

TROPICAL ECOLOGY

**Animals' adaptations to desert and
arid habitats**

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Fizjologia zwierząt

Adaptacja do środowiska



Knut Schmidt-Nielsen

WYDAWNICTWO NAUKOWE PWN

K. Schmidt-Nielsen:
**Animal
physiology.
Adaptation to
environment**

Polish edition III, PWN 2008
(original Vth edition).

Environmental Physiology of Animals

PAT WILLMER, GRAHAM STONE &
IAN JOHNSTON



*P. Willmer, G.
Stone and I.
Johnston:*
**Environmental
Physiology of
Animals**

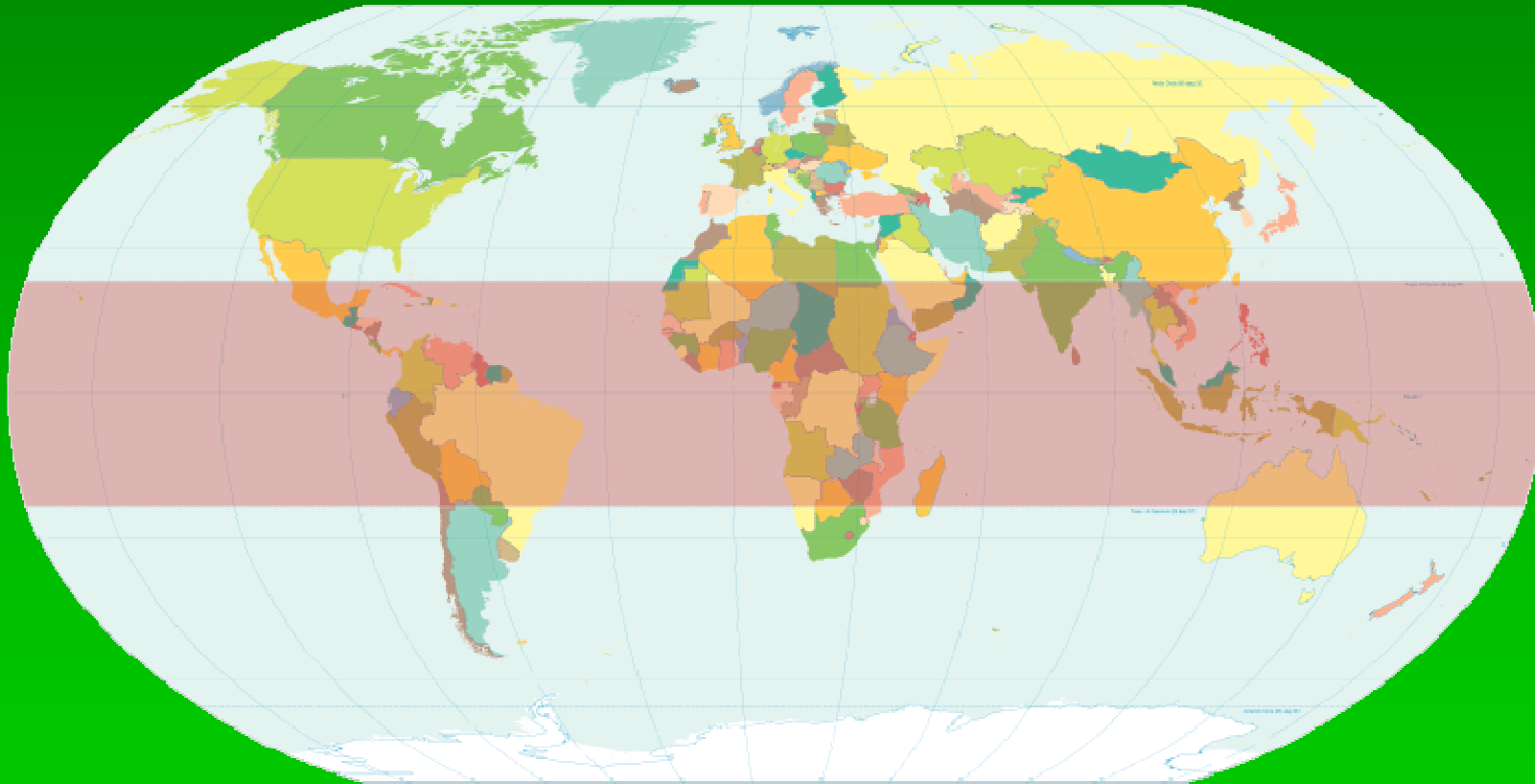
Blackwell Science,
2000

Plan of the lecture

- What are deserts and how do they form?
- Coping with high temperature
- Coping with low water availability
- Coping with low and unpredictable food availability

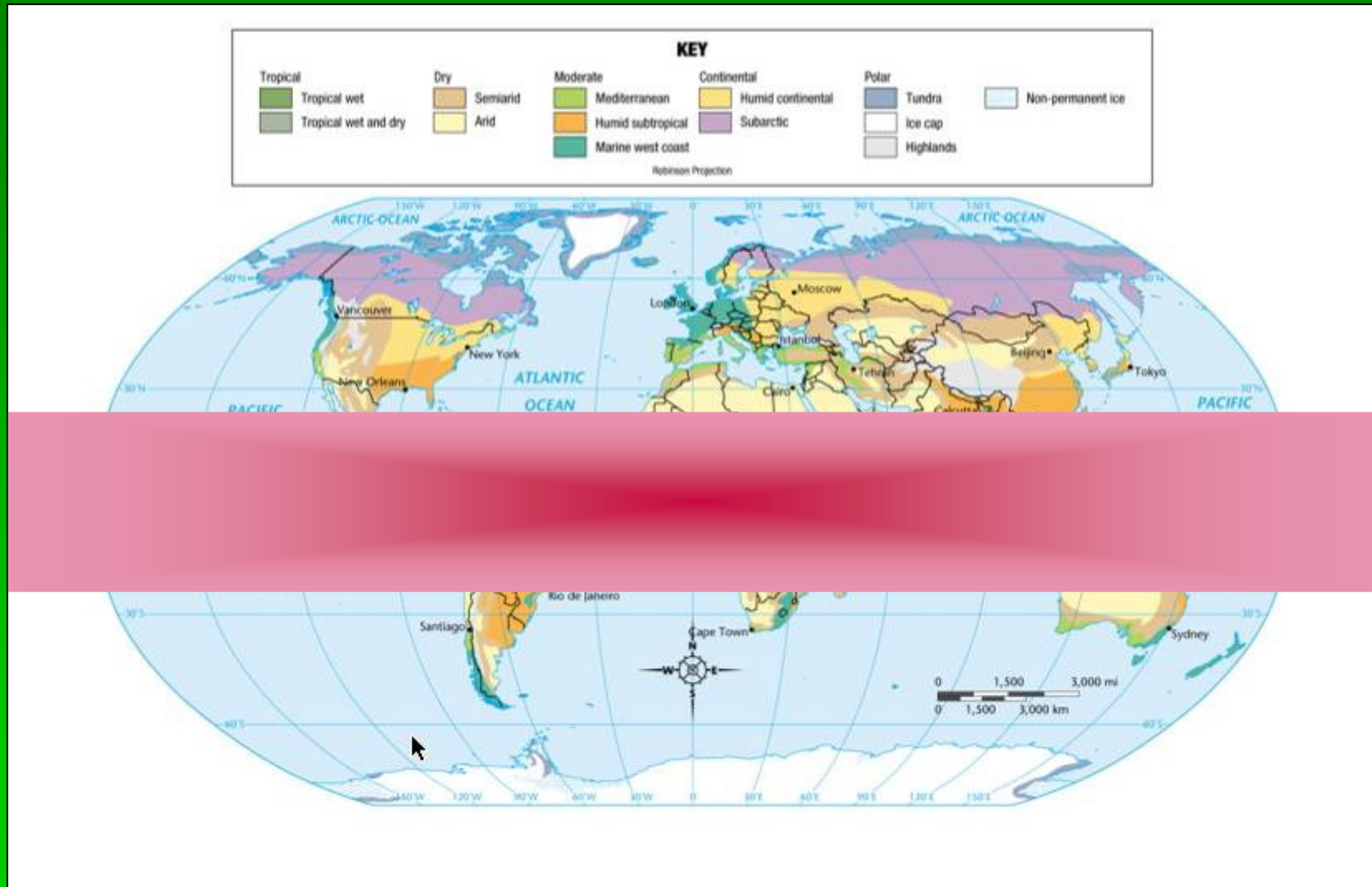
Where are the tropics?

The area between
the Tropic of Cancer and the Tropic of Capricorn



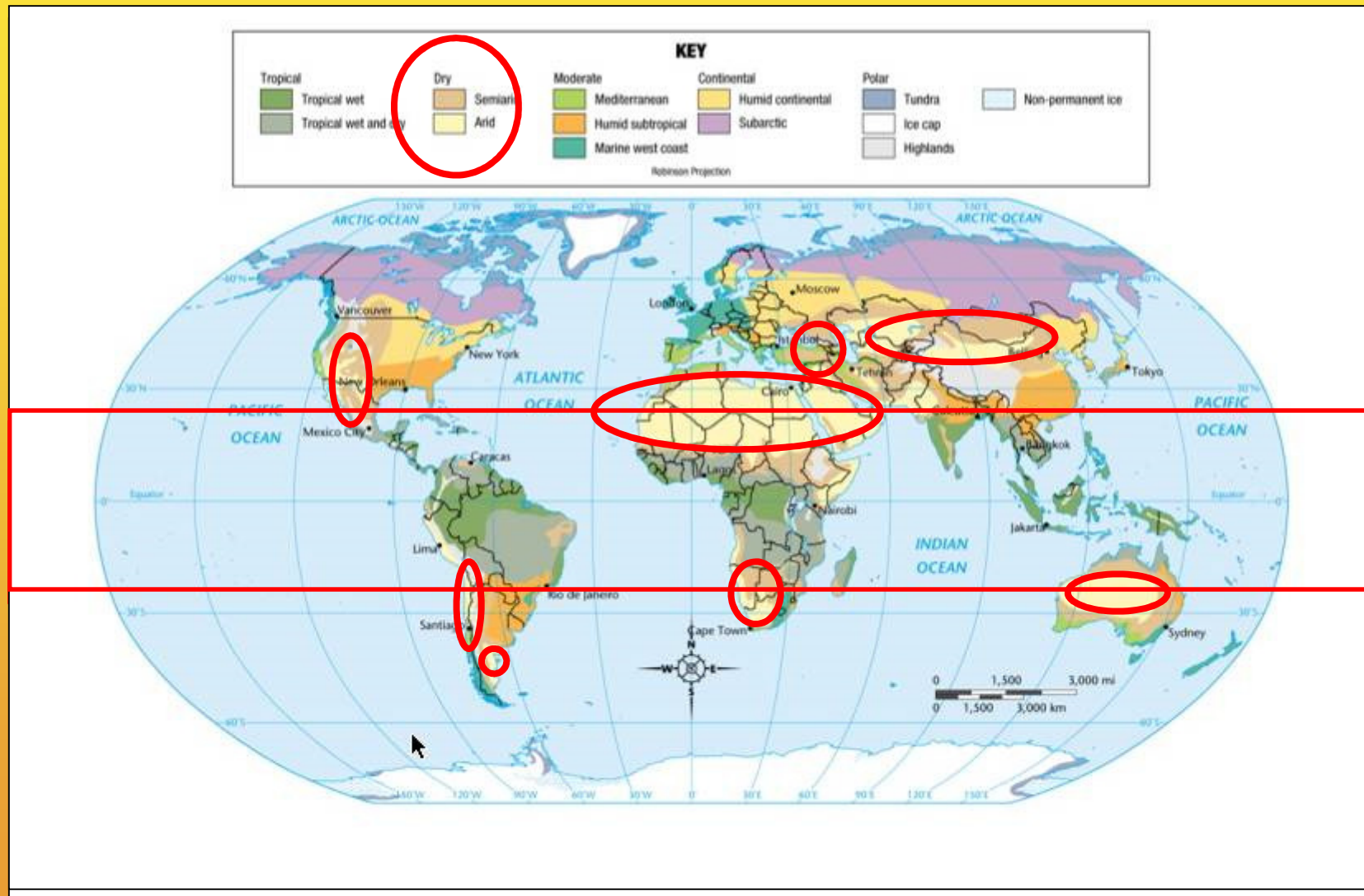
from the lecture of Professor R. Laskowski

Tropics and types of climate according to Wladimir Köppen

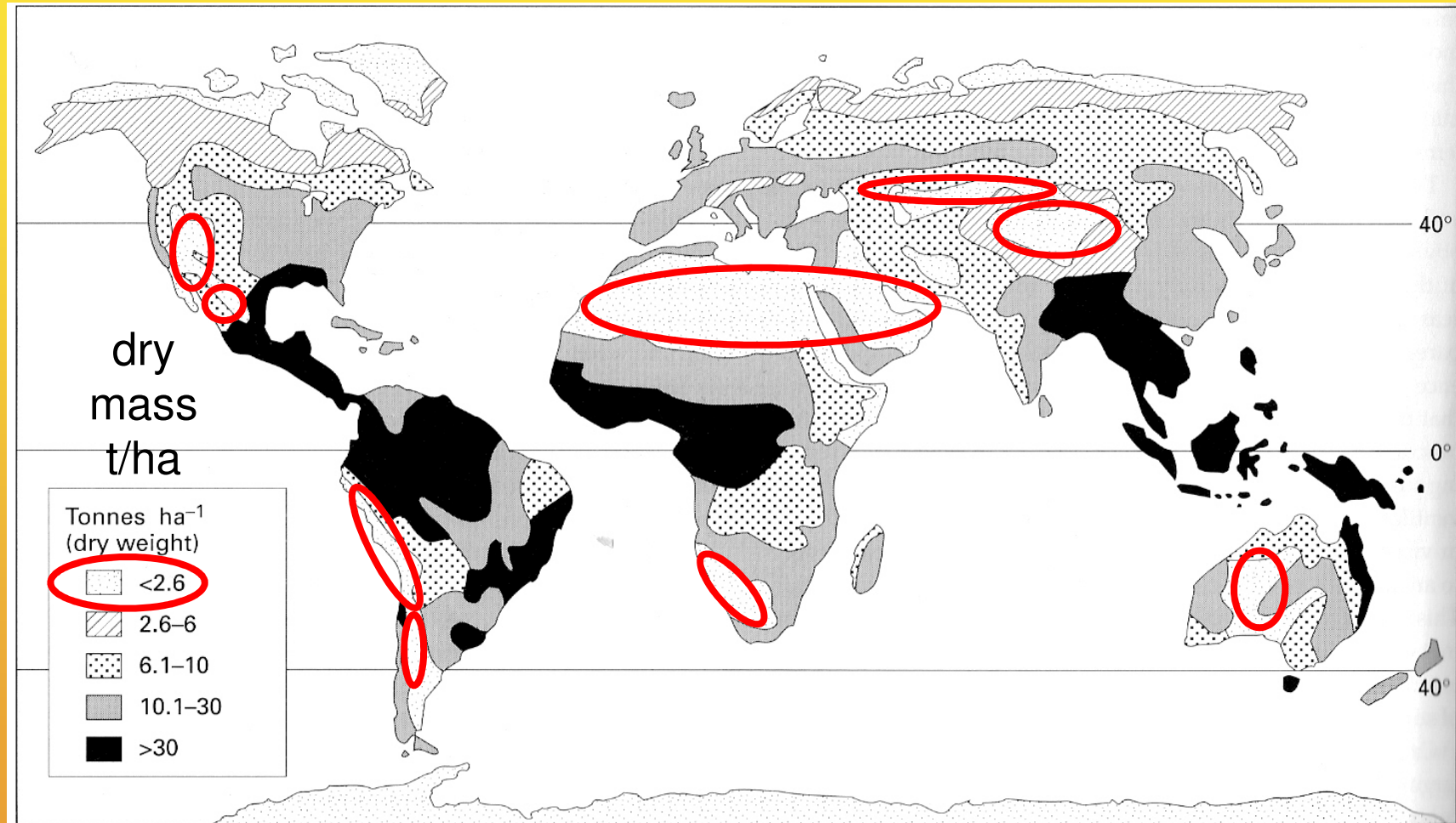


from the lecture of Professor R. Laskowski

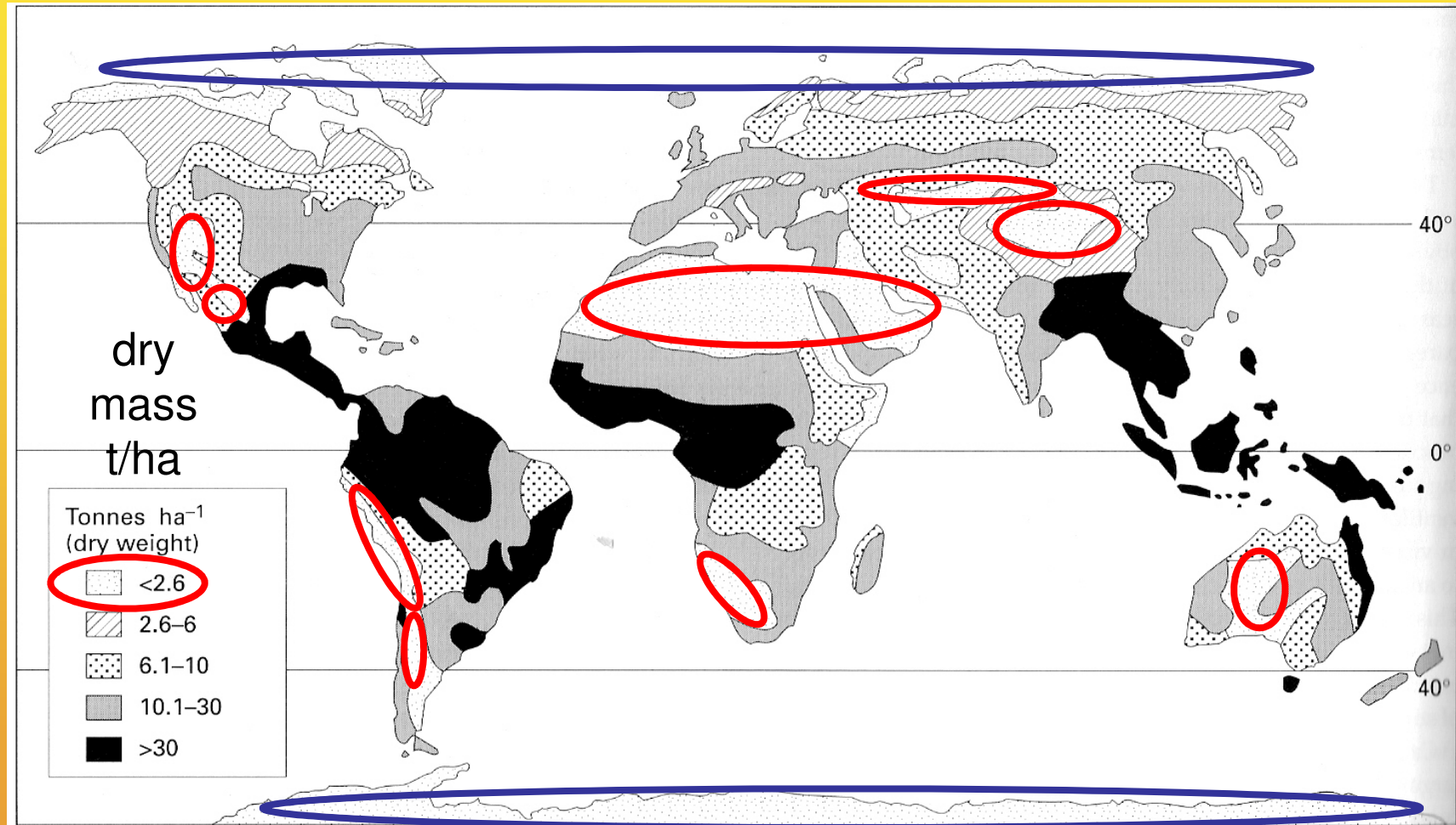
Areas of arid and semi-arid climate: deserts, semi-deserts, dry grasslands



"Trophic" deserts: areas of low primary production



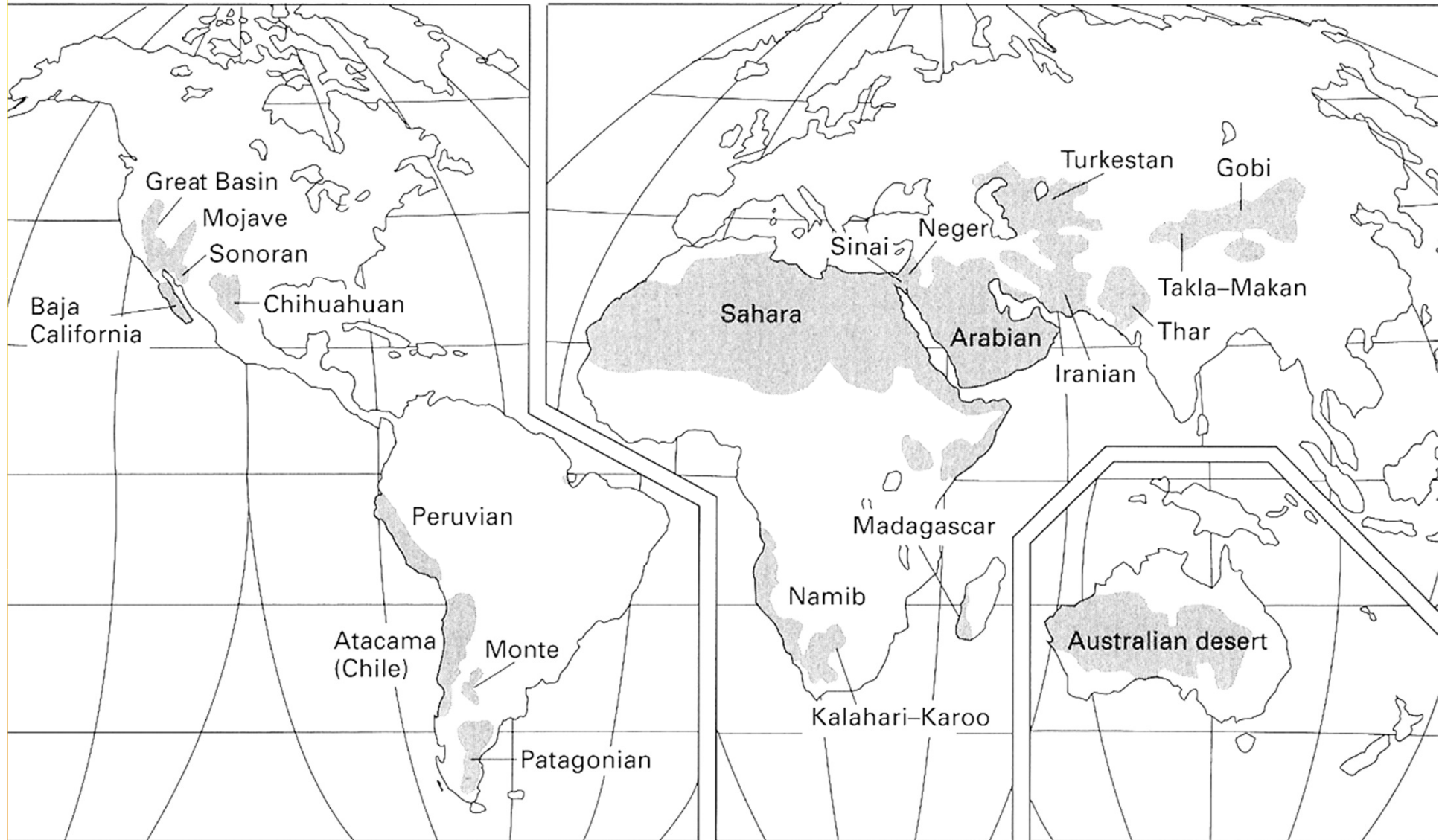
"Trophic" deserts: areas of low primary production



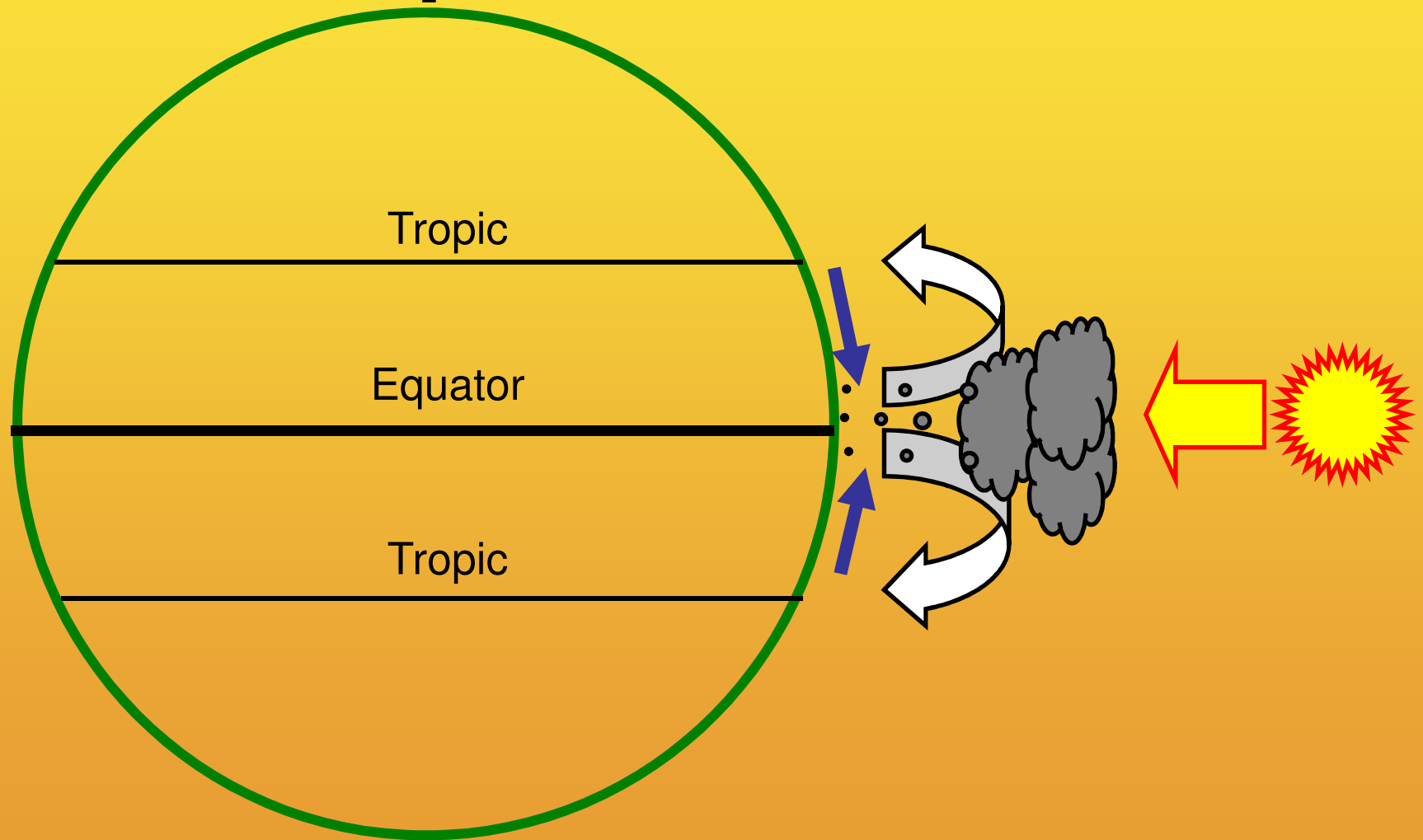
Characteristics of deserts

- **Low primary production: low food abundance**
- **Low water availability**
- **In tropical and subtropical zone: high temperature**
- **High daily amplitude of temperature**
- **Unpredictability of resource (food and water) availability**

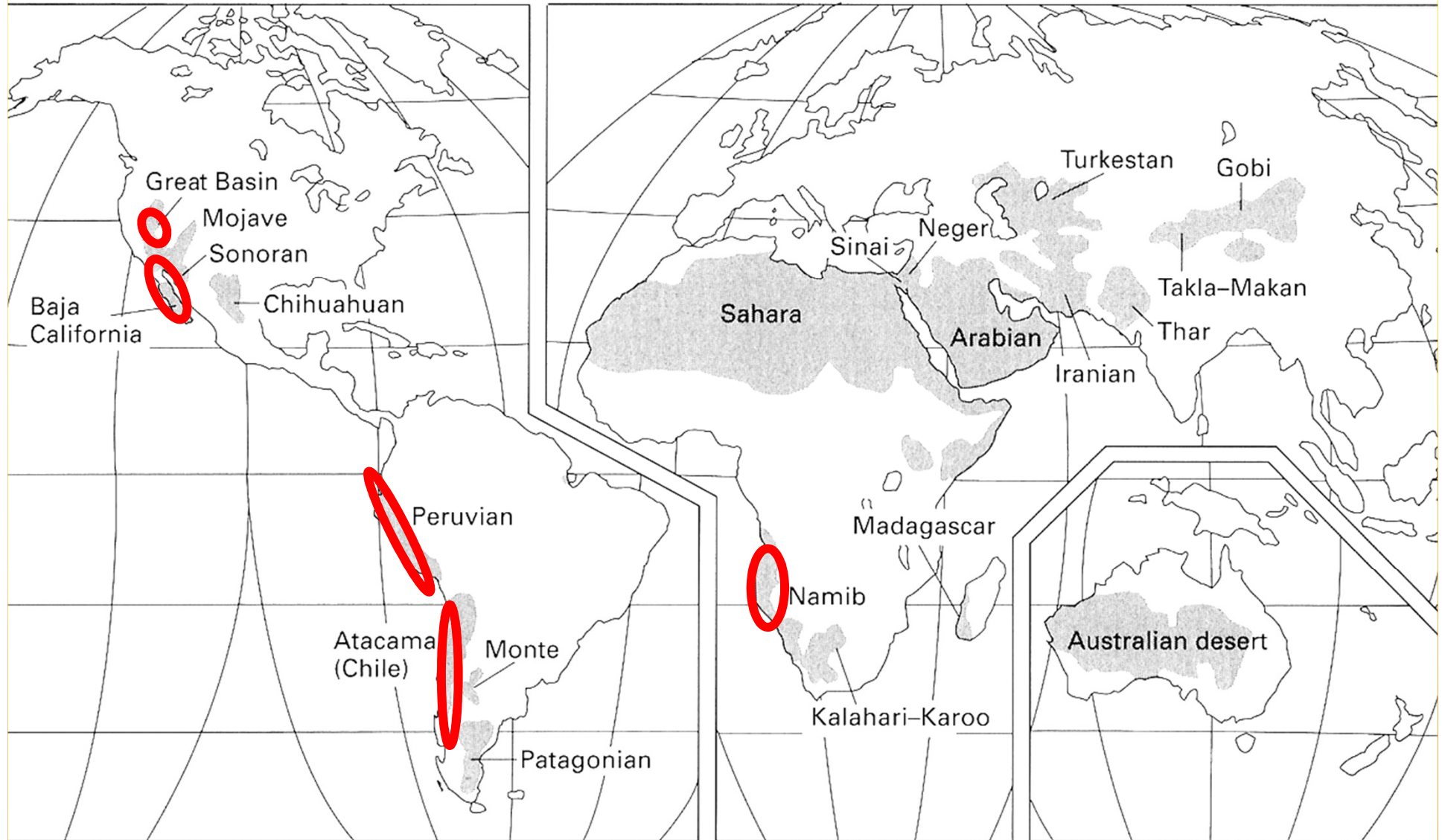
Main deserts



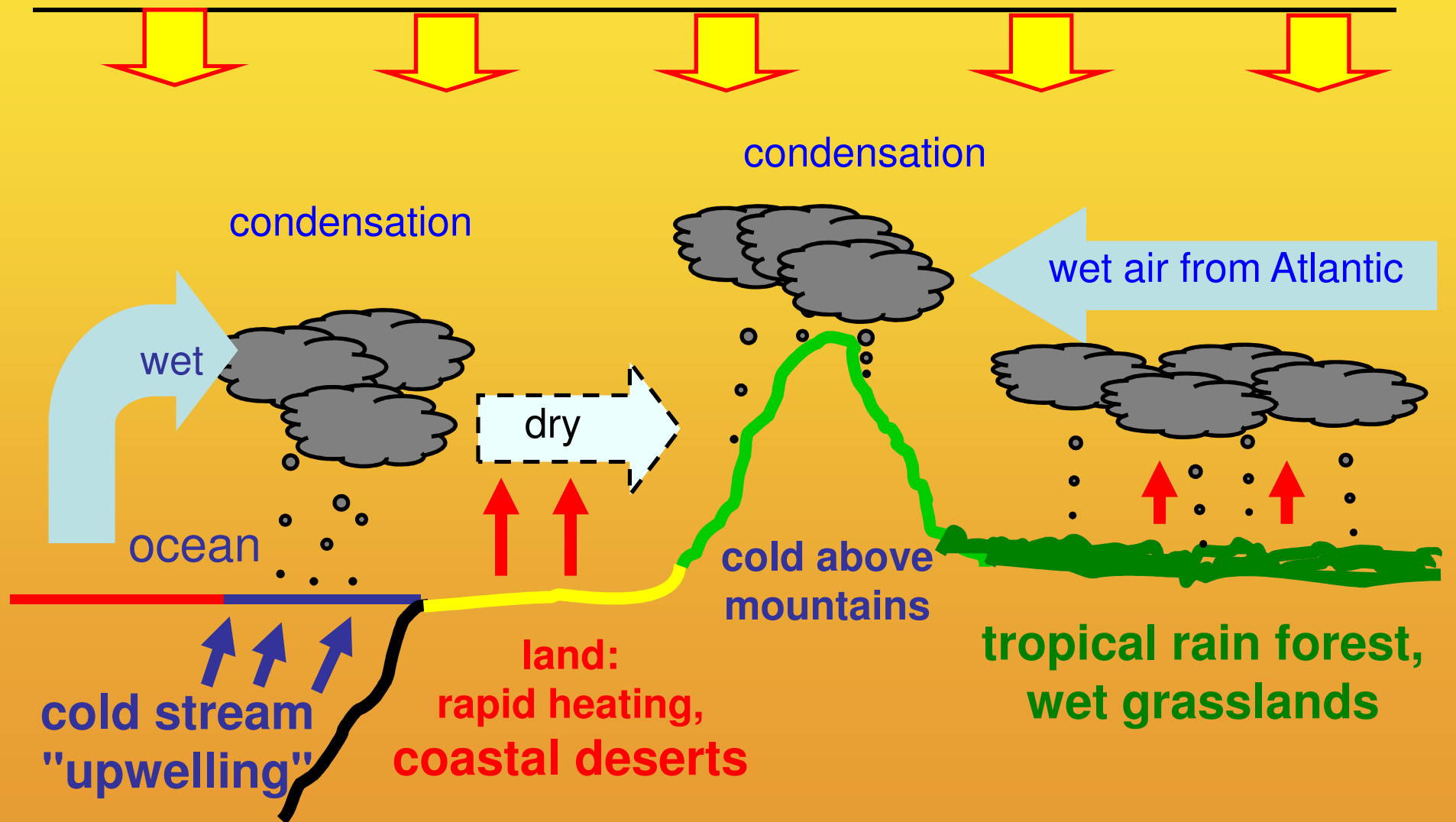
Mechanism of formation of a tropical-zone desert



