Avian Thermoregulation

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Thermoregulation

I. Introduction

Physiological processes similar to mammals

- double circulation (birds r. aortic arch)
- shiver to generate heat
- evaporative water to dissipate heat
- change thickness of insulation

Birds maintain high body temperature

use an array of adaptations

- structural
- physiological
- behavioral
- ecological

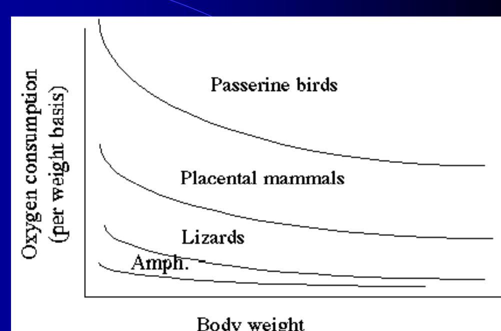
Temperature Regulation

Birds are endothermic thermoregulators – use metabolism as well as behavioral mechanisms to maintain constant body temperature.

But metabolic rates of birds generally much higher than in mammals

MR small bird ~ 70% higher than mammal of similar wght.

WHY?



II. Body Temperature

A. Normal range

Hottest animals, ~ 40°C (104°F) but ranges from 38 - 44°C for different species

Brown Pelican – 40.3

Rock Pigeon – 42.2

Black-billed Magpie – 41.8

House Sparrow – 43.5

B. Variation

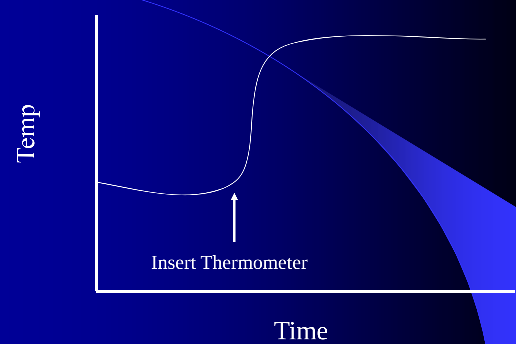
Unlike mammals, T_b can be variable

Difficult to measure

many variables can influence T_b

1. Stress

handling elevates T_b

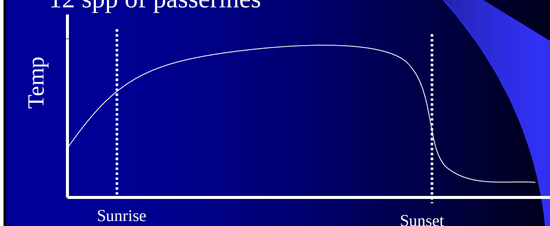


2. Diurnal variation

Deep T_b varies during 24-hr period.

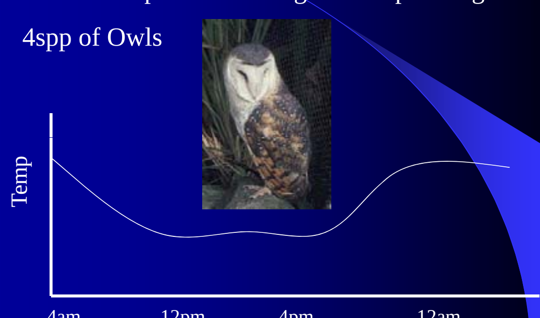
Diurnal birds - T_b highest during day –

12 spp of passerines

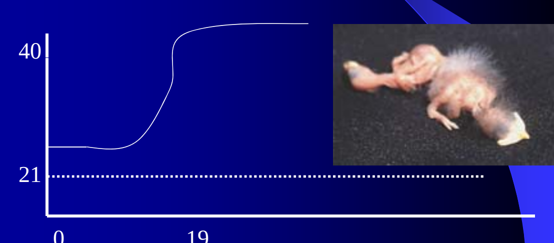


Nocturnal species have highest temps at night

4spp of Owls



3. Age – T_b nestlings are lower than adult bird but increase until adult levels ~ 20 d.



4. Molting – When birds replace feathers insulation efficiency not effective. Internal heat production increases to compensate.

C. Why so hot?

Little argument for ultimate answer to question.

Ability to be continuously metabolically active independent of the environment is certainly adaptive.

What is the cost to maintaining constant T_b

require constant energy supply

But why maintain higher body temps than mammals?

Consider gradients between birds body and environment.

Avg sea T = 15C; g = 25

Avg earth T = 13-14C; g = 26

Mean annual T in Tropics = 25 – 27C; g = 14

Numerous hypotheses exist which explain the high temps maintained by birds.

