**Title:**

Simulation Games for Animal Behavior: *Exploring Tradeoffs of Group Living in Lions*

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**Abstract:**

Animal behaviorists study the mechanisms of behavior using both an empirical approach and theoretical modeling of the costs and benefits of a particular strategy. These models follow logical rules and generate simulated outcomes that help researchers who study dynamics of animals in their natural environments. Students of behavior can appreciate the wide-ranging contexts in which these are applied. To develop a model, costs and benefits of alternative strategies for an animal are translated into a system of units that serves as a proxy for fitness. These units, such as the rate at which an animal acquires calories, typically correlate with fitness. An individual animal is expected to behave in ways that promote this fitness after weighing costs and benefits of employing alternative strategies. We present here one of a series of games to use in conjunction with published studies. Students role-play, follow simple behavioral rules based on game theory, and are rewarded or penalized for the choices made with a goal of maximizing individual fitness. In general, these games are designed to enrich the classroom experience and to help students more thoroughly understand theoretical concepts in animal behavior and evolution.

**Learning objectives:**

This activity focuses on principles of evolution by natural selection, which is a core concept important to undergraduate education (AAAS 2011). Students will apply a theoretical framework that underlies the study of animal behavior, namely how a behavior, such as foraging or breeding, is ultimately enacted by individuals of a population. Alternative strategies are typically available, and which one an animal chooses is likely the outcome of many trials and errors. The costs and benefits of these strategies can be modeled using basic economics so that the animal can maximize efficiency or fitness. This simulation game offers an opportunity for students to explore the consequences of different individuals choosing different strategies. Fitness rewards are represented by candy or some other “treat” and those individuals with the most rewards at the end of the game would enjoy the greatest fitness. Although this activity stops short of developing true mathematical models to simulate dynamics in animal behavior, students will learn how optimal strategies may evolve and how scientists can test theoretical models of how these strategies should be enacted.

**Time frame:**

This game can be incorporated into a 50-min class period. Student participants read the student handout and assigned published article before the activity (Mosser and Packer 2009). The instructor prepares specific materials (see below) and distributes the article for discussion. Several discussion questions for post-activity assessment are provided.

**List of materials:**

* enough dice for each player to have one
* Candy or other token of fitness reward (one piece = 1 fitness unit)

**Procedure and general instructions (for instructor):**

Prior to introducing and playing this game, students should read the article by Mosser and Packer (2009) cited below. The statistical analyses and modeling used in this paper are quite advanced, so some students may have difficulty understanding the results that lead to Mosser and Packer’s (2009) conclusions. We suggest that students skim these results with the assumption that the concluding statements are supported by rigorous analyses. For classes that emphasize modeling and statistical analysis, this article offers an opportunity to explore more advanced data analysis and modeling. Additionally, students should have a general understanding of terms and concepts related to and including altruism, competition, territoriality, and sociality. Many of these are described in the student handout. We refer to tokens in the description below, and these can be candy or any other representation of fitness. Discussion questions can be made available to students before, during, or after the exercise.

**How to play**

*General rules:*

* Lion prides share all their tokens equally.
  + Students should note that in the wild lions would not share food equally. Natural selection predicts that even within a pride, a lion should attempt to eat as much food as possible from joint kills. It would not be an evolutionarily stable strategy for a lion to stop eating and allow his or her pride mates to get their fair share of the food. Lions should always attempt to get the “lion’s share” of the food.
* Lions can refuse to join prides.
* Once a pride forms, no member can leave.
* Students should note that in the wild lions might leave their pride for a variety of reasons.
* Once a pride or individual has three or more tokens (collectively for a pride), it may move into the “plains.”
* If a pride or individual has two or fewer tokens, it must remain in the “woodland” area.
* Prides are composed of three to five individuals.
* If you or your pride lose(s) a challenge and have no tokens left, then you sit out a turn. When you return to the game, you or your pride gets one token and must go to the “woodland” area.
* Lions may only interact (join into prides, partake in challenges) with individuals or prides that are in their habitat area.
* The goal of the game is to have the highest number of tokens per individual, which reflects individual fitness.

