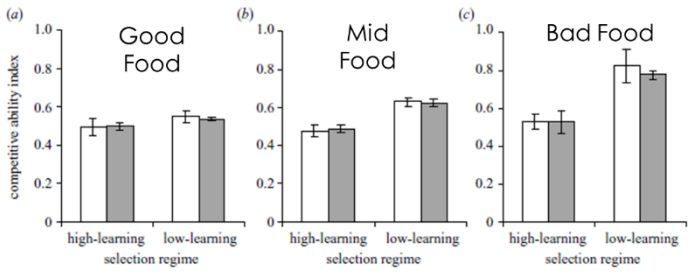
Lecture 07 – Animal Behavior

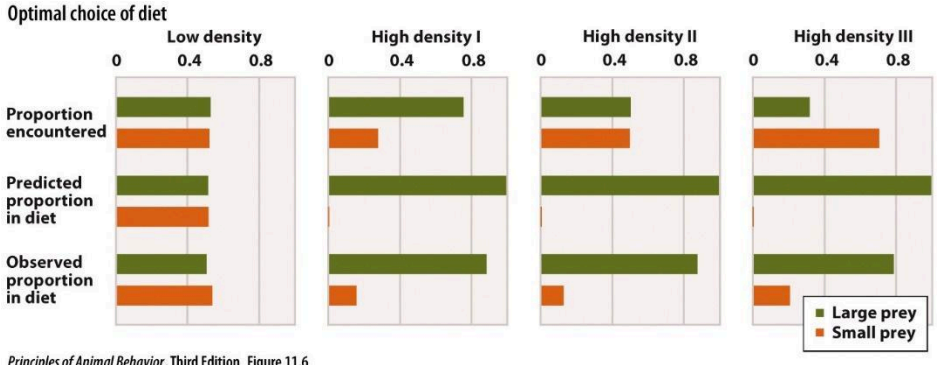
1. What is behavior?
    a. coordinated responses of whole living organisms to internal and/or external stimuli
    b. Two types of questions when studying behavior:
        i. Proximate Questions: How? What is immediate, mechanistic cause of behavior?
        ii. Ultimate Questions: Why? What is evolutionary root of behavior?
    c. Natural selection impacts behavior
2. Innate vs Learned Behavior
    a. Innate behaviors:
        i. Strong genetic component; Independent of environmental influences
        ii. Fixed Action Patterns (FAPs)
            1. invariant behavior triggered by simple stimulus
            2. Typically operate via fixed rules
            3. Can be exploited by "code breakers"
                a. Brood parasitism
    b. Learned behaviors:
        i. Result from environmental conditioning
        ii. Phase-dependent Learning
            1. Imprinting
        iii. Classical Conditioning
            1. Creates a link between some stimulus and some response
                a. Famous example: dog salivates in response to bell
            2. Components:
                a. Conditioned Stimulus (CS): no initial response
                b. Unconditioned Stimulus (US): has initial response
                c. Conditioned Response (CR): Learned response to CS
                d. Second Order Conditioning**:** Once you have some CR, pair it with a new CS (call it CS2)
        iv. Operant Conditioning
            1. Reinforces or suppresses some response via reward or punishment
                a. Law of Effect: if stimulus/ response is followed by positive event, response will be strengthened, and *vice versa*
        v. Why do animals learn?
            1. Wasp example:
                a. *Polistes fuscatus*: social
                b. *Polistes metricus*: solitary
                c. *P. fuscatus* capable of pairing facial stimuli with response; *P. metricus* unable to do so
            2. Cost of learning
                a. Gaining experience can be costly



Mery and Kawecki 2003

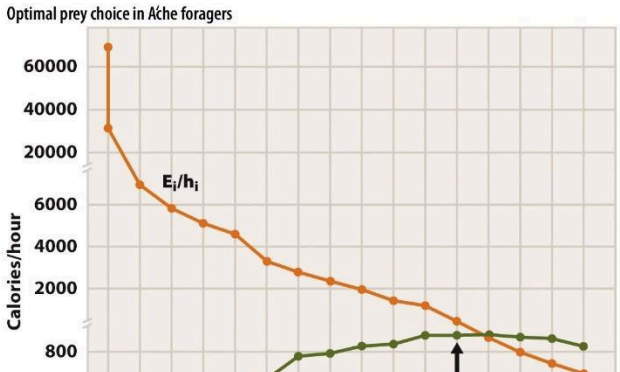
   b. Ability to learn carries tradeoffs
3. If environment is moderately changing, select for learning (worth cost!)
4. If environment is constantly changing, or never changing, select for innate behavior