1. Maxithermy Hypothesis

Birds maximize metabolic rate (higher T_b) so that growth rate (reproductive rate) will be maximized.

Evidence –

a. unpregnant sloths regulate T_b rather poorly, when pregnant much better

b. Indian Rock Python elevates T_b 3-5 when incubating eggs.

2. Hot enough to trot hypothesis – aka Phil Osterhaus hypothesis.

Birds want to maintain a T_b at the highest level they would experience under stress.

Want to ensure they operate metabolically.

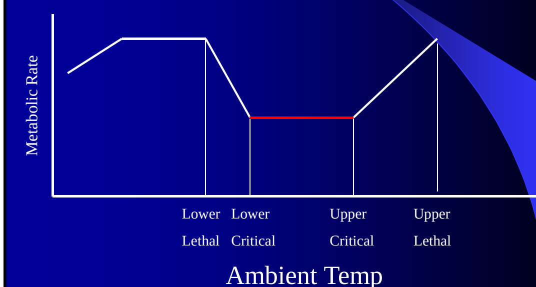
If too low??

3. O_2 transport Hypothesis – Transport of O_2 is Temp dependent.

Warm blood carries more than cold blood.

4. Law of the Minimum Hypothesis

a. Need understanding of definitions



b. Model

Assume 2 birds with same metabolic rates, wght, insulation.

T_{b1} = 26°C

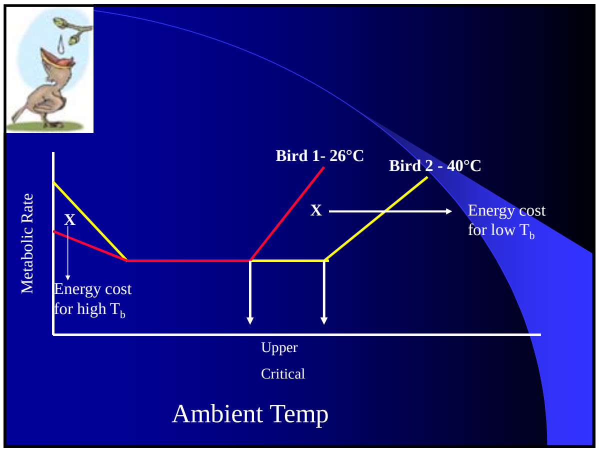
T_{b2} = 40 °C

When T_a < 20°C energy cost for 2 is higher then 1 ~ 68% less than energy cost of bird 2.

When T_a = 46° C, 1 suffers higher evaporative water loss than 2.

Difference results in 1 becoming hyperthermic at 30°C, 2 hyperthermic at 43°C.

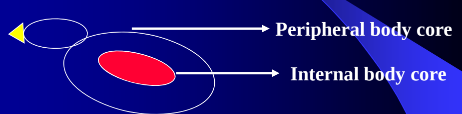
Hyperthermia = elevation of body temp above normal range. Lethal limit for most birds is ~ 46°C (115°F).

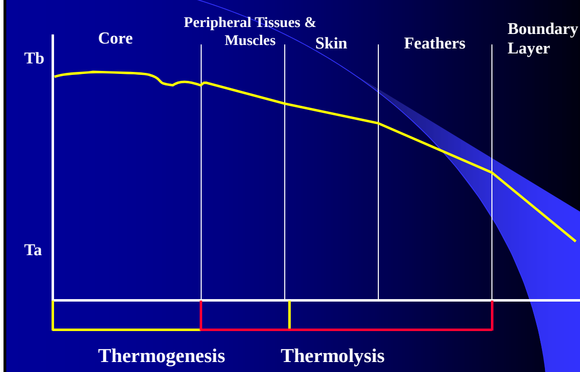


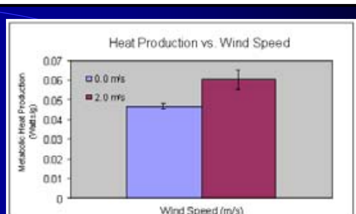
This hypothesis proposes –

Birds opt to use more energy during colder periods (to maintain high T_b) rather than incur the cost (energy + water) of lower T_b during periods of high T_a.

D. Core-shell concept







Infrared Thermography image of a House Sparrow exposed to 15°C and no wind (left) vs. that of a sparrow exposed to 15°C and a wind speed of 2 meters/second (right). Red colors represent higher temperatures grading into cooler temperatures with blue colors.

III. Thermogenesis and Thermolysis

A. Definitions

Thermogenesis = heat production

Thermolysis = heat loss

Constancy in T_b is obtained by balancing thermogenesis with thermolysis

B. Hypothermia - affects metabolic rate.

Colder the bird the slower the metabolic rate. Slower the metabolic rate the colder the bird becomes.