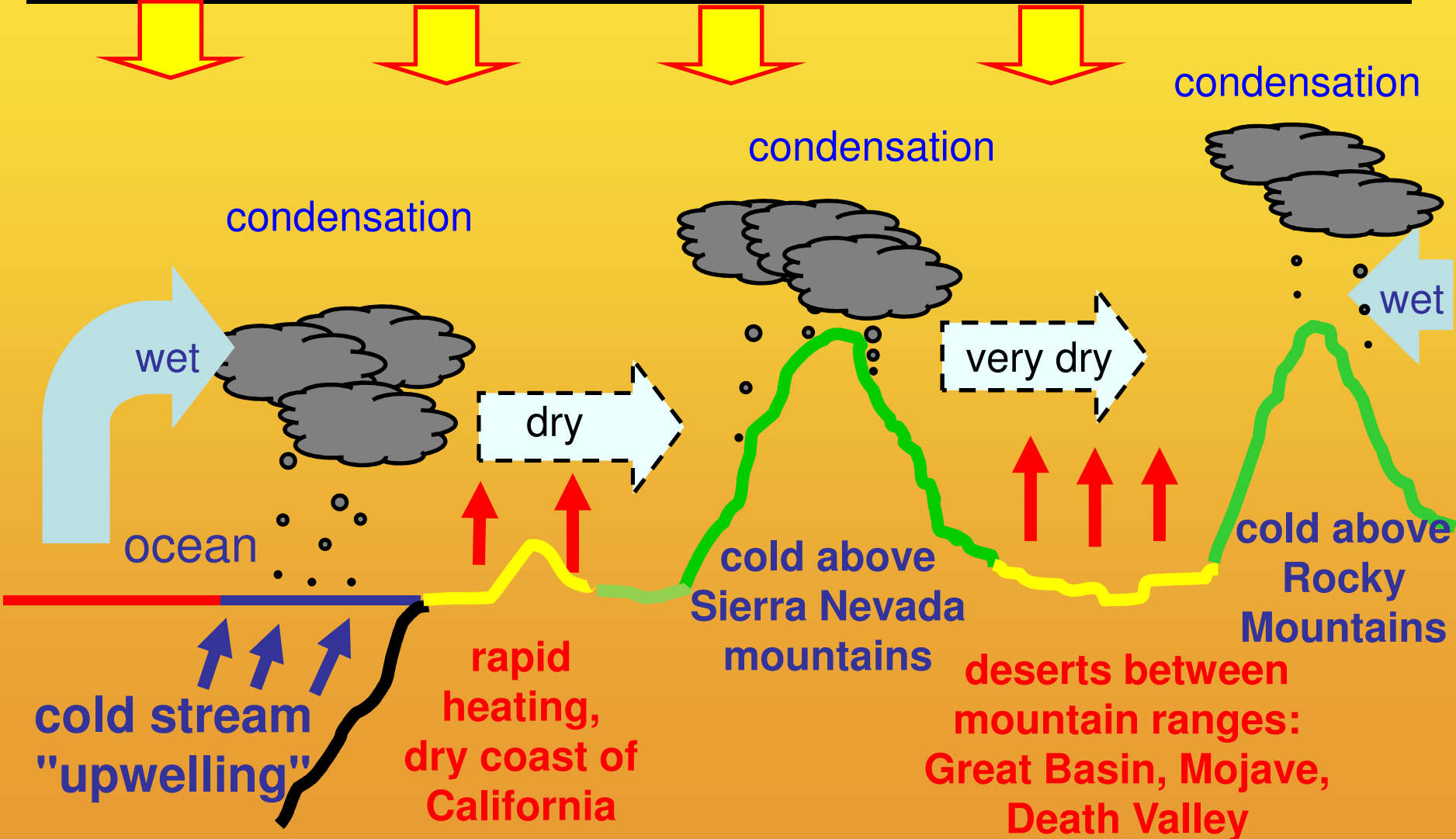
Main deserts



Mechanism of formation of a coastal desert: Peruvian, North part of Chilean (Atacama)



Mechanism of formation of a coastal and interior deserts in California and Nevada



Characteristics of deserts: challenges

- **Low primary production: low food abundance**
- **Low water availability**
- **In tropical and subtropical zone: high temperature**
- **High daily amplitude of temperature**
- **Unpredictability of resource (food and water) availability**

Coping with high temperature

EFFECTS of TEMPERATURE

- **Effects of body temperature on the rate of metabolism**
- **Thermal balance**
- **Effect of ambient temperature on the rate of metabolism in homeotherms**
- **Thermal conditions on deserts**

Thermodynamics: rate of processes kinetics of chemical reactions, effects of temperature

- **Arrhenius equation (form 1)**

$$k = k_{\max} e^{(-\mu/RT)}$$

k_{\max} - maximum reaction constant

(when each collision of molecules results in a reaction)

μ - energy of activation

$e^{(-\mu/RT)}$ - proportion of molecules that have energy exceeding μ

Thermodynamics: rate of processes kinetics of chemical reactions, effects of temperature

- Arrhenius equation (form 2)

$$k_{T_2} = k_{T_1} e^{\frac{\mu R(T_2 - T_1)}{T_2 T_1}}$$

k_{T_1} , k_{T_2} - reaction constants at temperatures
 T_1 and T_2

Thermodynamics: rate of processes kinetics of chemical reactions, effects of temperature

- **A simplified relation, the rule of van't Hoff:**

**A 10C increase of temperature results in
a 2-4-fold increase of the rate of a process**

$$Q_{10} = V_{(t+10)} / V_t = (V_{t2} / V_{t1})^{10/(t2 - t1)}$$

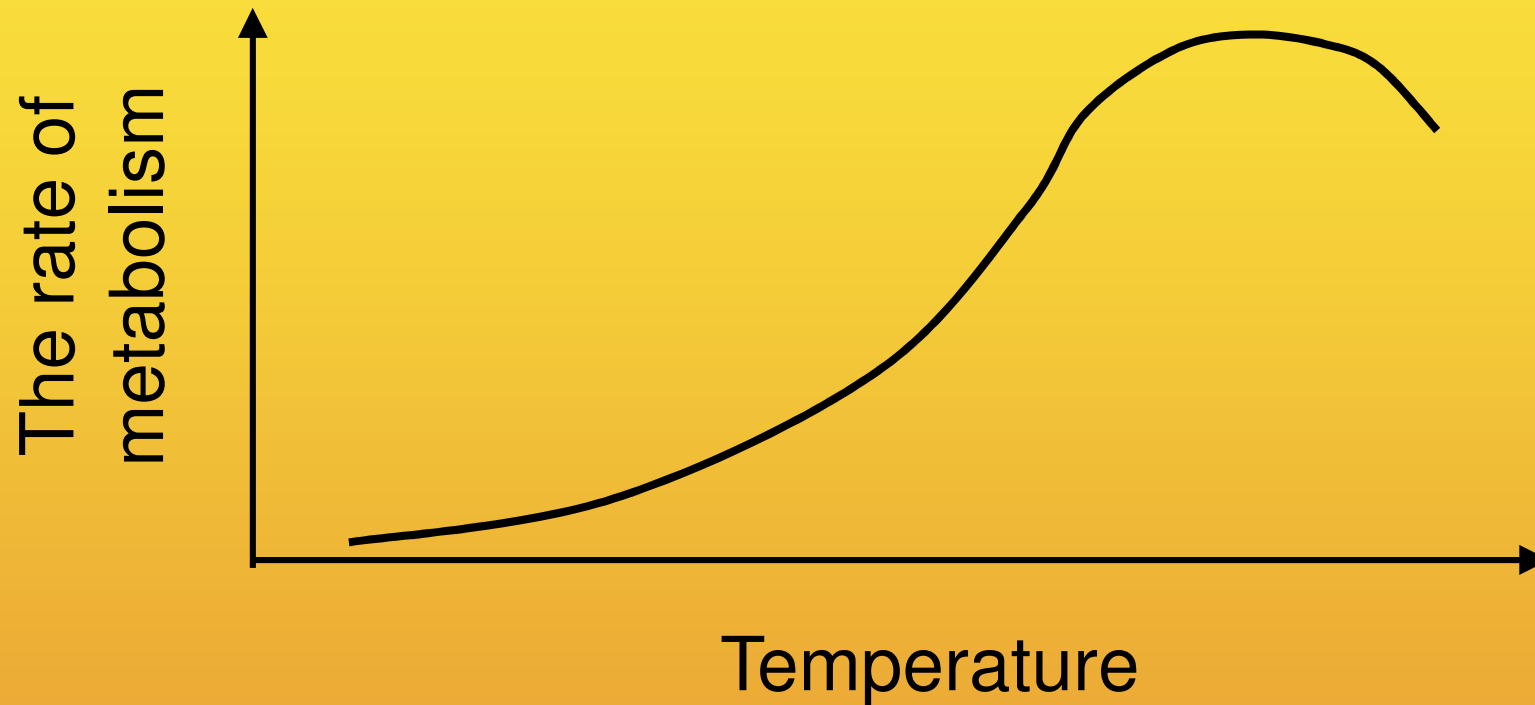
$$V_{t2} = V_{t1} Q_{10}^{(t2-t1)/10}$$

$t, t1, t2$ - temperature;

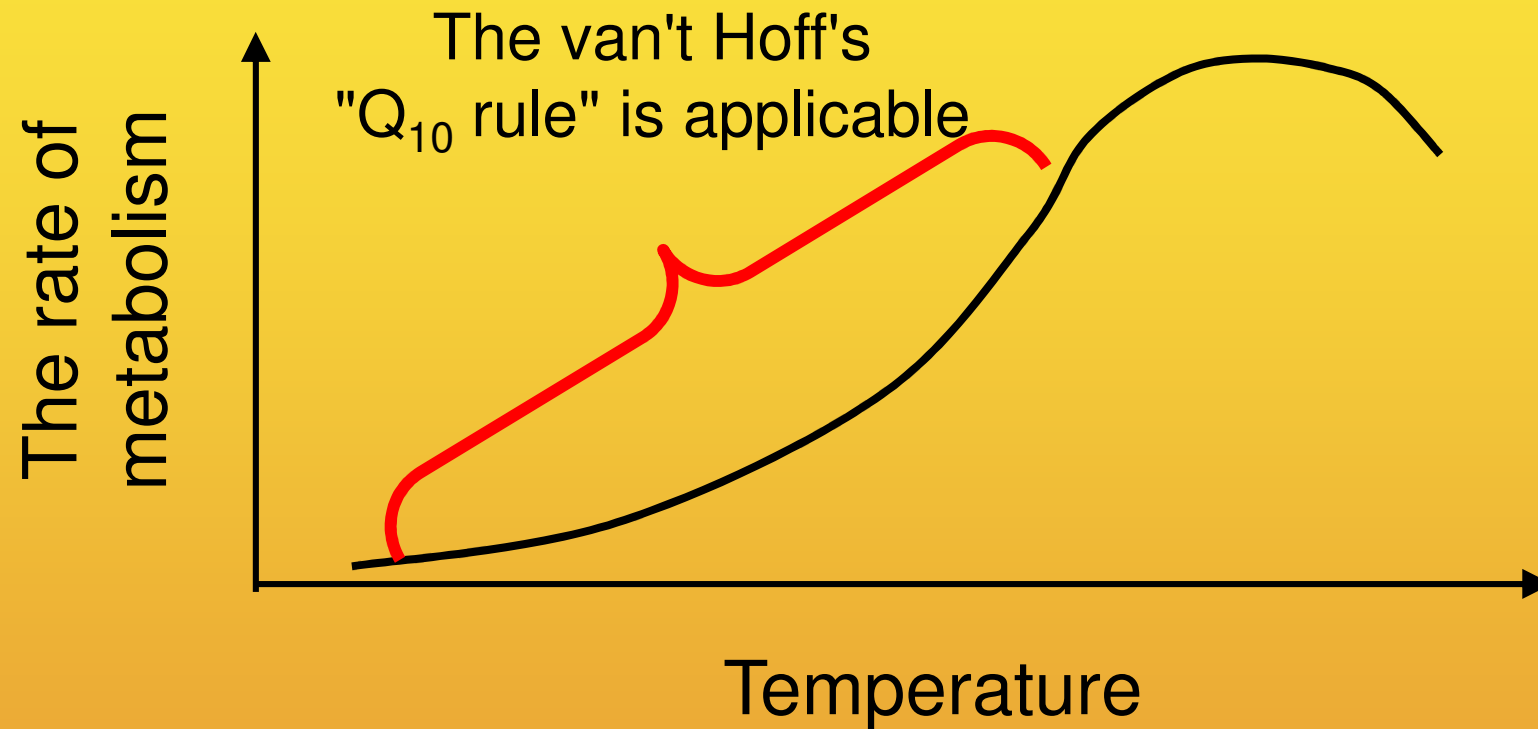
V - rate of a process at temperature t

Q_{10} - an empirically determined coefficient (NOT a physical constant)

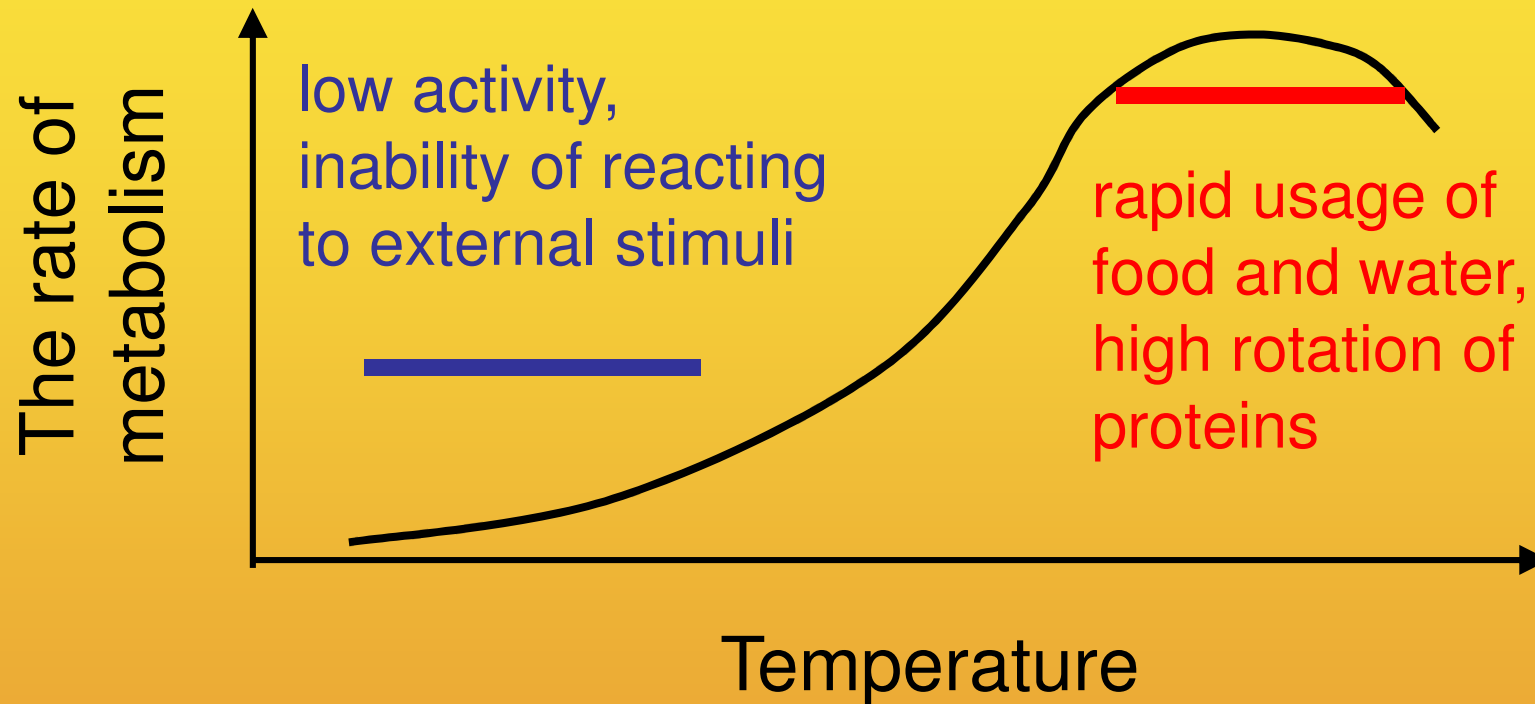
Rate of biochemical processes: combined effects of temperature



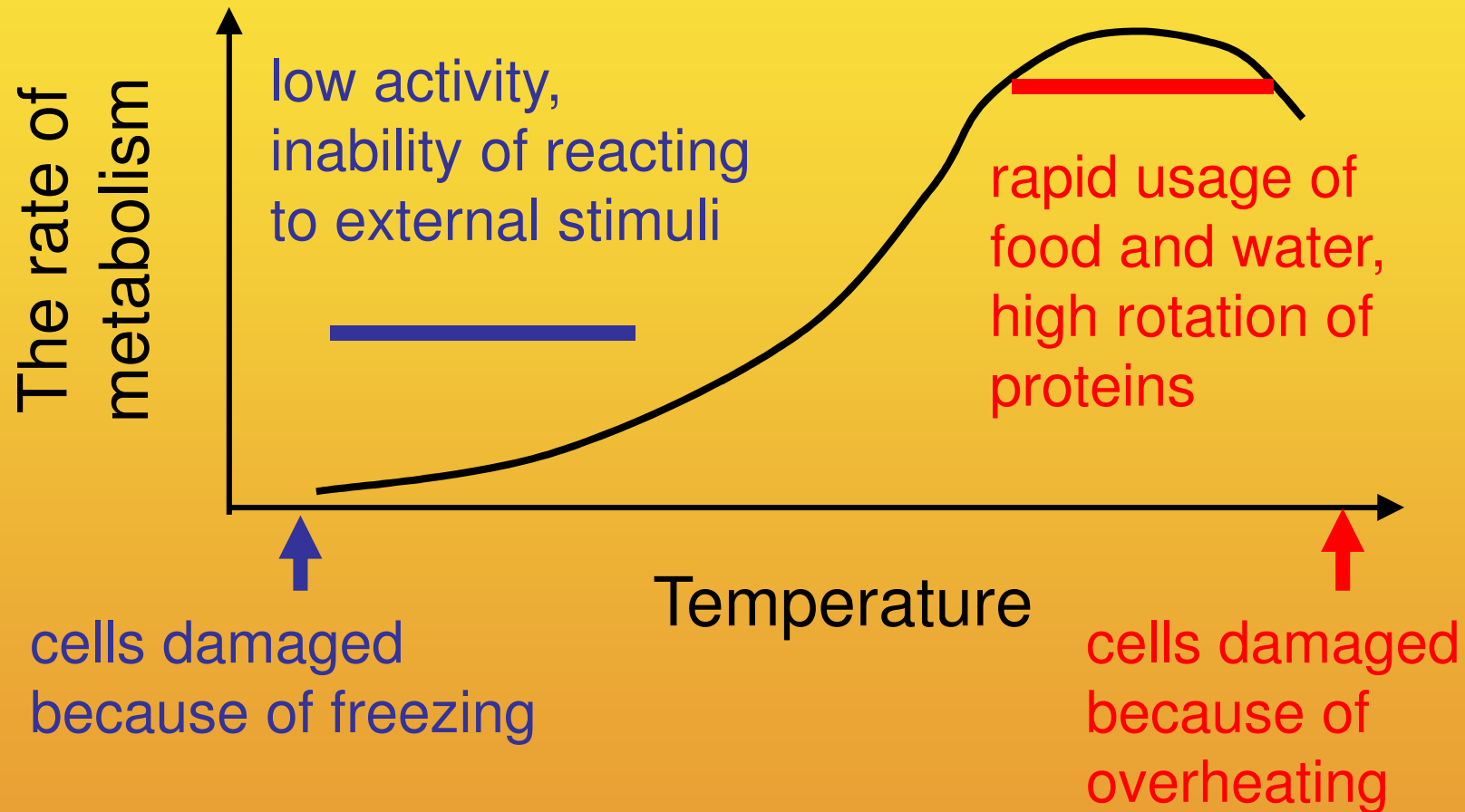
Rate of biochemical processes: combined effects of temperature



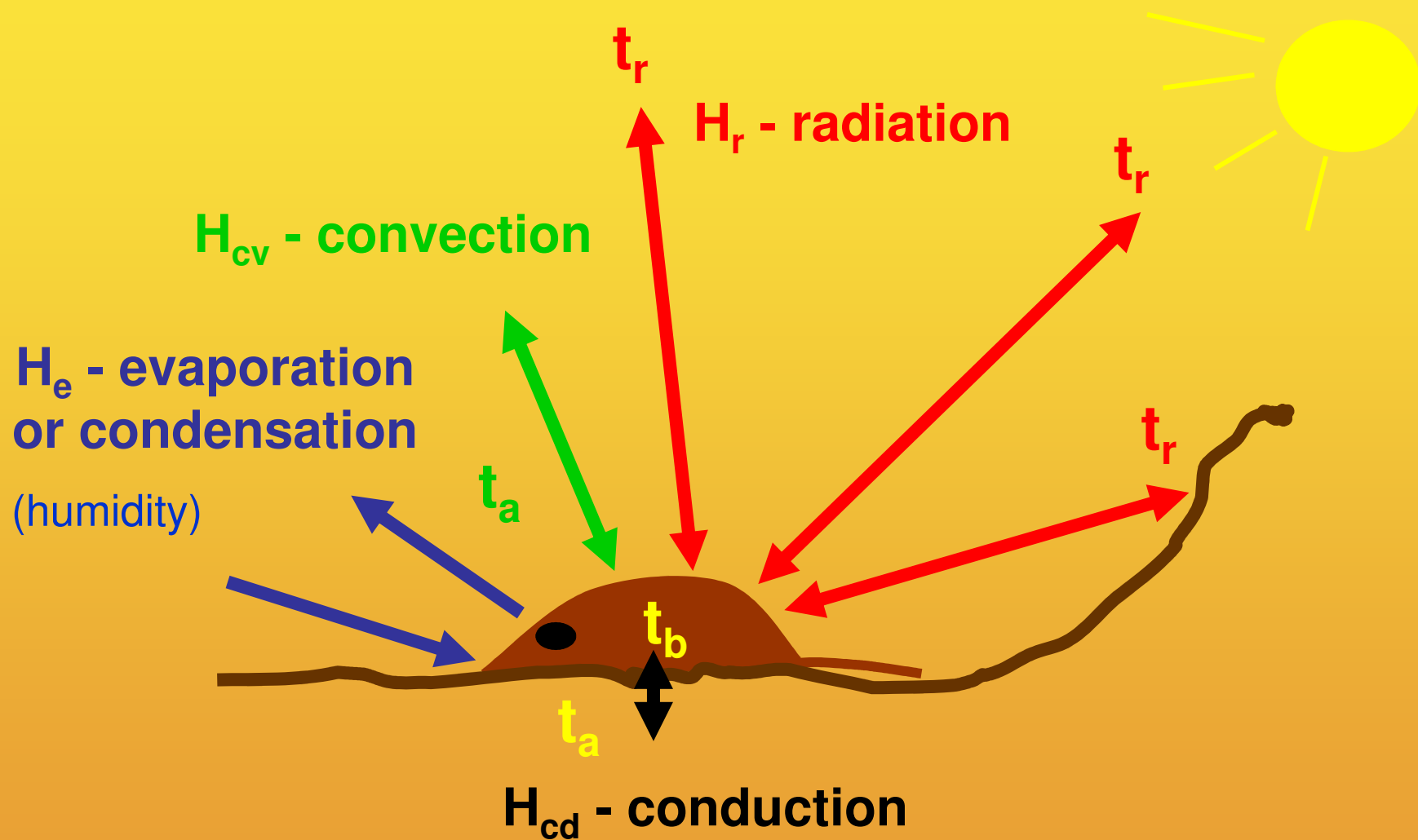
Rate of biochemical processes: combined effects of temperature



Rate of biochemical processes: combined effects of temperature



Components of heat balance



Components of heat balance

H_{cd} : conduction

H_{cv} : convection

H_r : radiation

H_e : evaporation

$$\left. \begin{array}{l} H_{cd} \\ H_{cv} \\ H_r \end{array} \right\} H \approx c(T_b - T_a)$$
$$H_e \approx f(T_b, T_a, W\%)$$

H_a : accumulation of heat = $\Delta t_b \times M_b \times q$

Q : metabolic heat production

$$H_a = \pm H_{cd} \pm H_{cv} \pm H_r \pm H_e + Q$$

Components of heat balance under a strict homeothermia ($\Delta t_b=0$)

H_{cd} : conduction

H_{cv} : convection

H_r : radiation

H_e : evaporation

$$\left. \begin{array}{l} H_{cd} \\ H_{cv} \\ H_r \end{array} \right\} H \approx c(T_b - T_a)$$

