Sexual Selection:
A Missing Link in Evolutionary Theories of the Firm?[i]

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Biological theory has long been a source of inspiration for economists, and the analogy between market competition and what Darwin called 'the struggle for existence' has informed both neoclassical and heterodox views of the firm. What has gone largely unnoticed, however, is that Darwin's theory of evolution rests on two pillars. In nature, the process of 'survival selection' that has inspired economists is complemented by 'sexual selection'. Sexual selection is a fundamentally different process from survival selection and can lead to very different selective outcomes. This paper explores how the notion of sexual selection can inform economic theory. We argue that sexual selection theory provides the ontological foundation for incorporating social aspects of human organization into evolutionary theories of the firm. This foundation provides the basis for a theory that can explain differences between firms that theories based on survival selection alone cannot. Moreover, in contrast to the optimality arguments that have been made on the basis of the logic of survival selection alone, a theory of the firm that also incorporates the logic of sexual selection would predict that firms may evolve stable characteristics that are deleterious from the point of view of their efficiency in product markets.

Key words: Generalized Darwinism; Theory of the firm; Ontological foundations

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'The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!' (Charles Darwin, 1860)[1]

'Of the branches of biological science to which Charles Darwin's life-work has given us the key, few, if any, are as attractive as the subject of sexual selection' (Ronald A. Fisher, 1915)

1. Introduction

The theory of biological evolution has inspired a number of evolutionary views on organizations. Economists, sociologists and organization theorists have all drawn on the analogy between what Darwin called 'the struggle for existence' and competition in markets to develop explanations of how economies, industries and firms evolve. What has gone largely unnoticed, however, is that Darwin's theory of evolution by natural selection rests on two pillars. In nature, 'selection for reproductive success', or 'sexual selection', complements the mechanism of 'natural selection', or 'survival selection' that has inspired evolutionary theories in the social sciences. Evolutionary theories of socio-economic organization have generally ignored this second mechanism, and the purpose of this paper is to explore how it might help us better understand economic evolution in general, and the nature of the firm in particular.

Darwin (1859, 1871) proposed a second type of selection to account for phenotypic traits that survival selection could not explain. The archetypal example in biology is the peacock's tail. This extravagant tail reduces the peacock's chances of survival, and without a countervailing force, its existence would be proof against the theory of natural selection. Sexual selection provides this countervailing force, and offers an explanation for traits that are deleterious in the struggle for existence. As Jones (1999, p.100) has aptly described it, '[biological evolution] is an examination with two papers. To succeed demands a pass in both. The first involves staying alive long enough to have a chance to breed, while the mark in the second depends on the number of progeny'. We here ask if the evolution of firms should also be seen as an examination with more than one paper. The fact that evolutionary theories of the firm have all equated natural selection with 'survival selection' begs the question if we have not been overlooking important additional selection mechanisms in theorizing about economic organization.

This paper argues that this question has to be answered in the affirmative. We will demonstrate how sexual selection theory provides an ontological basis to incorporate the social aspects of economic selection into the theory of the firm. We will argue that a theory of the firm that incorporates the explanatory logic of sexual selection explain organizational traits that a theory based on survival selection alone cannot. Moreover, we will show how the application of the logic of sexual selection to firms leads to a testable

[1] Quoted in Cronin (1991). The quote is from a letter by Darwin to the American Botanist Asa Gray.

prediction that runs counter to the optimality arguments that have been made on the basis of a survival selection logic alone (Alchian 1950, Friedman 1953).

Our arguments will not merely be based on sexual selection as metaphor or analogy. In keeping with recent contributions on the use of biological theory in economics, our focus is on exploring the implications of sexual selection in terms of ontological continuity (Witt, 2003) and ontological similarity (Hodgson 2002, 2003; Hodgson and Knudsen 2005). The second section of the paper will clarify these terms by reviewing the current status of discussions about the use of biological theory in economics. Section three then explains the general idea of sexual selection theory and its link to the theory of the firm. We argue that the fact that all organizations need to attract members to survive points to the possibility that there may indeed be selection mechanisms other than selection by the market at work in the evolution of firms.

In order to derive possible ontological similarities between sexual selection and socio-economic selection, section four takes a closer look at the specific mechanisms that sexual selection theory has proposed to explain traits that are deleterious from the point of view of survival selection. Section five then develops an explanatory framework that is based on the causal logic of sexual selection theory, but abstracts from specific biological content. This framework captures the general logic of selection driven by preferences, of which sexual selection is a special case. Section six applies the framework to the ways in which firms attract members, and shows that 'mutual preference selection' can explain differences in organizational culture between firms that theories based on survival selection cannot.

Section seven takes a closer look at what sexual selection theory can contribute to the theory of the firm from the point of view of ontological continuity. Here the argument is that the impact of sexual selection on the genetic basis of human behavior points to the importance of 'status seeking' as a driver of our behavior. Section eight then combines this insight with the general explanatory logic of preference selection to argue that a theory of the firm that incorporates these two ontological foundations leads to a testable proposition that differs from a theory based on survival selection alone. In contrast to the optimality arguments that have been made on the basis of the logic of survival selection, firms can be expected to evolve stable organizational traits that are deleterious from the point of view of selection by the market. Section nine concludes the paper.

2. Evolutionary theory and evolutionary economics

Economics and biology have always inspired each other. Darwin's theory of evolution by natural selection was inspired by Malthus' *Essay on Population*, and both orthodox and evolutionary economists have since used Darwin's ideas as a point of reference for better understanding competitive dynamics in markets (for overviews see Hodgson, 1993, 2004; Vromen, 1995). The seminal work of modern evolutionary economics, Nelson and Winter's *An Evolutionary Theory of Economic Change*, develops a theory based on biological metaphor and analogy, and one of Nelson and Winter's accomplishments is

that they ground their theory more firmly in biological principles than their predecessors in evolutionary economics (Hodgson, 2002). However, as Nelson and Winter are themselves aware, there are limits to what biological metaphors and analogies can do for economic theory (Winter, 1964; Nelson and Winter, 1982; Nelson, 1995). The idea that economics needs a theory of evolution that abstracts from the specific manifestation of evolutionary processes in nature is now widely supported among evolutionary economists (e.g. Dopfer, 2004; Dopfer, Foster and Potts 2004; Loasby 2002; Metcalfe 1998; Nelson, 1995; Witt, 1999, 2003; Knudsen, 2002; Hodgson, 2002, 2003, Vromen 2004). Recent work has therefore moved beyond metaphor and analogy and has explored the ontological basis of evolutionary economics.

