

Chapter-wide Learning Outcomes for Behavioral Ecology

Upon completion of *Behavioral Ecology*, students should be able to:

1. Persuade a lay audience that evolution selects for behaviors that improve an individual's fitness, which is why behavior makes no sense absent evolution's lens.
2. Demonstrate how ecologists use the scientific method to analyze behavior.
3. Show how models are used to generate testable predictions from a given hypothesis.
4. Show how hypotheses predictions can be tested with observational and/or experimental data.
5. Defend why ecologists continue to use models, even though their assumptions are often violated.
6. Develop prediction graphs for a given experiment from a verbal hypothesis.

Behavioral Ecology, Part 1: So Many Choices

Upon completion of *Part 1: So Many Choices*, students should be able to:

1. Defend Theodosius Dobzhansky's assertion that "nothing in biology makes sense except in the light of evolution."
2. Contrast Tinbergen's four key questions about behavior (Causation, Development, Function, and Evolution).
3. Break down the fitness benefits and costs of a given behavior.
4. Explain why ecologists often rely on proxies like energy gain, reproductive output, and survival when estimating fitness.
5. Show how phylogenies can be used to test hypotheses about evolution.
6. Explain how the ecology of fear is expected to influence foraging behavior.
7. Show how giving-up densities can be used to assess a forager's perception of predation risk.
8. Provide examples of studies supporting the hypothesis that animals select foraging sites that reduce their perceived predation risk.
9. Predict the optimal foraging distance for a central-place forager from a model showing how benefits and costs are expected to vary with distance traveled.
10. List the major assumptions of optimality theory (i.e., costs and benefits are measured in the same currency; and the costs and benefits of different behavioral choices can be estimated).
11. Identify optimum behavior based on difference between the cost and benefit curves.
12. Recognize that shape of the cost-benefit curves includes information about the underlying relationship between variables.
13. Modify a graphical cost-benefit model of foraging to account for predation risk, given assumptions about how the risk of predation varies.
14. Show how the predictions of a simple, graphical cost-benefit model of foraging behavior can be tested with observational data.

Behavioral Ecology, Part 2: Behavior in the Marketplace

Upon completion of *Part 2: Behavior in the Marketplace*, students should be able to:

1. Choose an appropriate model to evaluate the hypothesis that an individual is foraging optimally—that it is maximizing its fitness gain.
2. List the major decisions an animal makes when foraging.
3. Predict when an optimal forager should broaden its diet to include an additional prey item based on Charnov's model of prey choice.
4. State Charnov's model of diet choice, its terms, and its assumptions.
5. Explain why Charnov's model of diet choice, predicts that the decision to switch between foraging as a generalist and as a specialist should be abrupt and should depend on S_1 , the search time for the preferred prey, but is independent of S_2 , the time required to find the less preferred prey.

6. Discuss how aspects of food quality, other than energy content, may cause an optimal forager to expand its diet.
7. Show how energy content and handling time affect prey quality.
8. Show how Krebs et al. (1977) were able to experimentally test the predictions of the optimal diet model using great tits.
9. Predict how long an optimally foraging central-place forager should spend in a patch and how large a load it should collect according to the marginal value theorem.
10. Explain the graphical model of the marginal value theorem, including its terms, curves, and what it predicts about optimal foraging time and optimal loads.
11. State the assumptions of the marginal value theorem.
12. Explain why the marginal value theorem predicts that an optimal forager should spend less time foraging in near versus distant patches.
13. Explain why the marginal value theorem predicts that an optimal forager should spend less time foraging in a high quality patch than in a low quality patch.
14. Provide examples of how optimality models have been able to provide insight into human behavior.

