

# Does Market Theory Apply to Biology?

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## ABSTRACT

Traditionally, market models in economics describe interactions in which the commodities traded are subject to complete contracts that are enforceable at no cost. Such contracts do not exist among other animals. In conventional economic models, there is also no account of who meets whom, what the traders know, and how they settle on a transaction, whereas these aspects play a major role in biological market models. From this point of view, the scope for applying market theory to biology appears very limited. Recent developments in economics, however, may allow for fruitful interdisciplinary cooperation. These developments include what one leading economist termed “the abrogation of the law of supply and demand” accomplished by the introduction of principal-agent models, based on the incomplete nature of contracts and the traders’ limited information. There is an important convergence of thought in both disciplines, and biologists have recently identified a variety of interesting examples beyond the basic mating market. Some of these examples resemble labor markets and may be illuminated by principal-agent models. A look at the mating market shows that adopting an economist’s perspective provides a comprehensive model of the market, the components of which are now well understood by biologists. Finally, there are striking parallels between the signaling games studied in biology and economics, the value of education and the peacock’s tail having much in common.

## INTRODUCTION: WHY BOTHER WITH MARKETS?

When we buy a basket of apples, the interaction with the farmer is mutually beneficial: we receive a commodity while the farmer gets money in return. Mutual benefits alone, however, are not sufficient to explain cooperation. We tend to refuse a particular trade if we know that a better deal can be obtained elsewhere and is worth the effort of moving and searching. Similar market phenomena seem to exist in the nonhuman animal world. When a female mates with a male,

she receives sperm while the male “cashes in” on the eggs that his sperm fertilize. The mutual benefits, however, do not imply that they are worth the trade. Females often refuse a particular mate if superior partners are available. The preferred partners might offer “nuptial gifts,” more valuable sperm, lower risk of picking up sexually transmitted diseases, or better abilities to care for the offspring (if this can be expected at all).

Ever since 1838 when Charles Darwin read the classical economist Thomas Malthus, the emergent properties of competitive interactions have been prominent in biological thinking. The analogy between animal mating and human trade led much later to the metaphor of *mating markets* in behavioral ecology. Recently, a more general field of research on *biological markets* has emerged (Noë and Hammerstein 1994, 1995; Schwartz and Hoeksema 1998; Noë et al. 2001; Simms and Taylor 2002). The reason behind this broadening in scope is that *partner choice* plays an important role in social interactions other than mating (Hammerstein, Chapter 5, this volume) and that many cooperative *exchanges* take place within and between species.

In songbirds called Lazuli buntings (*Passerina amoena*), for example, the following exchange seems to take place: territorial males give juvenile-looking males access to their high-quality territories<sup>1</sup> and are compensated through offspring benefits that result from copulations with the juvenile’s mate (Greene et al. 2000). The juvenile-looking males are yearlings. In general, yearlings differ markedly in their plumage color, ranging from very dull to bright (adult looking). Color plays a crucial role in social partner choice. Adult males behave very aggressively toward brightly colored yearlings. In contrast, they sometimes show extreme tolerance toward dull-looking males, who then use this opportunity to settle near the adult in its high-quality habitat. Greene and his collaborators interpret this as a cooperative relationship, whereby the dull yearling benefits from the habitat quality as it allows him to attract a female and produce offspring with her. Rather than posing a threat to the adult, the presence of the dull male makes it possible for the adult to obtain extra-pair fertilizations — a mutually beneficial trade (revealed by DNA fingerprinting). Young birds with bright plumage coloration probably compete for territories as if they were adults. Green et al. report that both the dullest and the brightest yearlings generally obtained high-quality sites. It would be difficult to understand this empirical result without considering the *trade* among males in the *social partner market*. Noë and Hammerstein (1994) analyzed a similar scenario for purple martins.

Experimentalists have conducted several other market studies in which social partnerships are observed. For example, Bshary investigated the relationship between cleaner fish and their “customers” (i.e., other fish from which they remove ectoparasites). Cleaners live in coral reefs and have customers from the immediate neighborhood as well as from the open sea. Local customers for which long-distance moves are costly are cleaned less well than long-range

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<sup>1</sup> We refer to territory in a broad sense as the habitat controlled by the adult male.

travellers, who can easily switch between cleaning stations and thereby exert partner choice (see Bshary and Noë, this volume). This is exactly what one would expect from the economic theory of *monopolistic competition*: buyers with few alternative sources of supply will have less advantageous transactions than those who can shop around.