Two somewhat dissimilar attempts to specify ontological foundations for evolutionary economics are Witt's continuity hypothesis (Witt, 1999, 2003) and the application of Universal Darwinism to economic evolution (Hodgson, 2002, 2003; Hodgson and Knudsen 2005; Knudsen, 2002; Stoelhorst, 2005).

Witt's position is illustrated by the following quote:

> 'The continuity hypothesis … suggests conceiving the historical process of economic evolution as emerging from, and embedded in, the constraints shaped by evolution in nature. To understand the origin of economic evolution in human phylogeny and the fact that it has lasting influence through innate elements of human behavior, Darwinian theory is *directly* relevant. Yet in the further course of economic evolution, human behavior and, correspondingly, economic activities and their collective outcomes underwent a metamorphosis into the distinct, idiosyncratic forms observable in present-day economies. To explain the emergence of the latter, Darwinian theory is not sufficient. A theory of cultural evolution is required' (2003, p.16, emphasis added).

It may be clear that Witt takes the possibility of the application of biological evolution to economic behavior seriously, while being careful to avoid the pitfall of reducing the evolution of human behavior, economic institutions, and culture to genetic mechanisms alone. However, he does not see much relevance for Darwinism in understanding economic and cultural evolution beyond its use as an explanation of the genetic basis of human behavior. Once evolution has given rise to human creativity and cultural learning, these latter mechanisms become increasingly important to explain economic and cultural evolution. While natural selection has shaped '…innate dispositions and adaptation mechanisms and programs in humans … which define the basic behavioral repertoire upon which other forms of evolution rest' (2003, p. 16), the '… invocation [of Darwinian principles] outside biology would amount to an analogy construction or, since such analogies rarely hold, to the use of an abstract biological metaphor' (2003, p.13).

Witt extends his critique of using Darwinian concepts in economics to Campbell's (1960, 1965, 1974) formulation of 'variation', 'selection' and 'retention' as the general features of an evolutionary process, and dismisses this triumvirate as 'an abstract reduction of the Darwinian principles and, as such, still domain specific' (2003, p.12). This is in contrast to the notion of 'universal' or 'generalized' Darwinism, which holds that the principles on which Darwin's theory of natural selection rests are sufficiently general to explain the evolution of all open, complex systems. Dawkins (1983) originally coined the term Universal Darwinism as a label for the idea that Darwin's theory is sufficiently general to

explain the evolution of all possible life in the universe. However, the term has since been used for the notion that the variation-selection-retention algorithm on which Darwin's theory is based can be used as a general explanation of all evolutionary processes (cf. Cziko, 1995; Plotkin, 1994; Dennett, 1995). This is an ontological claim that goes beyond the construction of analogies. In fact, the central idea of Universal Darwinism is to derive a generalized logic by *abstracting* from the specific biological content in Darwin's theory. The idea of generalizing Darwinism is *not* to reduce other forms of evolution to biological principles, and a theory constructed along the lines of generalized Darwinian principles will therefore always need to provide a domain specific explanation of the mechanisms of variation, selection and retention that govern the evolution of the system in question (Hodgson and Knudsen, 2005).

The position taken here is that the ontological continuity proposed by Witt, and the role of Darwinian principles in illuminating the ontological similarity between all evolutionary processes as advocated by Hodgson and others, should both play a role in further developing the ontological basis of evolutionary theory in economics. They complement each other, and can both help evolutionary theory in economics move beyond metaphor and analogy. Each of them also points to interesting questions with respect to the possible role of sexual selection in economic theory. Witt's continuity hypothesis gives rise to questions about the innate behavioral dispositions that have been shaped by sexual, rather than survival, selection, and how these dispositions may affect economic behavior. Universal Darwinism's ontological commitment to the generic similarity of all evolutionary processes gives rise to questions with respect to the nature of selection, and the possibility that more than one type of selection process may have to be taken into account to explain the evolution of economic institutions.

3. Sexual selection and the theory of the firm

While most of the arguments to follow may apply to institutions in general, our analysis in the remainder of this paper will focus on firms, and our argument will be developed in terms of the ways in which sexual selection theory can contribute to an evolutionary theory of the firm. To the extent that the aim of a theory of the firm is to offer an explanation for the existence, boundaries, and internal organization of firms (Holmstrom and Tirole 1989; Foss 1996), it is not necessarily clear that an evolutionary theory of the firm exists (Foss 2001). Yet, evolutionary theory has been applied to the analysis of firms in a number of ways. The most prominent applications are as a bulwark for neoclassical efficiency arguments (Alchian 1950, Friedman, 1953), as a basis for understanding industry level population dynamics (Hannan and Freeman 1977), and as a source of analogies for constructing a more realistic alternative for the neoclassical theory of economic growth (Nelson and Winter, 1982). What these three ways of applying evolutionary theory to firms have in common is that they see firms as units of selection that are exposed to competitive pressures. Where they differ is in the sophistication of their view of the firm. On this latter point, Nelson and Winter's work is most developed. Their view of the firm as a repository of productive knowledge made up of boundedly rational individuals whose behavior is coordinated in organizational routines will serve as

our point of reference for exploring the possible value of the theory of sexual selection for the theory of the firm.

Darwin defined sexual selection as a process that depends on 'the advantage that certain individuals have over others of the same sex and species solely in respect to reproduction' (Mayer, 2001). Sexual selection works through competition for reproductive success rather than through competition for survival, and its causes and effects are different from those of survival selection (Andersson, 1994; Miller, 2000). Both survival selection and sexual selection involve competition between individual members of a species, but the relevant context within which this competition takes place is different. Under survival selection, species adapt to their natural environments, while under sexual selection, they adapt to sexual rivals and mates (Andersson, 1994). Survival selection takes place as a result of the challenges set by the organism's physical environment and the predators, prey, parasites and germs that occupy its ecological niche, while sexual selection takes place within the context of the preferences of the other sex. Survival selection is driven by *scarcity* of resources and is an inherently *convergent* process that can explain *efficient* adaptations to the organism's natural environment. Sexual selection is driven by differences in *preferences* and is an inherently *divergent* process that can explain traits that seem *wasteful* from the point of view of survival selection (Miller, 2000).

