Animal Physiological Ecology

Regulation: Temperature

- Most terrestrial vertebrates are temperature regulators
- **Endotherms** (birds, mammals):
  - regulate by internally generated metabolic heat
  - cool by evaporation
  - 37- 40 ^{o} C
- **Ectotherms** (reptiles, amphibians)
  - regulate by behavioral choices
  - choose environments to alter heat gain/loss

Components of Heat Balance

Equilibrium Temperature: Heat input = Heat output

- Inputs
  - Radiation (direct, reflected)
  - Conduction (solid -- solid)
  - Metabolism
  - Convection (solid -- fluid)
- Outputs
  - Re-radiation
  - Conduction (solid -- solid)
  - Evaporation
  - Convection (solid -- fluid)

$$H_s = H_m \pm H_{cd} \pm H_{cv} \pm H_r - H_e$$

Hs = heat stored in body

Hm = heat gained from metabolism

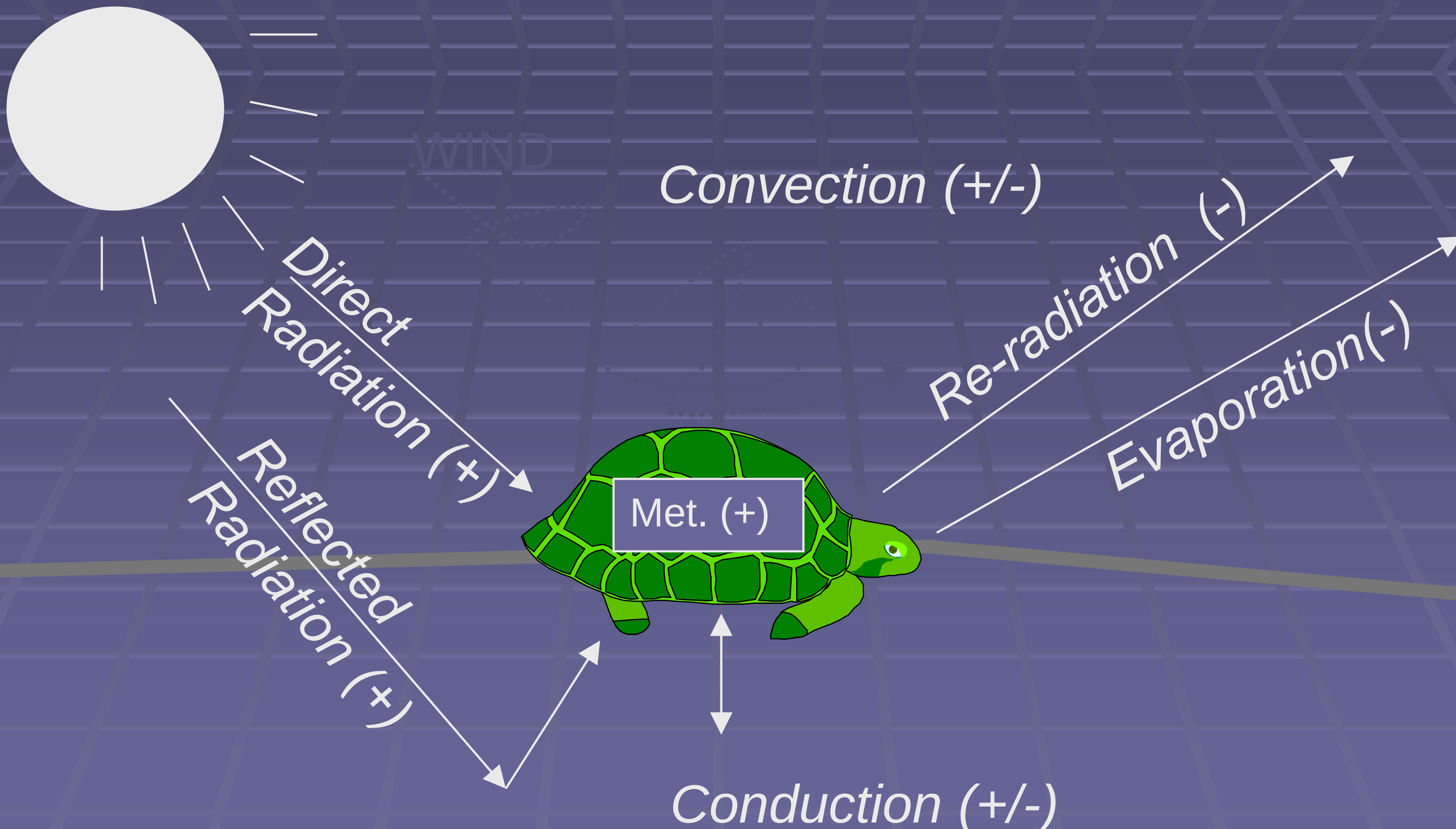
Hcd = heat gained or lost through conduction

Hcv = heat gained or lost through convection

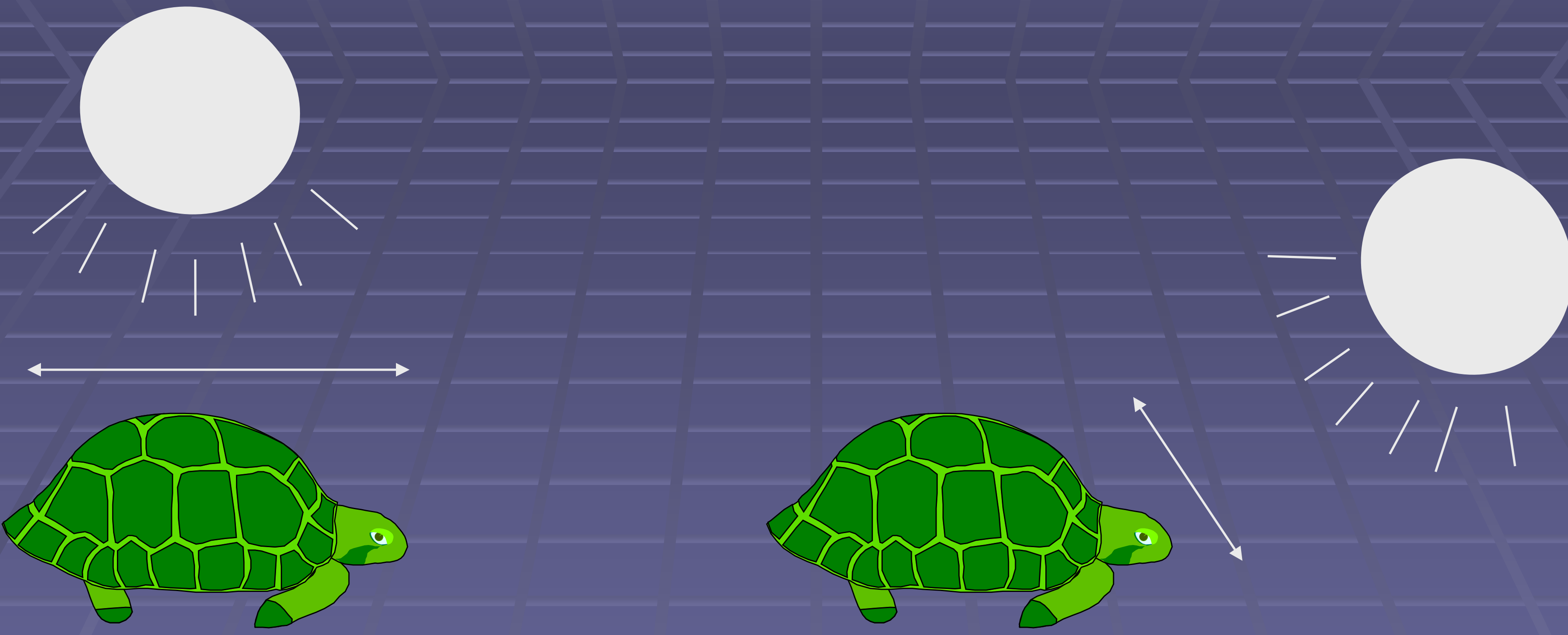
Hr = heat gained or lost through radiation

He = heat lost through evaporation

Heat balance for an ectotherm



Position and radiant heat input



Maximize surface
Low Tb

Minimize surface
High Tb

Three views of thermoregulation

- How do animals thermoregulate?
  - Behavioral mechanisms
  - Physiology
  - Precision of control
- Why thermoregulate? What is the advantage?
  - Optimize function (e.g., enzymes)
  - Ultimate fitness value
- How does thermoregulation affect distribution and abundance?

