

Genes as Entrepreneurs

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ABSTRACT

The signals of profit and loss play a fundamental role in how economic actors learn to behave. Profit informs and incentivizes in such a way that resources can be allocated through the market process according to our material demands. This paper will argue that this arbitrage process is not exclusive to monetary prices but functions similarly for a far older unit of economic analysis: the calorie. Biological evolution is governed by the differential replicability of genes, and these differences are the result of genes building survival machines that are more or less suited to their environment. The ability of a survival machine to acquire sufficient calories is a necessary condition for meeting the Darwinian goals of the gene, so genes that code for a higher than average ability to utilize the calories within an environment would be able to support a larger population in that environment. This enhanced carrying capacity provides positive selection pressure for mutations that allow for the exploitation of novel sources of calories. To model this process, a system of differential equations is developed where a mutant subset of a population is able to achieve enhanced growth in the presence of surplus food resources. The theoretical claims of this paper are tested by examining the urbanization process of birds.

KEYWORDS

Economics, Arbitrage, Calories, Discovery, Genes, Specialization, Population Model, Urbanization

INTRODUCTION

Our understanding of the way in which the market process allocates resources is underpinned by the role of profit signals. As demand for a material good drives up the price, the firms providing that good will be able to sell above cost and hence achieve profit. However, the existence of profit in the considered market will be a signal for others to enter the market with the resources they can bring to bear. This process will continue until economic profit is brought to zero and a stock of resources roughly corresponding to society's desired allocation has been achieved. Of course, the same process is happening within innumerable markets

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across the economy in an arbitrage that directs resources to their most desired use. This mechanism also allows entrepreneurs to test the desirability of new productive schemes. Put another way, a simple thought experiment can illustrate this process. What would happen if almost no one was producing a desired widget? The scarcity of the widget would drive its price up, and potential producers would be drawn in by the unexploited profit opportunity. Producers would continue to enter until the widget market yielded no profit.

This paper posits that this economic process applies as much to evolutionary biology as to human societies because the scarcity of resources is a fundamental feature of the environment in which a gene attempts to replicate. In the case of biological evolution, an economic unit to consider is the calorie, not profit. As before, consider a strategy or region that no lifeforms have colonized. Again, the lack of an incumbent will mean the existence of a caloric surplus. Mutant genes that allow for enhanced exploitation of this surplus will receive positive selection pressure. This is because the environment will support a larger population of those endowed with the mutant gene as such mutants can better utilize the scarce resources of the environment. Any caloric surplus will initially be exploited at the bottom of the food chain, but the same process will operate in every chain link upward. This selection pressure will continue until the caloric surplus has been brought to an equilibrium of zero. Thus, the mechanism that regulates which strategy to implement is the same in the case of the replicating gene and the profit-maximizing entrepreneur as both engage in an arbitrage process regulated by relative scarcity.

It is worth noting that any anthropomorphizing language used to describe the behavior of genes is entirely figurative since it is difficult to describe the process of evolution without some anthropomorphic description. The caloric arbitrage process of genes is different than that of entrepreneurs in that entrepreneurs consciously consider ways to exploit profit opportunities whereas genes randomly mutate. Despite the difference in the origin of strategy, or whether the subject even knows they are using a strategy, the process regulating the appropriateness of a given strategy is the same. Genetic strategies for exploiting a caloric surplus will be selected for until an equilibrium of no remaining unexploited calories is achieved, just as the market tends to achieve the equilibrium of no remaining profit opportunities. It should also be pointed out that this paper is not referring to the decision-making of animals. The decision-making of animals only matters for the present purpose in that the programmed behavior of an animal is a way to express a strategy for exploiting caloric surpluses.

The fundamental goal of the gene is to replicate, so the acquisition of calories is only a means to that end (Dawkins, 1976). Genes will not code for the continued pursuit of calories beyond that which will aid in the goal of replication. However, the acquisition of calories is a necessary condition for successfully meeting the gene's Darwinian goals, so adaption to the scarcity of resources in an environment plays an important role in evolution. The analog of the entrepreneur is, again, useful; economists generally assume entrepreneurs only desire profit for the sake of consumption utility. We would not expect a rational entrepreneur to pursue profit at the expense of their utility, but we do expect entrepreneurs to care deeply about profit opportunities because income is what allows them to achieve utility.

Just as profit opportunities incentivize entrepreneurs to enter a market, a surplus of calories will allow enhanced replication for any genetic mutation conducive to its exploitation. Thus, selection pressure will guide genes to act as entrepreneurs in their discovery of new strategies to exploit caloric surpluses. This process will be referred to as the *Genes as Entrepreneurs* theory for the remainder of the paper.