It is sexual selection's ability to explain such seemingly wasteful traits that makes it an essential feature of Darwin's theory of evolution. Without an additional mechanism to explain traits that are costly to evolve but that do not confer any survival advantage, the theory of evolution by natural selection would be incomplete. In fact, from the point of view of survival selection, the feathers of the peacock's tail are not just useless embellishments; they actually reduce the chances of survival of its bearer. Without a good explanation for why they evolved, their existence would constitute proof against the theory of evolution by natural selection. Sexual selection through mate choice provides this explanation: the feathers in the peacock's tail are sexual ornaments that evolved to attract mates. They are adaptations that increase their bearer's chances of reproducing. Because evolutionary success depends on the number of progeny, survival as such is not the only criterion by which the phenotypic traits of sexually reproducing animals are selected. The extravagance of the peacock's tail is the result of generations of peahens selecting their mates on the basis of a preference for long, colorful and patterned feathers.

Darwin's theory was not very well received by his Victorian contemporaries, and its publication in 1871 was essentially followed by a century of neglect.[2] Despite the fact that Ronald Fisher (1915), one of the architects of the Modern Synthesis of Darwinian evolution with Mendelian genetics in the 1930s and 1940s, already outlined the two ways in which sexual selection through mate choice is now believed to work, it took until the 1960s until a new generation of biologists picked up on the idea (Andersson, 1994).

[2] Perhaps the fact that one of the central mechanisms in Darwin's theory of sexual selection is mate choice by females may help explain its frosty reception among his male contemporaries. Even Alfred Wallace, who had independently discovered the principle of survival selection and was a staunch defender of the theory of evolution, was opposed to it, and in fact became the theory's main critic (Cronin, 1991).

When, in 1975, Amotz Zahavi proposed a link between sexual selection and survival selection called the 'handicap principle', the controversy over his paper became the true revival of sexual selection theory (Miller, 2000). The theory got increasing attention in the 1980s, and in the 1990s it became one of the most successful areas of biology (Andersson, 1994), as well as the most fruitful idea in evolutionary psychology (Miller, 2000). Biologists now take sexual selection seriously, and 'evolution through natural selection' is generally understood as 'evolution through survival and sexual selection'[3]

Why might the second pillar of Darwinism be relevant when theorizing about firms? Before moving on to ontological considerations, let us make this point by way of metaphor and analogy. At the most general level, the important role of sexual selection in biology calls attention to the possibility that other than merely survival selection mechanisms may also be at work in shaping firms. An exclusive focus on the competition between firms may have left us blind to selection mechanisms other than market pressures. In addition to this general notion, sexual selection can also be seen as a metaphor for the idea that firms may have traits that simply cannot be explained by their survival value in the competition between firms. In fact, firms may have characteristics that are deleterious with respect to survival selection because they are adaptations to other selection pressures. Seen in this way, the metaphor of sexual selection may serve as a heuristic lens to uncover aspects of economic organization that theories of the firm have so far overlooked, or worse, would not be able to explain.

The social aspect of firms is an example. Economic theories of the firm are largely silent about how firms differ in their social dimensions. More specifically, they miss the fact that (1) membership of a social organization is typically voluntary, so that individuals have a choice in which firm to join, and (2) that this choice may be at least in part motivated by social, as opposed to economic, reasons. We believe that the combination of these two caveats makes a broader perspective on selection necessary. The evolution of organizations is not just driven by their success in product markets, and is indeed 'an examination with more than one paper'. Organizations also need to attract members to survive. If membership of an organization is voluntary, then organizations need to be attractive to their members. This immediately points to a potential role for selection mechanisms other than survival selection in explaining differences between firms. If members have a choice in joining an organization, we may expect a process analogous to sexual selection, whereby employees select attractive organizations and organizations select attractive employees. If we accept that any form of human organization needs members to function, it follows that some traits of the firm may need to be understood in terms of their value in attracting employees. Moreover, some of these traits may be genuine adaptations, yet deleterious from the point of view of survival selection in

[3] In addition to the relatively recent resurrection of this part of Darwin's theory of evolution, this lumping together of survival and sexual selection helps explain why economists have so far overlooked the second pillar of Darwinism. Popular labels for the theory of evolution such as Herbert Spencer's 'survival of the fittest' add to the emphasis on survival over sexual selection, as does the fact that the theory is still given relatively limited attention in many books on biology. Even today, the leading textbook on evolutionary biology (Ridley, 1996) does not mention sexual selection until page 296, while an explanation of evolution to the general reader by one of the 20th century's leading biologists devotes a mere two pages to it (Mayr, 2001). We may be forgiven for our oversight.

product and/or financial markets. We will pick up on this point in section six, where we will further develop this line of reasoning to explain the emergence and nature of organizational culture. But to be able to do so, we must first develop our argument beyond metaphor and analogy.

4. Sexual selection theory

To better understand how the theory of sexual selection could contribute to the ontological foundations of an evolutionary theory of the firm, we first need a better understanding of how it works. Darwin proposed that sexual selection operates in two different ways: through competition among the members of the same sex, or through choice of one of the sexes for specific characteristics in the other. The first case, called *intrasex selection*, usually takes the form of competition or fighting among males, while the second case, called *intersex selection*, usually takes the form of female choice of males with attractive features (Mayr, 2001). The effects of these selection mechanisms should be most noticeable in polygynous species, where successful males mate with more than one female. This makes mating opportunities for other males scarce, and this scarcity enhances the selective effects of both intrasex and intersex selection. The most pronounced cases of sexual dimorphism such as the antlers of deer and the tail of the peacock should therefore be found among polygynous species. In *The Descent of Man*, Darwin provides extensive evidence that sexual dimorphism is indeed mainly found in polygynous species.[4] However, Darwin had no real explanation for why males compete and females choose. Nor did he address the question why females would have a preference for such seemingly useless ornaments as the peacock's tail.

