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CONCEPT

Looking at the bid picture: A framework for identifying reverse auctions in ecological systems

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Abstract

1. Biological market theory can be used to explain intraspecific cooperation, interspecific mutualism, and sexual selection through models of game theory. These models describe the interactions between organisms as two classes of traders (buyers/sellers) exchanging commodities in the form of goods (e.g. food, shelter, matings) and services (e.g. warning calls, protection). Here, we expand biological market theory to include auction theory where bidding serves to match buyers and sellers.
2. In a reverse auction, the seller increases the value of the item or decreases the cost until a buyer steps forward. We provide several examples of ecological systems that may have reverse auctions as underlying mechanisms to form mutualistic relationships.
3. We focus on the yellow baboon (*Papio cynocephalus*) mating system as a case study to propose how the mechanisms of a reverse auction, which have the unintended but emergent consequence of producing a mutually beneficial outcome that improves collective reproductive benefits of the troop in this multi-female multi-male polygynandrous social system. For the yellow baboon, we posit that the “seller” is the reproductively cycling female, and the “buyer” is a male looking to mate with a cycling female. To the male, the “item for the sale” is the opportunity to sire an offspring, the price is providing safety and foraging time (via consortship) to the female. The “increasing value of the item for sale” is the chance of conception, which increases with each cycle since a female has resumed cycling post-partum. The female's sexual swelling is an honest indicator of that cycle's probability of conception, and since resident males can track a female's cycle since resumption, there is transparency. The males presumably know the chance of conception when choosing to bid by offering consortship.
4. Across nature, this reverse auction game likely exists in other inter- and intraspecific social relationships. Considering an ecological system as a reverse auction broadens our view of social evolution and adaptations through the lens of human economic structures.

KEYWORDS
biological markets, economics, evolutionarily stable strategy, game theory, mutualism, primates, reproduction

1 | BIOLOGICAL MARKETS AND AUCTION THEORY

Biological market theory was proposed to explain intraspecific co-operation, interspecific mutualism, and sexual selection through a model of game theory while taking into consideration how the two players or traders come together to consummate a mutually beneficial transaction (e.g. partner choice; Noë & Hammerstein, 1994). Biological markets describe the interactions between two classes of traders (e.g. buyers/sellers, males/females or breeders/helpers) exchanging commodities in the form of goods (e.g. food, shelter, mating) and services (e.g. warning calls, protection; Noë & Hammerstein, 1994, 1995). These relationships are termed as markets because the supply and demand changes which influences the behaviour of the buyers and sellers. These transactions may occur in intra- or interspecies relationships. For instance, male and female Barbary macaques (*Macaca sylvanus*) spend more time grooming mating partners than others they do not mate with (Lhota et al., 2019). In an interspecies scenario, aphids (*Metopeurum fuscoviride*) are protected by ants (*Lasius niger*) from predators which increases aphid fitness and the ants benefit by harvesting the honeydew that the aphids secrete (Flatt & Weisser, 2000). However, the fact that two traders receive mutual benefits does not imply that the exchange of commodities is worth the transaction (Hammerstein & Noë, 2016). A trader could refuse to engage with another trader if there is a better deal elsewhere, which highlights the importance of considering these relationships as part of a market with changing supply and demand. Because selection acts on the mechanisms of cooperation at the individual level, not the cooperation itself, it is necessary to understand how a trader's tactics drive evolutionarily stable strategies (Hammerstein & Noë, 2016). One major advantage of looking at biological systems through a lens of market theory is the wide breadth of knowledge already formed by experts in economics that can be used to understand complex evolutionary mechanisms.