MODEL

This paper will develop a model of the above process using a system of differential equations loosely inspired by the model developed by Wilson and Turelli (1986). Consider an environment with food resources R that replenishes at a rate of α per unit time. Now consider a species residing in that environment with population P broken into mutants of population X and incumbents of population Y . The relevant mutation that differentiates the population creates changes in its holders such that the mutants can better utilize a novel source of calories in the environment. The change in food resources is then the replenishment rate minus what is consumed by the members of the species' population, and the mutants and incumbents follow typical population growth patterns with the mutants gaining an advantage proportional to the caloric surplus of the environment. The variable α is meant to change as a reflection of the introduction of a novel source of calories that the mutants are marginally more adapted to exploit. Such an increase could reflect an exogenous increase in calories, such as an anthropogenic increase, or the discovery of a niche source of calories. Thus, we have the equations:

$$(a) \frac{dR}{dt} = \alpha - X \left(\beta + \frac{R}{\delta} \right) - Y\beta$$

$$(b) \frac{dX}{dt} = \left(\frac{R}{\omega} \right) X + hX \left(1 - \frac{P\beta}{\alpha} \right)$$

$$(c) \frac{dY}{dt} = hY \left(1 - \frac{P\beta}{\alpha} \right)$$

where the mutants specialize in such a way as to gain greater benefit through the enhanced consumption of a caloric surplus in this environment. β is the normal consumption rate for the species, while R/δ is the additional consumption achieved by the mutant population. The species has a logistic growth rate with a growth constant of h and a carrying capacity that is achieved when population multiplied by consumption is equal to the replenishment rate. Additionally, the mutant population gains a benefit from a caloric surplus with a growth constant of R/ω .

From this model, we can derive the rate of change of the proportion of mutants in the population with the equation (proof in appendix):

$$(d) \frac{d(X/P)}{dt} = \frac{XY \left(\frac{R}{\omega}\right)}{(X+Y)^2}$$

Note this equation only gives coherent results when the rate of change is non-negative because all of the terms on the right-hand side are only reasonable when non-negative. Thus, the degree to which a caloric surplus changes the proportion of mutants in the population can be predicted.

To simulate the model, consider a scenario where the environment is in equilibrium: $P\beta = \alpha$ and $R = 0$, but there is an increase in α that is conducive to exploitation by the mutants. The following table and figures simulate such a situation using the deSolve package in R software. Figures 1 to 3 are the output of a plotting function in the R software. A time change interval of 0.01 was used to compute the simulation, and values in the table were rounded to the nearest tenth. For starting conditions, let α increase from 40 to 120, $\beta = 4$, $\delta = 40$, $h = 0.3$, $\omega = 300$, $X = 2$, and $Y = 8$. Numbers were selected for the sake of a reasonable, qualitative approximation of a natural scenario. Note that R becomes negative for a time, but this can be understood as a fully consumed surplus of food and does not substantially change the analysis.

Table 1

time	R	X	Y	d(X/P)/dt
0	0	2	8	0
1	73.2	2.7	9.6	0.04
2	127.9	4.5	11.3	0.09
3	152.6	8.2	12.7	0.12
4	135.1	14.2	13.5	0.11
5	83.6	20.4	13.4	0.07
6	31.7	23.3	12.7	0.02
7	0.5	23.1	11.9	0
8	-12	21.7	11.5	-0.01
9	-14	20.2	11.2	-0.01

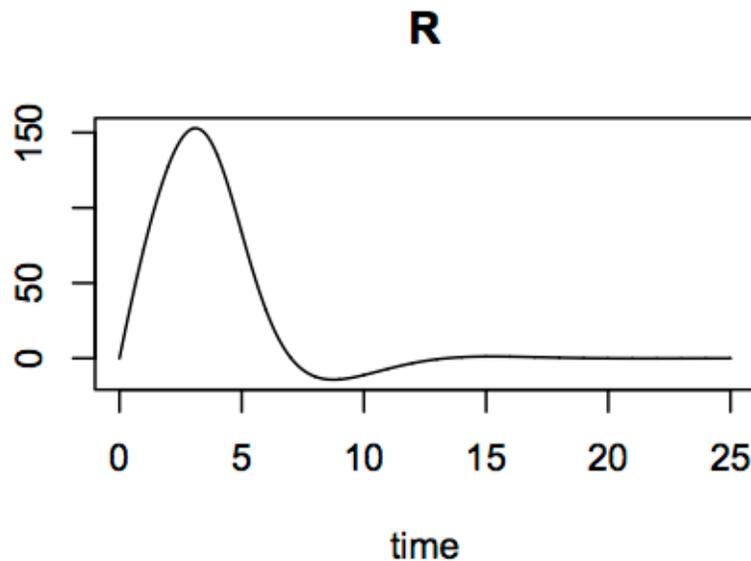
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10	-11	19.2	11.1	-0.01
15	1.2	18.5	11.3	0
20	0	18.7	11.3	0
25	0	18.7	11.3	0

