Animal Behaviour and Chronobiology

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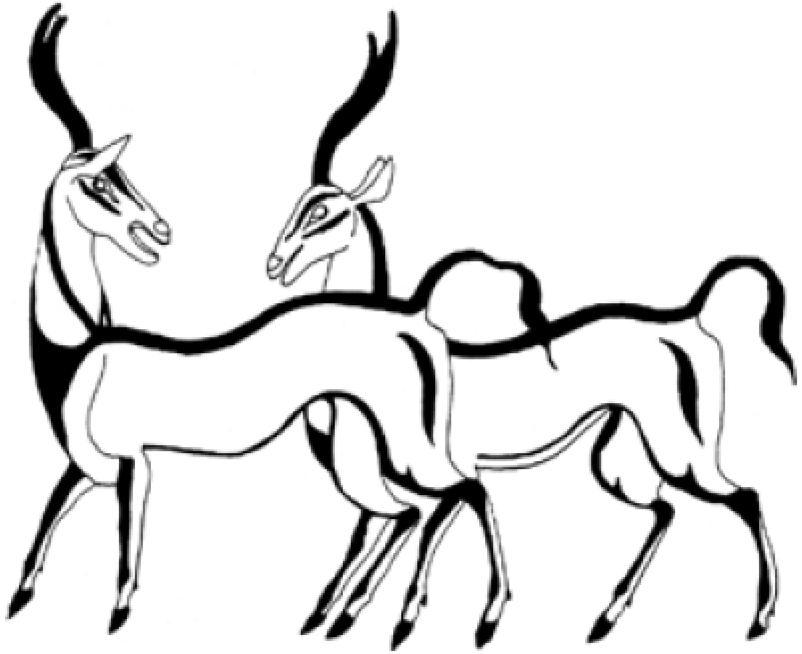
Unit 1: Introduction to Animal Behaviour

1. Origin and history of Ethology
2. Brief profiles of Karl Von Frish, Ivan Pavlov, Konrad Lorenz, Niko Tinbergen
3. Proximate and ultimate causes of behaviour
4. Methods and recording of a behaviour

What animal does is called animal behaviour

Art captures animal behavior. This pendant from the Chrysolakkos funeral complex in Crete suggests that some members of the ancient culture had a detailed knowledge of wasp behavior. *(From Gianni Dagli Orti/ The Art Archive at Art Resource, NY)*



Minoan wall paintings of "white antelopes." The drawing may depict a "lateral intimidation" during an aggressive encounter between the animals. *(From Masseti. Courtesy Ministry of Culture, Hellenic Republic)*

Fantastic images from a cave. A drawing of a herd of antelope found on the walls of a cave at Dunhuang, China. *(Photo credit: Pierre Colombel/Corbis)*

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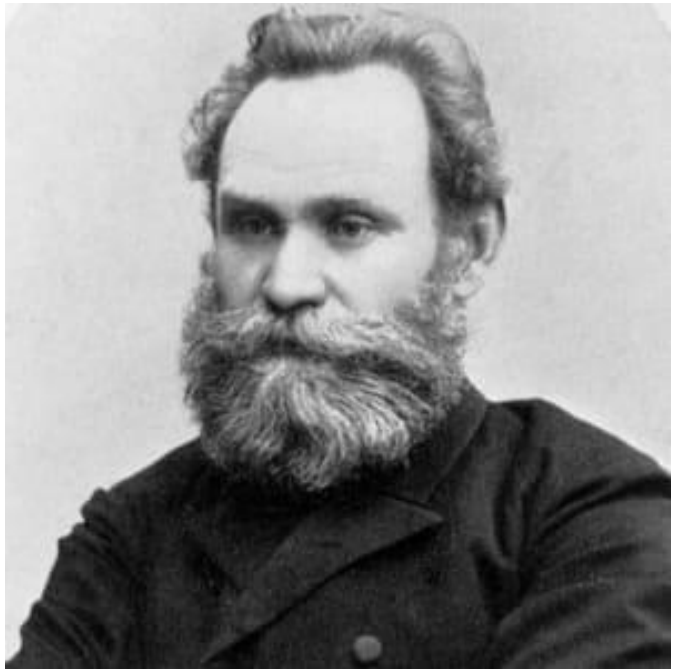
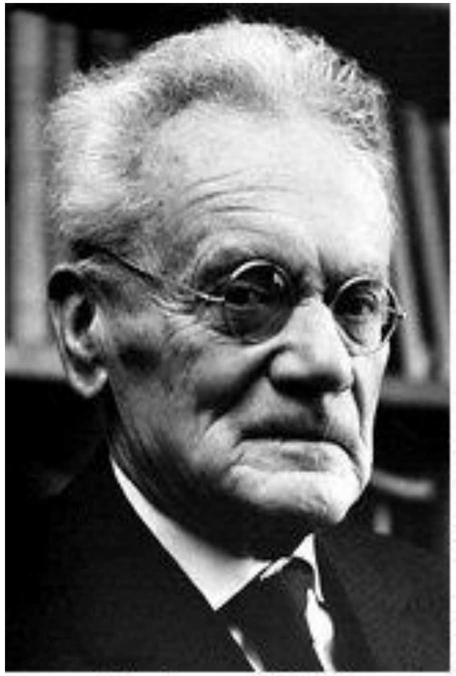
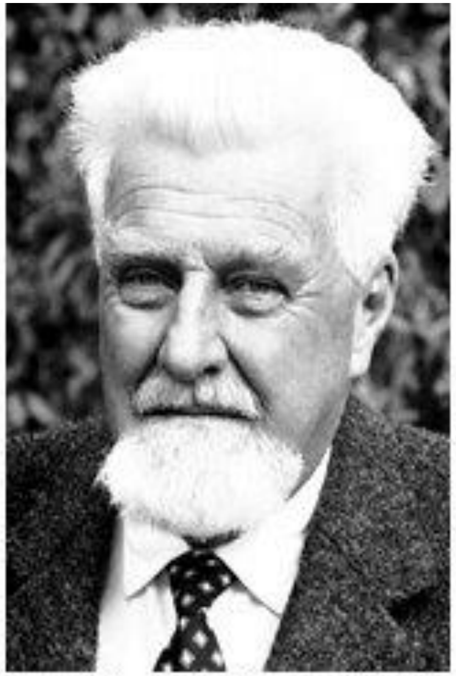
The Nobel Laureates of Ethology



Ivan Pavlov
(1849-1936)



Karl von Frisch
(1886 - 1982)



Konrad Lorenz
(1903 - 1989)

Nikolaas Tinbergen
(1907 - 1988)

•Ivan Petrovich Pavlov was a Russian physiologist known primarily for his work in classical conditioning. Pavlov won the Nobel Prize for Physiology or Medicine in 1904.

•Karl Ritter[a] von Frisch, was an Austrian ethologist who received the Nobel Prize in Physiology or Medicine in 1973, along with Nikolaas Tinbergen and Konrad Lorenz. His work centered on investigations of the sensory perceptions of the honey bee and he was one of the first to translate the meaning of the waggle dance.

•Konrad Zacharias Lorenz was an Austrian zoologist, ethologist, and ornithologist. He shared the 1973 Nobel Prize in Physiology or Medicine with Nikolaas Tinbergen and Karl von Frisch. He is often regarded as one of the founders of modern ethology, the study of animal behaviour. He developed an approach that began with an earlier generation, including his teacher Oskar Heinroth. Lorenz studied instinctive behavior in animals, especially in greylag geese and jackdaws.

•Nikolaas "Niko" Tinbergen was a Dutch biologist and ornithologist who shared the 1973 Nobel Prize in Physiology or Medicine with Karl von Frisch and Konrad Lorenz for their discoveries concerning organization and elicitation of individual and social behavior patterns in animals. He is regarded as one of the founders of modern ethology.

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Niko Tinbergen’s 4 Types of questions

Niko Tinbergen outlined in a classic paper entitled “On the Aims and Methods of Ethology” (N. Tinbergen, 1963). These questions centre on:

- **Mechanism—**What stimuli elicit behavior? What sort of neurobiological and hormonal changes occur in response to, or in anticipation of, such stimuli?

- **Development—**How does behavior change as an animal matures? How does behavior change with the ontogeny, or development, of an organism? How does developmental variation affect behavior later in life?

- **Survival value—**How does behavior affect survival and reproduction?

- **Evolutionary history—**How does behavior vary as a function of the evolutionary history, or phylogeny, of the animal being studied? When did a behavior first appear in the evolutionary history of the species under study?

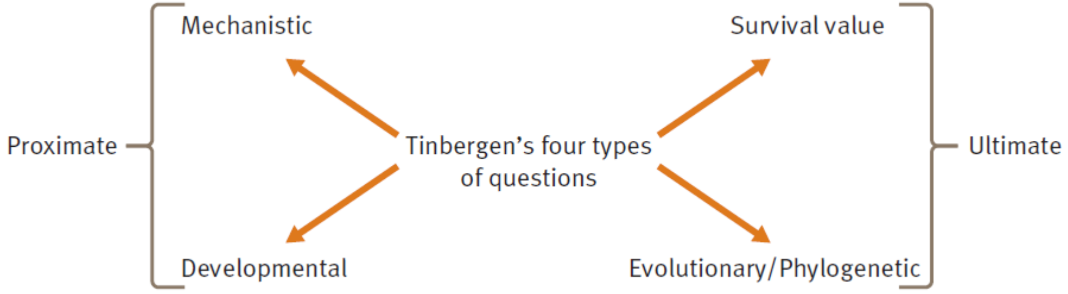
Tinbergen’s four questions can be captured in two different kinds of analyses—proximate analysis and ultimate analysis

Proximate analysis is focuses on *immediate causes, whereas*

Ultimate analysis is *defined in terms* of the *evolutionary forces that have shaped a trait over time.*

ultimate causation (factors) Those aspects of behavior that are concerned with why the behavior evolved and its functional significance in an ecological context.

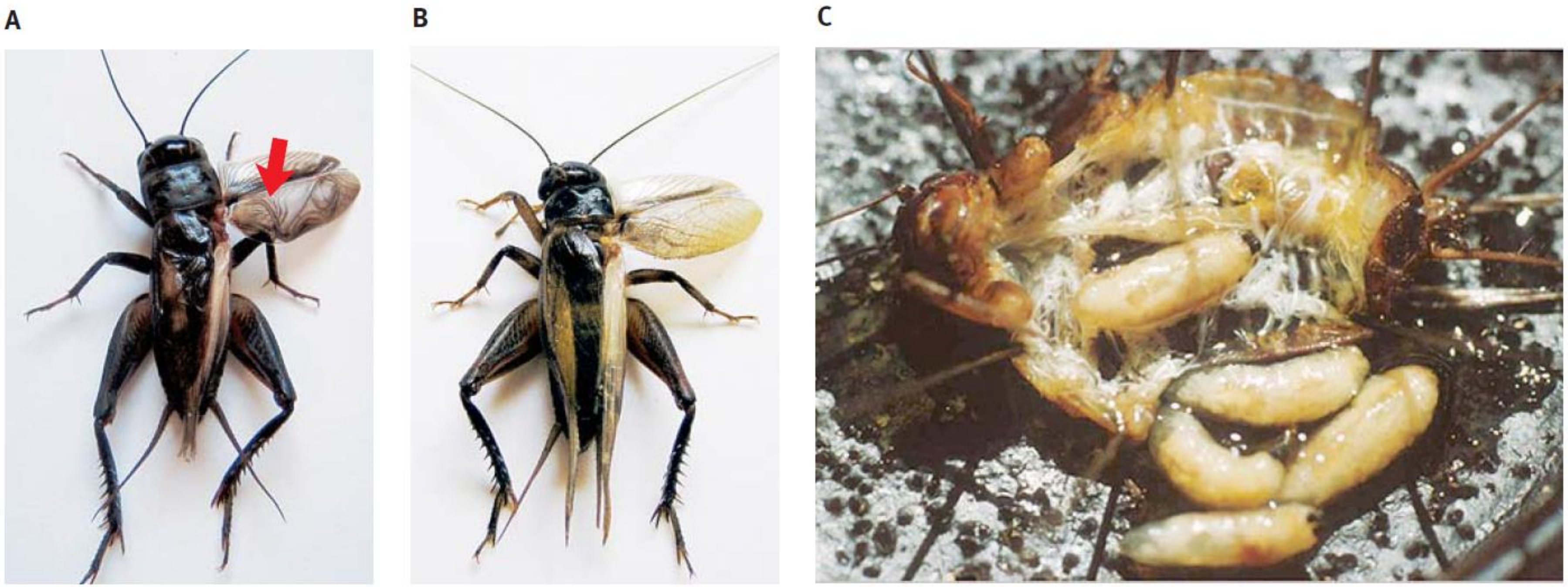
proximate causation (factors) Mechanistic explanations for how behavior occurs, including, in particular, hormones, the nervous system, and behavior development.



