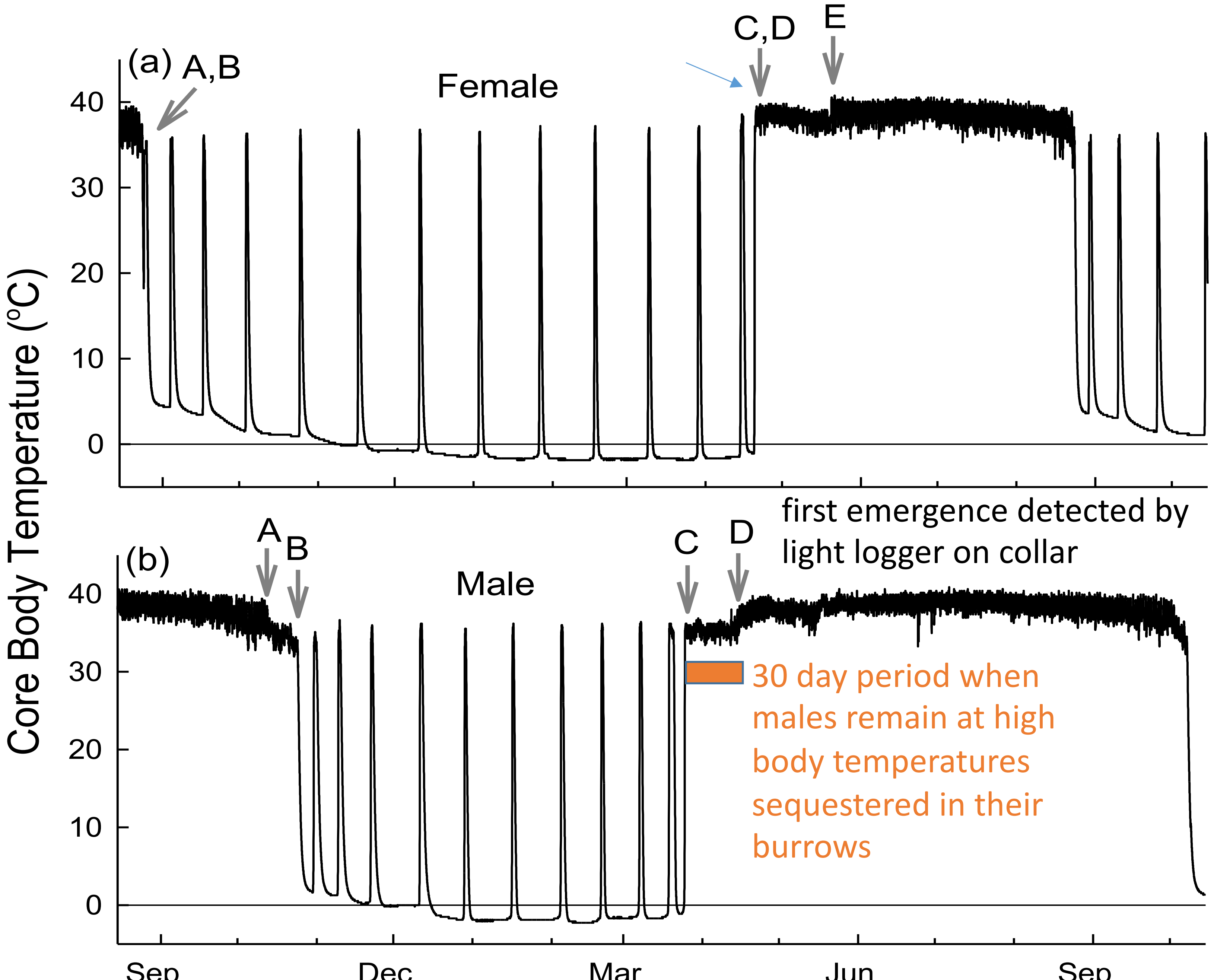
Sex differences in hibernation phenology