Biology does not lack market examples, and it is obvious that many important insights can be gained if the market is properly reflected in studies of cooperation. Biologists have only begun, however, to develop a general market theory, and thus it seems important at this stage to ask what might be learned from economics. At first glance, the scope for simple interdisciplinary “trade” may seem rather limited. Traditional concepts of economic markets appear to be particularly unsuitable for biologists. A cursory look at biological mating markets confirms this view. Some outstanding puzzles in biological market theory, however, demonstrate that there is some convergence of theory development in biology and economics.

### **MARKETS IN BIOLOGY AND ECONOMICS ARE NOT THE SAME**

The recent success of the market analogy in biology comes somewhat as a surprise to economists, for standard market models in economics appear to be a poor template for studying interactions among nonhuman animals. There are three reasons for this:

- First, canonical economic agents deploy extraordinary cognitive capacities unique to humans in pursuit of their self interest. By contrast, biological market traders at most perform an “as if” fitness maximization, and this is the product of population-wide dynamics, not of intentional behavior.
- Second, conventional economic models determine prices and other equilibrium outcomes in markets without representing the actual interactions among traders. In contrast to biological market models, there is no account of who meets whom, what the traders know, and how they settle on a transaction. In this sense, there is not even an economic theory of the price-setting process.
- Third, most market models describe interactions in which the goods and services traded are subject to complete contracts that are enforceable at no cost to the exchanging parties. This means that the explicit terms of the exchange cover all aspects of the trade of interest to the trader, and, once decided upon, these terms are not subject to cheating. Human contracts of this type are unique in nature.

As a result, conventional market models are silent on issues of considerable interest to biologists, including the determinants of bargaining power, how cheating is controlled, how the terms of a trade are determined in a biological exchange, and how power can be exercised in a highly competitive environment

in which all traders have many alternative transactions (Bowles 2003). Henzi and Barrett (2002) conclude from their study of grooming among chacma baboons that “if biological markets are to be fully applicable to primate groups (and those of other social animals), then the potentially distorting effect of dominance needs to be incorporated into the framework.” Economic models taking account of the importance of power (Coase 1937; Simon 1951) and social and genetic affinity in the exchange process (Sahlins 1974) have long existed, as have approaches that eschew the conventional but unrealistic assumptions concerning the cognitive capacities of economic agents (Becker 1962; Alchian 1950; Simon 1955). However, these contributions have made little impact on economic theory until recent years.

### MATING MARKETS AND THE ABROGATION OF THE LAW OF SUPPLY AND DEMAND

Let us now return to the oldest market paradigm in biology. Mating markets are *implicitly* involved in most evolutionary studies of partner choice, reproduction, and sex differences. They also set the stage for conflict among and between the sexes (for a review, see Hammerstein and Parker 1987). It is, therefore, interesting to give an *explicit* picture of these markets.

Driven by a strong inclination to take facts into account, biologists have collected numerous pieces of evidence suggesting that the *supply* of sperm exceeds *demand* in many animal species. Let us take Bateman’s (1948) famous mating experiment as an example. He demonstrated that male fruit flies (*Drosophila melanogaster*) can strongly increase their reproductive success by copulating with several partners, whereas the reverse is not true for females. Combined with the *sex ratio* argument that males and females are produced in roughly equal numbers, this indicates the following: The aggregated fertilization services offered by males substantially exceed female demand in the fruit fly population. It would seem that females should require commodities other than sperm as the appropriate “price for their eggs.” But in fruit flies, *sperm is all they get*.<sup>2</sup> The law of supply and demand does not apply.

This “law” states that, in a market economy, the forces of supply and demand push the price toward the level at which the quantity supplied and the quantity demanded are equal, a result termed “market clearing.” Biologists have many reasons to be critical of such a simplistic view of the world, and recently the same holds true for economists. Joseph Stiglitz, recipient of the Nobel Prize in economics, wrote of the “abrogation of the law of supply and demand” accomplished by recent development in microeconomics. The conventional market model, termed *Walrasian* after Leon Walras (1834–1910), one of the founders of

<sup>2</sup> Note, however, that female insects can receive other material with the seminal fluid. The advantages to the female are often marginal, and in the case of *Drosophila* seminal fluid actually shortens the life span of the female (Fowler and Partridge 1989).

neoclassical economics, has for the most part been superseded. The new market theory is quite different from the old and takes as its foundational assumptions the incomplete nature of contracts (biologically speaking, the possibility of cheating, exploitation, etc.) and the traders' limited information about the trades being offered and accepted by other traders. The new *post-Walrasian* microeconomics provides models of markets — labor markets, credit markets, markets for goods of variable quality — in which market clearing does not occur, even in a competitive equilibrium (Bowles 2003). We will see that this new approach may help resolve some outstanding puzzles in the theory of biological markets.