*Play the game:*

* Designate one side of the room as “woodland” and one side of the room as “plains”
  + “Woodland” habitat is less desirable because it has fewer resources, as represented by the tokens held by each individual or pride
  + “Plains” habitat is more desirable because it has more resources as represented by the tokens held by each individual or pride
  + Have students (lions) count off, repeating numbers 1-4 until all students are assigned a number.
* Give each student the number of tokens proportional to their designated number (1-4)
* A lion’s fitness allocation, or number of tokens, determines which habitat it inhabits
  + Lions with three or four tokens go to the “plains” area
  + Lions with one or two tokens go to the “woodland” area
* For each round, lions have the option to

i. Join with other lions to form a pride

*OR*

ii. Challenge other prides or individuals for tokens:

* To challenge, bet a number of tokens against your competitor
  + Each lion rolls. This means that if a pride includes five lions, the pride gets five rolls.
  + The highest roll wins the all tokens in the challenge.

*OR*

iii. Do nothing. A lion may choose not to challenge another player or pride, or to join into a pride. However, a lion cannot say no to a challenge. So if another player challenges a lion, he or she must accept.

* Play as many rounds as time allows, and compare fitness units at the end of the final round.

**Concepts to consider:**

How did the number of prides or individuals in each area affect the other lions in those areas?

* + *Because individuals or prides may only challenge players in their own area, the more individuals or prides in your location, the more likely you are to be challenged.*
  + *Mosser and Packer (2009) found that female lions were subjected to higher rates of mortality and wounding in areas with more neighbors. Further, they found that prides with more neighbors were at higher risk of losing territory. When subjected to these risks of attack and territory loss in environments with many neighbors, lions were more likely to form larger prides in defense. In the simulation, assume that when more players occupy the same area, more “challenges” would occur.*

What strategy was most successful: was it best to join a pride, and if so what size pride? Was it best to remain as an individual?

* *Larger prides have superior resource holding power, represented in the game by more opportunities for dice rolls and winning tokens. On the other hand, smaller prides have lower resource requirements because they have fewer members.*

**Discussion questions, based on the article by Mosser and Packer (2009):**

1. Why does pride size, particularly number of adult females in the pride, correlate with territory size only in woodland regions but not in the plains?
2. Would the results of this study have been different if it was conducted in an area where interspecific competition and threats from animals like hyenas exceeded the threat of other lion groups?
3. How would the results have changed if the scientists used data on male territoriality and survival in the final results instead of just female data?
4. Why is it evolutionarily advantageous for mothers to treat their daughters as rivals after two years of independence?
5. Is it adaptive for lionesses to kill lionesses from neighboring prides?
6. Is it adaptive for male lions to kill adult females from other prides? In the long run is it more adaptive to keep females alive and possibly mate with them or to kill them based on resource allocation?

*Mosser and Packer (2009) conclude that it is adaptive for male lions to kill adult females from other prides if the females are not sexually receptive. They may be competing for food.*

1. When female lions raise their young communally and strategically group themselves together for safety, would you consider this altruism?
2. Why is it adaptive for male lions to kill the cubs sired by other males?

*It is adaptive because it minimizes competition for food and it shortens the time for lionesses to become sexually receptive again.*

1. Given that Mosser and Packer (2009) suggest that it is advantageous for lions to exist in large prides, why do some lions remain in smaller groups? Why have pride sizes not stabilized at a standardized large number?
2. The foundation of the scientific method is that science advances through the refutation of false hypotheses. An earlier hypothesis to predict lion pride size was that larger prides were more effective at hunting and killing large prey (Schaller 1972). Why is this no longer a viable hypothesis to explain the size of lion prides?