THREE FOUNDATIONS OF ANIMAL BEHAVIOUR

1. The force of *natural selection*
2. The ability of animals to learn (*individual learning*), and
3. The power of transmitting learned information to others (*cultural transmission*)

Hawaiian island, Kauai



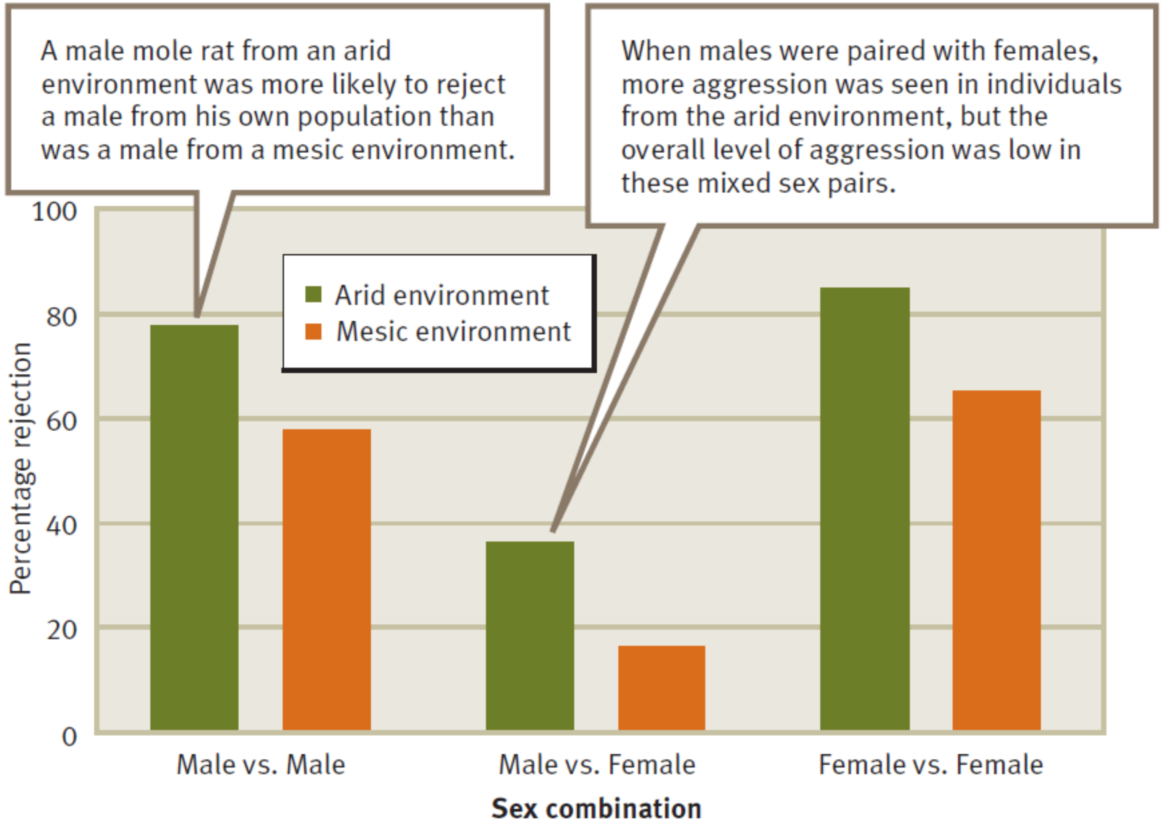
Natural selection in crickets. Marlene Zuk and her colleagues have been studying the field cricket *Teleogryllus oceanicus*. Pictured here are **(A)** a field cricket with normal wings (the arrow points to the file on its outstretched wing); **(B)** a field cricket with flat wings, in which the file section on the outstretched wing has evolved to a much smaller size and is visible only under a high-powered microscope; and **(C)** fly larvae in a parasitized cricket. *(Photo credits: Robin Tinghitella)*

Zuk and her colleagues hypothesized that flatwing males do this by staying near the handful of singing males still on Kauai, and mating with females as they approach singers.

And indeed, Zuk and her colleagues suggest that the mutation leading to the loss of song occurred only fifteen to twenty generations ago and has quickly increased in frequency, so that now most males on Kauai are flatwing males.

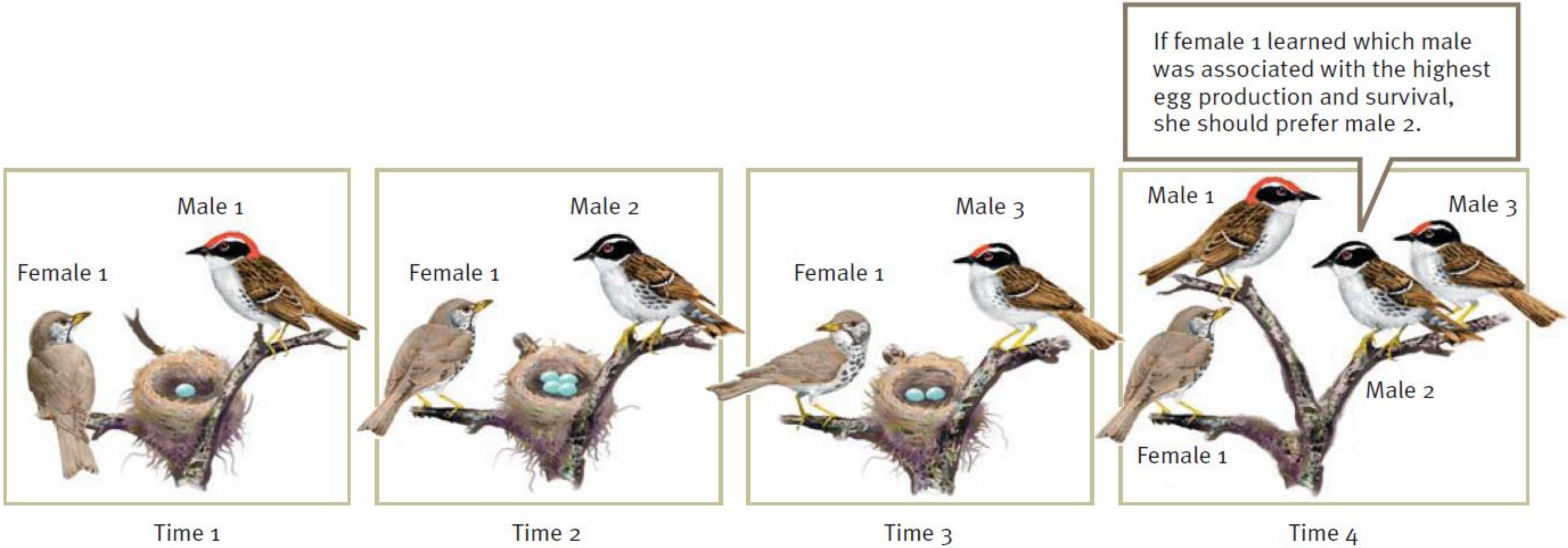
Natural Selection

Common mole rat. This xenophobic common mole rat *(Cryptomys hottentotus)* is showing an aggressive stance in response to a stranger. *(Photo credit: Graham Hickman)*



Xenophobia in common mole rats. Spinks and his colleagues found that mole rats from an arid environment (green bars) were more likely to reject a potential partner from their own population than were mole rats from a resource-rich mesic environment (orange bars). *(From Spinks et al., 1998, p. 357)*

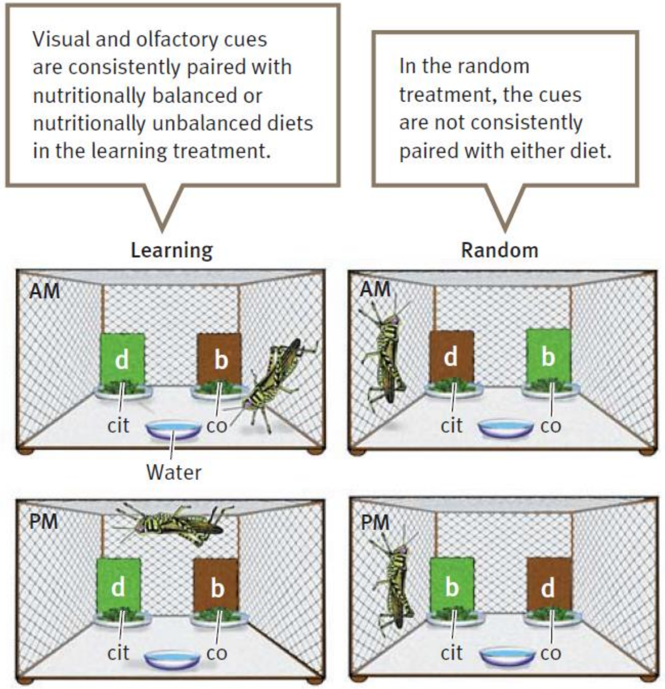
Natural Selection



A role for learning. Imagine a female that mates with different males over the course of time. Such a female might learn which male is a good mate by keeping track of the number of eggs she laid after mating with each male.

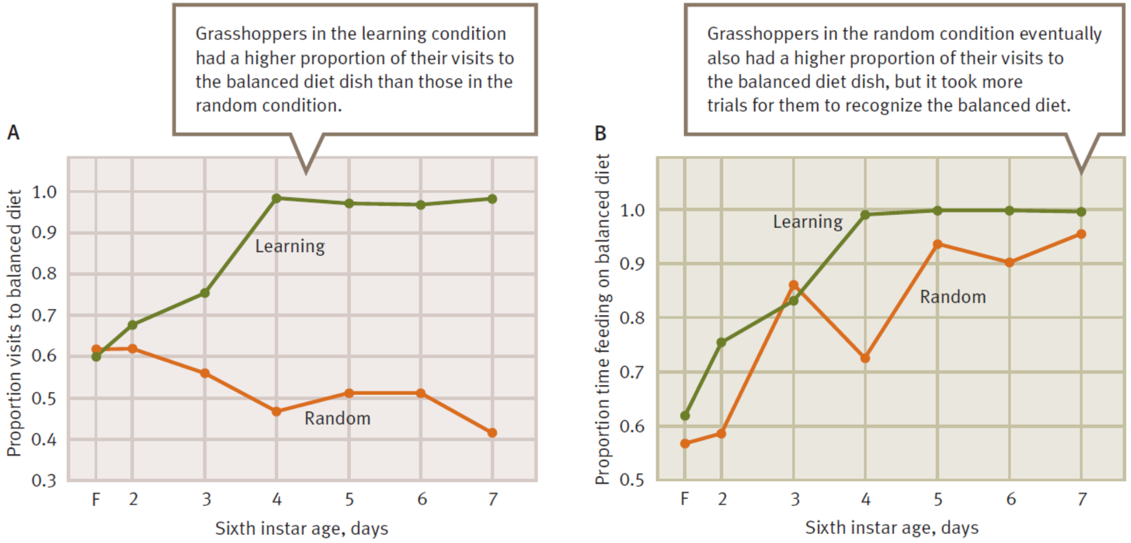
Individual Learning

Individual Learning

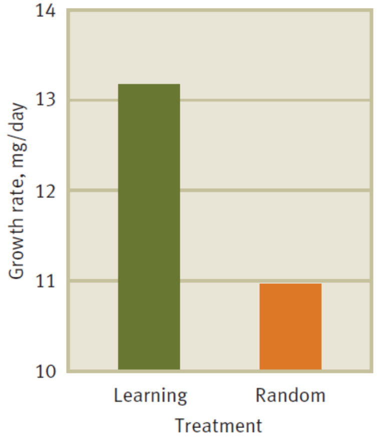


Learning, foraging, and fitness in grasshoppers. A schematic of the set-up showing the learning and random conditions. In the learning condition, the set-up consisted of a water dish in the center of the cage and a nutritionally balanced dish (b) on one side of the cage and a nutritionally deficient dish (d) on the other side of the cage. Each dish was paired with one odor (citral [cit] or coumarin [co]) and one colored card (brown or green). *(Base Bernays, 2000)*

Some aspects of foraging in grasshoppers are learned. *Schistocerca americana* grasshoppers learned to associate various cues with food sources. *(Photo credit: Stephen Dalton/ Naturepl.com)*

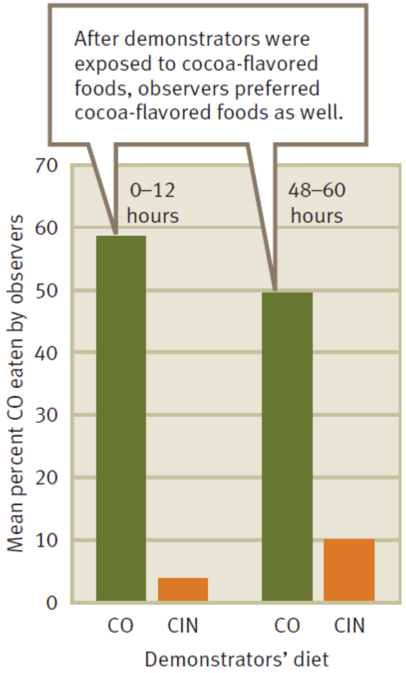


A balanced diet in grasshoppers. Grasshoppers in the sixth instar stage of insect development were given a choice between a balanced diet or a deficient diet, and researchers recorded the proportion of visits and feeding times of those in a learning treatment and those in a random treatment. In the learning condition, the food was presented in a way in which grasshoppers could learn to associate colored background cards and odors with balanced and unbalanced diets. In the random condition, grasshoppers could not make such associations. *(From Dukas and Bernays, 2000)*

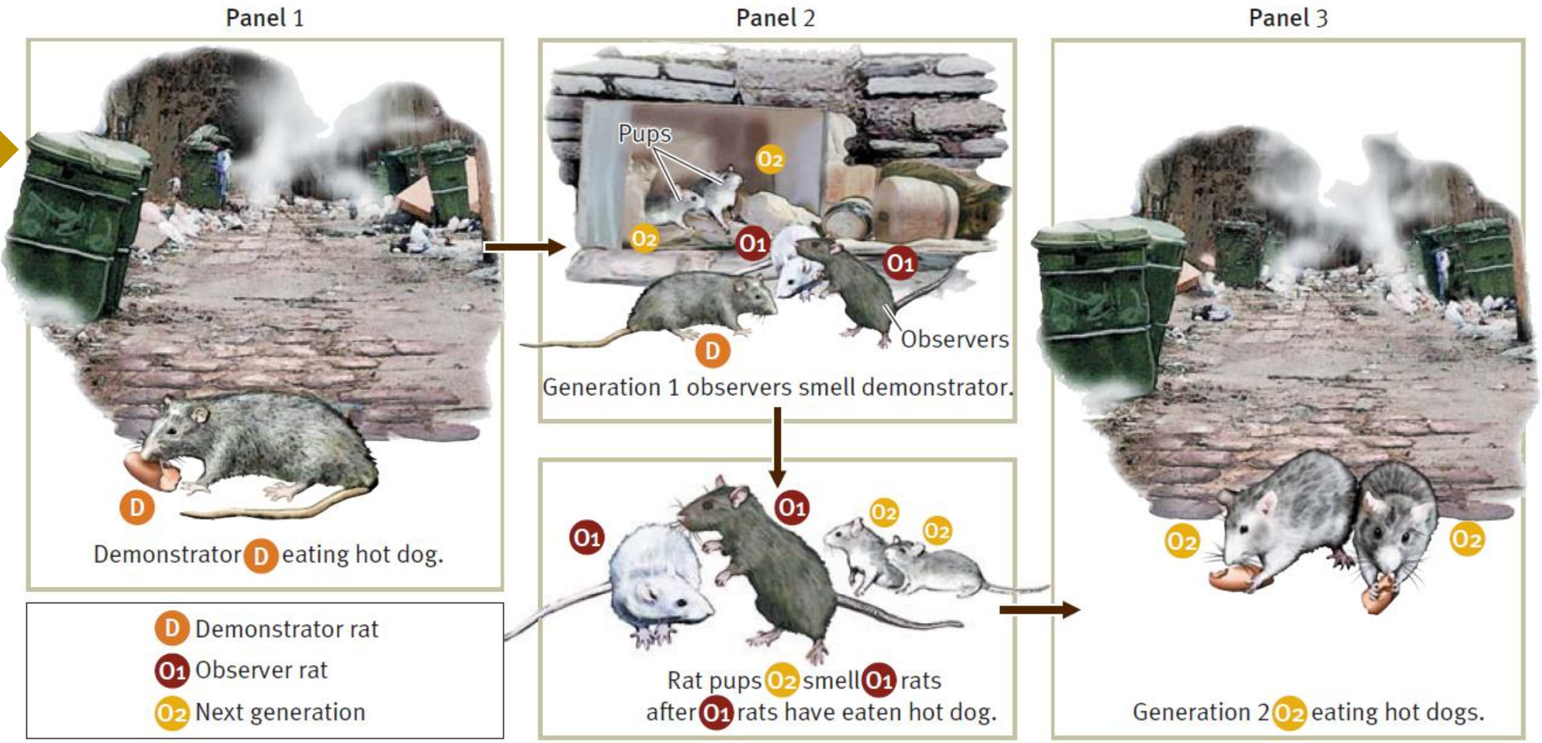


Fitness and foraging. Not only did grasshoppers in the learning condition approach the balanced diet dish more often, but this translated into quicker growth. Growth rate in grasshoppers is positively correlated with egg size and number. *(From Dukas and Bernays, 2000)*

