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RESEARCH ARTICLE

Property rights and domestication

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Abstract

This paper combines the property rights approach of Barzel with models from renewable resource and evolutionary economics to examine the domestication of wild animals. Wild animals are governed by weak property rights to stocks and individuals while domesticated animals are governed by private ownership of stocks and individuals. The complex evolutionary process of domestication can be viewed as a conversion of wild populations into private property, as well as a transition from natural selection to economic selection controlled by owners of populations and individuals. In our framework domestication is not the explicit goal of any economic agent, but it emerges as a long-run outcome of an innovation in hunting strategies in a hunter–gatherer society. Our formal model also suggests that the domestication process moves slowly at first but then proceeds rapidly, and is aligned with the archeological evidence on domestication events.

Keywords: Domestication; property rights; evolutionary economics; wildlife

1. Introduction

Yoram Barzel's contribution to economics is predominantly associated with his analysis of property rights (Barzel, 1997). This important work developed a framework for analyzing a wide range of problems by focusing attention on the economics that govern complex assets. In this paper we use this property rights approach to examine the domestication of wild animals.

The domestication of wild animals and plants was a crucial precursor for the development of human civilization (Clutton-Brock, 1989; Diamond, 1997). Before domestication, humans depended on their ability to kill or collect wild species for food, shelter, clothing, and tools. The great advantages afforded by domestication are obvious. To be able to confine and selectively breed animals and plants – using them for power, transportation, food, and clothing – do not only allow a better diet and shelter but also the development of markets (for products) and specialized human and physical capital. Domestication is crucial to the development of human societies, but its details are not well understood, particularly from an economic perspective.

Barzel applies his property rights model to a variety of topics from human slavery to the formation of the state and the allocation of water, but never extends his framework to the domestication of animals. Barzel's approach, however, is applicable because of its recognition of complex assets and how the ownership of those assets can itself be a complex mixture of ownership regimes. For wild and domestic animals there are two complex assets at issue: the population and the habitat (land for the cases we examine). Lueck (1989) uses Barzel's approach to analyze different systems of governance for wildlife but does not consider the economics of domestication. A property rights approach to domestication is also promising because wild and domesticated animals are governed by different property regimes. Wild animals are governed by weak property rights to stocks and individuals while domesticated animals are governed by private ownership of stocks and individuals. Thus, the complex evolutionary process of domestication can be viewed as a conversion of wild populations into private property.

This paper develops an economic approach to the question of human domestication of wild species with a focus on the establishment of property rights to animals and its effect on evolution.[1] We begin by examining literature from archeology–anthropology and genetics to describe the current understanding on the temporal and spatial history of domestication. We briefly discuss theories of domestication from within and outside economics and suggest how the economics of property rights combined with models from renewable resources and evolutionary economics can be used to develop a framework for understanding the domestication of wild populations. We then develop a model in which hunter–gatherers have the option of hunting (and killing wild animals) or capturing (and rearing animals for use) to show how economic forces can generate a process consistent with our current archeological and genetic understanding of domestication.

2. A summary of evidence on domestication

In this section we summarize the available evidence on the dates, locations and spatial and temporal diffusion of domestication. We then review the main sources and methods that support this evidence.

The domestication of animals – mammals in particular – began between 10,000 and 15,000 years ago (Clutton-Brock, 1989; Price, 2002; Sauer, 1953; Zeder, 2012; Zuener, 1963). Scholars consider domestication 'dates' as a point in time when there is strong morphological evidence that a species has become distinct from its wild ancestor. Dogs (*Canis lupus familiarus*) were the first to be domesticated (from wolves or *Canis lupus*) between 14,000 and 15,000 years ago. Dogs were followed by the familiar hoofed mammals – goats and sheep first (11,000 years ago) and later cattle and pigs (10,000 years ago). Horses were domesticated by 4,000 years ago,[2] while camels, llamas, and reindeer are more recently domesticated.[3]

Most of the major domestication events are considered to have taken place in just two regions – the Near East (southwestern Asia) and Asia. Indeed, domestic livestock – sheep, goats, cattle, and pigs – were domesticated between 10,000 and 11,000 years ago in southwest and southern Asia. In the Near East, domestication seems concentrated in the Fertile Crescent, while in Asia domestication was stretched between many regions and was accomplished by different groups of people.[4] Most of the major livestock animals known today were domesticated in southeastern Turkey and the Zargos Mountains of Iran.[5]

Sources of evidence: genetics and archaeology

The most comprehensive empirical studies on the origins and spread of domesticated animals come from interdisciplinary efforts between archaeologists and geneticists (see Edwards *et al.*, 2007; Gotherstrom *et al.*, 2005, Zeder *et al.*, 2006).[6] Archaeologists use skeletal morphology (the shape and size of bones) to establish similarities and differences between populations of animals, and various

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[1] Our focus is on animals rather than plants, though similar forces are likely at play.

[2] Archeologists use the more precise term "calibrated years before present" (cal BP), which refers to the correcting of radiocarbon 14 dates with other information. Radiocarbon dating can be off by substantial amounts of time, but can be calibrated with dates from other sources, such as tree ring dates. Cal BP dates are preferred over non-calibrated dates, which are indicated with YBP, or Years before Present. In this paper we simply use Years before Present.

[3] Lueck and Torrens (2019) present more detail on domestication evidence and consider a wider range of species.

[4] The Fertile Crescent is the region that stretches in a northward arch from modern-day Israel and Jordan, through southern portions of Turkey and Iran, and southward into the northern regions of Iraq. The term "Levant" refers to the western region of the Fertile Crescent (Verhoeven, 2004).

[5] The suite of plants, animals, and tools originating from southwest Asia is sometimes referred to as the "Neolithic Package" (Zeder, 2008).

[6] New evidence is continually changing the agreed-upon dates and specific location, but for this paper the evidence presented is sufficiently precise.

signs of muscle alteration and bone damage to understand the life history, death, and butchering processes of animals. Dating methods (especially radiocarbon dating and stratigraphic analysis) and the geographic relation of archaeological sites are also used by archaeologists to identify the origin and spread of domesticates (Reitz and Wing, 1999). Geneticists use a variety of chemical methods, computerized analyzers, and statistical methods to analyze the relationship between non-coding sections of DNA to establish the genetic similarity or distance between populations of a species.

