how would ***you*** define behavior?

How to define *behavior*

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Behavioural biologists do not agree on what constitutes behaviour

Daniel A. Levitis*, William Z. Lidicker, Jr, Glenn Freund

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How to define *behavior*

1. 'the total movements made by the intact **animal**' -Tinbergen (1955)
2. an expressed **motor** program -behavioral neuroscience
3. 'interaction between an animal's machinery, its **bones, muscles, nervous system**, etc. and its outside world, such as its food, enemies and social practice' -Hall & Halliday (1998)
4. undefined: we "know" it when we see it -Alcock (2005)

Glossary

Action potential The neural signal; a self-regenerating change in membrane electrical charge that travels the length of a nerve cell.

Adaptation A characteristic that confers higher inclusive fitness to individuals than any other existing alternative exhibited by other individuals within the population; a trait that has spread or is spreading or is being maintained in a population as a result of natural selection or indirect selection.

Adaptationist A behavioral biologist who develops and tests hypotheses on the possible adaptive value of a particular trait. Persons using an **adaptationist approach** test whether a given trait enables individuals to propagate their special genes more effectively than if they were to behave in some other manner.

Adaptive value The contribution that a trait or gene makes to inclusive fitness.

Allele A form of a gene; different alleles typically code for distinctive variants of the same enzyme.

Altruism Helpful behavior that raises the recipient's direct fitness while lowering the donor's direct fitness.

Arbitrary culture theory The view that human behavior is the arbitrary product of whatever cultural traditions people are exposed to within their society; thus, our actions are not expected to be explicable in evolutionary terms.

Artificial selection *See* Selection.

Associated reproductive pattern A seasonal change in reproductive behavior that is tightly correlated with changes in the gonads and hormones in contrast to a **disassociated reproductive pattern** in which the onset of reproductive behavior is apparently not triggered by a sharp change in circulating hormones.

Biological clock An internal physiological mechanism that enables organisms to time any of a wide assortment of biological processes and activities.

Brood parasite An animal that exploits the parental care of individuals other than its parents.

By-product hypothesis An explanation for a maladaptive or nonadaptive attribute that is said to occur as a by-product of a proximate mechanism that has some other adaptive consequence for individuals.

Causal question In the scientific method, a question about the cause of a natural phenomenon.

Central pattern generator A group of cells in the central nervous system that produces a particular pattern of signals necessary for a functional behavioral response.

Chase-away selection *See* Selection.

Circadian rhythm A roughly 24-hour cycle of behavior that expresses itself independent of environmental changes.

Circannual rhythm An annual cycle of behavior that expresses itself independent of environmental changes.

Coefficient of relatedness The probability that an allele present in one individual will be present in a close relative; the proportion of the total genotype of one individual present in the other, as a result of shared ancestry.

Command center A neural cluster or an integrated set of clusters that has primary responsibility for the control of a particular behavioral activity.

Communication The cooperative transfer of information from a signaler to a receiver.

Comparative method A procedure for testing evolutionary hypotheses based on disciplined comparisons among species of known evolutionary relationships.

Concession theory *See* Transactional theory.

Conditional strategy *See* Strategy.

Convergent evolution The independent acquisition over time through natural selection of similar characteristics in two or more unrelated species.

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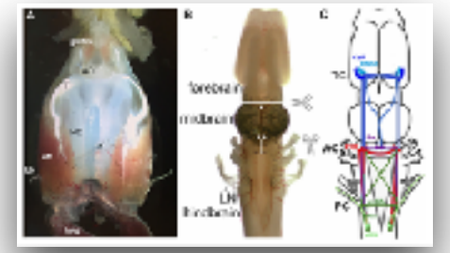
→ Do plant movements constitute “behavior”?

→Do ‘unintact’ animal movements constitute “behavior”?



“larynx in a dish”

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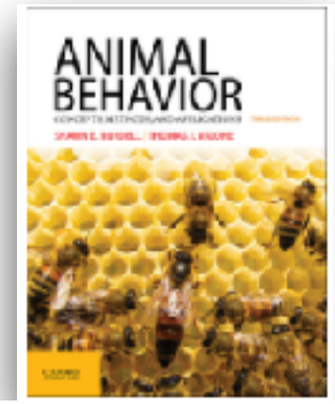
→ Is *growth* 'behavior'?

Our working definition this semester

Behavior **is any internally coordinated, externally visible pattern of activity that responds to changing external or internal conditions.**



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- internally coordinated: internal information processing
  - sensory processing, endocrine signaling
  - ultimately: neurally actualized (motor event=muscle contraction)
  - movement of a lion's mane in the wind ≠ behavior

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  - *questing in ticks = behavior*
  - *the thoughts in your neighbor's mind ≠ behavior*

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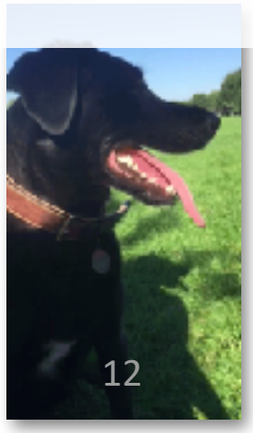
- Responsive to changing conditions
  - external: bird courtship vocalizations commence w/ long days
  - internal: panting as evaporative cooling (no sweat glands)

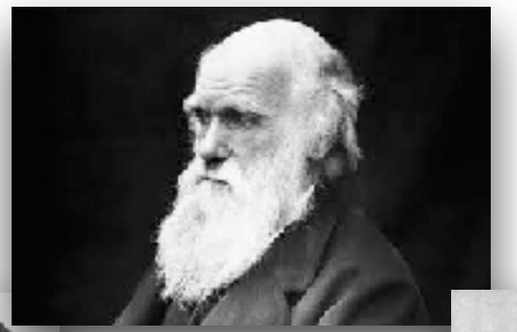


Ethology: roots of modern behavioral biology

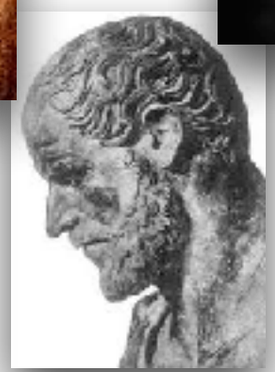
Ethologists

Niko Tinbergen
The study of instinct

Ethology: roots of modern behavioral biology



Darwin
Origins



Aristotle*:*
De partibus animalium

von Uexkuell
Umwelt

Ethologists

Reflexologists

Vitalists

Behaviorists

Niko Tinbergen
The study of instinct

Pre-ethology

Early art (Paleolithic, 40,000+ years ago) provide evidence that early *Homo sapiens* carefully observed the behavior of animals

- gregarious species in herds
- non-gregarious species in isolation
- animal migration
- certain predators hunting in packs

Pre-ethology

"Ought we, for instance, to begin by discussing each separate species man, lion, ox, and the like – taking each kind in hand independently of the rest, or ought we rather to **deal first with the attributes which they have in common** in virtue of some common element of their nature, and proceed from this as a basis for the consideration of them separately?"

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(in Harvey and Pagel, 1991, p. 35)

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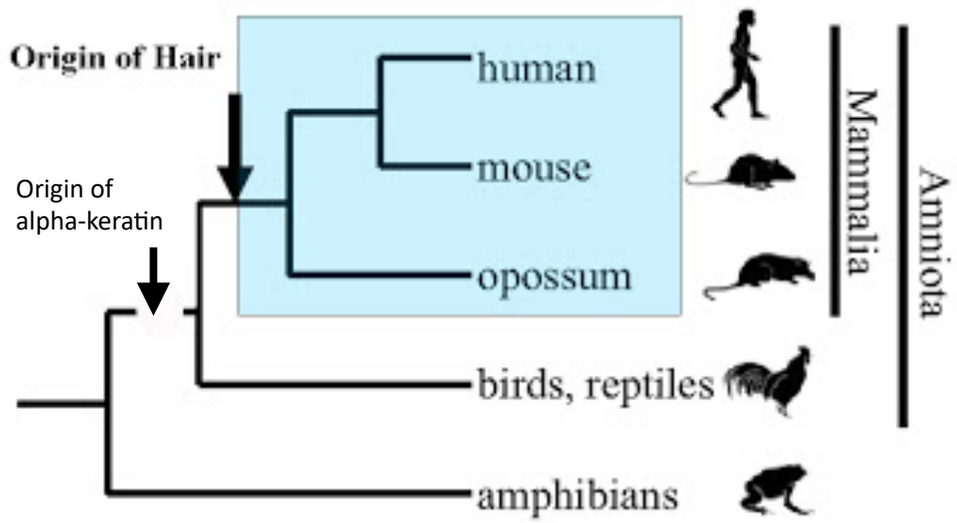
- birth of ***comparative*** thinking
- all mammals have hair, no non-mammals have hair (*synapomorphy*)



Modified From: Sasaki T. et.al. PNAS 2008;105:4220-4225

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- the ***pattern*** and ***process*** of evolution

order in nature
(e.g. some animals have hair)

drivers generating that order
(e.g. natural selection for thermoregulation)

Pre-ethology

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order in nature

e.g. some frogs evolve visual gestures for agonistic interatactions instead of vocalizations

A foot flagging Micrixalus frog displaying in a fast flowing stream found in the Western Ghats of India

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- the ***pattern*** and ***process*** of evolution

order in nature

e.g. some frogs evolve visual gestures for *agonistic* interactions instead of vocalizations

drivers generating that order

e.g. vocalizations are selected against because its too loud to hear them

A foot flagging Micrixalus frog displaying in a fast flowing stream found in the Western Ghats of India

- the ***pattern*** and ***process*** of evolution

order in nature

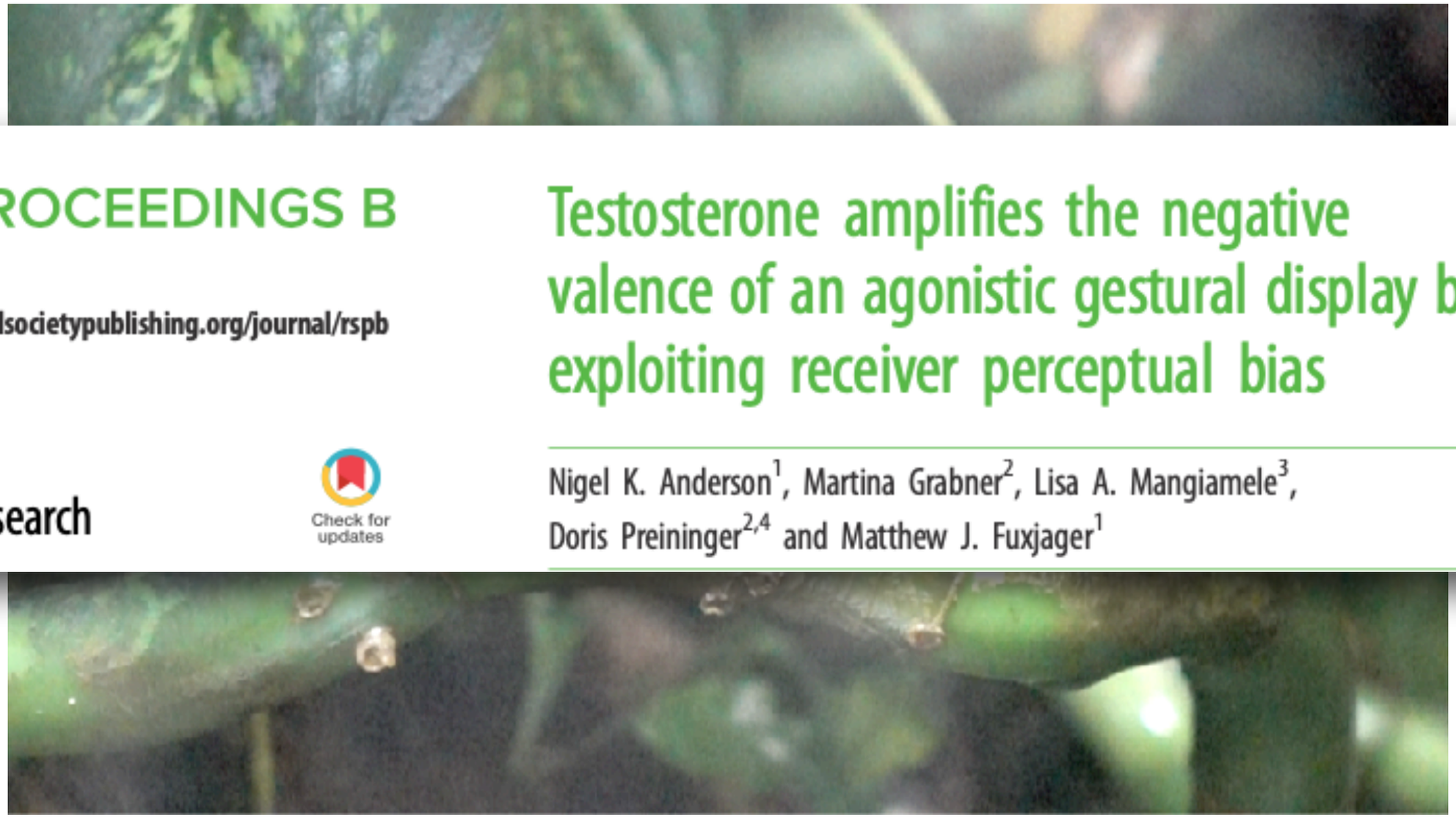
e.g. foot flagging frogs use a **perpendicular axis of movement**?