Lizard thermoregulation

- *Sceloporus* -- Spiny desert lizards
- Insectivorous
- *Sceloporus merriami*
  - Texas
  - Oviparous -- lays eggs
- *Sceloporus jarrovi*
  - Arizona
  - Viviparous -- gives birth, no eggs laid

Sceloporus merriami

Sceloporus merriami
(from Grant 1990 *Ecology* 71:2323-2333)

- Summer active period:
  - 7:30 AM - 2:00 PM
  - 6:00 PM - 9:00 PM
- Avoids heat of midday
- retreats to burrow within its home range
- Body temperature (T_b) mean $\pm$ SE
  - Morning: 33.3 $\pm$ 0.10 ^{o}C
  - Evening: 37.0 $\pm$ 0.20 ^{o}C

Why 2 different temperatures?

- Lizards behave similarly morning & evening
- at 33^{o}C
  - sprint speed is 25% greater than at 37^{o}C
  - water loss is 33% less than at 37^{o}C
  - metabolic rate is 40% less than at 37^{o}C
- Why have a 4^{o}C greater T_b in the evening?

What temperatures are *available* to the lizard?

- What are its choices, particularly in the evening?

Determine thermal properties of the Lizard

- Copper model of the lizard
- Thermocouple implant
- Paint lizard colors
- Place in locations within home range and allow to equilibrate
- Yields possible T_b

Results

- **Evening:** 50-60% of locations within the home ranges yield 36ºC $\leq T_b \leq$ 38ºC
- If lizard avoids those high temperatures, hunting areas would be greatly reduced
- Cost of maintaining ideal T_b (i.e., 33ºC) high

Results

- **Morning:** <20% of locations within home ranges yield 36ºC $\leq T_b \leq$ 38ºC
- Cost of maintaining ideal T_b low

Results

- **Midday:** Nearly all locations yield T_b>38ºC
- Maintaining ideal T_b impossible
- Lethal T_b likely
- Become inactive

Why 2 different temperatures?

- Higher-than-optimal T_b in evening represents a **Constraint**
- A limitation imposed by the environment
- Maintaining a non-ideal temperature is necessary to realize benefits of activity (foraging, mating, etc.)
- Limits placed on distribution

Sceloporus jarrovi

Sceloporus jarrovi

- **Mathies & Andrews 1997. *Functional Ecology* 11:498-507**
- ALSO … Beuchat & Ellner 1987. *Ecological Monographs* 57:45-60

Sceloporus jarrovi

- Viviparous
- T_b in the field (from Beuchat & Ellner 1987)
  - Adult males   Mean T_b = 34^{o}C (SD = 1.4^{o}C)
  - Nonpreg. females

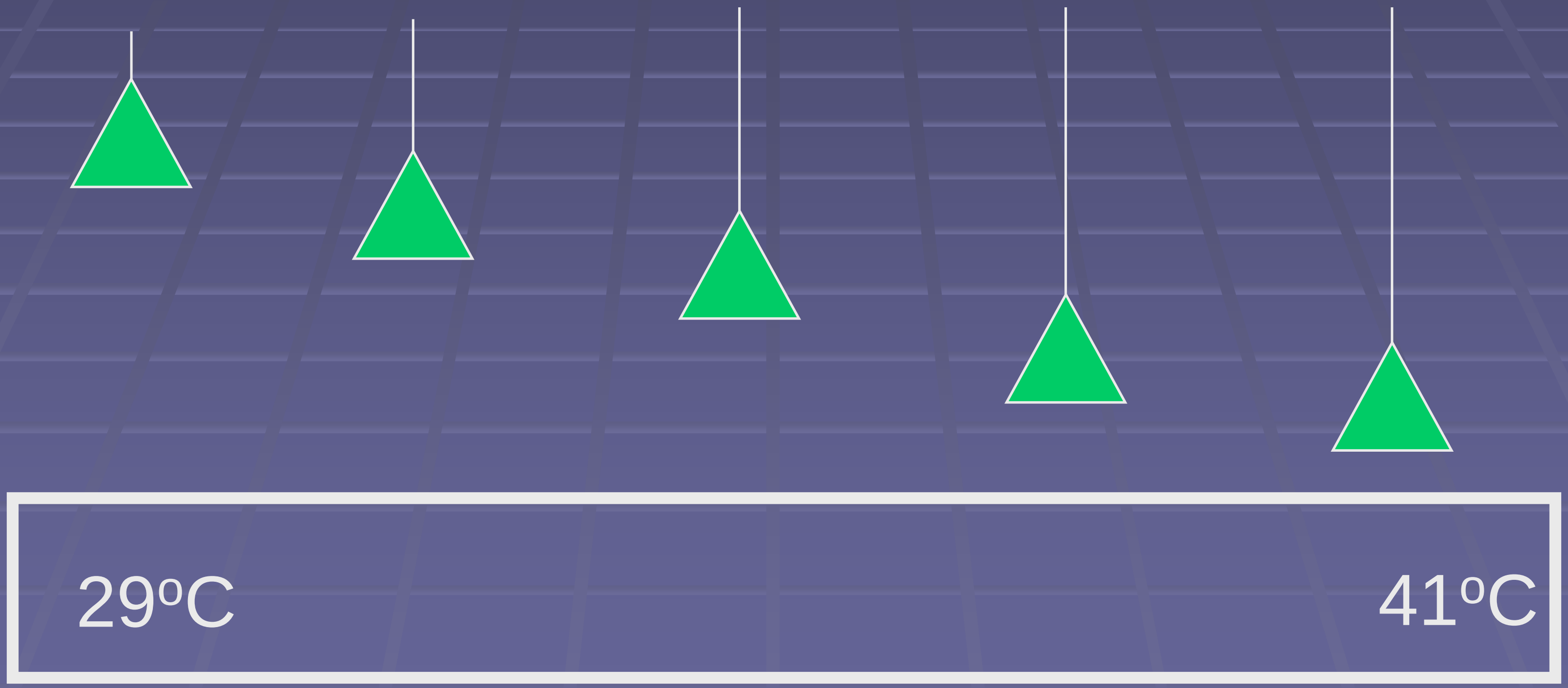
  Mean T_b = 34^{o}C (SD = 1.4^{o}C)
  - Pregnant females   Mean T_b = 32^{o}C (SD = 1.4^{o}C)
- SD -- Average deviation from mean
- 68% of observations within 1 SD of mean
- Why is there a difference in T_b?

Hypotheses
(Mathies & Andrews)

- Pregnant females actively select lower temperatures
- Higher T_b would reduce fitness of pregnant females, because it would be harmful to:
  - pregnant females
  - embryos
  - both

Testing Hypothesis 1

- Environmental chamber
- Post-partum females, Pregnant females



Thermal Gradient experiment

- Place females in the gradient box
- Measure T_b of females allowed to range freely
- Compare pregnant vs. post-partum females
- Three times during the day