Genetic comparisons can be used to determine how related modern sub-populations of a species are to each other, and how related modern populations are to ancient specimens of the species found in archeological sites. These comparisons can be used to pinpoint the original archeological populations from which modern domestic populations are descended. In some cases, such as domestic cattle and pigs, there seem to have been multiple points of domestication at different times.[7] Related analysis can be conducted to determine the degree to which domestic sub-populations have been interbred with other domestic sub-populations or related wild populations.[8]

The primary data used by geneticists studying the origins and spread of domesticates are similarities and variances within the genetic code (Reitz and Wing, 1999) using one of two comparative approaches. In the first method, the DNA of domestic populations are compared to the DNA of wild species from which they are thought to have descended, if that wild species is still extant. In the second method, the DNA of domesticates is compared to Ancient DNA (aDNA) extracted from archeological specimens of the presumed wild ancestor. If possible, both methods are used.[9]

There are three primary means by which archeologists can determine when an animal species has been domesticated (Reitz and Wing, 1999). The first, most traditional, method is to examine the appearance of distinct morphological traits (the physical shapes and characteristics) in the skeleton that distinguish domesticates from their wild relatives. The second technique, developed recently, is to calculate the mortality profiles of the animal remains from archeological sites to examine if animals killed there were done so in accord with the standard culling profile of domestic food animals. The third approach is to determine when a species starts appearing in regions outside its native habitat. This last method is particularly useful when the wild ancestor species had a limited range, or when the regions being investigated are separated by major geographical features such as oceans or mountain ranges.

Morphological changes

Morphological differences can signal the appearance of a domesticated version of a wild species. These differences include changes in body size, and changes in cranial morphology and related features such as horn size and shape, or greater or less uniformity in several characteristics (Zeder, 2008, Zeder *et al.*, 2006). Changes in cranial morphology is considered among the more universal characteristics signaling the appearance of a domestic species, particularly changes that are related to neoteny – the retention of juvenile characteristics. Retained juvenile characteristics of the skull include a shortened snout or face, crowding of the teeth, simplification of the cusps on teeth, the deduction or smoothing of muscle attachment ridges, and changes in the overall dimensions of the skull that suggest selection for particular traits or an easing of selective pressures.[10]

The appearance of greater uniformity or greater variance in other biological traits can also signal domestication. Greater uniformity can occur because the whole domestic population was derived from

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[7] Also see Larson *et al.* (2007); Edwards *et al.* (2007); and Loftus *et al.* (1994).

[8] For example, domestic cattle were apparently allowed to interbreed, occasionally, with aurochs, their wild ancestor. This appears to be also true for pigs, dogs, chickens, and most likely other domesticates.

[9] Conspecifics refers to two or more varieties of one species, particularly when these varieties exist in distinct or isolated populations, or for other reasons are distinct enough from each other that it worth noting that two or more sub-populations are actually of the same species.

[10] For example, domestic dogs have short snouts and floppy ears, which are present only among juveniles in wolves. These characteristics are documented in the fox study (Dugatkin and Trut, 2017).

a relatively small subgroup of the wild population. Greater variance can occur either because new traits are being actively selected for, or because in reducing the pressures of natural selection, through controlled breeding and by providing protection, humans allow variations (e.g. color) to appear in domesticate populations that would not have been able to survive naturally. Some morphological changes occur well into the domestication process, or toward the end of the initial domestication event.[11] As such, the appearance of a morphologically distinct domestic species may signal the final product of a domestication event and not the beginning of the process.

In archeology, the term "domestication event" refers to the period during which a wild species evolves into a relatively genetically, biologically, and behaviorally stable domesticated species.[12] Since a domestication event can take several hundred to several thousand years the appearance of a morphologically distinct domesticate species does not necessarily tell us much about the conditions of the process itself, it only tells us that it has already occurred. It does give, however, an end point from which to look further back in time for evidence of the domestication process itself. The search for this evidence often focuses on the environmental, social conditions, and human behaviors, such as species management, which likely caused or aided in the domestication process.

Herd management

Another useful method of understanding the origins of domesticated herd animals has been to collect evidence of herd management, since most of the major domesticated species are social (herd) mammals such as cattle, dogs, and sheep (Zeder, 2008, 2012).[13] Herd management can include the selective culling, or killing, of certain animals within a population so as to achieve human objectives such as meat production while still maintaining herd size and the breeding potential of a population. In general, males are preferentially killed relatively young, while females are allowed to survive until their prime reproductive years have ended. This differs from the way that hunter–gatherers typically kill the social mammals. This management strategy also closely resembles the typical mortality profile for modern domesticated animals, though it seemed to have taken some amount of time for it to develop fully.

Archeological evidence for herd management is a demographic shift in collections of animal remains recovered from kill sites. Hunter–gatherer sites typically show a fairly indiscriminate killing of all members of species regardless of sex or age, or with only a slight preference for large adult males. As ancient peoples shifted toward herd management the demography of animals killed started to more resemble that of more modern domesticated animal kill profiles. In this profile most males are killed just after they reach adulthood, but before they become sexually mature, while females are kept alive until after their reproductive prime. This management approach (correlated with this demographic profile) allowed humans to maintain, if not increase, the size of a herd while still obtaining a substantial amount of meat from it. Zeder (2008) and Zeder *et al.* (2006) argue that a shift from the kill profiles of hunter–gatherers to the herd-culling profiles of pastoralists occurred some 500 to 1,000[14] years before the appearance of morphologically distinct sheep and goats.[15] At around

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[11] For example, the shape of horns in both goats and sheep changed drastically from those of their wild ancestors, however this distinct physical difference did not occur until well after the domestication process had begun (Zeder *et al.*, 2006). Similarly, in recent domestication experiments with silver foxes, physical traits comparable to domesticated dogs did not occur until later in the experiment and after behavioral traits associated with domesticity had already begun to appear (Belyaev, 1979, Dugatkin and Trut, 2017).

[12] The term however is an abstract term without reference to set amounts of times, specific events, nor does it mean that no further alterations are made to the species through further selective breading – it only means the appearance of a genetically distinct sub-species that serves as the basic form of the domesticated variety of a species (Gotherstrom *et al.*, 2005; Price, 1984; Zeder *et al.* 2006).

[13] Indeed, scholars can measure the deviation from ancestral demographic distributions by comparing measures of central tendency and dispersion.

[14] This time frame might be taken as the time needed for a domestication process to occur.

[15] Morphological changes are well documented in the fox domestication study (Dugatkin and Trut, 2017).

10,900 YBP these demographic changes appear in goat remains in Iraq, while morphological changes in goats do not appear until 9,900 YBP. Similarly, demographic changes appear in sheep populations at 10,500 YBP, with other signs of domestication (translocation from original habitat) do not appear until 10,200 YBP. There is further evidence that manipulation of herd demographics began as early as 12,000 YBP for sheep, though these appear to be a first attempt as the culling profile had not yet fully come to parallel that of fully domesticated animals. In particular, it seems that males were allowed to get into adulthood, but females were being preserved until late in life (Zeder, 2008).[16]

Appearance of a species in a non-native habitat

The final form of evidence of domestication is the appearance of an animal species in a non-native habitat. This form of evidence has also been used as an index of the domestication of plants. In cases in which there were local varieties of the same species, or closely related species, it is still necessary to establish that animals at archeological sites are indeed domesticates through either morphology or genetics, or both.