drivers generating that order

- the ***pattern*** and ***process*** of evolution

order in nature
e.g. foot flagging frogs use a **perpendicular axis of movement**?

drivers generating that order
e.g. preexisting sensory bias for foraging (worm/anti-worm display)



PROCEEDINGS B

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Research

Testosterone amplifies the negative valence of an agonistic gestural display by exploiting receiver perceptual bias

Nigel K. Anderson[1], Martina Grabner[2], Lisa A. Mangiamele[3], Doris Preininger[2,4] and Matthew J. Fuxjager[1]

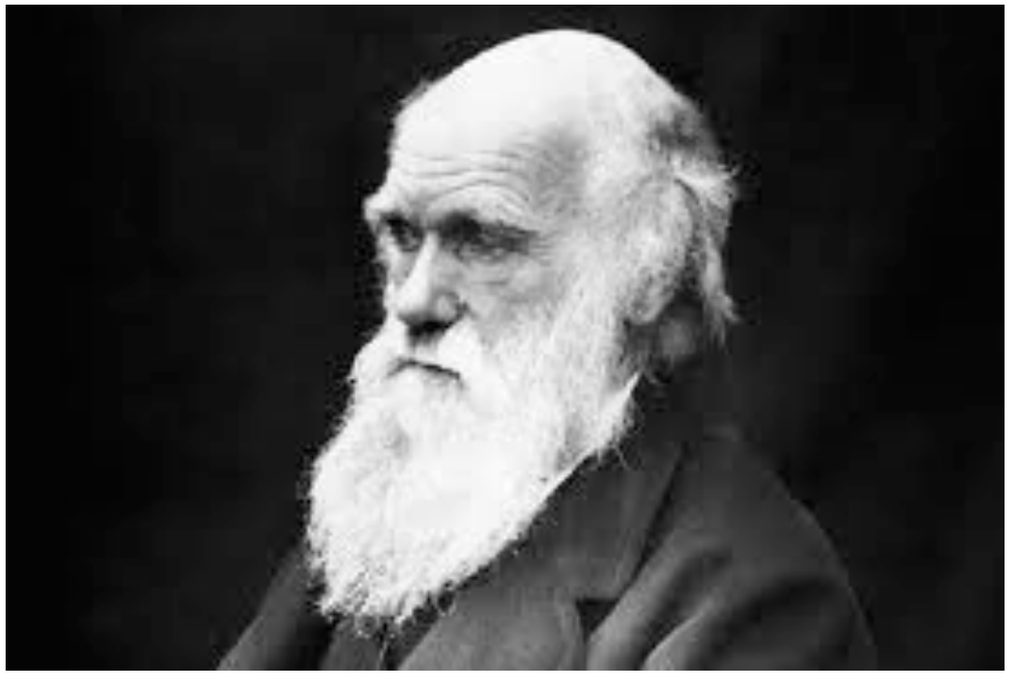
- the ***pattern*** and ***process*** of evolution

order in nature
e.g. foot flagging frogs use a **perpendicular axis of movement**?

drivers generating that order
e.g. preexisting sensory bias for foraging (worm/anti-worm display)

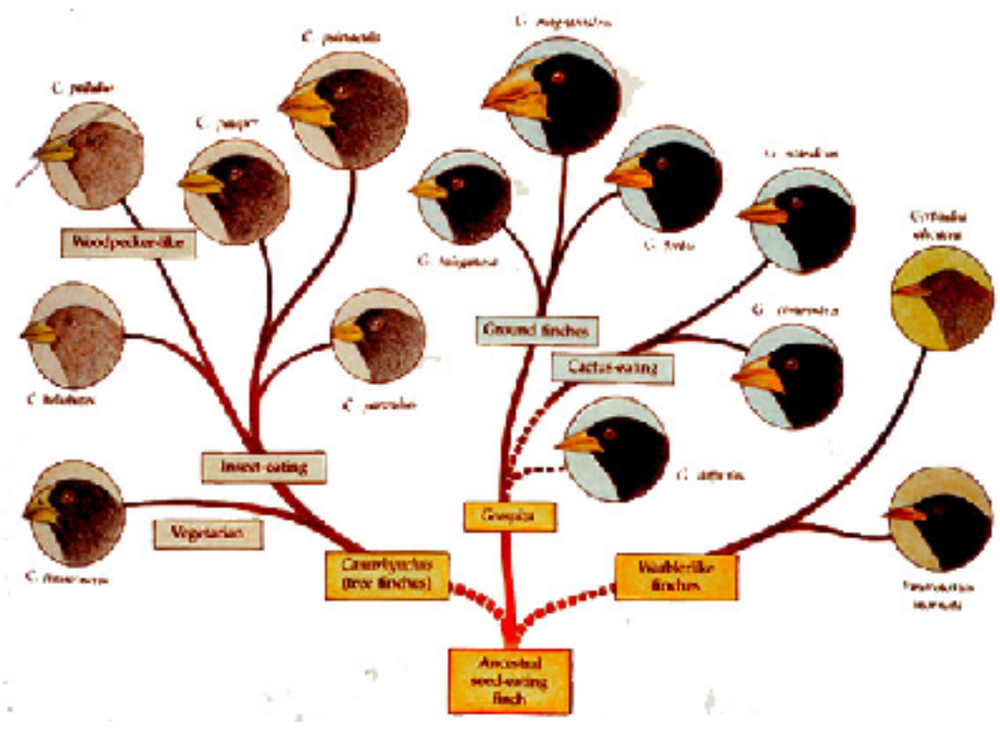
Selection had to act on mechanisms that give rise to this behavior: **androgens**