Biologist Robert Trivers answered the first of these two questions in the early 1970s (Trivers, 1972). Most species consist of two sexes, and because of how sexual reproduction works, males and females have conflicting interests and use different strategies to pass on reproductive information to the next generation. The fundamental sex difference is that females invest more nutrient energy in offspring than males, and Trivers realized that from this difference in 'parental investment', all else follows. Females can get pregnant only a limited number of times during their lives, whereas males can in theory inseminate a large number of females over a much longer period. It seems logical that their lower reproductive potential will make females a limited commodity and the object of competition by the other sex, and this allows them to be choosier. Put simply, 'males invest less and seek quantities of mates, while females invest more and seek quality of men' (Ridley 1993, p.129). The ensuing 'battle of the sexes' can be observed at every possible level, from sending the first signals to the other sex of potential availability or interest, through the act of mating and the 'sperm wars' of procreation, to the delivery and upbringing of offspring.

Of the two mechanisms of sexual selection, female choice poses the deepest theoretical questions. That intrasex selection driven by male competition may lead to characteristics

[4] In polyandrous birds, sexual selection and sexual dimorphism is reversed, and the females are the more colorful and ornate sex.

that may come at a cost in terms of the organism's chances of survival is easily understood. If males with larger antlers are more successful in securing mating opportunities because their antlers help them win fights and thus control larger harems, then the genes for large antlers will be disproportionally passed on to the next generation. This process will continue until the disadvantages of large antlers in terms of survival (for instance the cost of growing them, or limited maneuverability) put a limit on further growth. Intersex selection driven by female choice poses a bigger problem, because the advantage of, for instance, the peacock's tail, other than the fact that it is apparently attractive to females, is not clear, while its disadvantage in terms of survival value is. Why would females have evolved a preference for a characteristic that limits the chances of survival of their (male) offspring? There are two theories to explain this: Fisher's theory of sexual selection as a runaway process and Zahavi's handicap theory.[5]

Fisher's runaway process

Fisher's (1915, 1930) theory of sexual selection as a runaway process in essence explains deleterious characteristics as a result of the positive feedback mechanism of genes choosing copies of themselves. This can happen when genes for a certain sexual trait become genetically correlated with the sexual preference for that trait. Such a situation can occur quite easily. Consider a population of polygynous birds with relatively short tails. If some females where to develop a preference for longer tails they would choose male birds with longer than average tails as mates. The other females in the population would mate randomly, but the small segment of females that do actively choose longer tailed males would give the male birds with such tails an initially small advantage in producing more offspring. The crux of the runaway process is that this offspring has both the genes for growing a longer than average tail *and* the genes for preferring such a tail. The former will only get expressed in male offspring, and the latter in female offspring, but all descendents will contribute to the runaway effect on average tail length because the female preference is now genetically linked to the male trait. At the heart of this process is the positive feedback mechanism that females which choose males with longer than average tails will be increasingly likely to not only be choosing genes for the ability to grow such tails, but also copies of their own genes for preferring this trait. Each subsequent generation will therefore consist of a rapidly increasing percentage of females with a preference for long tails and males with a capacity to grow them.

As with all positive feedback processes, Fisher's runaway process is very sensitive to initial conditions and random events, and it is very difficult to predict its specific outcomes. It doesn't much matter what the initial reason for the female preference is, and random mutation may be enough to allow a species to evolve in an arbitrary direction under its own momentum. But there is also the possibility that the process is set in motion by an initial correlation between the trait preferred by females and the fitness of the males that posses it (say a longer tail allows more maneuverability in flight). Again, the correlation may be random, but if it exists, sexual selection and survival selection may start out as reinforcing each other. As the positive feedback process takes over, however, sexual selection will subsequently push the trait past its optimum from the point of view of survival.

[5] See Anderson (1994) or Ridley (1996) for details.

Fitness indicators and Zahavi's handicap theory

Zahavi's 'handicap theory' explains deleterious characteristics as a costly advertisement of good genes (Zahavi, 1975). This theory picks up on the notion of fitness indicators that Fisher first discussed in 1915. The idea of fitness indicators is based on the view that mate choice is a strategy for getting the best genes for your offspring. The variation in genetic quality among possible mates is not observable in itself, and fitness indicators are traits that evolved to reveal genetic information to the other sex. Fitness indicators are proxies for good genes, and under this theory, females don't choose mates for arbitrary reasons, but for traits that advertise their overall fitness. Zahavi's theory is that only *costly* fitness indicators are reliable. Males have an obvious incentive to cheat about their true fitness, so it is in the interest of females to select males on the basis of traits that only truly fit males possess. The costlier a trait is in terms of survival value, the more fit a male has to be to afford it. Sexual ornaments can thus be understood as 'handicaps' that advertise the true fitness of an individual by showing the costs they can bear in the competition for survival.

The reason that fitness indicators look maladaptive from the point of view of survival selection is that the wastefulness of sexual ornaments is what keeps males honest. Fitness indicators are not like other adaptations. As Miller (2000) puts it: they serve a meta-function by sitting on top of other adaptations and signaling their virtues. In contrast to the adaptations that are the result of survival selection, they show large individual differences, high costs, and high correlations with other mental and physical abilities, so that they provide as large a window on the genetic quality of the individual as possible. They are themselves legitimate adaptations, but are the result of a selection mechanism driven by the preference of the opposite sex.

We may conclude that sexual selection driven by intersex selection is not unlike artificial selection, by which humans selectively breed domesticated species according to their economic, aesthetic or alimentary value. The difference is that artificial selection is driven by the preferences of humans, while sexual selection is driven by the preferences of the species itself.[6] More specifically, in most species, sexual selection is driven by female preferences. This explains sexual dimorphism: why sexual ornamentation is almost always more developed in males than in females. Moreover, the fact that sexual selection is driven by differences in preferences may help explain why species diverge. The most widely used biological definition of a species is 'a set of interbreeding organisms' (Ridley, 1996), and diverging sexual preferences may explain why speciation tends to occur more rapidly than can be expected from the convergent process of survival selection. Darwin's theory of sexual selection can thus explain three things that survival selection cannot (Miller, 2000): the ubiquity of costly traits that do not confer survival advantage, sexual dimorphism within species, and the tendency for species to rapidly diverge.