In summary, the combination of archeological and genetic data has both increased the precision of our knowledge of domestication and has also generated greater certainty about the origins and spread of domestic animals. In some cases, the two sources verify each other while in other cases they contradict each other. Genetic analysis allows researchers to determine which specimens found at archeological sites are truly the ancestors of modern domesticates. In addition, genetic evidence has been used to unravel the history of domestic species as they spread out from their point of origin and interbreed with domestic or wild conspecifics (animals or plants of the same species, but of different subpopulations, such as different varieties or breeds). The dating of archeological sites gives a chronology to the history of domestication that genetic analysis is still not capable of providing.

3. Property rights economics and domestication

Despite using the best evidence available from archeology–anthropology and biology–genetics, the current domestication literature does not have a governing theoretical framework within which to offer explanations and develop the implications needed to further our understanding of the domestication process. For economics the key questions are: What are the social and economic interactions that produced the domestication of wild animals? What determines which species were domesticated? What determines where and when these species were domesticated? In this section, we discuss the basic economic issues of property rights, renewable resources, and evolutionary economics pertinent to building an economic theory of domestication. In the following section we illustrate the economic approach to domestication with a formal model.

Economics offers a framework in which individual and groups make decisions that can be studied as a social equilibrium. The economic approach makes explicit the benefits and costs of domestication, which will put some structure on the topic by separating parameters (e.g. habitat, alternative food sources) from the economic choices made by prehistoric, and sometimes more modern, peoples. The benefits of domestication are both obvious and important. Domestication leads to increases in food production (e.g. meat, grains, milk) and reduces the temporal variance in this production.[17] Domestication results in increases in the production of shelter and clothing (e.g. hides, furs) and

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[16] This empirical analysis is possible because the age and sex of animals can be determined from the osteological (bone) remains of animals found in archaeological sites (Reitz and Wing, 1999). By carefully reconstructing the demographics of the animals slaughtered at a particular site it has become possible to see the emergence and evolution of management strategies within the regions in which some domestic animals first appeared. Management appears to have occurred in the domestication process of sheep, goats, and cattle. This method, to date, has not been used to examine the origins of other domesticates, such as pigs and horses, and it is currently thought that it did not play a part in the domestication of either dogs or cats which are currently thought to have largely “self-domesticated.”

[17] More indirectly, dogs protect livestock and cats kill rodents that feed on stored crops.

tools (e.g. bone). Domestication lowers the cost of power (e.g. cattle pull carts, plows, and logs) and transportation (e.g. horses allow long-distance travel). Taken together, domestication allows a move away from a hunter–gatherer economy toward an agricultural economy with increased specialization and greater wealth.[18]

The costs of domestication have several components. There are costs of capture, rearing, and control, as well as the opportunity cost of hunting–gathering activities foregone. The costs of capture, confinement, and control of wild populations (or individuals from such populations) are likely to be key to understanding the origins and spread of domestic animals. For example, is it cheaper to capture juveniles and rear them in small groups? Or is it cheaper to capture a small group with a mix of sexes and ages to keep the social structure in place? The cost of confining and controlling wild animals is likely to vary across species and across habitat as well. Knowledge about the variation of characteristics within a species or within population of a species can also lead to insight about the cost of capture and control.

In economic terms, a domesticated animal is distinguished from a wild animal by ownership and by the time path of ownership (Lueck, 1989, 2002). Domestication can be viewed as an economic process by which the forces of natural selection are (at least largely) replaced by the forces of human selection by owners of populations.[19] This process ultimately results in individuals that become dependent on human control and will be unlikely to survive (or certainly thrive) in a setting solely governed by natural forces.

Barzel's (1997) approach, which focuses on property rights to attributes of assets, is important in our framework. In this case, for wild populations or animals generally, it is useful to consider property rights to the habitat (land) and animals (stocks or populations). Table 1 shows some possible property rights regimes (for details on this characterization, see Lueck and Miceli, 2007). Open access, common property, and private property are considered as possibilities for both land and animals, resulting in nine possible regimes. The upper left cell is the simplest regime common to the earliest hunter–gatherers, while the lower right cell shows the fully developed private property regime for both land and animals. The case in the middle of the matrix, in which both land and animals are governed by common property, is the prototypical case of a hunter–gatherer society that controls hunting territory and, thereby, implicit access to a wild population.

The economic theory of property rights states that the equilibrium level of ownership of an asset (or an attribute of an asset in Barzel's approach) is determined by maximizing the net present value of the rent stream derived from the asset given the relative costs and benefits associated with the definition and enforcement of those property rights. Moreover, property rights theory suggests a pathway from open access to common or private ownership (Anderson and Hill, 1975; Demsetz, 1967; Field, 1989; Libecap, 1989; and Lueck, 1995, 2002). The same logic most likely also applies to domesticates (i.e. species that have come to be domesticated).[20]

The property rights framework can be merged with models of renewable resources to examine how the incentives for ownership of a population change as parameters change (Clark, 1990; Gordon, 1954).[21] To illustrate this, consider a hunter–gatherer group that controls a territory with a population

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[18] Some authors argue that the transition to an agricultural economy caused a reduction in the quality of life of humans because cereals and other food-based domesticated plants cannot replace the nutrients in meat (e.g. Hermanussen and Poustka, 2003; Sands *et al.*, 2009). In the long run, there is little doubt that agriculture leads to greater income per capita. In any case, the argument does not immediately apply to the domestication of animals.

[19] Selection can take place over the quality of the animals for draft, hides, and meat as well as for docility or other handling characteristics. Indeed, the Siberian fox study suggests that selecting for docility might be the dominant force (Belyaev, 1979, Dugatkin and Trut, 2017).

[20] Original ownership of domesticates was held by groups (Baker, 2003; Bailey, 1992; Ostrom, 1990; Sethi and Somanathan, 1996; Smith, 2000).

[21] Gordon (1954) was the first to link property rights to renewable resources, while Clark (1990) is an important theoretical development in renewable resources.