Pre-ethology



Father of
comparative biology

Galapagos Finches

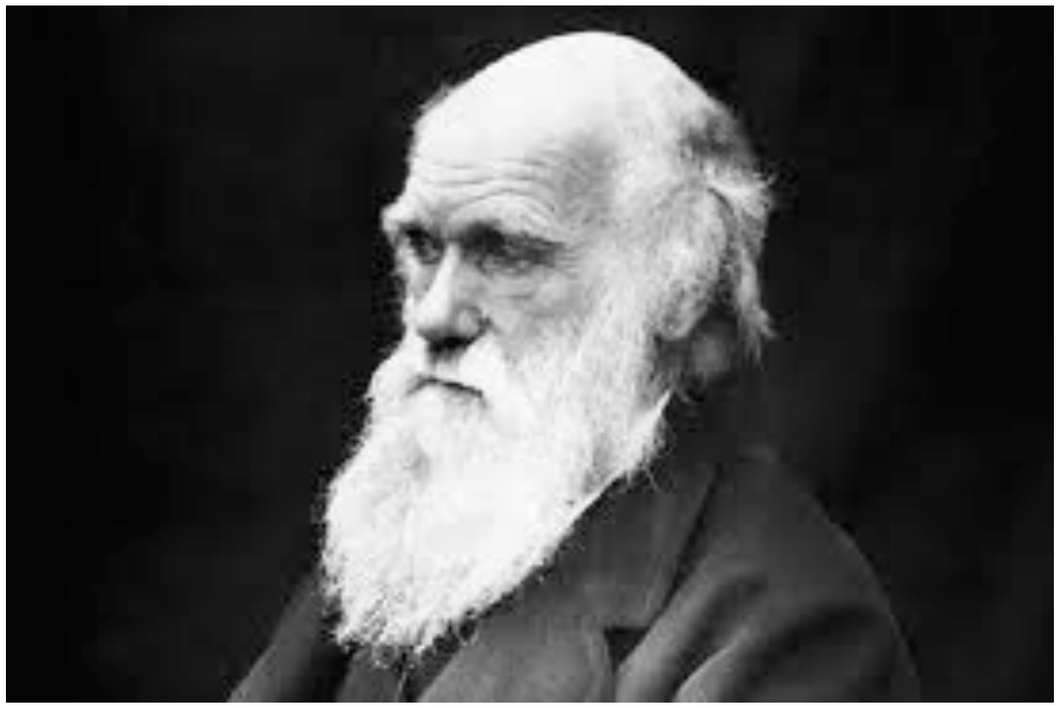


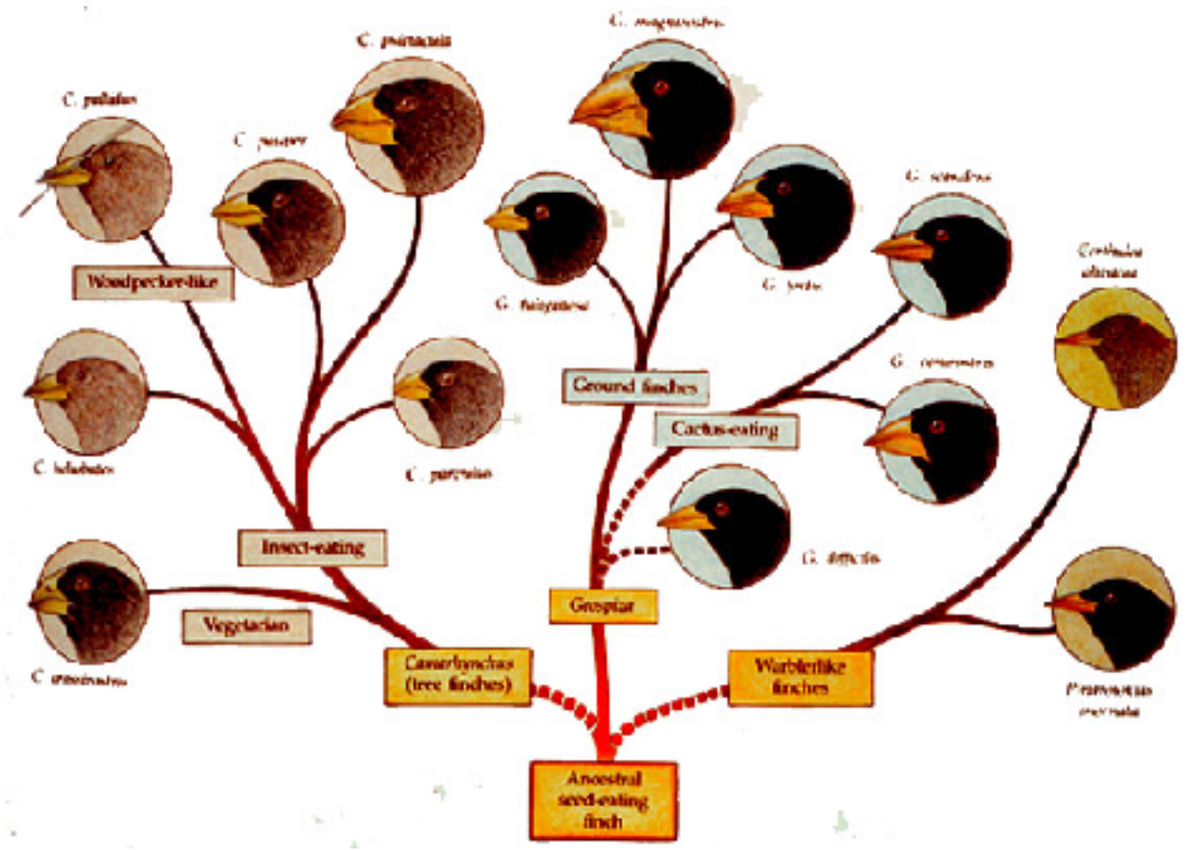
Birds of Paradise

Natural Selection

Sexual Selection

Pre-ethology

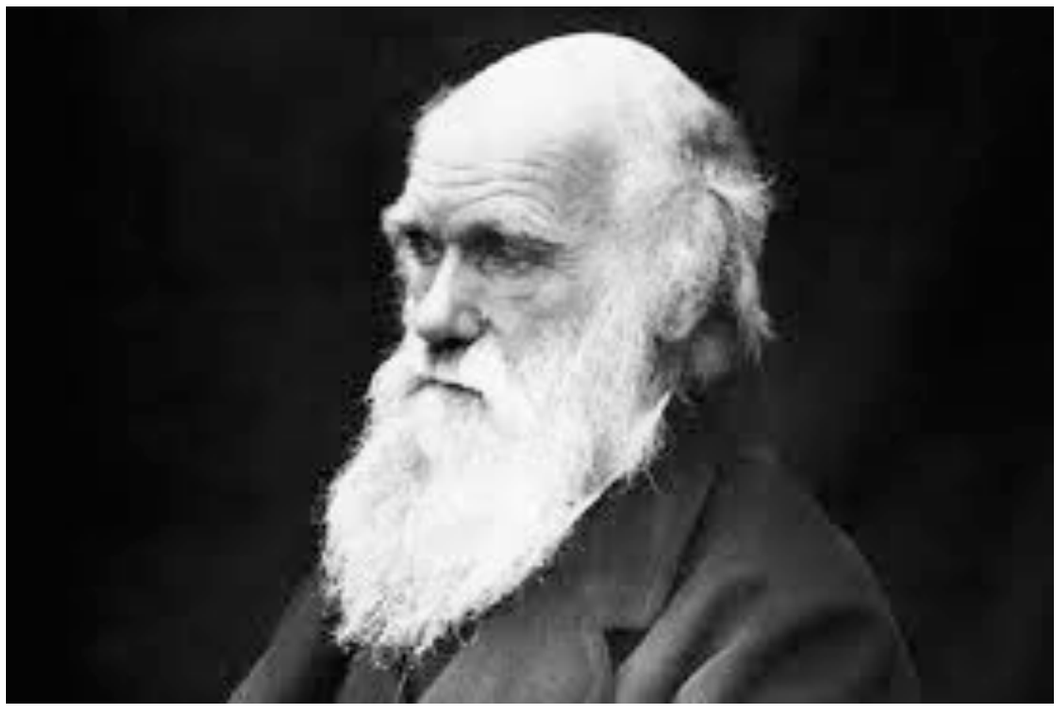




Natural Selection

non-random process by which certain biological traits become more/less common in a population as a function of differential survival and reproductive success of individuals bearing those traits. Over evolutionary time this generates phenotypes **well-adapted to their environments by disfavoring poorly suited phenotypes**. Therefore, *populations* evolve.

Pre-ethology

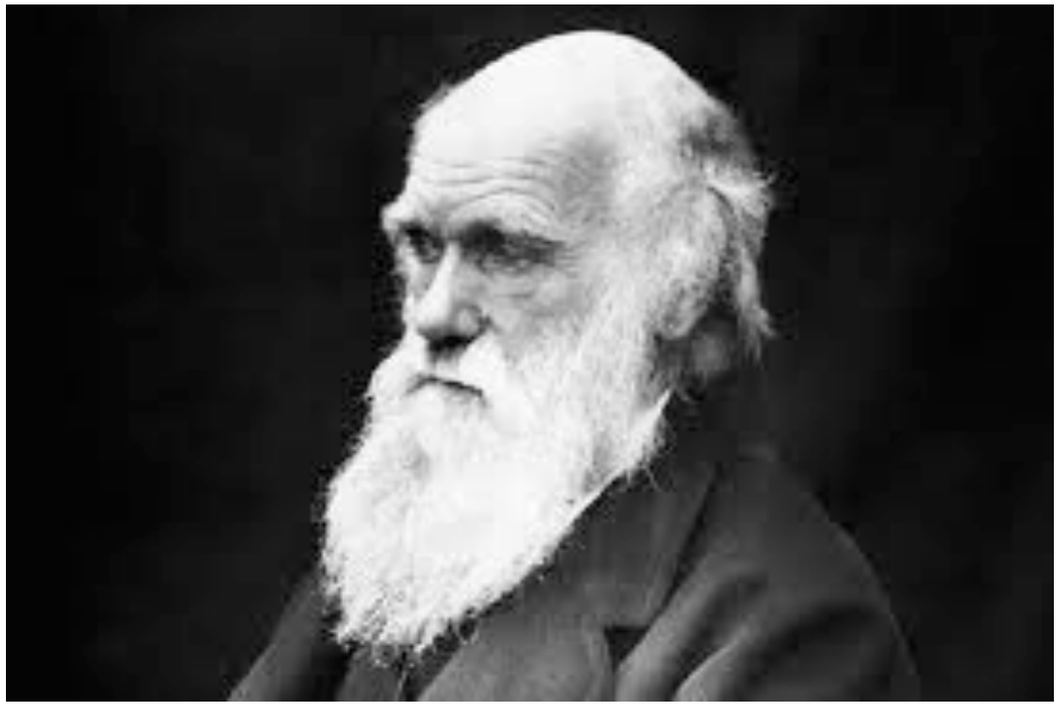


Sexual Selection

variance in the number of mates due to traits. Often favors certain secondary sexual characters that can be maladaptive for survival.

1. Intrasex competition (principally male-male competition)
2. Intersex choice (principally female choice)

Pre-ethology



An aesthetic sense

grounded in sensory biology, psychophysics,
and ecology that **is shared across animal species.**

Such conserved aesthetics appear to be widespread and predictable based on sensory biology.

frog visual system is
frog visual system is
frog visual system

Pre-ethology

Umwelt

• interested in how organisms **subjectively** perceive **their** environment (i.e. *not* anthropomorphizing)

• subjective sensory "inner worlds" (**Umwelt**)

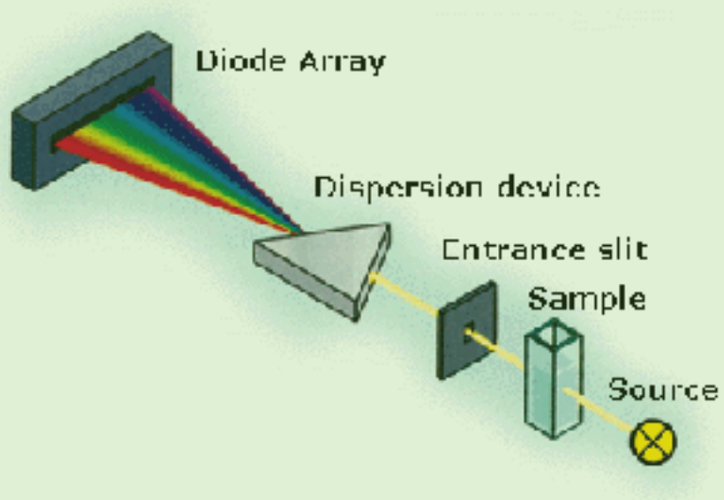
•e.g. what insect eye detect

Jakob von Uexküll (1903)

Merkwelt

• Umwelten are distinct from **Merkwelt** which represents an objective reality

• e.g. what a spectrophotometer detects



Pre-ethology

Instincts can be elicited by *external* stimuli (***conspecific*** signals, chemicals)

von Uexküll called triggers of instinctive stereotyped behaviors **sign stimuli** and they elicit **fixed action patterns (FAPs**)

FAPs: *invariant* within a species, once started these behavioral sequences run to *completion*

Jakob von Uexküll (1903)

PHOTO: ISTOCKPHOTO

tick – the importance of Umwelt in understanding how a tick gets a blood meal

Pre-ethology

"The whole rich world around the tick shrinks into a scanty framework consisting … of three receptor cues – her *Umwelt*."

Jakob von Uexküll

Jakob von Uexküll (1903)

The "inner world" of the tick reduces down to 3 **sign stimuli**:

1. **Odor** of butyric acid (emanates from the sebaceous follicles of mammals)
2. **Temperature** of 37C (blood temperature of all mammals)
3. **Texture** of hair (mammals)

Pre-ethology

• **Vitalists** believed in the instincts as mystical, wise and inexplicable forces inherent in the organism, governing the behavior of the individual.

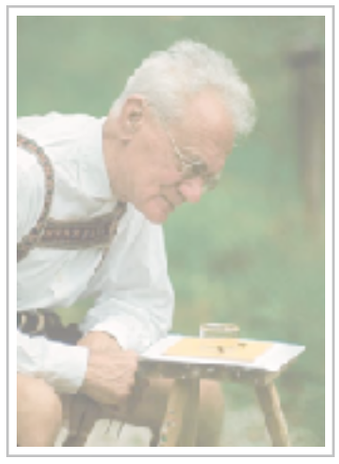
• **Reflexologists** interpreted behavior in an one-sided mechanical way (i.e. all behaviors are essentially FAPs)

• **Behaviorists** were largely preoccupied with *learning* as an explanation for *all* behavioral variation.