We suggest expanding on biological market theory to further include auction theory, which in economics evaluates how markets match buyers and sellers via bidding. Auctions generally evoke the idea of the *forward auction*, or English auction, where the highest bidder wins the item for sale. However, there are other auction types. Here, we highlight the *reverse auction*, or Dutch auction, where the seller decreases the cost or increases the value over time until a buyer concludes the transaction (i.e. the buyer gets a better deal by waiting; Milgrom & Weber, 1982). Two simplified examples that constitute a reverse auction are: (1) a storeowner lowers the price of an item until it sells, or (2) the value of the item up for auction increases until a bid is received (e.g. a farmer selling grain keeps the price the same but augments the amount until a buyer emerges). In reverse auctions, the buyer, by waiting too long, risks losing the item to another who accepts the offer sooner. Reverse auctions are used in an economic setting because they allow small investors to take part in the offering and they aim to optimize the value of the item through transparency (Carter et al., 2004), which minimizes the difference between the value of the item and the bid. The reverse auction for the females provides continuous consortship as lower ranking males have an incentive to accept a smaller reward. Alternatively, the lower ranked or inexperienced males may be uninformed, and "bid" earlier than otherwise would be optimal for them thus subjecting themselves to the "winner's curse" (Kagel & Levin, 1986). Either way the female strategy of increasing the chances of conception with each cycle enhances their fitness. We propose that biological traders could have evolved reverse auction strategies to establish evolutionarily stable mating and mutualistic relationships.

2 | LOOKING FOR REVERSE AUCTIONS IN ECOLOGICAL SYSTEMS

The key components of a reverse auction are the seller, the buyer, the item for sale, an understanding of how the cost of an item for sale decreases or the value of the item for sale increases over time, an honest offer advertisement of the item for sale, and a strategy that ultimately benefits both the seller and buyer. If reverse auctions exist in natural systems, they will eventually become an evolutionarily stable strategy in certain intra- and interspecific relationships. One way to begin looking for reverse auctions in ecological systems is to identify items for sale (e.g. goods or services) where the value (e.g. quality or quantity) increases over time. Next, there needs to be an honest signal to the buyer that indicates the value of the item for sale is increasing. Next, there needs to be competition for the item for sale so that the buyer must decide when to purchase the item. At last, this system needs to accommodate both the seller and the buyer due to the probabilistic nature of the "game" and associated payoffs results in an evolutionarily stable strategy.

We have identified several mating and mutualistic relationships that possibly resemble reverse auctions. Table 1 lists some potential reverse auction strategies involving both within species mating systems and between species mutualisms. We also list knowledge gaps that if answered may reveal if these systems are truly using a reverse auction. The two-spotted goby (*Gobiusculus flavescens*) mating system where males guard nests might be an example of a reverse auction (Svensson et al., 2009). This relationship initially appears to be a candidate to fit the reverse auction model because female abdominal colour increases during the mating season and males prefer mating with females with more colourful abdomens. Sexually mature females develop orange abdomens from the carotenoid-rich

TABLE 1 Intra- and interspecific interactions that may use reverse auctions to balance costs and benefits and form an evolutionarily stable strategy. The seller is the individual with the honest signal that advertises the item for sale. The buyer is the individual that can either buy the item for sale now or later.

Species	Seller	Buyer	Item for sale	How value increases	Honest offer advertisement	Risks and costs	Strategy	Gaps in knowledge	Reference
Chacma baboon (*Papio ursinus*)	Female	Male	Consortship	Chances of conception increases with each cycle since resumption	Female sexual swelling indicates fertility	Males risk missed mating opportunities, but costs foraging time	Resident males know which cycles have higher chances of conception	Costs of consortship were inconsistent; uncertain how males track cycles	Henzi et al. (2003)
Olive baboon (*Papio anubis*)	Female	Male	Consortship	Unknown if conception probability is different amongst cycles	Female sexual swelling indicates fertility	Unknown	Males track fertility through female sexual swellings	Unknown if there are multiple cycles since resumption until next pregnancy	Higham et al. (2009)
Two-spotted goby (*Gobiusculus flavescens*)	Female	Male	Egg fertilization	Over time, the female invests more carotenoids into the eggs	Transparent abdomen that changes colour and shows ovaries	Males invest in nest guarding; females must use valuable carotenoids to display colour change	Females invest in colour change towards end of breeding window when males are fewer	Unknown if egg quality change over the spawning season	Svensson et al. (2009)
Straight-tailed razorfish (*Xyrichtys martinicensis*)	Female	Male	Egg fertilization	Ovaries become more visible as spawning time window approaches	Transparent abdomen with visible ovaries	Polygynous mating system where males are territorial and must track multiple females' fertility	Females possibly receive spawning priority	Unknown if male sperm quality or quantity declines over time which would incentivize females to spawn with male earlier in the season	Baird (1988)