Scavenging rats and cultural transmission. **(A)** When a rat scavenges
:ounter new food items that are dangerous or spoiled and that can
death. **(B)** Smelling another rat provides olfactory cues about what it
er of information from one rat to another about safe foods is a form of
(Photo credits: Stephen Dalton/Mindon Pictures; Tom McHugh/Photo

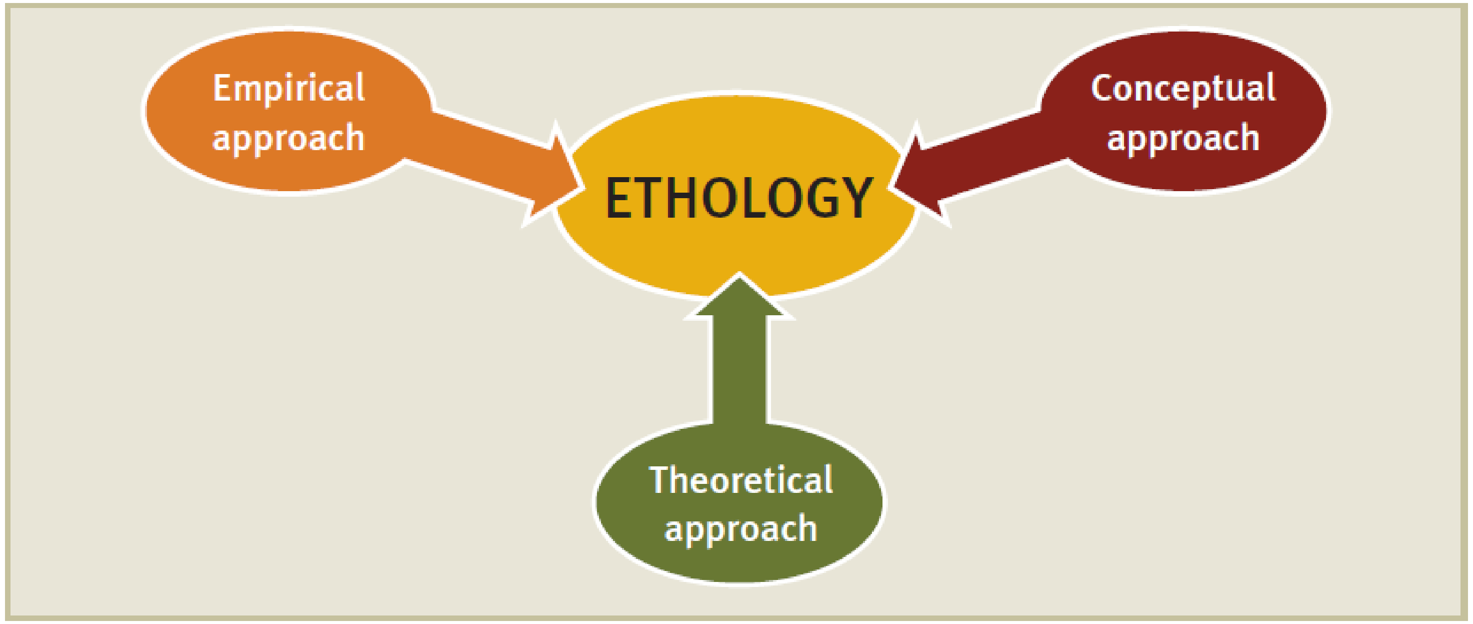


Social learning and foraging in the Norway rat. Observer rats had a "tutor" (demonstrator) that was trained to eat rat chow containing either cocoa (CO) or cinnamon (CIN) flavoring. After the observer rats had time to interact with a demonstrator rat, the observer rats were much more likely to add their tutor's food preferences to their own. *(From Galef and Wigmore, 1983)*



A role for cultural transmission. In panel 1, a rat eats a new food type (hot dog). When this rat (D for demonstrator rat) returns to its nest (panel 2), observer rats (O1) smell the rat and then are more likely to add hot dogs to their diet when they encounter such an item. Multigenerational cultural transmission occurs when rats from the next generation (O2) smell generation O1 rats after they have eaten hot dogs and subsequently add hot dogs to their own diet (panel 3).

Cultural Transmission

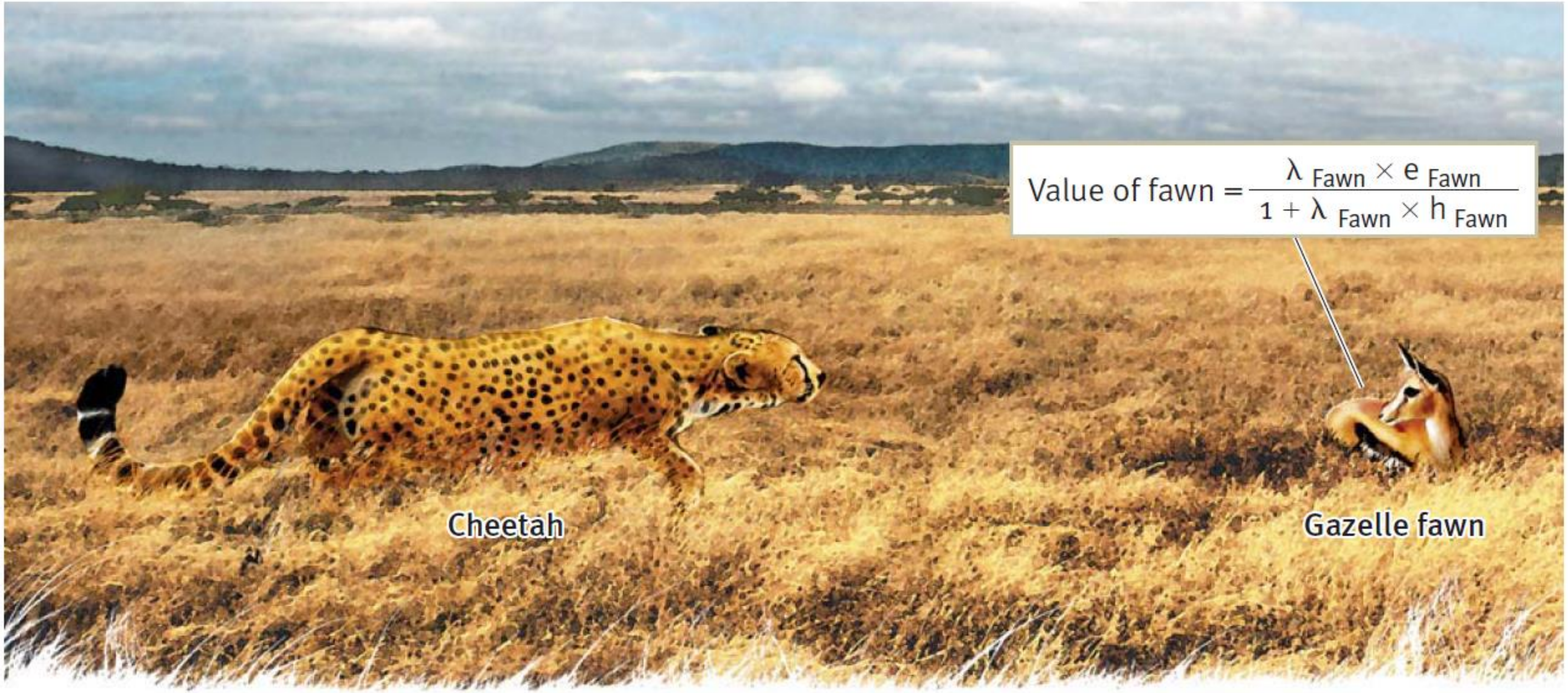


Different approaches to ethology. Ethology can be studied from a conceptual, theoretical, or empirical approach.

Kin selection and the mother-offspring bond. In many species, like the vervets shown here, mothers go to extreme lengths to provide for and protect their young offspring. W. D. Hamilton's kin selection ideas provided a conceptual framework for understanding the special relations that close genetic relatives share. *(Photo credit: Ben Cranke/Getty Images)*

- **Kin selection**
- **Direct fitness**
- **Indirect fitness**
- **Inclusive fitness**

Conceptual Approach



- **OFT**
- **Game theory**

Mathematical optimality theory and foraging. Cheetahs can feed on many different prey items, including a gazelle fawn. Ethologists have constructed mathematical models of foraging that determine which potential prey items should be taken. The value assigned to each prey is a composite of energy value (e), handling time (h), and encounter rate (λ).

Theoretical Approach

Observation and experimentation. Imagine your observations led you to believe that red-winged blackbirds decrease foraging when under predation pressure. To experimentally examine causality, you could allow a trained falcon to fly over a red-winged blackbird area and observe how its presence affects the amount of foraging.

- **Observational**
- **Experimental**

Empirical Approach

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Basic consideration

Approaches in behavioural studies

1. observational
2. experimental
3. ethological

Will discuss at practical…

Unit 2: Patterns of Behaviour

1. Stereotyped Behaviours (Orientation, Reflexes)
2. Individual Behavioural patterns
3. Instinct vs. Learnt Behaviour
4. Associative learning, classical and operant conditioning, Habituation, Imprinting

Stereotyped response

- Unlearned behavioral reaction of an organism to some environmental stimulus
- It is an adaptive mechanism and may be expressed in a variety of ways
- All living organisms exhibit one or more types of stereotyped response
- Stereotyped responses are the result of a continuing process of evolutionary modification and refinement
- Those actions that most successfully aid the animal or plant in its basic drives (e.g., reproduction, search for nourishment, escape from predators) are the ones most likely to be retained in succeeding generations
- As environmental conditions change, inherently determined responses also become modified in order to ensure continuation of the species
- **Types: Orientation (Taxis and kinesis) & Reflexes**

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Types of behaviours

1. Taxis and kinesis
2. innate and learned
3. egocentric and altruistic

Maintaenance

Body surface maintenance

- ***Body care***
- ✓ ***Bathing***
  - ➢ ***Water bathing***
  - ➢ ***Mud bathing***
  - ➢ ***Sand bathing***
  - ➢ ***Fire bathing***
- ✓ ***Powdering***
- ✓ ***Cleaning***
- ✓ ***Moving tail***
- ✓ ***Grooming***

Comfort movement

- ***Rubbing***
- ***Rutting***
- ***Scratching***
- ***Shaking***
- ***Stretching***
- ***Niblling***
- ***Yawning***
- ***Panting***
- ***Sub bathing/ basking***

Anting

- ***Active***
- ***Passive***

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Motivation and drive

- ***What compels an animal to do what it does is motivation***
  - All the internal and external factors which cause an organism to behave in a goal seeking way is motivation
  - Motivation leads to build-up of drives for the animal to perform appropriate behaviour (appetitive and consummatory)
  - Motivation helps to optimize stimulation to the homeostasis
  - *There is no behaviour without motivation except strict Pavlovian reflex*
  - Instincts are important to understand motivation
  - **Instincts are unlearned behaviours and responses which help them to survive and reproduce**
  - Animals have needs which motivate it to perform a behaviour

- ***Drives are internal state of arousal (e.g. thirst or hunger etc.) which animals tried to reduce and re-establish the homeostasis***

Drive Motivational state; urge to behave in some particular manner. The term has been used in various ways in psychology and ethology, often in one of the senses of "instinct," with which it shares a reputation for causing mischief because of its multiple meanings. In psychology drive has been invoked to account for learning; in this sense it means the mobilization of action as a consequence of bodily need, such as food or water deficit. The reduction of the deficit reinforces and strengthens the associated stimulus-response connection. In an experimental context the operational definition of drive might be hours of food deprivation, rate of bar-pressing, or some quantitive factor relating the independent and dependent variables in an equation.

In ethology the term "drive" has much the same history as motivational energy; initially it was thought of as an endogenous force propelling behavior, then was operationally construed as measurable in terms of overt behavior, and now is more or less avoided except in contexts that do not pretend to theoretical precision. Sometimes a distinction is drawn between "drive" and "urge": drive being the latent readiness to act in a particular manner, and urge being manifest motivation as expressed in behavior. "Mood" is sometimes used in a sense that overlaps with one of the senses of "drive."

Hierarchy of drives

1. **First level drive**
   (reproductive drive)

2. **Second level drive**
   (territoriality, mating, nest building, parental care)

3. **Third level drive**

Sign stimulus

Specific external stimuli that triggered stereotyped responses from conspecifics, usually called fixed action pattern

learning The relatively permanent change in behavior or potential for behavior that results from experience.

experience All of the interactions between an organism and its environment, beginning at conception and including both external and internal influences.

fixed action pattern (FAP) An innate behavior pattern that is stereotyped, spontaneous, and independent of immediate control, genetically encoded, and independent of individual learning.

innate releasing mechanism (IRM) A neural process, preprogrammed for receiving a particular sign stimulus, that mediates specific behavioral responses.

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HOW ANIMALS LEARN?

*This discussion of how animals learn follows an outline developed by **Cecilia Heyes,** both because of its conciseness and its attempt to tie how animals learn to why they learn (Heyes, 1994)*

learning The relatively permanent change in behavior or potential for behavior that results from experience.