A = entry

B =start of heterothermy

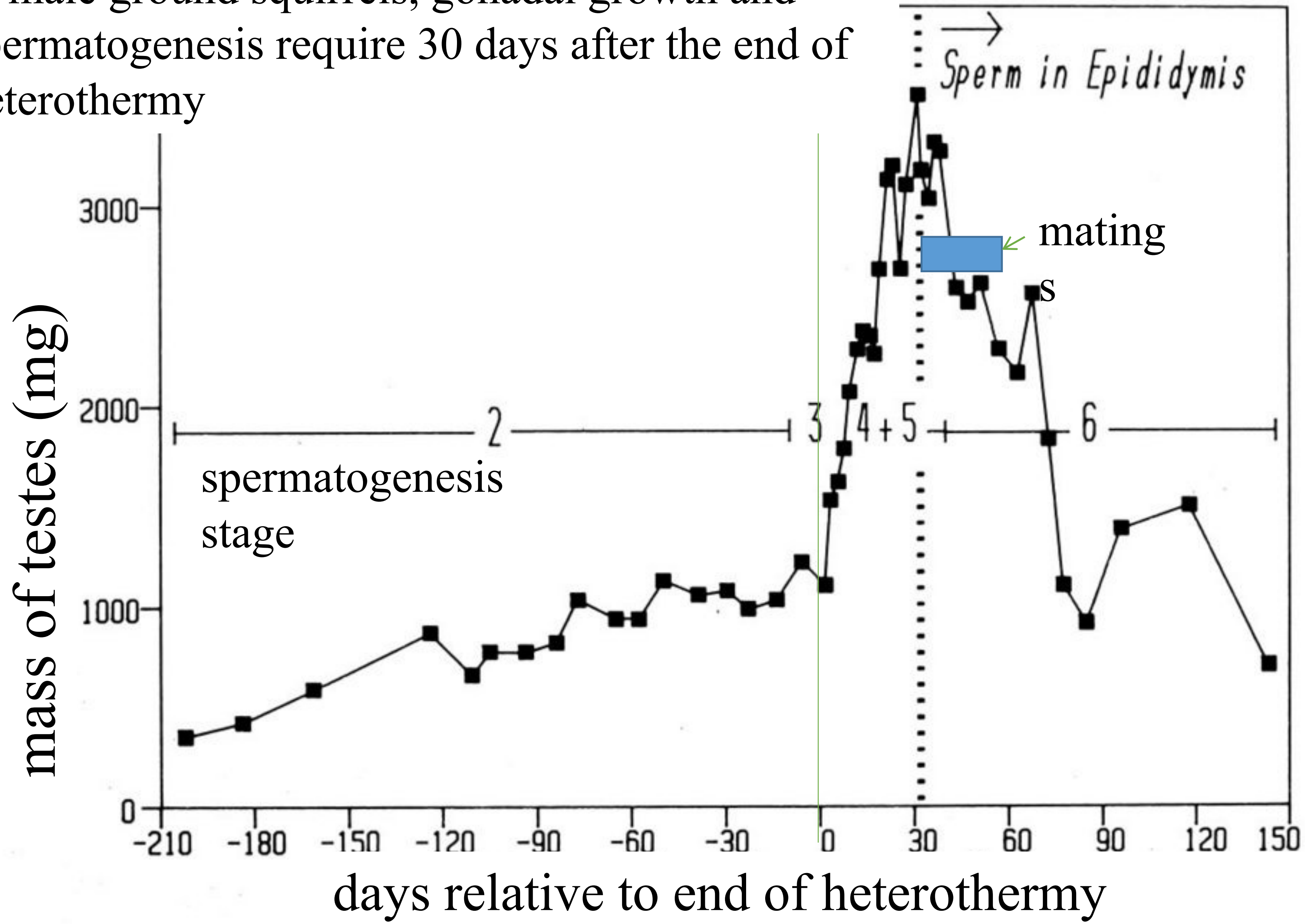


C = end of heterothermy

D = emergence

E = parturition

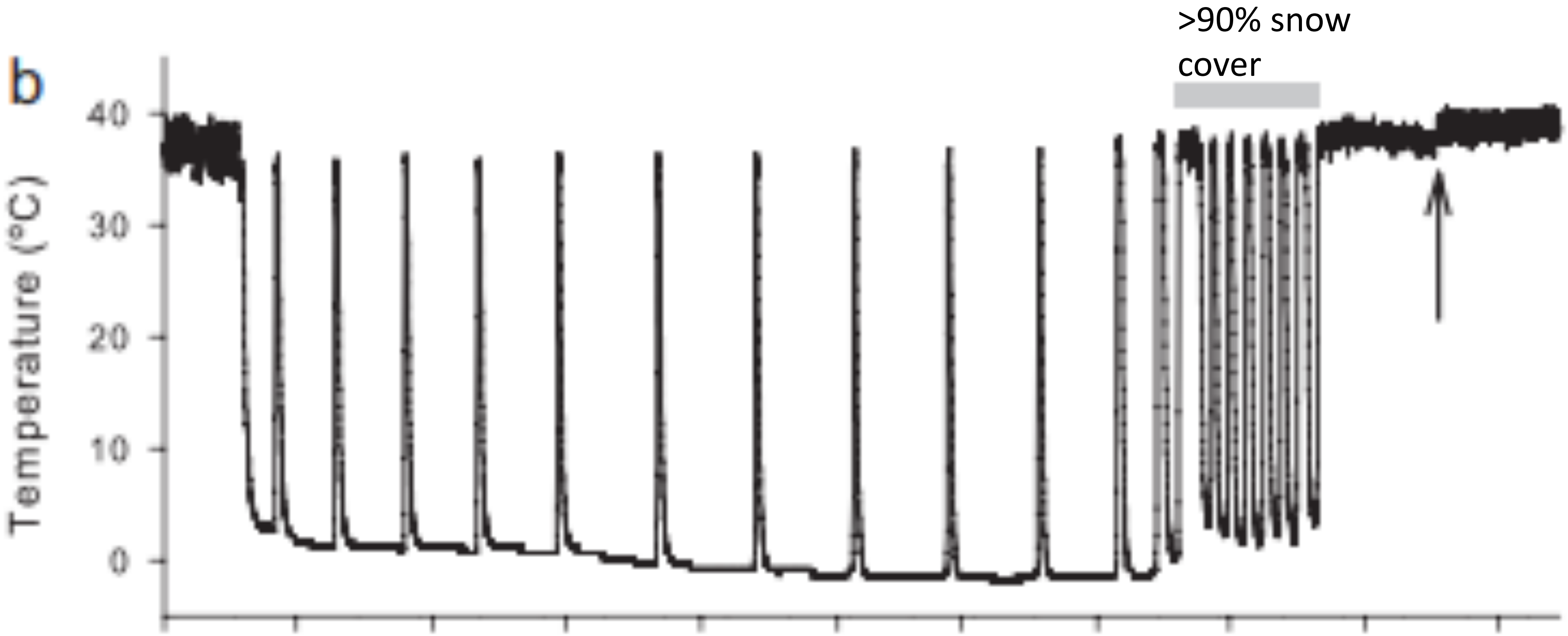
in male ground squirrels, gonadal growth and spermatogenesis require 30 days after the end of heterothermy



Barnes BM, Kretzmann M, Licht P, and Zucker I (1986) Influence of hibernation on testis growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis*. *Biol Reprod* 35:1289-1297.


In females, ripening of eggs takes 2-3 days after ending hibernation; ovulation occurs only after females choose to copulate.
This sex difference in how long it takes for gametogenesis results in much higher flexibility in reproductive timing in females vs. males.

In snowy springs, female ground squirrels repeatedly assess the above ground environment and only emerge for good once snow free ground appears.



Williams, C.T., Buck, C.L., Sheriff, M.J., Richter, M.M., Krause, J.S. and Barnes, B.M., 2017. Sex-dependent phenological plasticity in an arctic hibernator. *The American Naturalist*, *190*(6), pp.854-859.