Table 1. Possible property regimes for habitat and animals

Habitat/ Animals	Open access	Common property	Private property
Open access land	Simplest hunting society for wild species.	Cattle on open range (share herds)	Cattle on open range
Common (group) land	Wild species on a common pasture	Hunter–gatherers. Pastoralists – sheep, cattle, goats, reindeer	Typical of European commons for cattle, sheep, goats
Private land	Wild species on private land with open access for hunting		Typical modern livestock setting (e.g. cattle on ranch)

of wild animals.[22] Suppose that the evolution of the stock of wild animals is described by the following difference equation $W_{t+1} = W_t + \gamma W_t\left(1 - \frac{W_t}{W_K}\right) - hW_t$, where W_t is the stock of animals in period t, W_K is the environmental (habitat) carrying capacity, $\gamma > 0$ is the intrinsic growth rate, and $h \in (0, \gamma)$ is the proportion of animals hunted by the group in each period.[23] Given W_K and γ, the hunting rate h induces a steady-state stock of $W^{SS} = \frac{(\gamma - h)W_K}{\gamma}$ animals. Suppose that the payoff of the group is given by $v_H = hW^{SS} - c_h h$, where c_h is the marginal cost of hunting for the group and $c_h h$ is the total cost of hunting. Then, the level of h that maximizes v_H is $h^* = \frac{\gamma(W_K - c_h)}{2W_K}$, which induces a steady-state stock of $W^* = \frac{W_K + c_h}{2}$ wild animals, a steady-state harvest of $h^*W^* = \frac{\gamma[(W_K)^2 - (c_h)^2]}{4W_K}$ animals, and a payoff for the hunter–gatherer group of $v_H = \frac{\gamma(W_K - c_h)^3}{4W_K}$. Note that h^*W^* and v_H^* are both increasing in the environmental carrying capacity and the population growth rate, and decreasing in the marginal cost of hunting.[24]

Using the notation above, imagine a population of wild cattle in a natural landscape with a carrying capacity of $W_K = 25,000$ and an intrinsic 20% growth rate ($\gamma = 0.20$). In the simplest case in which there is no hunting cost ($c_h = 0$) there would be a harvest of $h^*W^* = 1,250$ and a sustainable population of $W^* = 12,500$ wild cattle.[25] This means that this wild cattle herd could provide a harvest of up to 1,250 cattle per period in perpetuity (what biologists call the maximum sustainable yield/harvest). More generally, as hunting costs increase, the optimal harvest decreases and, hence, the size of the population increases.

This population growth model can be used in harvest models or in models of optimal crop rotation, both of which might be applicable to the question of domestication, depending on the mechanism of

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[22] We assume the stock has no significant interaction with other stocks, so it can be viewed as a single resource. We also assume that the group is acting as a sole owner of the stock and not treating the stock as common property (Caputo and Lueck, 2003). Under common property, groups hold exclusive access to the stock and allocate its use among members subject to the costs of policing those members. Several models show that common property may be a cheaper alternative than private property because of economies of enforcement and use of a relatively large-scale resource (Bailey, 1992; Lueck, 1994; Ostrom, 1990). In section 5 we consider the case in which hunter–gatherers are exploiting a wild population under open access.

[23] The harvest rate is constrained to be lower than the intrinsic growth rate, so the stock is not fully depleted.

[24] To keep the example as simple as possible we have assumed that the hunter–gatherer group selects h to maximize its steady state payoff. Qualitatively similar conclusions can be obtained if the group selects h_t in each period to maximize its discounted (at rate β^t) payoff. Formally, we must solve the following dynamic programing problem: $\max_{\{h_t\}} \sum_{t=0}^{t=\infty} \beta^t h_t(W_t - c)$, subject to $W_{t+1} = W_t + \gamma W_t\left(1 - \frac{W_t}{W_K}\right) - h_t W_t$ and $W_0 > 0$ given. In such case the steady state level of W^* is given by the unique solution to $W^* - c = \frac{\beta\gamma(W_K - W^*)W^*}{(1-\beta)W_K + \beta(2-\gamma)W^*}$ and $h^* = \gamma\left(1 - \frac{W^*}{W_K}\right)$. Also note that focusing our attention on steady state values, we ignore transitional dynamics; that is, we do not explore the path to the steady state.

[25] In this symmetric growth function the stock at the maximum sustainable yield is half the carrying capacity (Clark, 1990).

initial domestication.[26] If hunter–gatherer groups live-captured small groups (i.e. populations) and managed them as pastoral herds, as with goats and sheep, then the optimal harvest model is more appropriate because the herd is maintained intact and harvest is more or less continuous. If, however, just a small number of juveniles were captured to start a new herd, then the rotation model is more appropriate because the population is allowed to grow and then be harvested as a cohort. In either case these biological parameters will depend on the natural environment and vary across space and time.[27]

The forces of evolution also can be used to examine how economic selection can in turn affect population characteristics.[28] Ownership of a wild population effectively substitutes natural selection for artificial (Clutton-Brock, 1989) or what we call economic selection. This economic selection changes the parameters of the evolutionary process (Dugatkin and Trut, 2017; Geist, 1971; Trut, 1999). This process can be incorporated into evolutionary models. For example, assume that a portion of the individuals are "docile" and a portion are "aggressive." Then, economic selection over time for docile individuals (which should reduce capture and confinement costs) will lead to a population of domestic animals distinct from the wild ancestor. Indeed, in the following section we formally develop such an approach.

4. An economic model of domestication

In this section we illustrate the economic approach to domestication with an evolutionary model of a hunter–gatherer group that interacts with a wild population which provides products (e.g. meat or clothing).[29] In the model, the group has exclusive access to the wild population and begins indiscriminately hunting individuals in this population, which contains docile and aggressive individuals. The group eventually gains access to a new hunting technology that gives the group the ability to capture and confine a subgroup of the wild population and to identify docile and aggressive individuals within the confined population. This allows the group to slaughter animals selectively based on their aggressiveness or (economic) cost of control. Being able to control live animals is the beginning of ownership and the domestication process. This economic selection under ownership and control changes the confined populations and, over time and many generations, creates domesticated, confined populations. Because this economic selection takes place over a long time frame, no single economic actor has domestication as an explicit goal.[30] The group slaughters more aggressive animals because it is cheaper to confine more docile individuals. The model includes a dynamic link in which the cost of confining animals and extracting products from docile animals decreases in the future because the captured docile animals generate relatively more docile individuals in the future. From this connection the model generates path dependence.

The basic model

Consider again a hunter–gatherer group that controls an exclusive hunting territory populated by a stock of wild animals. The territory has a carrying capacity of $W_K > 0$ animals, which allows the group to hunt a steady-state level of $h^* W^*$ animals maintaining the population at $W^* < W_K$. As noted above the associated payoff of the group is given by:

$$v_H = h^* W^* - c_h h^* \tag{1}$$

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[26] Continual harvest models are typical of fishery analysis, and cropping models are typical of forest analysis.

[27] For example, caribou are found in tundra and forest habitat and the populations have distinct characteristics in these distinct environments (Ingold, 1980).

[28] See, for example, Friedman (1998), Maynard Smith (1982), and Sigmund and Young (1995).