Ethology: roots of modern behavioral biology

- <u>Ethologists</u> (EU)

Konrad Lorenz

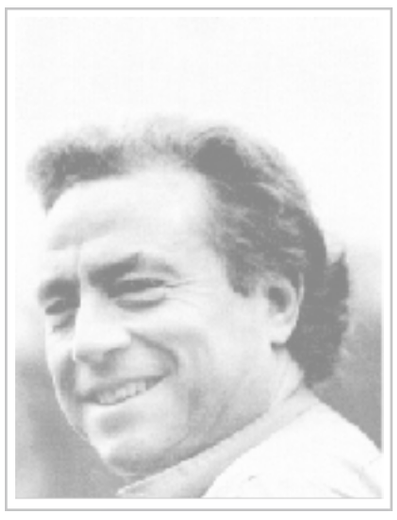


Karl von Frisch

Niko Tinbergen

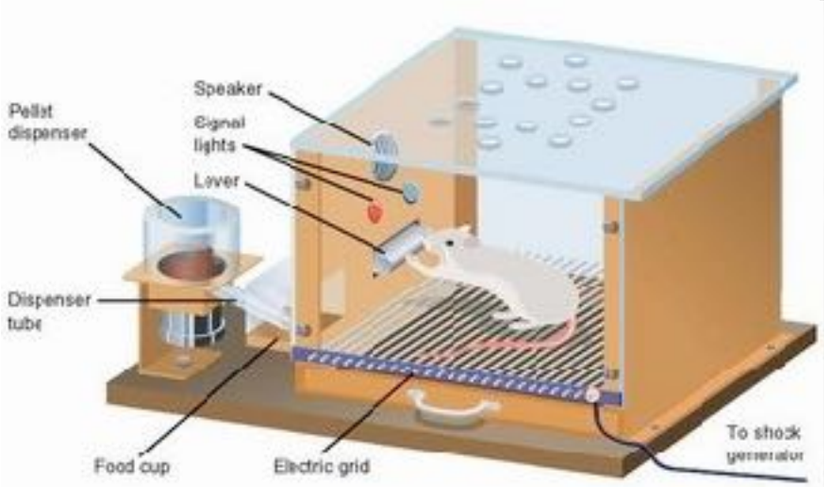
<u>Contemporaries</u> (USA)

B.F. Skinner
Behaviorism



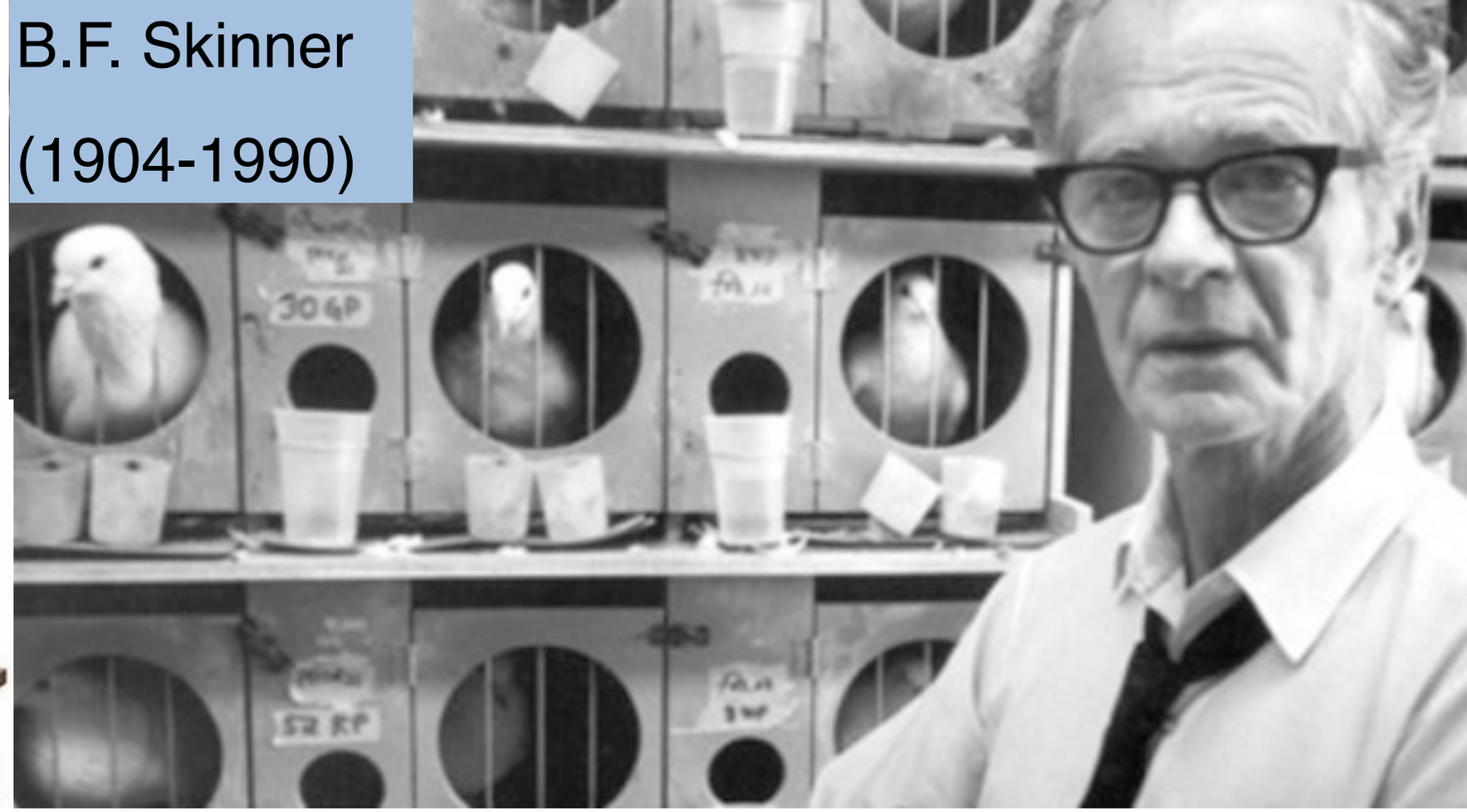
Daniel S. Lehrman
Comparative Psychology

Behaviorism (radical)



B.F. Skinner

(1904-1990)



Behaviorists focused on experimental studies of mechanistic basis of behavior in the laboratory (rats, pigeons)

Learning: classical and operant conditioning.

→ Behavioral tendencies are a consequence of a history of **reinforcing** experiences

- *associations* between experience and outcome (reward, punishment) can be made and are *equally* easy to learn across species (*equivalence of association assumption*).

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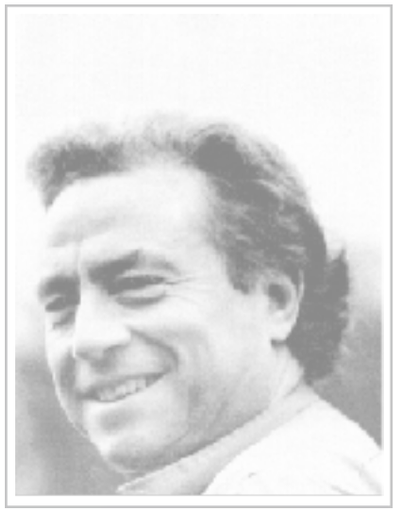


Daniel S. Lehrman
Comparative Psychology

Ethologists: focused on ***natural*** **behaviors** in **natural contexts**

Karl von Frisch

Konrad Lorenz

Niko Tinbergen

sensory biology

- bee dance language
- fish visual systems (brightness vs color)
- bee sun compass (polarized light)

learning

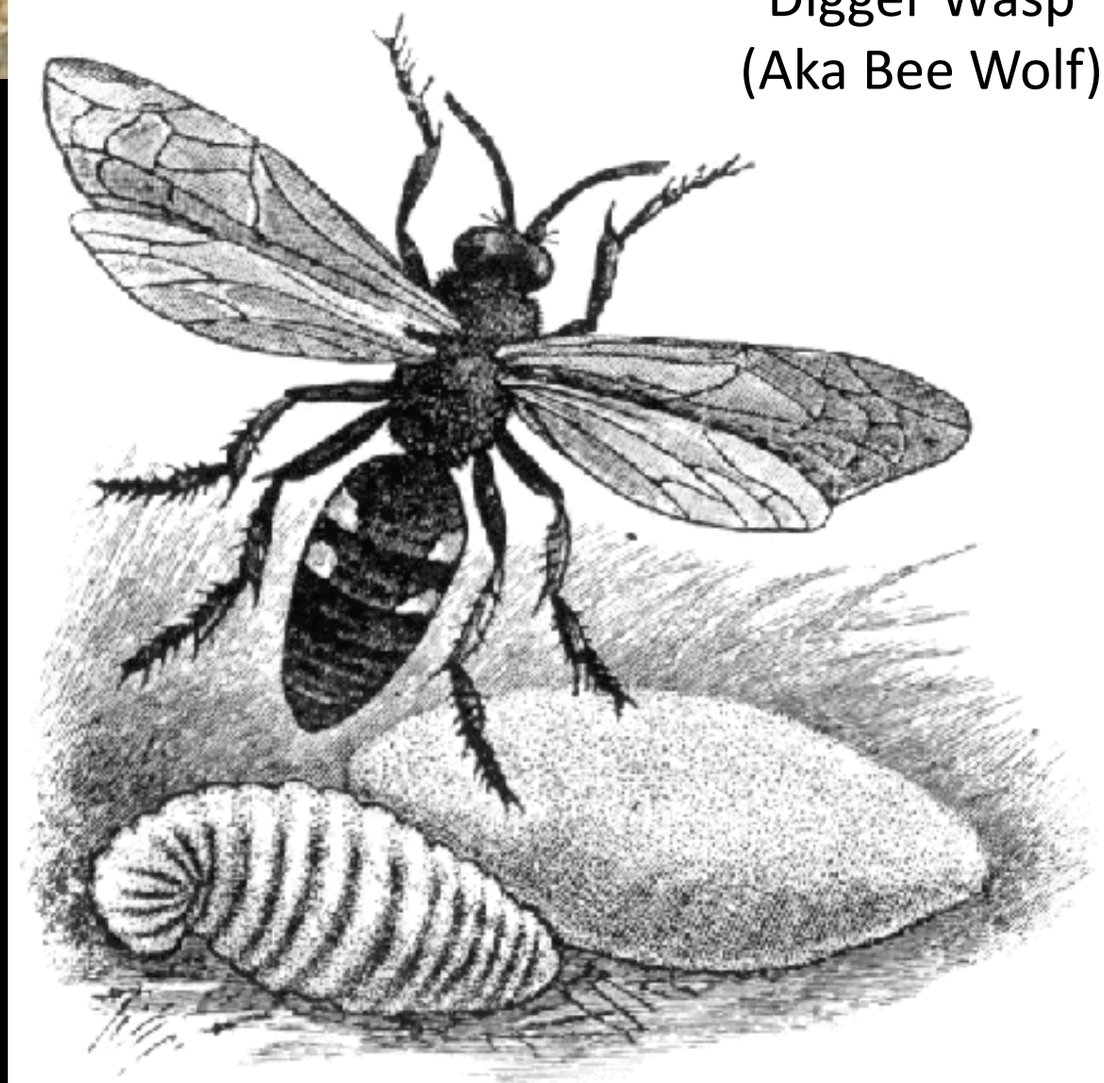
- **imprinting** in ducks & geese
- behavioral development
- aggression

field biology

- *The Study of Instinct*
- emphasis on natural conditions
- mating behavior
- orientation (landmarks in digger wasps)

Niko Tinbergen, Ph.D.