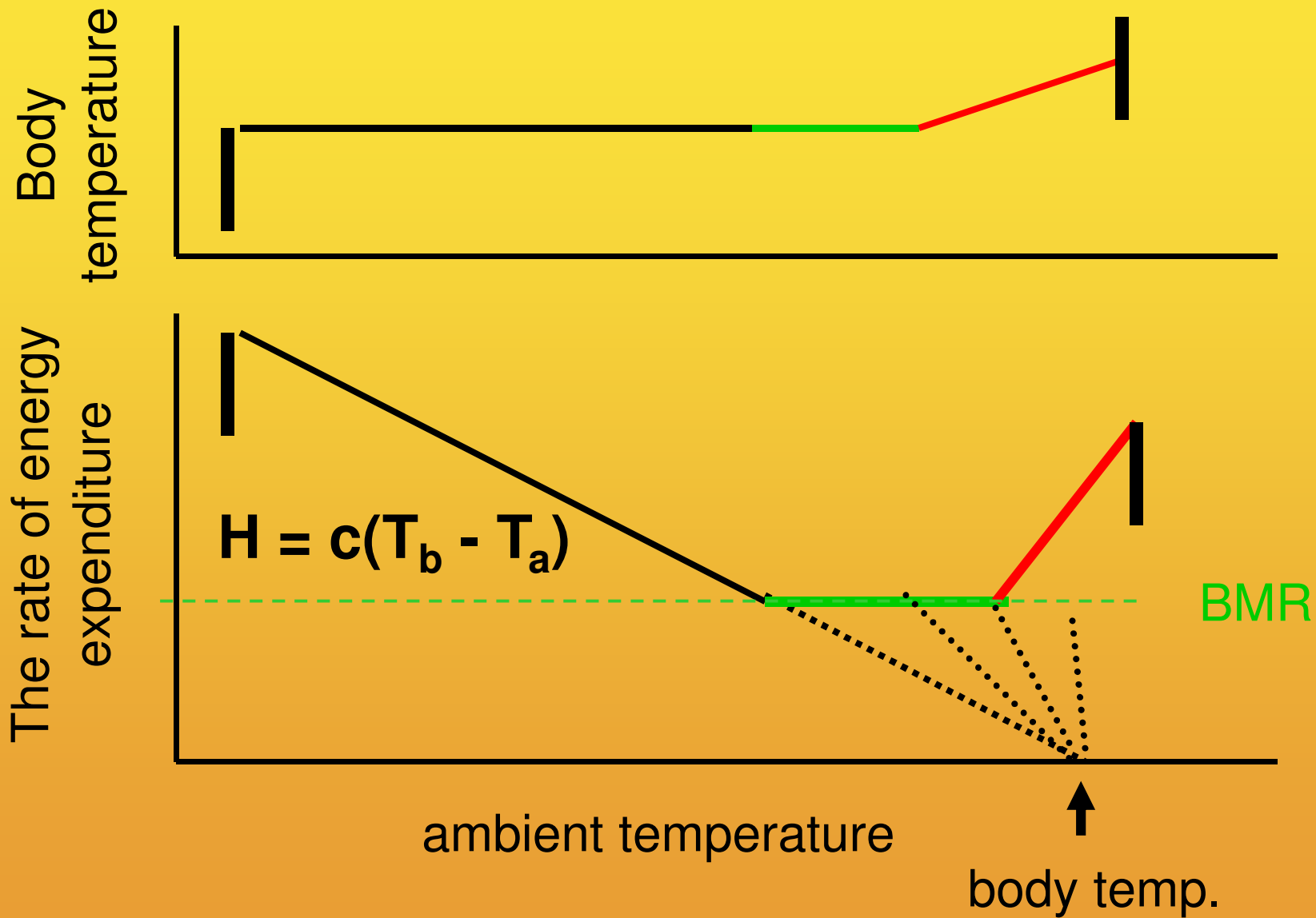
$$H_e \approx f(T_b, T_a, W\%)$$

H_a : accumulation of heat = $\Delta t_b \times M_b \times q = 0$

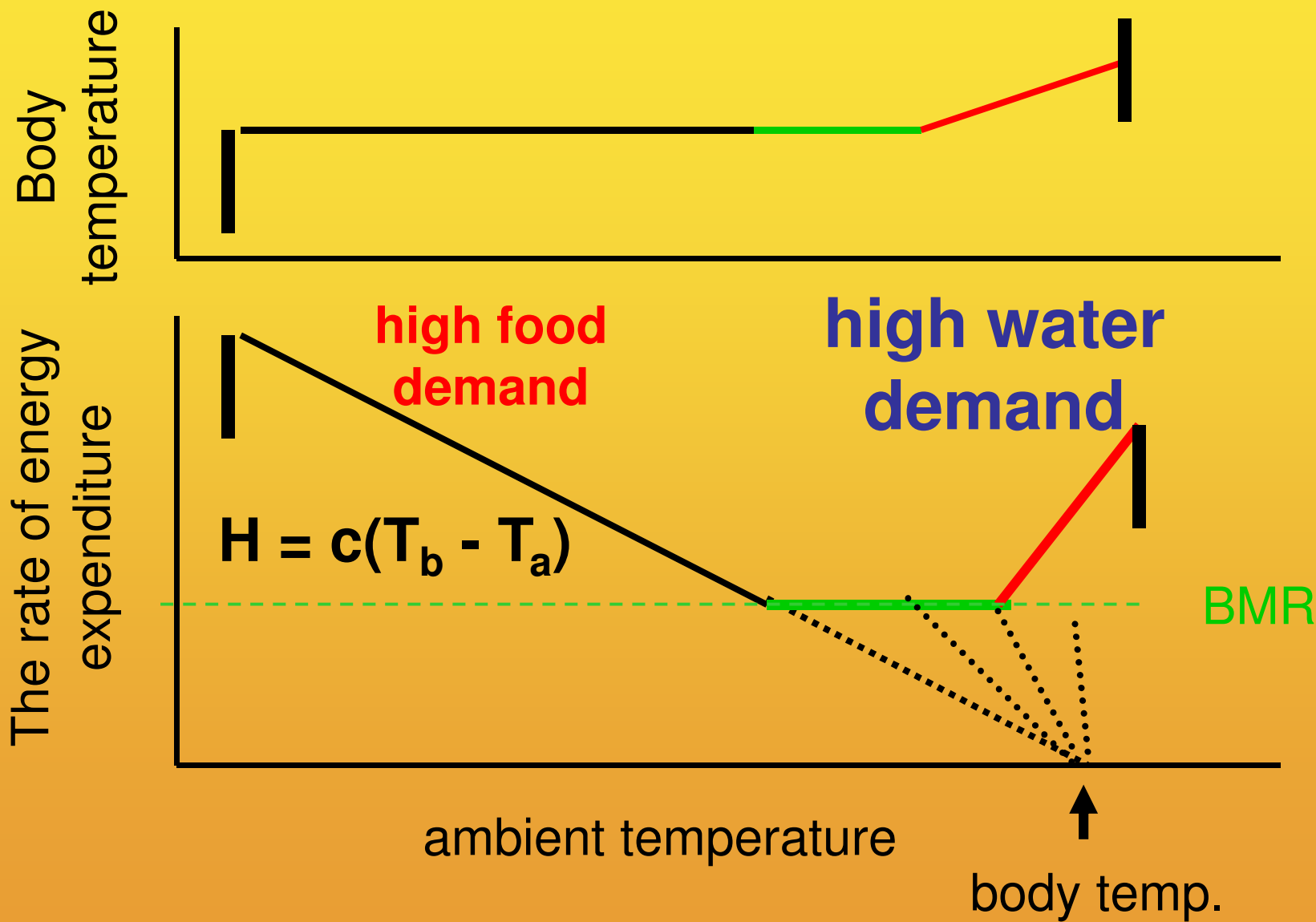
Q : metabolic heat production

$$Q = \pm H_{cd} \pm H_{cv} \pm H_r \pm H_e$$

A simplified model of thermoregulation

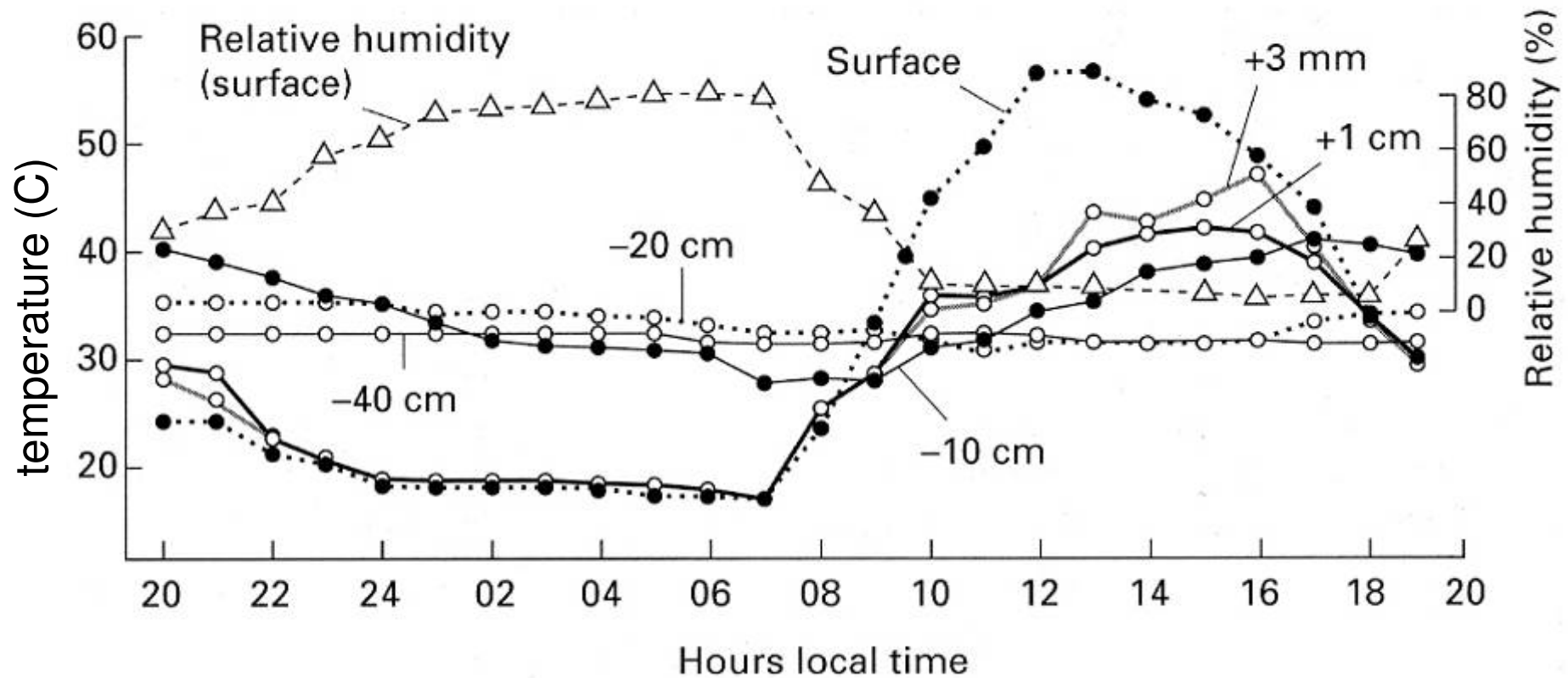


A simplified model of thermoregulation



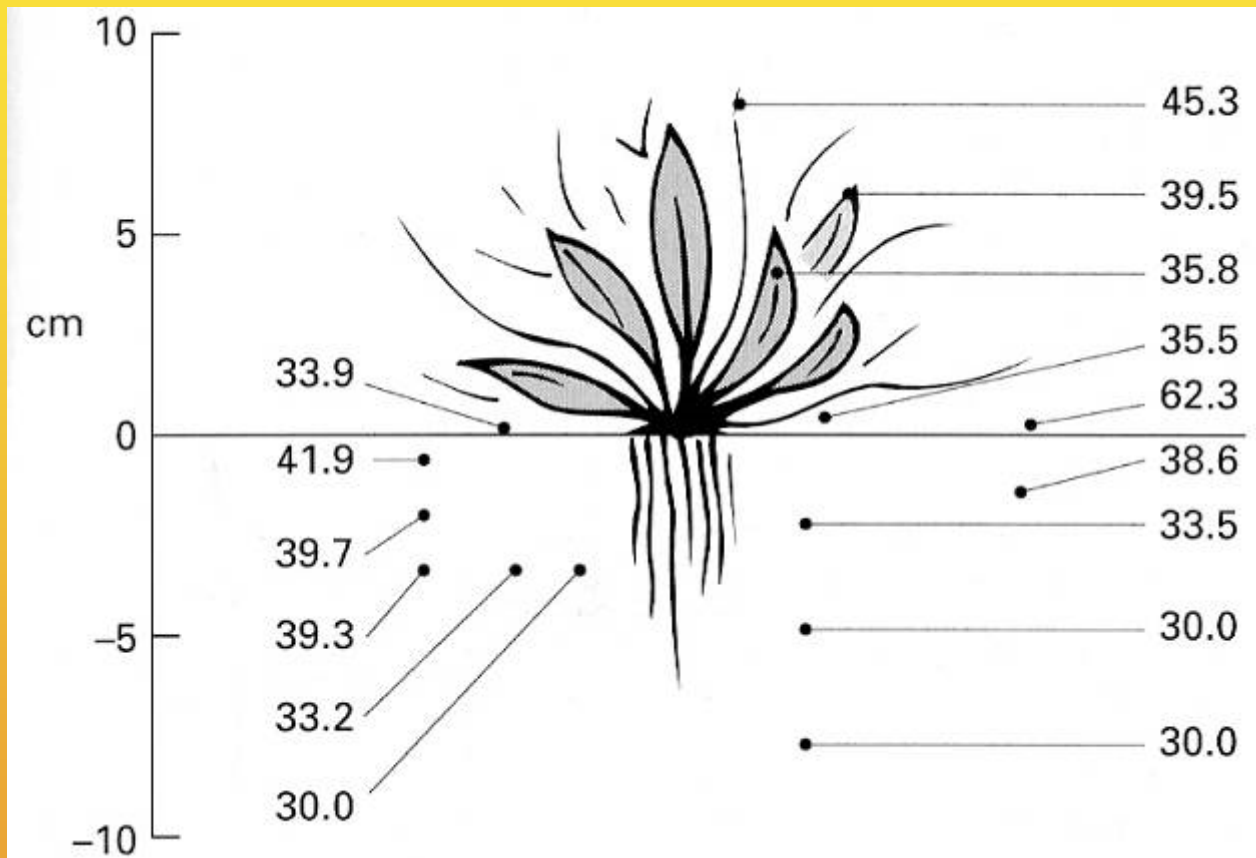
Thermal conditions on a hot desert

Daily cycle of temperature and humidity



Thermal conditions on a hot desert

Temperature near a clump of a plant

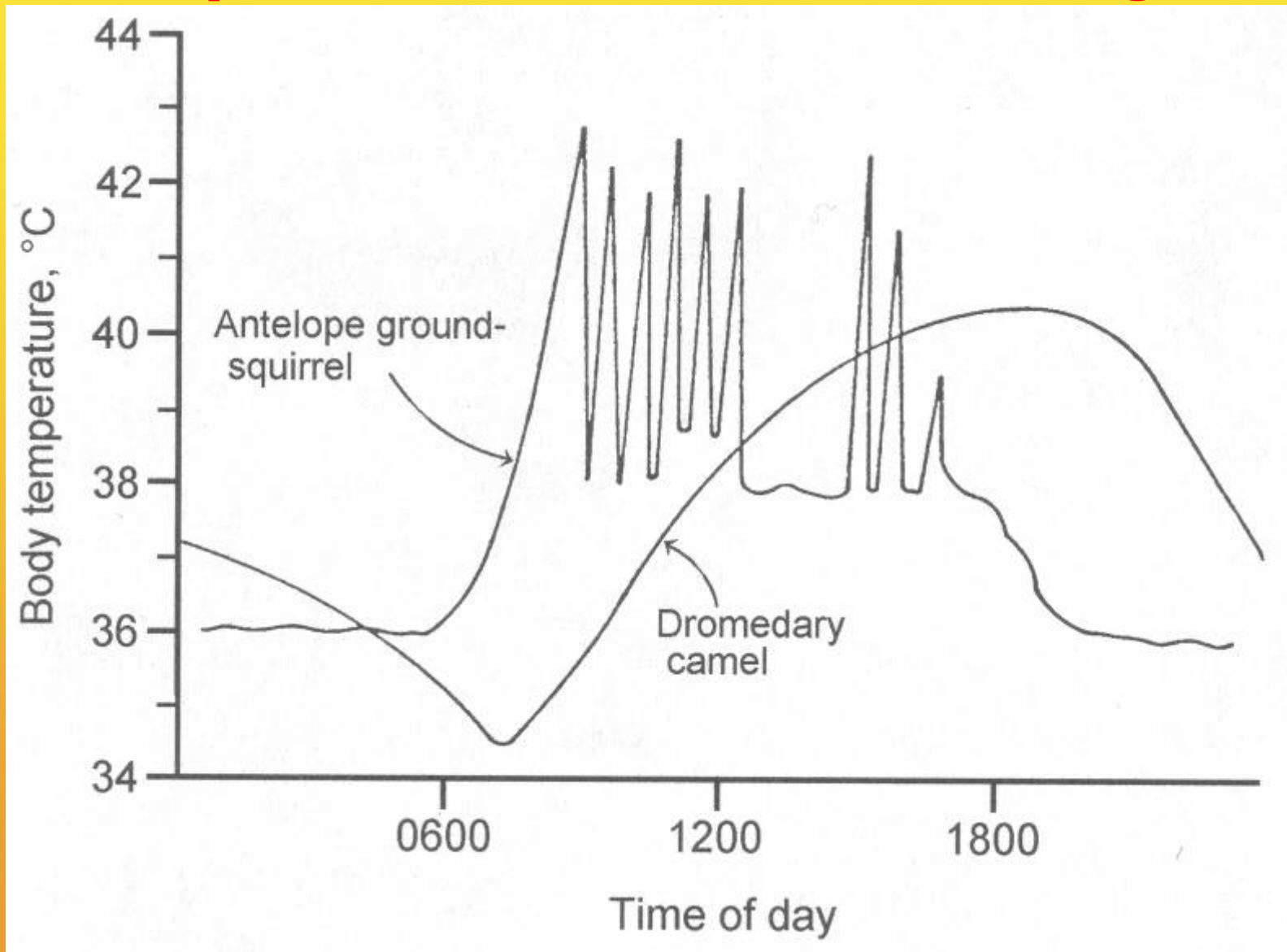


Microclimate experienced by small beetles
in, under, and near a desert shrub

Main strategies

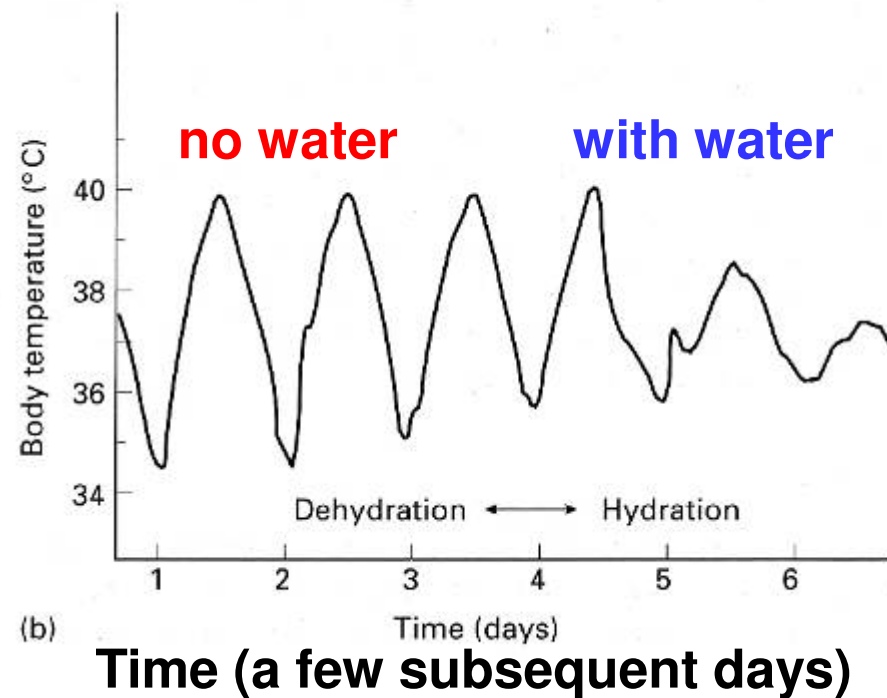
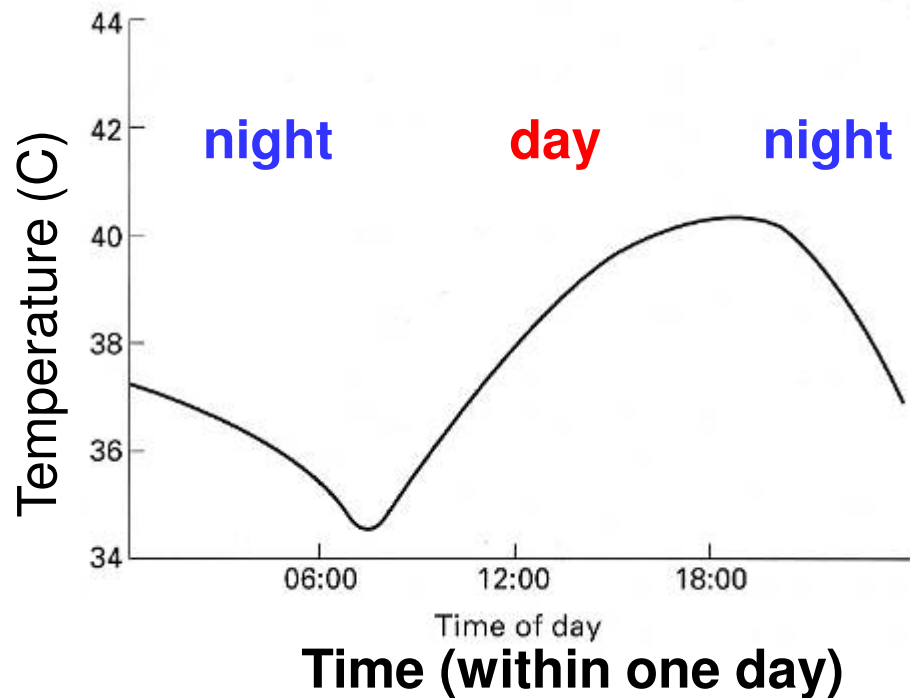
- **"Endurers"**
 - large body mass,
 - thermal inertia;
- **"Evaporators"**
 - intermediate mass,
 - leave on desert edges,
 - daily migrations;
- **"Evaders"**
 - small body mass
 - escape to suitable microhabitats

Comparison of distinct strategies

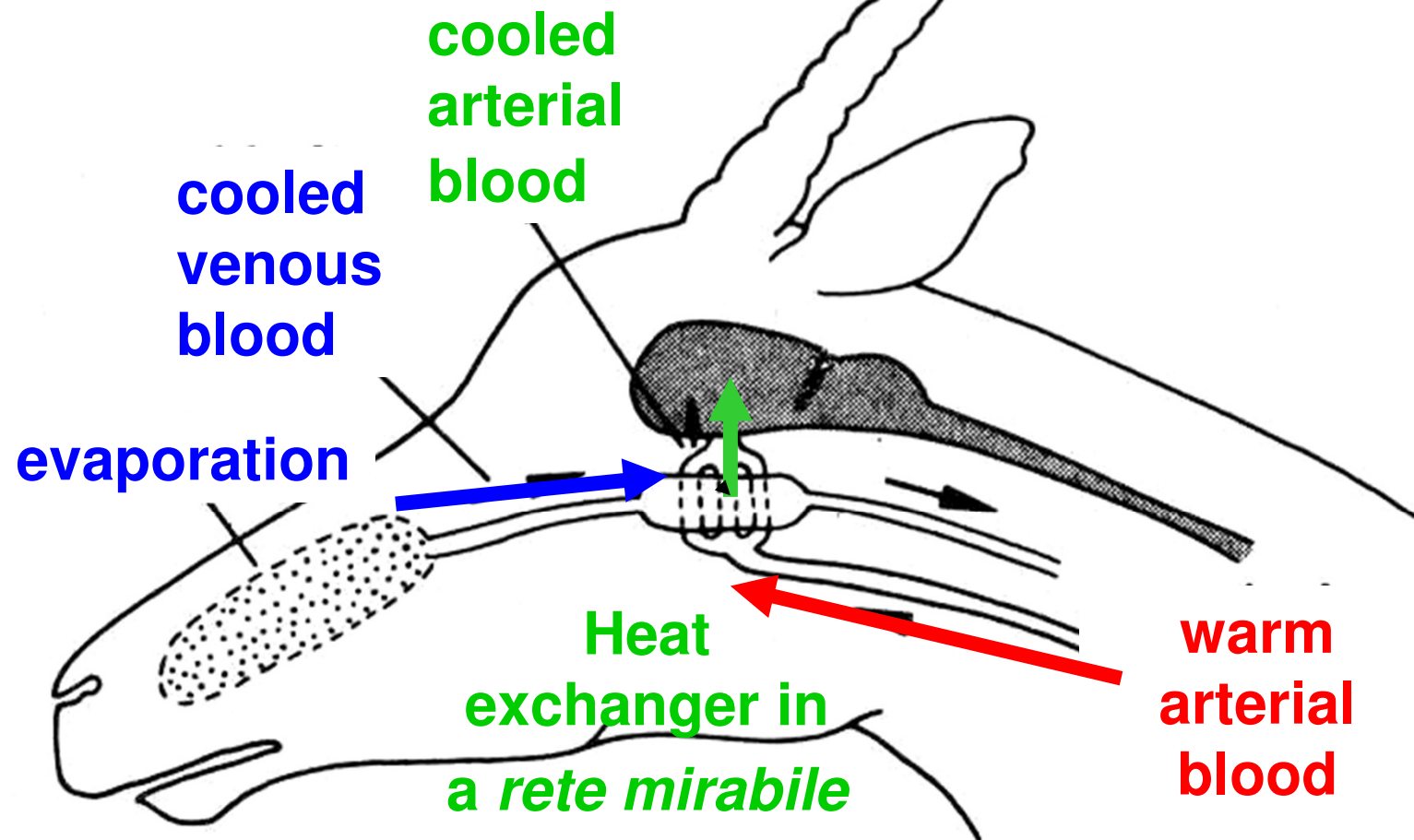


The strategy of an "inertial endurer"

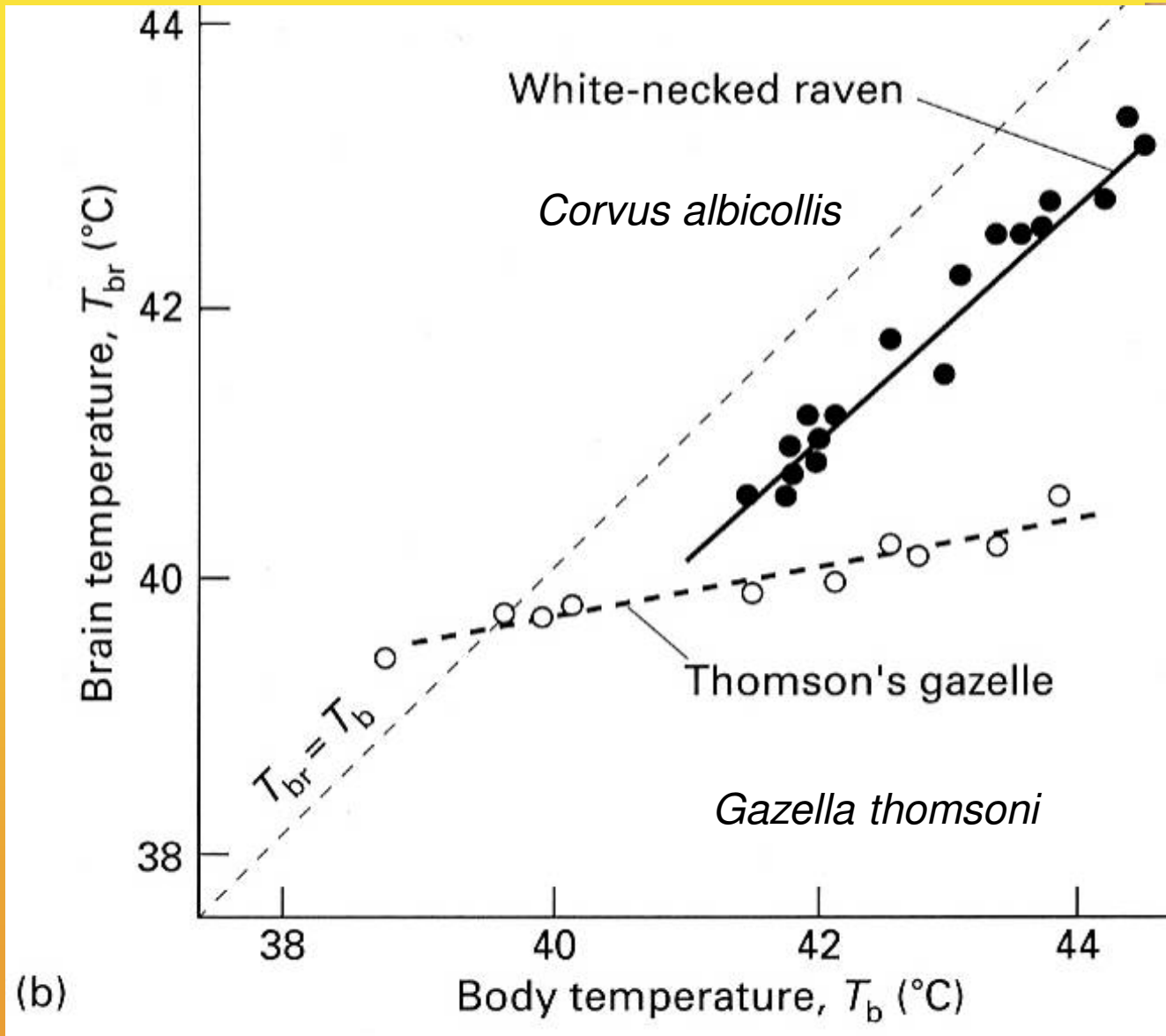
Changes of body temperature in a dromedary camel



Selective brain cooling



Selective brain cooling

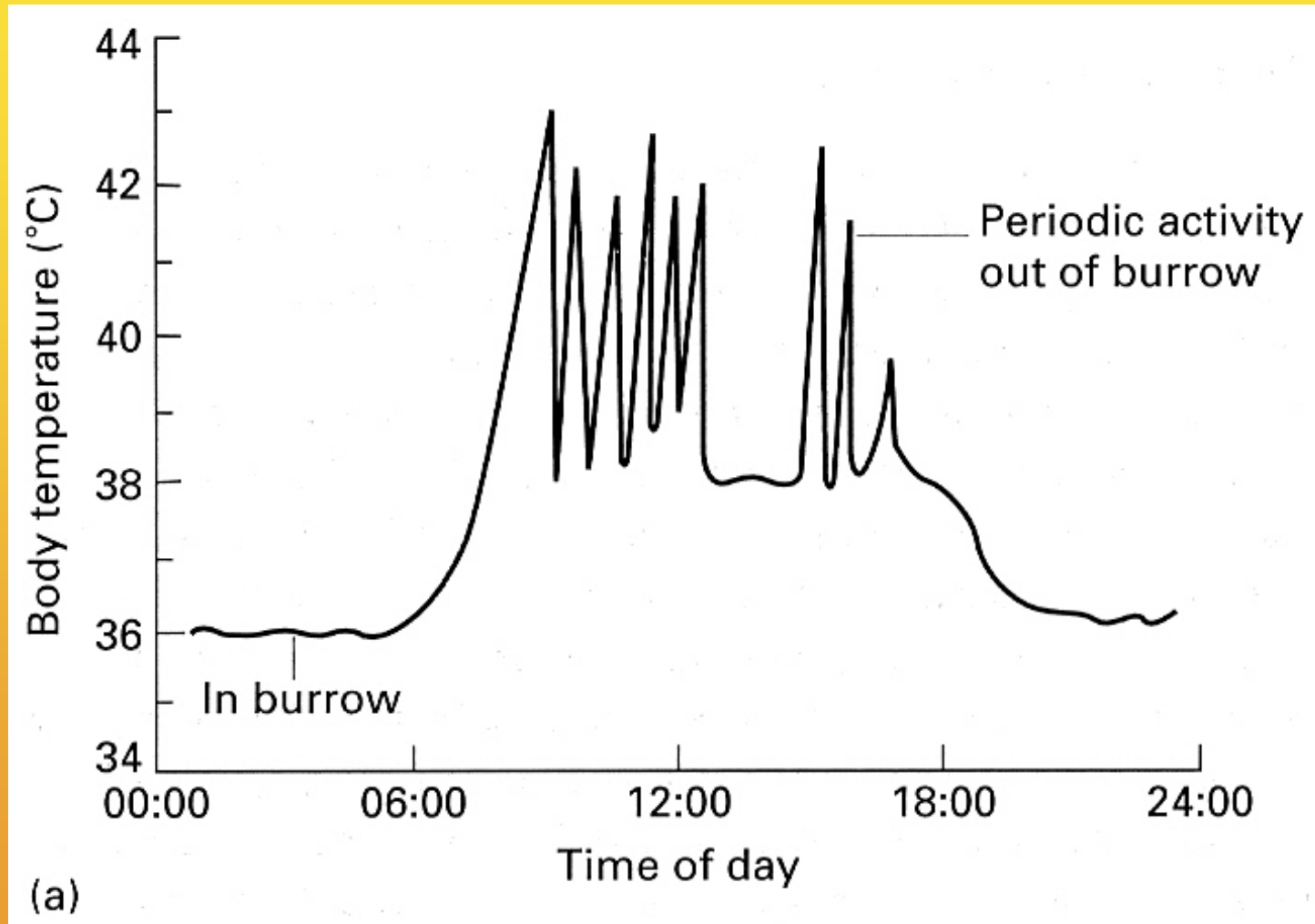


photos: Wikipedia

Willmer et al. 2000

Escape underground...

Body temperature in a rodent: the antelope ground squirrel



Escape underground...

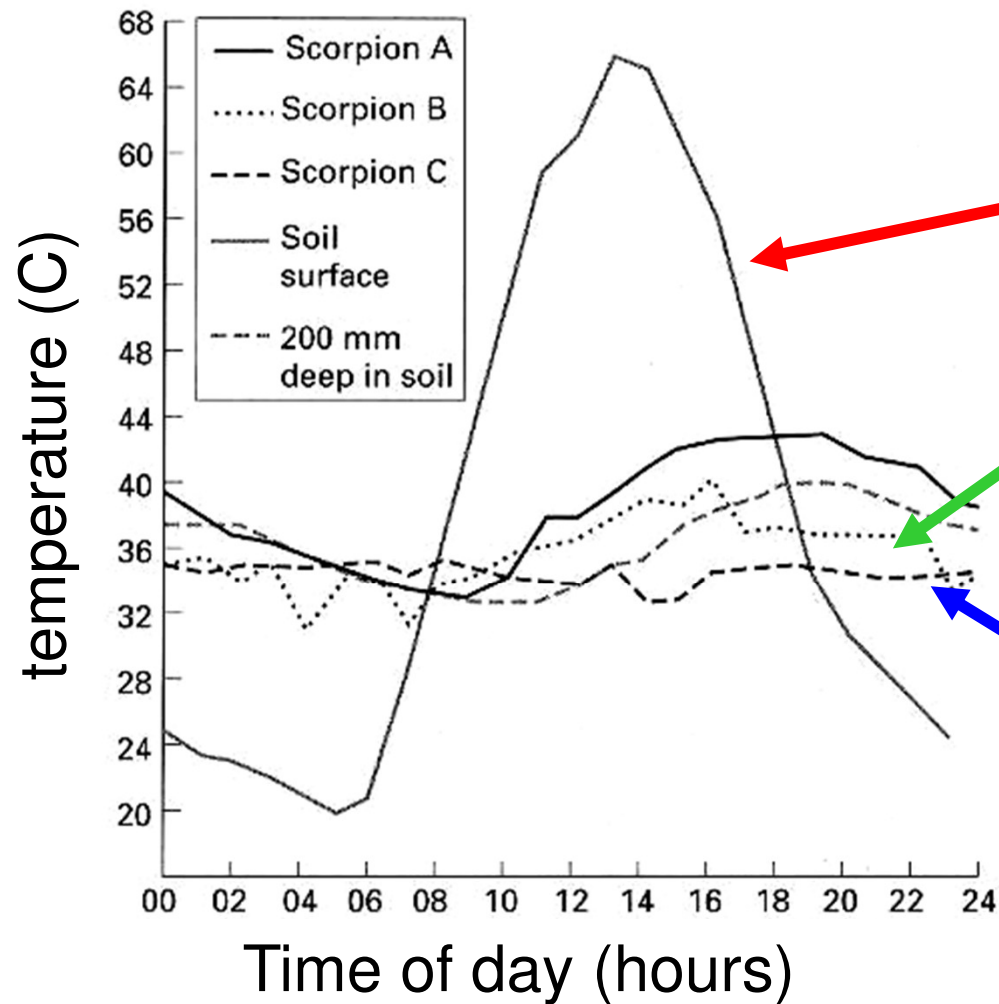


Fig. 14.5 Temperatures in the burrow of the scorpion *Hadrurus*, compared with temperatures at the soil surface and at a depth of 200 mm. (Adapted from Hadley 1970.)