Returning to the mating scenario, let us now look at the *market entry problem*. Given the excessive supply of sperm, why is half the population entering the “male side of the market” instead of producing eggs? In other words, why are males and females often produced in roughly equal numbers? The initial attempt to explain *sex ratio evolution* was made by Darwin in the first edition of his monograph on *The Descent of Man* where he implicitly resorted to group selection reasoning. But he abandoned this in the second edition. Almost in a state of despair he had to admit that “the whole problem is so intricate that it is safer to leave its solution to the future” (Darwin 1874, p. 399). The evolutionary explanation of sex ratios is not quite as difficult as it appeared to Darwin. Sex ratio theory developed soon after he raised the problem but only reached the attention of later generations via Ronald Fisher (1930).

Fisher's presentation of the theory can be rephrased in economic terms. Assuming that mothers determine the sex of their offspring, a female acts like an *investor*, allocating resources to sons and daughters to obtain as many grandchildren as possible. As soon as the population sex ratio is biased, it pays to invest in the rarer sex. This is so because, looking at the entire population, members of the less abundant sex produce collectively as many offspring as those of the more abundant sex (in diploid organisms, every grandchild has exactly one genetic father and one genetic mother so the only way there could be fewer fathers in the population is that they would on average have more offspring). On average, therefore, individuals of the rarer sex have more children. Thus selection acts in favor of the unbiased sex ratio. Of course, this is only the basic idea; it has since been elaborated (e.g., Charnov 1982). In particular, one can allow the organism to choose being a male or female independent of the mother. Under many circumstances, the result is the same.

Even if, for these reasons, the *supply of males* cannot adjust we still have to ask why males do not adjust the *supply of sperm* to a “sperm-saturated market.” The answer lies again in Bateman's fruit fly experiment and in the assumption that sperm production is not very costly. If males can increase their reproductive success by having more than one mate, they should produce enough sperm for fertilizing the eggs of two or more females. In addition, the more sperm competition there is, the more sperm is required (Parker 1970; Parker and Ball 2001). Sperm competition results from successive inseminations by different males,

whose sperm compete for access to eggs. Comparing different primates species, Harcourt et al. (1981) showed that the size of testes correlates with the degree of promiscuity typically found. Even in animal populations with social monogamy, a somewhat excessive production of sperm is to be expected, since extra-pair copulations are not unheard of in humans and have been demonstrated for a number of socially monogamous animal species.

In contrast to males whose reproductive potential is enhanced by the low cost of sperm, females are severely limited in their reproductive potential by the high cost of egg production (or in mammals by viviparity). This sex difference in reproductive potential gave rise to the term *asymmetric mating market*. Biologists think that the asymmetry in reproductive potential is perhaps the main key to understanding the morphological, physiological, and behavioral *differences* between the sexes.

The asymmetric mating market explains nicely why males *compete* for access to females and why females are in a strong position to exert precopulatory or postcopulatory *mate choice*. The peacock's tail has probably evolved in response to female choice. But why do females not use this advantage and sell their eggs at a higher price instead of contenting themselves with a beautiful tail? In the presence of excess supply of sperm, what prevents price adjustment from clearing the mating market as the Walrasian market model would predict? It would seem that females should prefer male partners who offer "commodities," such as nutrients or parental care, in addition to sperm.

The same puzzle arises in the theory of human labor markets. If labor is chronically in excess supply, what prevents the unemployed workers from offering employers a more attractive package, promising to work harder for the same wage? Or given that markets do not clear, so that jobs are typically scarce and workers abundant, why do employers not sell jobs, charging a fee to the prospective worker as a condition of employment?

The problem in both human and other markets is that the relevant contracts are not enforceable and this appears to be a serious impediment to the "package deal." The workers' promise to work harder is not enforceable, nor is the employer's promise not to fire the worker once the fee has been paid. Among other animals, it is easy to "promise" paternal care and forgo the effort when it is due.