Digger Wasp
(Aka Bee Wolf)

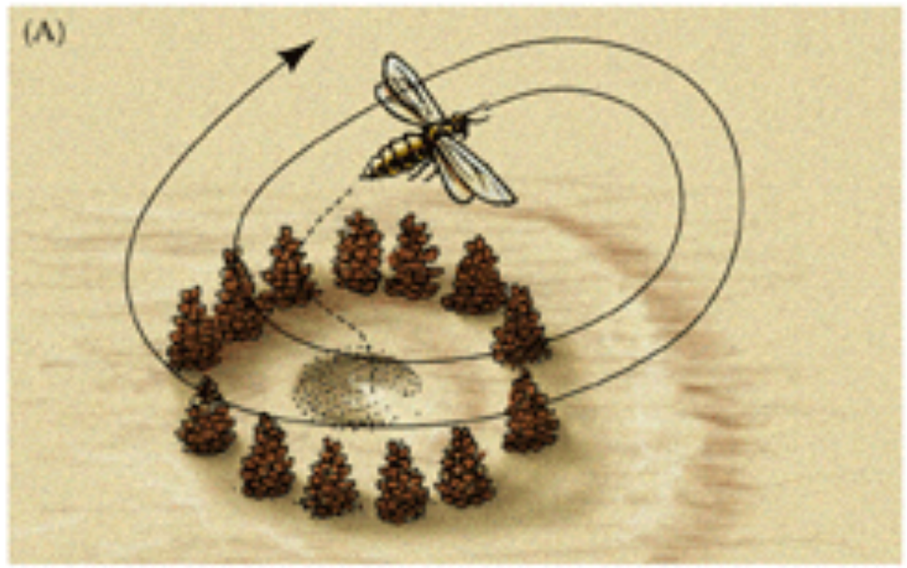


Tinbergen's observations of the digger wasp *(Philanthus triangulum)*

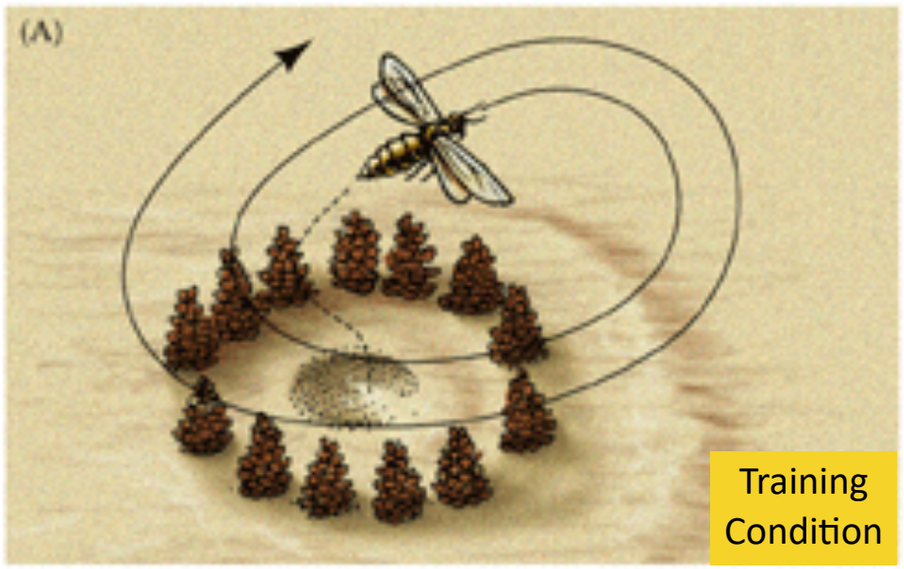
*behavioral biology research begins with **observations** which spur basic **questions***

Tinbergen's observations of the digger wasp *(Philanthus triangulum)*

Observation: females fly in a circle before a foraging trip. Why?



Tinbergen's observations of the digger wasp *(Philanthus triangulum)*



Observation: females fly in a circle before a foraging trip. Why?

• **Hypothesis:** female memorizes visual landmarks to relocate nest after foraging/hunting expedition

• **Method to Test**:

• **Prediction**:

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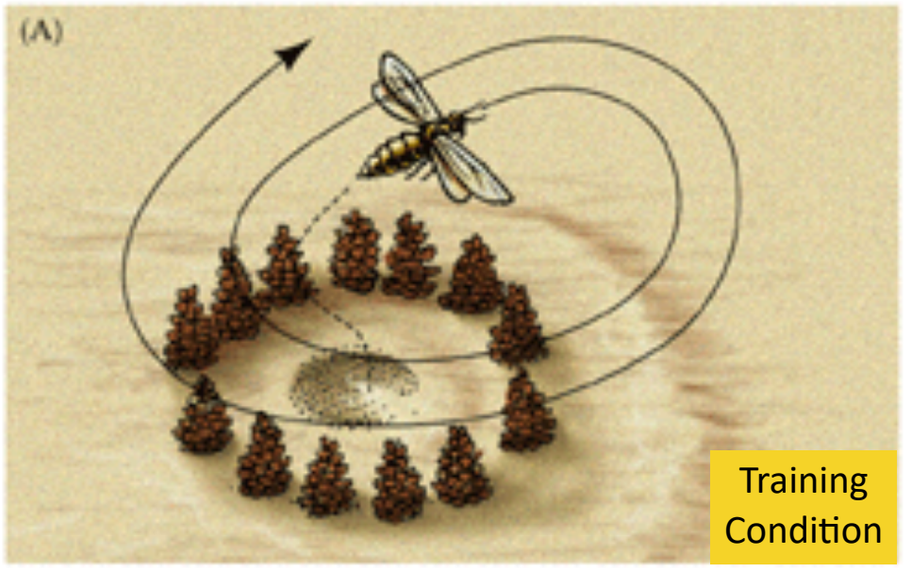
• **Method to Test**: move artificial landmarks when female is away

• **Prediction**: female will return to center of translocated landmarks



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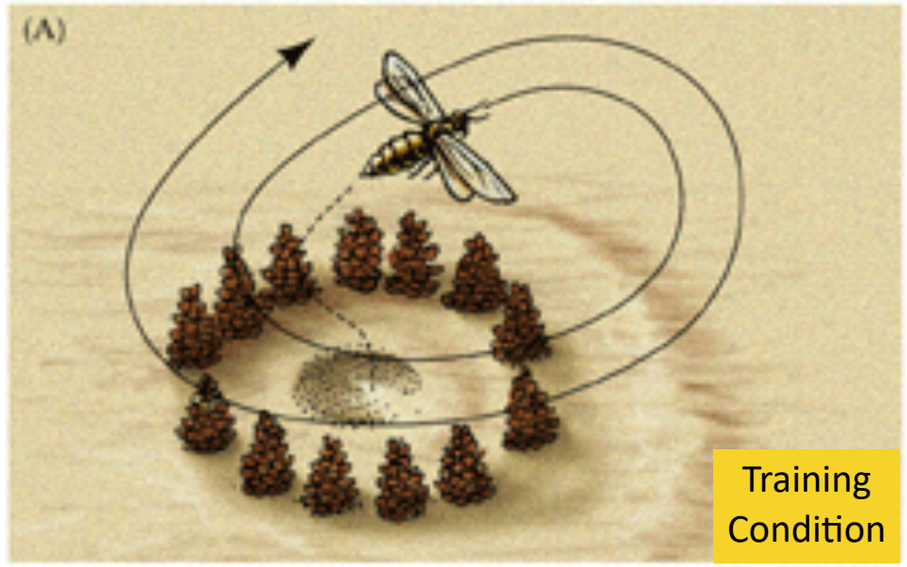
• **Prediction**: female will return to center of translocated landmarks

• **Result**: female orients to translocated landmark

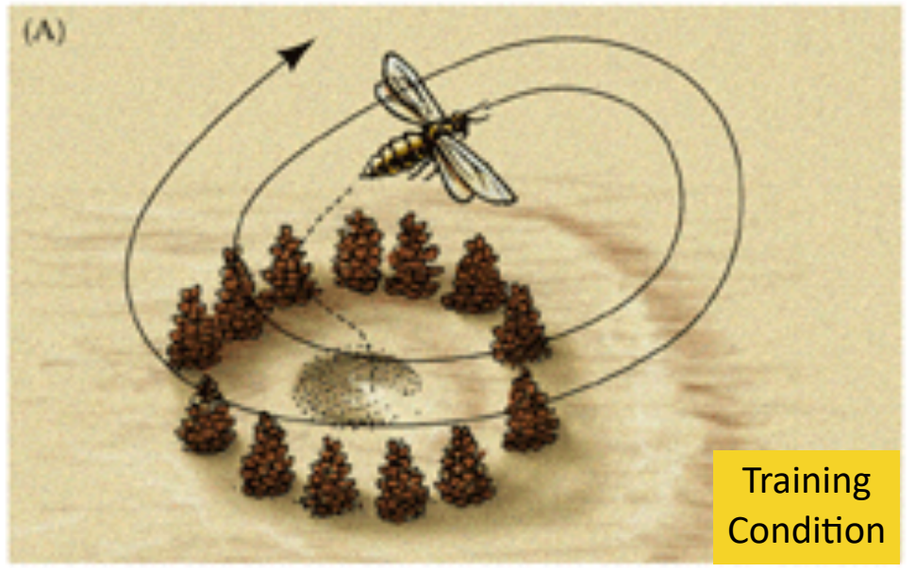


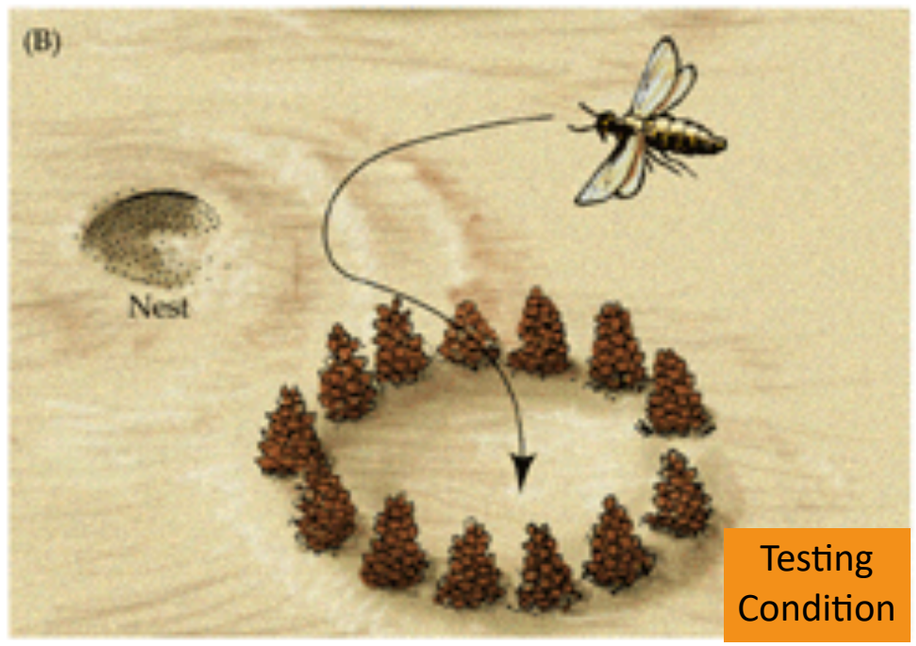
Tinbergen's observations of the digger wasp *(Philanthus triangulum)*

Theoretical importance:

Wasps can **learn this visual task easily** (fast) without conventional reward/punishment.