Temperature:

- soil surface

- in burrows of scorpions *Hadrurus sp.* (3 individuals)

- 20cm deep in soil

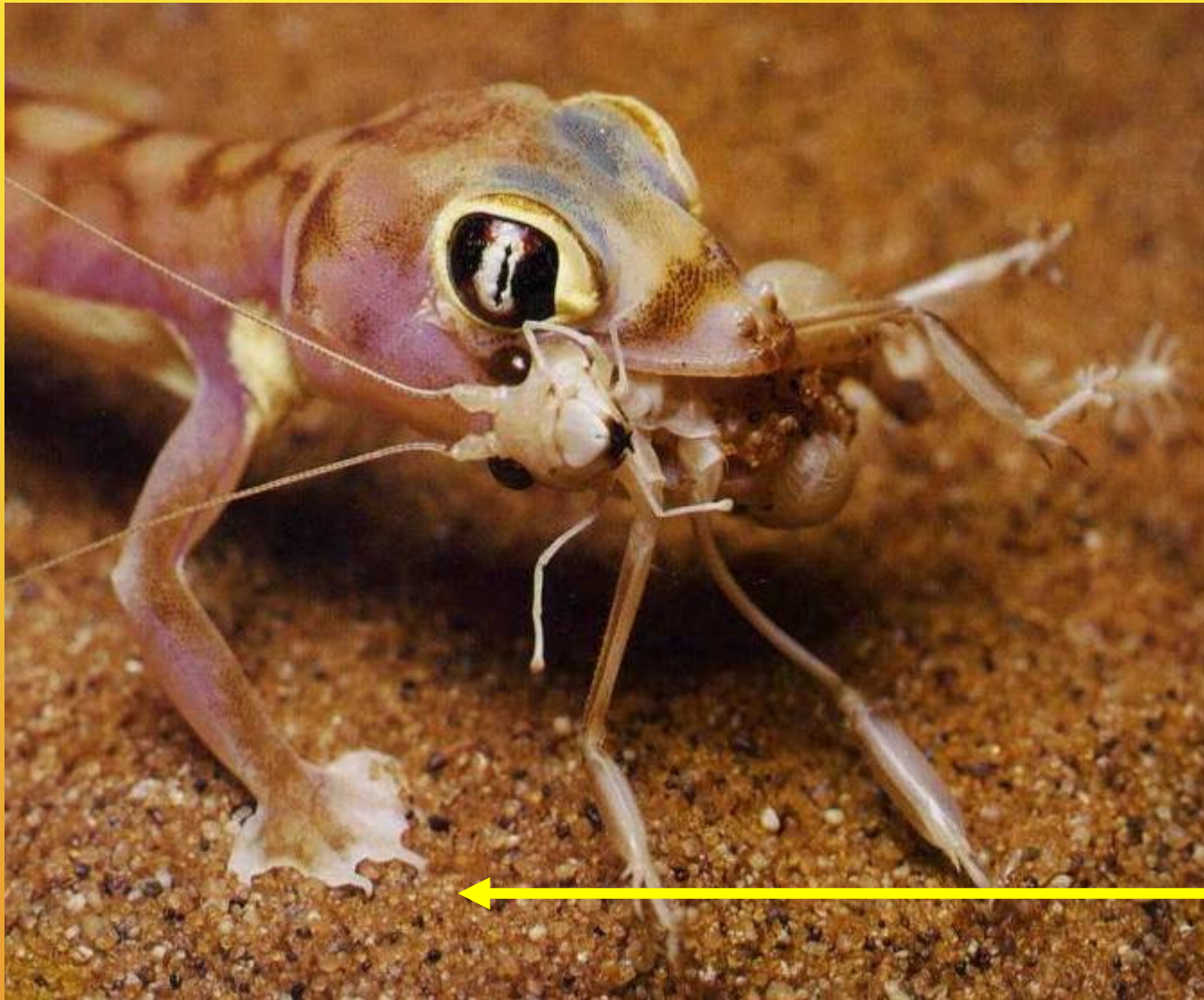
Escape underground...

A lizard:
sand diver
Meroles cunierostris
South Africa



photo: Anthony Bunnister/NHPA; copied from: *Encyklopedia zwierząt gady i płazy*; ELIPSA, Warszawa 1993

Escape underground...



A lizard:
gecko
*Palmatogecko
rangei*

South Africa,
Namib Desert

food adapted for
digging in sand

Escape underground...

A lizard: skink
Lenista labialis

Australia,
Simpson Desert



reduced food;
the lizard "swims"
in sand

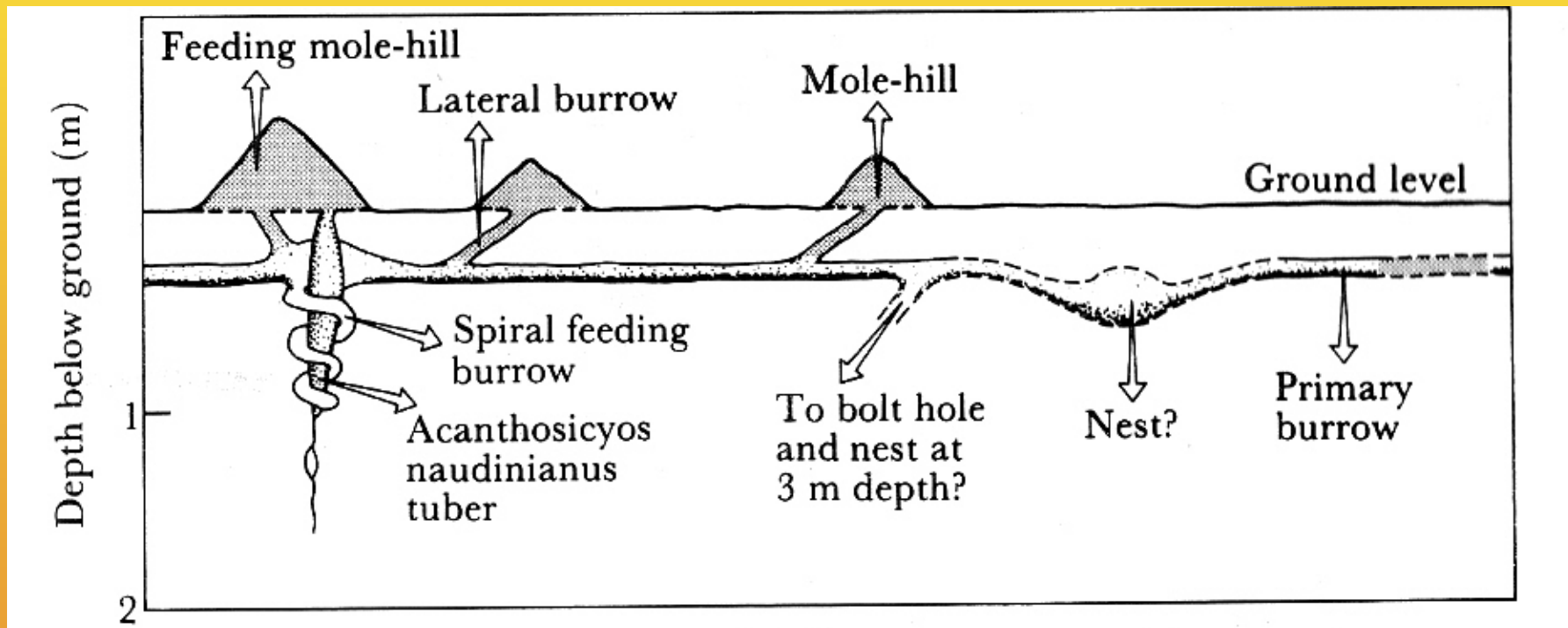
Naked mole rat (in Polish: "golec")
Heterocephalus glaber (Rodentia, Heteromyidae)



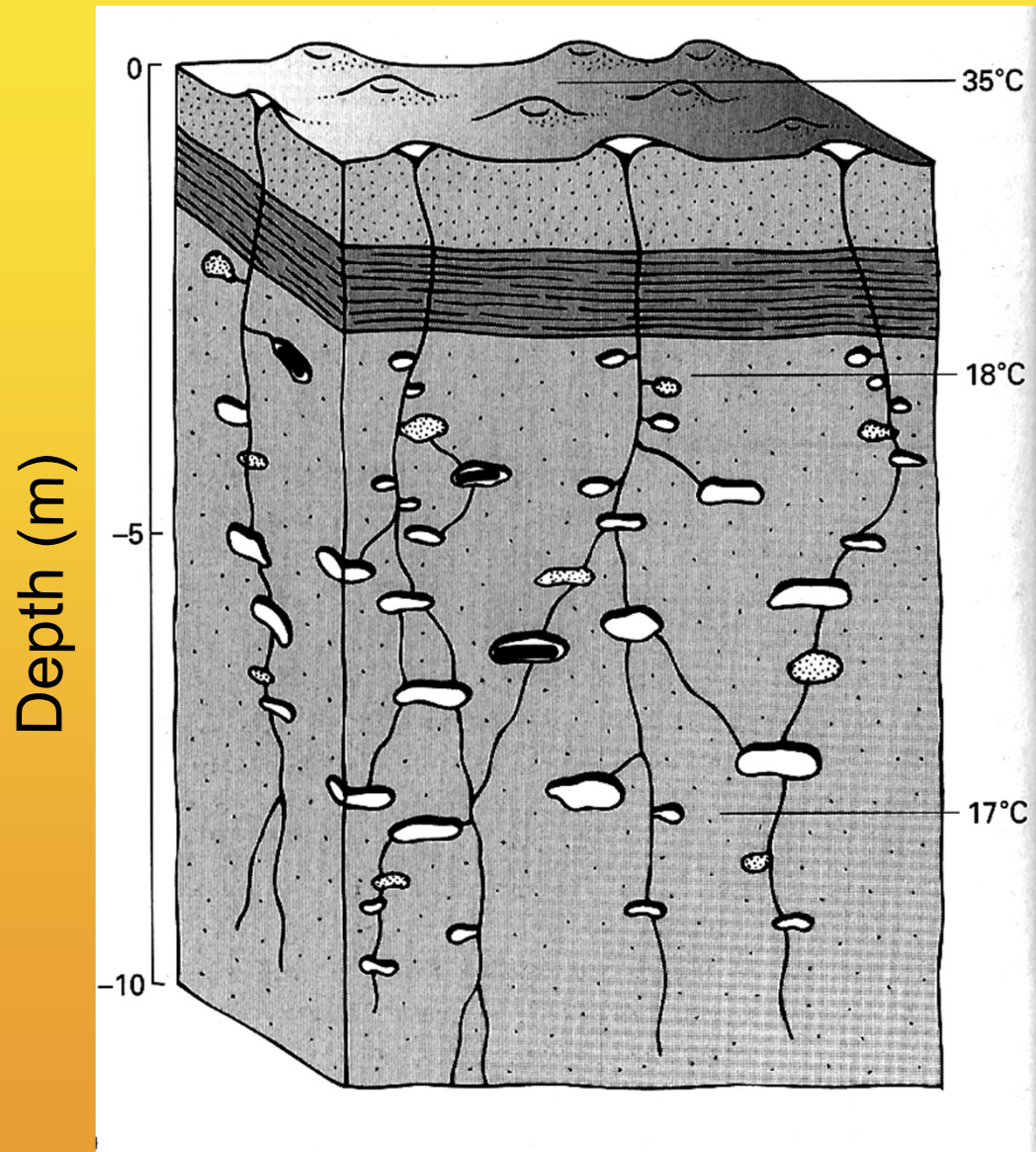
Heterocephalus glaber from www.animalpicturesarchive.com (also on Wikipedia)

Escape underground...

**Burrow system
of the Damaraland mole rat
Cryptomys (=Fucomys) damarensis
South Africa, Namib desert**



Escape underground...



Willmer et al. 2000

Temperature on and below ground: a nest of leaf-cutter ants *Atta sp.*



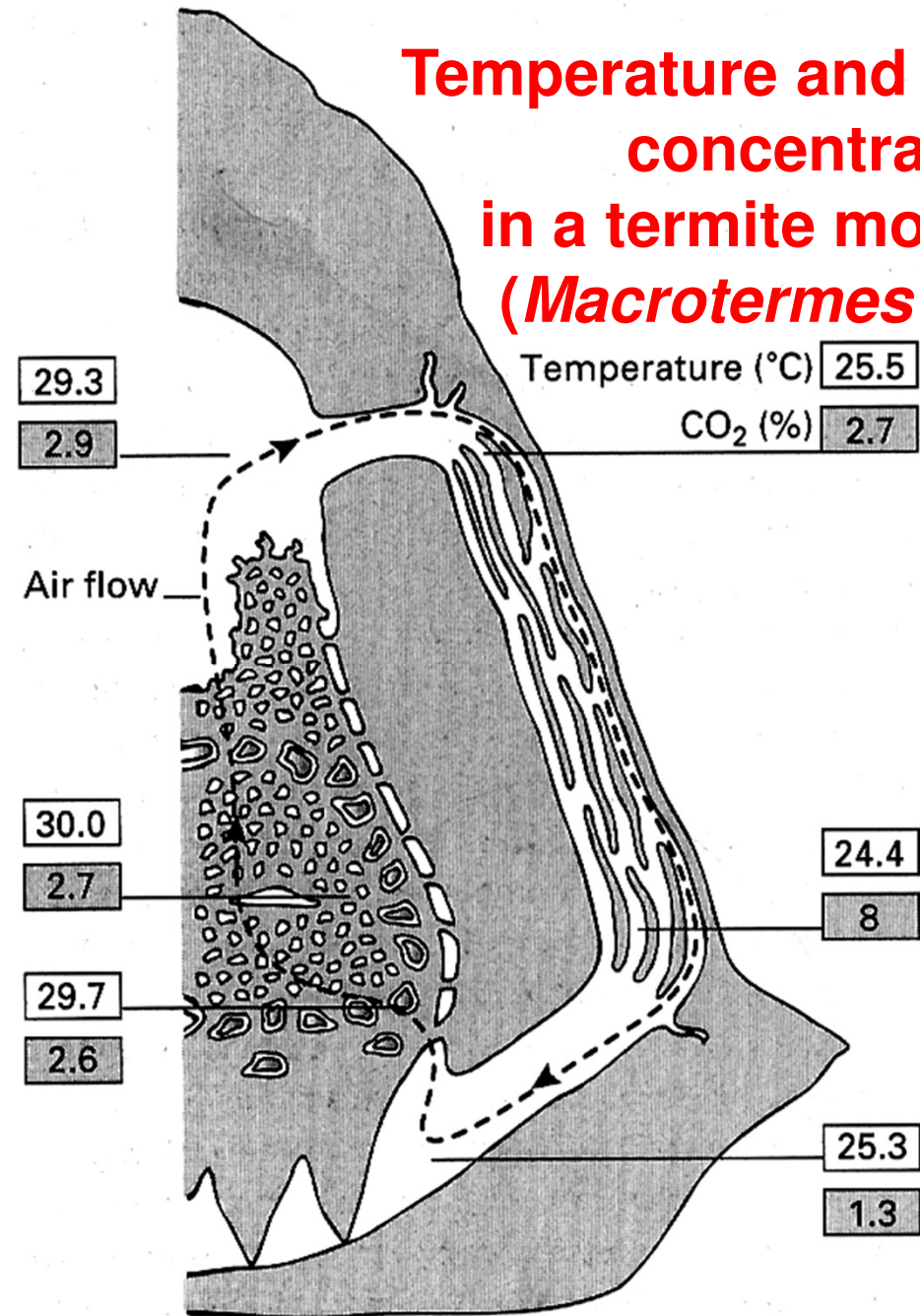
photo: Wikipedia

Escape to "buildings"...

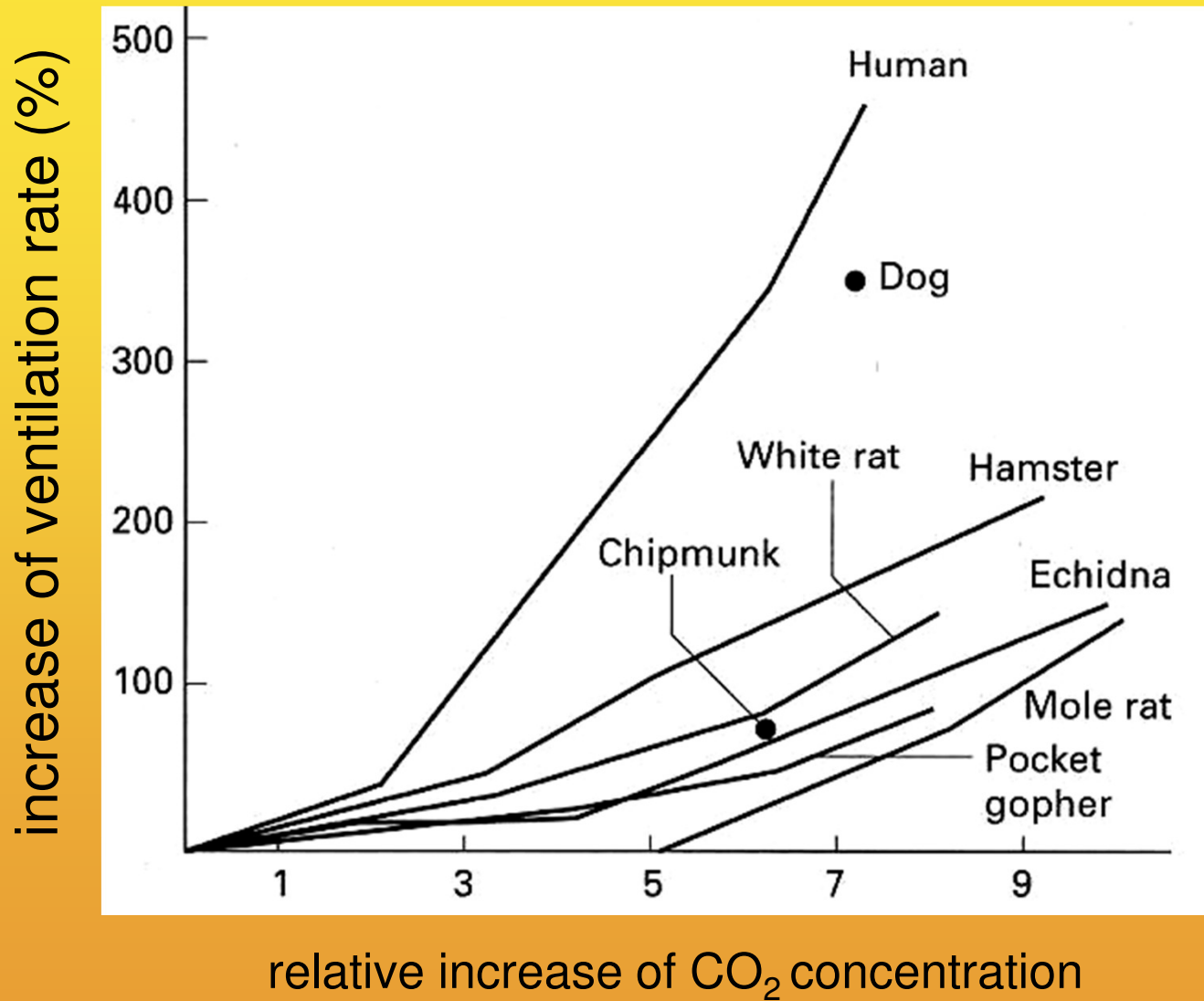


photo: Wikipedia

Temperature and CO₂ concentration in a termite mound (*Macrotermes sp.*)



Life underground...



**requires
tolerance
of a high CO₂
concentration**

If on the ground surface, than how...?

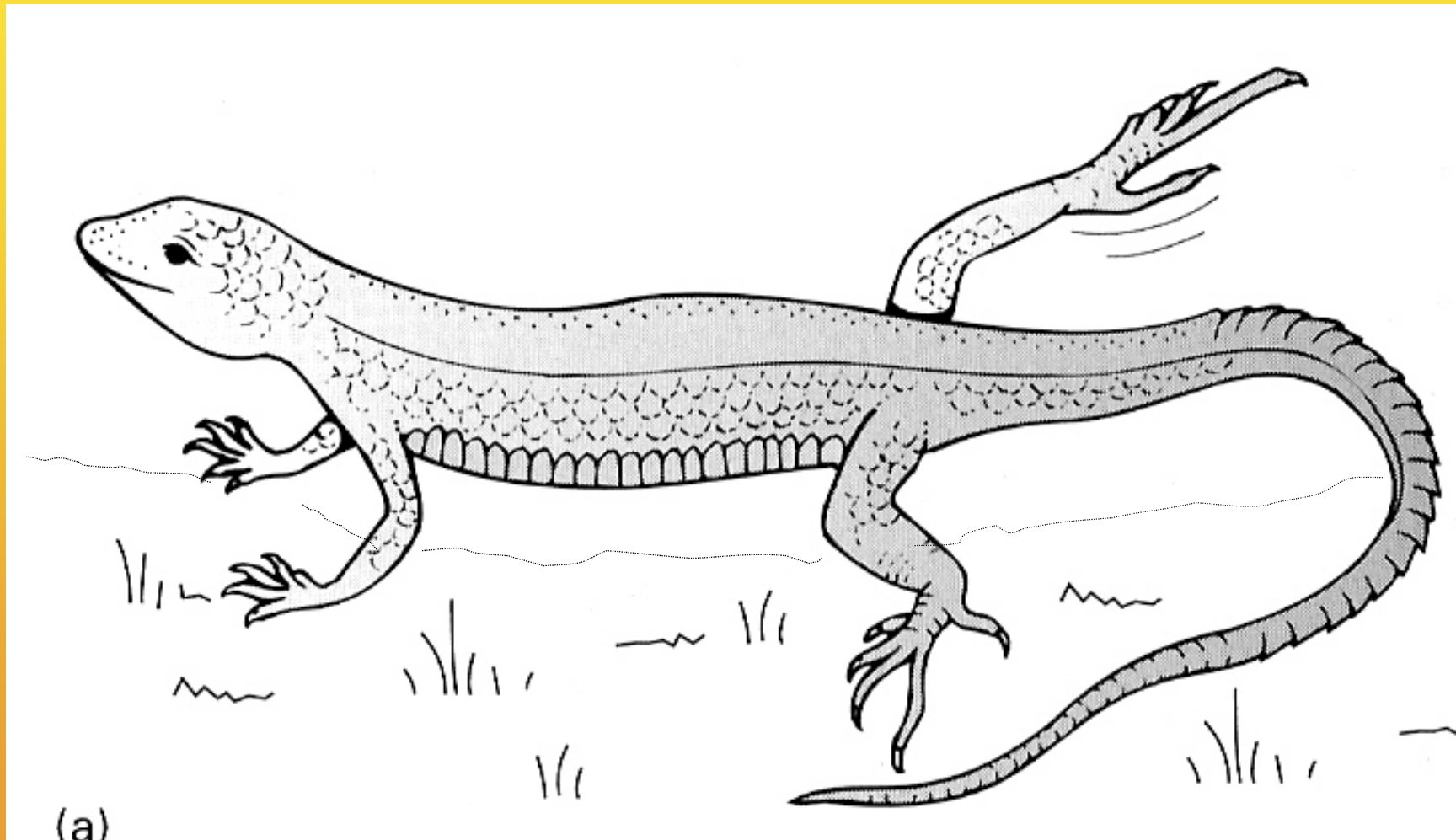
Locomotion on a hot surface: keep your body up!



SOME DESERT ANTS forage (in this case, for a researcher's cheese) at temperatures above 45 degrees Celsius. Photo: Rüdiger Wehner.

If on the ground surface, than how...?

Locomotion on a hot surface: keep your body up!



Legs up!

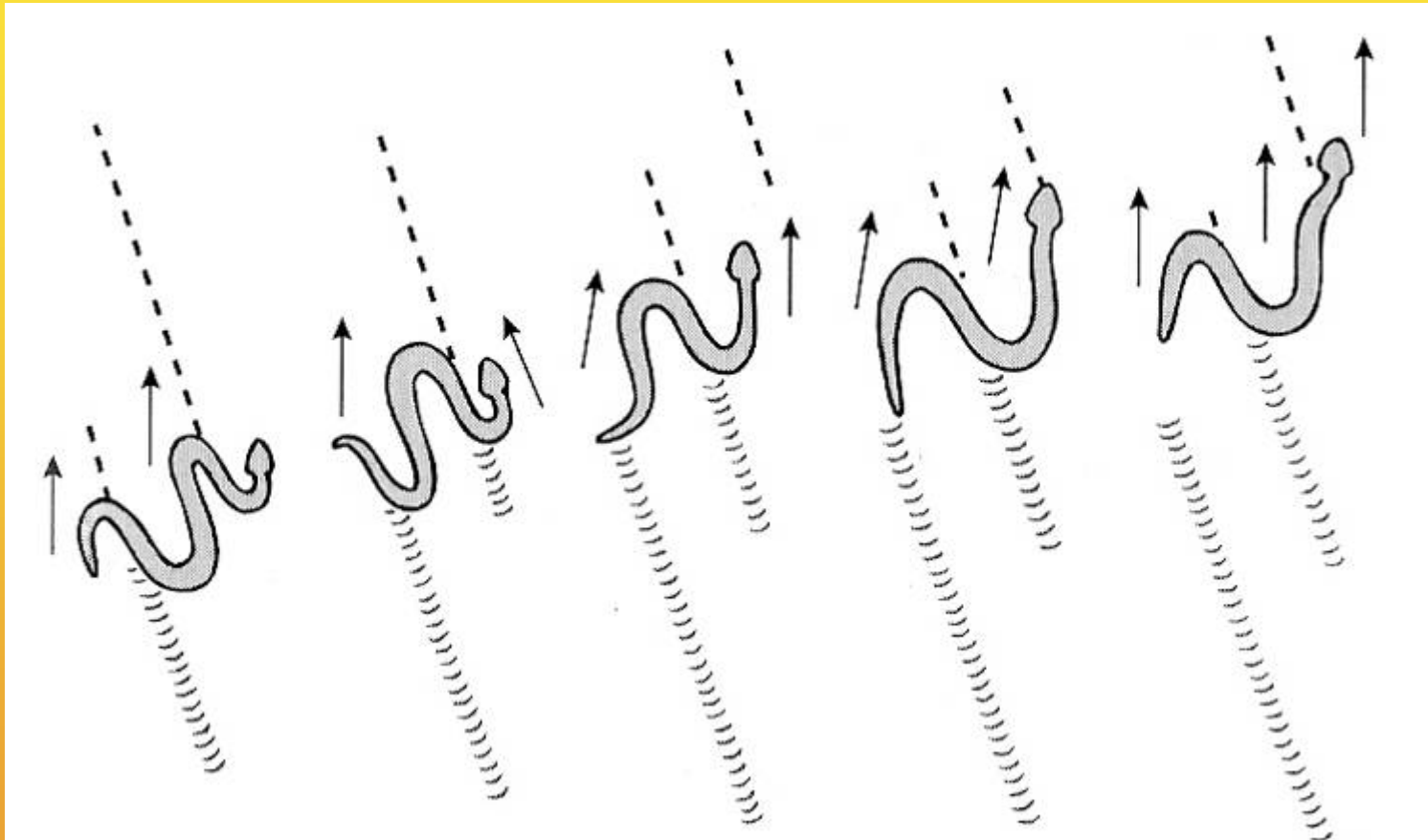
A lizard
Meroles anchieteeae
balances on two legs
South Africa,
Namib Desert



photo: M. i P. Fogden; copied from: *Encyklopedia zwierząt gady i płazy*; ELIPSA, Warszawa 1993

If on the ground surface, than how...?

Locomotion on a hot surface: keep your body up!



Locomotion of a sidewinding adder

Keep your body up!

The sidewinding adder
Bitis peringueyi
"glides" on the sand surface
supporting the body
on only two points.
South Africa, Namib Desert

Keep your body up!