Positive feedback loop leads to death. Proximate cause is direct effect of low T_b on cellular functions (chemical reactions).

Adaptations for thermoregulation under cold stress center on -

• reduce thermolysis

• increase thermogenesis

C. Hyperthermia – speeds up metabolic rate. Results in positive feedback loop.

Unlike hypothermia death usually does not always result from the direct effects of elevated temperature.

Death can be due to problems arising from hyperventilation of the bird for heat dissipation.

Adaptations for thermoregulation under heat stress really only involve increase thermolysis.

IV. Heat Flow

Need an understanding of physical mechanisms birds use to exchange heat with environment

A. Conduction

Matter composed of molecules in motion.

Hot molecules move faster then slow molecules.

Thus hot molecules impart their energy to slower moving cold molecules when two objects are in contact.

Conduction occurs between birds body and substrate bird is resting on.

Also between skin, feathers and boundary layer of bird.

Matter varies in ability to conduct heat.

Water – good conductor

Air – poor

Down - poor

B. Convection

Takes place in gases and liquids (actual movement of gases and liquid).

Flowing air or water can carry with it heat energy.

Circulatory system of birds transports heat through the body (responsible for internal convection)

C. Radiation

All matter in the universe is continually radiating energy. Main source is sun.

No conducting or transporting medium is required.

Cold bodies - net thermal gain through radiation exchange.

Warm bodies - net thermal loss.

V. Adaptations for reducing thermolysis under cold stress.

Birds LCT not all that low! 20 – 30 °C

Few birds below 10°C.

American Dipper (50g) feeds in Montane streams in Great Basin. LCT = 11.5°C

Common Raven = 0°C

A. Anatomical

1. Reduction in peripheral tissues in exposed extremities.

- Birds minimize blood flow to extremities
- Few muscles in lower leg

2. Seasonal changes in plumage density

Species	Winter	Summer
White-throated Sparrow	2600	1500
Carolina Chickadee	1700	1100
Dark-eyed Junco	32% heavier	
Common Redpolls	31%	
Stellar's Jay	45%	

3. Counter-current heat exchange

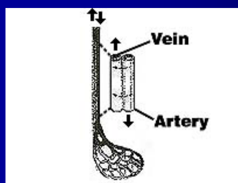
Rete mirable present in extremities

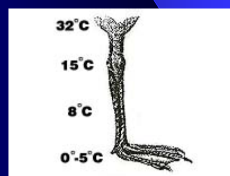
Outgoing arterial blood gives up heat to incoming cooler venous blood.

Glaucous-winged Gull

T_a = -16°C

T_b = 36 °C





4. Bergman's Rule – In a species inhabiting a variety of climates there is a trend toward larger size in colder areas, hence reduced s:v ratio.

Inverse relationship between body size and mean ambient temperature.

What does increased size do for the organism in cool environments?

Many species exhibit this pattern.

Downy Woodpecker

House Sparrows

What about Canada Geese?

Branta canadensis

B.c. hutchinsonii – 1.6kg
B.c. minimus – 2.3kg
B.c. interior – 4.1kg
B.c. maxima – 6.8kg

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B.c. hutchinsonii – 1.6kg

5. Importance of surface to volume ratio

The s:v ratio has important consequences to metabolism and hence thermoregulation.

SA proportional to Weight $^{0.67}$

MR related to W as - Kcal/day = 86.4 W $^{0.668}$

Thermogenesis must balance thermolysis (function of SA)

Heat loss is proportional to W of the organism raised to 2/3 power.

Calculate separately for Passerines & Nonpasserines

Nonpasserines = Kcal/day = 78.3 W $^{0.723}$

Passerines = Kcal/day = 129 W $^{0.724}$

Convert to linear function –

Nonpasserines = Kcal/day = 78.3 + 0.723 log W

Passerines = Kcal/day = 129 + 0.724 log W

For same W, passerines metabolism ~ 50% > than nonpasserines within ZTN.

If calculate metabolism below LCT (0°C) relate to W relationship changes – slopes change, becomes less steep.

i. small birds are more greatly affected by low T relative to large birds.

ii. slope of passerines is less steep than non-passerines (nonpasserines more affected by cold)

iii. more derived passerines are better adapted to cold

Hypothesis – Passerines may not need to migrate

How could we test this hypothesis?

Lat.	# Censuses	Mean Total Sp	% Non-passerines	% Passerines
50 N	11	25	39	61
37N	10	64	45	55
26N	4	128	55	45

B. Behavioral Adaptations

1. Roosting in cavities

Birds also regulate by seeking changes in microclimate during hottest and coldest time of day.