(Continues)

TABLE 1 (Continued)

Species	Seller	Buyer	Item for sale	How value increases	Honest offer advertisement	Risks and costs	Strategy	Gaps in knowledge	Reference
Fruit-bearing plants and European blackcap (*Sylvia atricapilla*)	Fruit-bearing plants	Seed-dispersing animal (e.g. European blackcap bird)	Food (e.g. fruit)	Beneficial antioxidant (e.g. anthocyanin) concentrations increase as fruit ripens	Fruit changes colour that is distinguishable to the birds and they choose fruit with higher antioxidants	Unknown. Plants possibly deplete nutrients to bearing fruit; birds possibly incur more foraging competition	Unknown. Birds possibly keep track of ripeness of plants	Unknown. Possibly more intra- or interspecies competition at plants with more ripe berries; possibly a strategy to choosing berries at a certain time for certain birds	Schaefer et al. (2008)
Plants with coloured nectar and Mauritius ornate day gecko (*Phelsuma ornata*)	Plants with coloured nectar	Pollinator (e.g. Mauritius ornate day gecko)	Food (e.g. nectar)	More nectar accumulates over time	Coloured nectar indicates nectar reward quality and quantity through palatability which corresponds with flower sexual maturity	For plants, there is no pollination when there is no nectar available	Unknown. Geckos possibly skip flowers with less nectar	Are there other costs to the plants such as nutrient loss? Unknown. Plants possibly sacrifice nutrients to produce nectar; possibly more intra- or interspecies competition at flowers with more nectar	Hansen et al. (2006)

eggs that are visible through their semi-transparent abdomen as well as increased skin colour surrounding the abdomen. The females (i.e. sellers) display the eggs available for fertilization (i.e. item for sale) to the males (i.e. buyers). As the mating season progresses and fewer males become available to mate, the female increases the intensity of orange of her abdomen by investing more carotenoids into the visible eggs (i.e. honest signal). Carotenoids are important nutrients that maintain many health functions and they must be ingested. We presume this increases the value of the item for sale as the female invests more beneficial carotenoids into her eggs. She uses the colour intensity of her abdomen as an honest signal to the males to show the quality of her eggs. Both males and females have an interest in producing high quality offspring that have the highest chance of survival. Males must strategize by seeking out females with valuable eggs but also not missing mating opportunities by waiting too long. Females must titrate how much of their precious carotenoids to invest in their eggs versus their own bodies. It would be beneficial to know the survivorship of offspring based on the intensity of colour of their mother's abdomen to see if the carotenoid investment is beneficial to the offspring.

Plants may also use reverse auction tactics in mutualistic relationships to attract pollinators and seed-dispersers at an optimal time by indicating the quality of a reward using an honest signal (Hansen et al., 2006; Schaefer et al., 2008). Some plants (i.e. sellers) produce fruits (i.e. items for sale) that ripen over time resulting in a change in colour (i.e. honest signal) and increase in valuable antioxidants (i.e. increase in value). The plants produce these fruits for frugivores, like the European blackcap bird (*Sylvia atricapilla*) (i.e. buyers), that ingest the fruit, excrete the seeds, and disperse and propagate more fruit-bearing plants. The blackcap is interested in eating fruit that is the ripest because it will have the highest concentration of antioxidants. However, the strategies for the plants and blackcaps and how they fit into the reverse auction model are vague. It is possible there is more competition for riper fruit which is only accessible to older or more dominant blackcaps. Therefore, younger or less dominant blackcaps might be forced to eat less ripe fruit or miss out on the fruit all together if another bird or animal eats it first. Older or more dominant birds might also be better seed dispersers, which might be beneficial to the plants and the reason they increase the investment of antioxidants in the fruit over time to select for better seed dispersers.