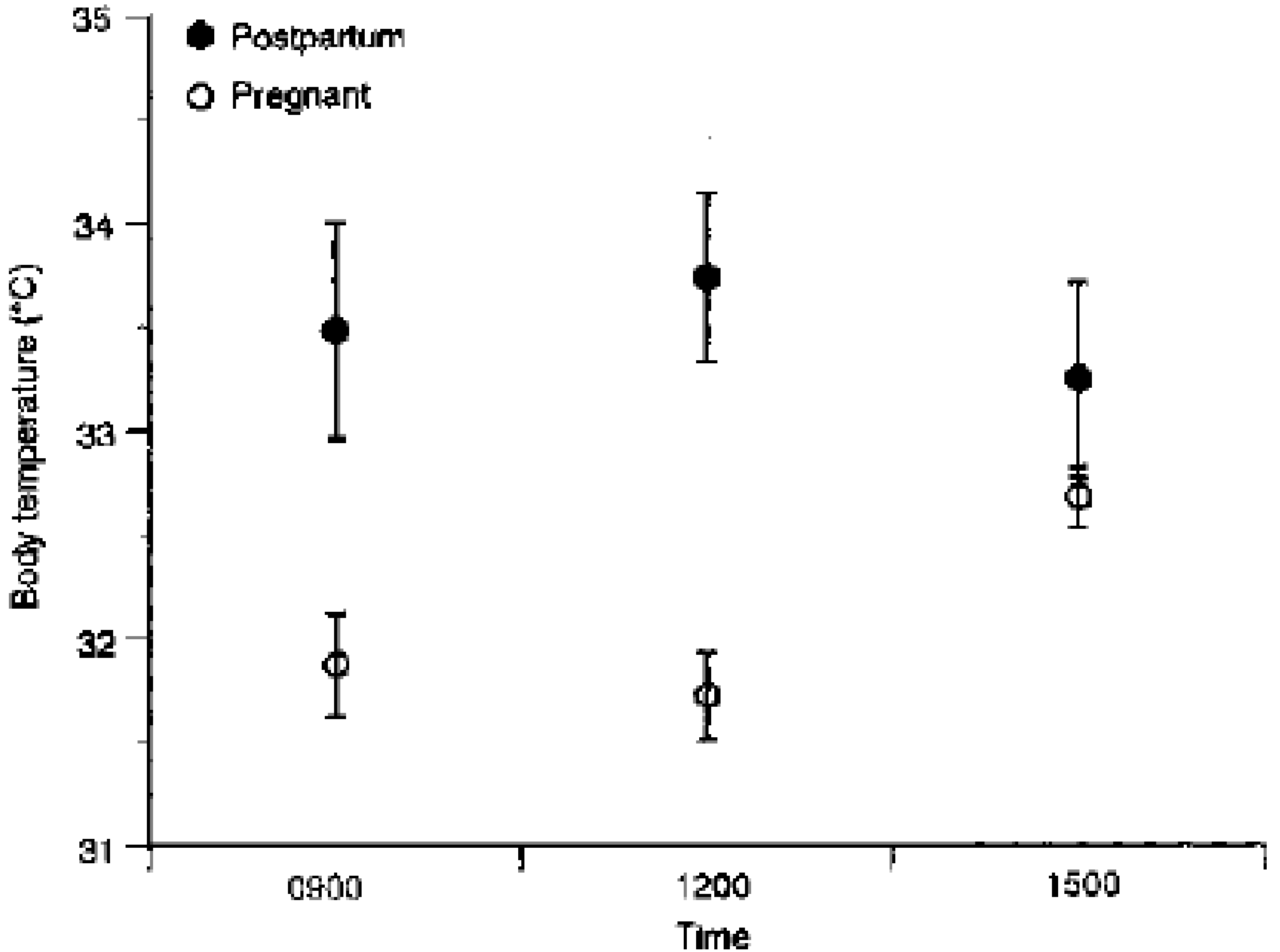


Fig. 3. Mean selected body temperatures (± 1 SE) of female *Sceloporus jarrovi* ($n = 18$) when pregnant and postpartum measured at three times during the main portion of the daily activity period.

Results & Conclusions

- T_b Significantly lower for pregnant females
- Overall:
  - pregnant females 32.1 ± 0.1°C
  - post-partum females 33.5 ± 0.5°C
- T_b less variable for pregnant females

First hypothesis supported

- Females choose a lower T_b when pregnant
- Temperatures chosen in the laboratory similar to temperatures observed in the field
- So, what is detrimental about higher T_b?

Testing Hypothesis 2

- Pregnant females
- Incubator temperatures:
  - Day = 35.7^{o}C, Night = steady decline to 15^{o}C
  - Day = 32.0^{o}C, Night = steady decline to 15^{o}C
- Thermoregulation treatment
  - females in terraria with incandescent light
  - able to regulate T_b
  - light off at night

Testing hypothesis 2

- Maintain pregnant females in three conditions (35^o, 32^o, & T_{reg}) until young are born
- Record:
  - growth of female (increase in mass, SVL)
  - abnormalities of neonates
  - dry mass of neonates
  - yolk in neonates
  - growth of neonates over 9 days (mass, SVL)

Testing hypothesis 2

- **Predict:** If high T_b harms pregnant females, then 35º treatment should have
  - lower survivorship
  - lower growth in mass or length
- **Predict:** If high T_b harms embryos, then 35º treatment should have
  - more abnormalities
  - smaller size at birth (mass, SVL)
  - smaller sizes at 9 days

Results: Effects on females

- None
- Survival = 100% for all
- Growth not significantly altered by treatment
- High temperature has no effect on females performance

Results: Abnormalities

- Of 15 females in each treatment:
  - at 35ºC … 4 females produced 1 or more abnormal or dead offspring
  - at 32ºC … 1 female produced 1 or more abnormal or dead offspring
  - in T_{reg} … no females produced abnormal or dead offspring
- abnormalities rather rare, hard to say much

Results: Effects on embryos

Variable	35^o	32^o	T_{reg}	Significant
Devel. Time (d)	32.7 ± 1.9	37.3 ± 1.9	40.0 ± 2.0	$P<0.05$
SVL (mm) Day 0	25.83 ± 0.19	26.85 ± 0.19	26.72 ± 0.20	$P<0.001$
SVL (mm) Day 9	29.45 ± 0.28	30.66 ± 0.28	30.33 ± 0.28	$P=0.012$
Mass (g) Day 0	0.59 ± 0.02	0.66 ± 0.02	0.66 ± 0.02	$P=0.002$
Mass (g) Day 9	0.89 ± 0.03	0.98 ± 0.03	0.96 ± 0.03	$P=0.08$

Conclusions

- High temperature actually **increases** development rate of embryos
- However, high temperatures reduce mass and SVL at birth
- Effects of high temperatures remain for up to 9 days after birth
- This size effect is probably sufficient to affect offspring fitness (survival)

Overall conclusions

- Pregant females actively regulate at a lower T_b because of negative effects of high temperature on offspring fitness
- How might this evolve?
  - Quantitative trait: T_b when pregnant
  - Fitness differential (S): females with T_b = 32°C

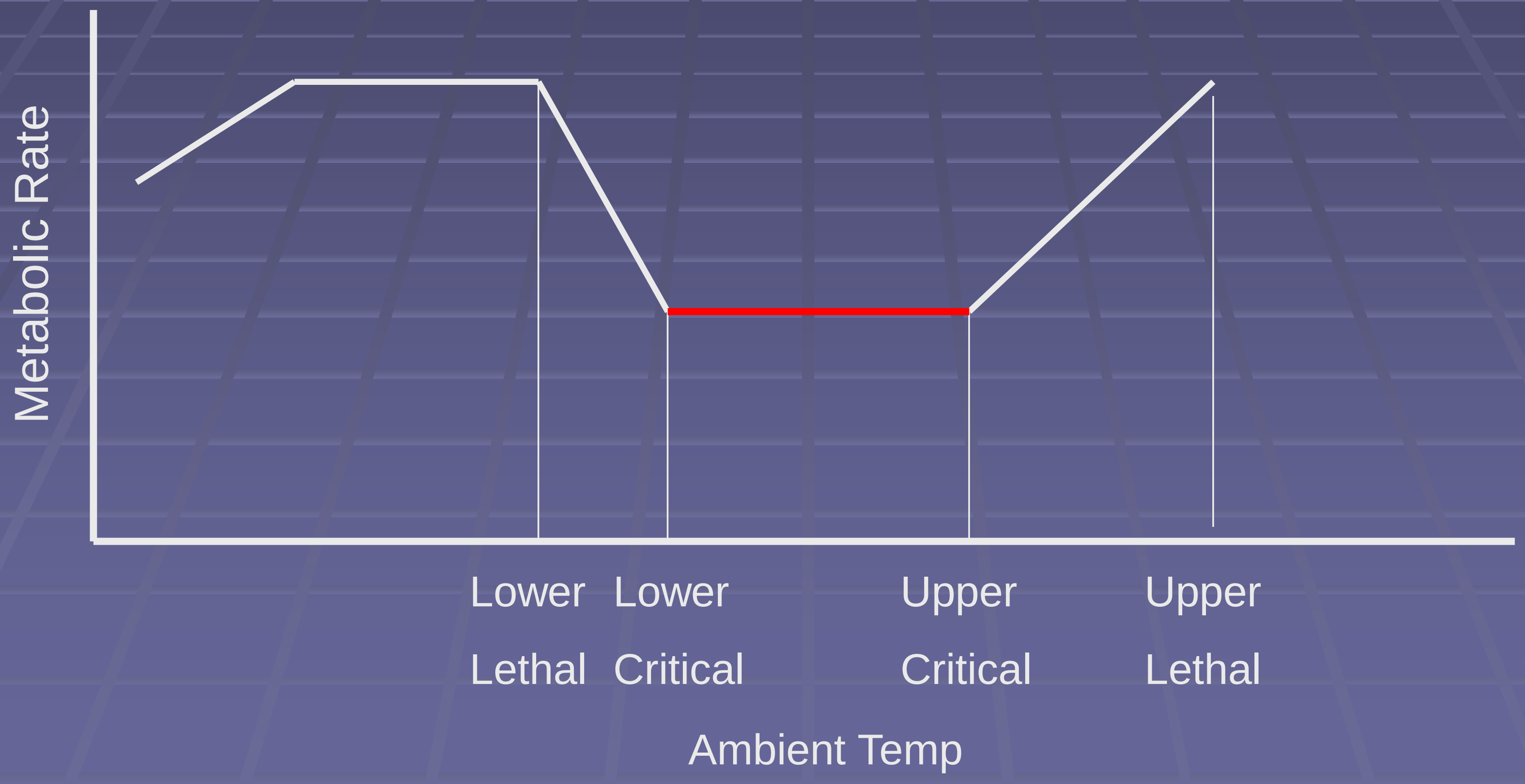
Temperature regulation

- Poikilotherms – don’t regulate internal temperature; temperature varies with environment
- Ectotherms – rely on external sources of energy to regulate body temperature
- Endotherms – rely on internally derived metabolic heat energy
  - homeotherms: birds and mammals (maintain relatively constant body temperature, as opposed to certain fish and insects that only heat critical organs)

Endothermic Thermoregulation

Thermal Neutral Zone - Range of temps over which metabolic rate of homeothermic animal doesn’t change

What causes increase in MR at low temps? High temps?