**Procedure and general instructions (for students):**

**Student Handout:**

*Exploring Tradeoffs of Group Living in Lions*

**Key terms:** altruism; inclusive fitness; indirect fitness; direct fitness; competition; territoriality

In the animal kingdom, many species live in social groups. These include pods of killer whales, packs of wolves, herds of elk, schools of fish, colonies of insects, and prides of lions. Such social groups are often composed of closely related individuals or family units that may or may not have a dominance hierarchy. In general, group living offers many advantages including better access to resources (e.g., food, mates, and shelter), protection from predation, and division of labor. However, individuals also face costs of exposure to disease, competition for resources, and increased conspicuousness to predators and competitors. The decision to live in a group or to live alone is one of many contexts in which alternative behavioral strategies exist simultaneously, and the outcome of such a decision may be predictable based on the fitness benefits for an individual. This is where scientists can use theoretical models to estimate costs and benefits of particular behavior strategies, compare the outcomes for each, and suggest how an individual might optimize its fitness. The activity described here provides an opportunity to actively apply the costs and benefits and have participants take on roles of individuals deciding between alternative behavior strategies.

In this simulation, players function as lions and make choices about whether to live in a pride or as an individual. When joining a pride, an individual may sacrifice some of its fitness (represented by tokens) to the benefit of others. For example, if player #1 has five tokens and joins a pride with players #2 and #3 who have only three tokens, then player #1 would be sacrificing some of its individual fitness for the benefit of the others. In the wild, seemingly sacrificial behaviors that have fitness costs to a donor may provide higher overall fitness for that individual if a recipient is related to the donor. This is a form of **altruism**, where the donor experiences a reduction in fitness and the recipient gains a fitness benefit. Kin selection enhances the motivation for altruistic behavior because the donor enjoys a boost in **inclusive fitness** when the recipient is a relative(Alcock, 2013)**.** **Inclusive fitness** is derived from effort put into ensuring survival of one’s own offspring (**direct fitness**) as well as non-descendant kin (**indirect fitness**). According to **Hamilton’s rule** (Hamilton 1964) altruistic behavior will spread among members of a population as long as the loss of direct fitness for an individual is less than indirect fitness gains. This is an interesting problem that invokes a mathematical model to calculate and compare estimated fitness values (see details in Alcock 2013).

The simulation presented here does not specifically consider relatedness of the players, though this can be an underlying motivation. The game does, however, factor in other tradeoffs of social living. The competition between different prides and individuals in this game, labeled as “challenges,” reflects the ecological costs and benefits of group living in terms of food acquisition and allocation. In the wild, a possible benefit of group living is improved foraging through the **information** **center** **effect** of a group home base (Ward and Zahavi 1973). By making decisions as a group, the members of the social unit rely on collective intelligence, and are therefore better able to determine the best course of action. In our game simulation, players experience how group living affects food acquisition; players gain more chances to roll a high number while disputing territory or resources (represented by tokens). In a “challenge,” one pride or individual bets tokens against another, and each player rolls their die to determine a winner over the disputed tokens. Each member of a pride rolls, so when there are more members of a pride (up to five), the chances of rolling a high number are greater. However, in the wild and in this game, there is a resource cost to group living. A single lioness can catch and eat a gazelle by herself, but in a pride, that lioness must share the food with the other members of the pride. When living as a group, there is more competition for food among group members but also potentially cooperation in the hunt. This means that if a pride of five individuals collectively has ten tokens, each member has a lower individual fitness (two tokens each) than an individual living alone with three tokens.