The sidewinding adder

Bitis peringueyi

South Africa; Namib Desert

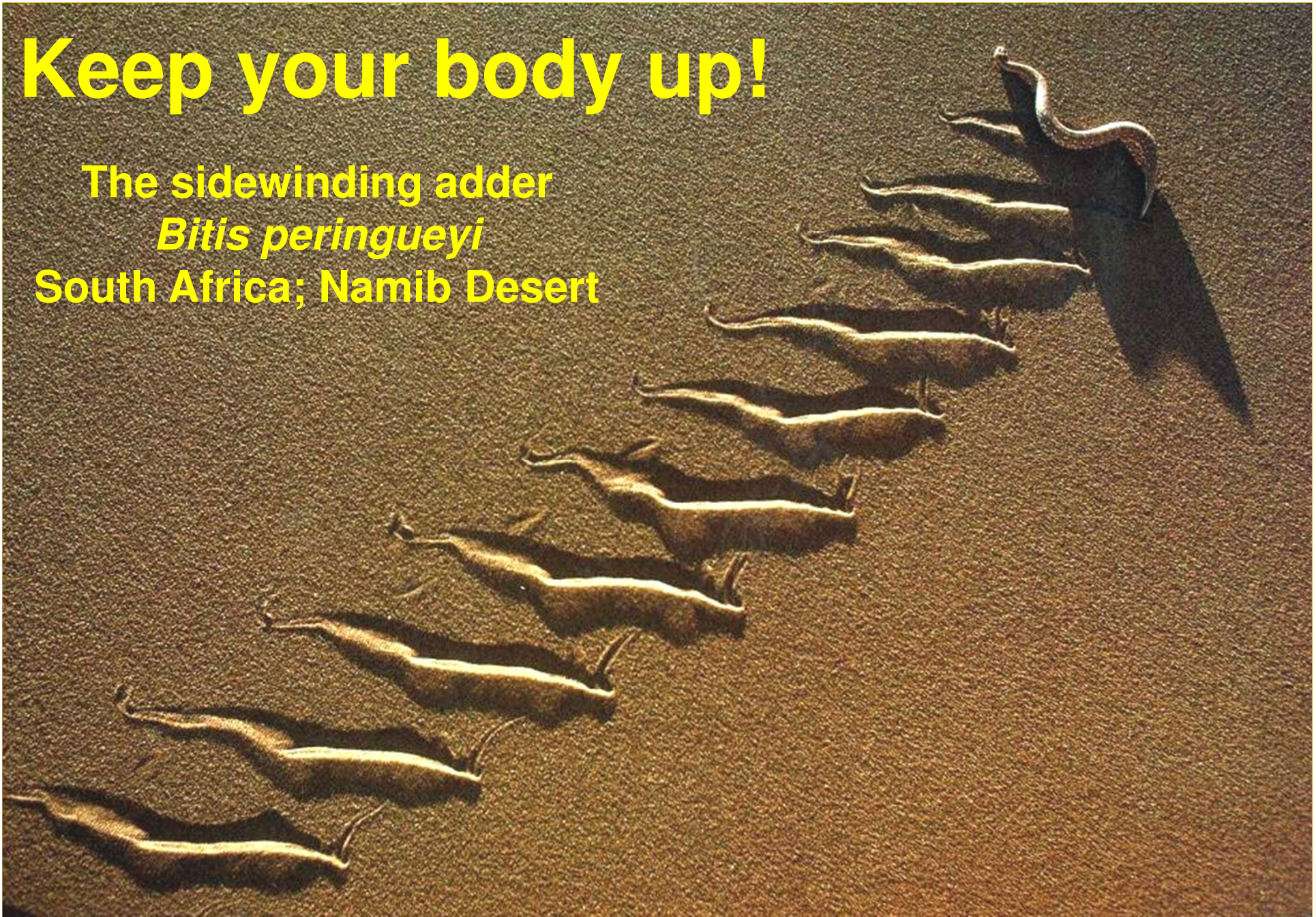
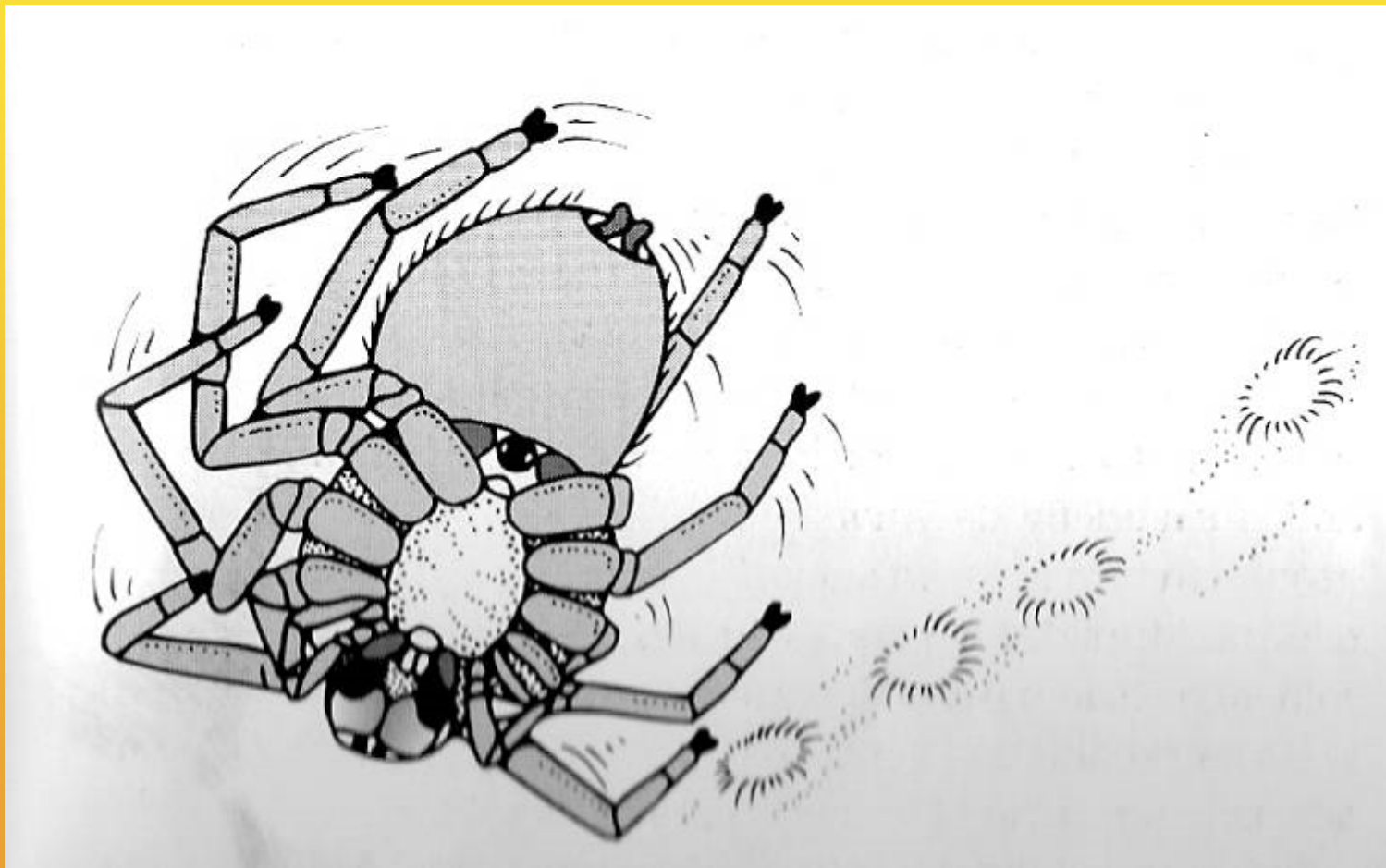


photo: C. i D. Hughes, National Geographic, Polish ed. : wrzesień 1983 (zeszyt specjalny: "100 najlepszych fotografii")

If on the ground surface, than how...?

Locomotion on a hot surface: keep your body up!



The spider *Carpachne* sp. rolling down a dune

If on the ground surface, than how...?

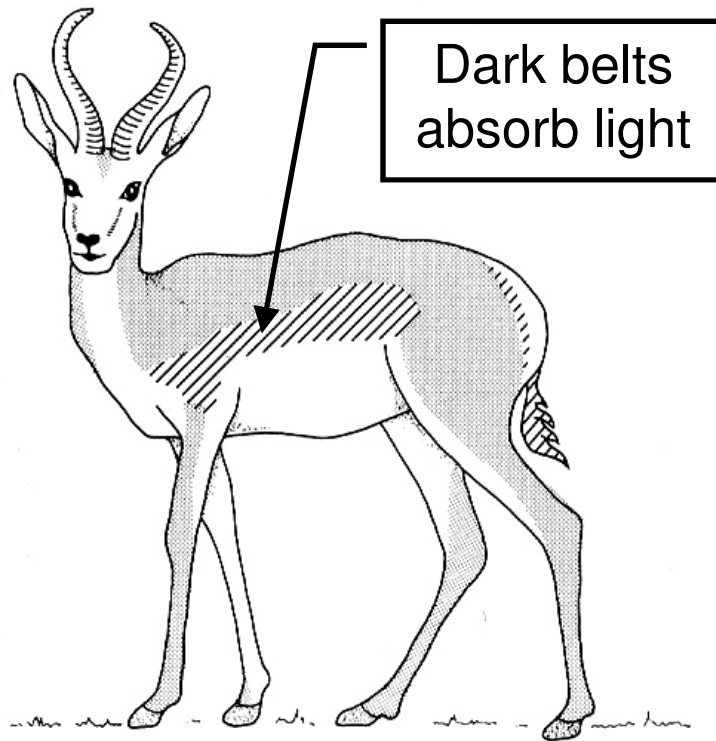


Springbok gazelle
Antidorcas marsupialis
South Africa, Namibia

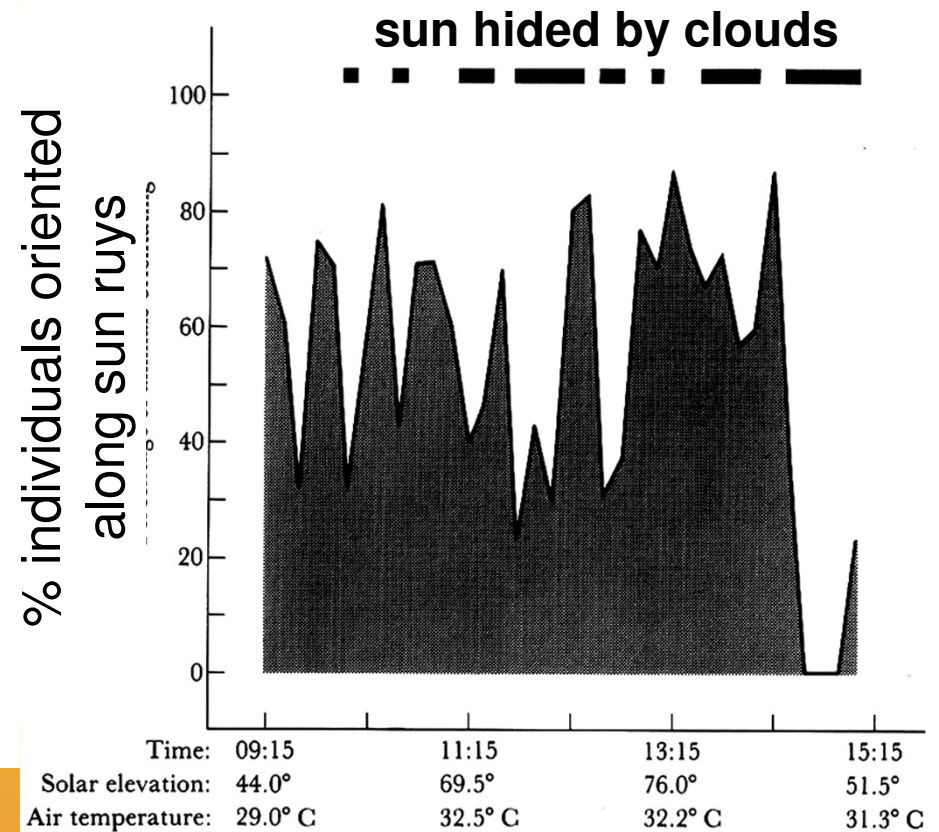


If on the ground surface, than how...?

Manipulation with coloration and body orientation



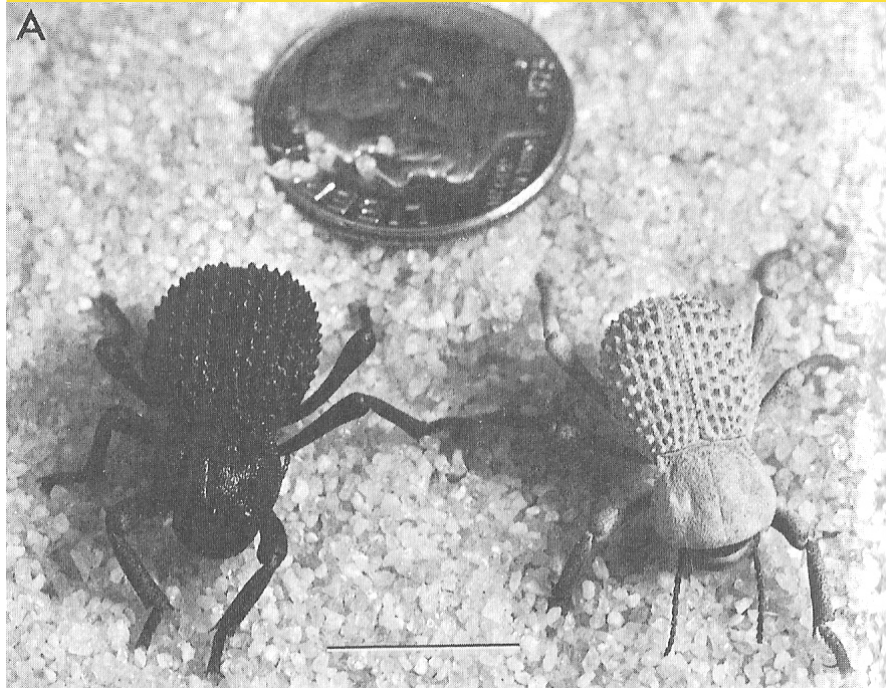
Springbok gazelle
Antidorcas marsupialis



morning, cooler - noon, hotter

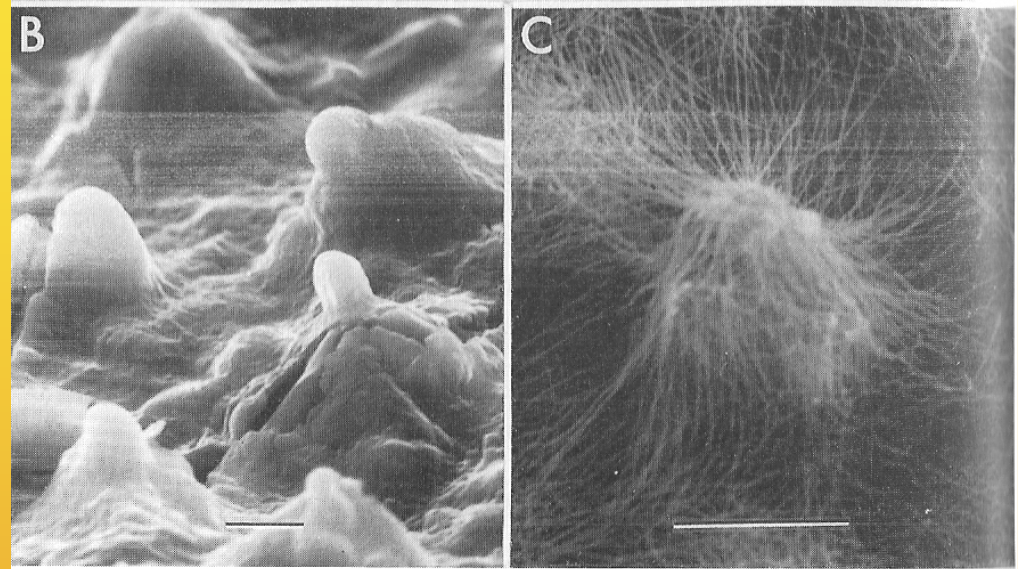
If on the ground surface, than how...?

Manipulation with coloration and permeability



high <- humidity -> low

A tenebrionid beetle
Cryptoglossa verrucosa
North America, Sonoran Desert



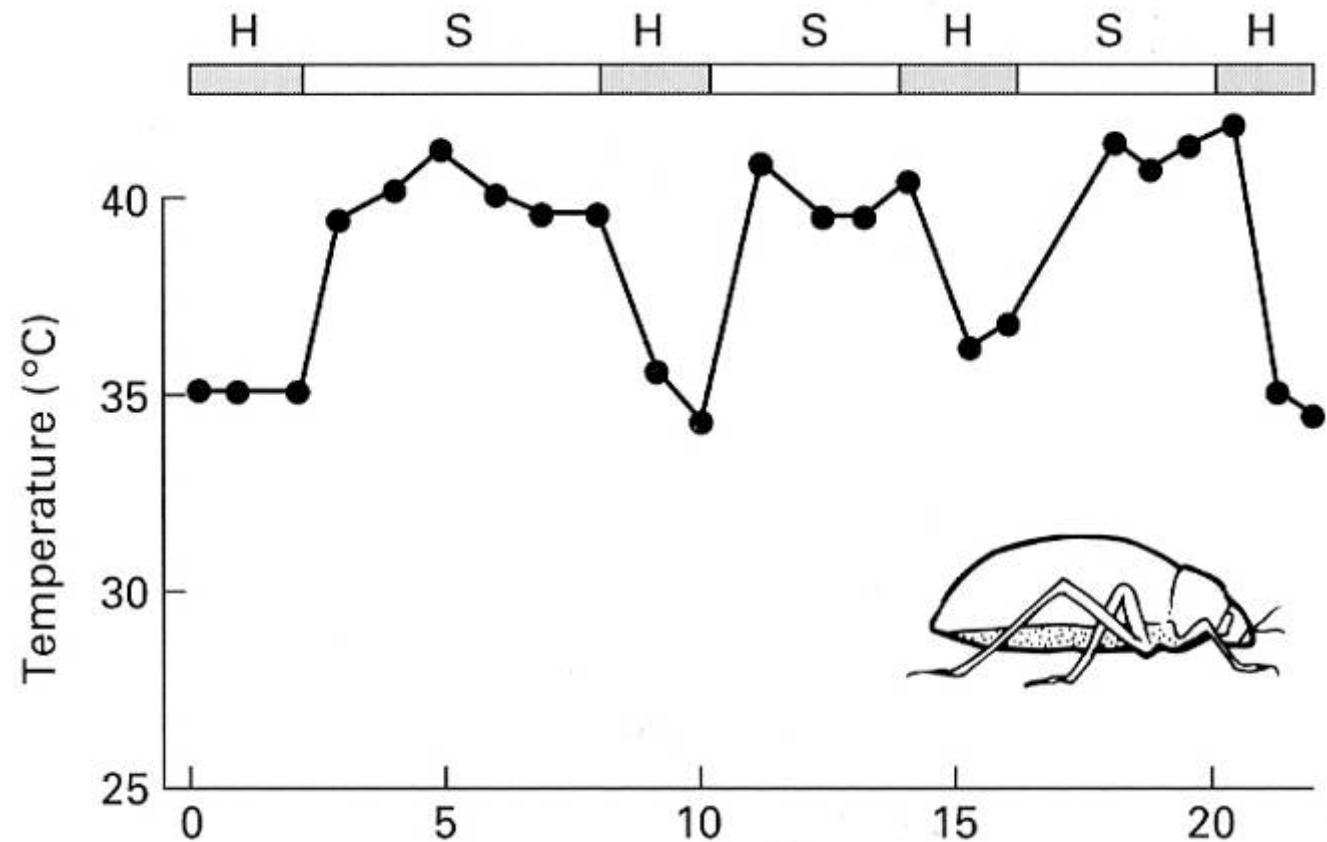
Wax filaments produced by tubercles
waterproof the surface of elytra
and give a light blue color

If on the ground surface, than how...?

Manipulation with coloration and body orientation

Orientation: H - head towards sun; S - side towards sun

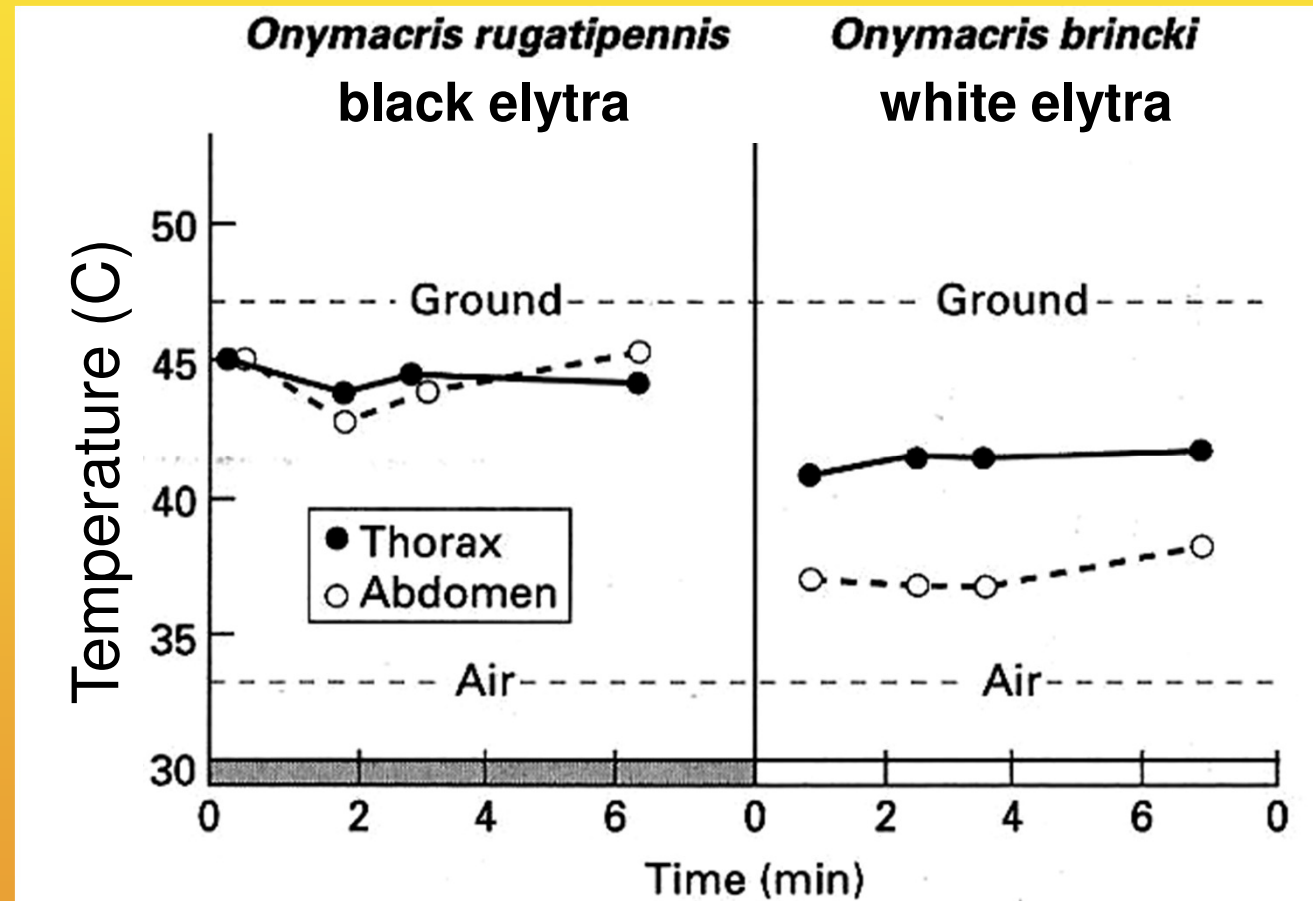
Thorax
temperature
in a desert
beetle



If on the ground surface, than how...?

Manipulation with coloration and body orientation

The effect of elytra color on body temperature of desert beetles



Coping with low water availability

Evaporation: water lost by breathing

Changes of **temperature** and **humidity** of inspired (I) and expired (E) air in the African ostrich: breath-by-breath analysis

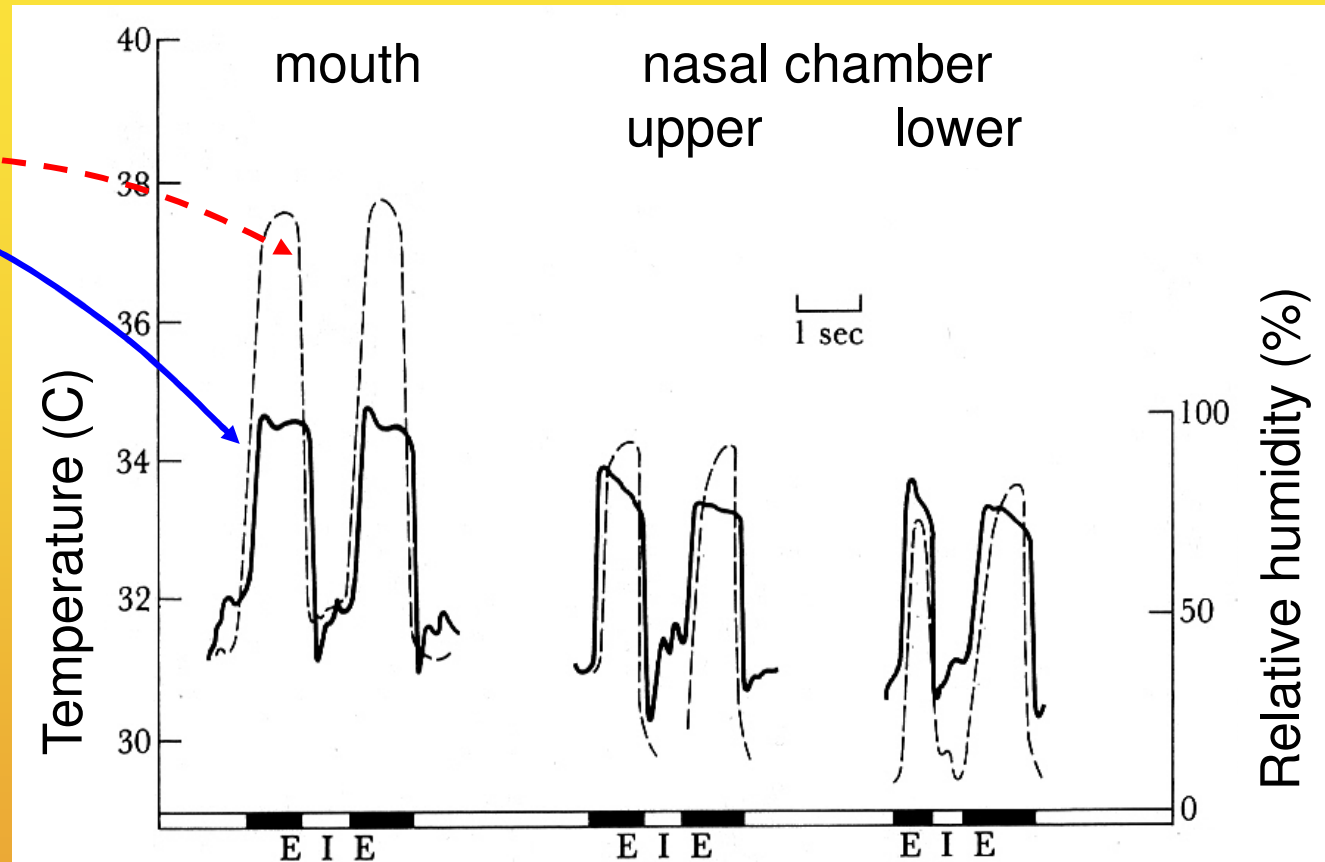


Figure 2.22 Breath-by-breath recorder tracings of relative humidity and temperature of inspired and expired air in the mouth, upper nasal chamber and lower nasal chamber of the ostrich (relative humidity, solid line; temperature, broken line; E, expiration; I, inspiration). From Withers *et al.* (1981).

Evaporation: water lost by breathing

Changes of **temperature** and **humidity** of inspired (I) and expired (E) air in the African ostrich: breath-by-breath analysis

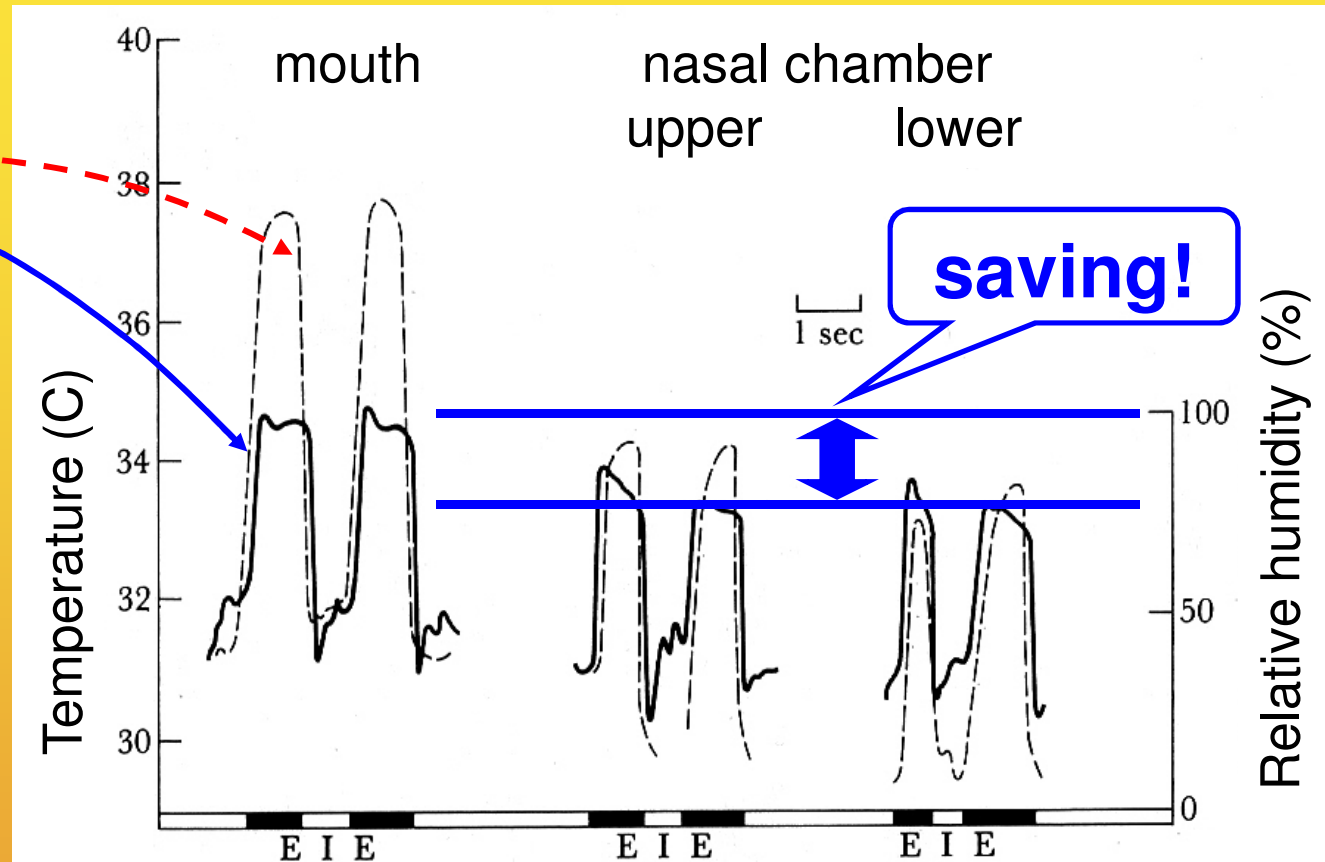
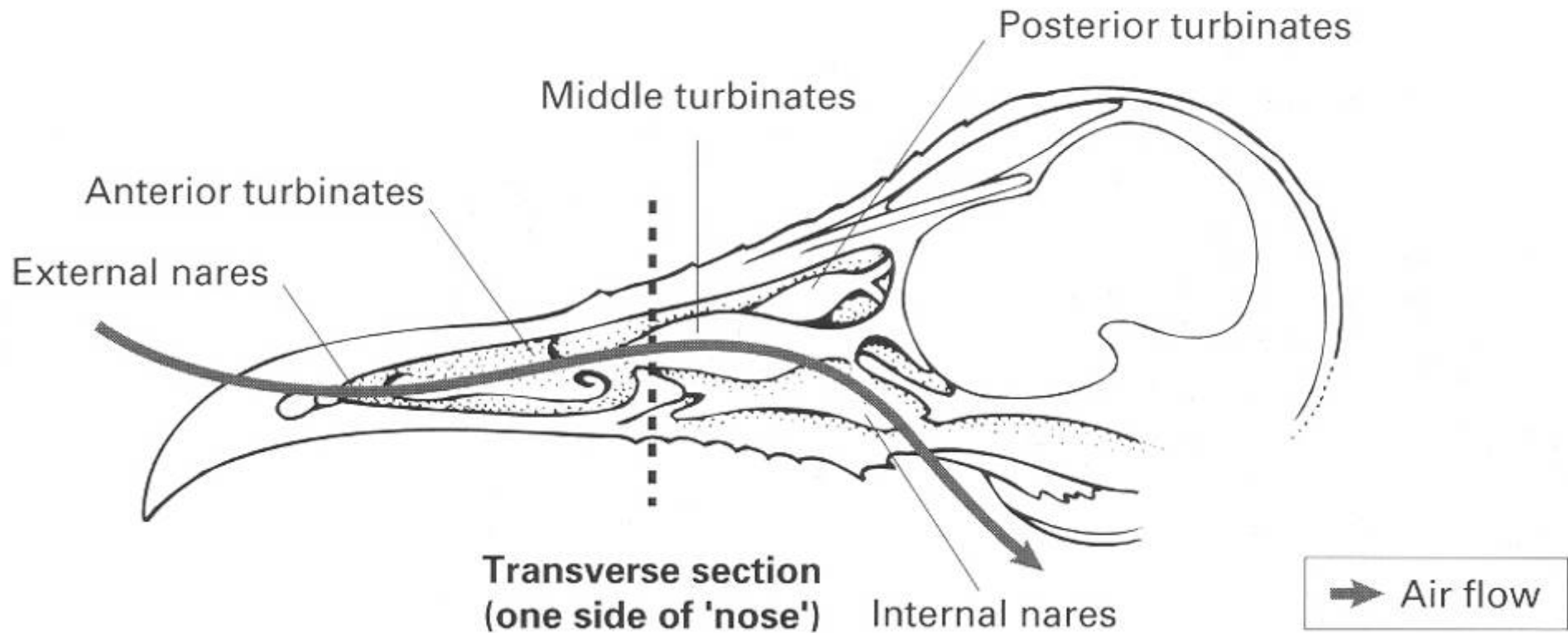


Figure 2.22 Breath-by-breath recorder tracings of relative humidity and temperature of inspired and expired air in the mouth, upper nasal chamber and lower nasal chamber of the ostrich (relative humidity, solid line; temperature, broken line; E, expiration; I, inspiration). From Withers *et al.* (1981).