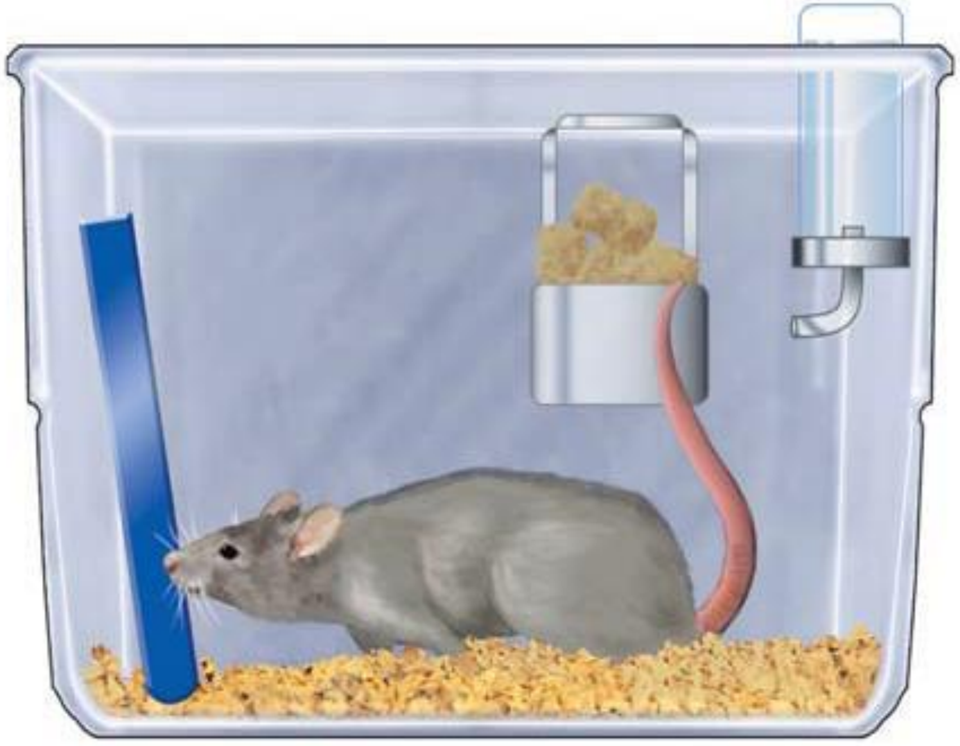
experience All of the interactions between an organism and its environment, beginning at conception and including both external and internal influences.

Heyes notes that there are **three** commonly recognized types of experience that can lead to learning—namely,

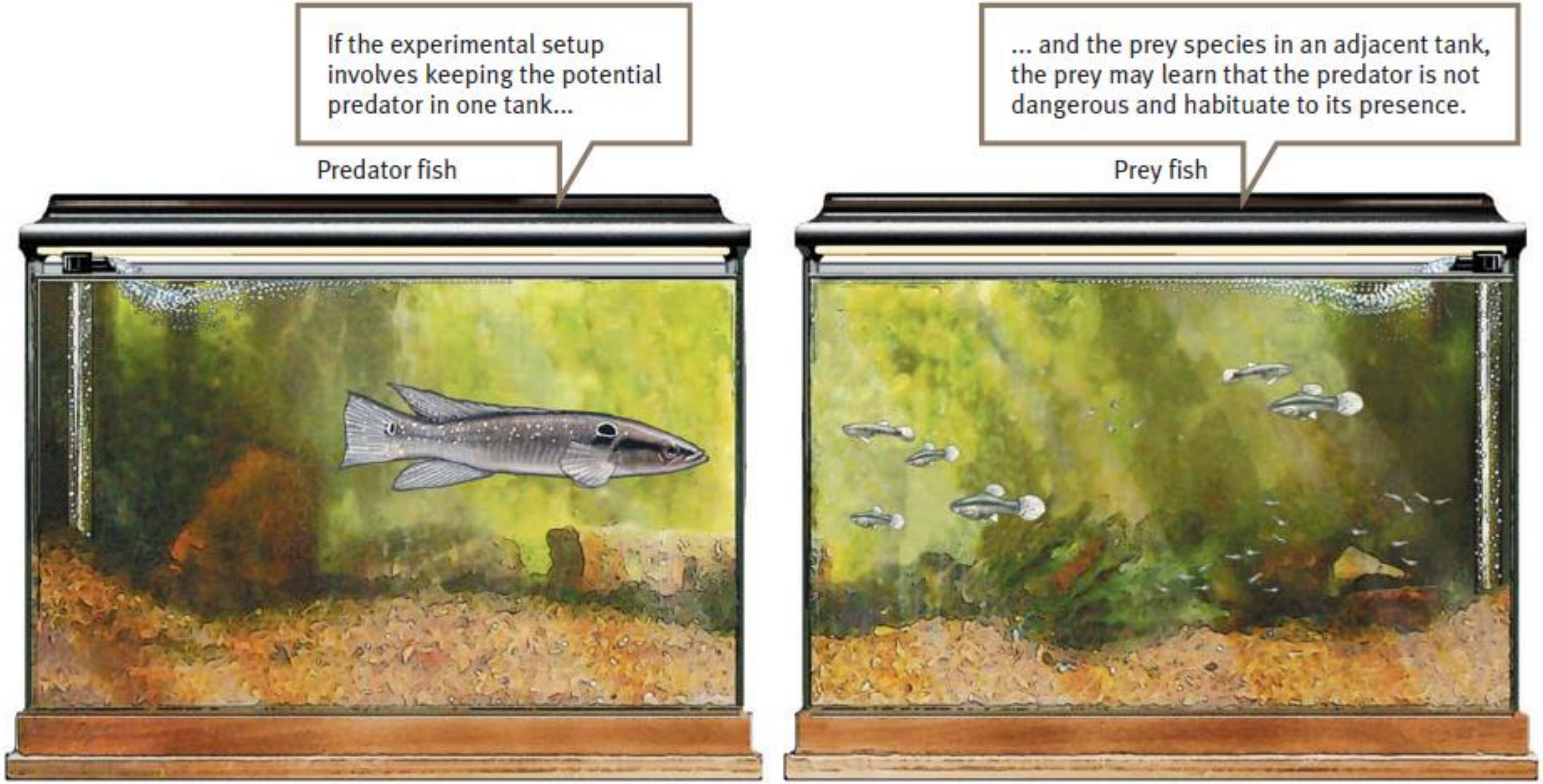
1. Single stimulus
2. Stimulus-stimulus (Pavlovian (classical) conditioning), and
3. Response-reinforce (Operant conditioning)— each of which facilitates certain forms of learning.

Single-stimulus learning

Sensitization and habituation are two simple single-stimulus forms of learning

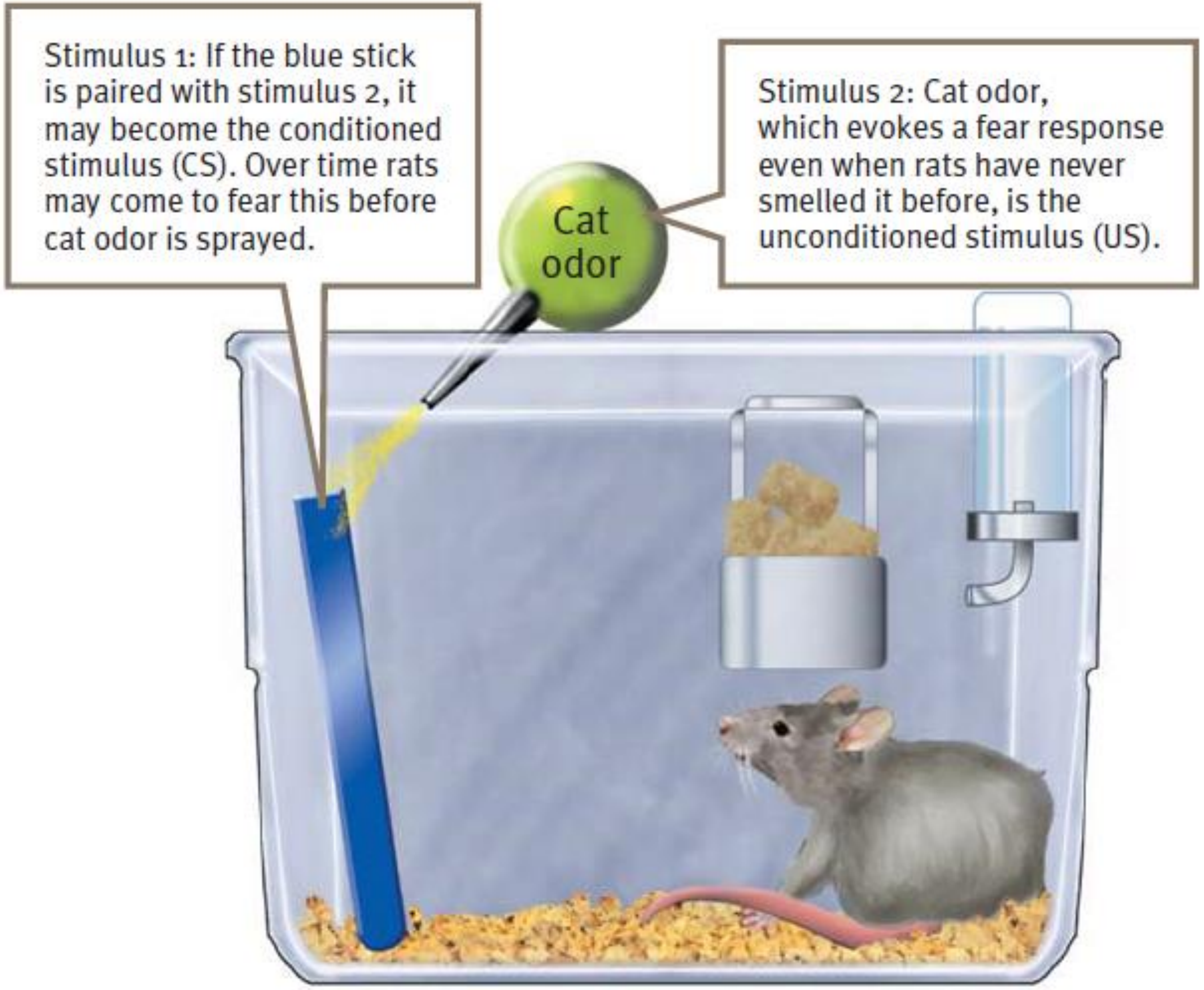


Habituation and sensitization:
Numerous times each day, a blue stick is placed in a rat's cage. If the rat takes less and less notice of the stick, habituation has occurred. If the rat pays more attention to the blue stick over time, sensitization has taken place.



Habituation as an problem

Pavlovian (classical) conditioning



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Paired stimuli

Five seconds after a blue stick (stimulus 1) is placed in a rat's cage, the odor of a cat (stimulus 2) is sprayed in as well. The question then becomes: Will the rat pair the blue stick with danger (cat odor)?

classical (Pavlovian) conditioning A type of learning whereby an unconditioned stimulus (US) that elicits a specific response (unconditioned response [UCR]) is paired with a neutral stimulus. (After it becomes associated with the US, the neutral stimulus, becomes the conditioned stimulus (CS), and results in a conditioned response (CR).

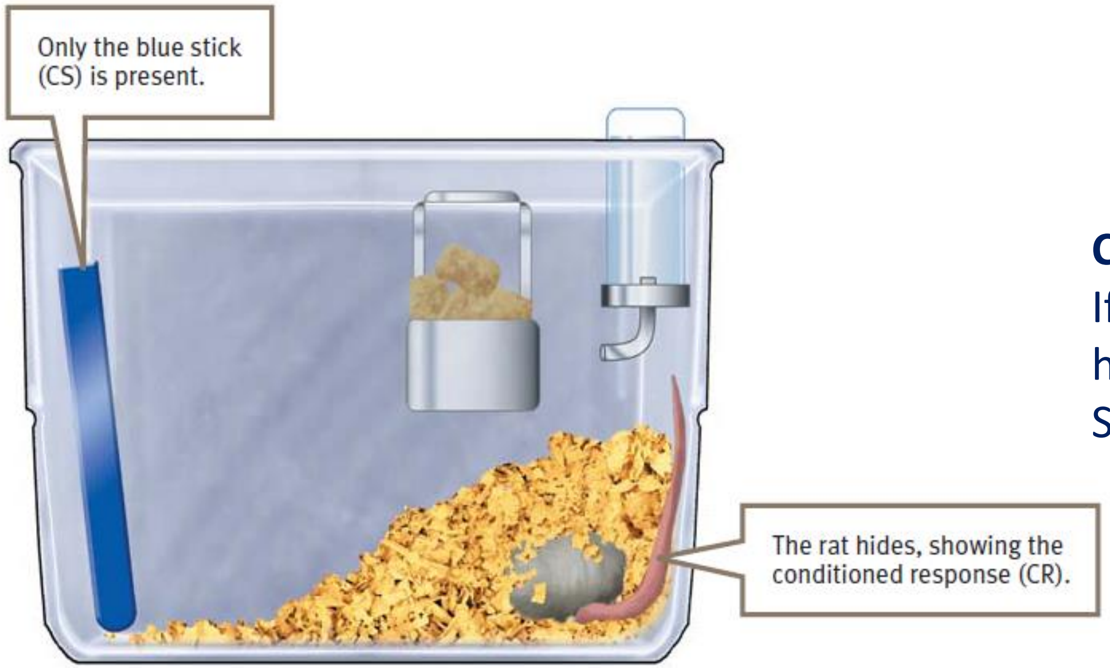
unconditioned response (UCR) In classical conditioning, the animal's response that is initially given to the unconditioned stimulus.

unconditioned stimulus (US) In classical conditioning, the stimulus that produces what is initially the unconditioned response.