- Sociable Weavers
- Black-capped Chickadees

Goldfinches roosting in evergreens reduced energy demands by 1/3 compared to those roosting in open sites.

Overhead shelter from night sky also important.

Radiation losses can be large.

Calliope Hummingbird

2. Huddling

Grouping together decreases the group’s s:v ratio.

- Brown Creepers
- Pygmy Nuthatches

3. Migration
4. Body positioning

Tuck bill into plumage, sitting on legs, flying with legs pulled into plumage.

C. Physical

Changing physical properties of insulative shell affects heat conductivity.

1. Pteroerection

a. Ring Doves – overall erection increases depth of plumage by 400% & thermal resistance by 56%.

b. Occurs within ZTN and below LCT

2. Reduction of peripheral blood flow

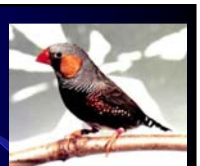
- constrict surface vessels to shunt blood away from surface.

V. Adaptations for Thermogenesis under Cold Stress

A. Ectothermic Strategy – Plumage coloration

1. Melanic Zebra Finches – use 23% less energy at the same temp than albinistic birds

2. Wind reduces this advantage



3. Why are Snowy Owls white?

Plumage very thick to protect against heat loss.

B. Shivering

Only metabolic response available to birds.

C. Tolerance of hypothermia

If can survive low T_b then gradient with T_a is reduced – thermolysis is reduced.

1. T_b lowered 2 - 3°C each night
2. Heterothermia can occur under temporary cold stress

a. Anna's Hummingbird would require 10.23 Kcal/day at normal T_b , but when in torpor only 7.55 Kcal/day (27% savings)

b. MR drifts lower until 2nd arousal reached, bird initiates thermogenesis

c. Torpor common in Apodiformes and Caprimulgiformes. Also known in Snowy Owl, Black-capped Chickadee, Swallows, Rosy Finches, Manakins.

3. Heterothermia under seasonal cold stress.

Hibernation in at least 1 spp. Common Poorwill.

December 29, 1946 Edmund Jaeger discovered torpid Poorwill in S. California.

Returned to same crevice following winter (Nov – Feb). T_b ranged from 18 – 19.8°C

At T_b 10°C mr slows to 1/10 normal resting value.

1g fat support hibernating Poorwill for 10days.

Torpid Common Poorwills able to attain flight at low T_b 27.4 – 30.8°C

Lowest reported flight temps for a bird.

D. Latitudinal Relationships of Thermogenesis and LCT

Arctic	Temperate	Tropic
Snow Bunting 9	N. Cardinal 18	Waxbill 28
Gray Jay 6	Blue Jay 18	Manakin 20
Herring Gull 10	Horned Lark 20	Budgerigar 34
	Dark-eyed Junco 24	
	Turkey Vulture 26	

2 ways to decrease LCT

- increase metabolic rate

- increase insulation

Tropical birds have thinner skin and less dense feather coat than temperate and arctic birds.

House Sparrows – MR in coastal Texas 20% lower than in Colorado.

E. Seasonal shift in LCT

1. Seasonal changes in plumage density
2. Arctic and temperate birds carry more subcutaneous fat in winter than in summer.
3. Seasonal preference for lipids rather than in carbohydrates in muscle metabolism
4. No change in aerobic thermogenic capacity of avian muscle but hematocrits increase in winter.

V. Adaptations for increasing Thermolysis under heat stress.

A. Evapotranspiration

Heat dissipated by evapotranspiration.

Liquid water to vapor – 580 kcal/g at 30°C

50% water loss in small birds through skin. No water loss in Ostriches.

Rest of water loss is through respiration.

Both skin and breathing system water loss can be controlled, in part.

B. Physiological Control

At T_b of 41 – 44 °C hypothalamic panting center takes over from medulla.

Panting rates are 16 – 27 x resting breathing rates

At T_b of 46 °C, panting volume of air exchange blown off so much CO_2 that alkalosis could potentially occur.

Alkalosis – abnormally high pH in ECF

Increased breathing rate causes loss of CO_2 which normally disassociates into carbonic acid in blood.

$H_2O + CO_2 \rightarrow H_2CO_3 \rightarrow H^+ + HCO_3^-$

Death follows from enzyme inactivation by high pH rather than temperature.

Mechanisms to prevent alkalosis

1. Tracheal dead air space.

In Rock Pigeons, panting begins at T_b of 43°C but volume of air exchange is small because tracheal dead air space. No alkalosis.