Note. Results listed from simulation in R.

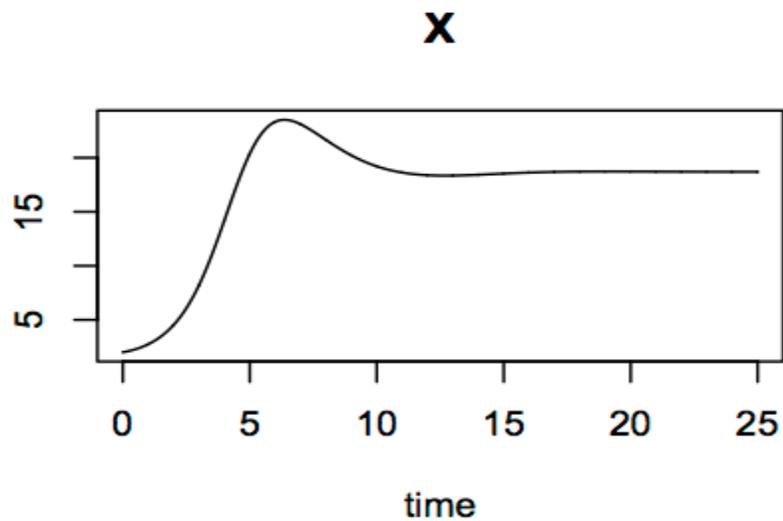
Table 1 shows the values of the three variables in consideration, as well as the change in the proportion of mutants, as time increases. The mutants begin as the minority in the population but overtake the incumbents at some point between time three and four. This is, unsurprisingly, sometime around the point at which surplus food peaks. While approximate, the relationship between caloric surplus and proportion of mutants is also reflected in the fact that caloric surplus and change in proportion of mutants rise and fall together and reach their respective peaks at roughly similar times.

Figure 1



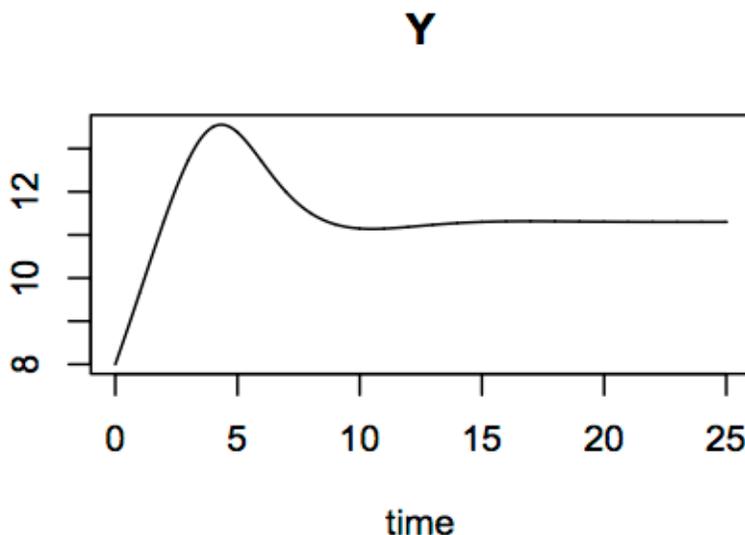
As figure 1 demonstrates, the introduction of a new source of calories creates a surplus of calories that is promptly consumed. The growth in food surplus outpaces the population's consumption for a time, but the population then grows in response. This population growth is biased in favor of the mutants as the existence of a caloric surplus provides them with an additional benefit. The system then begins to reach an equilibrium as the surplus is brought to zero.

Figure 2



Both subgroups of the population grow beyond what can be sustained, but the mutants are able to keep more of their gains before reaching equilibrium. The incumbent population begins to decline while the mutant population is still increasing, and the mutant population gains from the existence of surplus, even as the surplus declines. Once the surplus is brought to zero, both mutants and incumbents settle into an equilibrium where the food is replenished at a rate equal to consumption.