3. Foraging
   a. Search Image
      i. Key into simplified search image to detect important features of envi
      ii. May be simplified total prey, prey color, etc.
      iii. As organisms gain experience, often become better foragers
         1. May be due to improved search image
   b. Optimal Foraging Theory
      i. Natural selection acts on foraging such that they <u>appear</u> to undertake complex mathematical decision making to optimize energy intake/unit time
      ii. What to eat:
         1. Parameters:
            a. Energy Value of Food (e_i)
            b. Encounter Rate (λ_i)
            c. Handling Time (h_i)
         2. Net Profitability of food item $E_i = e_i/h_i$



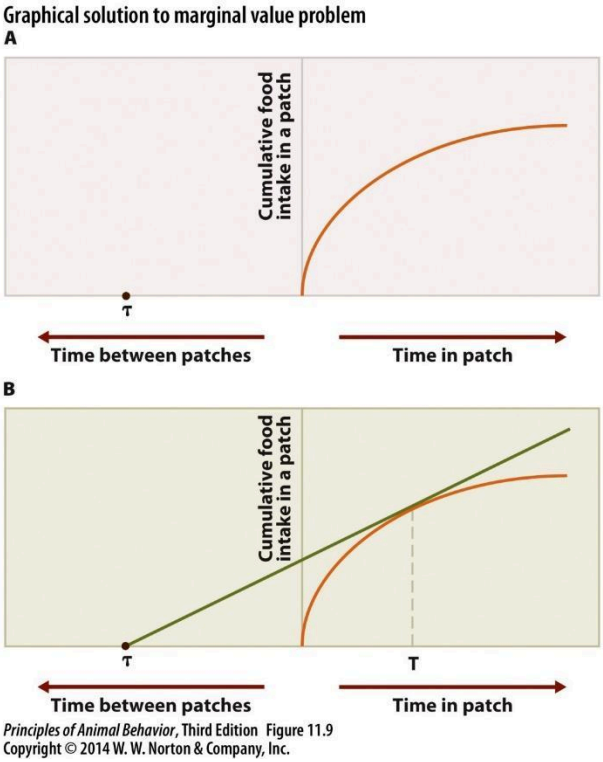
Principles of Animal Behavior, Third Edition Figure 11.6
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         3.
         4. Interesting result: so long as high quality food has high enough encounter rate, encounter rate of low quality food does not matter at all
            a. Ache forager example



      iii. Where to eat:

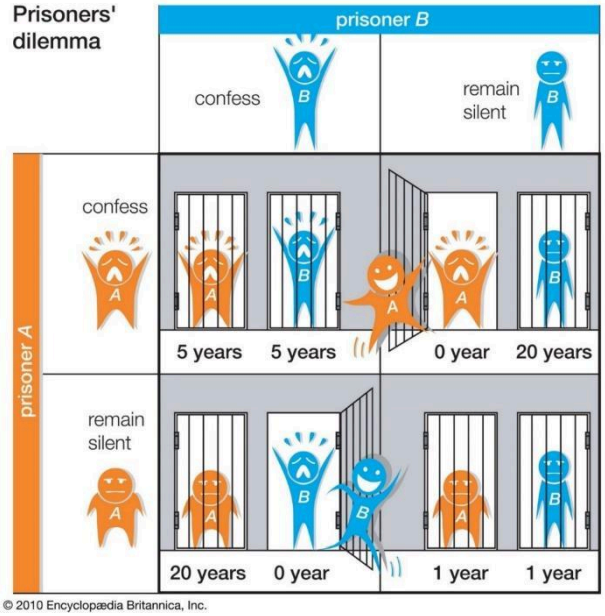
1. Patches: clumps of food that can be depleted by forager
2. OFT predicts animals will maximize speed with which food is taken from patches
3. Marginal Value Theorem: used to describe situations where organisms face diminishing returns
    a. As animals feed in a patch, patch value declines
    b. When should organisms seek another patch?
    c.