[29] This model does not distinguish between species used for protection, power, food, clothing, and transportation. These distinctions are examined in (Lueck and Torrens, 2019).

[30] In the Siberian fox experiment, however, domestication was the explicit goal.

where c_h measures the marginal cost of hunting. The wild population contains a mix of aggressive and docile individuals. The porportion of aggressive individuals in the wild population is $a_w \in (0, 1)$. These animals are more difficult to control, though not more difficult to kill. We assume the vast majority of individuals in a wild population are aggressive and hunting does not affect the distribution of aggressiveness in the population. Before period $t = \tau_C$, hunting is the only technology available to the group and, hence, the size of the population of wild animals, the distribution of aggressiveness, and the payoff obtained by the hunter–gatherer group remain constant over time. Formally, $W_t = W^\star$, $a_t = a_w$, $v_t = v_H$, respectively, for all $t < \tau_C$. This outcome is the pure hunter–gatherer equilibrium for a group exploiting a single wild population.

In the absence of any technological (or environmental) change the group remains in the hunter–gatherer equilibrium shown above. One way to introduce a change that can lead to domestication is to assume that the group innovates in a manner that allows it to confine wild animals. We assume that such innovation occurs in period $t = \tau_C$.[31] The innovation creates a technology that gives the group the ability to confine a group of animals and identify aggressive and docile animals within the confined population. Specifically, after the innovation, the group can confine a proportion $y \in (h^\star, 1)$ of the wild population and selectively slaughter a steady-state level of $h^\star W^\star$ animals.[32] This technology allows the group to harvest $h^\star W^\star$ animals from a confined population of $yW^\star$. Hunting, however, requires a population of $W^\star$ wild animals to generate the same steady-state level of output and the total amount of habitat (land) remains the same, though as y increases, less habitat will be available for wild animals.

Keeping animals confined is costly and we assume that the cost of confinement is higher for aggressive than docile animals. Specifically, when the group uses the confinement technology its payoff is $v_{C,t} = s_{a,t}A_t + s_{d,t}D_t - c_C(1 - s_{a,t})A_t$, where A_t and D_t denote the stock of aggressive and docile animals, respectively, in the confined population at the beginning of period t, $s_{a,t} \in [0, 1]$ and $s_{d,t} \in [0, 1]$, respectively, denote the proportion of aggressive (docile) animals slaughtered in period t, and $c_C(1 - s_{a,t})A_t$ is the cost of confining the remaining aggressive animals. To simplify we assume that the cost of confining docile animals as well as the cost of slaughtering animals in a confined population are both zero. Thus, the new problem for a hunter–gatherer group choosing capture and confinement in period t is given by:

$$\begin{aligned} &\max_{s_{a,t}, s_{d,t}} \{v_{C,t} = s_{a,t}A_t + s_{d,t}D_t - c_C(1 - s_{a,t})A_t\} \\ &\text{subject to} : s_{a,t}A_t + s_{d,t}D_t \leq h^* W^* \end{aligned} \tag{2}$$

The constraint indicates that the total number of animals slaughtered in period t (a mix of aggressive and docile individuals) cannot exceed $h^\star W^\star$, the maximum number that the group can slaughter maintaining the population at $W^\star$.[33] It is easy to verify that, if $A_t > h^\star W^\star$, then the solution to (2) is $s_{a,t}A_t = h^\star W^\star$ and $s_{d,t} = 0$, while if $A_t \leq h^\star W^\star$, then the solution is $s_{a,t} = 1$ and $s_{d,t}D_t = hW^\star - A_t$. Because the cost of confinement is higher for aggressive animals, the group will slaughter as many aggressive animals as possible and confine relatively more docile individuals. As a consequence, while the stock of aggressive animals is greater than the steady-state level that can be slaughtered ($A_t \geq h^\star W^\star$), the group slaughters only aggressive animals. Alternatively, when $A_t < h^\star W^\star$, the group completely wipes out all the aggressive animals and starts slaughtering docile animals.

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[31] The origins of such an innovation might be taking advantage of a geographical location or some other unique situation. We do not distinguish between adults and juveniles in the wild population, though it seems likely that the capture and control costs of juveniles will be lower than for adults.

[32] Slaughter is simply harvesting in confinement. Hunting and slaughtering are differentiated by ownership of the live animals. In this concept of confinement, aggressive and docile are not identified until after separation from the main population.

[33] To keep the model simple, we hold constant the harvest level under confinement *versus* hunting and gathering. Domestication is likely to increase the productivity of the stock, for example, through investments in predator control and nutrition (which are more likely to occur under confinement). In section 5 we discuss this possibility.

After the group makes the slaughtering decisions in period t, the proportion of aggressive animals remaining in the confined population is $(1-s_{a,t})A_t/[(1-s_{a,t})A_t+(1-s_{d,t})D_t]$, where the numerator is the number of aggressive animals remaining and the denominator is the total number of animals remaining. We assume that the animals in the confined population will reproduce to replenish the original population level, namely yW^*. More impotantly, we assume that all individuals have the same chance of successfully reproducing. Thus, at the beginning of period $t+1$ the stock of aggressive and docile animals in the confined population will be given by:

$$A_{t+1}=\frac{(1-s_{a,t})A_t}{(1-s_{a,t})A_t+(1-s_{d,t})D_t}yW^*, \tag{3}$$

and:

$$D_{t+1}=\frac{(1-s_{d,t})D_t}{(1-s_{a,t})A_t+(1-s_{d,t})D_t}yW^*, \tag{4}$$

respectively. If in period $t=\tau_C$, the group adopts the new technology, then yW^* wild animals are captured and confined, a proportion a_w of which are aggressive and $(1-a_w)$ are docile. Thus, $A_{\tau_C}=a_w yW^*$ and $D_{\tau_C}=(1-a_w)yW^*$. Introducing the optimal slaughtering decisions of the group into (3) and (4) and solving the corresponding difference equations, we obtain the following proposition.[34]

Proposition 1:

Suppose that in period τ_C *the group adopts the new technology. Then, the paths of* A_t *and* D_t *for all* $t\geq\tau_C$ *are given by:*

$$A_t=\begin{cases} yW^*\left[1-(1-a_w)\left(\dfrac{y}{y-h}\right)^{t-\tau_C}\right]\text{if } t\leq\tau_D \\ 0 \text{ if } t>\tau_D \end{cases}, \tag{5}$$

and:

$$D_t=\begin{cases} yW^*(1-a_w)\left(\dfrac{y}{y-h}\right)^{t-\tau_C} \text{ if } t\leq\tau_D \\ yW^* \text{ if } t>\tau_D \end{cases}, \tag{6}$$

where $\tau_D=\tau_C-1+\dfrac{\ln(1-a_w)}{[\ln y/(y-h)]}$.[35]

Figure 1 illustrates Proposition 1 for specific parameters. In period τ_C the group captures and confines a population comprised of $A_{\tau_C}=a_w yW^*$ aggressive animals and $D_{\tau_C}=(1-a_w)yW^*$ docile animals. For many periods, the group selectively slaughters only aggressive animals in order to make the confinement cost as low as possible. As a consequence, the population of aggressive animals slowly but steadily declines until it reaches $A_t\leq h^*W^*$. At this moment (formally, when $t=\tau_D$) all the remaining aggressive animals are slaughtered and, thereafter, the confined population comprises just docile animals. The domestication process has been completed at time τ_D, and this would be a 'domestication event.'[36] In the long run, only docile individuals are maintained as property. Figure 1 also shows that

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[34] The proof of Proposition 1 is provided in the appendix.