Figure 3



Therefore, the model is consistent with the predictions of the Genes as Entrepreneurs theory as the system has reached a new equilibrium with a fully consumed surplus and the mutant gene having made a significant gain. Parameters can then be chosen in such a way as to match an observed environment.

EVIDENCE

To examine the theoretical claims of this paper, urban bird colonization will be considered as the exogenous changes of urbanization have happened quickly enough to provide a discontinuous change in environment. The Genes as Entrepreneurs theory predicts that the existence of a caloric surplus will precipitate evolutionary changes leading to organisms adapted to the exploitation of the excess calories. A paper by Møller et al. (2012) examining the population density differences in European bird species between urban and rural habitats found that the urban habitat population density is on average 30% higher than that of rural habitats, with some species achieving a 100-fold increase. While this data is consistent with the theoretical predictions of this paper, the description of the evolutionary process provided by this paper goes beyond the positive relationship between caloric surpluses and carrying capacity. More to the point, Møller et al. (2012) found that urban bird species that colonized over longer periods of time achieved the greatest increases in population density over that of their rural counterparts. The evolutionary process that causes bird species to adapt by exploiting the caloric surpluses created by anthropogenic food waste requires time, so longer periods of colonization allow the evolutionary changes predicted by this paper to occur. Those changes, in turn, allow bird species to achieve greater

population density through better adaptations that exploit the caloric surpluses of the urban environment.

The question then is what sort of changes are typical of species that have colonized urban environments and whether these changes are consistent with the Genes as Entrepreneurs theory. Luniak (2004) examines the changes typical of a species undergoing synurbization, or the adaptation of animal species to the novelty of an urbanizing environment. Many of these changes are considered within plausible behavioral plasticity of the species considered, but behavioral plasticity is itself a genetic trait that bestows an advantage as bird species that are more generalist and behaviorally flexible have had greater success in urban environments (Møller, 2009).

The adaptations described by Luniak (2004) originated from a variety of causes including the diminished effect of winter in urban environments, the lack of predator pressure, or the abundance of anthropogenic food. There were several changes with a connection to the caloric surplus from anthropogenic food. Reduced migratory behavior has been observed partially because of the abundance of food and the reduced requirement for travel that this abundance implies. Several urban populations of birds in Central Europe, including the mallard (*Anas platyrhynchos*), blackbird (*Turdus merula*), mute swan (*Cygnus olor*), coot (*Fulica atra*), and rook (*Corvus frugilegus*), live sedentary lifestyles with much of the winter spent in breeding areas. The sedentary life allowed by the abundance of anthropogenic food has in turn allowed longer breeding seasons with urban blackbirds generally beginning their breeding season one to four weeks sooner than their rural counterparts (Luniak, 2004). Finally, urban bird populations have changed their behavior towards humans. This includes changing feeding habits to find or receive the excess calories from human societies and an increased docility towards humans (Luniak, 2004).

Further evidence of the adaptation of urban bird species to human interaction is examined through changes in flight distance (Møiler, 2008). A bird's flight distance is the proximity that a potential predator must achieve to trigger the bird's flight response. Møiler (2008) found that urban bird populations have consistently smaller flight distances than their rural counterparts. Moreover, the variation in flight distance had a positive relationship with both the number of generations since urbanization and the population differential between the urban and rural variants of a species. Thus, there is evidence that the adaptation of shorter flight distance is the result of genetic evolution. The tradeoff that dictates the optimal flight distance is the benefits of an uninterrupted activity versus the danger of an approaching threat. The benefit of anthropogenic food increases the desirability of leaving an activity uninterrupted, and calm in the face of human presence allows access to the caloric surpluses that those humans leave behind.

Many of the behavioral adaptations described above are not exclusively caused by the existence of a caloric surplus as the quest for calories is, of course, not the only source of selection pressure. That being said, the Darwinian value of gaining access to the novel calories brought about by urbanization has had a significant effect on the behavior of those bird species adapting to the urban environment. To what degree these adaptations are a result of genetic changes unique to the urban species is not well understood (Luniak, 2004). However,

behavioral differentiation between blackbirds with forest and urban origins that have been reared in a lab has been interpreted as genetic (Walasz, 1990). Additionally, the positive relationship between colonization time and population density established by Møller et al. (2012) implies that the adaptations associated with synurbization have a significant genetic component.