Behavioral Ecology, Part 3: Playing Games

Upon completion of *Part 3: Playing Games*, students should be able to:

1. Analyze how decisions made by other actors influence the costs and benefits associated with a given behavioral choice and thus which strategy is expected to yield the greatest fitness gain.
2. Demonstrate how game theory can provide insight into conflicts between individuals, including when these conflicts are likely to escalate.
3. Show how the expected payoffs associated with a given strategy will vary depending on the strategy adopted by two or more players.
4. Explain the Hawk-Dove game and what it describes, including its assumptions, strategies, and payoff matrix.
5. Explain how the ESS for the Hawk-Dove game can be pure Hawk or mixed, but can never be pure Dove.
6. Distinguish between a pure and mixed ESS.
7. Explain the two mechanisms that can produce a mixed ESS.
8. Describe two distinct situations in which males should be willing to fight for mates.
9. Calculate the expected payoffs for the Hawk-Dove game.
10. Provide examples of a conditional strategy.
11. Explain how adding the Bourgeois strategy to the Hawk-Dove game can add realisms.
12. Explain why frequency-based selection is important using examples.
13. Describe how individually rational decisions can lead to a collectively poor outcome in a game known as the Prisoner's Dilemma.
14. Define the Prisoner's Dilemma in terms of the relative payoffs of the four outcomes that are possible when two players can either cooperate or defect.
15. Explain why the conflict between marauding bowerbirds is a good example of the Prisoner's Dilemma.

Behavioral Ecology, Part 4: Family Matters

Upon completion of *Part 4: Family Matters*, students should be able to:

1. Construct logically consistent verbal hypotheses about sexual selection, mate choice, and sexual conflict.
2. Explain variation in mating strategies, male and female morphologies, parental investment, and sexual conflict using the theory of sexual selection.
3. Explain how differences in investments between males and females set up an asymmetrical contest where evolution favors different strategies for each sex (i.e., choosy females promiscuous males).
4. Graphically illustrate the relationship between variation in fitness of males and females and strength of sexual selection.
5. Explain how mating strategies tend to be influenced by strength of selection.

6. Provide examples of the four most common mating strategies, monogamy, polygyny, polyandry, and polygynandry.
7. Predict whether males or females are likely to provide parental care based on mating system, parental certainty, and other relevant factors.
8. Evaluate evidence suggesting that male parental care can vary with certainty of paternity.
9. Provide examples of when divergent evolutionary interests leads to sexual conflict.
10. Summarize the conditions that favor intrasexual selection (male-male conflict) vs. the conditions that favor intersexual selection (female choice).
11. Describe the traits that male-male conflict tends to favor.
12. Describe some of the alternative strategies smaller males have adopted in order to gain mating opportunities when direct conflict with large males is unlikely to be successful.
13. Explain what must be true if both dominant males and sneaky males are to coexist in a population—i.e., if the ESS is mixed.
14. Describe multiple hypotheses for why females may prefer certain males over others (including both direct and indirect benefits).
15. Design a set of experiments to evaluate the various hypotheses explaining why a certain species of females prefers some males over others.
16. Generate logical, graphical predictions that would allow you to discriminate between competing hypotheses for how females choose their mates.

Behavioral Ecology, Part 5: Cooperation

Upon completion of *Part 5: Cooperation*, students should be able to:

1. Describe the potential costs and benefits of group living.
2. Provide examples of the four types of social interactions (i.e., cooperation, mutual benefit, selfishness and spite).
3. Summarize the evidence suggesting that while kin selection may help maintain eusociality, it cannot fully explain its origin.
4. Defend the claim that altruistic behaviors can be explained without invoking group selection.
5. Design a set of experiments that could distinguish between the three primary hypotheses for altruistic behavior (i.e., behavior benefits actor, behavior benefits relatives, behavior is reciprocated).
6. Show how reciprocal altruism may explain the sharing of blood meals by vampire bats.
7. Explain how the repeated prisoner's dilemma can be solved with strategies like tit-for-tat.
8. Evaluate the evidence suggesting that Belding's ground squirrels call for two different reasons depending on whether they are being attacked by a terrestrial or an aerial predator.
9. State Hamilton's rule including both its terms and its assumptions.
10. Illustrate how both direct and indirect behaviors can contribute to an individual's inclusive fitness.
11. Show, using Hamilton's rule, that subordinate males benefit from helping dominate toms mate.
12. Provide examples of how "patient males" in some cooperative breeding may directly benefit by waiting until the dominant male dies to breed.
13. Explain why ecologists are reluctant to invoke group selection as an explanation for altruism or eusociality.