[6] Another difference is, of course, that the selection pressures in artificial selection result from a conscious choice, whereas sexual selection in nature does not.

5. A generalized framework: the explanatory logic of preference selection

We are now ready to consider how sexual selection theory may be able to contribute to the ontological foundations of evolutionary economics. A later section will consider this question from the point of view of ontological continuity. This section will answer the question on the basis of the notion of ontological similarity. We will generalize the explanatory logic of sexual selection theory and then, in the next section, apply it to the firm. The generalization in this section will proceed by, first, specifying what sexual selection explains, second, how it explains it, and then abstracting this explanation from the mechanisms that are specific to sexual reproduction.

Discussions of the general characteristics of selection processes in biology (e.g. Cziko 1995; Hull et al. 2001) and economics (e.g. Knudsen, 2002, 2004) have implicitly focused on 'survival selection'. If sexual selection theory is to have any value in attempts to unravel the ontological similarity of all evolutionary processes, it should add something to our understanding of evolution that these discussions do not capture. As noted above, sexual selection theory addresses three explananda that survival selection cannot account for:

- Costly traits that do not confer survival advantage and that may even be deleterious from the point of view of survival selection
- Sexual dimorphism within species
- Rapid divergence between species

The first and second of these explananda are explained by intrasex selection and/or intersex selection, while the third is explained solely in terms of intersex selection. Remember that the first explanans, *intrasex* selection, revolves around contests among one sex in *competition* for scarce mating opportunities, while the second, *intersex* selection, takes place as a result of the *preferences* of the other sex exercised in mate choice. Of these two explanations, intrasex selection fits the rubric of selection as it has generally been understood in economic theory, i.e. selection resulting from the competition for scarce resources. This part of sexual selection theory can be understood from the same general logic as 'survival' selection, and therefore does not add much to our understanding of the selection pressures that firms may face. Intersex selection, however, points to a fundamentally different selection mechanism. It is a type of selection that is driven by preferences rather than scarcity, and this makes it a process with different characteristics than the ones that economic selection theory has traditionally focused on.

Sexual selection theory thus offers a potentially valuable additional explanans for the outcome of evolutionary processes: selection driven by preferences rather than scarcity. This type of selection would seem especially interesting from the point of view of the firm as a social environment, where humans with similar innate behavioral dispositions, but differently evolved preferences, interact. However, we still face the task of abstracting from the specific mechanisms of sexual reproduction, and while the explanans 'selection driven by preferences' seems to fit this bill, at least two of the three explananda

of sexual selection theory don't. Sexual dimorphism requires sexes, and, other than the obvious fact that the employees of most firms represent both biological sexes, at the level of firms there is just no meaningful equivalent to this concept. Similarly, the concept of species as exclusive reproductive communities that is central to the third of the explananda, does not hold up in the world of firms and economic institutions. In other words, we need to either drop these explananda or generalize them.

We may generalize the explanatory structure of intersex selection as follows, and refer to it as 'preference selection', of which sexual selection by mate choice is a special case. Preference selection occurs in situations when:

- Two parties are interested in a transactional relationship;
- There is variation in the traits of the potential transaction partners;
- There is variation in preferences regarding the traits of the other party;
- At least on of the parties can exercise a choice of transaction partners.

Note that this implies that there must be a population of entities to choose from. In these situations we can expect divergence of the overall population of entities into sub-populations that are characterized by more or less mutually exclusive transactions, in a process akin to assortative mating. The third explanandum of sexual selection theory above is a specific example of such a selective outcome.

We may also expect the entities involved to evolve costly traits, but only if additional conditions apply. One of the ways in which this can happen is when there is a scarcity of transaction partners and the party exercising the choice cannot evaluate the quality of all the relevant traits of the entities among which it can choose. This is a generalization of the situation to which Zahavi's handicap theory applies. The other way in which costly traits can evolve is when the choices made over time involve a positive feedback mechanism. This may occur if the entities choose copies of themselves and is a generalization of Fisher's runaway process. Table 1 summarizes the generalization of the explanatory logic of sexual selection to preference selection.

Preference selection applies to a broad class of socio-economic situations, including some processes that affect the nature of firms. The selection of board members or merger candidates would come to mind, and preference selection processes may also help explain competitive outcomes in product markets. However, here we focus on how firms attract members. The next section shows how the explanatory logic of preference selection can explain cultural differences between firms that extant economic theories of the firm based on survival selection cannot.

6. An application to organizational culture

To substantiate our claim that sexual selection provides the ontological basis for incorporating the social aspects of the firm into economic theory, consider the case of organizational culture. Schein (1990) defines culture as a pattern of assumptions

developed by a group through finding solutions to problems with respect to external adjustment and internal integration. Thus defined, culture is something that emerges in the interactions between individuals.[7] Economic theories of the firm do not pay much attention to organizational culture. Yet, culture can be a source of competitive advantage (Barney, 1986), as well as a source of inertia and organizational failure (Schein, 1985). There are obvious differences between organizational cultures (e.g. Hofstede et al., 1990), even if the firms in question are competing in the same product markets (e.g. Chatman 1991). If a theory of the firm is to explain how and why firms are different (Holmstrom and Tirole 1989; Nelson 1991; Foss 2001) then it should also be able to explain cultural differences. An explanation based on survival selection would find it difficult to do so. Because survival selection is an inherently convergent process that steadily moulds firms to fit their competitive environment, we would expect firms to become more and more alike. In contrast, organizational culture is a trait of firms that seems to display the characteristics of a preference selection process: even firms that follow similar survival strategies differ in their cultures, and firms may have cultures that are deleterious from the point of view of their economic performance and survival. Organizational culture thus seems to be a phenomenon that is better explained as the outcome of a divergent preference selection process.