Another benefit for animals living as members of a social group is the amplified ability to defend resources from competitors. **Territorial** animals can monopolize high-quality habitats and resources, often forcing conspecifics to make use of less desirable areas. Through aggressive territorial defense, animals can increase their access to food resources or mating areas. However, territorial animals incur a cost in the form of energy expenditure and potential injury. Individuals with superior competitive ability are able to control the highest quality habitat but may be challenged often. Mosser and Packer (2009) observed and compared lions contending for control of habitat in short-grass plains and in lower quality woodland areas. For lions, group defense of a territory provides a competitive advantage that can facilitate the control of those higher quality habitats. In Mosser and Packer’s (2009) study, and in our simulation, the woodland habitat is less desirable because it has fewer resources. The plains habitat has more resources and is therefore more desirable. In this game, tokens represent resources. Prides and individuals with three or more tokens inhabit the plains area while those with two or fewer tokens inhabit the woodland area. When one player or pride challenges another, they fight for control of resources, as represented by the tokens that they bet. However, players must remember the costs of sharing resources (tokens) within their own pride. Even when an individual with two tokens inhabits the less desirable woodland habitat while a pride of five with six tokens occupies the plains, the individual maintains a fitness advantage by holding more tokens than are available to each of the pride members.

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iii. Do nothing. You may choose not to challenge another player or pride, or to join into a pride. However, you cannot say no to a challenge. So if another player challenges you, you must accept.

* Play as many rounds as time allows, and compare fitness units at the end of the final round.

**Concepts to consider:**

How did the number of prides or number of individuals in each area affect the lions in those areas?

What strategy was most successful: was it best to join a pride, and if so what size pride? Was it best to remain as an individual?

**OPTIONAL SECTIONS:**

*The following narrative was developed as an introductory overview for the instructor and students:*

Animal behaviorists take many different approaches in unraveling the proximate and ultimate mechanisms of behavior of animals in their natural environment. One approach for testing hypotheses about behavior is to use mathematical techniques to model the costs and benefits of a particular behavior strategy, and compare the value of different strategies (Goodenough et al. 2009). These models, based largely on those used in economics, follow logical rules and generate simulated outcomes that can be supported by empirical data. Behavior models are useful for researchers examining dynamics of animals in their natural environments, and students of behavior can appreciate the wide-ranging contexts in which these are applied.

To develop a model, costs and benefits of strategies for an animal are translated into common units that serve as a proxy for fitness. These units, such as the rate at which an animal acquires calories, typically correlate with fitness. For example, the faster an animal takes in energy, the greater fitness it will achieve. This proxy for fitness oversimplifies a system, but it generates much more information than waiting for the actual fitness measures of long-lived animals. In the end, once all relevant variables have been identified, a good model can be used to discover an optimal behavioral strategy under different conditions tested, and predict how an animal might behave, following simple behavioral rules, to maximize the difference between the costs and benefits, and hence its fitness. For many of these models, the goal is to maximize an individual’s fitness, and to behave in ways that promote this fitness after weighing costs and benefits of employing alternative strategies.

We present here one of a series of animal behavior games in which students role-play, follow simple behavioral rules, and are rewarded or penalized in terms of their “fitness” for the choices made. Fitness rewards can be in the form of candy. So the more candy an individual earns, the greater his or her fitness for choosing a particular behavioral strategy. These games use game theory, as described below, and are designed to enrich the classroom experience and to help students more thoroughly understand theoretical concepts in animal behavior. Through the use of such simulation games, students are able to take abstract concepts and examine them in a fun way, breaking down the concepts into logical and simple parts. These games are meant to augment class discussion by making more tangible the costs and benefits of choosing particular behavioral strategies over others.

Game theory was introduced to ecology and evolutionary biology by John Maynard Smith (Maynard Smith & Price 1973, Maynard Smith 1982), who demonstrated that competition between individuals can be assessed as a battle of “strategies” for which mathematical criteria can be used to predict outcomes of alternative behaviors. The well-known game theory model “The Prisoner’s Dilemma,” (von Neuman & Morgenstern 1944, Axelrod 1984) presents a scenario where different behavioral strategies have different consequences depending on how each of the two individuals behave. This model has been adapted as a simulation game that is fun to play in the biology classroom (Lynch 1994; Morgan, 2003).