Occasionally, a package deal has evolved. In sea horses and giant water bugs, for example, males make a major parental effort and care intensively for their offspring, whereas females "only" provide the eggs. How does evolution force a male to carry the burden of parental care? To address this, we describe an abstract scenario inspired by R.L. Smith's work (1997) on the giant water bug.

Suppose we look at a stage in the evolution of an abstract animal species where parental care is absent. Females deposit their eggs on plants that line their freshwater habitats. Female foraging, however, takes place at other locations. Since males compete for access to females, they defend territories that contain the plants required for egg laying. Females deposit their eggs in male territories.

At this stage in our evolutionary story, there is no reason for a female to remain with her eggs. To the contrary, she will pursue foraging activities to produce more offspring.

Next, a change in the environment occurs that calls for parental care to ensure egg survival. In principle, both males and females have an interest in the survival of their joint offspring. However, if she leaves after depositing the eggs, he is caught in a situation where he has the last move in the interaction sequence. If he does not care, the brood is gone. Sometimes it is bad to have the last move. Since he would not benefit from deserting his territory, he cannot benefit from ending the spatial association with the eggs. Strategically he is thus in a weak position to “pass the buck” in the parental investment game. What does he do? It is easy to imagine evolution imposing the burden on his broad shoulder. (The game theoretic logic behind mate desertion is discussed by Hammerstein [2001].)

Our scenario shows that sex role reversal is possible in evolution. The effects of the basic market asymmetry are indeed more subtle and less supportive of our cultural stereotypes than popular presentations of sociobiology would make us believe (for further discussion of reversals in the relative strength of sexual selection on males and females, see Lorch [2002]).

To conclude this section on mating markets, it would appear that the advancements in this impressive field of research have mostly been made by biologists. Yet, as we just saw, there are many bridges to economics, and we maintain that looking at mating markets through the economist’s eyes is extremely useful if one aims to “assemble” the various pieces of sexual selection theory to study the whole picture that emerges.

## PRINCIPALS, AGENTS, AND POWER IN BIOLOGICAL EXCHANGES

In the animal world, egalitarian societies are the exception rather than the rule. Often, a fraction of the male population controls access to high-quality habitats, leaving the rest of the males to contend with what is left. The weak receives permission to settle within the otherwise defended territory, but a service to the strong must be rendered in return. What kind of service would this be, and why can the strong rely on this service when opening the door to his “estate”? The answer provided by post-Walrasian microeconomics is that the *power* of the strong males to keep weak males off their territories enables them to act as *principals* in trades with *agents*. A *principal* benefits from the actions of an *agent* but cannot use an enforceable contract to bind the agent to do the actions that are optimal from the principal’s standpoint. The principal must therefore exercise power to induce the agent to act in accordance with the principal’s interests. What follows is a biological example (worked out mathematically by Bowles and Hammerstein, unpublished manuscript).

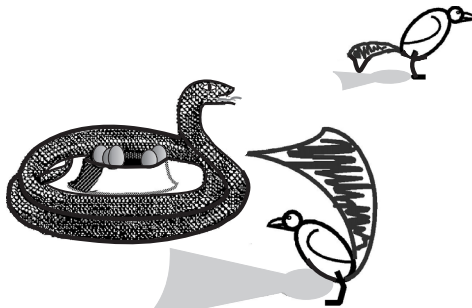


Among Lazuli buntings, the adult territory owner is the principal. He allows a dull-colored yearling — his agent — to settle in the habitat area that he controls. The yearling, of course, is interested in attracting a mate and producing offspring with her, and the habitat of the territory owner increases his chances. Due to the imbalance of power between the males, the adult can “steal” copulations from the yearling by mating with the yearling’s partner. Copulation is one service the territory holder gets, and he can count on it as long as the yearling’s mate agrees. It is not, however, in the interest of territory holder to push the “adultery” to an extreme. Monopolizing all copulations could be countered by the yearling withdrawing his investment in parental care, another service that he provides. If this logic drives the adult male’s behavior (via natural selection), the yearling is better off with the trade than without it, just as the employed worker is better off with the job than without it.

In an evolutionary equilibrium that reflects this logic, the trade can take place and the birds do not have to “worry” about commitment and enforceable contracts. The exercise of power is thus essential to the way the market works.