The literature on organizational and personnel psychology provides evidence that this is indeed the case. An interesting strand of research in this literature concerns the fit between individuals and the organizations they work for (for a review, see Van Vianen, 2005). One of the person-organization fit models that initiated much empirical research is Schneider's attraction-selection-attrition model (Schneider 1987; Schneider et al., 1995). Leaving aside the superficial resemblance to the Darwinian algorithm, this framework describes the process by which the fit between an individual and the organization is established. People are not randomly assigned to organizations, but select themselves into and out of organizations. There are three mechanisms at work in this process. First, people find organizations differently attractive as a function of their judgment of the congruence between the characteristics of the organization and their own characteristics. Second, the firm selects those people that have the characteristics that the firm desires. Third, once people have become members of the organization and find that they do not fit their work environment, they tend to leave.

This literature gives credence to the idea that the membership of firms results from a mutual preference selection process. Consider the four conditions for a mutual preference selection process described in the previous section. In the case of personnel selection: (1) both firms and individuals are interested in a transaction relationship, (2) both firms and individuals have a choice of transaction partners, (3) there are variations in the traits of firms and individuals, and (4) there are variations in the preferences for the traits of the transaction partner on both sides of the potential transaction relationship. We would thus expect the population of firms and prospective employees to sort themselves out

[7] Note that Schein's definition of culture in terms of two types of problems, those with respect to external adjustment and those with respect to internal integration, makes it likely that solutions to the former problem are subjected to convergent selection pressures from the market, while solutions to the latter problem are more likely to result from the divergent preferences of the members of the different firms.

according to their mutual preferences, and the person-organization fit literature suggests that such a process does indeed take place. Firms will select (and, we may add, retain) those individuals that fit their preferences. However, they can only select from among those individuals that apply for a job. Before there is anything for the firm to select, prospective individual employees have already self-selected on the basis of their own preferences for the type of firm they want to join, and if, upon accepting a job, the firm turns out to be not that attractive after all, they can always vote with their feet and end their membership by changing jobs. If, in keeping with Schein's definition, organizational culture emerges from the interactions between the members of an organization, then we can expect the composition of the organization's membership to affect its culture. In the words of Schneider (1985), 'the people make the place'. And if the membership of an organization is the result of a mutual preference selection process in which people sort themselves out into relatively homogeneous groups, then we can expect stable cultural differences between firms to evolve. Such differences are an empirical fact and cannot be explained by the logic of survival selection.

Could it also be that organizations evolve cultures that are deleterious from the point of view of their survival? Again the empirical facts would seem to bear out that this may be the case. Following the general framework developed above, this could be explained in two ways. First, there may either be a situation of scarcity of transaction partners combined with information asymmetry impeding proper evaluation of all the relevant characteristics of the potential partner. Second, there may be a situation in which transaction partners sustain a runaway process by choosing 'copies of themselves'. It is likely that these situations may obtain in personnel selection. For instance, we can expect similarity attractions between (groups of) individuals to play an important role. The similarity attraction mechanism, through which people feel more attracted to individuals with similar attitudes and values, is well established in social psychology. A more detailed analysis of person-environment fit shows that the fit between person and organization may be better understood in terms of the fit between an individual and the team of which the individual is part (Van Vianen, 2005) Also, the person-to-person interaction between the prospective employee and the recruiter plays an important role in deciding the firm's membership. At these levels of analysis, similarity attraction helps explain why recruiters have tendency to select employees they perceive as similar to themselves. With such a psychological mechanism in place the condition for a Fisherian 'runaway process' akin to genes selecting copies of themselves is fulfilled.

In short, organizational culture has the characteristics of a trait that is the outcome of a divergent selection process. The role of mutual preferences in establishing and maintaining group cohesion and organizational culture can explain these characteristics. Prospective employees pre-select themselves on the basis of their preferences for the traits of firms, and firms select on the basis of their preferences for the traits of employees. The result will be that the populations of firms and employees will sort themselves into more or less exclusively interacting communities according to their mutual preferences. Moreover, if the natural tendency for people to let the mechanism of similarity attraction play a central role in the process is left unchecked, this may lead to the type of positive feedback related to 'choosing copies of oneself'. This may result in a

runaway process whereby certain types of people create a certain type of culture, which attracts more people of the same type, which strengthens the culture. If we accept that firms need members to survive in addition to making profit in product markets, then we must accept that it is possible that the membership selection process leads to organizational cultures that are deleterious from the point of view of survival selection. This may even obtain if the original culture was conducive to the firm's performance. In the presence of a positive feedback mechanism, the membership selection process may push an organizational culture past its optimum from the point of view of profitability in product and financial markets.

7. Sexual selection and the behavioral foundations of the theory of the firm

We now shift our attention from matters of ontological similarity to matters of ontological continuity. What can the theory of sexual selection contribute to our understanding of the genetic basis of economic behavior? As Witt's (2003) elaboration of the notion of ontological continuity shows, we need not fall prey to 'greedy reductionism'[8] when we accept that human behavior has a genetic basis. This is not to deny the importance of the cultural mechanisms that influence behaviors learned during one's lifetime. But evolutionary biology and evolutionary psychology have firmly established that human behavior is in part driven by innate preferences that have evolved to increase our genetic fitness (cf. Witt 1991, 2003). To this general insight, sexual selection theory adds the notion that our genes have not just been shaped by competition for survival, but also by the preferences of the opposite sex. A substantial part of our innate behavioral tendencies has evolved to attract mates. From the point of view of ontological continuity, the question we face is how this insight relates to economic behavior. What are the behavioral assumptions that follow from sexual selection theory, and what can they contribute to economic theory in general, and the theory of the firm particular?