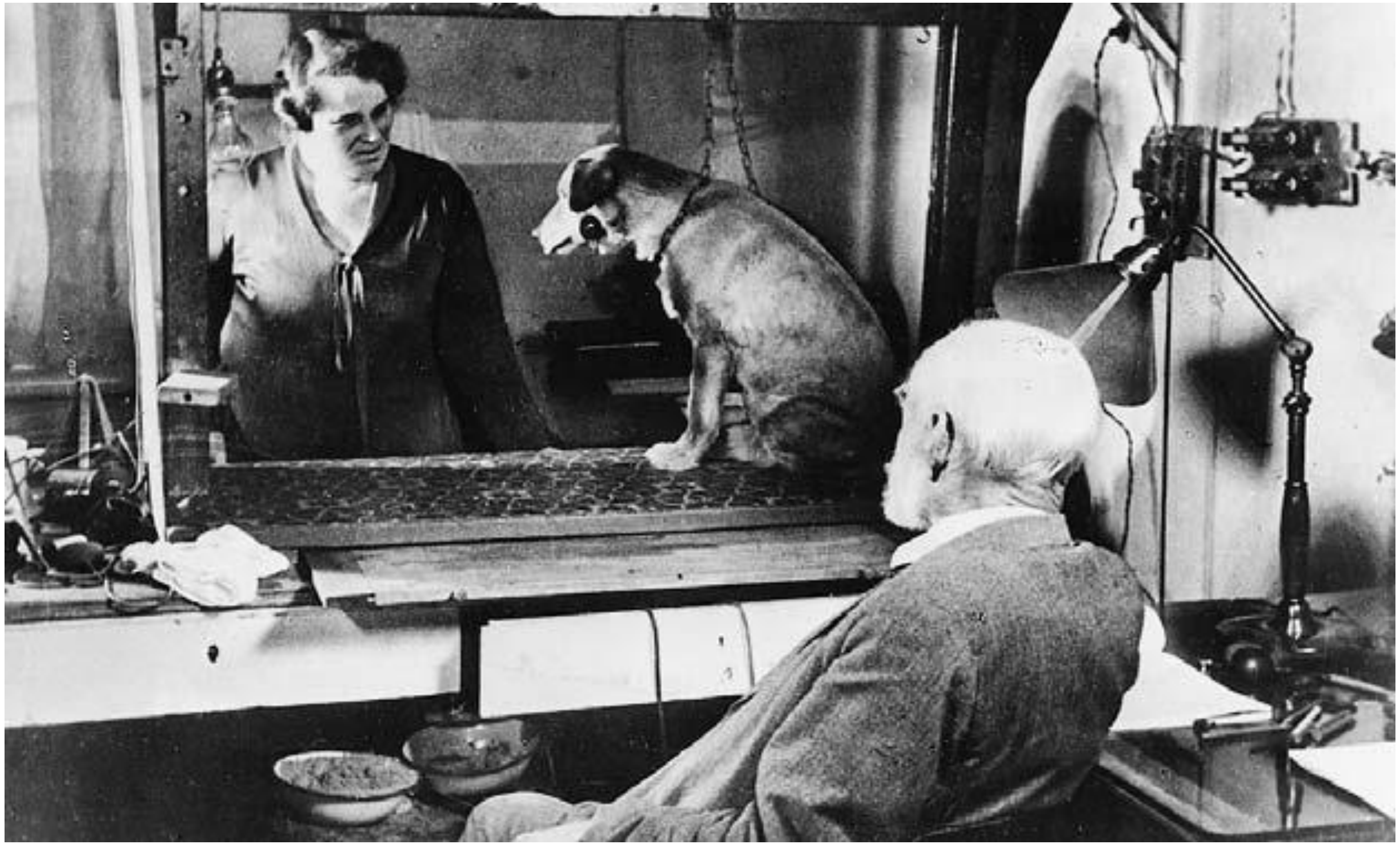
conditioned response (CR) The behavior pattern that becomes conditioned during classical conditioning.

conditioned stimulus (CS) The previously neutral stimulus that, through classical conditioning, now elicits the conditioned response.

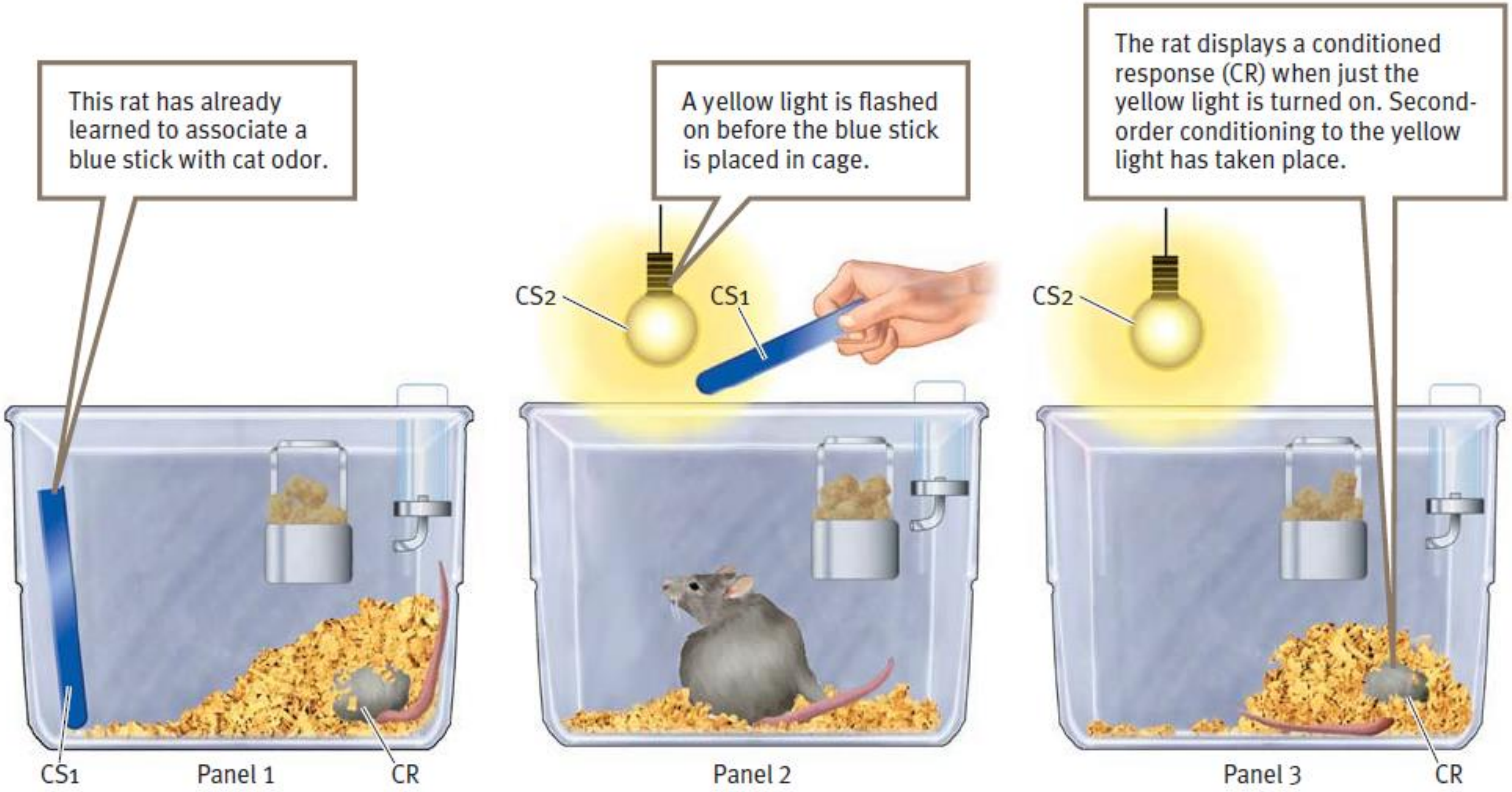
In nature, US=UR
Upon pairing, US+NS=UR/R
When, NS=R
Then, NS=CS & R=CR



Conditioned response
If the rat pairs the blue stick (CS) and the cat odor (US), it will hide under the chips when the blue stick alone is presented. Such hiding represents a conditioned response (CR)



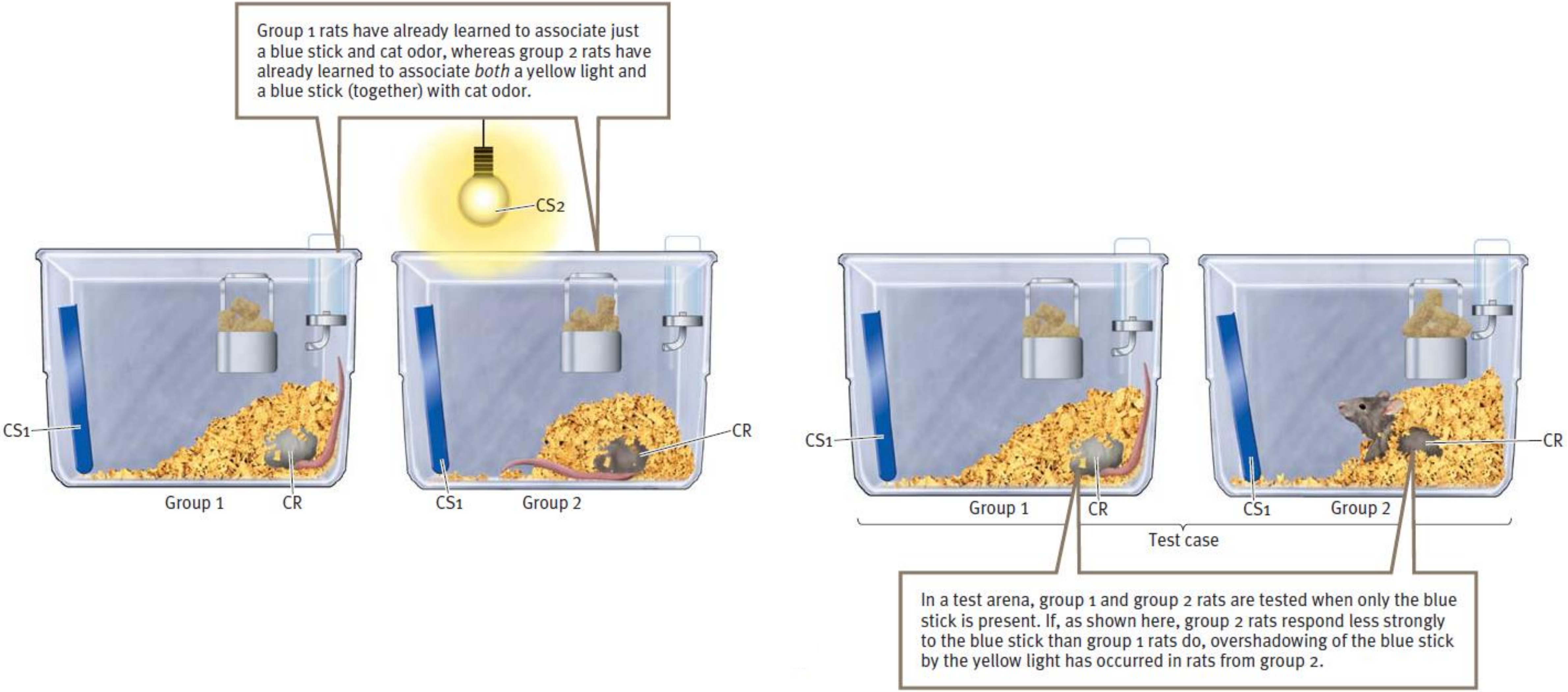
Ivan Pavlov and classical conditioning. Pavlov watches a classical conditioning experiment as it is being conducted in his laboratory. In the experiment, a device to measure salivation has been attached to the dog’s cheek, the unconditioned stimulus is a dish containing meat powder, and the conditioned stimulus is a light. (Photo credit: Sovfoto/Eastfoto)



Second-order conditioning The rat learns to respond to a second CS—the yellow light—with the conditioned response.

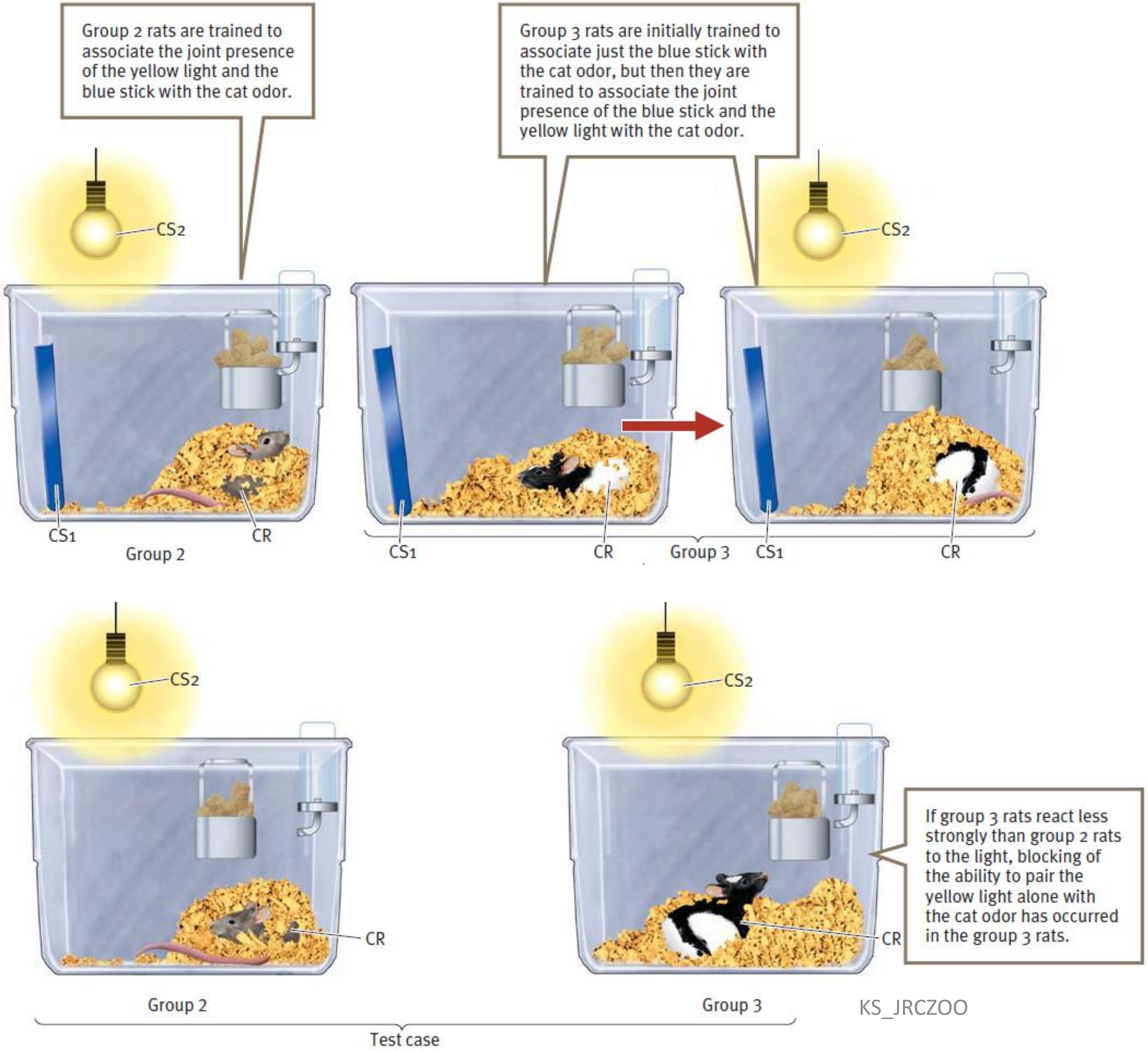
- ✓Pavlovian conditioning affects not only behavior per se but also what is referred to as ***learnability*** (that is, the ability to learn under certain conditions).