Low Temps Humans – shivering – heat through muscle contraction
Release hormones – increase metabolic rate (rate at which metabolize energy stores) – increases generation of heat.

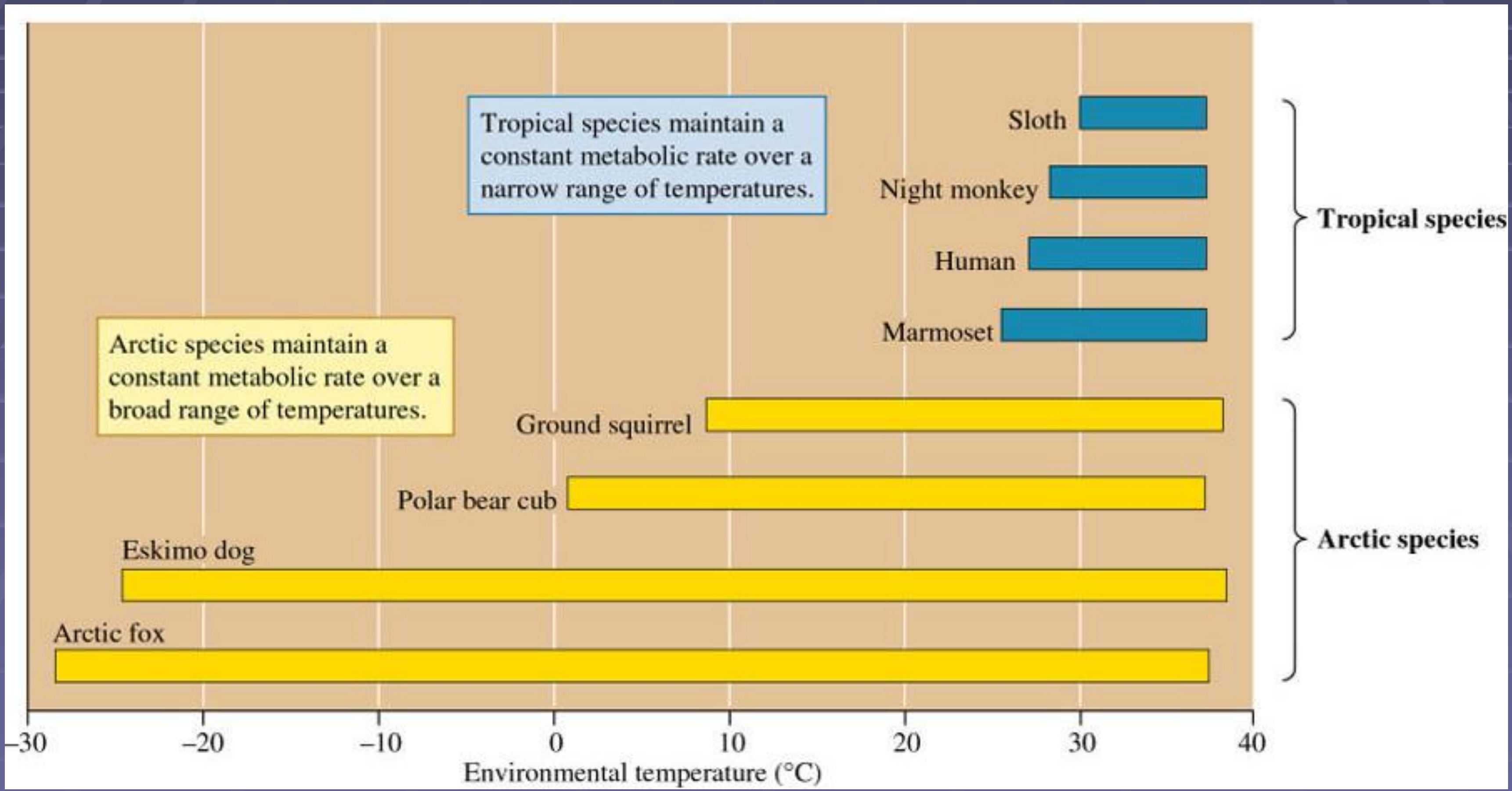
High Temps – heart rate and blood flow to the skin increases – transports heat from the body to skin increases convective heat loss,

Evaporative cooling accelerates heat loss (large endotherms -horses, humans, camels sweat, Dogs birds - pant, marsupials, rodents moisten body surfaces with saliva).

Can define two groups based on differences in the widths of thermoneutral zones

Tropical species – narrow zone

Arctic Species – broad zone


Tropical species maintain a constant metabolic rate over a narrow range of temperatures.
Arctic species maintain a constant metabolic rate over a broad range of temperatures.
Sloth
Night monkey
Human
Marmoset
Ground squirrel
Polar bear cub
Eskimo dog
Arctic fox
Tropical species
Arctic species
–30
–20
–10
0
10
20
30
40
Environmental temperature (°C)

Important point – thermoregulation outside of thermal neutral zone costs energy which could otherwise be directed to other processes.

Te = G+M+R

Life History Theory - the schedule and duration of key events in an organism's lifetime are shaped by natural selection to produce the largest possible number of surviving offspring.

Life history characteristics are traits that affect the life table of an organism, and can be imagined as various investments in growth, reproduction, and survivorship.

The goal of life history theory is to understand the variation in such life history strategies.

This knowledge can be used to construct models to predict what kinds of traits will be favored in different environments.

The key to life history theory is that there are limited resources available, and focusing on only a few life history characteristics is necessary.

Examples of some major life history characteristics include:
Age at first reproduction
Reproductive lifespan and aging
Number and size of offspring

Temperature regulation in aquatic endotherms

- Water temperature much more stable than that of air (takes much greater change in energy content to heat/cool water)
- Convective and conductive heat loss in water is far more rapid (20-100x) than in air
- Gills expose a large surface area to this vast heat sink
  - Because of these constraints, few aquatic animals are endothermic

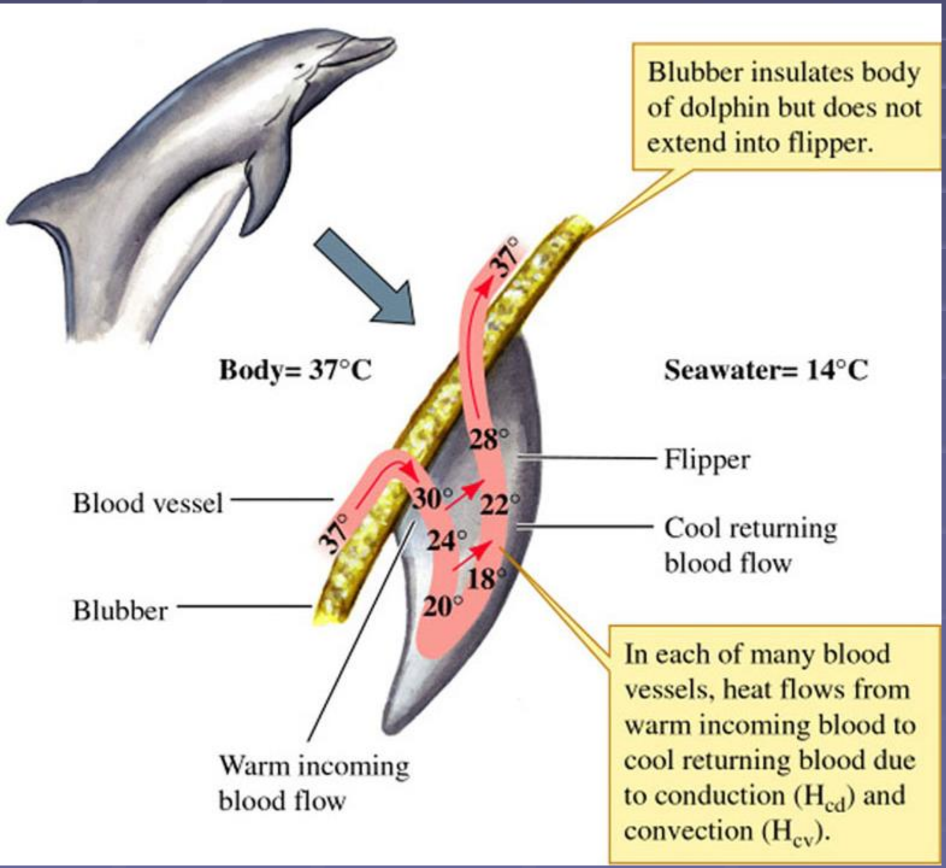
Temperature regulation in aquatic endotherms