[35] x denotes the integer part of x.

[36] Note also that our model does not examine morphological and hormonal changes that arise from domestication but rather we assume docility is strongly correlated with these features.

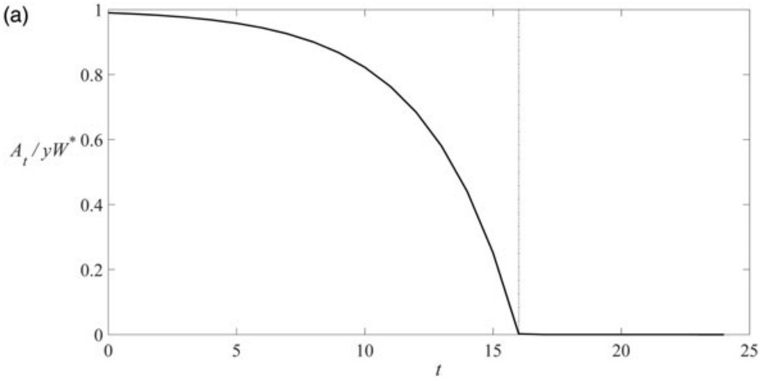

Figure 1a. Proportion of aggressive animals in the confined population

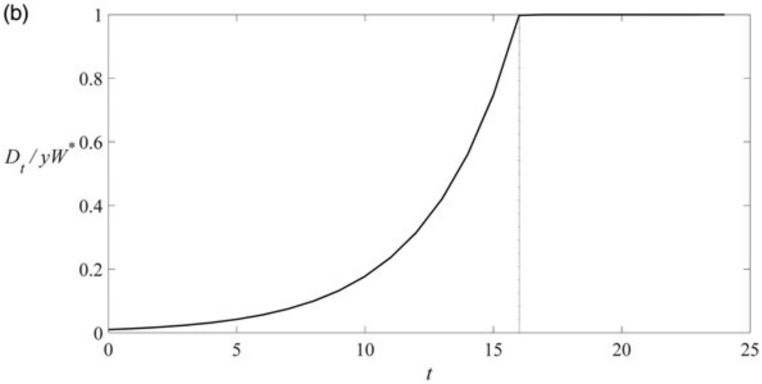

Figure 1b. Proportion of docile animals in the confined population
Notes: Example uses the following parameters: $a_w = 0.99$ (proportion of aggressive animals in the wild population), $W^* = 1,000$ (size of the wild population), $y = 0.2$ (proportion of W^* captured) and $h^* = 0.05$ (proportion of W^* harvested).

the domestication process moves slowly at first but then proceeds rapidly. Figure 1a shows the proportion of aggressive individuals and Figure 1b symmetrically shows the proportion of docile individuals. Although obtaining a population of fully docile animals could take many periods,[37] at some point the process will gain momentum and the proportion of docile and aggressive animals in the confined population will experience significant changes in a relatively short time.

Comparative statics

The model can also generate implications about how the time required to fully domesticate a population will depend on the parameters of the model. First, the time to domestication, $\tau_D - \tau_C$, is increasing in a_w.[38] Thus, as the proportion of aggressive animals in the wild population is higher the longer it takes to completely wipe out the aggressive individuals from the confined population. This effect is illustrated in Figure 2 which uses the same parameter values as in Figure 1, while allowing the proportion of aggressive animals to change.

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[37] For example, if we interpret a period as 30 years (approximately, one human generation), the domestication process depicted in Figure 1 would take 480 years.

[38] As noted earlier, archeologists label this entire period as a “domestication event.”

Second, the time to domestication $\tau_D - \tau_C$ is increasing in y. Thus, as the new technology requires the group to confine a higher fraction of the wild population prior to selectively killing the aggressive animals, it takes longer to eliminate all the aggressive ones. Finally, the time to domestication $\tau_D - \tau_C$ is decreasing in $h^\star$. Thus, as the proportion of animals that the group can slaughter increases, it takes less time to obtain a domesticated, confined population.

Endogenous adoption of domestication technology

We have assumed that the group exogenously switches to the new technology in period τ_C but the adoption decision can be made a choice of the group. We consider two possible cases. First, suppose that the group is completely short-sighted, i.e. it only takes into account its payoff in period t. Second, suppose that the group takes into account the payoff in the current and future period and has a discount factor $\beta \in (0, 1)$, so the group maximizes $V_t = v_t + \beta v_{t+1}$, where $v_t = v_{C,t}$ $(v_t = v_H)$ if the group has (not) adopted the capturing technology. The following proposition summarizes the adoption decision in each case:[39]

Proposition 2

Suppose that the group is completely short-sighted. Then it adopts the new technology if and only if

$$c_C < \frac{c_h h^*}{(a_w y - h^*)W^*}.$$

Suppose that the group maximizes $V_t = v_t + \beta v_{t+1}$*. Then, it adopts the new technology if and only if*

$$c_C \le \frac{(1+\beta)c_h h^*}{W^*\left[(a_w y - h^*) + \beta(y - h^*) - \beta y(1 - a_w)\left(\frac{y}{y - h^*}\right)\right]}.$$

Proposition 2 states that the domestication process begins only if the cost of confinement is below some threshold. Intutitively, the cost of obtaining $h^\star W^\star$ animals hunting from the wild population is $c_h h^\star$, while the cost of obtaining the same level of output using the new technology is $c_C(a_w y - h^\star)W^\star$. The most important implication of Proposition 2 is that it is possible that some hunter–gatherer groups never transition to a domestication path simply because the initial costs of confining and selectively slaughtering animals is not low enough relative to the costs of hunting from a wild population. If somehow the hunter–gatherer group found a way of partially internalizing the future cost reductions associated with the domestication path, then adoption of this technology would be easier. Formally, the threshold in Proposition 2.2 is higher than the threshold in Proposition 2.1. This suggests that not only environmental, but also social and organizational factors could have played a role in the path followed by different groups.

