Beasts with Best Reponses:
Fresh Examples for Teaching Game Theory in Undergraduate Biology Courses

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Abstract
Game theory has been central to understanding animal behavior for over fifty years, yet undergraduate biology students are often exposed to only a narrow set of canonical examples, such as the hawk-dove game and the prisoner's dilemma. This paper introduces two fresh, research-grounded examples designed to enrich game theory instruction in undergraduate biology courses: (1) gray wolf self-domestication as a hawk-dove game and (2) northern lapwing nesting decisions as a coordination game. Each example highlights distinct strategic dynamics – competition and coexistence in the wolf game, and coordination and payoff dominance in the lapwing game – while extending naturally to discussions of evolutionary stability. To support flexible teaching, we provide handouts, an in-class activity, simulation tools, and AI tutoring prompts that help students engage with the material both in and out of class. Our aim is to make game theory more accessible, engaging, and biologically relevant, thereby strengthening students' quantitative reasoning.

Keywords: Game theory, animal behavior, evolutionary biology, active learning, classroom activities, quantitative skills, AI tutoring.

Biologists have used game theory to understand strategic inter- and intraspecific interactions in nature for more than 50 years (Maynard Smith and Price, 1973), but undergraduate biology students receive relatively little training in game theory, with many textbooks in animal behavior and evolutionary biology devoting just a page or two to the topic (e.g., Rubenstein and Alcock, 2018; Herron and Freeman, 2020; Futuyama and Kirkpatrick, 2023). This may be a missed opportunity. Because game theory is a subfield of mathematics, incorporating it into undergraduate courses addresses students' growing interest in quantitative skills (Coffey, 2024). And because game theory is widely used in economics (Dixit et al., 2025), political science (McCarty and Meirowitz, 2007), and international relations (Kydd, 2015), game theoretic examples have broad interdisciplinary appeal. Game theoretic examples also naturally lend themselves to classroom activities that can make the topic more engaging and, as a result, more memorable.

We present a pair of examples that are grounded in scientific research, that complement the hawk-dove and prisoner's dilemma examples found in many textbooks, and that highlight the importance of competition and coordination in animal behavior. Instructors can use one or both of these examples in different ways depending on how much time they wish to devote to game theory. We also provide handouts, assignments, instructions for an in-class activity, and interactive AI tutoring prompts instructors can use alongside these examples.

The most straightforward approach is to use the first example (gray wolf domestication) in class as way to explain concepts like best response and Nash equilibrium without simply restating the classic hawk-dove example (Maynard Smith and Parker, 1976) often found in textbooks. This would require no more class time than the standard presentation but may be more interesting for students who have already read about the classic game.

Instructors interested in spending a bit more time on game theory can pursue one or both of the examples further, introducing students to evolutionary stability. Alternatively, an instructor could walk through one of the examples in class, reserving the other example for an assignment students complete outside of class.

Gray wolf self-domestication as an example of a hawk-dove game

Dogs (*Canis familiaris*) are domesticated gray wolves (*Canis lupus*). Some researchers (e.g., Larson and Fuller, 2014) hypothesize that wolves initially domesticated themselves, with the friendliest, least timid wolves approaching human hunter-gatherer groups in order to eat the humans' food scraps.

This can be modeled as a hawk-dove game where two wolves must simultaneously decide whether to play Friendly or Timid. The payoff matrix presented in Figure 1 shows two wolves' payoffs in fitness points as a function of how each wolf behaves around humans. The row wolf's best response is to play Timid with humans when the column wolf plays Friendly, and its best response is to play Friendly with humans when the column wolf plays Timid. The same reasoning applies to the column wolf, so the game has two pure-strategy Nash equilibria: (***Friendly***, Timid) and (***Timid***, Friendly). At either of these equilibria, neither player can improve its own payoff by changing its own strategy. Unlike the prisoners' dilemma (Tucker, 1983), which has a unique Nash equilibrium, this game has multiple possible equilibria. Some students may find this counterintuitive. If the row wolf gets its highest possible payoff when it plays Friendly, why not always play Friendly? But game theory does not ask which strategy yields the best absolute payoff, it asks which strategy is the best response to the other player's behavior. If the row wolf anticipates the column wolf will play Friendly, then playing Timid earns it 3 fitness points, which is more than the 2 it would earn by matching friendliness.

