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Privatization and property in biology

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ABSTRACT

Organisms evolve to control, preserve, protect and invest in their own bodies. When they do likewise with external resources they privatize those resources and convert them into their own property. Property is a neglected topic in biology, though examples include territories, domiciles and nest structures, food caching, mate guarding, and the resources and partners in mutualisms. Property is important because it represents a solution to the tragedy of the commons; to the extent that an individual exerts long-term control of its property, it can use it prudently, and even invest in it. Resources most worth privatizing are often high in value. To be useful to their owner in the future, they are typically durable and defensible. This may explain why property is relatively rare in animals compared to humans. The lack of institutional property rights in animals also contributes to their rarity, although owner-intruder conventions may represent a simple form of property rights. Resources are often privatized by force or threat of force, but privatization can also be achieved by hiding, by constructing barriers, and by carrying or incorporating the property. Social organisms often have property for two reasons. First, the returns on savings and investments can accrue to relatives, including descendants. Second, social groups can divide tasks among members, so they can simultaneously guard property and forage, for example. Privatization enhances the likelihood the benefits of cooperation will go to relatives, thus facilitating the evolution of cooperation as in Hamilton's rule or kin selection. Mutualisms often involve exchange of property and privatization of relationships. Privatization ensures the stability of such cooperation.

The major transitions in evolution, both fraternal and egalitarian, generally involve the formation of private clubs with something analogous to the non-rivalrous club goods of economics.

Keywords: property, privatization, evolution, ownership, investment, territoriality, sociality, kin selection

INTRODUCTION

Organisms have evolved to live not just for the immediate present but also for the future. They work to preserve their bodies, to protect them against external threats, to control how they are used and, under some conditions, they invest in improving them. More rarely, they also preserve, protect, control and invest in resources that are not part of their own body. In humans, such external resources are very important – we call them property. In this paper, we consider the role of property in non-humans. When do organisms preserve and protect resources aside from their own body and the bodies of their offspring or kin? A central feature of our argument is that such resources must be partly or wholly privatized; they must come under the control of an owner. If an organism is to expend effort and energy in preserving or investing in a resource, it must be able to reap sufficient gains from doing so. If non-kin end up harvesting the resources instead, the investment would not pay and so the act of investing would not evolve.

Table 1 give definitions and examples of property and privatization. We expand on these below, but note now that property and privatization, though closely linked, are not synonymous. One can have each without the other. Organisms may engage in privatization that does not fully succeed in excluding others and generating property. Conversely, organisms may sometimes have property for their exclusive use that they did not have to actively privatize. Both concepts are distinct from privacy, defined as physical or informational separation from conspecifics (Klopfer & Rubenstein 1977)

Property and privatization are neglected concepts in biology. There are many known examples, such as territoriality, but these are not usually grouped together. There are at least two ironies here. First, the field of sociobiology has been criticized for being a crude extrapolation of capitalist economics into biology (Gould & Lewontin 1979), but if this were true, wouldn't a biological theory of property have emerged long ago? Yet, so far as we know, this review is the first attempt to argue that property and privatization are concepts that might be useful across many evolutionary contexts.

The second irony is that while biologists have expended great effort in understanding possible cooperative solutions to tragedies of the commons, they have tended to ignore the most obvious solution. The obvious, though not necessarily best, solution to Garrett Hardin's paradigmatic example of cattle overgrazing a pasture owned in common is privatization of the pasture (Hardin 1968).

Here we explore the range of privatization and property in the non-human world.. We ask why property seems to be uncommon in nature. Why do organisms not preserve, protect, and enhance their resources more often? We also identify the kinds of privatization and property that do exist. We assemble cases, drawn from the existing literature, for example on territoriality, on hiding resources or sequestering them in fortresses, and on privatizing partners in interactions. Our goal is not mainly to identify new phenomena but rather to begin exploring privatization commonalities among known phenomena. Privatization is a key element of the Hamiltonian view of sociality because it allows property to benefit kin (Hamilton 1964).

TERRITORIES

Territoriality, which is widespread in animals (Maher & Lott 2000)(Burt 1943; Klopfer 1969), is perhaps the best-recognized form of privatization, so we use it to introduce many points that may be more general.. It is an ancient concept. Around 300 BC, Aristotle realized that eagles need a large area for food and so exclude others (Lack 1944). In a review of the topic in birds, Nice traces territoriality to Olina's 1622 book, Uccelliera, that explicitly mentions male territory invasion by nightingales (Nice 1941). It is no surprise that these earliest references are to birds since they are particularly active in their territorial defenses.

A territory can be defined as property in the form of an area that an organism controls, uses, and defends. The territory is an unusual form of property in that the area defended is not really the resource. Instead of defending a particular resource only when it is specifically threatened, a territory holder follows a more general strategy of keeping intruders away from an entire area. For birds, the actual resources can be food for their young, a safe nesting place, or their mates. Birds may defend their territory against others of the same or different species (Peiman & Robinson 2010). Males of many species may also guard their mates to preserve paternity of young for the caring male – the privatization of his mate or mates (Jormalainen 1998; Møller & Birkhead 1991). Such privatization is imperfect, as shown for example, by the often high frequencies of young in the nests that are not the progeny of the attending male (Petrie & Kempenaers 1998). A large part of the challenge for territorial males is that they are attempting to privatize a living conspecific who may have conflicting interests (Arnqvist & Kirkpatrick 2005).