Noë and Hammerstein (1994) created a tale between a fictitious boa “constructor” and “shadowbirds” to make a similar point. The female boa “constructs” a nest mound in an open desert environment upon which she lays her eggs. The snake has all it takes to guard her nest successfully against egg predators, but her eggs are still at risk from solar radiation. To protect the eggs from thermal stress, the snake benefits from cooperation with a shadowbird. If permitted by the boa (the principal), the female shadowbird adds her eggs to the boa’s nest and subsequently shades the nest with a fan-like tail. The trade is mutually advantageous because the boa protects her social partner from predation. The amount of shade is determined by a morphological characteristic, namely tail length. Cheating by the bird is, therefore, not an issue. Conversely, it is assumed that the bird serves the boa better for shade than for a meal, so that the boa has no incentive for “breaking the social contract.”

The larger the bird’s tail, the larger the fitness of the boa. However, it is the bird that pays the price for the tail in this tale, as it could shade its own eggs with relatively shorter feathers. If there are typically fewer birds than boas, evolution will tune the boa’s mind to accept birds with short tails. This resembles the situation of an employer seeking employees when few are available; almost anyone





who meets minimum needs has to be accepted. As we all know, when there are many candidates, the job market looks different. For the boa constructor this means that it can exert choice and thereby create a selection pressure on shadow birds to evolve elongated tails.

This shows, at least theoretically, that exaggerated or understated morphological traits may result from social partner choice, not just from sexual selection. Let us interpret the Lazuli bunting example in this spirit. Among the males that are able to reproduce, some are dull and resemble juveniles whereas others are brightly colored and thus look like adults. What incentive does a male capable of reproduction have to delay plumage maturation? Dull plumage seems to signal the denial of territorial claims in the Lazuli bunting. The signal comes with the moult and cannot be changed during the season. At first glance, this appears to be a self-imposed obstacle, but social choice exerted by territorial adults generates the advantage of being “dressed as a juvenile.” The market determines the extent to which this dress code holds.

The Lazuli bunting example and the boa–shadowbird tale share a strong resemblance with human labor markets. Both adult bunting and boa act as principals hiring a helper, whose job it is to increase the principal’s breeding success. We think that it is, therefore, possible to draw on recent developments in economics and model the biologist’s boas and buntings in the spirit of modern market models, in which cheating is a theme and workers may be lazy if they wish.

## EDUCATION AND THE PEACOCK’S TAIL

As shown above, signaling can play a crucial role in biological markets. The peacock’s tail demonstrates this even more impressively than the coloration phenomena observed in Lazuli buntings. Although it is tempting to compare the peacock’s signal with advertising observed in human economic activities, there are important differences. Human advertising can easily manipulate mental mechanisms because they operate in the modern world and not in the environment of evolutionary adaptation. For animals, however, this situation is much simpler: we expect countermeasures to work. Empirical attempts to understand male advertising and female choice have kept an industry of biological research busy for at least two decades and it remains difficult to understand all the details (e.g., Bradbury and Vehrencamp 1998, 2000).

At the theoretical level there has been a long-lasting discussion about the so-called *handicap principle* which goes back to Zahavi (1975). When Zahavi first expressed his idea, that animals acquire costly handicaps just to impress others, he failed to convince the community of theoretical biologists. However, subsequently Pomiankowski (1987), Grafen (1990), and Gintis, Smith and Bowles (2002) showed that the handicap principle can be expressed in coherent mathematical models. The basic idea is that a signal that is costly to send—and more costly for some than others—will not be easily faked, so other animals can infer that those sending the signals are those with lower costs.

Let us have a quick look at the easiest way to approach this issue (following Siller and Hammerstein, in prep.) and compare it with modeling in economics.

Consider a theoretical bird population in which males have elongated tail feathers and females base their mating decisions on tail length. Assume that males have the opportunity to adjust the intensity of their signal  $s$  (tail length) to their own physical condition (i.e., health state, vigor, etc.). We call this condition the sender's type  $t$  and allow the signal to be conditional on  $t$ . The signal  $s$  is received by the female who rewards the sender an amount  $b(s)$  in terms of offspring, where  $b$  is increasing in  $s$ . Tail length is not for free and the male has to pay an amount  $c$  for its signal, where  $c$  is increasing in  $s$ . Now, to create an appropriate model for Zahavi's handicap principle, we have to assume that this cost depends not only on the level of the signal  $s$  but also on the male's type  $t$  (i.e., on its physical condition).

In this signaling game, the payoff  $w$  to a male is the reward from the female minus the cost of the tail, i.e.,  $w = b - c$ . Let us assume that the population is at an evolutionary equilibrium and that females prefer males with longer tails. Consider two males with the following characteristics:

Male 1: signal  $s_1$ , type  $t_1$

Male 2: signal  $s_2$ , type  $t_2$ .