An instructor might ask the students whether it is realistic to assume that non-human animals think through their options strategically. If not, why use game theory to describe animal behavior at all? The answer is natural selection. Wolves do not need to think rationally; some are simply born with tendencies that approximate best responses to the social games they face. These wolves tend to reproduce more successfully, so over time the population evolves with increasing numbers of individuals employing strategies that are best responses, even in the absence of conscious thought.

An instructor can take things a step further by discussing whether a given population state is evolutionarily stable, meaning it cannot be successfully invaded by mutants playing a different strategy. To do this, the instructor could rewrite the payoff matrix solely in terms of the

		Column wolf	
		Friendly	Timid
Row wolf	***Friendly***	(***2***, 2)	(***5***, 3)
	Timid	(***3***, 5)	(***2***, 2)

Fig. 1. Payoff matrix for the wolf-dog game. All payoffs are measured in fitness points, where a higher payoff is better. Each cell shows payoffs as (***Row payoff***, Column payoff). The two pure-strategy Nash equilibria are (***Friendly***, Timid) and (***Timid***, Friendly).

row wolf's payoffs, as seen in Figure 2, then calculate the row wolf's expected payoff assuming q is the proportion of column wolves playing Friendly[1]. Thought of another way, if the row wolf randomly encounters another wolf from the population, that wolf will play Friendly with probability q.

Figure 3 presents these expected payoffs graphically, with fitness on the vertical axis and the proportion of the population playing Friendly on the horizontal axis. Focusing on the monomorphic state where all wolves play Friendly (i.e., where $q = 1$), a mutant playing Timid will have a higher expected payoff (3 fitness points versus 2). It will therefore be more successful reproductively, and the proportion of wolves in the population playing Timid will increase over time. Likewise, in a monomorphic state where all wolves play Timid (i.e., where $q = 0$), a mutant playing Friendly will have a higher expected payoff (5 fitness points versus 2). It will therefore be more successful reproductively, and the proportion of wolves in the population playing Friendly will increase over time. This shows that either monomorphic state can be successfully invaded by mutants, meaning neither of these population states are evolutionarily stable.

Intrepid students might ask about the point where the two expected-payoff lines cross. This point represents a polymorphic population where

		Column wolf: Friendly (q)	Column wolf: Timid ($1-q$)	Row wolf's expected payoff
Row wolf	***Friendly***	***2***	***5***	$E(\pi_{Row}^{Friendly}) = 2q + 5(1-q) = 5 - 3q$
	Timid	***3***	***2***	$E(\pi_{Row}^{Timid}) = 3q + 2(1-q) = 2 + q$

Fig. 2. Payoff matrix showing Row wolf's expected payoff as a function of the population playing Friendly. The proportion of the population playing Friendly is denoted by q. Expected payoffs are measured in fitness points, where a higher payoff is better.

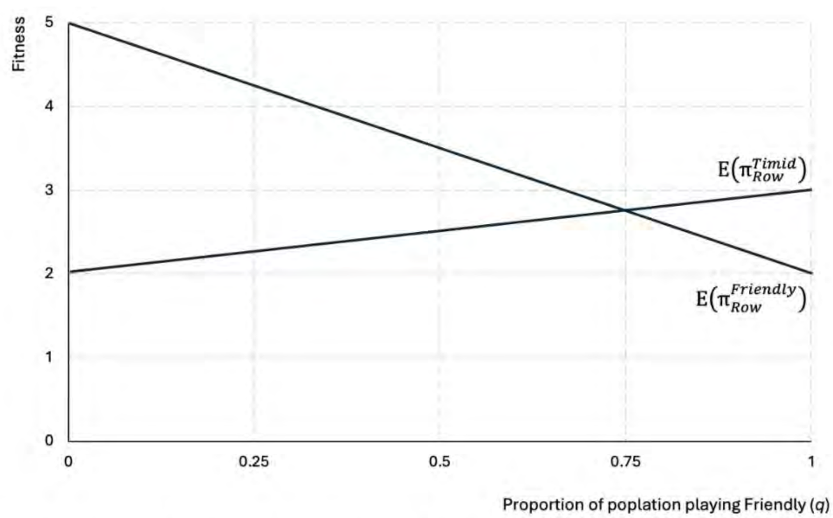

Fig. 3. Plot showing Row wolf's expected payoff as a function of the population playing Friendly. The proportion of the population playing Friendly is denoted by q. Expected payoffs are measured in fitness points, where a higher payoff is better.