Water-saving mechanism in nasal turbinates (maxilloturbinates)

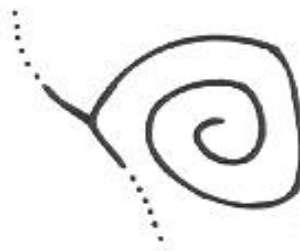


An increased surface of heat and humidity exchange in nasal channels

Cross-sections through nasal turbinates



Vulture



Fulmar



Rhea



Emu



Cactus wren



Kangaroo rat

An increased surface of heat and humidity exchange in nasal channels

Cactus Wren
*Campylorhynchus
brunneicapillus*
(pol.: strzyżyk kaktusowy)

North America:
Sonora,
Chihuahuan



Kangaroo rat (pol.: szczurowskoczek)
Dipodomys sp. (Rodentia, Heteromyidae)

Deserts
and arid
habitats
in North
America

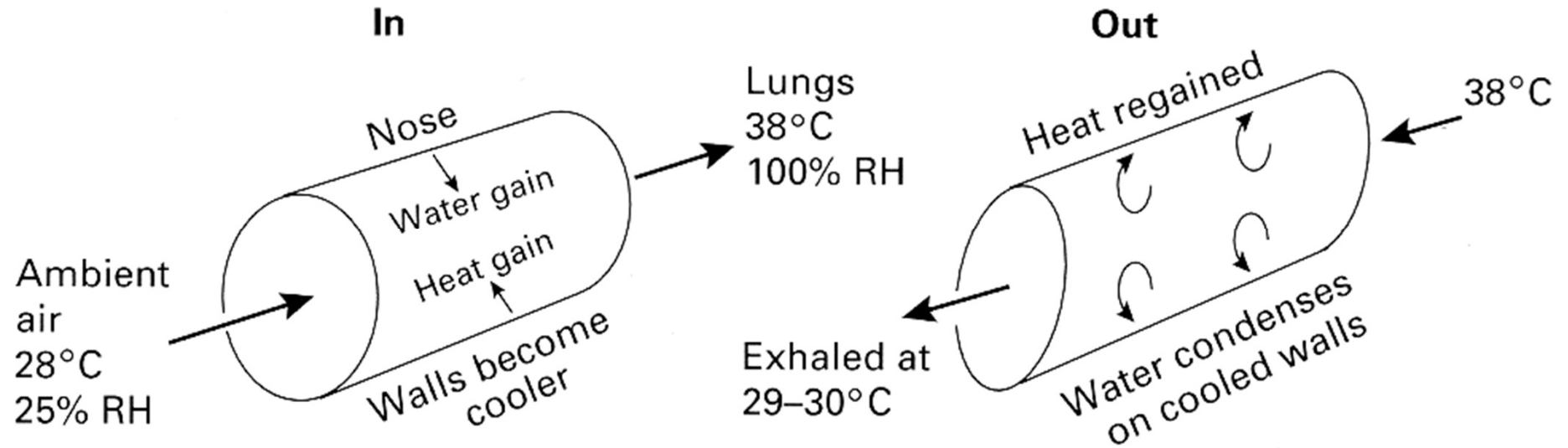


Kangaroo rat (Dipodomys ordii) from Wikipedia

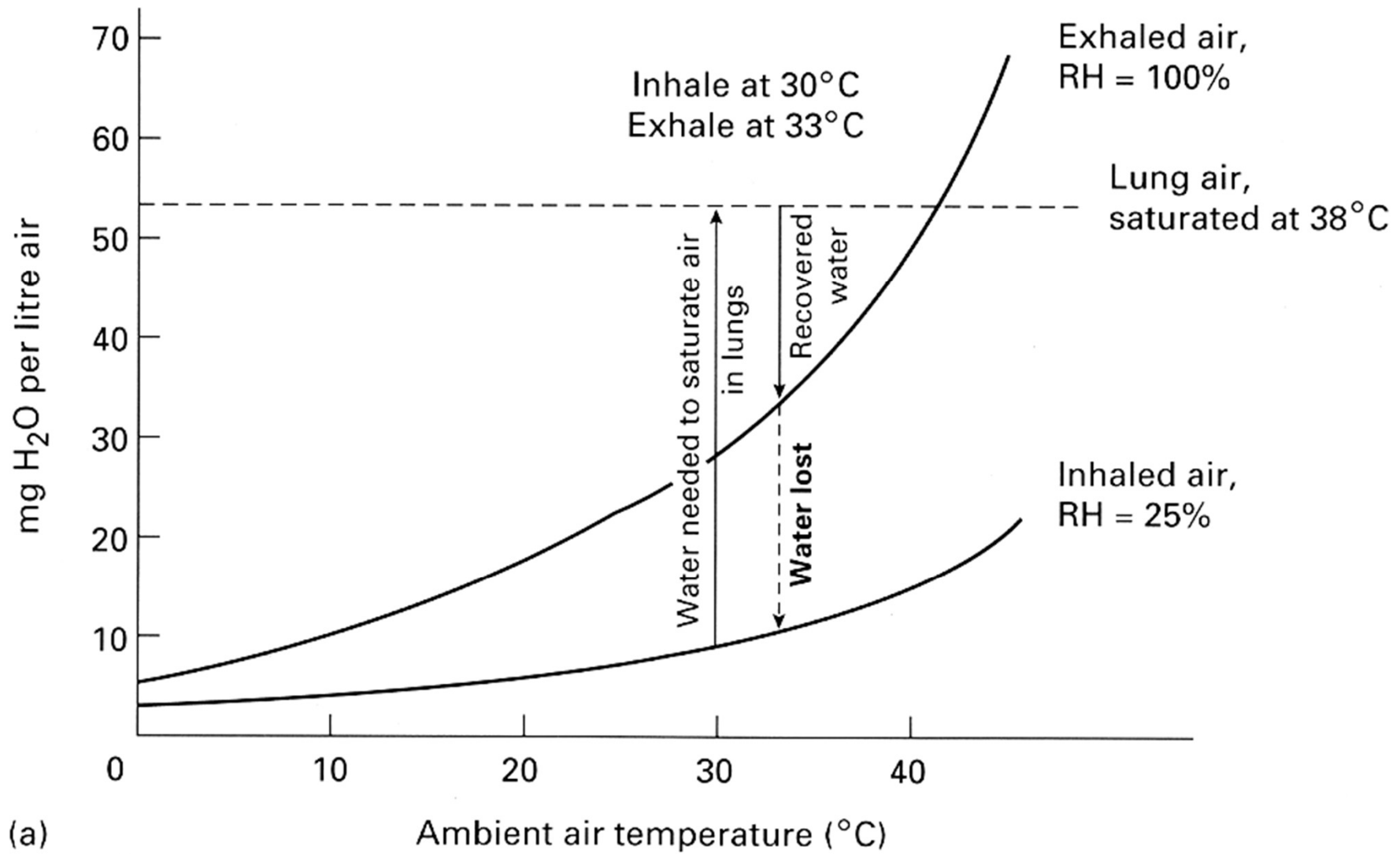
Water-saving mechanism in nasal turbinates

Inhale

Exhale

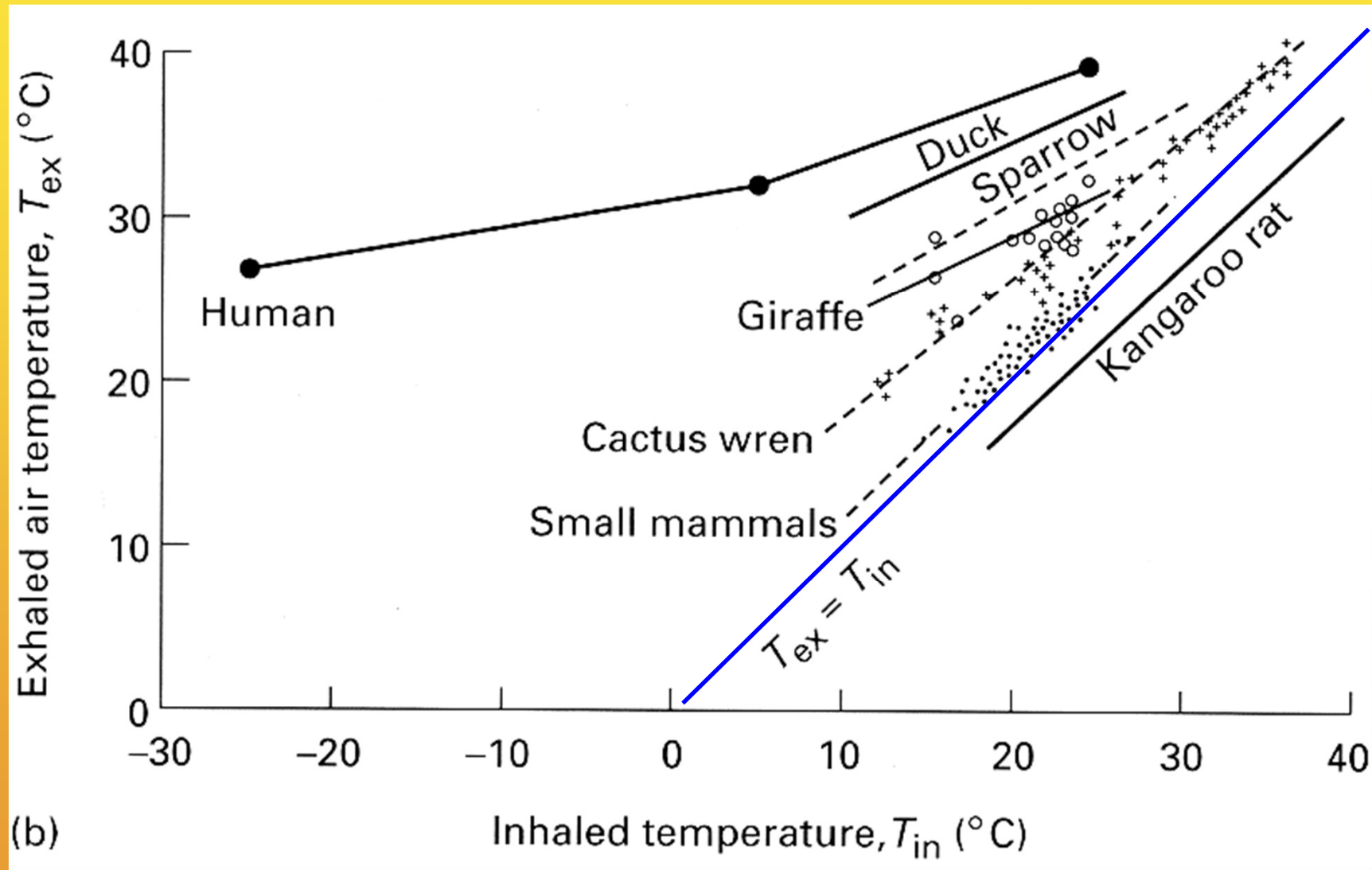


Water-saving mechanism in nasal turbinates



(a)

Water-saving mechanism in nasal turbinates: decreased temperature of exhaled air -> decreased water loss



Water balance in a kangaroo rat over 1 month

Conditions: Food: 100 g dry barley grain, no drinking water;
Temperature: 25C;
Humidity: 25%

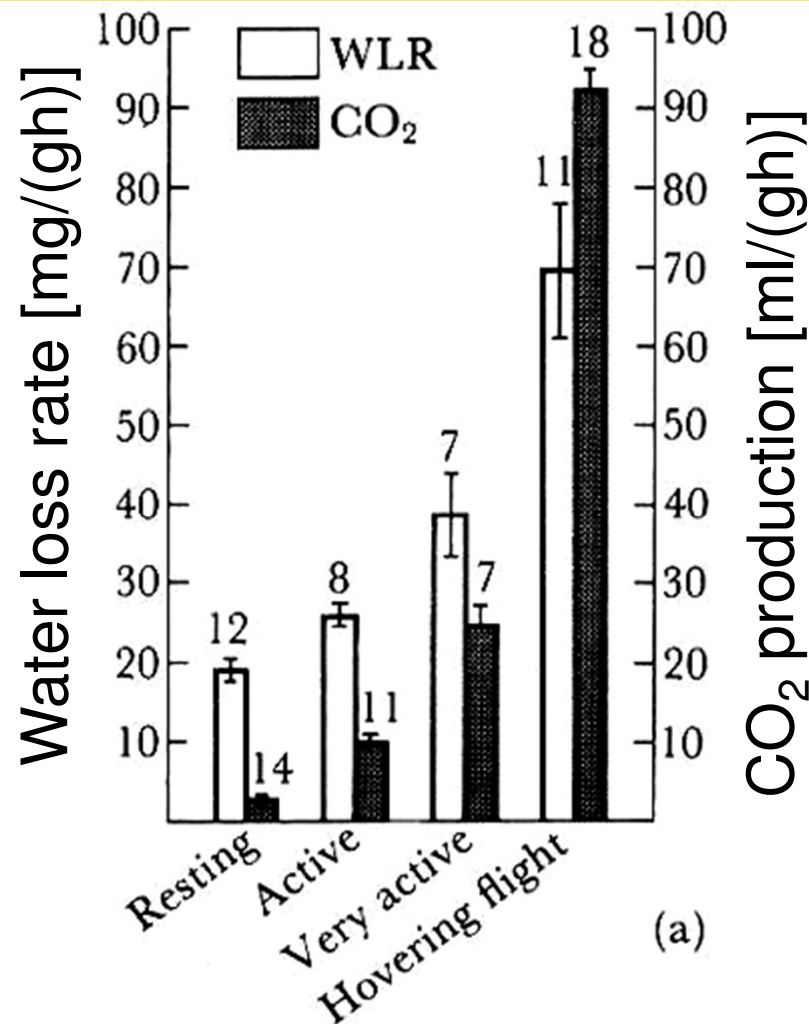
| Water gain | | Water loss | |
|--------------------------------|-------------|--------------|-------------|
| Source | ml | Source | ml |
| Metabolic water (oxidation) | 54.0 | Evaporation | 43.9 |
| Food | 6.0 | Urine | 13.5 |
| | | Faeces | 2.6 |
| Total | 60.0 | Total | 60.0 |

Food substrates as a source of energy... and water

Table 2.4 Relationship between the respiratory quotient (RQ), metabolic water production and energy production when the major nutrients are oxidised. From Prosser (1973) and Schmidt-Nielsen (1983)

| Food | RQ | g water g food ⁻¹ | l O ₂ g food ⁻¹ | l O ₂ g water ⁻¹ | kJ g food ⁻¹ | g water kJ ⁻¹ |
|---------------|------|---------------------------------|--|---|----------------------------|-----------------------------|
| Carbohydrates | 1.0 | 0.56 | 0.83 | 1.49 | 17.4 | 0.0320 |
| Fats | 0.71 | 1.07 | 2.02 | 1.89 | 39.7 | 0.0269 |
| Proteins | 0.79 | 0.40 | 0.97 | 2.44 | 17.4 | 0.0228 |

Water balance in active insects



Increasing level of activity

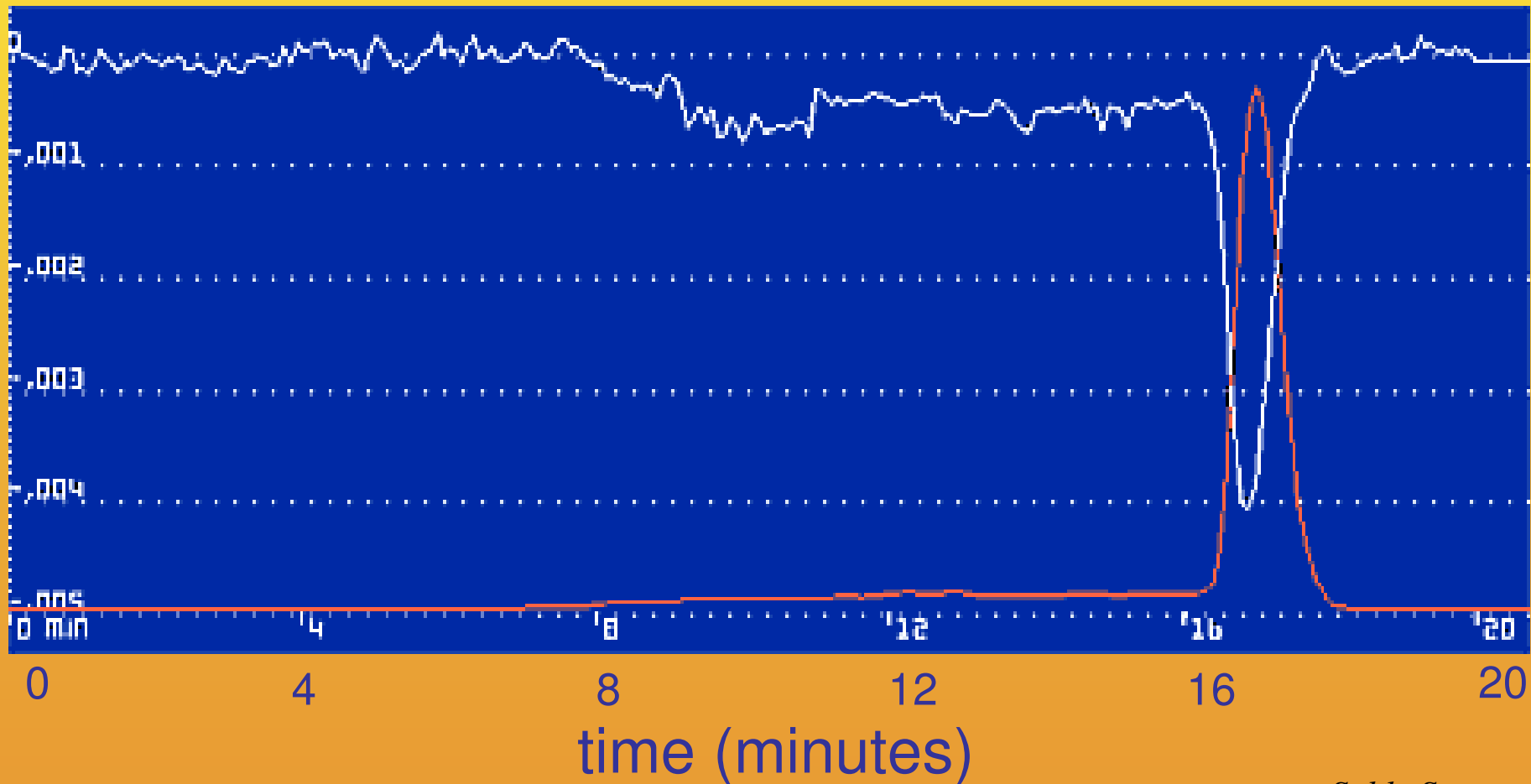
In a honey bee:

- A large increase in metabolic rate
- A smaller increase of water loss

Cycling respiration in an ant

Changes of gas content in the air flowing through a respirometric chamber

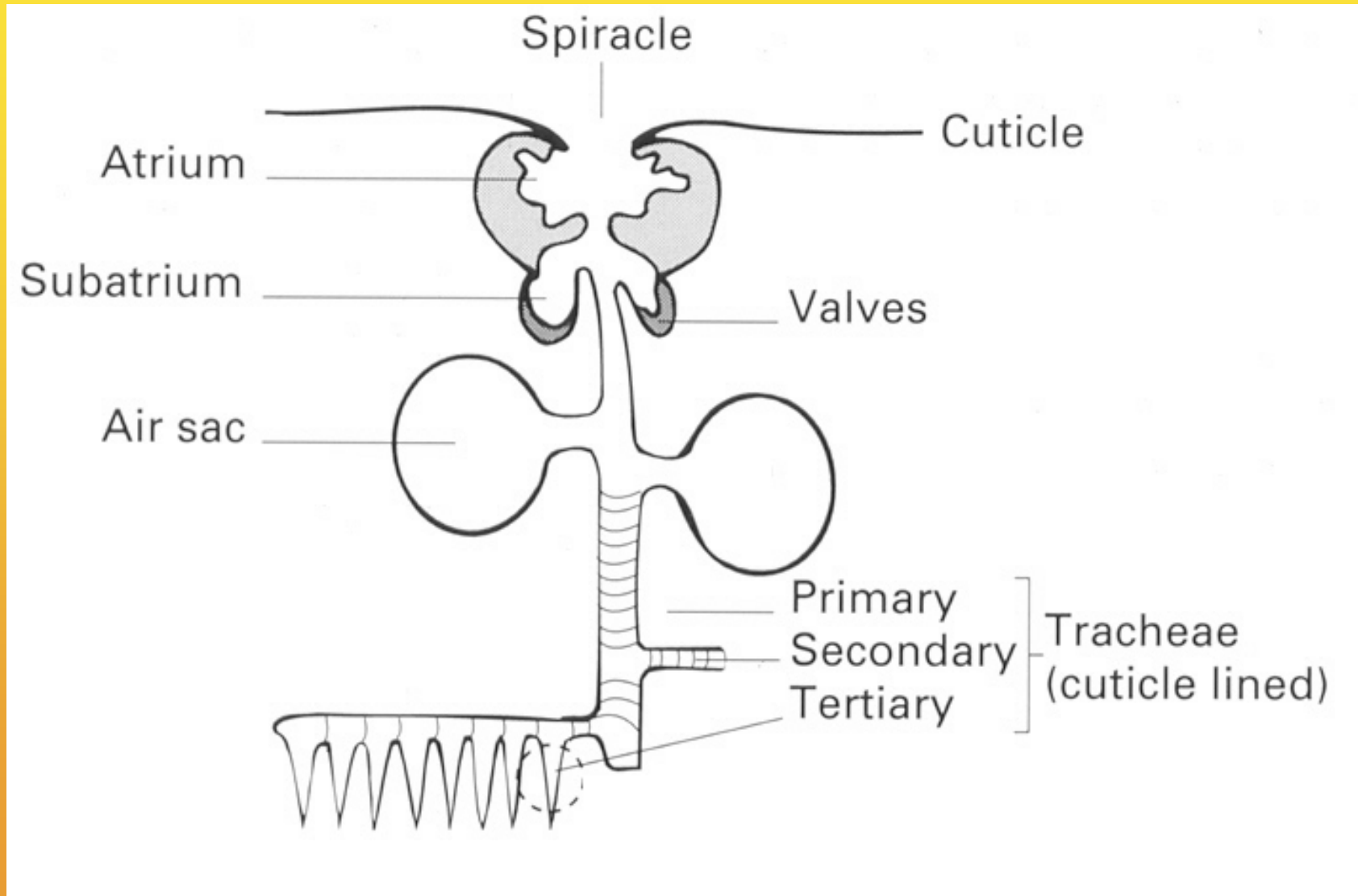
- decrease of O₂ content
- increase of CO₂ content



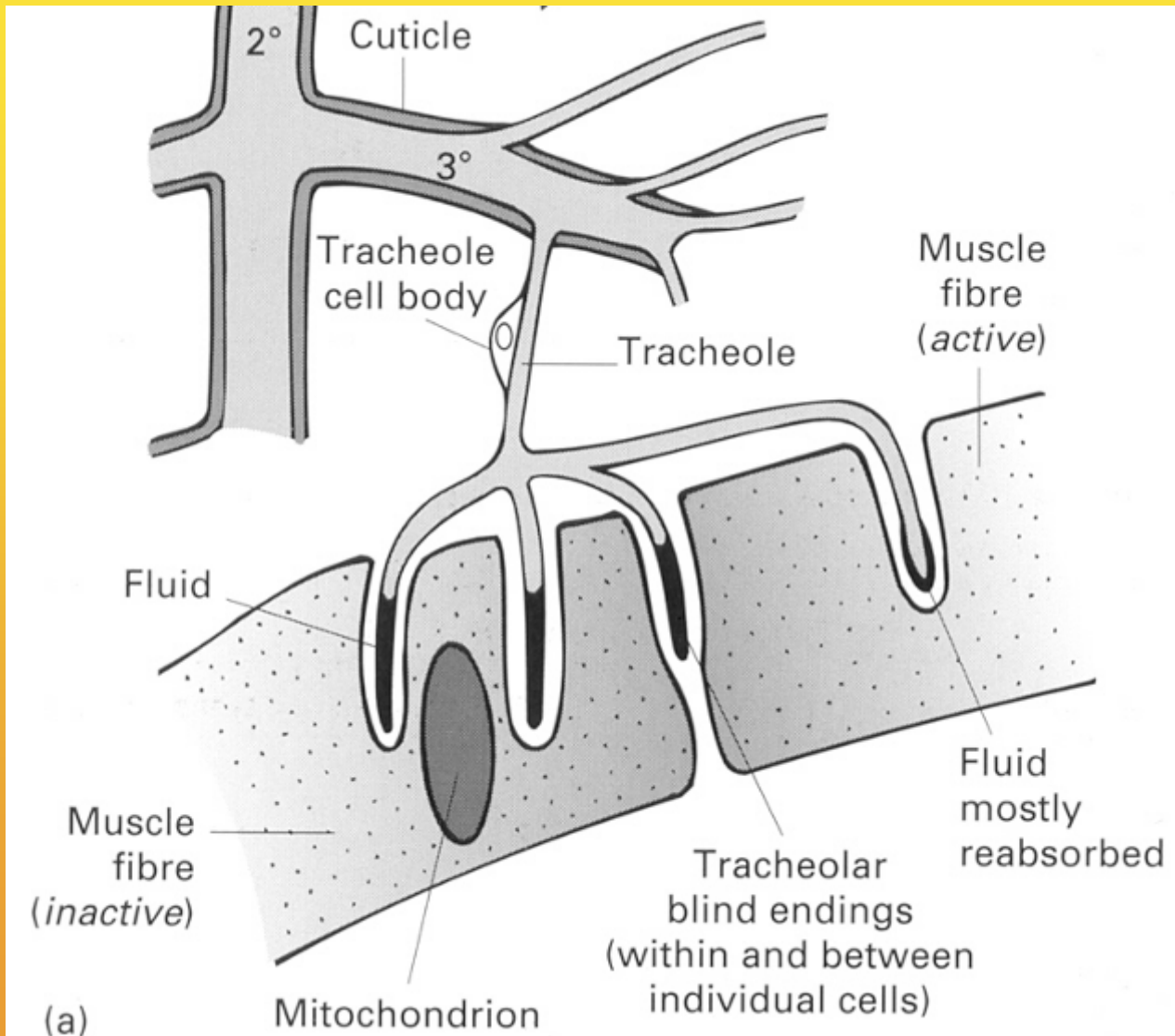
Cycling respiration in insects

- **Hypotheses:**
- cycling changes of metabolism?
- cycling ventilation?

Respiratory system in insects: direct oxygen delivery from air to working cells

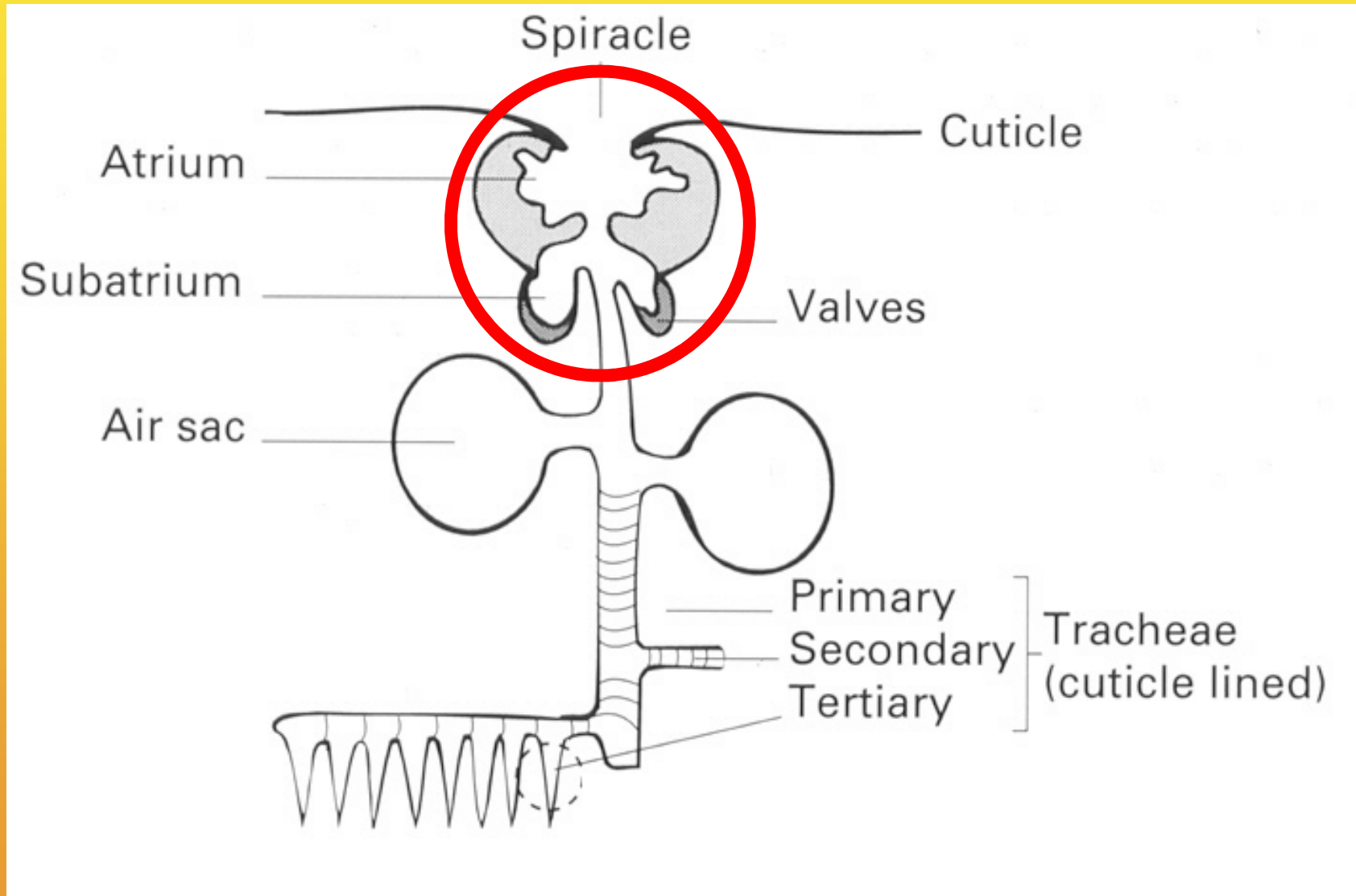


Respiratory system in insects: direct oxygen delivery from air to working cells

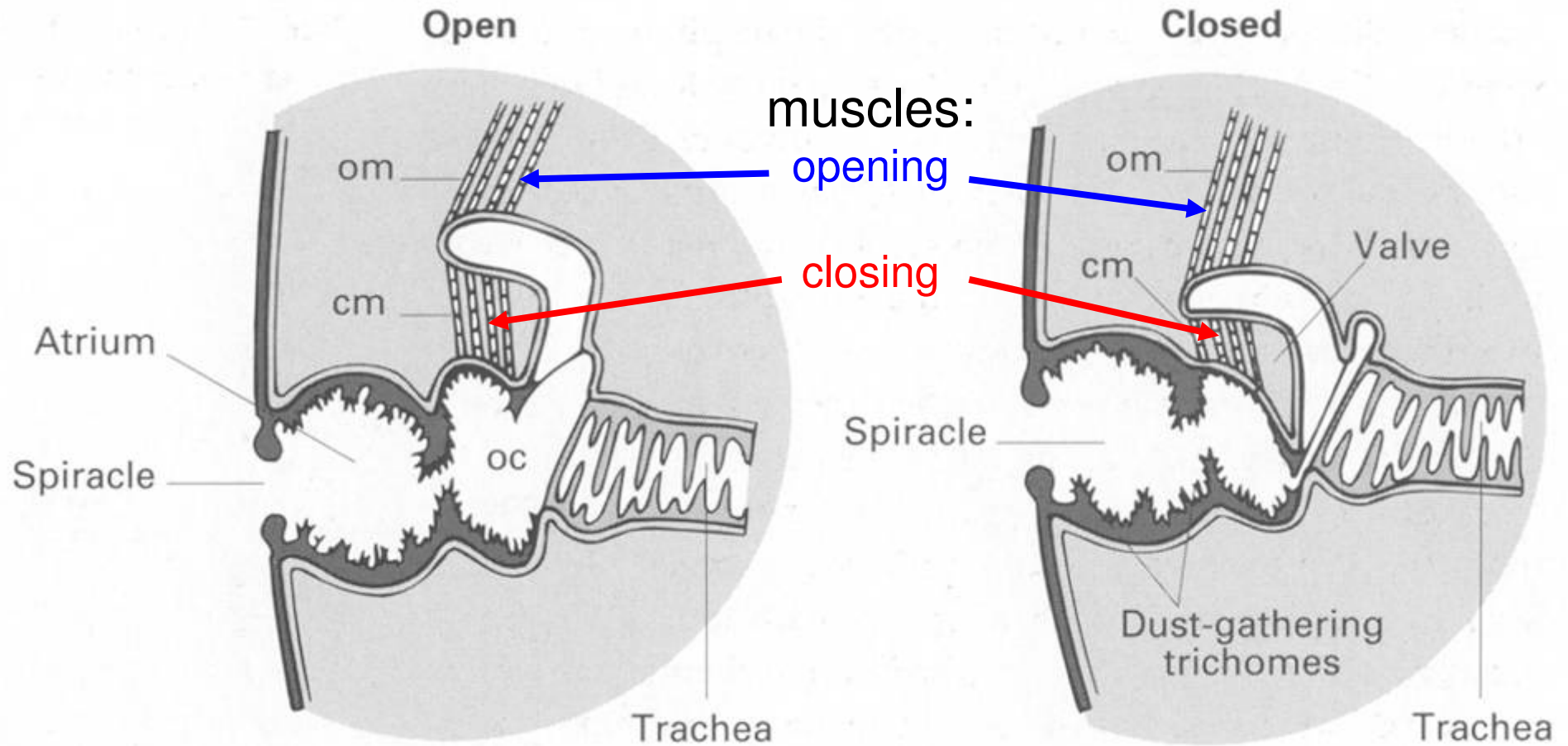


up to 10 mln
tracheoli
per fiber !