Table 2

Species	Adjusted Trend	# of Routes	Raw Trend	95% CI
House Sparrow	-3.6	3804	-3.6	(-3.8, -3.5)
Chimney Swift	-2.5	2537	-2.5	(-2.7, -2.3)
Common Grackle	-1.7	3438	-1.8	(-1.9, -1.6)
European Starling	-1.5	4211	-1.5	(-1.7, -1.3)
Rock Pigeon	-1.2	3401	-1.2	(-5.2, -0.9)
Purple Martin	-0.9	2333	-0.9	(-2.2, -0.6)
Blue Jay	-0.7	3072	-0.7	(-0.8, -0.6)
Chipping Sparrow	-0.6	3798	-0.6	(-0.9, -0.4)

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Northern Mockingbird	-0.5	2684	-0.5	(-0.6, -0.3)
Mourning Dove	-0.3	4361	-0.3	(-0.4, -0.2)
American Robin	0.1	4210	0.1	(0.0, 0.2)
Inca Dove	1.6	221	1.6	(0.5, 2.7)
Eurasian Tree Sparrow	5.7	38	5.8	(4.1, 7.7)
Eurasian Collared-Dove	27.8	1438	29.2	(24.6, 31.7)
House Finch	0.1	3069	0.1	(-0.2, 0.5)

Source: North American Breeding Bird Survey.

The above data represents trends in population for bird species with urban breeding patterns from 1966 to 2015. The data was collected through roadside observations across North America, and the trend values were created using procedures developed by Link and Sauer (1996). Unsurprisingly, one can see that there have been evolutionary winners and losers among the urban bird species. One species, the Eurasian Collared-Dove (*Streptopelia decaocto*), is an invasive bird that appears to have fared particularly well in an urbanizing continent (Bonter, Zuckerberg, & Dickinson, 2010). Data from the Christmas Bird Count in Florida of the average number of bird sightings per hour at sites with a Collared-Dove presence showed an increase from 0.025 in 1986 to 1.322 in 1996 (Romagosa & Labisky, 2000). The Genes as Entrepreneurs theory does not predict that the introduction of anthropogenic food will create a benefit for all lifeforms involved, but a problem would arise for the theory if, despite the caloric surplus, no species was able to adapt and exploit the surplus. Thus, the reasons for the success of the Eurasian Collared-Dove will be explored.

The Eurasian Collared-Dove is thought to have originated around India and spread to Turkey and the Balkans in the 16th century (Fujisaki, Pearlstine, &

Mazzotti, 2010). The species then rapidly colonized Europe, northwest Africa, and North America in the 20th century (Crooks & Soulé, 1999). The lagged, then rapid, colonization pattern is in keeping with the theory that urban specialization is the cause of the Collared-Dove's success (Isenmann, 1990). The Collared-Dove's broad diet is an adaptation that would lead to success in an urban environment, and the supplement of anthropogenic food to the diet of the Collared-Dove is also thought to be a significant factor in its high breeding productivity (Robertson, 1990; Romagosa & Labisky, 2000). Study of the species' habitats in Europe has shown unique levels of human commensalism (Fujisaki et al., 2010). A large-scale study conducted by Fujisaki et al. (2010) using the North American Breeding Bird Survey data found that road density, used as a proxy for human alteration of the landscape, is positively related to Collared-Dove abundance, so the expansion of the species is thought to follow human effects on environments.

Work by Bonter et al. (2010) studied the invasion of the Eurasian Collared-Dove by examining 444 sites in Florida for the relationship between occupancy of the invading species and habitat characteristics. The Collared-Doves were more likely to be found in areas that had been affected by human influence. This is consistent with work done by Coombs, Isaacson, Murton, Thearle, and Westwood (1981) where they studied the Collared-Dove in two British industrial areas and noted this species of bird is located exclusively around human settlements. Furthermore, Coombs et al. (1981) found that roosting patterns were formed to facilitate proximity to human grain sources and that population fluctuated with the supply of said grain sources. In fact, the impact of Collared-Dove exploitation of human grain supplies was so significant that regulations were put in place to reduce the food loss and spoilage problems the birds introduced (Coombs et al., 1981). These findings suggest that the increase in population of the Eurasian Collared-Dove in North America is related in part to adaptation to life in urban environments and the exploitation of the excess anthropogenic calories present in those environments. Other factors such as the ability to traverse long flight distances and the young age at which Collared-Doves can breed are also thought to be factors in their success (Romagosa & Labisky, 2000).