Social species may also evolve the reverse auction system to stabilize group living. Baboon species (*Papio ssp.*) exhibit complex and unique social systems, life histories, and ecologies. The properties of the mating system in the savanna baboon species (yellow *Papio cynocephalus*, chacma *P. ursinus*, olive *P. anubis*, Kinda *P. kindae*) contain the core features of a reverse auction system, specifically one where value increases. These baboon species all live in multi-male multi-female polygynandrous groups. They use a mating system based on the formation of a male–female consortship during the time when a female would be ovulating (Bercovitch, 1991; Seyfarth, 1978). The females also display exaggerated sexual swellings that are an honest indicator of sexual receptivity (Fitzpatrick et al., 2015). There have been several long-term research projects focused on these baboon species, which provide fine-scale data on social behaviours and physiology. To better highlight how auction theory can be combined with biological markets to understand evolutionary mechanisms, we will examine one species, the yellow baboon, more closely in the case study below.

3 | UNDERSTANDING THE YELLOW BABOON MATING SYSTEM

We believe the yellow baboon mating system evolved to possibly resemble a reverse auction, which evolved into an evolutionarily stable strategy that maximizes individual and group benefits. To begin understanding these relationships in a new light, we need to sort out the intricacies of their mating system to better fit auction theory to their biology. Yellow baboons inhabit most of eastern Africa residing in savanna ecosystems (Zinner et al., 2013). Yellow baboons live in troops of 12–100 animals and have a polygynandrous mating system (Markham et al., 2015). The females are socially bonded, and the males disperse at maturity resulting in female philopatry (Barton et al., 1996; Fischer et al., 2019). Yellow baboons live in areas with dispersed resources and high risk from predators such as leopards (Altmann, 1974; Jolly, 1993). This may explain their multi-male multi-female troops.

Yellow baboons exhibit sexual dimorphism (Clutton-Brock, 1989). Male yellow baboons choose female mates by assessing females' sexual swellings (Paul, 2002), which are attributes that have been well studied. Female sexual swellings provide an honest signal of female sexual receptivity during that reproductive cycle (Nunn, 1999). These sexual swellings develop during the follicular phase of their estrous cycle, with the 5 days preceding ovulation being the time that males compete to consort with the female (Bercovitch, 1987; Nunn, 1999). A female only accepts one consort at a time but may have multiple consorts during a reproductive cycle (Alberts & Fitzpatrick, 2012; Fitzpatrick et al., 2015). When a female resumes cycling after giving birth, she typically has multiple cycles (termed 'cycles since resumption'; two to eight cycles, mode = four cycles) before conceiving (Bercovitch, 1987; Fitzpatrick et al., 2015). Fitzpatrick et al. (2014) state that the likelihood of conception increases with each cycle since resumption. We agree with this statement; however, this has not been demonstrated empirically nor has the physiology of how the chance of conception increases been determined. There is clear evidence based on male behaviour towards cycling females that the later cycles since resumption are different than the earlier cycles. As the cycles since resumption increase, the highest-ranking male becomes more likely to be her consort and more males are likely to be 'followers' to this consort couple (Fitzpatrick et al., 2015) indicating that later cycles since resumption are more valuable. Additionally, higher-ranking males are more likely to mate during these later cycles in yellow baboons (Gesquiere et al., 2007) and chacma baboons (Bulger, 1993), and therefore sire more infants (Alberts et al., 2006). Fitzpatrick et al. (2015) found that female cycle fecundity changes over time and males monitor these cycles through an honest signal.