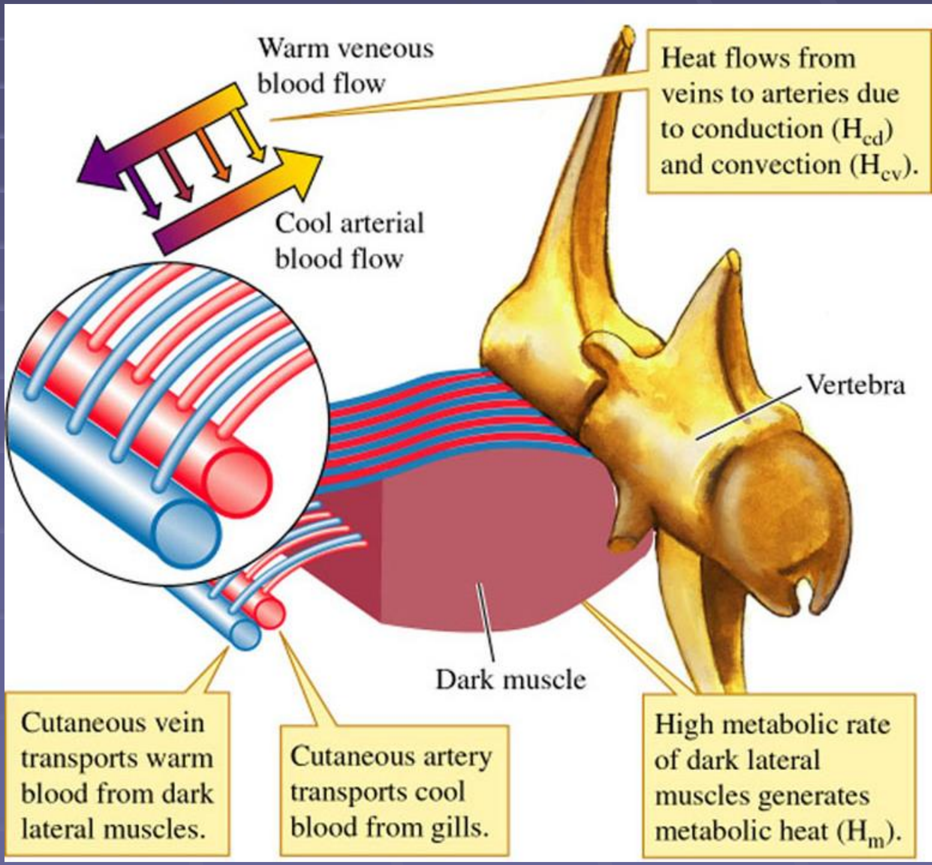
Aquatic mammals – can be endothermic due to:

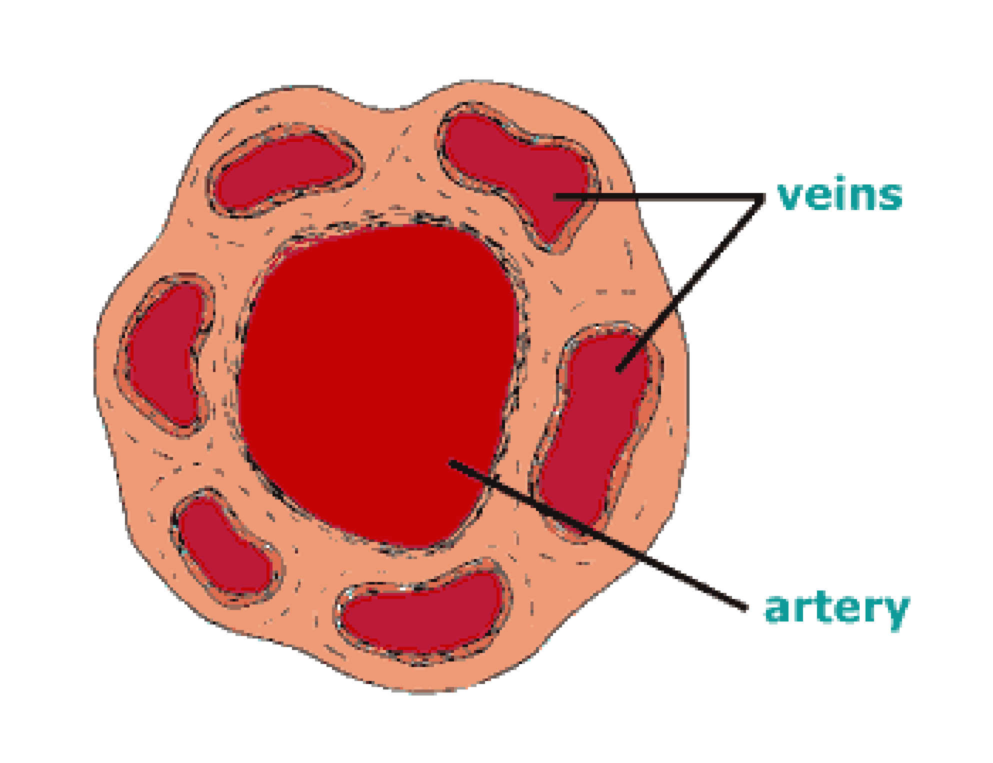
- Air-breathing (no gills)
- Insulation (blubber/fat or thick fur)
- Countercurrent heat exchangers (also found in endothermic fish, e.g., tunas and white sharks)

Countercurrent Heat Exchange

- Vascular arrangements reduce the amount of heat loss to the aquatic environment






veins
artery

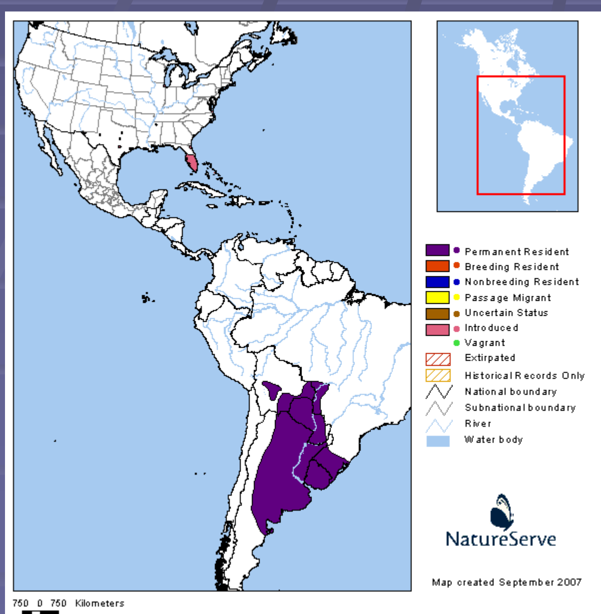
Sociable Weaver


Angola
Zambia
Etosha
Swakopmund
Windhoek
Botswana
Kalahari
Keetmanshoop
South Africa
Namib Desert
Escarpment
Central Plateau
Kalahari Desert


MADRID
ROME
LISBON
ANKARA
YEREVAN
BAKU
ALGIERS
TUNIS
TUNISIA
RABAT
MOROCCO
TRIPOLI
ALGERIA
LIBYA
EGYPT
CAIRO
WESTERN SAHARA
MAURITANIA
NOUAKCHOTT
MALI
NIGER
CHAD
SUDAN
KHARTOUM
ERITREA
ASMARA
DAKAR
SENEGAL
BAMAKO
NIAMEY
BURKINA FASO
GUINEA
CONAKRY
NIGERIA
N'DJAMENA
SIERRA LEONE
LIBERIA
CÔTE D'IVOIRE
ABIDJAN
ACCRA
LOME
CAMEROON
YAOUNDE
CENTRAL AFRICAN REPUBLIC
BANGUI
ADDIS ABABA
ETHIOPIA
SOMALIA
MOGADISHU
GABON
CONGO
LIBREVILLE
BRAZZAVILLE
DEM. REP. OF CONGO
KINSHASA
UGANDA
KAMPALA
KENYA
NAIROBI
TANZANIA
Dar Es Salaam
SEYCHELLES
LUANDA
ANGOLA
ZAMBIA
LUSAKA
MALAWI
MOZAMBIQUE
HARARE
ZIMBABWE
COMOROS
MADAGASCAR
ANTANANARIVO
MAURITIUS
Reunion
NAMIBIA
WINDHOEK
BOTSWANA
GABORONE
PRETORIA
MAPUTO
Johannesburg
SOUTH AFRICA
Durban
Cape Town
Canary Islands
KURDISTAN
Sicily
Crete