[1]Following common practice in game theory, we use π to represent *payoff* in Figure 2 and later in Figure 5. Instructors may want to point out that this is distinct from the more common use of π to represent the mathematical constant roughly equal to 3.14.

3/4 of wolves play Friendly and 1/4 play Timid. At this critical point, wolves playing Friendly have the same fitness as wolves playing Timid, meaning neither has an advantage over the other and there is no tendency for the population to change. This is the game's unique evolutionarily stable population state. If a population that starts at q = 0.75 is somehow perturbed such that $q > 0.75$, wolves playing Timid will be fitter than wolves playing Friendly, meaning the proportion of wolves playing Friendly will decrease over time until the population returns to q = 0.75. Similarly, if the population is perturbed such that $q < 0.75$, wolves playing Friendly will be fitter than wolves playing Timid, meaning the proportion of wolves playing Friendly will grow over time until the population returns to q = 0.75.

Instructors can find a handout presenting this example at bit.ly/4ltNBSs. Depending on what instructors think is most appropriate for their class, they can provide this handout to students to work through as the instructor presents the material on the board, they can provide class time when students can work through the packet on their own or in small groups, or they can have students complete the handout outside of class as an assignment. We also provide the instructions for an in-class activity at bit.ly/45z6SMS. In this activity, students are assigned the role of either a friendly or timid wolf, then play the game from Figure 1 with five of their classmates. A student's total fitness score from these five rounds determines whether they would have one, two or three offspring. If an instructor assigns relatively few students to the friendly role (e.g., q = 0.15), students will see that friendly wolves dramatically outperform timid wolves, such that virtually all wolves with three offspring are friendly. In the interest of time, an instructor can use the Excel simulation for this exercise (bit.ly/4oOFQsl) to show how the outcome would be different when a given wolf goes has a 90% chance of being friendly. In this case, wolves having multiple offspring are disproportionately timid.

If students complete the handout for this game as a homework assignment, instructors may also want to provide them with the AI tutoring prompt available at bit.ly/40ZwUWP. This closely follows a prompt developed by Mollick and Mollick (2025). Students can copy the entire text of this prompt, paste it into the AI of their choosing, and then upload the assignment. Using this prompt, the AI will provide students with guidance and useful hints but will not simply present them with answers. Early evidence from Bastani et al. (2025) suggests that the deliberate feedback provided by this kind of AI tutor has a large positive effect on homework performance without harming performance on exams[2]. Another alternative would be to provide students with the AI prompt in the lead up to the next exam. Students could then use the AI tutor as a way to quickly review the handouts as they prepare for the exam.

In the next section, we present another evolutionary game. Instructors can present this new game instead of or in addition to the wolf domestication game. Alternatively, instructors can present one game in class, then send students home with the handout for the other game to complete as an assignment.

Northern lapwings' strategic nesting decisions as an example of a coordination game

The northern lapwing (*Vanellus vanellus*) is a Eurasian shorebird that nests in wetlands and farmlands (Cevenini et al., 2025). Its choice of nesting site is strategic because a nest built on farmland is less likely to be preyed upon when other lapwings build their nests nearby (Tilgar et al., 2024).