Note that the development of theories based on realistic behavioral assumptions has always been a central part of the research agenda of evolutionary economists. It is no coincidence that Miller (2000), one of the advocates of the importance of sexual selection mechanisms, mentions Veblen's (1899) notion of conspicuous consumption as one of the sources of inspiration for developing his theory of how sexual selection through mate choice has shaped human nature. In keeping with the search for realism in evolutionary economics, Nelson and Winter (1982) make an important point of what they call 'appreciative theorizing' about what happens inside firms. In chapters four and five of their book, their main concern is to ground theories of competition and economic growth in more realistic behavioral assumptions than those of neoclassical orthodoxy. They achieve this by building on the behavioral theory of organizations developed by Cyert and March (1963). The central assumption of this theory is Simon's (1976) notion of 'bounded rationality', and it is this notion that underlies Nelson and Winter's view of the

[8] The term is from Dennett (1995) who uses it to differentiate between properly reductionist theories that allow for the fact that human behavior is partly explained by genetic dispositions and greedily reductionist theories that would want to explain all of human behavior solely in genetic terms.

firm as a set of decision-rules, or 'routines'. Contractual theories of the firm (e.g. Williamson 1975, 1985) are also based on the notion of bounded rationality, but add a second behavioral assumption. Human agents are also seen as prone to opportunistic self-interested behavior. The behavioral assumptions of bounded rationality and opportunism that underlie extant theories of the firm are entirely compatible with evolutionary insights. Humans have impressive, yet limited, cognitive abilities, and natural selection is driven by organisms acting in their own interest. But as fundamental as these assumptions may be, they can hardly be seen to represent all that is relevant about human economic behavior. Let us therefore ask if sexual selection theory would suggest any additional behavioral assumptions.

Taking the notion of the basic ontological continuity of evolutionary processes seriously means accepting that human behavior has historically been driven by the competition for survival and mates. The innate behavioral dispositions that are passed on genetically from generation to generation have been shaped by natural selection to reflect their 'fitness' in regard to staying alive and reproducing. These dispositions are the behavioral 'universals' that evolutionary psychologists are interested in. According to Miller (2000), creativity and morality are among the human traits that are likely to have evolved as a result of sexual selection rather than survival selection. If this is so, then what are arguable the main drivers of the evolution of economic institutions are to be understood as the products of a selection mechanism that economic theory has thus far ignored. Miller's theory of sexual selection as the source of creativity, morality and other features of human nature may still have to be classed as speculative, but the central feature of competition for mates in humans is nevertheless quite clear. Sexual selection theory and the empirical research in evolutionary psychology that it has spurred strongly suggest that the mechanisms of mate choice in humans have led to behavior that is driven by social status.

Buss summarizes the evidence on the importance of status as follows: '[i]f there were ever a reasonable candidate for a universal human motive, status striving would be at or near the top of the list' (2004, p.345). In the words of Robert Frank (1985), '[w]e come into the world equipped with a nervous system that worries about rank'.[9] Status is directly linked to dominance hierarchies, and Cummins goes as far as speculating that '[I]f one were to guess at which problems cognition evolved to solve, one would be hard pressed to come up with a better candidate than dominance' (1998, p.46).There is indeed evidence that children as young as three appear to reason about dominance hierarchies (Buss 2004). Dominance hierarchies are as widespread in nature as they are among different human cultures. The existence of a dominance hierarchy means that that some individuals within a group reliably gain greater access than others to key resources that contribute to survival or reproduction (Cummins, 1998). Among these resources are mating opportunities, and across cultures and over recorded human history, high status men have consistently acquired more mating opportunities. That status seeking has likely been affected by sexual selection is witnessed by the finding that men are higher in social dominance orientation, that men and women express their dominance in different ways,

[9] Quoted in Buss 2004, p.344.

and that across cultures women prefer men with higher social status as mates (Buss 2004).

Seeking social status may be especially relevant to understanding learned as opposed to innate drivers of behavior, and especially so in what Witt (1991) refers to as 'affluent' environments in which the pressures of survival selection are limited. As Witt notes, the biological universals such as hunger, thirst, sleep, pain and a sex drive, do not offer much help in explaining the specific preferences and behaviors that the economist is interested in. These would rather be the result of learned behavior: 'In an individual lifetime history of conditioning, a more or less long chain of learned associations leads from a few innate preferences to those actually revealed in current everyday life' (Witt, 1991, p. 567). We may expect that in economically developed environments, where day-to-day survival is not an immediate problem, social rather than natural selection pressures shape learned behavior. Social status can then be seen as a general measure of the success of an individual's behavior in the social interaction with other individuals that is related to the individual's access to economic resources and sexual mates.

In short, what sexual selection theory and its application to primates and humans suggest is that if we were to choose one additional behavioral assumption to the theory of the firm it should be 'status seeking'. Both evolutionary logic and empirical evidence underwrite the importance of this behavioral disposition in explaining human behavior. Anthropological and sociological theory and research have of course long emphasized status as a central feature of human culture, and its incorporation in the theory of the firm would open up interesting possibilities to integrate insights on the social aspects of human organization from other social sciences into economic theory.

8. Implications for the theory of the firm

What are the implications of our exploration of the possible value of sexual selection theory for the theory of the firm? We have argued above that sexual selection theory suggests both an additional behavioral assumption to bounded rationality and opportunism, and an additional selective logic to that of survival selection. Together, these two contributions can help us incorporate the social aspects of economic organization into the theory of the firm. In addition to views of the firm as a repository of routinized productive knowledge or a nexus of contracts between self-interested agents, sexual selection theory suggests a view of the firm as an entity involving *voluntary membership* and social interactions based on *preference selection* between *status seeking* individuals.

One of the interesting features of this view of the firm is that it provides a foundation to explain the existence of managerial hierarchies. Contractual and competence based theories of the firm have answered the Coasian question 'why do firms exist' in terms of the advantages that managerial hierarchies have over the market. But neither theory offers an explanation for the existence of the hierarchy as such. We may accept that firms can economize on transaction costs and avoid the problem of hold-up, or alternatively,

that firms are a superior vehicle for creating and retaining productive knowledge. But these explanations do not, in themselves, explain why these advantages over the market should involve a hierarchical form of organization. The behavioral assumption of status seeking offers an essential building block to account for the ubiquity of the managerial hierarchy.[10]