5. Theoretical extensions and empirical challenges

In this section we explore three directions for extending and modifying the model developed in section 4. First, we consider the possibility that several hunter–gatherer groups compete for the control of the hunting territory. Second, we discuss changes in management strategies under confinement that would allow a change in the biological parameters that govern the evolution of the animal population. Third, we explore a domestication path in which a hunter–gatherer group combines hunting and harvesting from a confined population. Finally, we also briefly discuss the empirical challenges associated with testing our theoretical predictions.[40]

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[39] The proof of Proposition 2 is provided in the appendix.

[40] These issues are examined in Lueck and Torrens (2019).

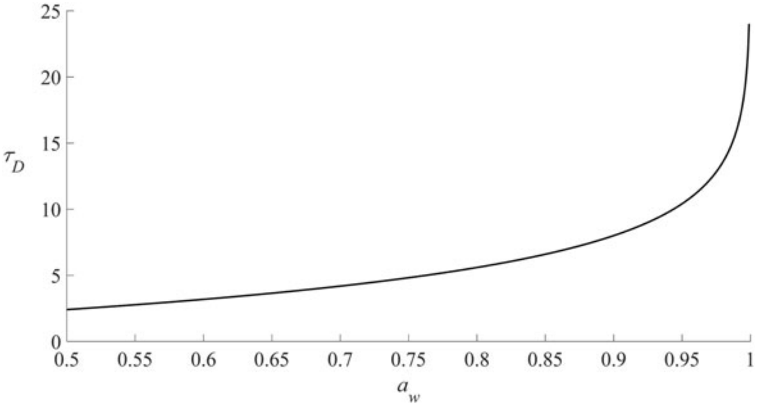

Figure 2. Time to domestication as a function of a_w
Notes: Example uses the following parameters: $W^* = 1,000$ (size of the wild population), $y = 0.2$ (proportion of W^* captured) and $h^* = 0.05$ (proportion of W^* harvested). Without loss of generality, we assume that $\tau_C = 0$.

Exclusive versus non-exclusive hunting territory

In section 4 we assume that the hunter–gatherer group has exclusive control over the hunting territory and manages the wild stock as common property. A promising modification of the model is to explore what would happen to the domestication path if several groups were competing for the same territory, so that the wild stock was effectively open access. We conjecture that beginning with open access rather than common property implies that domestication should take place earlier. The reason is that it should be easier to protect and defend a confined rather than a wild population of animals and that under open access the rent from the resource would be lower (potentially zero) than under common property (Gordon, 1954). Thus, a hunter–gatherer group facing competition from other groups would find it relatively attractive to capture, confine, and protect a proportion of the wild population, *ceteris paribus*, entering the domestication path earlier.

This mechanism could also help explaining spatial differences in the domestication process. In some locations, groups may have started with open access to or severe competition for the control of a given hunting territory. In these locations, groups are expected to transition simultaneously to common property and harvest selectively from a confined population. In other locations, a hunter–gatherer group might manage to fully control a hunting territory and, hence, incentives to confine and selectively harvest such populations would be less intense. Domestication times and the evolution of property regimes would differ across these locations. In locations with strong competition for the hunting territory, domestication is expected to occur earlier, and at the beginning of the process there was a change in the property regime from open access to common property. In locations with weak competition for the hunting territory, the domestication process would be delayed, and it would not be preceded by a change in the property regime to the wild stocks.

Change in the steady-state level of harvest under confinement

The optimization problem in equation (2) contains the constraint that the harvest level after confinement cannot exceed the harvest level under hunting and gathering. We imposed this assumption to isolate the effect that confinement has on the incentives of the hunter–gatherer group to selectively slaughter animals with different levels of aggressiveness. It is more realistic, however, to assume that domestication is also likely to increase the productivity of the stock. For example, confinement may facilitate investments in predator control, nutrition, and shelter, which surely increase the steady-state level of harvest. The model in section 4 could be modified to allow for this productivity-enhancing effect of confinement. The crucial question is to understand the economic logic behind these investments and how they change the evolutionary pressures operating in the confined population. One interesting possibility is that only when enough animals are docile can the group start selecting for other desirable features such as food or clothing potential. In such an environment, even before the domestication process ends (with all the specimens in the confined population being docile), economic selection also begins to proceed through other dimensions.

More gradual domestication path

In the model in section 4, the group makes an abrupt change from hunting to harvesting entirely from the confined herd. One possible way of relaxing this result is to assume that in each period the group can capture and confine only a very small number of animals from the wild population (e.g. a few juveniles), and hence it takes time to build a large confined herd. If this is the case, the group will continue hunting from the wild population while it slaughters the aggressive individuals of the confined herd. Eventually, the confined herd will be big enough and the group will stop hunting from the wild population.

An alternative way of inducing a smoother transition from hunting to harvesting for the group is to assume that the model in section 4 captures individuals from just one of the many species that inhabit the territory controlled by the group. A full model would determine how the group allocates its resources to exploit each species and, hence, which species will be domesticated. This extension of the model would be consistent with evidence suggesting that people exploited domesticated animals predominantly in their domesticated form and hunted other non-domesticated species (e.g. members of the deer family).[41]

Empirical challenges

Barzel emphasized empirical applications of his property rights approach. Indeed, he suggests property rights analysis leads to explanations that “can be tested against the facts” (1997: 1). Our analysis generates a wide range of implications both from the model in section 4 and from the extensions discussed above. The empirical applications would include examining the determinants of the choice of species to domesticate and the location of those domestication events and the timing and pace of those domestication events.[42] One can imagine natural experiments in which identical hunter–gatherer groups in adjacent and otherwise identical locations face slightly different wild populations of the same species.

The implementation of standard economic empirical testing, however, is daunting. An ideal data set for such analysis would be a panel of data on population–location observations and information on the land and human inhabitants at each point in time. In fact, the archeological-genetic data that are available do not remotely resemble such an ideal. Instead the data are based on archeological discoveries (and related genetic and data testing) from sites that have preserved evidence and been discovered and studied. It is far from a random sample of observations over time. Moreover, each ‘data point’ of a time- and place-specific observation has been generated by numerous competing archeological studies, which in turn are debated. Measurement error is large.

The limits of these data restrict the questions that can be reasonably tested.[43] For example, our model of domestication predicts that the path of domestication is expected to be slow at first, then relatively rapid. This prediction is generally consistent with the findings of the Siberian fox study (Dugatkin and Trut, 2017), which finds that early fox generations did not show much behavioral-morphological change but after a couple of decades the pace of change was rapid. The fox experiment,

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[41] One important exception is *sus scrofa*, the wild boar/domesticated pig, which is domesticated and hunted in its wild form in the same location.

[42] Zeder (2012) discusses information on the dates of initial changes in morphology among goats before they are considered fully domesticated. Such information might be used in empirical analysis.