4. Cooperation
    a. How do animals cooperate?
        i. Many ways!
        ii. Foraging
        iii. Hunting
        iv. Avoiding Predators
        v. Mating
        vi. Play
        vii. Aggression
    b. How does cooperation evolve?
        i. Evolutionary problem
        ii. altruism: behavior which lowers the fitness of the actor, but increases the fitness of another individual
        iii. An altruistic organism will be selected against, because cheaters will gain at the expense of altruists
        iv. Yet, many examples of altruism/cooperation in nature. How do we explain this?
    c. Pathways to cooperation
        i. Byproduct Mutualism
            1. No altruism required; individuals who do NOT cooperate suffer costs
            2. No temptation to cheat, as that would actually reduce fitness
            3. Cooperation is byproduct of natural selection
            4. House sparrow example
        ii. Reciprocity
            1. "You scratch my back, I'll scratch yours"
            2. Exchange of altruistic behaviors
                a. Individual A suffers some cost to help individual B, but recoups that cost later when B returns the favor
            3. Reciprocity in vampire bats
                a. Will regurgitate blood for starving individuals; individuals will reciprocate at later date
                b. Factors which make reciprocity possible in this population:

i. High likelihood of future interaction
ii. Huge benefit of blood meal to recipient, less cost to satiated bat
iii. Recognize one another

4. Modeling Cooperation with Game Theory – Prisoner's Dilemma
   a. T = temptation to cheat (highest reward)
   b. R = reward for cooperating (2nd highest reward)
   c. P = punishment for both cheating (2nd lowest)
   d. S = "sucker's payoff" (worst)
   e. T>R>P>S



   f. Using iterated prisoner's dilemmas, can assess repeated interactions (required for reciprocity)
   g. Evolutionary stable strategy: Strategy that, if used by most members, no mutant strategy could invade
      i. ALLD: Always defect
         1. Might be a lousy population (not cooperative makes fitness worse than it could be), but no strategy can invade
      ii. TFT: Tit for Tat
         1. Repeat your opponent's last move; stable
         2. 3 features:
            a. Nice (never cheats first)
            b. Retaliatory (responds to cheating with cheating)
            c. Forgiving (forgives earlier cheating)
         3. Stable, but only if TFT players at high frequency

5. Reciprocity in humans
   a. Played monetary prisoner's dilemma while in fMRI scanner
      i. Highest MONETARY award when you successfully cheat
      ii. Highest EMOTIONAL award when you both cooperate

b. When given the opportunity, tend to punish those who cheated against you
    i. Greater pleasure from more intense punishment

iii. Kin Selection
1. By helping relative, even if the actor suffers some cost, actor may be increasing frequency of genes in population
2. Hamilton's Equation: $\Sigma \mathbf{rB > c}$
    a. r = relatedness to actor
    b. B = benefit to receiver
    c. c = cost to actor
3. For parent-offspring, relatedness = 50% (should help spawn if benefit to child is 2x cost to actor)
4. Example: alarm calls in ground squirrels
5. Kin selection on antisocial behavior
    a. Homicide rates in humans
    b. In 1972 Detroit, large number of murders of related individuals
    c. Does this invalidate kin selection?

iv. Group Selection
1. Within a group, selection will always favor cheaters over altruists
2. However, if BETWEEN group pressures are high (groups behave aggressively toward one another, or compete for resources), selection can favor group with highest fitness
    a. One path to high fitness: cooperation and social cohesion!
3. Group selection can push toward altruism if between group pressures > within group pressures
4. Example in ants
    a. Queens cooperate with one another until colony gets off the ground
        i. Allows them to survive in an environment with slave-raiding ants
        ii. Here, between>within
    b. Once colony is established, queens turn on each other
        i. At that point within>between

Focal Questions:

1. What is behavior? What types of questions can we ask about animal behavior?
2. What is the difference between innate and learned behavior?
3. What are types of innate behavior? Learned behavior?
4. How is Classical different from Operant Conditioning?
5. Do all animals learn the same? Are all animals equally capable of learning? Why might selection NOT favor learning?
6. What is search image theory?
7. What is optimal foraging theory? What is important in determining energy value of food?

8. How do organisms know when to leave one patch for another? What factors are important?
9. Why is altruism an evolutionary problem?
10. What are the four pathways to the evolution of cooperation? Understand what each means and how it works
11. What is the prisoner's dilemma game? How is it used to model cooperation?