Respiratory system in insects: direct oxygen delivery from air to working cells



Respiratory system in insects: mechanism of ventilation control



opened

closed

Mechanism of cycling ventilation

spiracle movements:
fluttering - open - closed

intratracheal pressure

Tracheal gas composition:

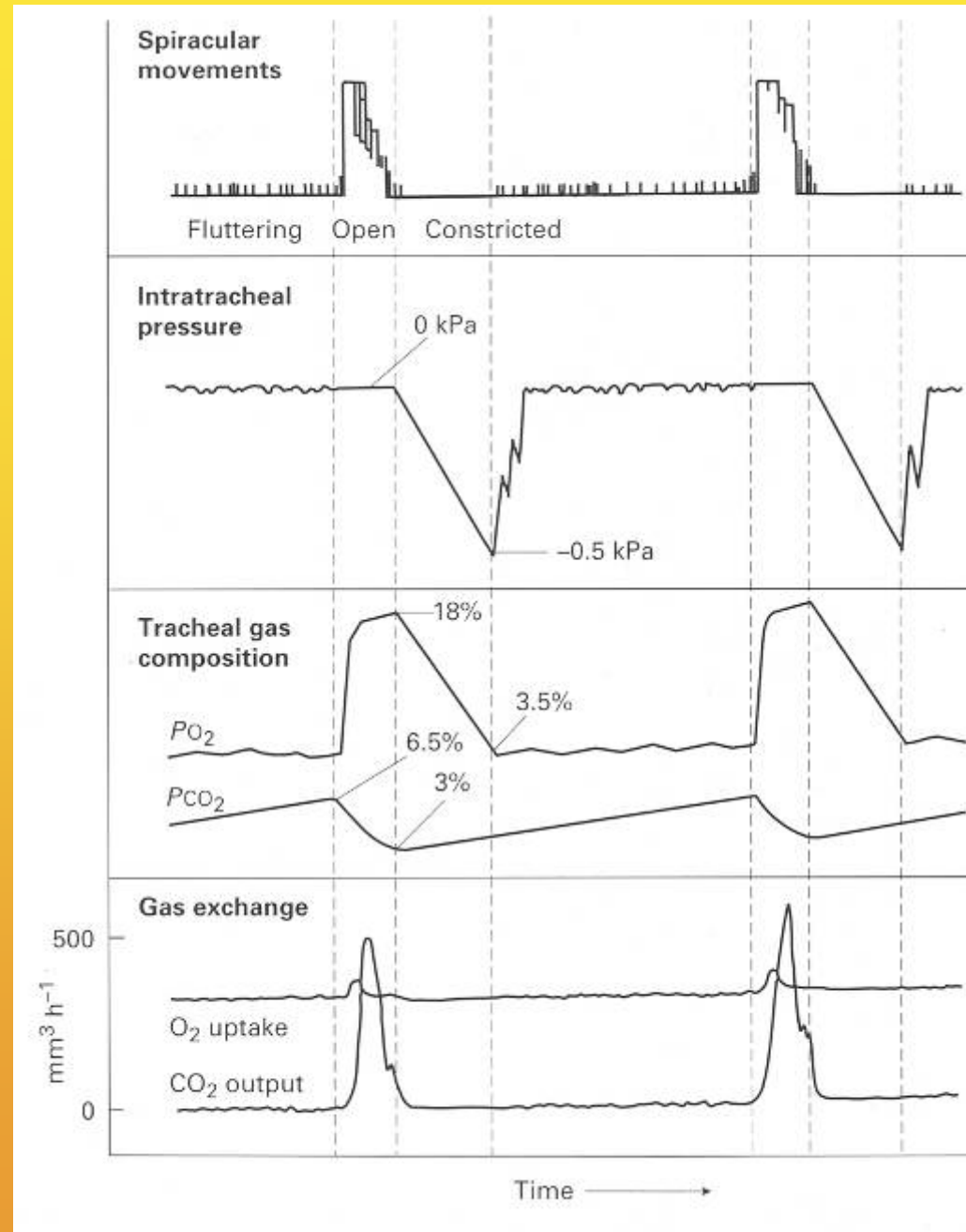
PO_2 - oxygen content (%)

PCO_2 - CO_2 content (%)

Gas exchange:

Oxygen uptake

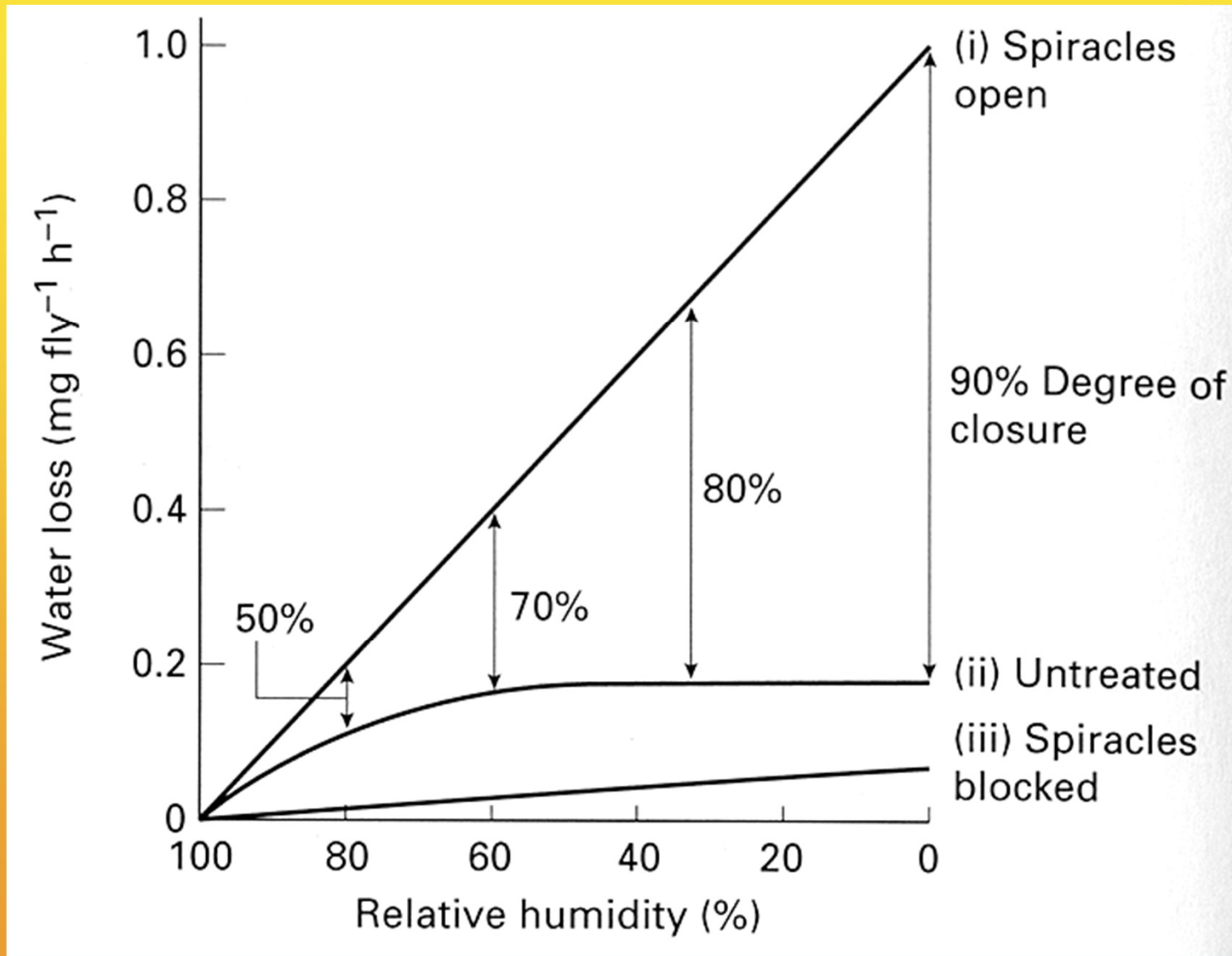
CO_2 output



Cycling respiration in insects

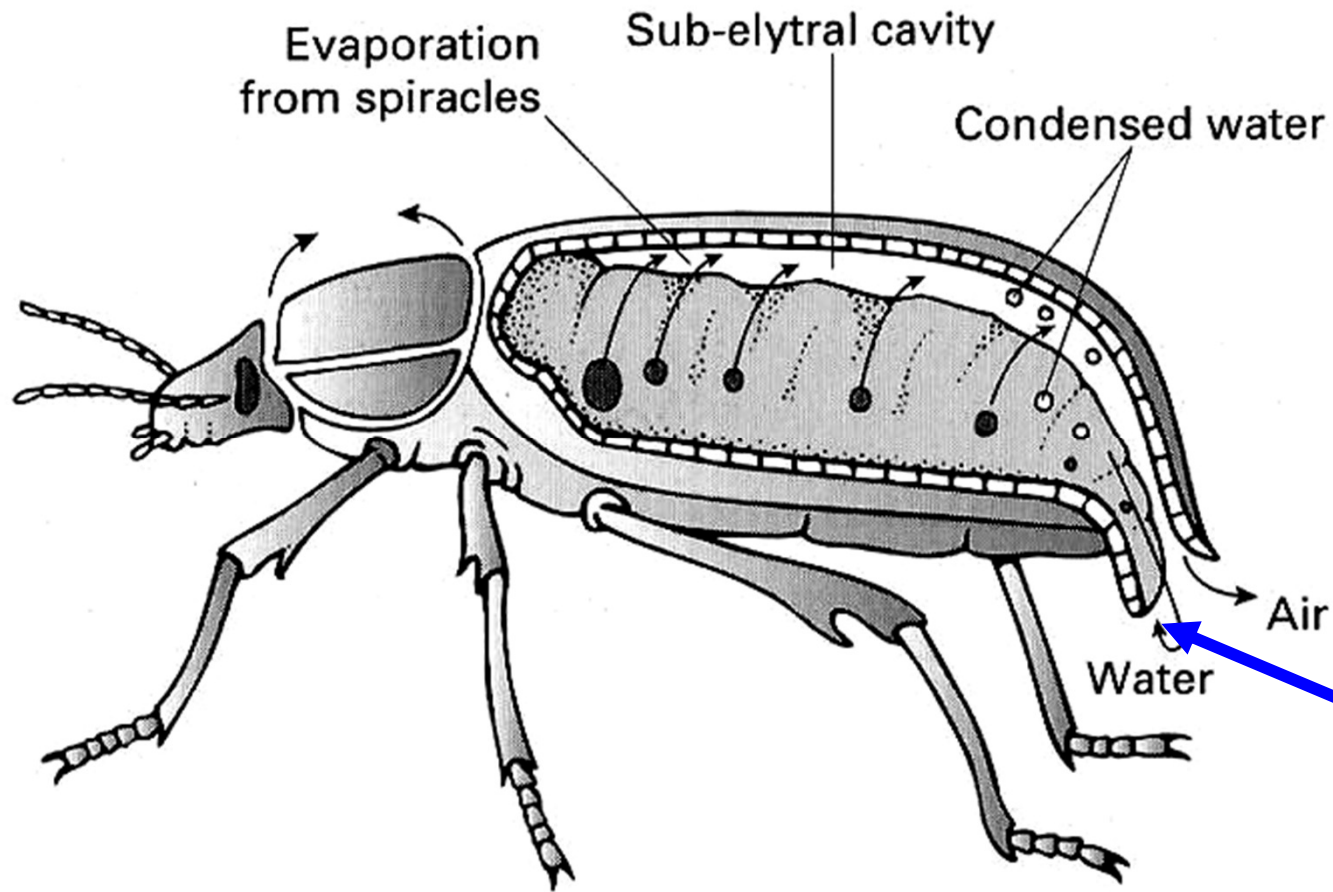
- **Hypotheses:**
- ~~cycling changes of metabolism?~~
- **cycling ventilation**

Cyclic ventilation: water savings



Respiratory water recovery

A tenebrionid beetle



condensed water returned to the body via the anus

Water acquisition: condensing water vapor by tenebrionid beetles

Mechanism:

- elytra covered by hydrophobic layer
- from which ultra-hydrophilic bristles („hair”) are sticking
- water condenses on the hydrophilic bristles
- and flows down along hydrophobic „ditches”

A tenebrionid beetle from the Namib Desert
Stenocara gracilipes



A tenebrionid beetle from the Namib Desert

Onymacris unguicularis



A tenebrionid beetle from the Namib Desert
Onymacris unguicularis

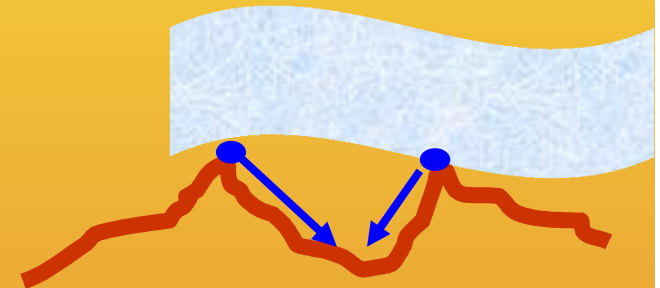


A tenebrionid beetle from the Namib Desert

Lepidochora discoidalis



- The beetle builds trenches
- Water from mist condenses on the edges of the trenches



Acquisition of water from the vapor without its condensation

Desert "sand cockroaches" *Arenivaga* sp.

A. floridensis

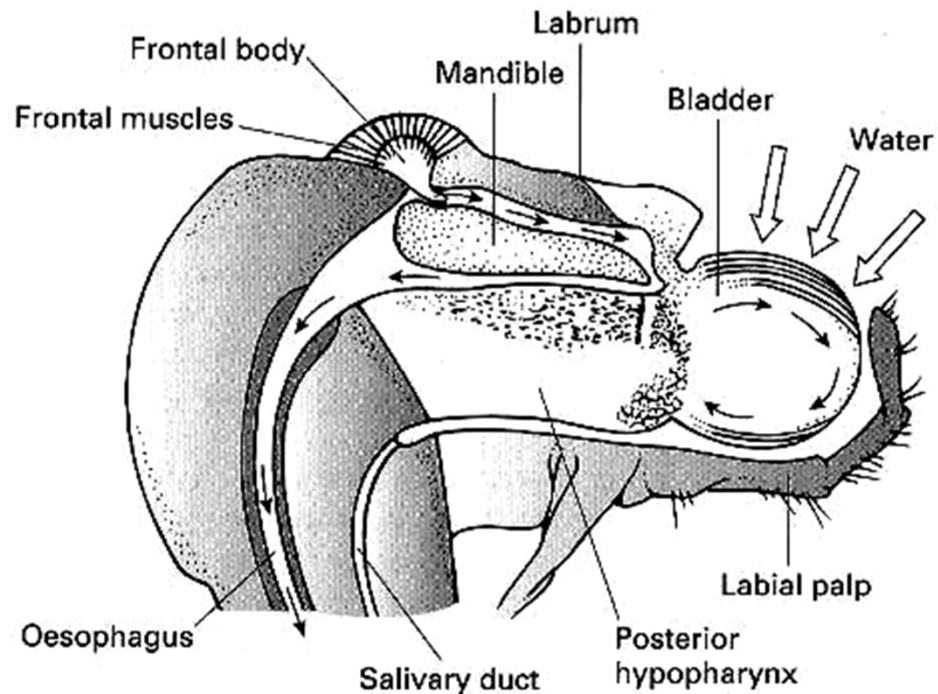


*A sand roach from deserts of
South-Western USA
(probably *A. investigada*)*

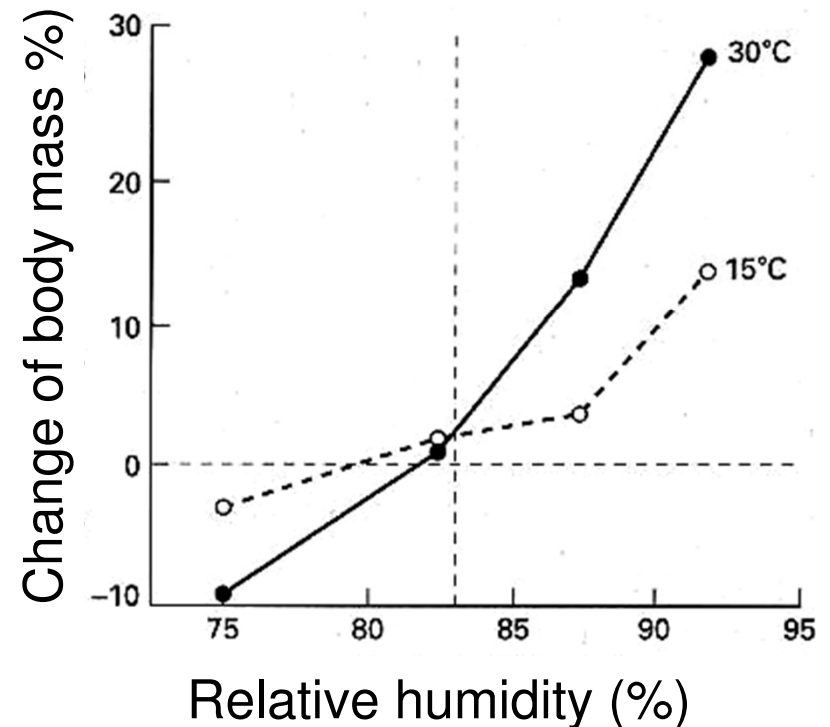


Acquisition of water from the vapor without its condensation

The mechanism described in *Arenivaga investigada*



Lateral section through the head



Water: the most potent solvent

Only few processes concern pure water:

- Evaporation associated with respiration
- Absorption of condensed water

Most processes concern solutions:

- thermoregulation by sweating
- drinking liquid water
- excretion
- regulation of osmotic pressure
- regulation of hydrostatic pressure

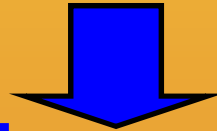
Water: the most potent solvent

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Water-mineral regulation

Key processes in water-mineral regulation

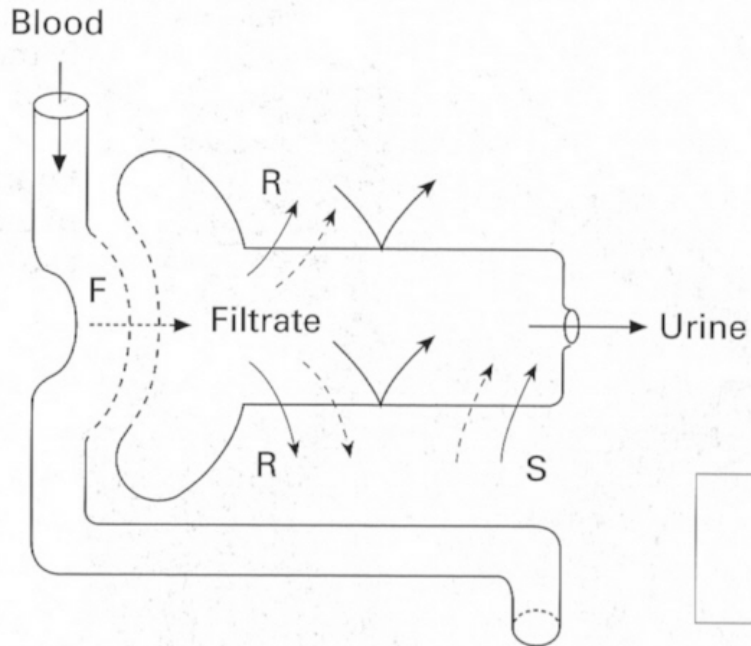
- Osmosis
- Ultrafiltration
- Selective diffusion through plasmatic membrane channels
- Regulation of membrane permeability
- Active transport through membranes
- Co-transport supported by osmotic gradients

Basic designs of excretory organs

Ultrafiltration

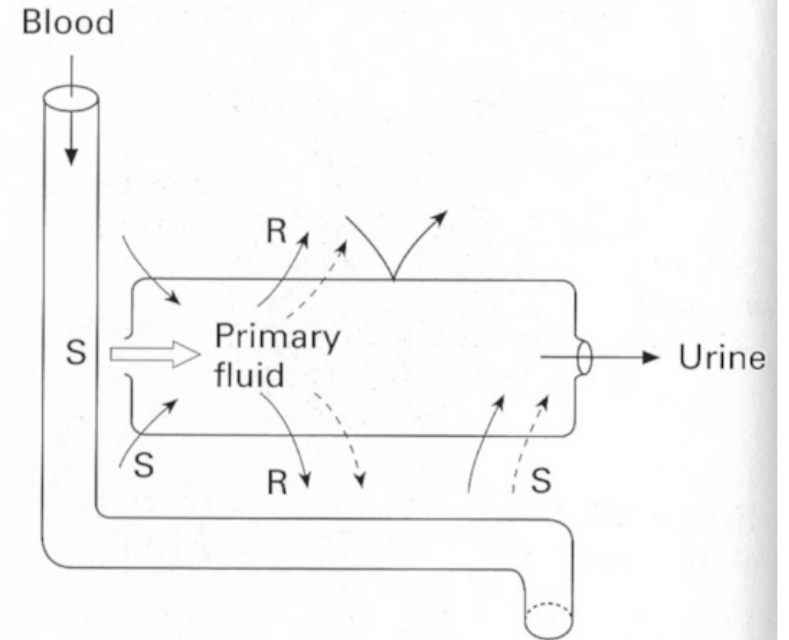
Secretion

Ultrafiltration



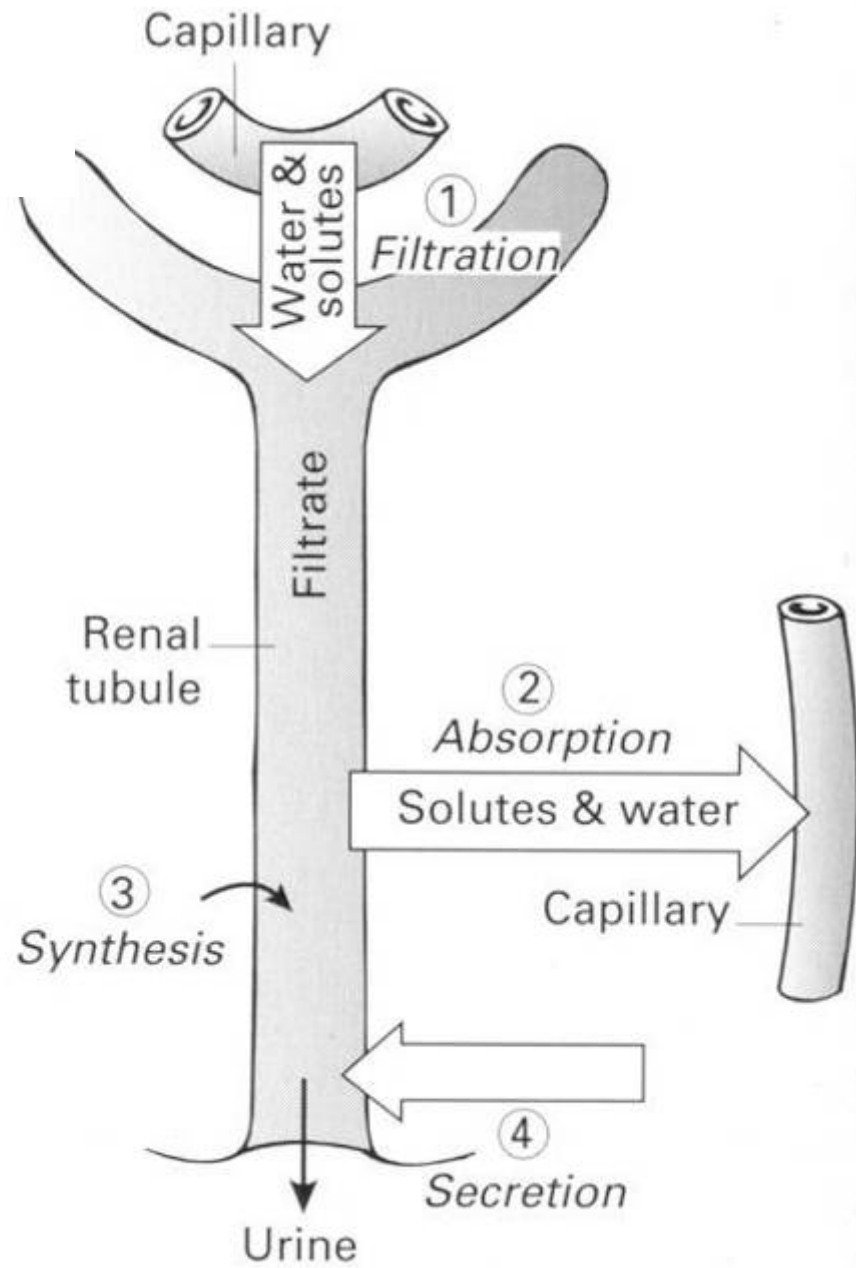
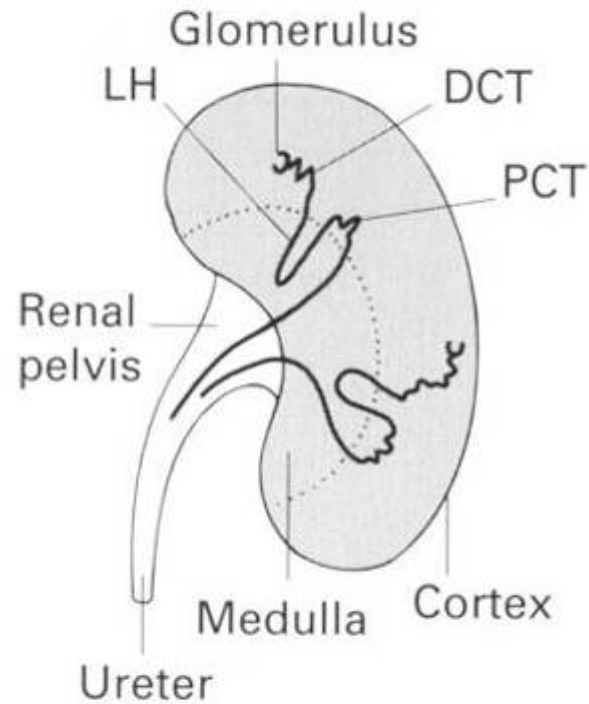
Basic designs

Secretion

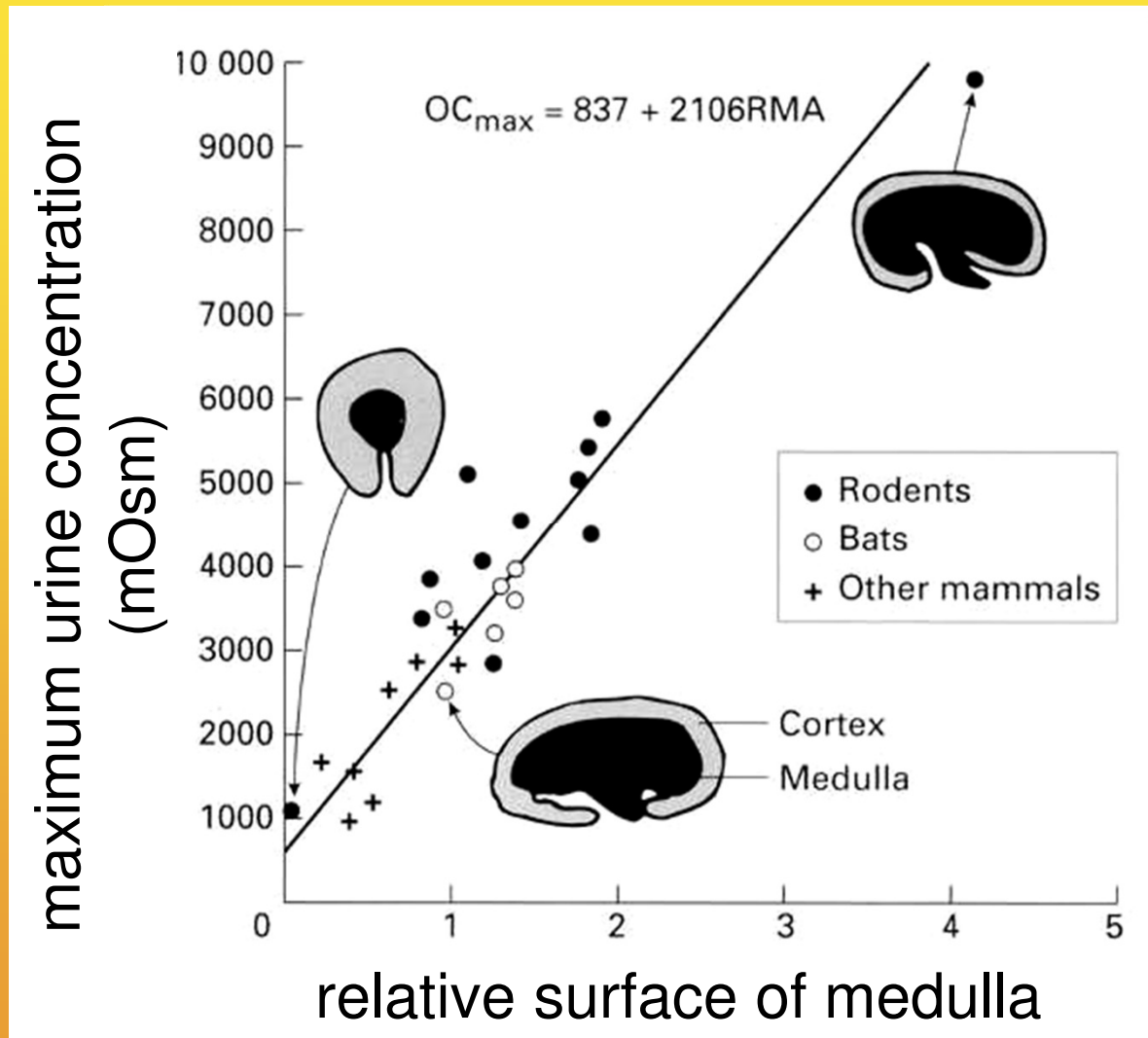


F Filtration
R Reabsorption
S Secretion

Design of a mammalian kidney



Relation between kidney morphology and urine concentration in mammals



Spiny mouse *Acomys cahirinus*

(Near East, North Africa)