4 | A CASE STUDY: ASSESSING THE YELLOW BABOON MATING SYSTEM AS A REVERSE AUCTION

The yellow baboon mating system may have evolved a reverse auction to optimize benefits to individuals and the group (Figure 1). Our goal is to identify the key characteristics of the complex yellow baboon mating system to propose a mechanism of female mate choice. We offer that the "seller" is the cycling female. We propose that the value of the mating opportunity increases with each subsequent estrous cycle because of increased likelihood of conception. The "buyers" are the males that exchange consortship for a mating opportunity. The female's sexual swelling provides an honest indicator of a female's sexual receptivity. Since resident males can track a female's cycles since resumption, there is transparency in the auction and males can choose whether to bid.

In a system where females are interested in balancing having high-ranking males sire their offspring and delaying their next pregnancy until they are in better condition, a reverse auction may be an ESS for both females and males, whereby once adopted by most members of the group no other strategies can offer higher reproductive fitness to an individual (Smith & Price, 1973). Our assumptions include: (1) females have an ideal interbirth interval that balances the value of having another young soon with the benefits of waiting to recover and improve body condition; (2) females benefit from male consortship by which a male in exchange for great assurance of paternity provides the female with vigilance allowing her greater access feeding time and places; (3) male–male competition is greatest when likelihood of conception is highest; and 4) dominant males require a greater assurance of paternity than subordinate. These assumptions may apply to yellow baboons inhabiting East African savannas. Their large social groups evolved in response to patchy resource distributions (in time and space) and high predation (Altmann, 1974).

Ideally the female would prefer continuous consortship while only offering a very high probability of conception at the ideal interbirth interval (Figure 2a). Yet, with such a mating strategy males would only provide consortship at this point (Figure 2b). Hence, it could benefit females to have cycles that offer less than 100% chance of conception within the cycle. Consider cycles with constant probabilities of conception (Figure 2c). The advantage would be continuous consortship (Figure 2d). The disadvantage for the female is that at a high probability of conception most conceptions would occur at early cycles well before the ideal. With a low conception probability the risk is that conception occurs well after the ideal. Hence, the ESS for the females would be to increase the probability of conception with each cycle (i.e. reverse auction) to gain continuous consortship and to reduce the likelihoods of conception too soon or too late (Figure 2e). Completing the reverse auction, the ESS for males sees low ranking males providing consortship during early cycles and high-ranking males doing so later; thus reducing male–male competition and diversifying paternity (Figure 2f). The reverse auction requires females and males of all ranks to remain in the group. Whether the auction itself determines the group size and composition as part of the evolutionarily stable strategy, or whether the group size emerges from other selective advantages, such as safety in numbers from predators, remains an open question as our model does not include the dynamics of group size.

5 | CONCLUSIONS AND NEXT STEPS

We have provided the framework to show how a reverse auction would fit into several mutualistic and mating ecological systems. We selected several systems that we believe have the components to fit the reverse auction based on the existing literature. We proposed that some mating systems in fishes (e.g. two-spotted goby and straight-tailed razorfish) and savanna baboons have evolved reverse auction strategies. Reserve auctions may have also evolved in mutualistic relationships (e.g. fruit-bearing plants and seed dispersers, and plants and pollinators). We used the yellow baboon mating system as a case study because there is more evidence to support our hypothesis.

Our hypothesis fits well into the established literature on female savanna baboons. Our work highlights the evolution of the stabilization of multi-male, multi-female groups that are necessary in areas of high depredation like the yellow baboon's range of East Africa (Stacey, 1986). The reproduction suppression model posits that females can increase lifetime fitness by waiting until conditions are more favourable because reproduction is costly and often unsuccessful (Wasser & Barash, 1983), which is exemplified by the delayed conception approach in a reverse auction. By consorting with multiple males during a cycle, the female confuses paternity and decreases infanticide success from immigrating males (Alberts & Fitzpatrick, 2012; Fitzpatrick et al., 2015). These relationships fit with Nunn's graded signal hypothesis showing that females evolved exaggerated swellings to adjust the costs and benefits of consortship to confuse paternity and increase the chances of having a dominant male sire their offspring (Nunn, 1999). However, the reverse auction considers both the females and males in the group.