Trachea heavily invested with arterial blood network – another rete mirable.

This system transfers heat from the blood to the surrounding air in trachea.

2. Esophageal pumping

Other Columbiforms use esophageal pumping (Ring Doves).

Plexus of blood vessels to transfer heat from the blood into the air within esophagus.

3. Gular fluttering

Pelican moves hyoid which causes pharynx to flap.

Found in Strigiforms, Columbiforms, Anseriformes, Pelecaniformes. No passerines do this.

C. Physical mechanisms

Birds can change physical properties of shell to increase thermolysis.

1. Increase peripheral flow by dilation
2. Fluffing feathers to disrupt shell and expose skin to air for increased cutaneous heat loss.

D. Anatomical

Plumage color

Why are tropical gulls dark while temperate gulls are gray and white, and arctic gulls are white?

Tropical gulls are dark because …

In still air, white birds have the advantage – less heat is actually absorbed.

As wind increases dark birds have the advantage.

WHY????

Gray Gull

- nests in Atacama desert of Chile
- morning plumage maximally depressed
- afternoon plumage becomes maximally erect
- if it were white would reflect heat back toward body

E. Temporary tolerance of Hyperthermia

Temporarily tolerate rises in T_b of 2 - 4 °C

decreases gradient with environment

This mechanism also used by birds to conserve water.

F. Behavioral Mechanisms

1. Decreasing activity
2. Flying with legs extended
3. Change body position

4. Urohydrosis – T_a above 45°C Wood Storks increase rate of defecation on legs. Provides additional evaporative cooling.

Known in 12 spp storks

G. Flight

Heat produced during flight could be lethal.

1. T_a of -5°C, evaporative cooling of flying Starling only 5% Metabolic heat production
2. T_a of 29°C, 19% of heat production
3. T_a above 7°, starling can become dehydrated when flying

Water Stress

I. Maintaining Water Balance

Most difficult at high Ta.

Continually evaporating from bird.

Understanding of how birds deal with stress comes from laboratory and field studies.

Joshua Tree National Monument

Fall migration very stressful time

Shade temps > 100°C , free water difficult to find.

100’s dead birds found.

A. Water Losses

1. Cutaneous and respiratory

Largest water losses for birds through skin and respiratory surfaces.

Drying capacity of air is dependent on T_a and its humidity.

Diurnal variation

High T_a – midafternoon

High humidity - night

• Convection can also contribute to water loss.

• Activity

• Body size – small birds more difficult to remain in balance.

25°C at rest

147g California Quail – 3.5%

19g House Finch – 17.2% of body wght/24rs

2. Urinary and fecal losses

Main excretory product – uric acid, urate salts

Uric acid highly insoluable – cannot reabsorb large amounts of water.

Excreted as semisolid.

Water stress – reabsorption can occur within cloaca, large intestine, back as far as gastrointestinal tract.

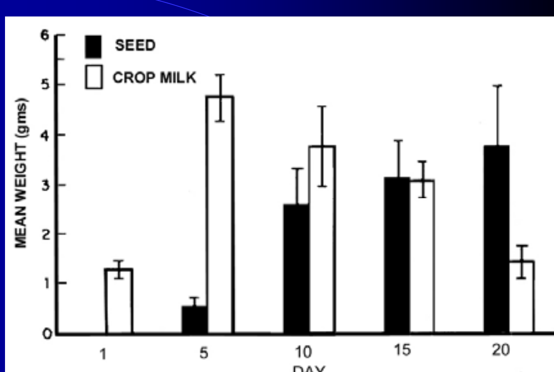
Brewer's Sparrow – reduces water content of excrement from 93 – 33%

2. Regurgitation

Major source of loss during nesting.

Can remove water from crop and esophagus.

Production of crop milk more of a stress 65 – 81% water



Young gain 5.8g/day

Protein content – 13 – 18%

Fat content – 7 – 13%

3. Egg laying

yolk and albumin high water content 70-80% by wght.

1 egg/24hr

B. Water gains

1. Metabolic – result from oxidation of organic compounds.

Quantity depends on type of food metabolized.

Fats release most water – more energy/g to breakdown than carbohydrates

No bird can survive solely on metabolic water

19g HOFI at 25°C

Gains ~ 5% of body mass over 24hr, loses 17% due to evaporation during same period.

2. Water from succulence

Insects 50 – 90% water content

Seeds 5 – 10%

Brewer's and Sage Sparrows able to survive on metabolic sources and those found in diet.

Reabsorption & minimizes losses – cools exhaled air reclaims from nasal passages

3. Surface Water

Few and far between.