< 10mm (0.4”) /yr





Permanent Resident
Breeding Resident
Nonbreeding Resident
Passage Migrant
Uncertain Status
Introduced
Vagrant
Extirpated
Historical Records Only
National boundary
Subnational boundary
River
Water body
NatureServe
Map created September 2007
750 0 750 Kilometers

Water Balance

Water content of most organisms 50-90%

Survival requires maintenance

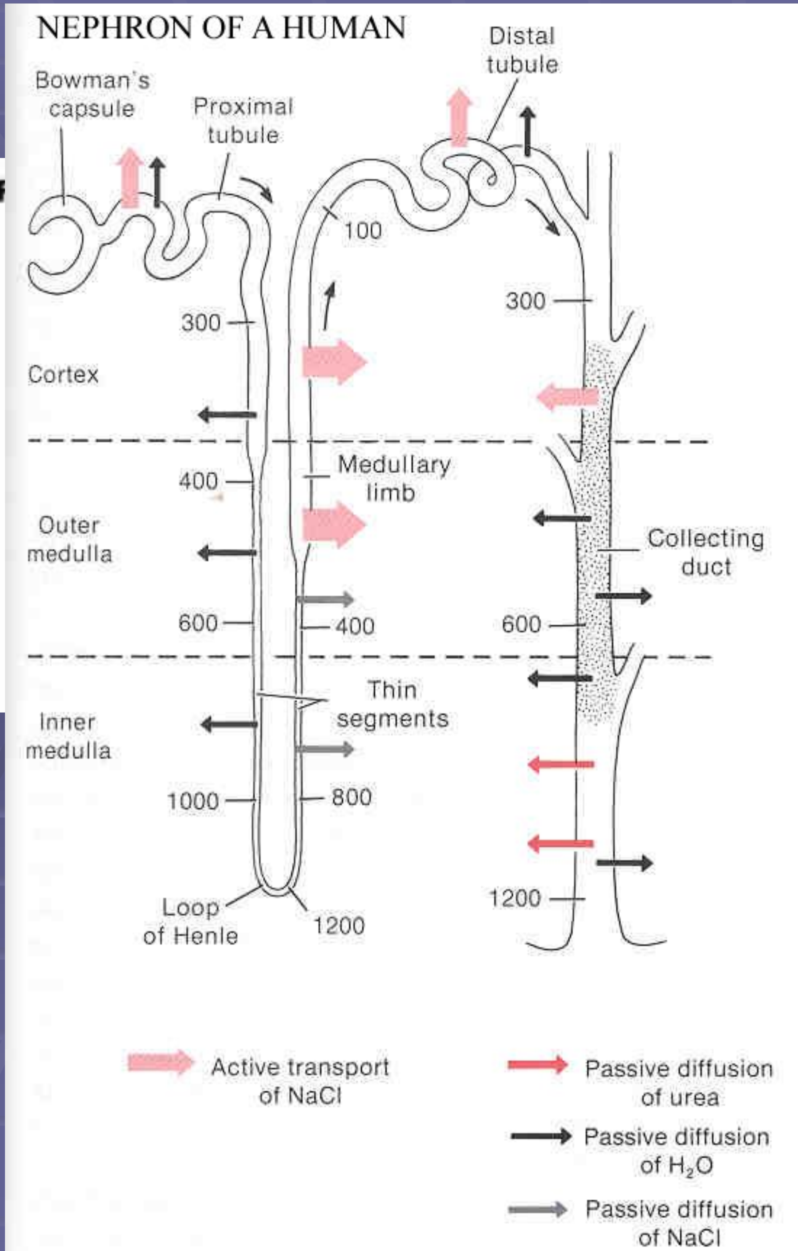
Water Conservation

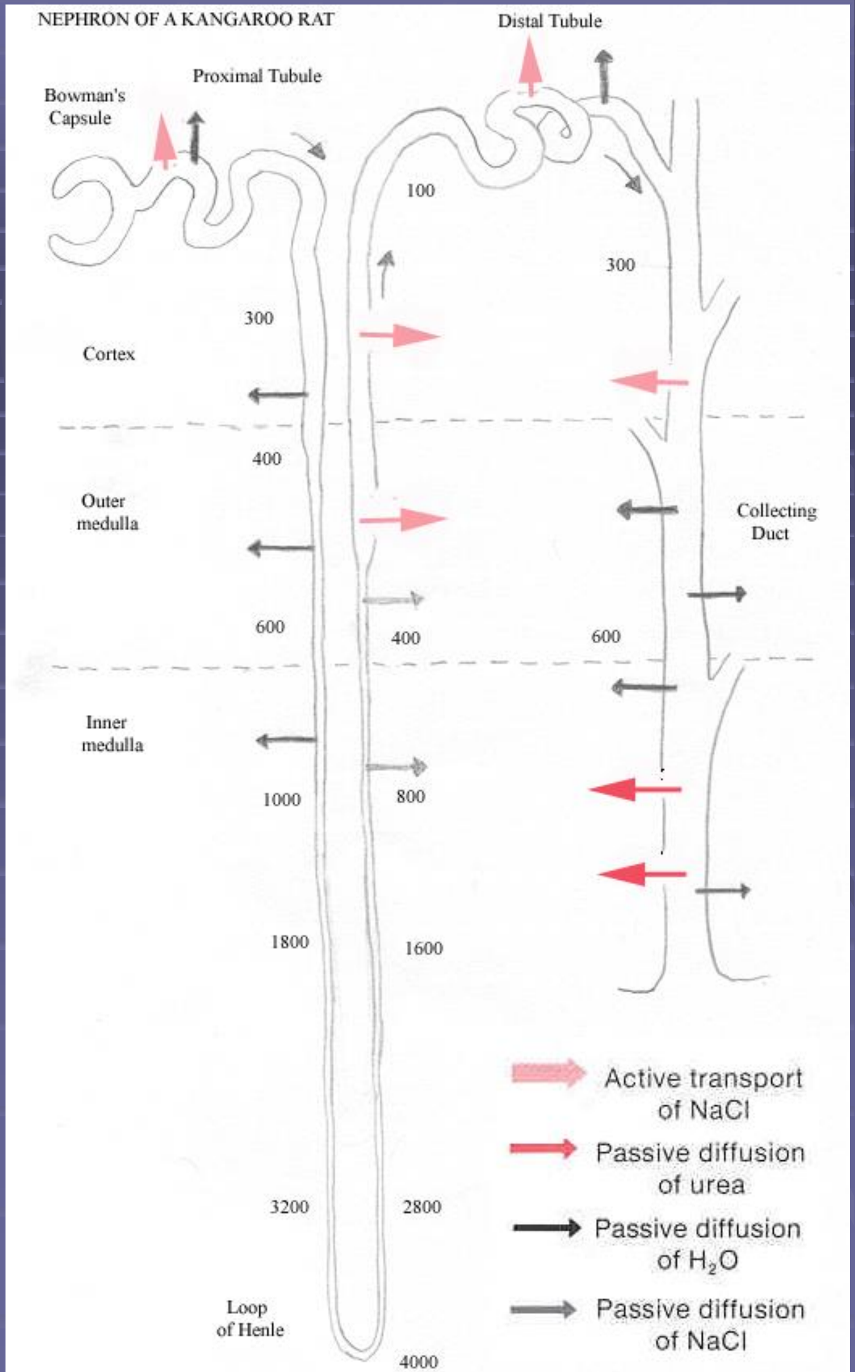
- water proofing to reduce evaporation
- concentrated urine or feces
- behavioral adaptions

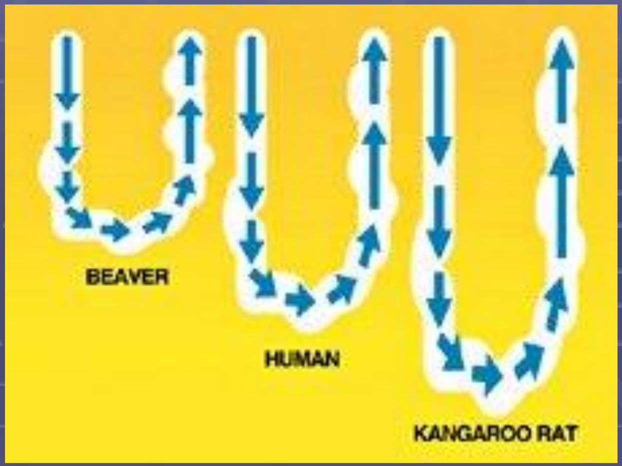
Case Study – Kangaroo Rats (*Dipodomys*)