Our hypothesis also complements existing literature on male savanna baboons. The consorting male still endures the costs of reduced energy intake through reduced quality in foraging (Alberts et al., 1996). Yellow baboon females tend to prefer young, high-ranking, newcomer males, but these males did not always have the highest mating success (Bercovitch, 1991). This fits into the concept of the a "winner's curse" where bidders that are unaware of the value of the item for sale are more likely to overpay, which for male yellow baboons, is to mate with a female that has a low chance of conception. Immigrating males are more likely to be subjected to

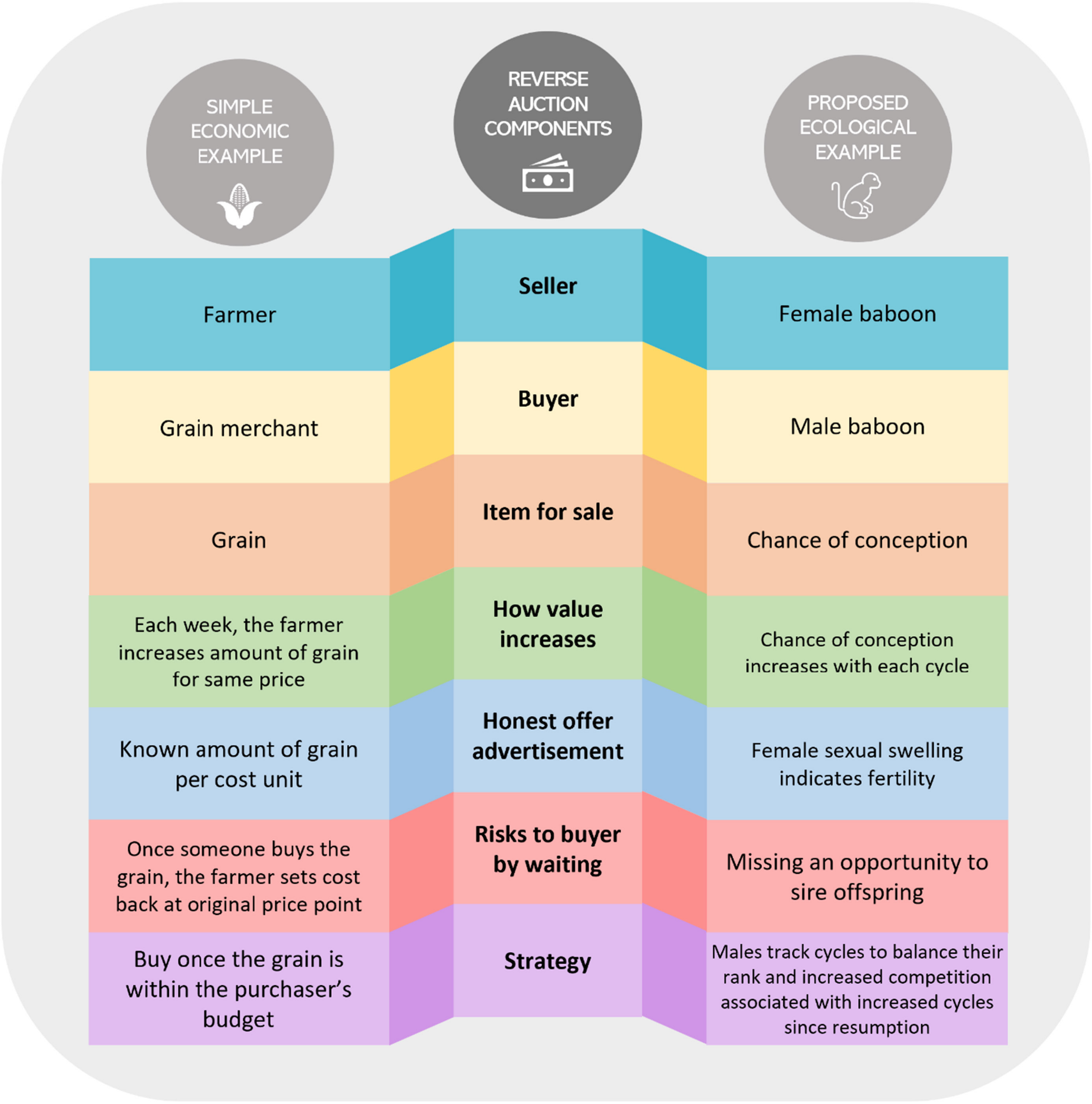

FIGURE 1 Using a traditional economic example (left column), we compare important components of a reverse auction (middle column) to the yellow baboon reproductive system (right column).