Another feature of this view of the firm is that it can explain differences between firms that extant theories cannot. Contractual theories can only explain differences in scale and scope between firms. Competence-based theories are limited to explaining differences in productive knowledge in terms of a path-dependent process of market selection acting on variations in routines generated in a boundedly rational process of local search. The incorporation of voluntary membership into the analysis helps us recognize that firms also differ in terms of the people they employ. By giving individuals and their preferences a central place in the analysis, we can in turn account for cultural differences between firms. Such differences are not just a matter of interest for behavioral and social scientists, but are also economically relevant. Cultural differences between firms have a direct impact on their performance in product and financial markets. In fact, if we accept the simple but powerful idea of culture as 'the way things are done around here', organizational culture rather than routines needs to be understood as the true repository of productive knowledge.[11]

A third feature of this view of the firm is that it points towards the necessity of a multi-level selection logic to explain the evolution of firms. By incorporating both voluntary membership and status seeking into the theory of the firm, the tensions between within and between group selection are brought into focus (Sober and Wilson 1998; Campbell 1994). Status seeking individuals can be both expected to find firms differentially attractive when deciding about membership, and to compete for positions in the hierarchy upon joining the firm. Firms compete among each other for both economic resources and members, and individuals compete with each other for membership of attractive firms and positions in the hierarchy within these firms. Economic organization thus needs to be understood as the outcome of a multi-level selection process in which within-group and between-group competition for economic resources and status interact. This is reflected Schein's (1990) definition of culture as a pattern of assumptions developed by a group through finding solutions to problems with respect to external adjustment and internal integration. Culture can thus be seen as way to arrive at workable solutions to combine

[10] It might seem tempting to see 'status seeking' as a sufficient assumption to explain hierarchical organization, but such an explanation faces a number of problems. For one, it should be noted that the evolutionary stability of status hierarchies suggests that there should also be an evolutionary advantage of group membership to individuals at lower levels of the hierarchy. This in turn suggests that hierarchies also require a behavioral disposition to accept authority. Simon (1990) has made the argument for such a behavioral disposition, which he labeled 'docility'. The evolutionary stability of hierarchies would seem to depend on an equilibrium resulting from the interaction of status seeking and docility.

[11] Viewing organizational culture as the repository of productive knowledge has distinct advantages over the more restrictive notion of routines, if only because it makes changes in the firm's knowledge base more amenable to analysis. Nelson and Winter's (1982, see also Winter 2003) solution of an infinite regress of routines, whereby higher level search routines explain changes in lower level routines may be mathematically elegant, but is not very convincing because it abstracts from the differential behavior of the individual human agents that create the variety from which productive knowledge can evolve.

internal stability with external success. Seen in this way, firms can be understood to compete with each other on the basis of their cultures. In this competition, the problem is to not let internal competition undermine external success, nor to let success in external competition for economic resources undermine the firm's attractiveness to members, or vice versa.

A final feature of this view of the firm is that it leads to a testable prediction that runs counter to predictions made on the logic of survival selection between firms alone. In their search for economic resources and social status, individuals have a choice in which firm they join. Given a variety in individual preferences, they will find firms differentially attractive. Firms, in turn, will find prospective employees differentially attractive, and we thus have the ingredients for a mutual preference selection process. A generalization of the logic of sexual selection driven by mate choice leads to the prediction that firms will evolve characteristics that are the result of their advantage in attracting members. These characteristics may be deleterious from the point of view of their efficiency in terms of competition in product and financial markets.[12] Such outcomes seem especially likely when we realize that membership preferences may not only driven by economic considerations but also by social status. But even from a purely economic perspective, the generalization of the explanatory logic of sexual selection points to conditions under which such deleterious characteristics may evolve. These conditions include the combination of scarcity with information asymmetry (the handicap principle), and the selection of new members that closely resemble existing members of the firm (Fisher's runaway process).

9. Conclusion

Acknowledging the important role of sexual selection in the theory of biological evolution can contribute to recent efforts to explore how Darwinism can improve the ontological basis of evolutionary theory in economics. These efforts have so far been limited to generalizing the logic of survival selection. Taking the notion of a generalized Darwinism seriously means that we should also acknowledge the second pillar of Darwin's theoretical framework. At the very least, sexual selection alerts us to the possibility that selection processes other than survival selection may play a role in the evolution of economic institutions. In addition, there are two ways in which sexual selection theory can help strengthen the ontological foundations of economic theory. The first is to apply insights in the genetic foundations of human nature from sexual selection theory directly to economic behavior. This line of reasoning suggests the incorporation of 'status seeking' as a central behavioral assumption in theories of economic institutions in general and the firm in particular. The second way in which sexual selection can contribute to the ontological foundations of evolutionary economics is to transcend the specific biological content of the concept and establish its similarity to selection processes in the cultural domain. This line of reasoning leads to the conclusion that we

[12] Executive compensation may be a case in point. Note that the effect also works the other way, with individuals evolving behaviors that may be economically inefficient, such as pursuing levels of education that over qualify them for the actual jobs they end up holding.

should distinguish selection processes driven by preferences from selection processes driven by environmental contingency and scarcity. The latter type of selection, of which survival selection in nature is an example, is an essentially convergent process, and it is this type of selection that economic theories have historically focused on. Preference selection, of which sexual selection in nature is an example, is an essentially divergent process that may have effects opposed to those of survival selection and can lead to characteristics that are deleterious from the point of view of survival.

Our exploration of the value of sexual selection theory for economics points to a view of the firm that incorporates the social dimension of economic organization in a way that is compatible with extant views of the firm based on the logic of survival selection. The fundamental behavioral assumption of such a view of the firm is that both economic resources and social status drive human behavior. This view of the firm also acknowledges that firms need members as well as profit to survive. In doing so it brings membership selection processes driven by status seeking individuals with different preferences into the analysis of economic organization. The value of theories built on the ontological precepts derived from sexual selection theory is underscored by two defining characteristics. First, they would be able to explain differences between firms, such as organizational cultures, that directly affect their economic performance, yet that theories based on survival selection alone cannot account for. Second, they lead to a testable prediction about the nature of firms that runs counter to the optimality prediction that follows from the logic of survival selection. The combination of the dynamics of selection processes driven by preferences with the fact that social status is not necessarily linked to purely economic criteria leads to the prediction that firms are likely to evolve stable organizational traits that are deleterious from the point of view of their efficiency in product and financial markets.

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