Metabolic water can also be important

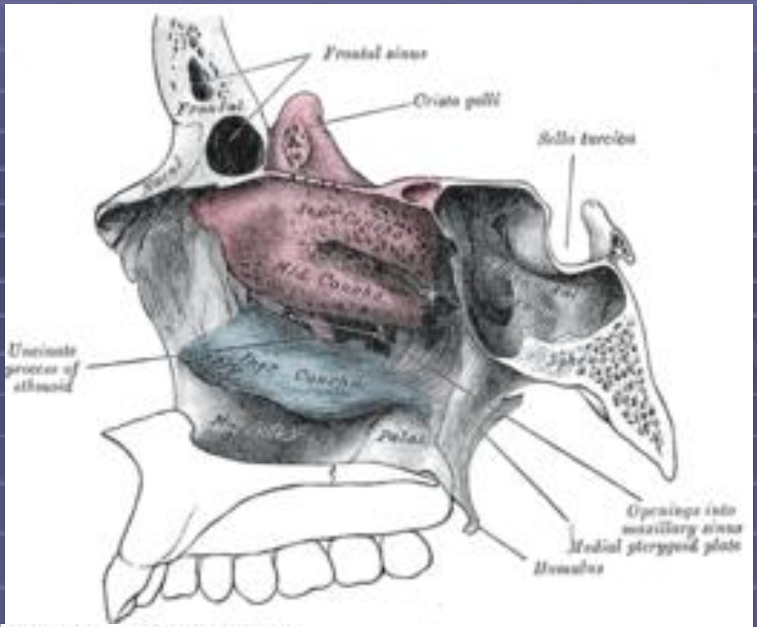
$C_6H_{12}O_6 + CO_2 \rightarrow CO_2 + H_2O$

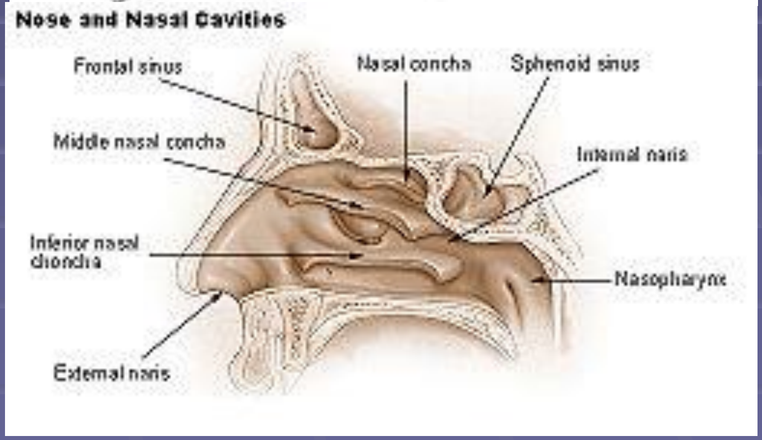

NEPHRON OF A HUMAN
Bowman's capsule
Proximal tubule
Distal tubule
100
300
300
Cortex
400
Medullary limb
Outer medulla
Collecting duct
600
400
600
Thin segments
Inner medulla
1000
800
1200
Loop of Henle
1200
Active transport of NaCl
Passive diffusion of urea
Passive diffusion of H_2O
Passive diffusion of NaCl


NEPHRON OF A KANGAROO RAT
Distal Tubule
Proximal Tubule
Bowman's Capsule
100
300
300
Cortex
400
Outer medulla
Collecting Duct
600
400
600
Inner medulla
1000
800
1800
1600
3200
2800
Loop of Henle
4000
Active transport of NaCl
Passive diffusion of urea
Passive diffusion of H_2O
Passive diffusion of NaCl

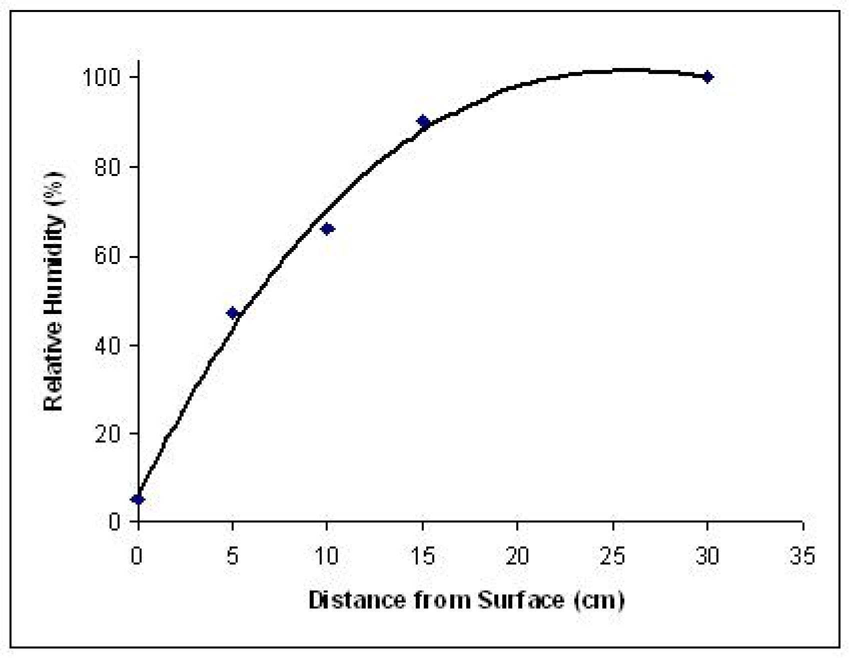


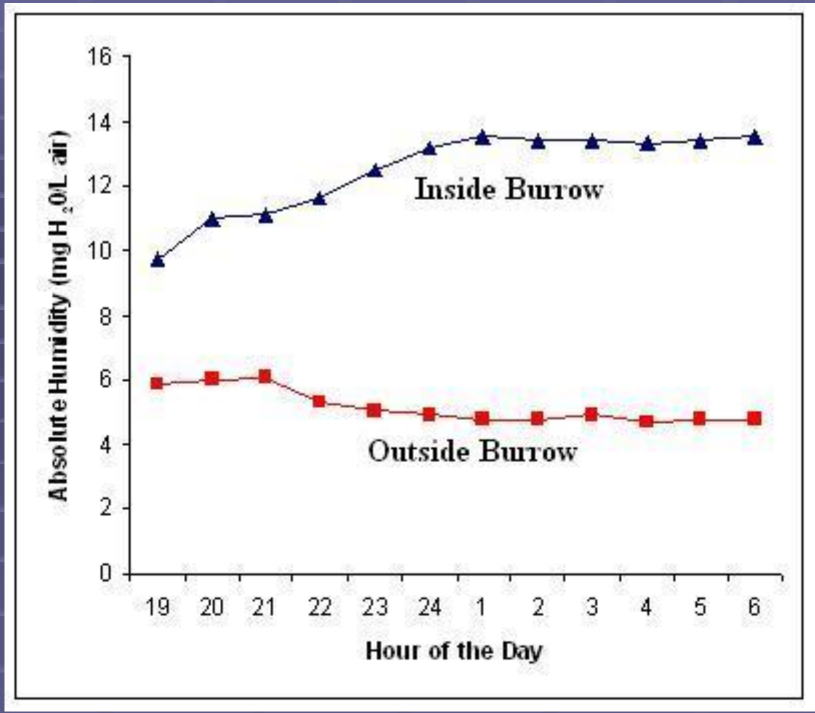
Result - Urine 17x more concentrated than blood