the "winner's curse" because they have not been able to track the females' cycles in their new group. This is in line with the hypothesis by Henzi and Barrett (2003) that males with longer residence in the group have more information about the females' current reproductive status which gives them a higher reproductive success. Our theory is in alignment with findings that mating frequency does not correlate with conception (Drea, 2005) nor male reproductive success (Bercovitch, 1987). Although our proposed theory fits well with savanna baboons, it does not fit with the mating systems of other baboons.

Because not all baboons evolved a polygynandrous mating system, we do not propose that these other species evolved a reverse auction in their mating systems. We do not believe hamadryas and Guinea baboons evolved a reverse auction reproductive strategy because they evolved a one-male harem reproductive system. Additionally, hamadryas baboons have been reported to use sexual swellings as a *dishonest* signal to deter infanticide from incoming males (Zinner & Deschner, 2000). These differences between closely related species with different life histories and ecologies highlight how the reverse auction theory is only useful in certain situations.

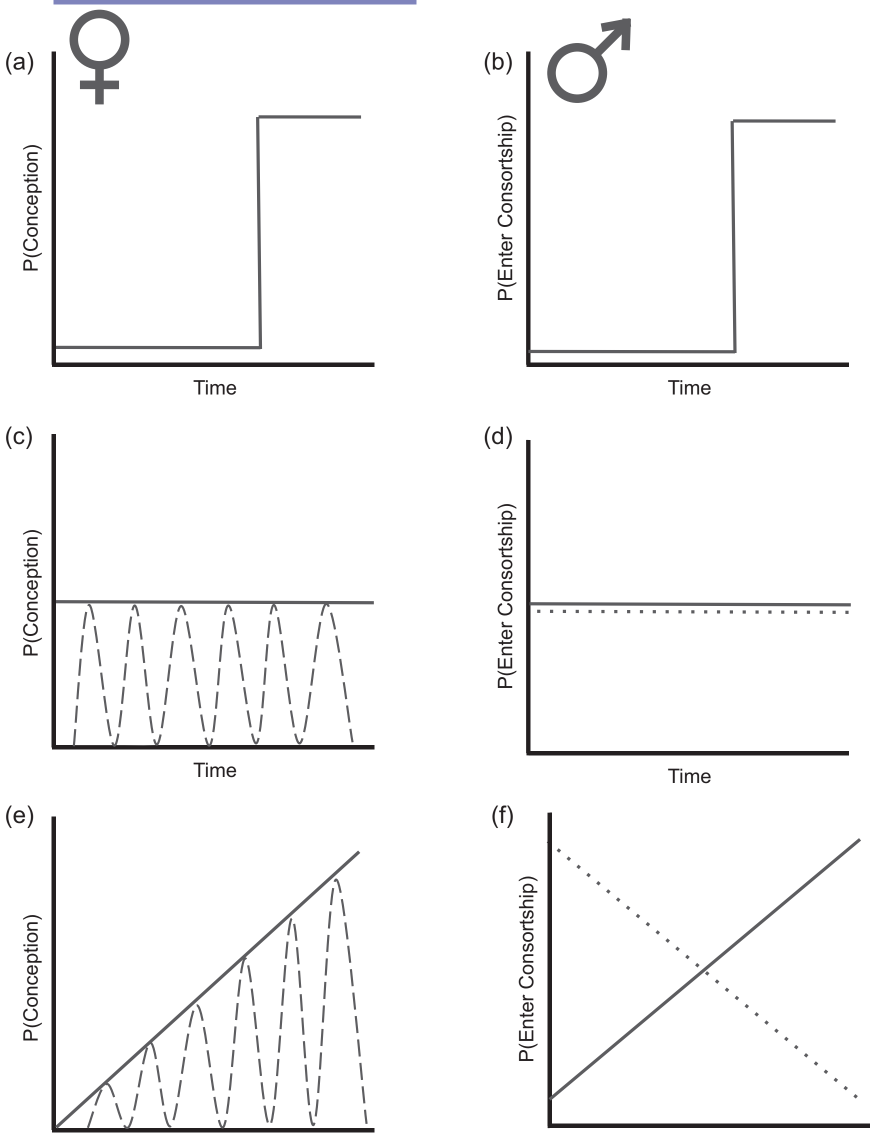

FIGURE 2 Alternative female reproductive strategies (a, c, e) and how males would respond (b, d, f). (a) The female's probability of conception (P(Conception)) is a step-function where the chance of conception (solid line) is continuously low and then jumps to a high chance of conception. This is ideal for the female if she could control conception while having continuous consortship. (b) However, males will not provide consortship until the step increase in P(Conception), and dominant males (solid line) should prevail. (c) In a system that female fecundity continually cycles over time with a moderate and constant P(Conception). (d) All males (high [solid line] and low [dotted line] ranking) will engage will consortship. In this case, females risk conceiving earlier or later than ideal for her body condition and males encounter higher competition for mates. (e) The yellow baboon system where P(Conception) increases with each cycle. (f) A female receives continuous consortship initially from low-ranking males (dotted line) and then later from high-ranking males (solid line) when her body condition is most likely better and it is more likely a high-ranking male sires her offspring.