[43] Lueck and Torrens (2019) develop additional models of domestication and use them to illuminate the archeological data.

however, was designed to test how selection for "tameness" affects the behavior and morphology of animals, which might not capture the decisions of a hunter–gatherer group.

Similarly, our comparative statics analysis generates predictions about the impact of the proportion of aggressive animals in the wild population and the size of the optimal harvest on the length of time to domestication (from initial confinement).[44] While such predictions may seem testable, the data are not up to the task. Consider the implication that more aggressive species are less likely to be domesticated. For example, it has been suggested that the reason the American bison was not domesticated is that it is too aggressive compared to cattle.[45] The data strongly indicate that cattle were domesticated from a wild bovine known as the auroch, which has now been extinct for several hundred years. The archeological and museum evidence suggests that auroch were as big and likely as aggressive as bison, but it is impossible to know.[46]

6. Conclusions

The domestication of wild animals and plants is undoubtedly an important innovation in human history. Domestication is fundamental to the transformation from hunter–gatherer societies to agricultural and ultimately industrial societies. Archeologists, anthropologists, biologists, historians and others have studied and continue to study domestication. Economists have been curious bystanders so far, but they need not be. Data on domestication are accumulating and economic models of property rights, renewable resources, and evolutionary games provide tools of analysis. It is our view that economics has great potential to illuminate our understanding of the human domestication of wild species.

Yoram Barzel's approach to economics has been to focus on the property rights to assets, and how those rights shape incentives and ultimately economic decisions. Our application to the domestication of wild animals relies on his framework to examine the incentives inherent in human decisions to move from hunting and gathering to a property rights-based system of using and managing animals. This paper has started this application but has by no means finished it. Among other things our analysis ignored the differences between animals domesticated for meat (cattle, sheep, pigs) and those domesticated for transportation or protection (dogs and horses).[47] The mechanism of ownership and economic selection is likely different across such species. The emergence of property rights to animals, the creation of markets, and the expansion of trade are also left for future work. It is noteworthy that 'chatel', the Old Norman term for personal property, has its origins in an ancient word for cattle.[48]

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[44] Note our model does not say anything about the level or magnitude of aggressiveness.

[45] Diamond (1997) and others have argued this.

[46] The data tend to show that domestication occurs in just a few spots. This alone implies that non-species characteristics are also important, perhaps because they influence the cost of confinement or the rents from wild stocks in a hunter–gatherer society.

[47] Zeder (2012) discusses different "pathways" of domestication that makes similar distinctions.

[48] See the discussion in https://www.merriam-webster.com/dictionary/chattel (accessed June 17, 2019).

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Appendix – Proof of Propositions 1 and 2

Proposition 1

If $A_t > h^\star W^\star$, then the solution to (2) is $s_{a,t}A_t = h^\star W^\star$ and $s_{d,t} = 0$, while if $A_t \leq h^\star W^\star$, then the solution is $s_{a,t} = 1$ and $s_{d,t}D_t = hW^\star - A_t$. Introducing these solutions into (3) and (4) we obtain: $A_{t+1} = \frac{A_t - h^* W^*}{A_t - h^* W^* + D_t} yW^*$, $D_{t+1} = \frac{D_t}{A_t - h^* W^* + D_t} yW^*$ when $A_t > h^\star W^\star$ and $A_{t+1} = 0$, $D_{t+1} = yW^\star$when $A_t \leq h^\star W^\star$. Since $A_t + D_t = yW^\star$ we have: $A_{t+1} = \frac{A_t - h^* W^*}{y - h^*} y$, $D_{t+1} = \frac{D_t}{y - h^*} y$ when $A_t > h^\star W^\star$ and $A_{t+1} = 0$, $D_{t+1} = yW^\star$when $A_t \leq h^\star W^\star$. Solving these difference equations with initial conditions $A_{\tau_C} = a_w yW^*$ and $D_{\tau_C} = (1 - a_w)yW^*$ we obtain:

$$A_t = \begin{cases} yW^* \left[1 - (1 - a_w)\left(\frac{y}{y - h} \right)^{t - \tau_C} \right] \text{if } t \leq \tau_D \\ 0 \text{ if } t > \tau_D \end{cases} \text{ and}$$

$$D_t = \begin{cases} yW^* (1 - a_w)\left(\frac{y}{y - h} \right)^{t - \tau_C} \text{ if } t \leq \tau_D \\ yW^* \text{ if } t > \tau_D \end{cases}$$

where $\tau_D = \tau_C - 1 + \frac{\ln(1 - a_w)}{[\ln y/(y - h)]}$. **QED**

Proposition 2

Suppose that the group is completely short-sighted. If the group does not adopt, its payoff is given by $v_H = h^\star W^\star - c_h h^\star$. On the contrary, if the group adopts, its payoff is given by $v_C = h^\star W^\star - c_C(a_w y - h^\star)W^\star$, where we have used that $A_{\tau_C} = a_w yW^*$, $s_{a,\tau_C}A_{\tau_C} = h^* W^*$ and $s_{d,\tau_C} = 0$. Therefore, the group adopts if and only if $c_C < c_h h^\star/(a_w y - h^\star)W^\star$.

Suppose that the group maximizes $V_t = v_t + \beta v_{t+1}$. If the group does not adopt, its payoff is given by $V_H = (1 + \beta)v_H = (1 + \beta)(h^\star W^\star - c_h h^\star)$. On the contrary, if the group adopts, its payoff is given by $v_{C,\tau_C} = h^* W^* - c_C(a_w yW^* - h^* W^*)$ and $v_{c,\tau_C+1} = h^* W^* - c_C W^* \left[y - h^* - y(1 - a_w)\left(\frac{y}{y - h^*} \right) \right]$, where we have used that $A_{\tau_C} = a_w yW^*$, $s_{a,\tau_C}A_{\tau_C} = h^* W^*$, $s_{d,\tau_C} = 0$, $A_{\tau_C+1} = yW^* \left[1 - (1 - a_w)\left(\frac{y}{y - h^*} \right) \right]$, $s_{a,\tau_C+1}A_{\tau_C+1} = h^* W^*$ and $s_{d,\tau_C+1} = 0$. Therefore, $V_C = h^* W^* - c_C(a_w y - h^*)W^* + \beta W^* \left\{ h^* - c_C\left[y - h^* - y(1 - a_w)\left(\frac{y}{y - h^*} \right) \right] \right\}$. Hence, the group adopts if and only if $c_C \leq \frac{(1 + \beta)c_h h^*}{W^* \left[(a_w y - h^*) + \beta(y - h^*) - \beta y(1 - a_w)\left(\frac{y}{y - h^*} \right) \right]}$. **QED**

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