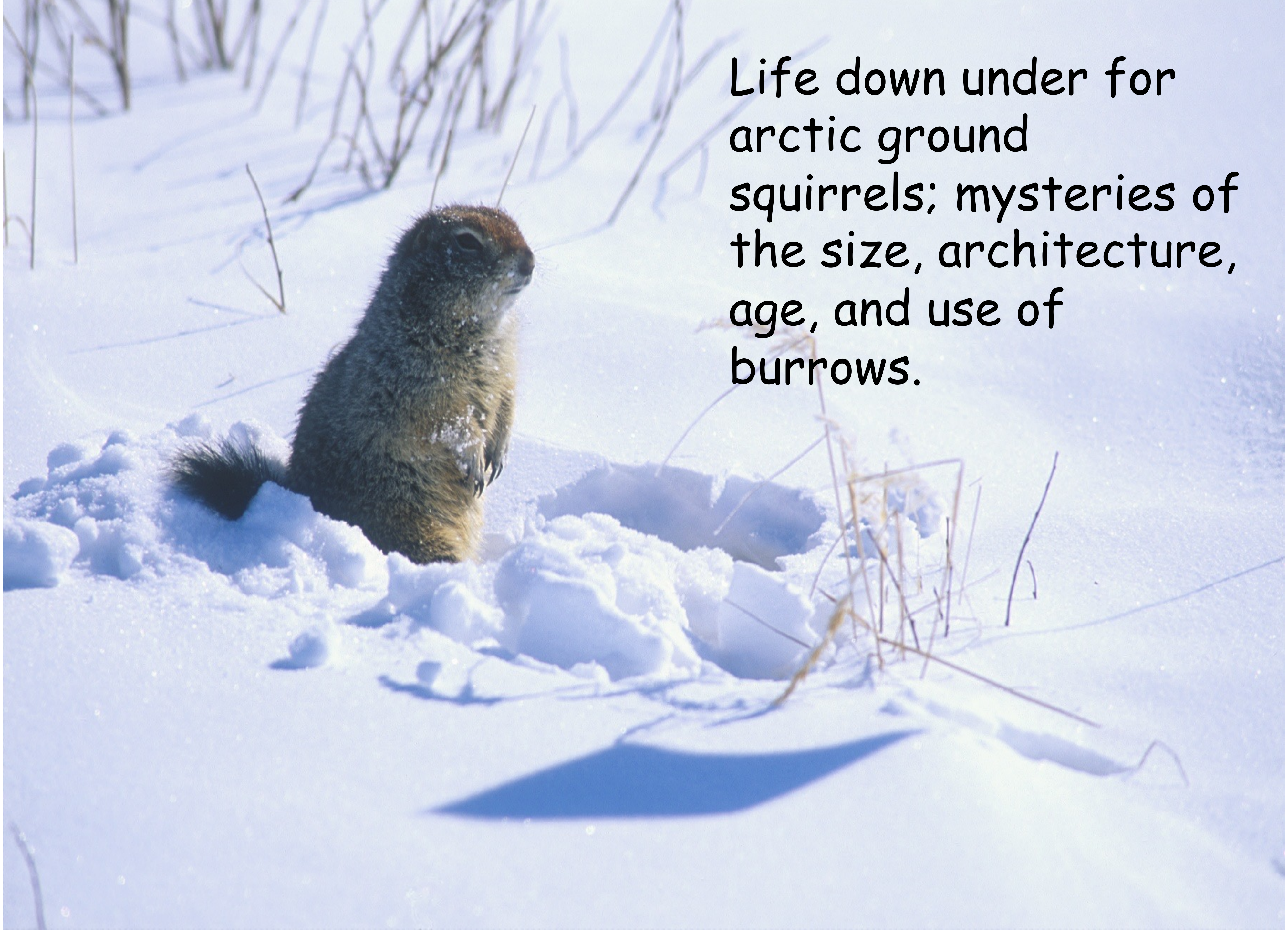

Life down under for arctic ground squirrels; mysteries of the size, architecture, age, and use of burrows.


Photo by R. Flanders