- ✓We will explore three types of learnability: **overshadowing, blocking, and latent inhibition**.



Overshadowing

The process of overshadowing is shown in two groups of rats.



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Blocking

Learning can be slowed down depending on prior association or lack of association between stimuli

Finally

- Let’s consider a fourth group of rats that is initially **exposed to a blue stick, but no cat odor**, for a long period of time
- We then **try to pair the blue stick with cat odor** at some subsequent point in time
- If we find that the rats in group 4 have more **difficulty learning** than the rats in group 1 (where standard Pavlovian pairing has occurred), then we would say that **latent inhibition** is responsible for this lack of learning in group 4

Instrumental (operant) conditioning

- ✓ **Instrumental conditioning**, also known as **operant** or **goal-directed learning**, occurs when the response that is made by an animal is reinforced (increased) by the presentation of a reward or the termination of an aversive stimulus, or when the response is suppressed (decreased) by the presentation of aversive stimulus or the termination of a reward.

- ✓ One of the most fundamental differences between Pavlovian and instrumental learning is that, in instrumental learning, the animal must undertake some action or response in order for the conditioning process to produce learning.

- ✓ Thorndike's law of effect: This law states that if a response in the presence of a stimulus is followed by a positive event, the association between the stimulus and the response will be strengthened. Conversely, if the response is followed by an aversive event, the association will be weakened.

Rats in a Skinner box

To test various theories of animal learning, rats are often placed in "Skinner boxes," where they have to take an action (here, pressing a button) to get a reward of food or water. *(Photo credit: Walter Dawn/Science Photo Library/Photo Researchers, Inc.)*

acquisition Gaining a response in a learning paradigm.

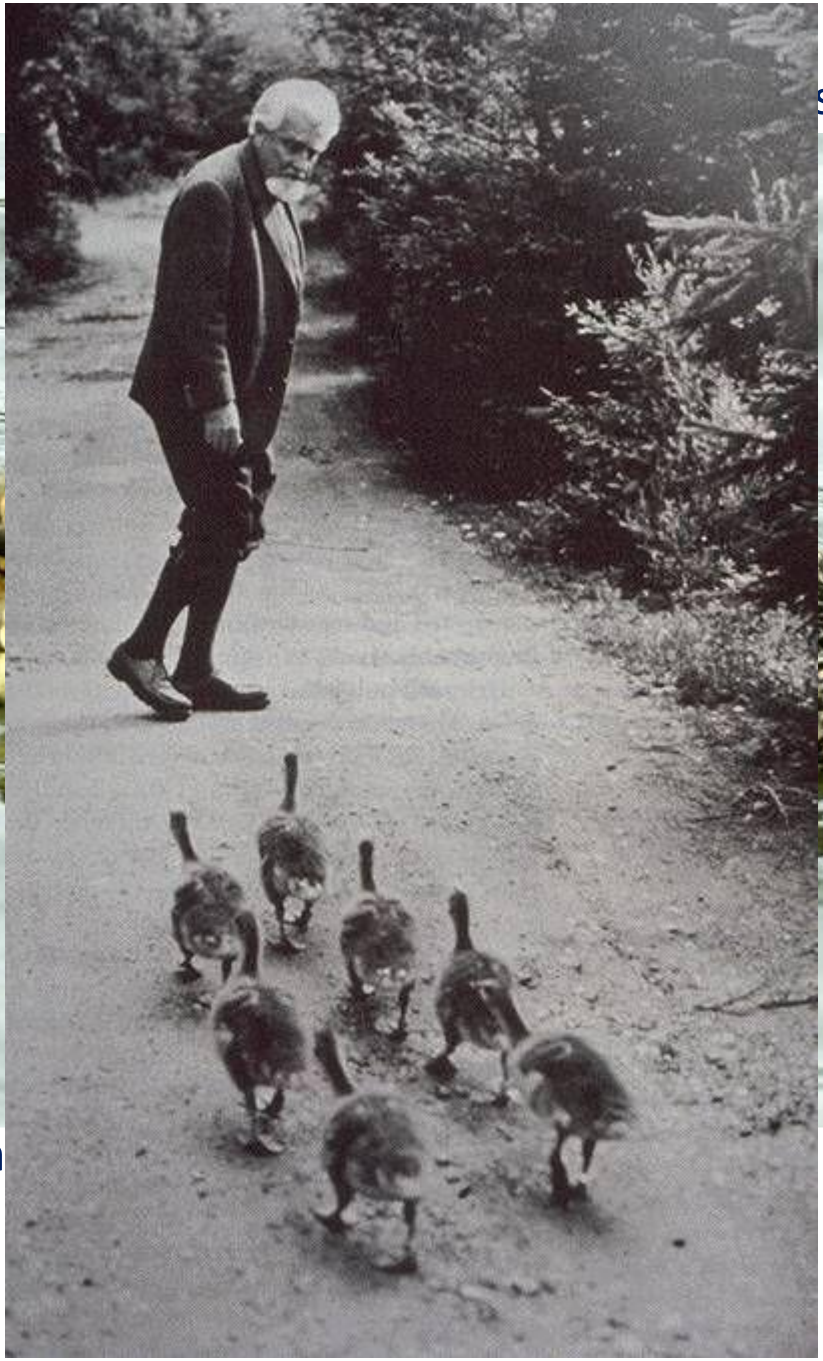
The act of first developing a response is termed **acquisition.**

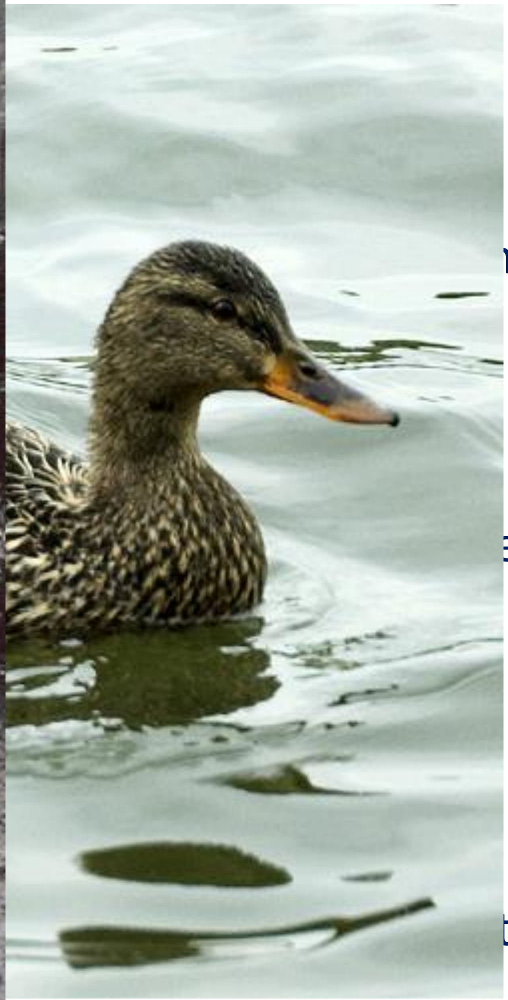
habituation The relatively persistent waning of a response that results from repeated presentations not followed by any form of reinforcement.

sensitization (1) Enhanced responsiveness to a repeated stimulus. (2) Strengthening of a response that was initially produced via a CS resulting from a pairing with a US and UR. (3) A stimulus priming the animal to pay particular attention to what follows.

Extinction In learning, the decrease of response rate or magnitude of response with lack of reinforcement in a learning situation

- **Imprinting** is a form of learning … s attention on the first object with
wh…





- I… …nate objects
hav…

- I… …eese, but a
co… fishes and
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- I… …t receptivity
to imprinting stimuli vanishes at th…

Unit 2: Social and Sexual Behavior

1. Social Behaviour: Concept of Society, Altruism (Insects' society with Honey bee as example, Foraging in honey bee and advantages of the waggle dance)
2. Communication and the senses
3. Sexual Behaviour: Asymmetry of sex, Sexual dimorphism, Mate choice, Intra-sexual selection (male rivalry), Inter-sexual selection (female choice), Sexual conflict in parental care

Special Topic

Theory of Decision Making

Game theory is a branch of applied mathematics that provides tools for analysing situations in which parties, called players, make decisions that are interdependent. This interdependence causes each player to consider the other player's possible decisions, or strategies, in formulating his own strategy.

Game theory was originally developed by…

John von Neumann
Hungarian-born American mathematician

Oskar Morgenstern
German-born American economist

Types of games…

1. One-person, two-person, or n-person game (based on **number of players**)

2. Games of perfect information vs. game of imperfect information (based on **available information** about the opponent's strategies, e.g. Chess vs. Poker)

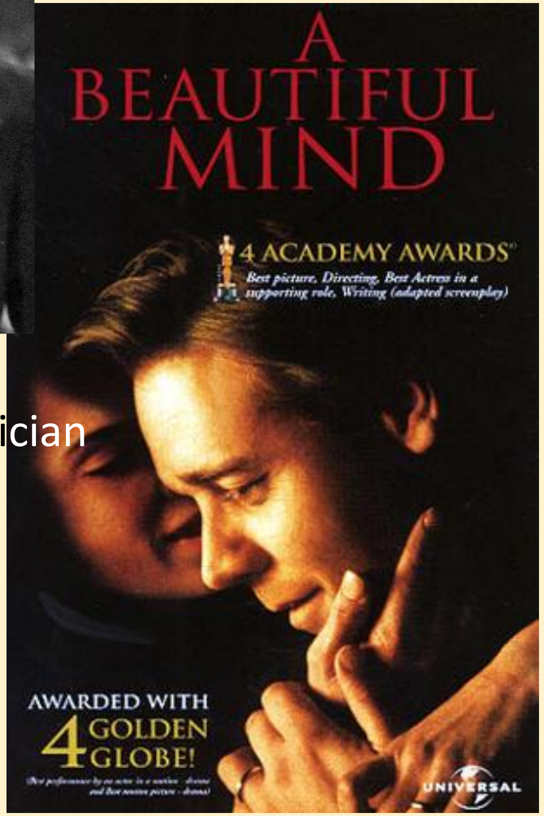
3. Constant-sum games *(game of pure competition e.g. poker)* vs. variable-sum game (based on the **distribution of resource**)

4. Variable-sum games can be further distinguished as being either cooperative or non-cooperative.

Prisoner’s Dilemma

Albert W. Tucker
(Canadian mathematician)

John F. Nash
American Mathematician



T = “Temptation to cheat” payoff,

R = “Reward for mutual cooperation” payoff,

P = “Punishment for mutual defection” payoff, and

S = “Suckers” payoff.

For the matrix to qualify as a prisoner’s dilemma game, it must be true that T > R > P > S

PD Matrix		Suspect 2	
		Cooperate	Cheat
Suspect 1	Cooperate	Suspect 1: R = 5 year in jail Suspect 2: R = 5 year in jail	Suspect 1: S = 15 years in jail Suspect 2: T = 0 years in jail
	Cheat	Suspect 1: T = 0 years in jail Suspect 2: S = 15 years in jail	Suspect 1: P = 10 years in jail Suspect 2: P = 10 years in jail

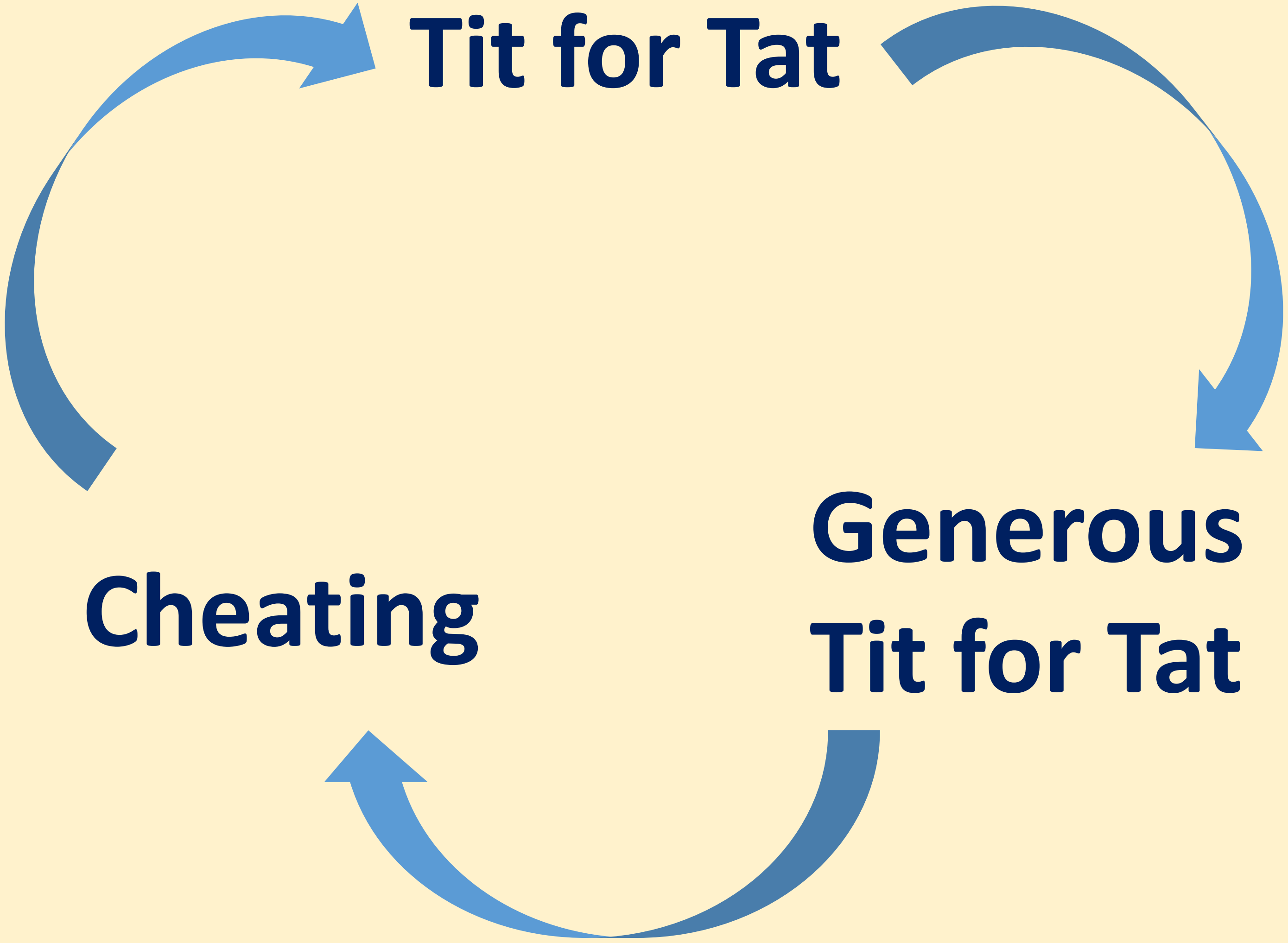
What should be the Evolutionary Stable Strategy (or the Nash Equilibrium)?