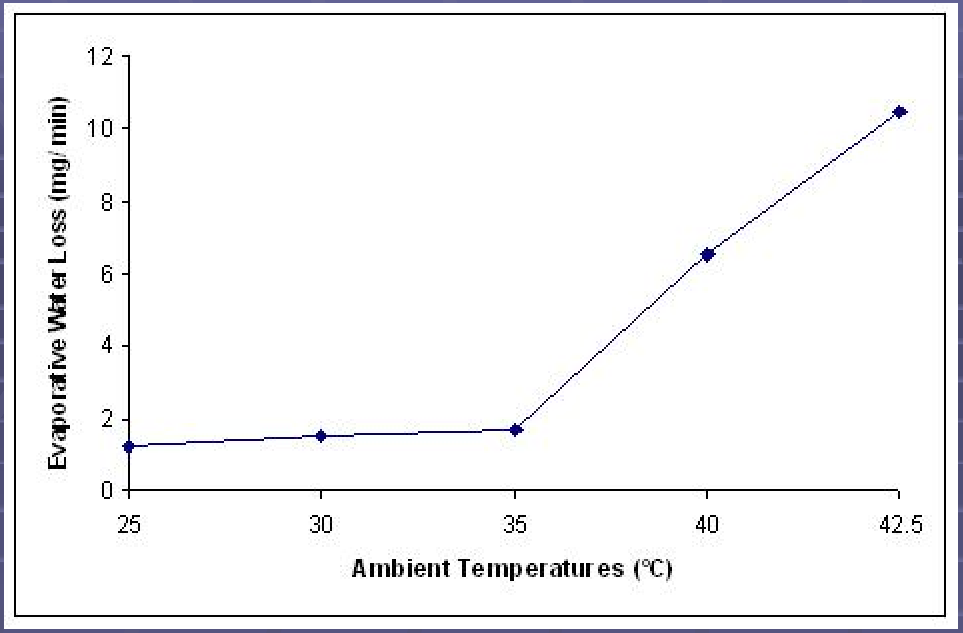

Frontal sinus
Crista galli
Sella turcica
Uncinate process of ethmoid
Openings into maxillary sinus
Medial pterygoid plate
Hamulus


Nose and Nasal Cavities
Frontal sinus
Nasal concha
Sphenoid sinus
Middle nasal concha
Internal naris
Inferior nasal choncha
Nasopharynx
External naris

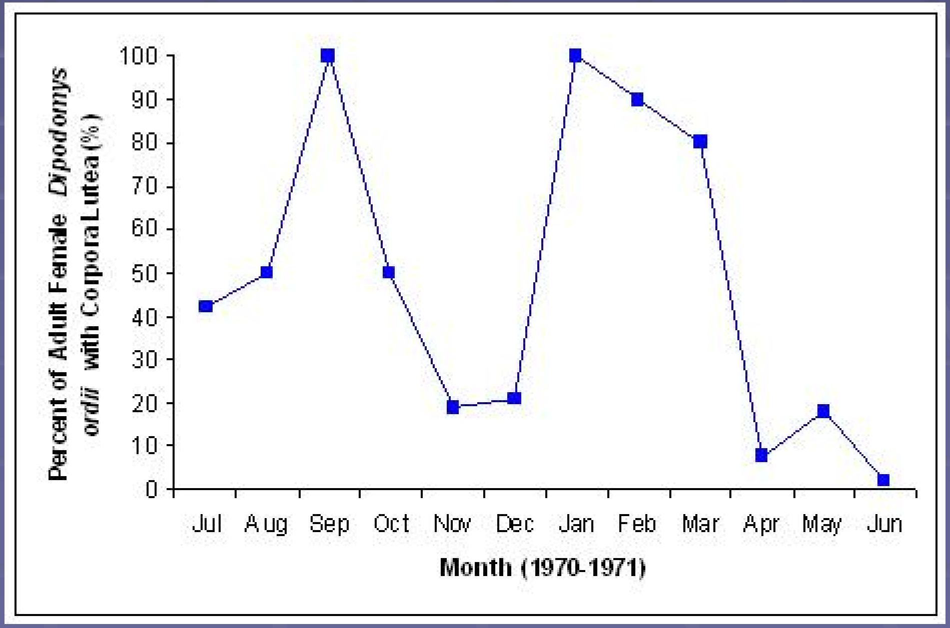
- food high in carbohydrates
- stored in burrows


Relative Humidity (%)
100
80
60
40
20
0
0
5
10
15
20
25
30
35
Distance from Surface (cm)


Absolute Humidity (mg H_2O/L air)
16
14
12
10
8
6
4
2
0
Inside Burrow
Outside Burrow
19
20
21
22
23
24
1
2
3
4
5
6
Hour of the Day



Nocturnal behavior largely due to water conservation not avoidance of high temperatures



Reproduction correlates with rainfall

Temperature regulation in endothermic insects

- Bumblebees use metabolic heat to warm their flight muscles
- Large moths maintain fairly constant metabolic rate and regulate temperature via conductive and convective cooling / heating

Physiological Ecology Summary

- Ecology of individuals
- Adaptive value of physiological traits
- Homeostasis (e.g., thermoregulation)
- “How” vs. “Why” questions
- Costs and constraints (e.g., *S. merriami*)
- Benefits related to fitness (e.g., *S. jarrovi*)

Behavioral Ecology

- Another aspect of the ecology of individuals
- The relationship between the living and nonliving environment and the actions of animals

Topics within behavioral ecology

- Foraging - how environment influences choice of what, how, when, where to eat
- **Social systems - how environment influences how individuals interact with conspecifics; living in groups**
- **Sex and mating systems - environmental determinants of mating and reproduction**

Behavioral ecology focuses on adaptation and evolution

- Main focus is on the adaptive value of observed traits in a given environment
- There can be questions of both **how** and **why** concerning behavior
- In both cases, approach is similar to that seen in physiologial ecology (costs, benefits, constraints)

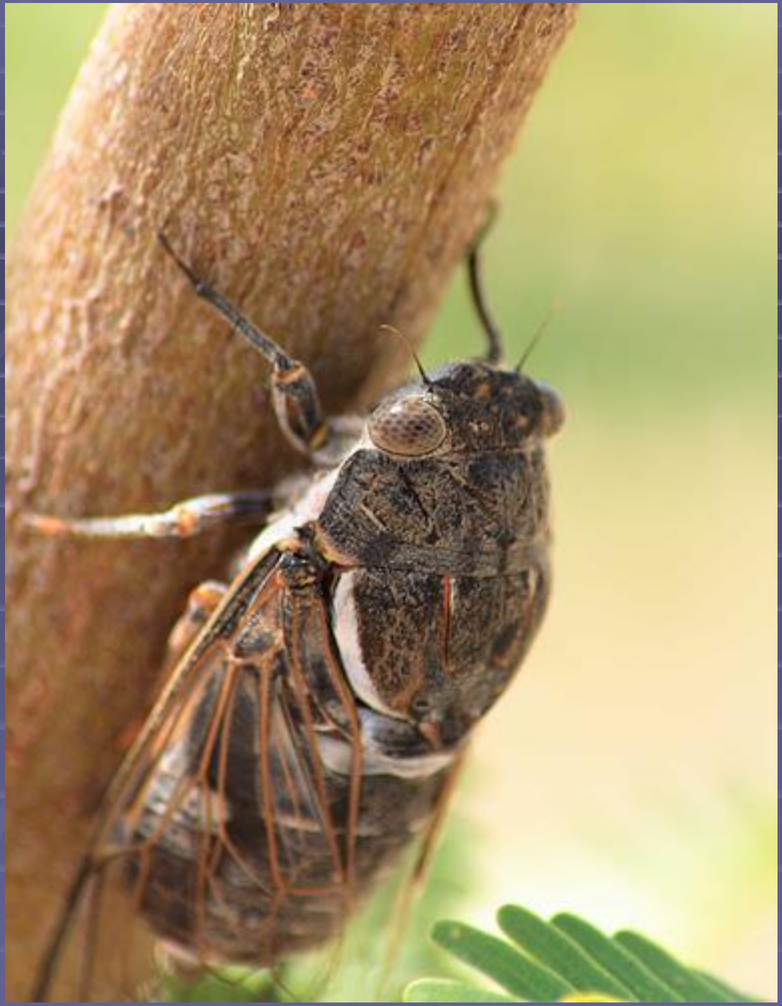
Living in groups

- Many animals live in groups with conspecifics
  - Birds form feeding flocks, migrating flocks
  - Herds of herbivorous mammals
  - Schools of fish
  - Insect aggregations (e.g., monarch butterflies)
- What determines group size?
- What are benefits and costs?

Major benefits of group living

- Improved foraging success
- Improved defense against enemies
- Improved ability to cope with the physical environment

Case Study – Sonoran Desert Cicadas



Ta = 46°C – higher than upper lethal
Tground = 70°C
Tb = 37°C

Actively calling during hottest part of day

Hyp1 – use microclimates effectively
Hyp2 – use evaporative cooling

Feeds on xylem from Mesquite trees

Found capable of evaporative cooling

Placed in Env Chambers – no access to cool microclimates

Ta = 45.5°C
Tb = 37 - 42°C

1. Relative Humidity 100%
Ta = 45.5°C
Tb = 45.5°C

2. Relative Humidity 0%

Ta = 45.5°C

Tb = 41°C

How are results consistent with evaporative cooling?

2nd group of experiments

-Placed humidity sensors above cuticle
- As Ta increased rate of water movement increased

- Rate of water loss highest ever reported for insect

Sonoran desert cicada. Pores 7X size of pore canals located on dorsal mesonotum + connected to special dermal glands via cuticular ducts are involved in water transport to the surface. Cooling of 2-5oC below ambient of 42-45oC.