The nesting decision can be modeled as a coordination game where two lapwings must simultaneously decide whether to play Farmland or Wetland. The payoff matrix presented in Figure 4 shows two lapwings' payoffs in fitness points as a function of each bird's nest site selection behavior. Each cell shows payoffs as (***Row payoff***, Column payoff). The row lapwing's best response is to play Farmland when the column lapwing plays Farmland, and its best response is to play Wetland when the column lapwing plays Wetland. The

[2]The authors find that access to AI without the tutoring framework has a smaller positive impact on homework performance and a negative impact on exam performance, suggesting students use the AI as a "crutch," perhaps by simply pasting questions into the AI, then copying the answers.

same reasoning applies to the column lapwing, so the game has two pure-strategy Nash equilibria: (***Farmland***, Farmland) and (***Wetland***, Wetland). At either of these equilibria, neither player can improve its own payoff by changing its own strategy.

While this closely resembles the hawk-dove game, coordination games differ in that the two pure-strategy Nash equilibria involve each player matching the other's strategy. This particular game also differs from the one in the previous section in that the (***Farmland***, Farmland) Nash equilibrium leaves both players better off than the (***Wetland***, Wetland) Nash equilibrium. Game theorists would say the (***Farmland***, Farmland) Nash equilibrium is payoff dominant.

An instructor could end the formal game-theoretic analysis here and segue into a discussion of whether we can be sure the lapwings will end up at the payoff-dominant equilibrium where both nest in farmland. Most students can quickly come up with examples of situations where evolution has produced an outcome that would clearly seem to leave individuals worse off than they could be. And that is consistent with the game. If one lapwing builds its nest in wetlands, the other lapwing can do no better than to build its nest in wetlands. That is true even though the birds would obviously be better off if they both built their nests in farmland.

In this sense, this game also resembles the classic prisoners' dilemma, where the unique Nash equilibrium leaves both players worse off than they would have been if they had both played their other strategy. But what makes this game different is that if one lapwing builds its nest in farmland, the other lapwing can do no better than to build its nest in farmland as well.

As with the previous example, instructors interested in devoting more time to game theory can extend this example by discussing whether a given population state is evolutionarily stable. To do this, the instructor could rewrite the payoff matrix solely in terms of the row lapwing's payoffs, as seen in Figure 5, then calculate the row lapwing's expected payoff assuming the column lapwing is a random draw from a population where q is the proportion of lapwings playing

		Column lapwing: Farmland	Column lapwing: Wetland
Row lapwing	***Farmland***	(***4***, 4)	(***2***, 3)
	Wetland	(***3***, 2)	(***3***, 3)

Fig. 4. Payoff matrix for the lapwing game. All payoffs are measured in fitness points, where a higher payoff is better. Each cell shows payoffs as (***Row lapwing***, Column lapwing). The two pure-strategy Nash equilibria are (***Farmland***, Farmland) and (***Wetland***, Wetland).

		Column lapwing: Farmland (q)	Column lapwing: Wetland ($1-q$)	Row lapwing's expected payoff
Row lapwing	***Farmland***	***4***	***2***	$\mathrm{E}\left(\pi_{Row}^{Farmland}\right) = 4q + 2(1-q) = 2 + 2q$
	Wetland	***3***	***3***	$\mathrm{E}\left(\pi_{Row}^{Wetland}\right) = 3q + 3(1-q) = 3$

Fig. 5. Payoff matrix showing Row lapwing's expected payoff as a function of the population playing Farmland. The proportion of the population playing Farmland is denoted by q. Expected payoffs are measured in fitness points, where a higher payoff is better.