Does this experiment contradict the **core tenant of behaviorism** that *all associations* are equally easy to learn across species, provided adequate reinforcement regime? (*equivalence of association assumption*)

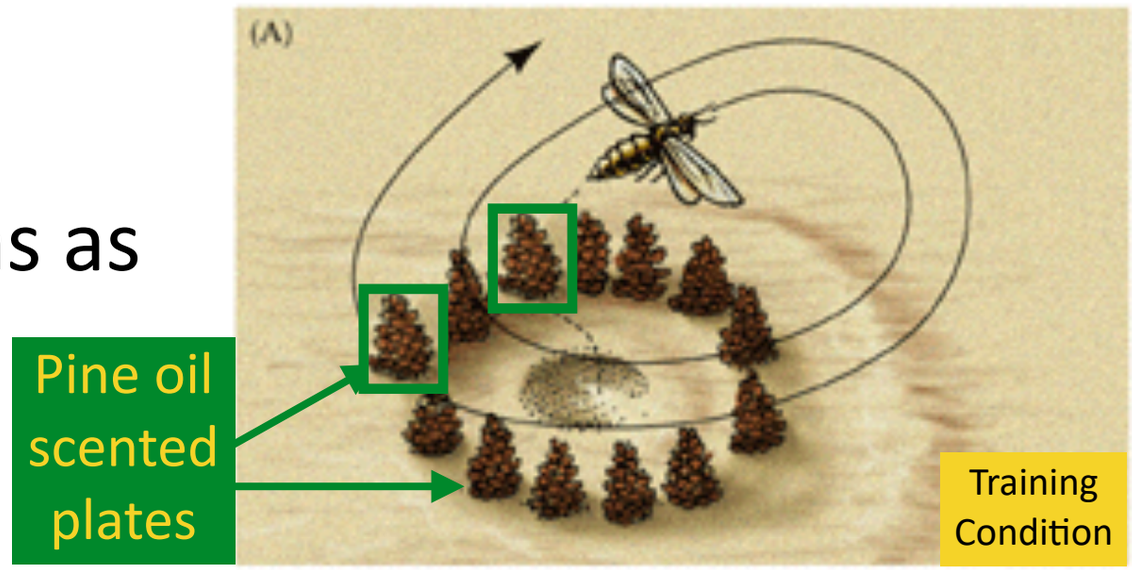




Tinbergen's observations of the digger wasp *(Philanthus triangulum)*

Theoretical importance:

Do wasps learn alternative associations as easily?



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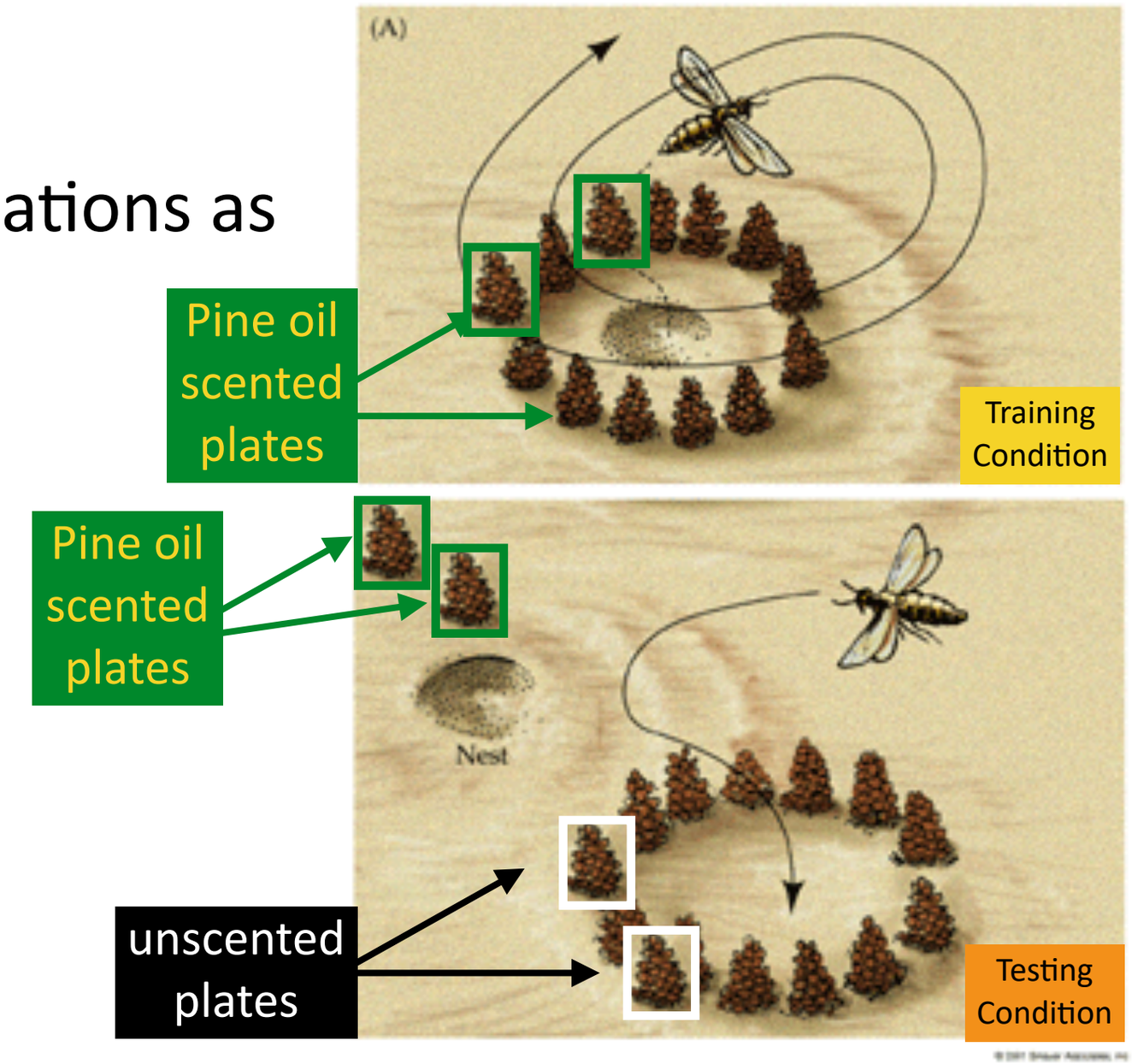


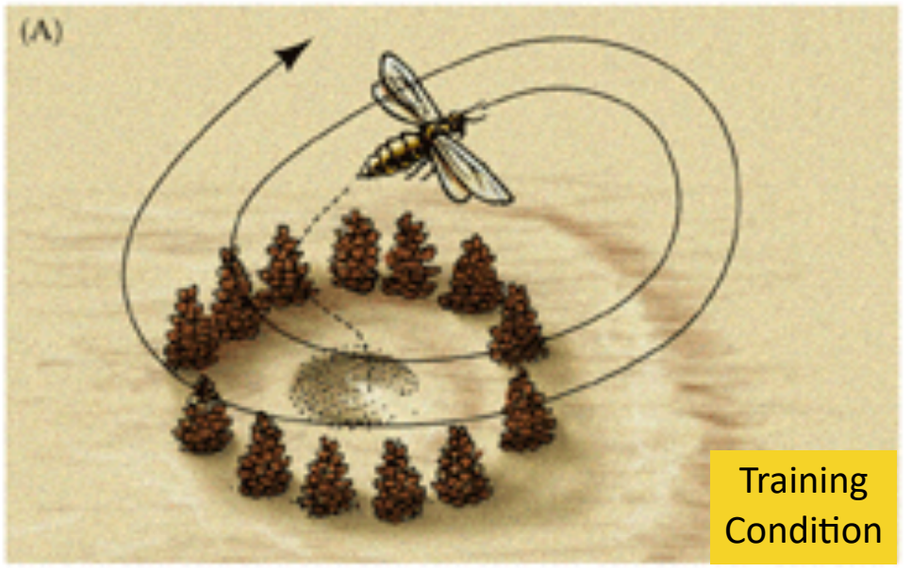
Tinbergen's observations of the digger wasp *(Philanthus triangulum)*

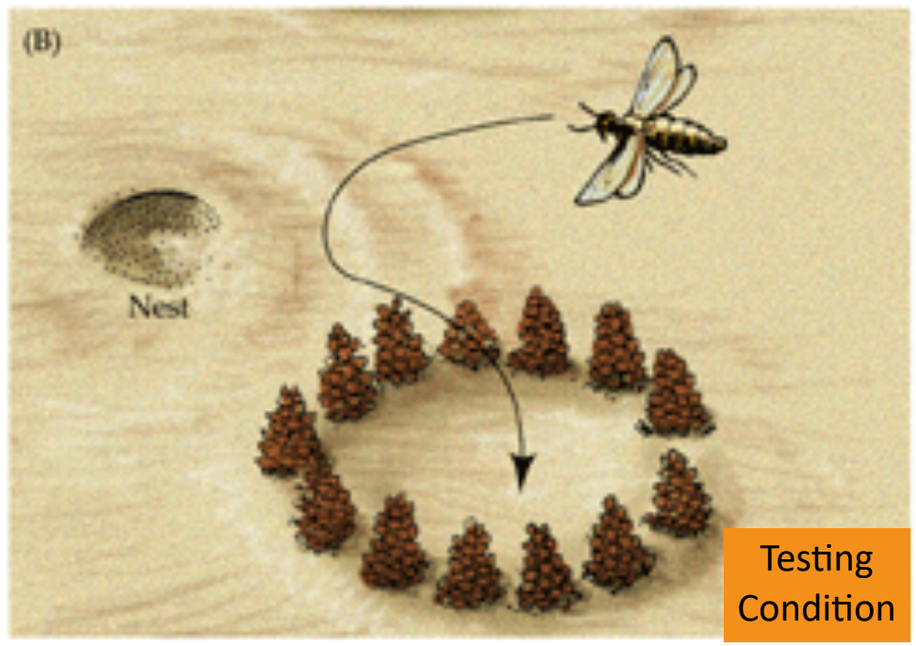
Theoretical importance:

Wasps can **learn the visual task easily** (fast) *compared to other learning tasks (olfactory)*.

Contradicts Behaviorism's equivalence of association assumption

Supported idea that each species has a unique set of typical behaviors (i.e. ***species-specific behavior***):
visual learning > olfactory learning





Concept: species-specific behavior

- No animal is a *tabula rasa* (blank slate)

- Organisms can have "**innate*"** (*inborn, intrinsic, inherent, hard-wired, instinct, built-in, genetically determined**) behaviors and **species-specific biases** (*predispositions, instinct-to-learn*) are key to behavioral evolution

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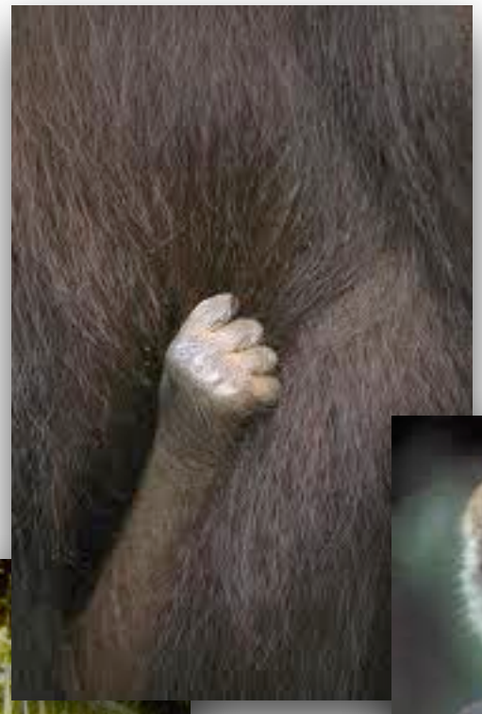
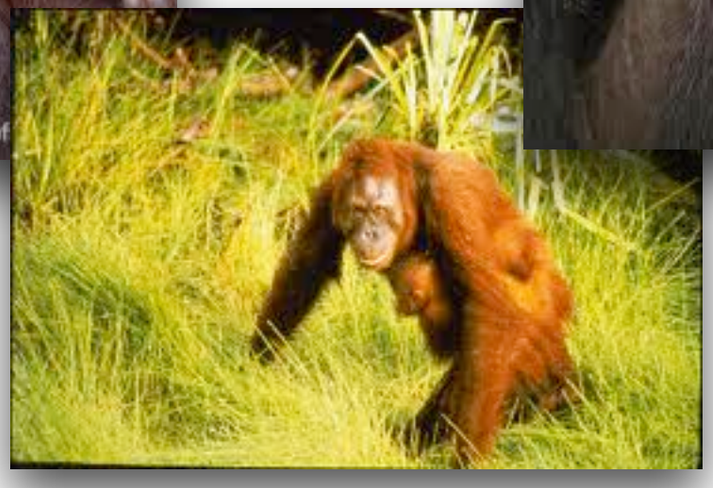
e.g., in humans or other primates?