- If cooperation adopted by most then cheating penetrate

- If cheating adopted by most then system collapses and cooperation penetrate

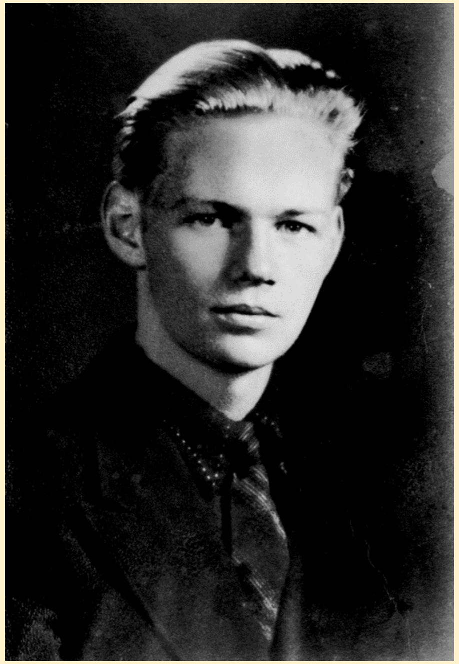
So…Tit for Tat

Among us…



The Hawk-Dove game

John Maynard Smith
British theoretical and mathematical evolutionary biologist



George Price
American geneticist

		Player 2	
		H	D
Player 1	H	$(v-c)/2, (v-c)/2$	$v, 0$
	D	$0, v$	$v/2, v/2$

c>v leads to hawk-dove

v>c leads to PD

(we have them in this room!!!)

What should be the Evolutionary Stable Strategy (or the Nash Equilibrium)?

A mixture of both

(can be calculated mathematically)

which is dynamic in nature

and

the third ***bourgeois behaviour***

Unit 3: Social and Sexual Behaviour

1. **Social Behaviour: Concept of Society**
2. Communication and the senses
3. Altruism: Insects' society with Honey bee as example, Foraging in honey bee and advantages of the waggle dance
4. Sexual Behaviour: Asymmetry of sex, Sexual dimorphism, Mate choice, Intra-sexual selection (male rivalry), Inter-sexual selection (female choice), Sexual conflict in parental care

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- **Communication** is the transfer of information from a signaler to a receiver
- It modulate the behavior of the receiver

The vervet monkey story of Amboseli National Park, Southern Kenya

Cough-Eagle

Barking-Leopard

Chutter-Snakes

Types and Evolution of Behaviour

Signaler	Receiver	
	+ve	-ve
+ve	True Communication Conspirational whispers	Manipulation Exaggerated signals
-ve	Exploitation	Ignorance

Krebs and Dawkins, 1978

one might expect from a salesman attempting to convince a prospective buyer that his product is the top of the line

signaling often involves some costs—for example, energy costs or drawing attention from predators—natural selection should favor minimizing these costs during conspirational whispers, **thus reducing the conspicuousness**

Communication and Honesty

- When what is good for the signaler is not good for the recipient, natural selection will favor signalers that send signals in whatever way best increases the fitness of the signaler, even if that means manipulating recipients
- But natural selection also favor recipients with the ability to unscramble what is honest and what isn't, so it can act in ways that maximize its own fitness. Krebs and Dawkins refer to recipients as "mind readers" and describe an "arms race" between signaler and recipient
- in which the signaler is selected to better manipulate the receiver, which then is selected to better filter out only that information that benefi ts it, and so on

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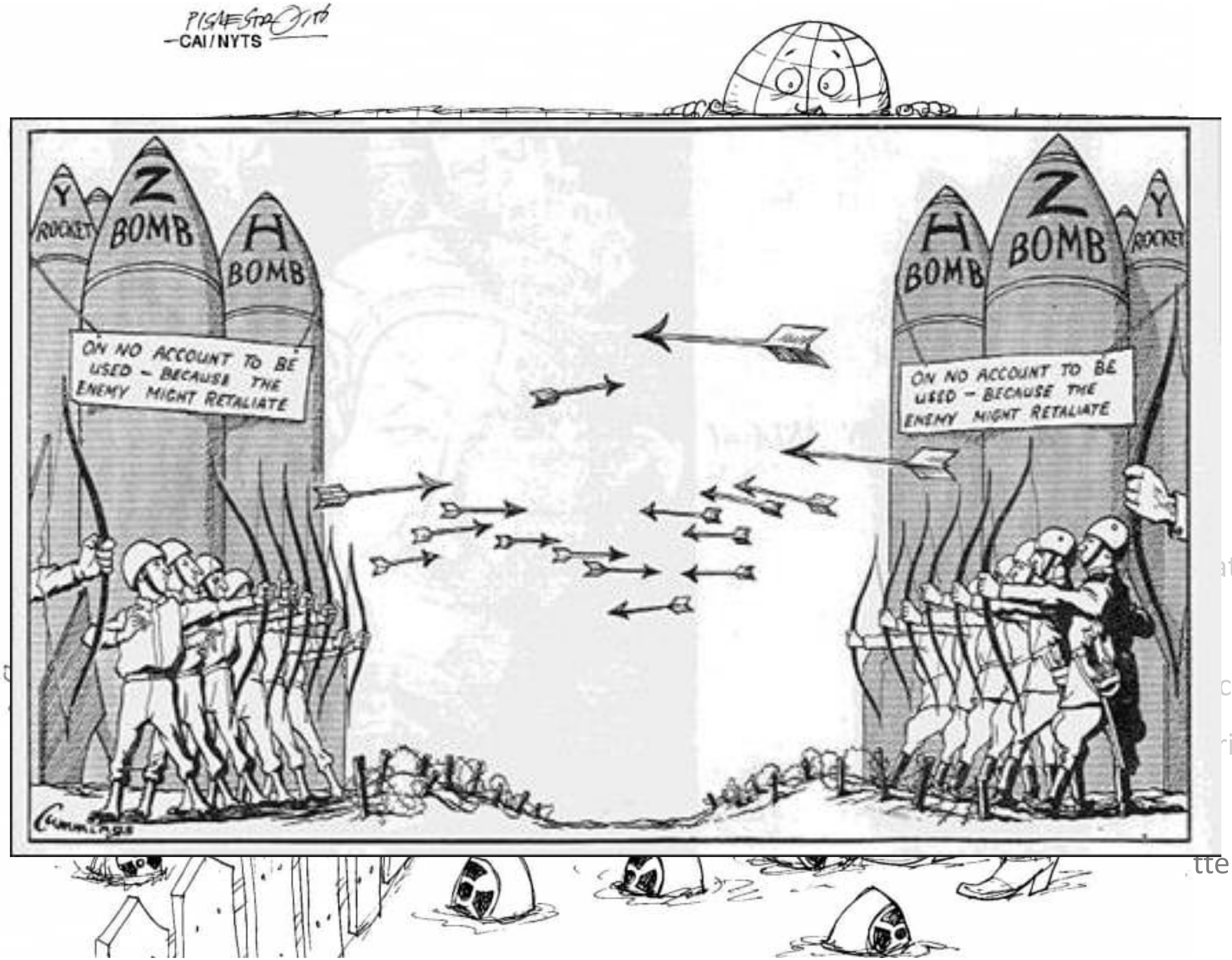
Krebs and Dawkins, 1978



Communicatio

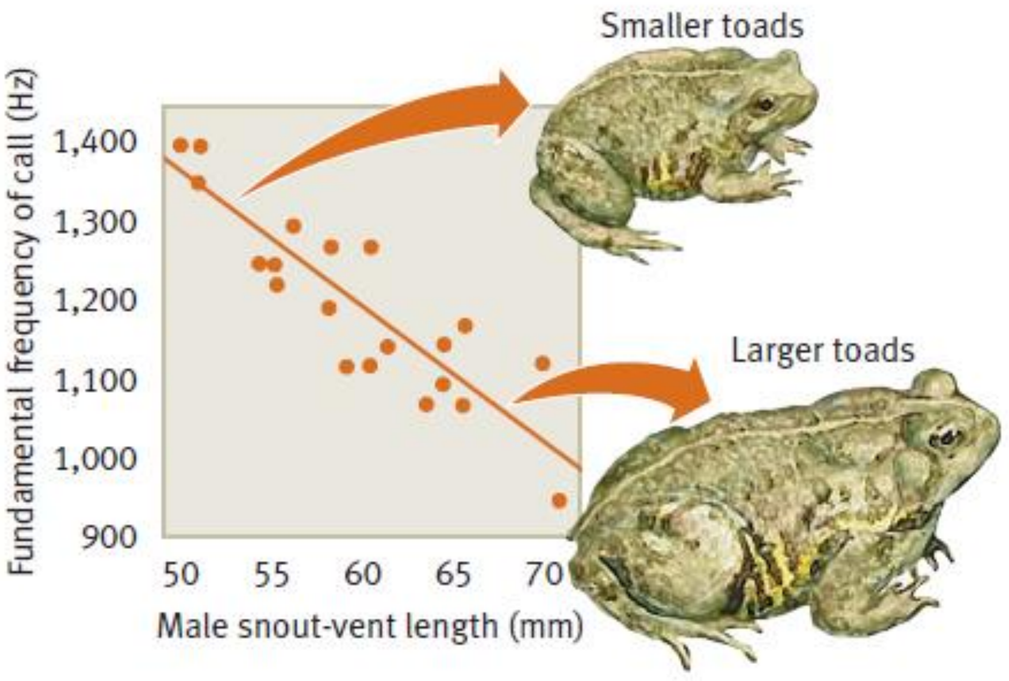
- When what is go … at send signals in whateve …
- But natural select … can act in ways that max … ribe an "arms race" betw …
- In 'arms race' whi … tter filter out only that infor …

Even within the manipulator/mind-reader view of communication, honesty might evolve:

- ❖ **Signals being sent are impossible**
- ❖ **Or at least, very difficult to fake**

But…

This appears to be the case in toads:
Deep croaks and physiological advantage



Under Zahavi's handicap principle

- ❖ Honesty is also possible when traits are not impossible but merely very costly to fake
- ❖ Honest communication may be an outcome even when deception is possible in principle, as long as deception is costly

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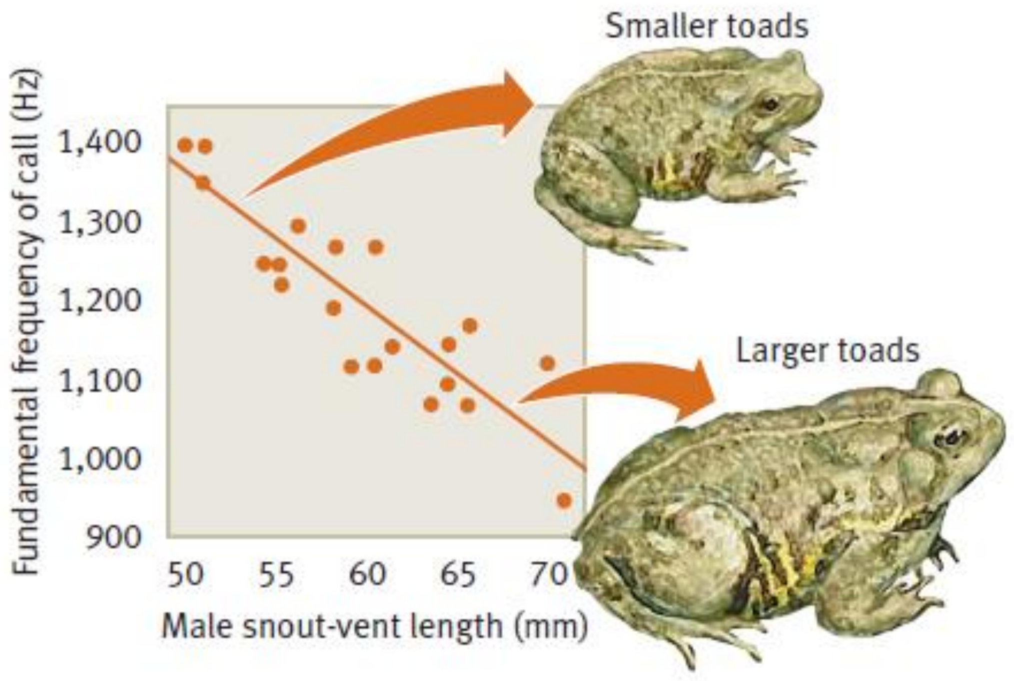