Although valuable, biological markets are not fully comparable to human economic markets. For most economic markets, the law of supply and demand dictates the exchange of commodities. This may not be the case for all biological markets (Bowles & Hammerstein, 2003). Standard market models in economics are often too simple to describe nonhuman interactions and need to include population-level dynamics. In social species like primate groups, for example, dominance rankings must also be included in the market framework (Bowles & Hammerstein, 2003; Henzi & Barrett, 2003). There are many discrete factors that play into this game (e.g. female rank, number of females in estrus at one time, number of males at each rank, resource availability, sneaky matings outside of consortships). We also do not know how males track female cycles. Crockford et al. (2007) hypothesize that chacma baboons eavesdrop on vocalizations in order to achieve extra-consortship matings. Therefore, vocalizations could be a way to track previous consortships, and therefore, matings. We hope this framework can be used to provide new perspectives on existing research and shape new hypotheses and methods in future work.

We have some recommendations for obtaining empirical evidence on how a reverse auction benefits both buyer and seller. In mating systems that we hypothesis evolved as a reverse auction, it is necessary to understand how these mating strategies impact lifetime fitness and offspring fitness. For the yellow baboons, it is important to establish if there are differences in survivability or fitness of individuals sired at later cycles. Additionally, if researchers could gain more insight into the female and male physiology during these cycles, this would indicate more about mate choice and strategy, specifically what physiological changes in the female as the cycles since resumption increase. If females are varying the chance of conception to delay their next pregnancy until they have reached a better body condition, it would be useful to measure body condition through the cycles since resumption noting the body condition during the conceptive cycle. For mutualistic relationships, considering the quantity and/or quality of the item for sale and the buyer could reveal the seller's strategy in gaining the best outcome. We have included a proposed mathematical model to explain these relationships in the Supporting Information S1.

Considering ecological systems as reverse auctions could broaden our view of evolution and adaptations through the lens of human economic structures.

AUTHOR CONTRIBUTIONS

Joel S. Brown conceived of the original idea. Katherine J. Fowler wrote the manuscript and did the majority of the background research and writing and creation of the figures. Emily J. Potratz completed the research on economic auctions, biological markets, mate choice and helped with editing. Abdel Halloway, Margaret Malone and Joel S. Brown conceived of the mathematical models. All authors helped edit and approve of the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were used for this manuscript.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Mathematical model of the auction strategy.

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