Concept: species-specific behavior

suckling and grasping

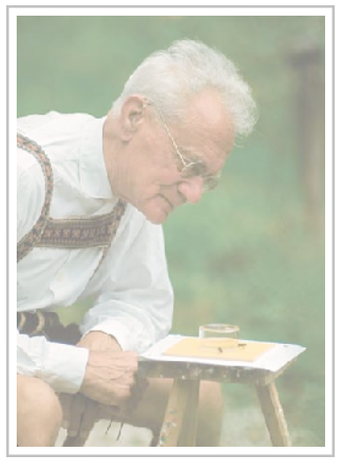




Ethology: roots of modern behavioral biology

- Ethologists (EU)

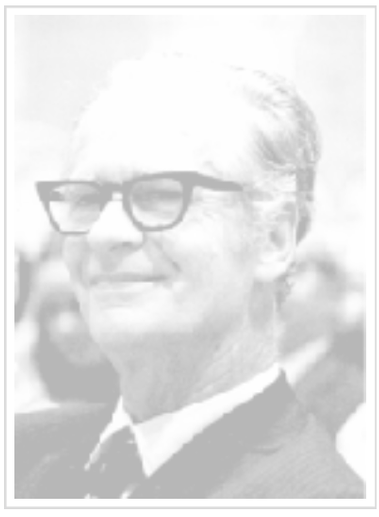
Konrad Lorenz



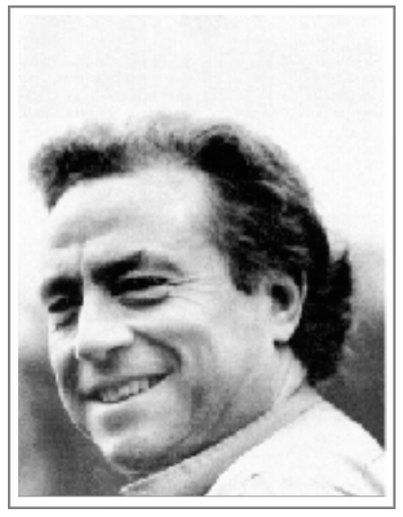
Karl von Frisch

Niko Tinbergen

Contemporaries (USA)



B.F. Skinner
Behaviorism



Daniel S. Lehrman
Comparative Psychology

Comparative Psychology

American school of thought:

Experimental lab studies: hormones, **ontogeny**, role of **experience** (incl. embryonic experience) shaping behavioral phenotypes

Daniel S. Lehrman

Comparative Psychology

American school of thought:

Experimental lab studies: hormones, **ontogeny**, role of **experience** (incl. embryonic experience) shaping behavioral phenotypes

Daniel S. Lehrman

"the statement "It is innate" adds nothing to an understanding of the developmental process involved"

Comparative Psychology

Pecking behavior in chicks

-**Lorenz**: “its innate b/c chicks don’t require experience”

Daniel Lehrman

Comparative Psychology

Pecking behavior in chicks

-**Lorenz**: “its innate b/c chicks don’t require experience”

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Comparative Psychology

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Pecking behavior in chicks

-**Lorenz**: “its innate b/c chicks don’t require experience”

-Kuo & **Lehrman**: No, pecking behavior can be traced back movements that developed in the unhatched chick, thus development of this ‘classically hardwired behavior’ involves practice

species-typical sensory biases:

psychophysically exaggerated stimuli

- **sign stimuli**
- **supernormal stimulus**

sign stimuli and the **supernormal stimulus**

breeding behavior in three-spined sticklebacks:

1. onset of male breeding physiology/behavior
   -> red throat and belly
2. males build nest
3. defend territories
4. attract females
5. fertilize eggs externally

sign stimuli and the **supernormal stimulus**

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sign stimuli and the **supernormal stimulus**

stimulus-response in males: AGGRESS

mirror test

aggressive response

sign stimuli and the **supernormal stimulus**

stimulus-response in males

how to decompose which stimuli are key?

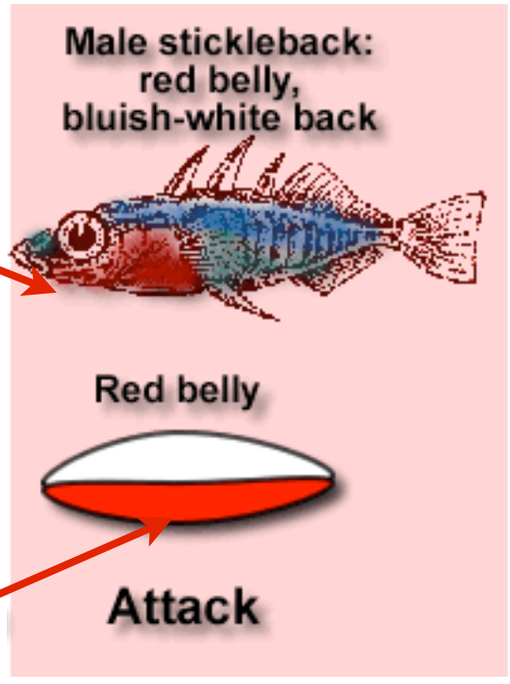
aggressive response

sign stimuli and the **supernormal stimulus**

sign stimuli elicit **FIXED ACTION PATTERN (FAP)** => AGGRESS

red throat/belly
normal (sign) stimulus

supernormal
stimulus



sign stimuli and the **supernormal stimulus**

FAP = AGGRESS

Supernormal stimulus

sign stimuli and **supernormal stimuli** elicit **FIXED ACTION PATTERN (FAP)** => AGGRESS

goes berzerk!

normal (sign) stimulus

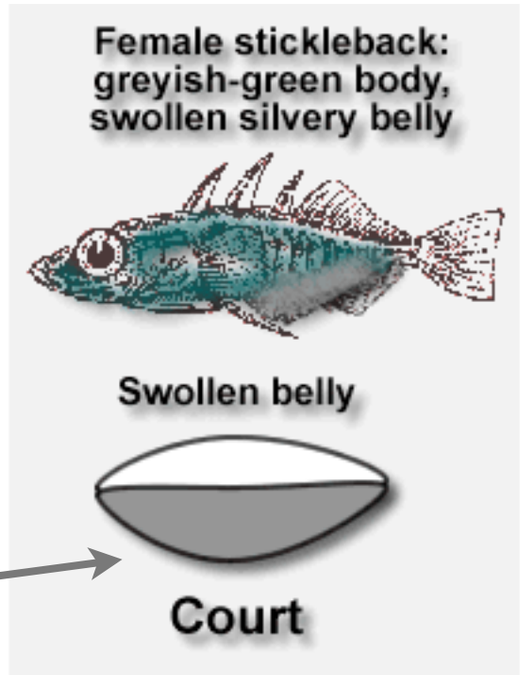
very supernormal stimulus

sign stimuli and the **supernormal stimulus**

FAP => COURT

grey body normal
(sign) stimulus

supernormal
stimulus



principles from early ethology

e.g. **FAPs**

- Replaced by "***behavioral patterns***"

    - Behavior is not as "fixed" as FAPs imply — variation (e.g. duration of components of behavioral sequence) *between* and *within individuals* of a single species (i.e. ***conspecifics***)

- FAPs are not simply "innate" — they can be subtly modified by experience

- Other extrinsic conditions in the environment can *inhibit* the triggering of FAPs

after ethology: balkanization and specialization

Behavioral Ecology

A synthesis between the evolutionary traditions of modern ethology, and the mechanistic studies of comparative psychology Krebs and Davies (1978)

Sociobiology

Ethology applied to the evolution of social behavior. The theory was the target of controversy due to its application to humans and a (false) belief that it supported biological determinism (nature versus nurture)

E. O. Wilson (1975)

Evolutionary Psychology

Applies an (often narrow) Darwinian **adaptationist** approach the to explain human behavior (murder, female choice, alcoholism, yellowing of finger nails)

John Tooby, David Buss

Neuroethology

The neural basis of natural behavior

Mark Konishi, Walter Heiligenberg (1970s)

Behavioral Neuroscience

Uses laboratory animal models (mice, rats, drosophila) to experimentally manipulate (e.g. lesions) neural basis of behavior (e.g. pathologies, disease models)

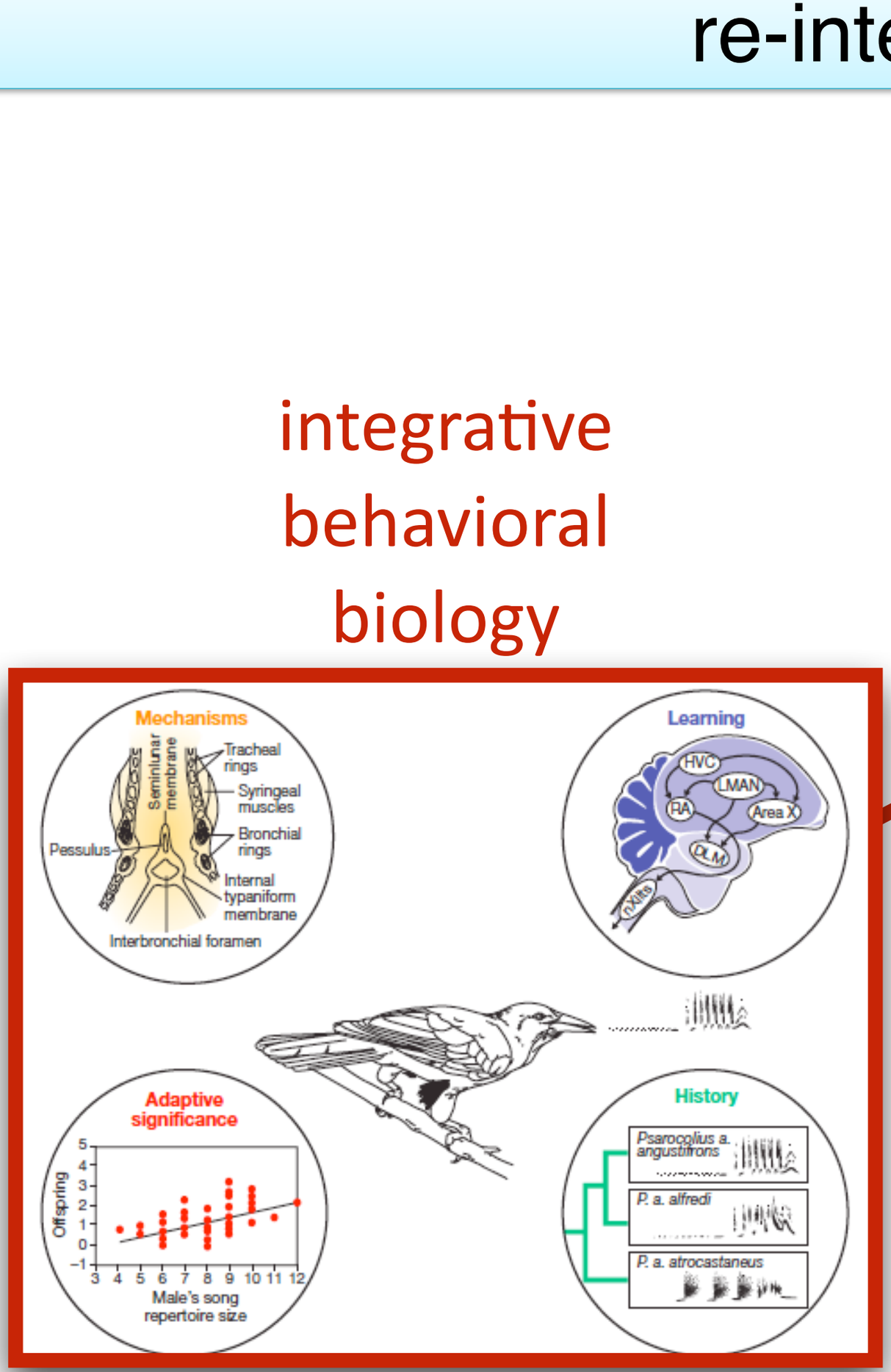
Behavioral Endocrinology

Hormones and Behavior

Daniel Lehrman (1970s)