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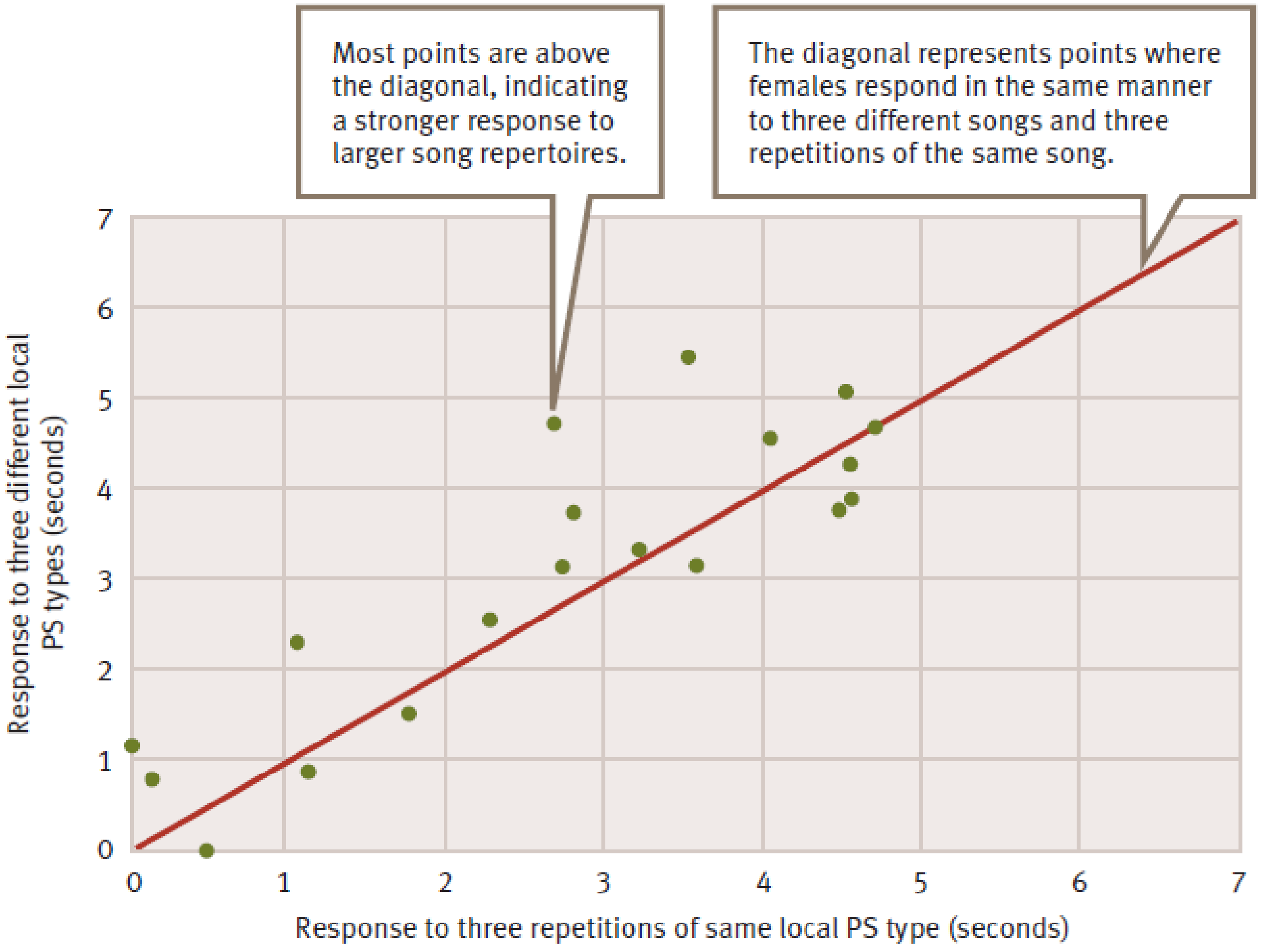
This thought leads Amotz Zahavi to *Handicap principle*

Competitive altruism: In Arabian babbler the helping-at-the-nest behavior often occurs among unrelated individuals- thus cannot be explained by kin selection-The altruistic act is costly to the donor, but may improve its attractiveness to potential mates

Obesity, a sign of ability to procure or afford plenty of food, comes at the expense of health, agility, and in more advanced cases, even strength; in cultures that experience food scarcity, this exhibits "fitness" to the opposite sex and is also often associated with wealth

Peacock to peahen 'I have survived in spite of this huge tail; hence I am fitter and more attractive than others'

Response to male cowbirds song by female:
Each point represents the copulation-solicitation displays (CSDs) of one female



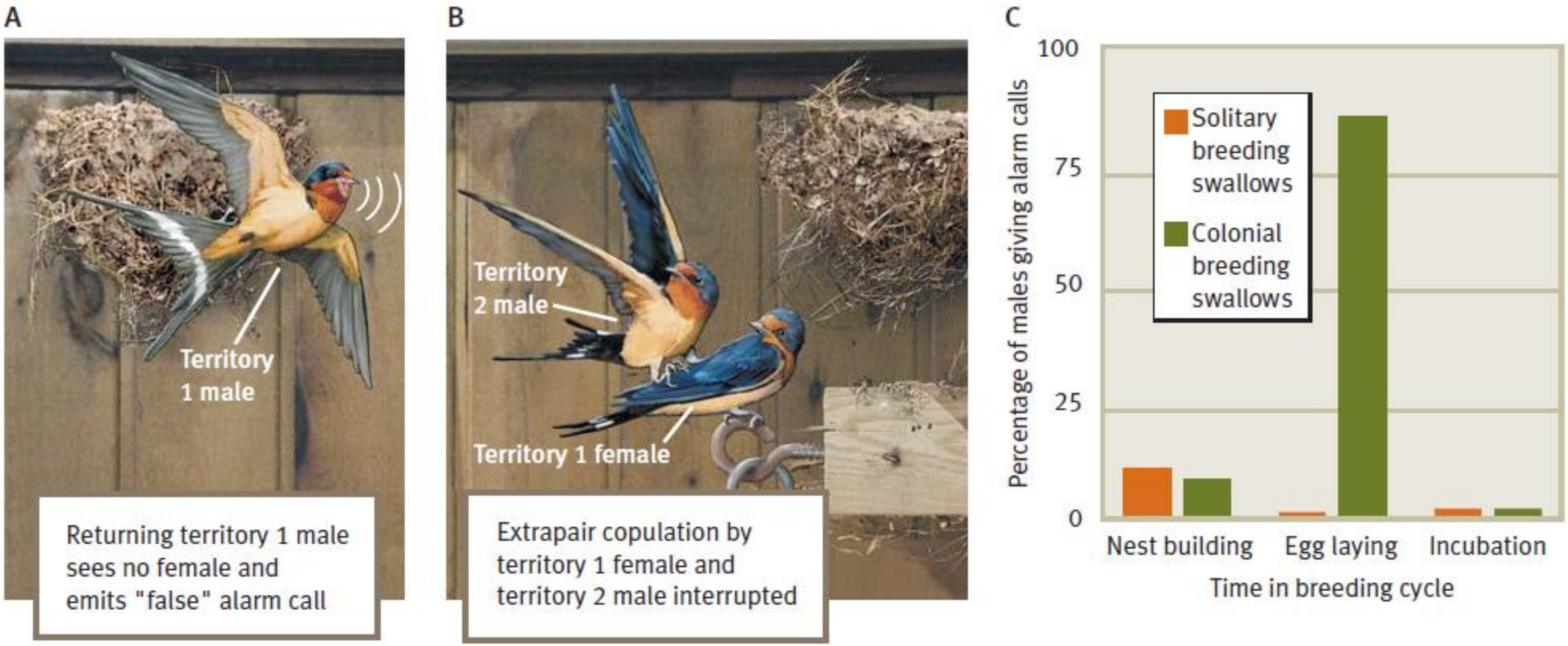


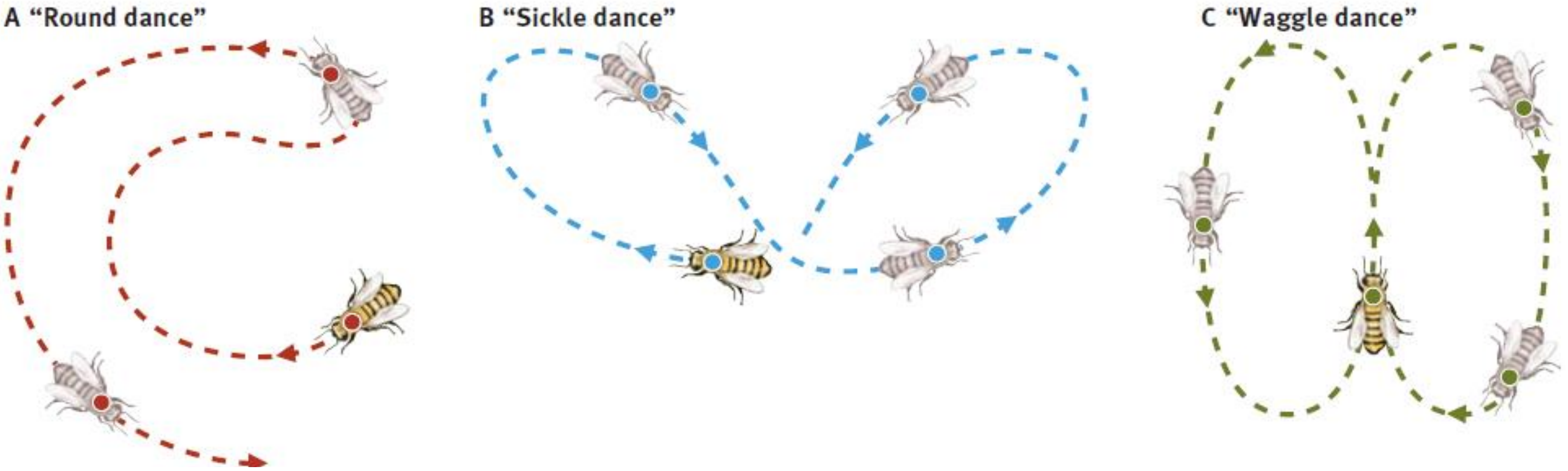
FIGURE 13.23. Dishonest alarm calls in swallows? (A) Male barn swallows often give false alarm calls when their fertile mates leave the nest vicinity. **(B)** These false alarm calls sometimes disrupt extrapair copulations (EPCs). **(C)** Møller hypothesized that male swallows would give false alarm calls when they were at the greatest risk of EPCs to disrupt the EPCs. To test this hypothesis, Møller removed a female from the nest at different stages in the breeding cycle for both solitary breeding swallows and colonial breeding swallows. Solitary breeding males almost never emitted alarm calls when their mate was temporarily gone. Colonial breeding males emitted false alarm calls during the period in which EPCs were most likely (during egg laying). *(Based on Møller, 1990)*

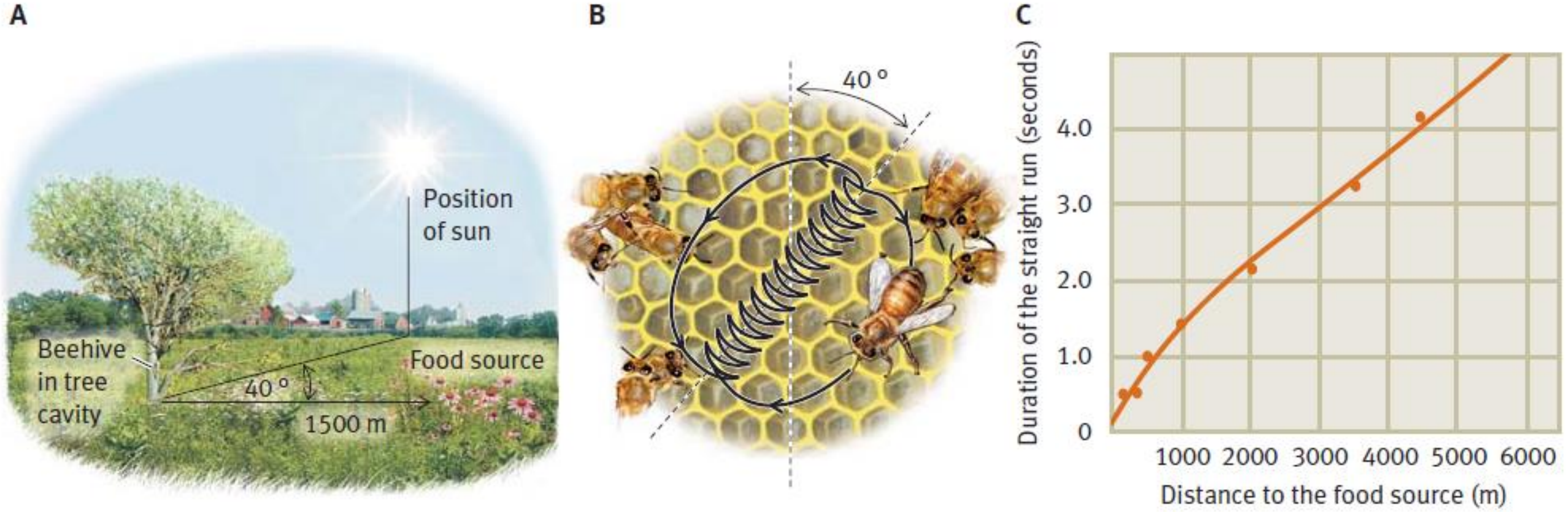
Deceptive Alarm Calls!!?

A B C

FIGURE 13.24. Deceptive alarm calling in topi. (A) A male topi (in background) has given a false alarm snort close to the boundary of his territory and now stares into the distance, as he does when a stalking predator has been detected. A sexually receptive female in the foreground (darker) looks toward the potential danger. **(B)** As the female begins to move away, the male looks toward the female (note the change in the orientation of his gaze and the different position of the ears. **(C)** Soon thereafter, the male mates with the female. *(From Bro-Jorgensen and Pangle, 2010)*

Honey Bee Dance Languages





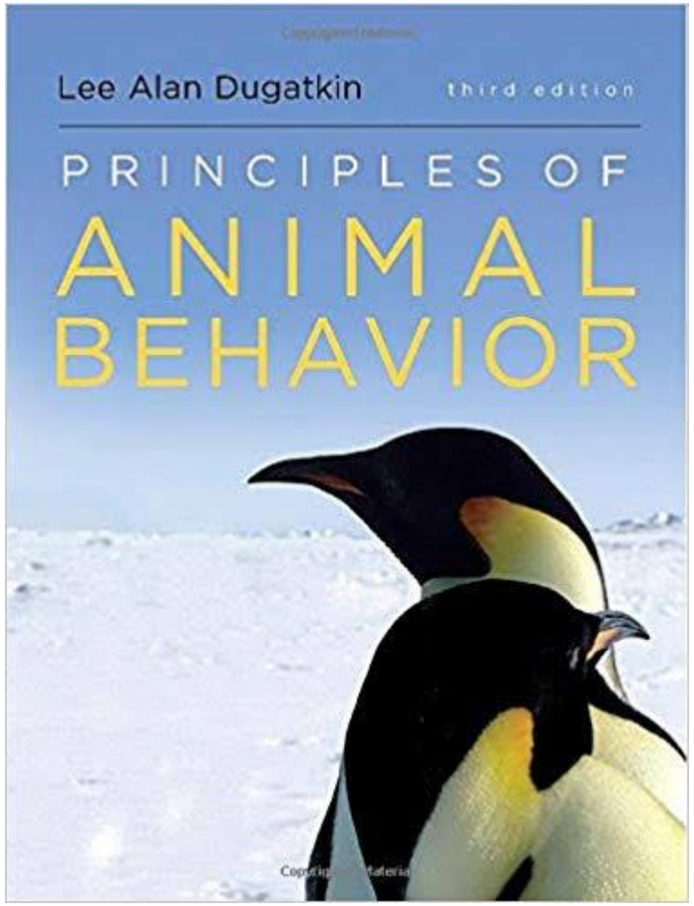
Modification of Behavior Due to Anthropogenic Disturbance

Cock-of-the-Rock (South America/Peru)

Altering forest canopy in or near lek (traditional place where males assemble during the mating season and engage in competitive displays that attract females) leads to…

(1) stop males from displaying at all because of increased exposure to predators,
(2) induce males to display so often that they become energetically drained, or
(3) lead to females no longer being able to assess male quality accurately

References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That's all Folks!