Urine concentration can exceed 9000 mOsm

Spiny mouse *Acomys russatus*

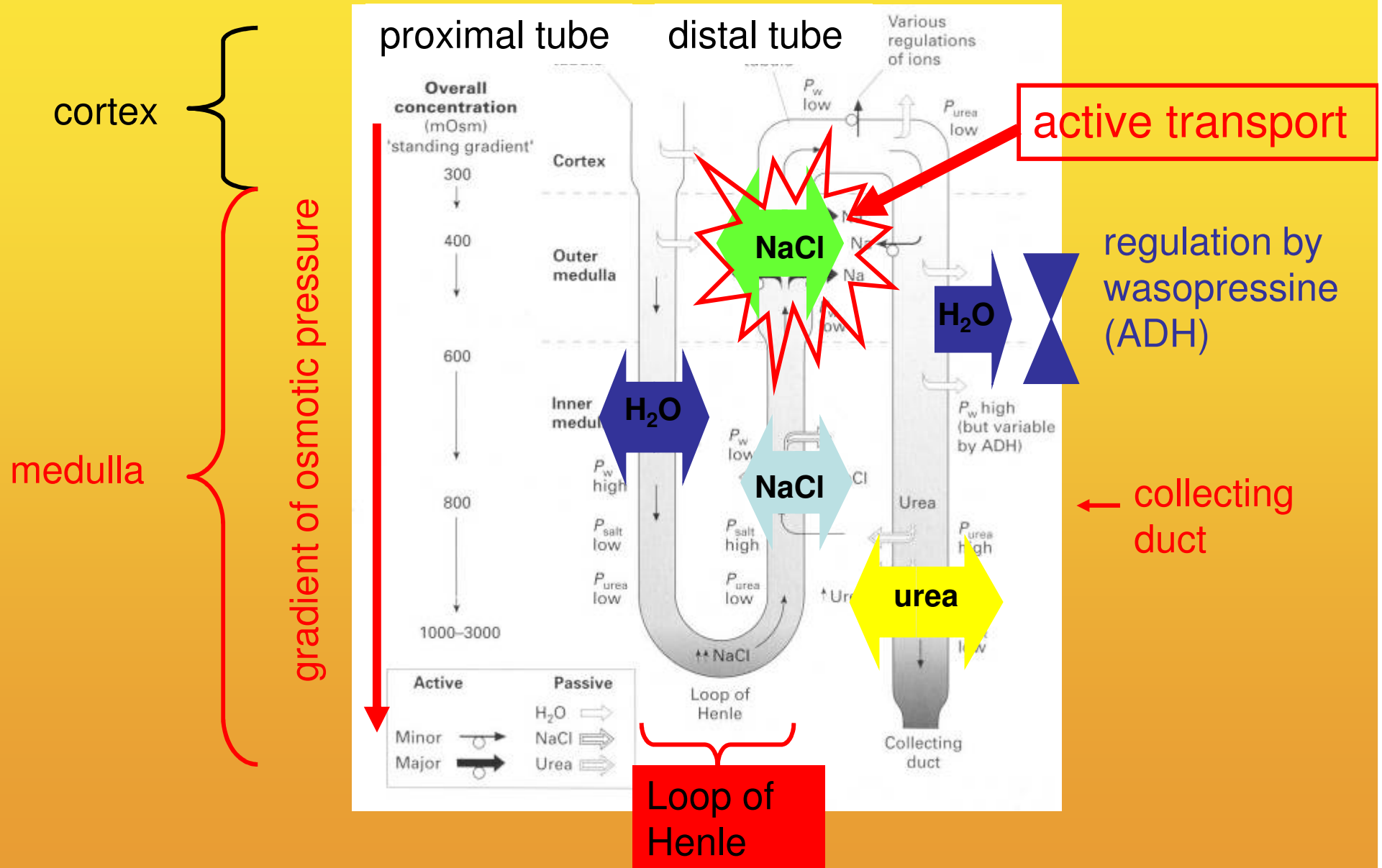
(Near East, Negev Desert)



Spiny mouse *Acomys nesiotes* (Cyprus)



Nephron - a countercurrent "amplifier"



Relation between kidney morphology and urine concentration

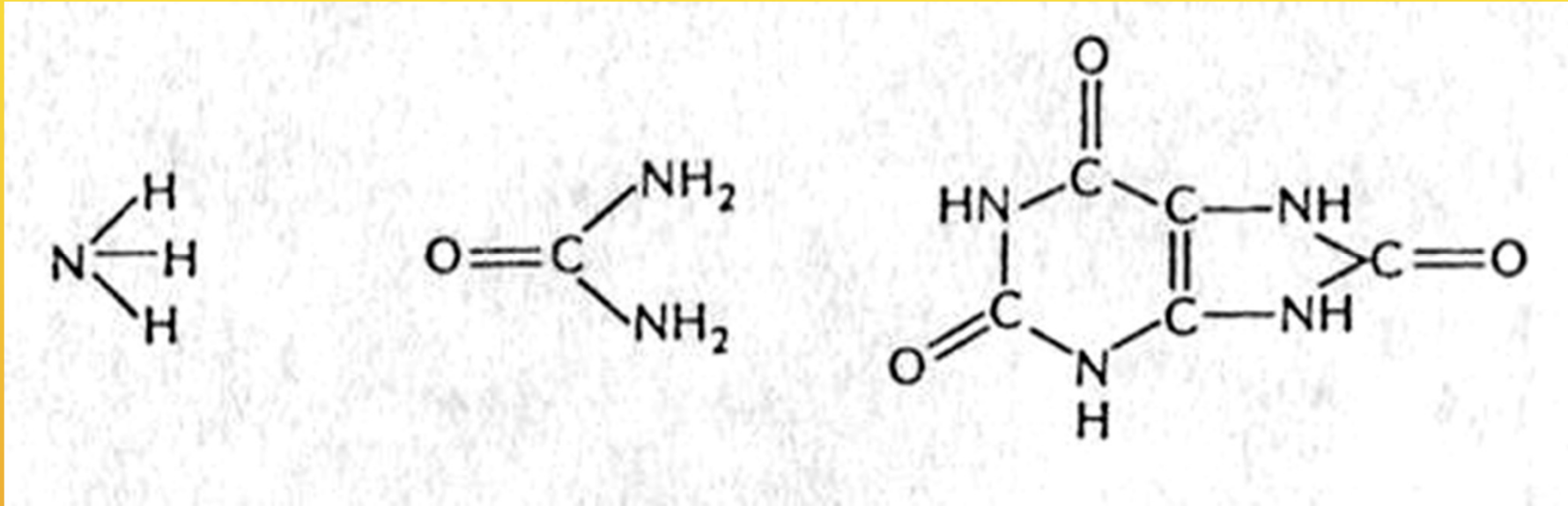
- Reptiles do not have the Henle's loop
- Birds have very short loops
- **How can they dwell in arid habitats?**

The most important forms of nitrogen excretion

Ammonia


Urea

Uric acid



The most important forms of nitrogen excretion

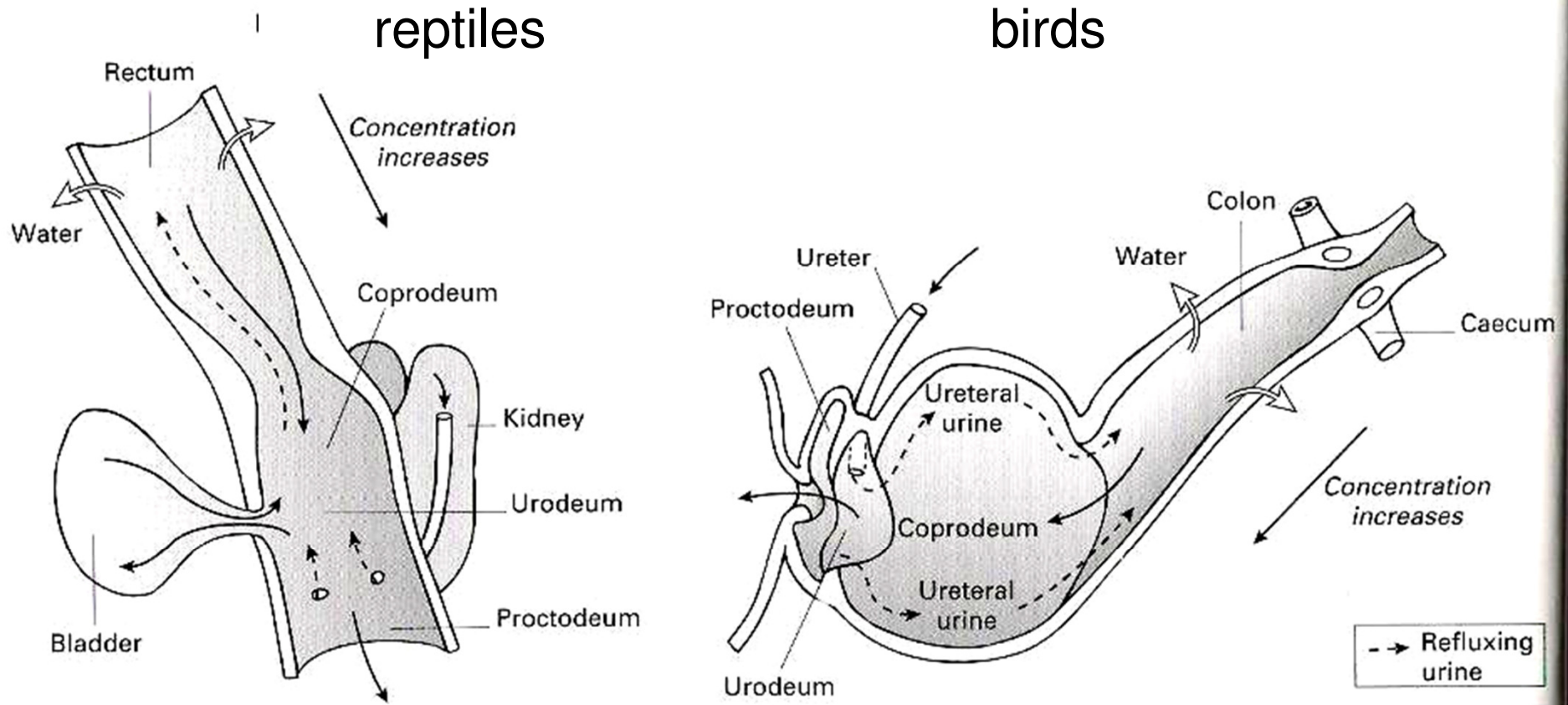
| Form | Toxicity | Cost | Solubility |
|-----------|----------|------|------------|
| ammonia | high | no | high |
| urea | low | low | high |
| Uric acid | low | high | low |


converts to crystal form

How do birds and reptiles cope with low water availability?

- Urine (not very concentrated) is removed to cloaca
- Water is resorbed in cloaca
- **Uric acid forms crystals:
the osmotic pressure is not increased!**
- The „urine” can be almost dry

How do birds and reptiles cope with low water availability?

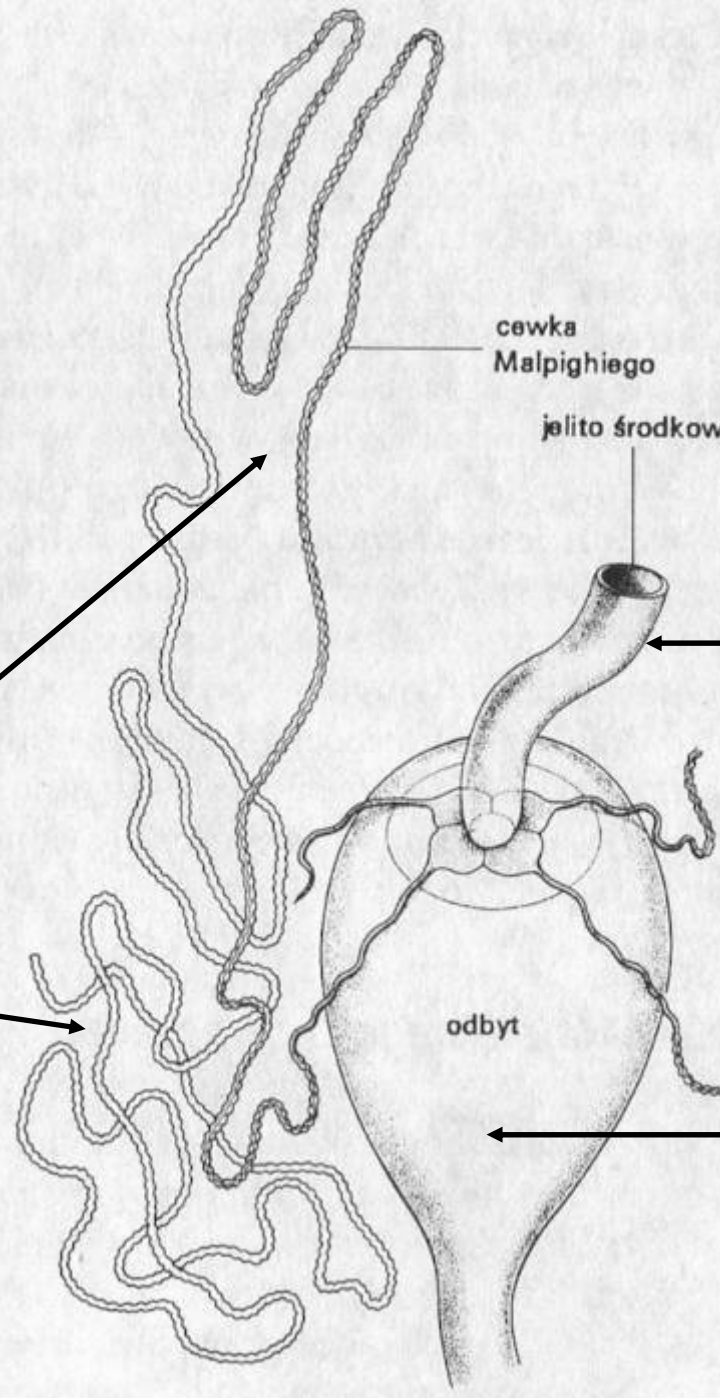


Water retrieval in cloaca

Other excretory systems

Malpighian tubule system in insects

Malpighian tubules

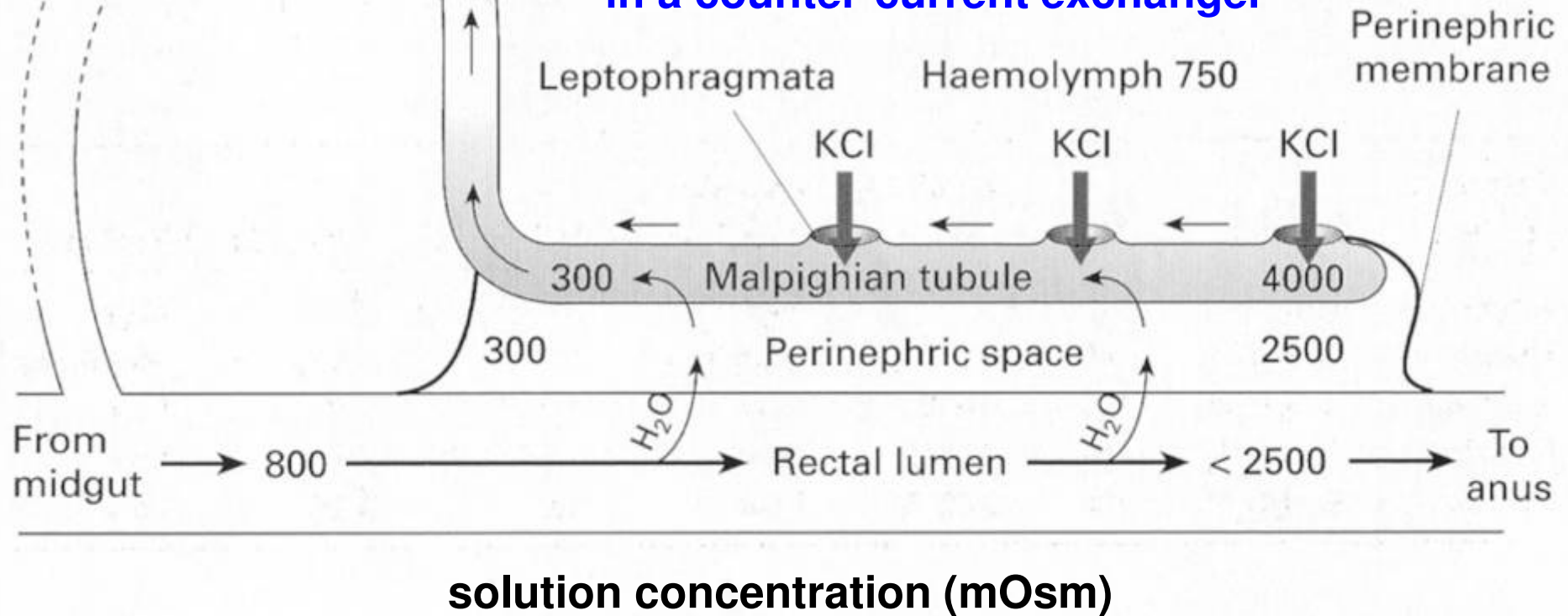


midgut

hindgut and rectum

Resorption of water in insects dwelling in arid habitats

- Active pumping of ions to the Malpighi tubes
- Osmotic "sucking" of water from hindgut in a counter-current exchanger

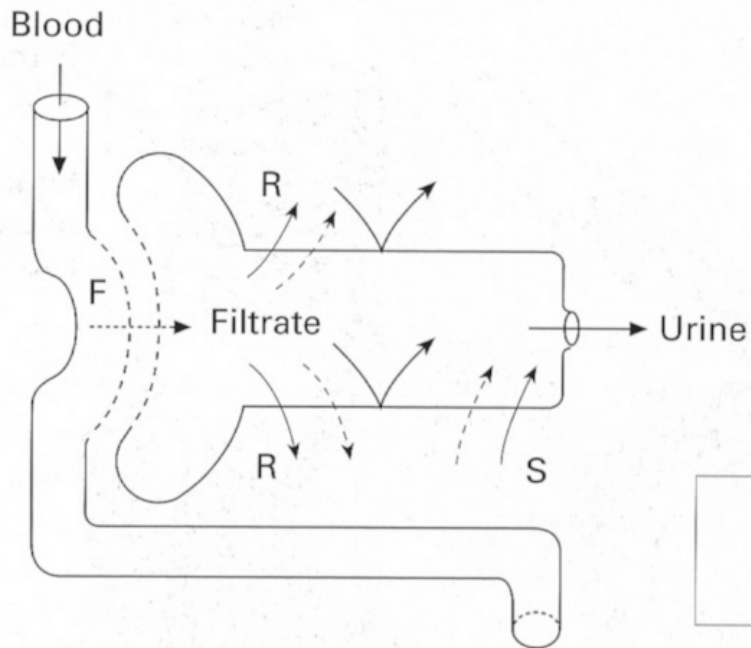


Basic designs of excretory organs

Ultrafiltration

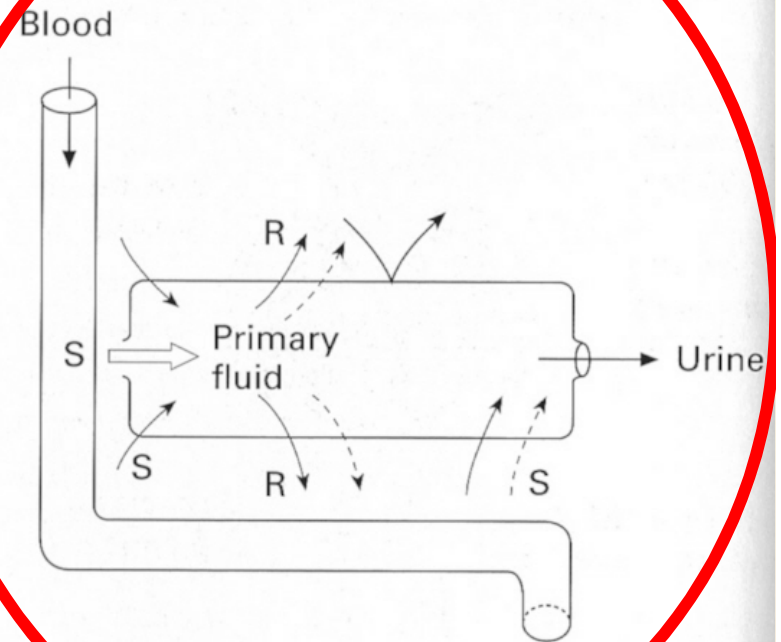
Secretion

Ultrafiltration



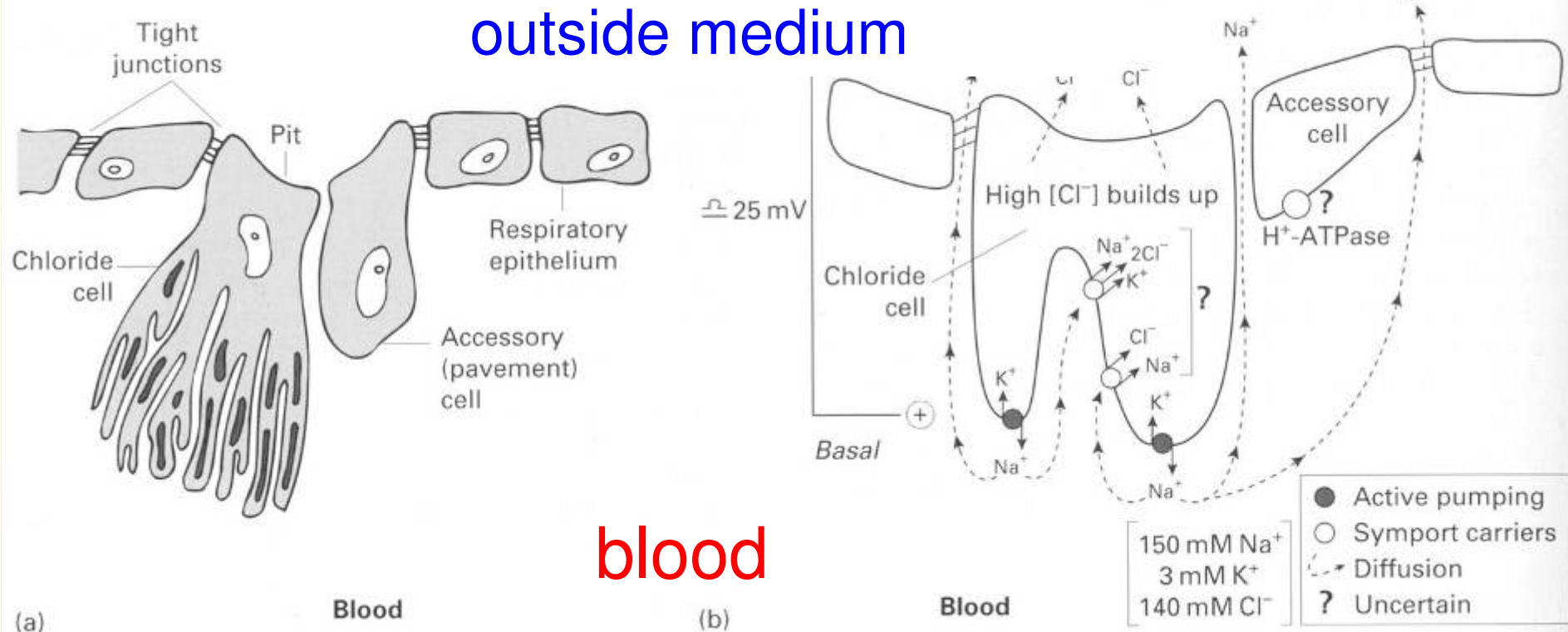
Basic designs

Secretion



F Filtration
R Reabsorption
S Secretion

Salt glands in desert reptiles and birds (similar to glands in some marine animals)



Active transport of Na^+/K^+ cations into chloride cells works as a pump drifting the transport of chloride anions (Cl^-)

Coping with low food availability

Food availability

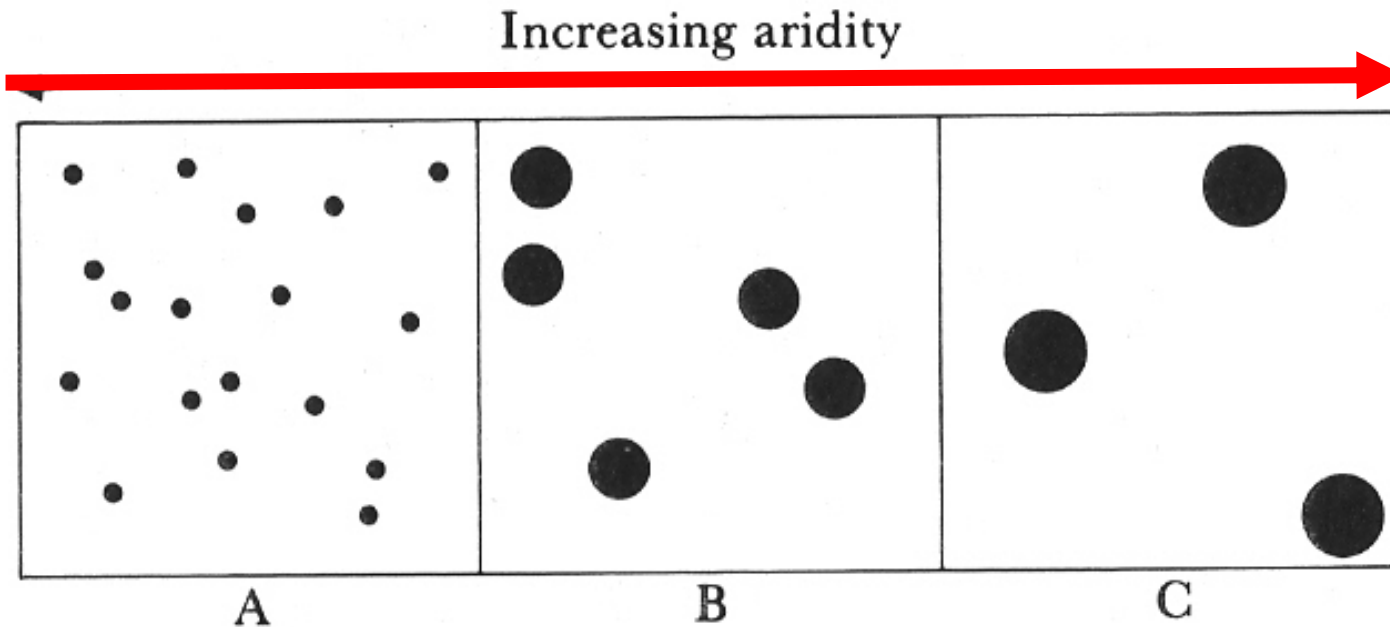


Figure 3.30 Diagrammatical representation of the general trend, with increased aridity, of increased plant tuber size and increased nearest-neighbour distance. Tuber distributions are markedly random for the situation depicted in (B) and (C), but are unknown for the mesic situation depicted in (A). Redrawn from Lovegrove and Wissel (1988).

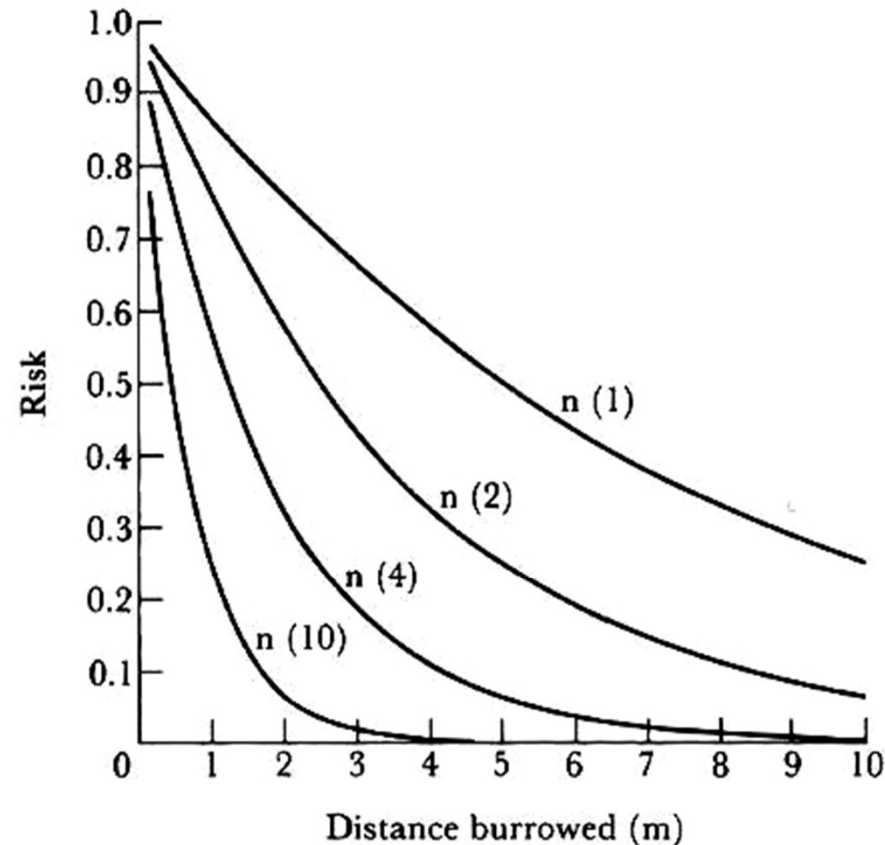
Food availability: clumps of plants on a desert (South Sinai)



photo: P. Koteja

Food availability

Risk of foraging failure is lower during cooperative foraging



32 The decay curves of foraging risk, quantified as the probability of no encounter with a plant tuber, as a function of distance burrowed for different numbers (n) of cooperatively foraging mole rats. The data show rapid reduction in risk with increasing numbers of cooperatively foraging mole rats. After Lovegrove and Wissel (1988).

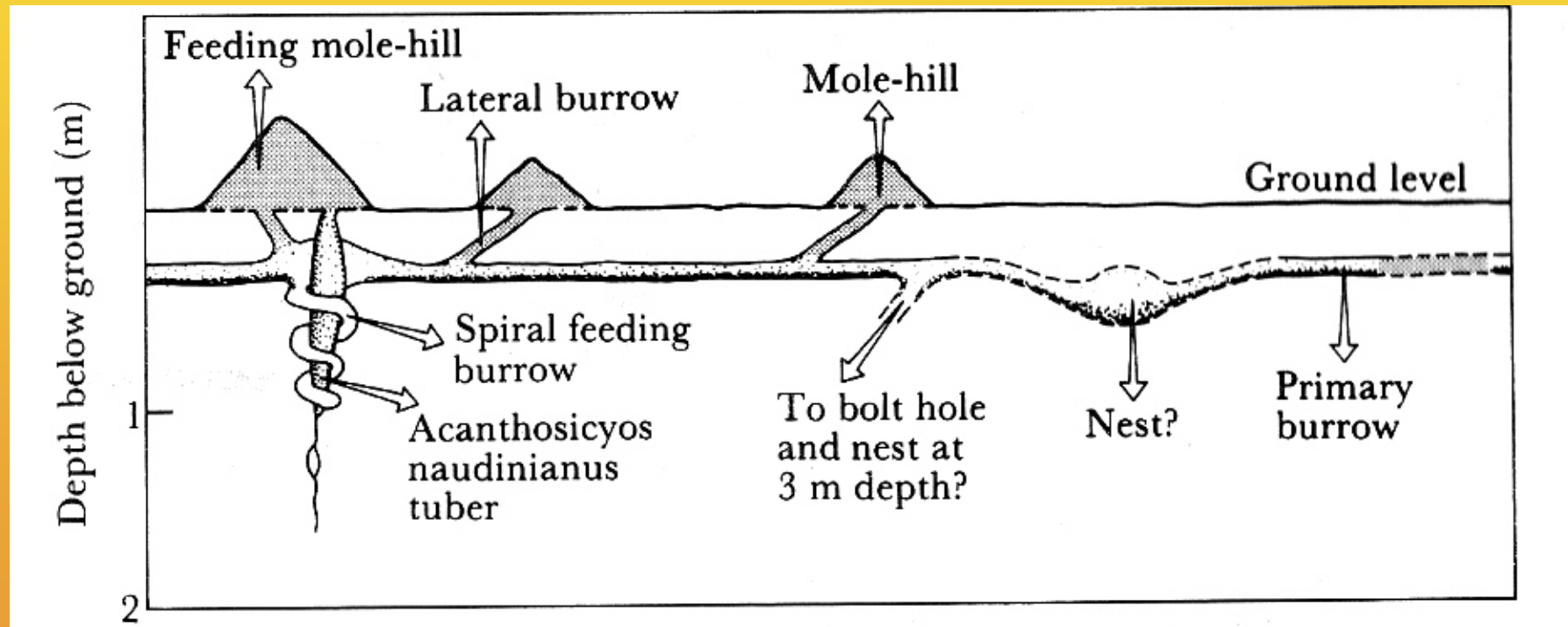
Social life...

Eusocial mammal !

Damaraland mole rat

Cryptomys (=Fucomys) damarensis

South Africa, Namib desert



Eusocial mammal

- casts
- only "queen" reproduces

naked mole rat
Heterocephalus glaber



Heterocephalus glaber from www.animalpicturesarchive.com (also on Wikipedia)

Social life...

Meerkat *Suricata suricatta*



Photo: Wikipedia

SUMMARY:

adaptation of animals to desert habitats

- **Minimizing overheating risk: fossorial (underground) microhabitat**
- **Water economy:**
 - minimizing evaporation
 - condensing urine
 - water acquisition from water vapor
- **Low rate of metabolism, extended lifespan (a topic for a separate lecture!)**
- **Life in groups: sociality**