re-integration

integrative
behavioral
biology

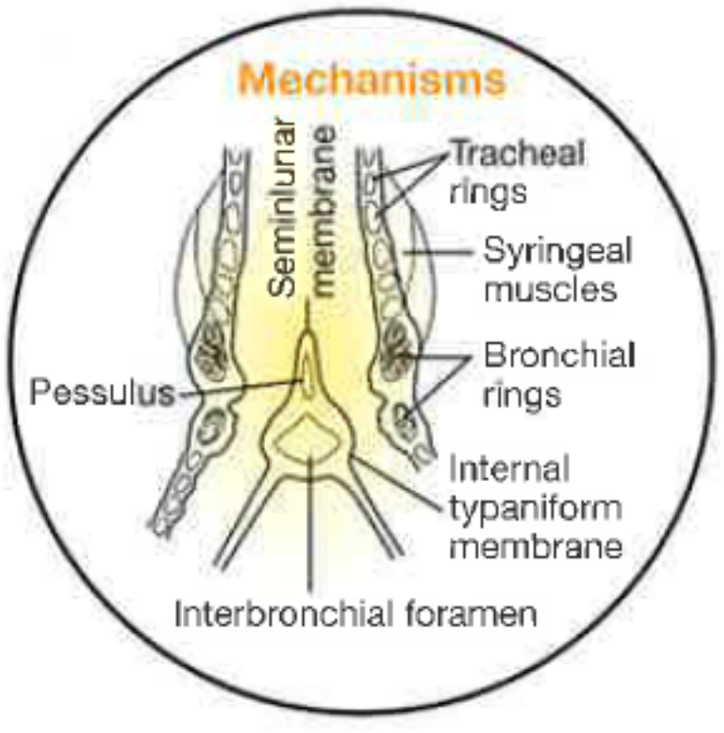


- Behavioral Ecology
- Sociobiology
- Neuroethology
- Evolutionary Psychology
- Behavioral Endocrinology
- Behavioral Neuroscience

birdsong

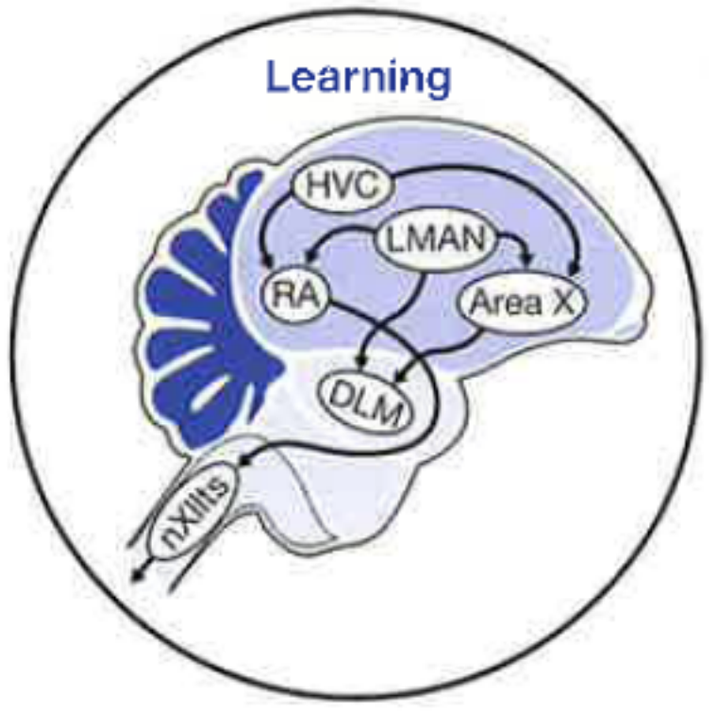
why does a songbird sing?

- this is at least four different but interrelated questions:
  - 1. *how* does he **make** the song?



why does a songbird sing?

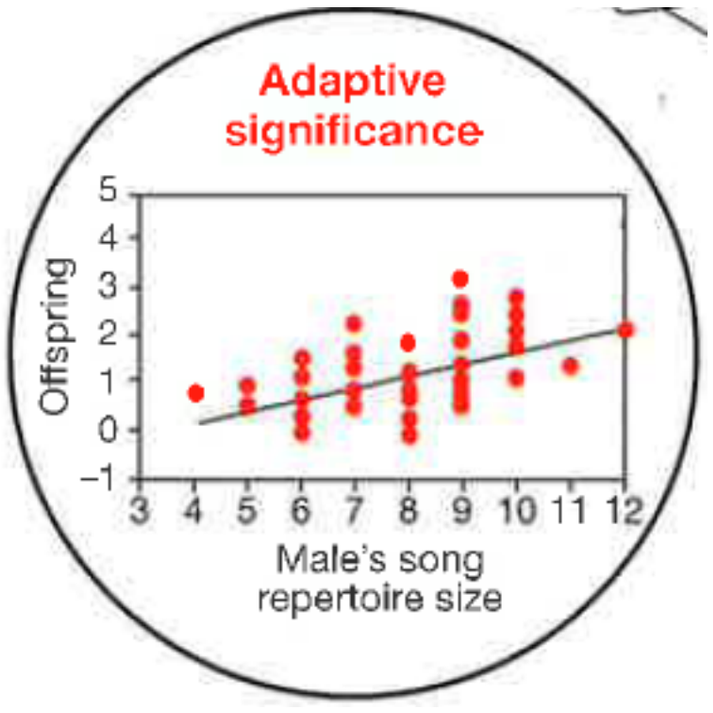
- this is at least four different but interrelated questions:
  - 2. *how* does he **acquire** the song?



why does a songbird sing?

- this is at least four different but interrelated questions:

  – 3. *why* does he sing, i.e. what is current function of song?



why does a songbird sing?

- this is at least four different but interrelated questions:

  – 4. *why* does he sing a **complex** song?

Cedar waxwing (*Bombycilla cedrorum*)

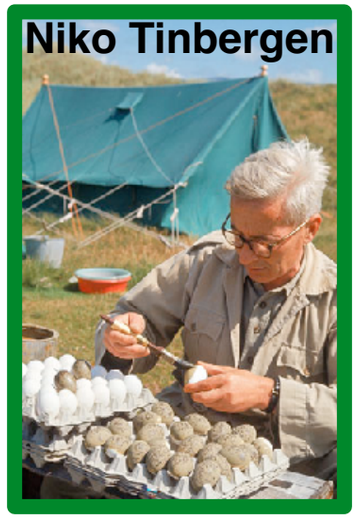
why does a songbird sing?

At least 4 basic answers:

- 1. because it has a complex syrinx
- 2. because it learned the song of an adult
- 3. because selection favors complex song
- 4. because it is a true songbird

Northern Cardinal (*Cardinalis cardinalis*)

Tinbergen's four questions



why does an animal behave the way it does [under natural conditions]?

proximate

how are behavioral traits manifested?

Mechanism of Control
physiology
genetics
neurobiology

Acquisition
innate*
learned*

ultimate

why do behavioral traits evolve?

Current Utility
current adaptive value

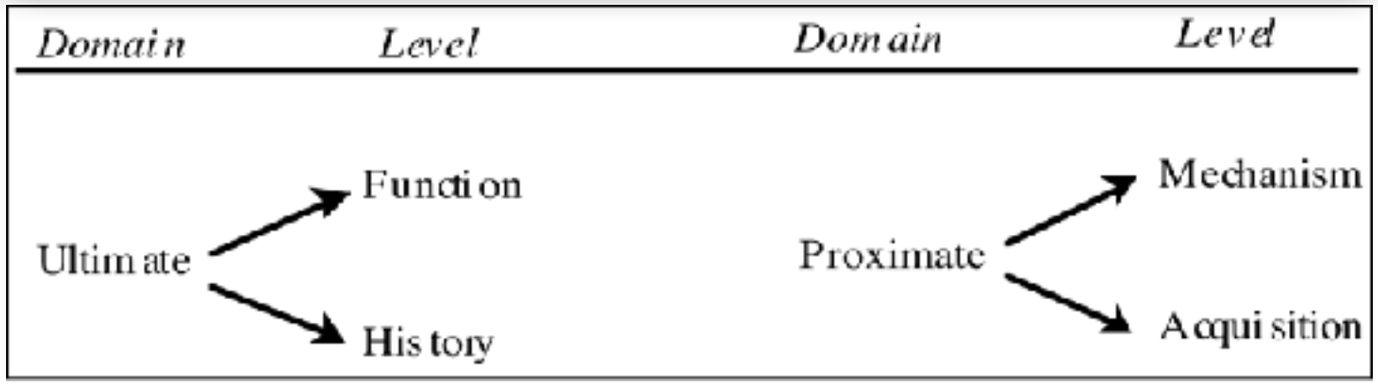
History
evolutionary origins

best understanding emerges from the synergisms of these levels

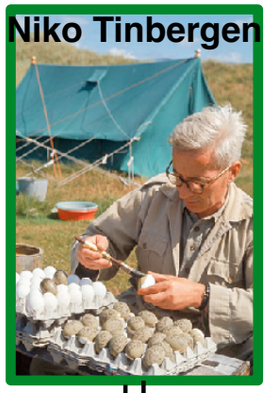
A biologist in Papau New Guinea observes a flash of blue movement in the tree nearby—it's a superb bird of paradise (a sexually reproducing bird) performing an elaborate song and dance using its bright feathers (pictured at right). The biologist immediately suspects these color and behavior traits are sexually selected.

Question: She decides to test the hypothesis that birds with *brighter* feathers attract more mates.

Which *domain* and *level* would this hypothesis test (figure to the right).



Tinbergen's four questions



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innate*
learned*

ultimate
why do behavioral traits evolve?

Function
current adaptive value

History
evolutionary origins

best understanding emerges from the synergisms of these levels

What should you be familiar with after today's lecture?

- Definition of behavior (and its components)
- Pre-ethology
  - What does "comparative" really mean in biology
  - Darwins two big ("dangerous") ideas
  - Umwelt concept
- Ethologists + Contemporaries
  - Reinforcement learning (equivalence of association hypo)
  - Instinct/innateness concept and its limitations
  - Species specific behavior
  - Sign stimuli, Supernormal Stimuli, 'Fixed' Action Patterns (FAPs)
  - Integrative behavioral biology
  - Tinbergen's 4 Questions Framework

Behavior is any internally coordinated, externally visible pattern of activity that responds to changing external or internal conditions.

why does an animal behave the way it does?

proximate
how are behavioral traits manifested

ultimate
why behavioral traits evolve

Mechanism
neuroendocrine

Acquisition
innate*
learned*
experience-dependency

Function
current adaptive value

History
evolutionary origins

***immediate causation**: what are the **neuroendocrine mechanisms** that constitute responses to internal and external stimuli?*

***immediate causation**: what mechanisms constitute <u>responses to internal and external stimuli?</u>*