Assume that male 1 has the longer tail. By just looking at tails in the equilibrium population what can we (and the females) conclude about the underlying types and costs?

Consider the difference in tail length,  $\Delta s = s_1 - s_2$ , with  $\Delta s > 0$ . For the two birds, what is the cost of having the longer tail as compared to the shorter tail? That is, given the type of each bird, how expensive would it be to increase tail length? We can express this by:

$$\Delta c_{male1} = c(s_1, t_1) - c(s_2, t_1) \text{ and } \Delta c_{male2} = c(s_1, t_2) - c(s_2, t_2).$$

In economics one would call  $\Delta c_{male1}$  and  $\Delta c_{male2}$  the comparative costs of signal 1 for male 1, male 2, respectively. At evolutionary equilibrium, where both males play best responses to the females' and other males' behavior, the long tails must be a best response for birds of type 1 and short tails a best response for birds of type 2, or  $w(s_1, t_1) \geq w(s_2, t_1)$  and  $w(s_2, t_2) \geq w(s_1, t_2)$ . These inequalities imply the following comparative fitness advantage for type 1:

$$w(s_1, t_1) - w(s_2, t_1) \geq w(s_1, t_2) - w(s_2, t_2). \quad (8.1)$$

If the benefit function  $b$  depends only on the signal and not on the bird's type, then this inequality implies that

$$\Delta c_{male2} \geq \Delta c_{male1}. \quad (8.2)$$

Thus, a necessary condition for the signaling equilibrium is that if either of the two males has a greater additional cost for growing the larger tail, this will be the

one that we observe with the shorter tail. The equilibrium does not permit males to cheat with their tails.

This is the essence of “handicap mathematics” and it gives the reader a good foretaste of how to formalize Zahavi’s idea. Of course one wants to complete the argument and inquire about sufficient conditions for an equilibrium that separates the types. Depending on the appropriate assumptions, evolutionarily stable states exist in which the sender’s type can be inferred from the signal observed by the receiver.

It must be emphasized that biologists have struggled with the handicap principle without paying much attention to the existence of similar models in economics, dating from about the same time as Zahavi’s initial paper. Anyone who knows signaling theory will recognize the striking similarity between what we just discussed in relation to Zahavi’s thoughts and signaling games in economics.

Ultimately, the worlds of biology and economics are perhaps not so different. Let us, therefore, end the chapter with celebrating this proximity. We move on to human affairs and present an *economic version of the peacock’s tail*.

In our school days, when we had doubts about the value of learning “exotic” things such as Latin, mathematics, or the capital cities of Europe, our teachers tried to console us by explaining that education serves to prepare us for our future lives and is not intended to just get us through school. It appears that Nobel Laureate Michael Spence (1973) was not quite convinced by his teachers’ advice because he posed the following theoretical question: Does the acquisition of *higher levels of education* lead to *higher wages* even if education fails to improve a person’s productivity? Spence’s model of the job market can be formulated as follows. A person’s type (health, talent, productive ability) is randomly determined. The person can then choose a level of education conditional upon talent, it being less costly for the more talented to continue in school. Following completion of schooling, two firms observe the person’s education (but not the person’s talent) and make simultaneous wage offers. The person accepts the higher offer or flips a coin in case of a tie.

Spence found that an equilibrium can exist in which education signals talent and higher education implies higher wage. The reason is that only the talented persist in long years of schooling, so employers use years of schooling as a signal of the unobservable trait, talent. This result is remarkable because education is costly in the model and does not increase a person’s productivity — quite like a peacock’s tail.



## CONCLUDING REMARKS

Biologists have discovered fascinating examples of market-like interactions and have made considerable progress in understanding these markets. In light of this success it seems unfortunate that traditional models from economics do not easily apply to biology. We have argued, however, that with the development of post-Walrasian microeconomics, the interdisciplinary gap is shrinking, and we have indicated how some bridges can be built. One bridge, however, remains to be mentioned. Inspired by the general equilibrium concept from economics, biologists should perhaps dare to step beyond the analysis of dyadic and other small numbers interactions and consider the population-level interactions among more than a single market. Such investigations would be essential to understand, for example, why the disadvantages of the locally based cleaner fish persist in equilibrium. Conversely, economists should take more seriously the idea that humans are animals after all and not quite as distinct from the rest of nature as traditional modeling approaches might make us believe.

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