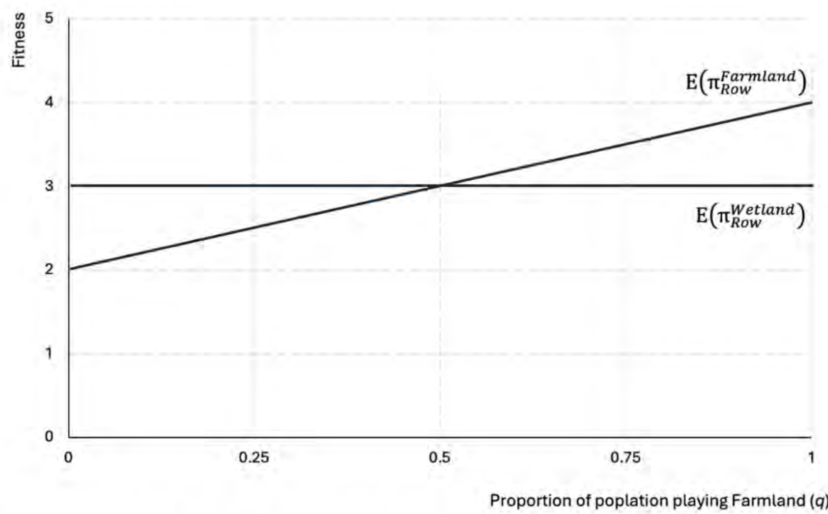

Fig. 6. Plot showing Row lapwing's expected payoff as a function of the population playing Farmland. The proportion of the population playing Farmland is denoted by q. Expected payoffs are measured in fitness points, where a higher payoff is better.

Farmland.

Figure 6 presents these expected payoffs graphically, with fitness on the vertical axis and the proportion of the population playing Farmland on the horizontal axis. Focusing on the monomorphic state where all lapwings play Farmland (i.e., where q = 1), a mutant lapwing playing Wetland will have a lower expected payoff (3 fitness points versus 4). It will therefore be less successful reproductively, and its mutant strategy will be unlikely to spread through the population. Likewise, in a monomorphic state where all lapwings play Wetland (i.e., where q = 0), a mutant lapwing playing Farmland will have a lower expected payoff (2 fitness points versus 3). It will again, be less successful reproductively, and its mutant strategy will be unlikely to spread through the population. This shows that neithermonomorphic state can be successfully invaded by mutants, meaning both of these population states are evolutionarily stable.

Again, students may ask about the point where the two expected-payoff lines cross. This point represents a polymorphic population where 1/2 of lapwings behave by playing Farmland and 1/2 behave by playing Wetland. At this critical point, lapwings playing Farmland are just as fit as lapwings playing Wetland, meaning neither has an advantage over the other and there is no tendency for the population to change. But unlike the example in the previous section, this critical point is not an evolutionarily stable population state. If a population that starts at q = 0.5 is somehow perturbed such that q > 0.5, lapwings playing Farmland will have higher fitness than those playing Wetland, meaning the proportion of lapwings playing Farmland will continue to grow until the population reaches to q = 1. Similarly, if the population is perturbed such that q < 0.5, lapwings playing Wetland will have higher fitness than those playing Farmland, meaning the proportion of lapwings playing Farmland will continue to decrease until the population reaches q = 0.[3]

Instructors can find a handout presenting this example at bit.ly/40pjvXW. The handout can be completed inside or outside of class. If completed outside of class, instructors may want to provide students with the AI tutoring prompt described in the previous section (bit.ly/40ZwUWP).

[3]In this example, we assume that lapwing breeding density never becomes high enough to cause overcrowding, which would otherwise reduce individual fitness or prompt birds to switch strategies and nest in an alternative habitat

Conclusion

Biologists have used game theory to explain animal behavior for more than 50 years (Leimar and McNamara, 2023.). The tools of game theory are so widely accepted that evolutionary biology and animal behavior textbooks now routinely include game theoretic examples complete with payoff matrices and discussions of Nash equilibrium (e.g., Bergstrom and Dugatkin, 2023; Nordell and Valone, 2024). However, this coverage is usually quite limited and rarely tied to a biologically relevant example grounded in empirical evidence. Instructors who are interested in presenting students with alternatives to the examples normally found in textbooks can use the framing and payoffs from either of the examples in this paper. Instructors who want to devote more class time to game theory can extend either or both of these examples through informal discussion or through a formal presentation of evolutionary stability. Interested instructors can supplement this formal presentation with the handouts and AI tutoring prompts we provide.

Acknowledgements

Our thanks to Arielle Cooley, Paul Whetstone, and an anonymous reviewer for comments that improved the paper.

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Corrigan, J.R & Levin: Appendices

Lapwing Game.docx

AI Tutor Prompt.docx

In-Class Activity.docx

In-Class Activity Simulation.xlsx

Lapwing Game.docx

Wolf Game.docx