Bonter et al. (2010) also examined the relationship between Collared-Dove and native dove populations to determine the effect of the invading species on the native species. To the surprise of the authors, they found that the native and invasive populations were positively correlated. This result would be explained if the population growth of the Collared-Dove was due to its exploitation of exogenously introduced resources that had yet to be fully exploited as is the case in the model presented in this paper. The additional competition for resources introduced by the invading species was expected to negatively affect the native species, but this zero-sum effect need not take place if the invading species was exploiting a new stock of resources.

A final prediction of the Genes as Entrepreneurs theory is that a caloric surplus should not remain indefinitely. Unfortunately, this prediction is muddled in the urban environment as food waste is disposed of by human institutions. However, the scarcity of calories has long been considered characteristic of natural settings. The natural tendency described by Malthus of population growth to outpace food supply had a significant influence on Darwin's original theorizing about natural

selection (Barnett & Morse, 2013). Thus, the scarcity of calories drives the process of caloric arbitrage and its contribution to biological evolution. Humans have, thus far, defied the limitations predicted by Malthus by creating knowledge of how to create food more efficiently. The Genes as Entrepreneurs theory creates an analogous dynamic framework for how genetic evolution can occasionally break through the Malthusian Trap by discovering new strategies for exploiting caloric surpluses.

CONCLUSION

The urban colonization process is not currently well understood, but the Genes as Entrepreneurs theory that this paper posits may contribute to the literature by advancing the understanding of urban species colonization in a rapidly urbanizing world (Evan et al., 2009). Urbanization has proceeded at an unprecedented scale in the last century and can be expected to continue into the indefinite future (Shochat, Warren, Faeth, McIntyre, & Hope, 2006). The selection pressure that will govern evolution going forward will largely be the result of human influence, so there is a great deal of practical knowledge to be gained by understanding the evolutionary dynamics of urban colonization. This paper seeks to demonstrate that the ongoing process of urban colonization is partially explained by the Genes as Entrepreneurs theory. More generally, the caloric arbitrage mechanism described in this paper may help to explain why life has colonized a wide variety of inhospitable, or novel, regions on Earth and will continue to do so as humans change the landscape. Further data should be collected to test the viability of the model developed in this paper.

The theoretical predictions of this paper are meant as a clarification of intuitions already present in biology. For example, the basic dynamics of the Genes as Entrepreneurs theory is taken as given in work done by Rohmer, Hocquet, and Miller (2011) that analyzes the evolution of pathogenic bacteria. They argue that the long-established fact that pathogens evolve new forms of virulence to access niche environments is true of metabolic functions as well. Pathogenic bacteria must compete for the nutrients present in its host with a myriad of resident bacteria; therefore, pathogens evolve strategies for gaining access to these scarce nutrients. Thus, the evolution of metabolic and virulence capabilities both play a role in the success of a pathogen.

The theory of evolution provides a starting point for the understanding of all biology. The Genes as Entrepreneurs theory is intended to be an explanation of one of the mechanisms in the evolutionary process through the help of the analytical tools of economics. The logic of profit arbitrage plays a central role in our understanding of the market process and its own evolutionary dynamic, but the idea of an arbitrage can reach beyond monetary transactions. By borrowing from the wealth of analytic tools in the discipline of economics, evolutionary biology can advance its understanding of the way scarcity affects the process of biological evolution.

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APPENDIX

Proof of (d):

$$\begin{aligned}
 \frac{d\left(\frac{X}{P}\right)}{dt} &= \frac{\left(\frac{dX}{dt}\right)P - X\left(\frac{dP}{dt}\right)}{P^2} \\
 &= \frac{(X+Y)\left(\left(\frac{R}{\omega}\right)X + hX\left(1 - \frac{P\beta}{\alpha}\right)\right) - X\left(\left(\frac{R}{\omega}\right)X + hX\left(1 - \frac{P\beta}{\alpha}\right) + hY\left(1 - \frac{P\beta}{\alpha}\right)\right)}{(X+Y)^2} \\
 &= \frac{X^2\left(\frac{R}{\omega}\right) + hX^2\left(1 - \frac{P\beta}{\alpha}\right) + YX\left(\frac{R}{\omega}\right) + hXY\left(1 - \frac{P\beta}{\alpha}\right) - X^2\left(\frac{R}{\omega}\right) - hX^2\left(1 - \frac{P\beta}{\alpha}\right) - hXY\left(1 - \frac{P\beta}{\alpha}\right)}{(X+Y)^2} \\
 &= \frac{YX\left(\frac{R}{\omega}\right)}{(X+Y)^2} \blacksquare
 \end{aligned}$$