For some students, the written description of the model or the verbal lecture can make the model clear. For others, the diagram representation serves as a sufficient explanation. By playing a game, however, students are able to test different strategies, experience the outcomes of punishment and reward, and are fully engaged with learning. This also helps to commit concepts and examples to memory and allows easy application of the concept to a variety of different situations. Indeed, active-learning methods can enhance understanding and retention in undergraduate science courses (Handelsman et al. 2007).

The game we present were is one of three designed by students enrolled in a semester-long upper level course, Animal Behavior (BI373) at Colby College in 2014. While the examples available here are tied to specific research articles that were concurrently under discussion, they serve well as examples and can be easily modified to meet classroom goals under different conditions. In general, the benefits to using these games to enrich curricula cannot be understated. The most obvious benefit is that difficult concepts are made enjoyable and memorable. Further, by combining lecture with the use of a simulation game, the instructor appeals to different leaning styles and enhances the students’ learning, maximizing the productivity of a class period. Students’ understanding of a concept, such as optimal foraging or reciprocal altruism, is reinforced by engaging with the lecture, reading the material, going through the physical motions of playing the game, and discussing the ideas stimulated from the readings and game-playing. Student collaboration and the breaking down of concepts through step-by-step play encourages discussion and consideration of behavioral aspects which might otherwise have been overlooked.

**Suggestions and materials for assessing student learning:**

Students should read the article by Mosser and Packer (2009), or another relevant article, before the class period, and can submit three to five questions of their own that they have about the article to the instructor or to the student discussion leaders. This helps to gauge how well they understand the concepts and the scientific approach used to address the hypothesis. After the exercise, students can work in small groups or all together to address discussion questions. Several of these are provided in the instructor handout, and additional questions can be drawn from those submitted by students before the class period. This calls for students to analyze information, formulate critical questions and hypotheses, evaluate and criticize evidence, or propose alternative solutions.

**Reference list:**

American Association for the Advancement of Science. 2011. Vision and change in undergraduate biology education: a call to action. <http://visionandchange.org/finalreport>.

Alcock, J. 2013. *Animal behavior: an evolutionary approach*. 10th edition. Sinauer Associates, Inc., Sunderland, MA, USA.

Axelrod, R. M. 1984. *The evolution of cooperation*. BASIC Books, New York, USA.

Goodenough, J., B. McGuire, and E. Jakob. 2009. *Perspectives on animal behavior, Parts 1-2.* John Wiley & Sons, New York, USA.

Hamilton, W.D. 1964. The genetic theory of social behavior, I, II. *Journal of Theoretical Biology* **7**:1-52.

Handelsman, J., S. Miller, C. Pfund. 2007. *Scientific teaching*. W.H Freeman and Company, New York, USA.

Lynch, A. 1994. The evolution of cooperative behavior. Pages 319–333 *in* C. A. Goldman, editor. *Tested studies for laboratory teaching, Volume 15*. Proceedings of the 15th Workshop/Conference of the Association for Biology Laboratory Education (ABLE), 390 pages.

Maynard Smith, J. 1982. *Evolution and the theory of games*, Cambridge University Press, Cambridge, UK.

Maynard Smith, J. and Price, G. 1973. The logic of animal conflict. *Nature* **246**: 15–18.

Morgan, K. N. 2003. Demonstrating strategies for solving the Prisoner’s Dilemma. Pages 359-378 *in* B. J. Ploger and K. Yasukawa, editors. *Exploring Animal Behavior in Laboratory and Field*. Academic Press, San Diego, CA, USA.

Mosser, A., and C. Packer. 2009. Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour* **78**:359–370.

von Neumann, J. and O. Morgenstern. 1944. *Theory of games and economic behavior.* Princeton University Press, Princeton, NJ, USA.

Shaller, G. B. 1972. *The Serengeti Lion.* University of Chicago Press, Chicago, USA.

Ward, P. and A. Zahavi. 1973. The importance of certain assemblages of birds as ‘information centres’ for food-finding. *Ibis* **115**: 517-534.