The early references and later discussions of territoriality make several important points (Klopfer 1969) that are relevant to privatization in general. First, the resource has to be sufficiently valuable to warrant the effort needed for privatization. Defense is frequently required because a resource that is valuable to its owner is likely to also be valuable to others. Defense can be viewed as what distinguishes a territory from a home range. The requirement of defense is also what limits territory size. Territories can be only as large as is feasible for defense (Brown 1964). Either an exceptionally poor or rich territory may not be worth defending, the former for inadequate resources, the latter for too many invaders. A classic example is the golden-winged sunbird which only defends territories of flowers yielding sufficient nectar reward (Gill & Wolf 1975).

Ownership of territories can sometimes lead to investment in the protected resources. Beavers are perhaps the most famous example for their investments in dams and the water bodies they create (Bradt 1938). These dams change the landscape in ways that can even be viewed as geologic (Ruedemann & Schoonmaker 1938), but it is unlikely beavers would evolve to build them if they could not keep the resource private. When territoriality privatizes partners, investments in those partners may be profitable. For example, at least two species of territorial damselfish weed their algal gardens and defend them against other damselfish and against sea urchins (Eakin 1987; Hata & Kato 2006). Social insects build elaborate nests to defend brood and stored resources (Hansell 1984).

WHAT IS PROPERTY?

We began with an analogy between preserving, protecting, controlling, and investing in bodies and doing likewise for entities outside of the body. Indeed, one's body is often regarded as property, the most fundamental property there is. There are many adaptations that keep an organism entire and out of the digestive tracts of others, for example camouflage, hiding, distastefulness, weapons, shells,swiftness and selfish herds (Hamilton 1971). However, here we focus on privatization of resources other than self and kin. Our point here is not to nitpick what should and should not be considered property. Instead, the narrower focus serves to limit the scope of the review and to concentrate on the more novel aspects. Preserving, protecting and investing in survival and reproduction is expected, common, and well understood. What we want to understand is when and why this sensitivity to the future that applies to ordinary phenotypes also applies outside the body, to extended phenotypes (Dawkins 1982).

Property includes not just territories, but also objects such as food sources or structures that are defended individually rather than as part of a general defended area. Simply taking a resource and consuming it immediately could be viewed as a sort of privatization, but we are interested in a narrower usage. We focus on privatization that can lead to property, a resource that is saved to draw benefits from later.

We will also consider goods exchanged with other individuals as a kind of property. Some of these stretch our definition a bit because these goods may be part of the owner's body until the time of exchange or shortly before it, for example nutritive spermatophores or nuptial gifts, flower nectar, aphid honeydew, and the nitrogen of nitrogen-fixing bacteria. But these are investments, much like human exchanges of property, and issues of privatization and owner control of the resource are often just as important here.

Other individuals, of the same or other species, can also be objects of privatization efforts. Humans treat some animals as property and have sometimes treated other humans as such. Our recognition that animals sometimes do likewise in no way justifies or condones such practices in humans. It is simply a recognition that animals sometimes attempt to privatize other living organisms in ways similar to the way they attempt privatize inanimate objects. The degree of control by the privatizer may be less complete given that the potential property is also an agent that can evolve and act according to its own interests.. Again, arguments over the precise definition are less important than the recognition that, even if control is incomplete, organisms do attempt to privatize others, from humans with their alpaca herds to fungi that host algae in lichens.

HOW TO PRIVATIZE

By privatization, we mean steps taken in the direction of gaining or protecting property. In humans, privatization often means moving resources from government control to private control, but in non-humans that lack governments it usually means taking resources out of public use. There are at several major methods of privatization. Physical force, or the threat of it, is perhaps the primary method of privatization. It is applicable not only to territories, but to more restricted types of resources. Resources may be gathered from and moved into a defendable cache, as is the case with many rodents that store seeds in their burrows for winter, or burying beetles that move a carcass and defend it. Alternatively, individual items of property may be defended in place, such as a nest or a particularly rich food site. When other living organisms are the resource they themselves may be defended. A male may defend a harem of females from other males. Ants may defend a group of aphids and their rich honeydew.

Property can also be privatized by chemical means. A common way that individuals protect their own bodies is to make them distasteful or unappealing to predators. Many plant secondary compounds serve this function, but some animals are also distasteful, often via sequestration of some of these plant compounds. This strategy appears to be less common for privatizing external resources, but it does occur. Jansen (1977) proposed that microbe-induced rot of rich resources like fruit and carcasses has often evolved as an adaptation of microbes to make these resources unpalatable to larger consumers such as vertebrates.

Examples of chemical protection by multicellular organisms do not appear to be very common. However, some protect their resources with antibiotics, often produced by mutualistic bacterial partners. Honeybees chemically protect their honey stores; burying beetles protect their carcasses (Rozen 2008). Farming ants, beetles (Oh et al. 2009; Scott et al. 2008) and social amoebas (Stallforth et al. 2013) use symbionts that chemically protect their crops.

Chemical privatization is usually directed against other species with different chemical vulnerabilities. It is generally more difficult to chemically harm conspecifics without harming oneself. However bacteriocins, chemicals that bacteria use to harm others of their species, are a major exception. In animals, chemical manipulation of the opposite sex provides some examples. For example, in *Drosophila*, male-produced proteins or peptides delivered in the ejaculate sometimes manipulate female behavior. For example, they can increase the female's immediate egg-laying rates (sometimes at a survival cost) and decrease her re-mating rate. Both of these chemical modifications serve to partly privatize the female, in the sense of ensuring that more of her progeny go to the manipulating male instead of to other males.

In addition to defense, privatization can be achieved by two other main kinds of actions: concealment and fortress construction. Scatter caching is one way of privatizing food resources without defense (Smith & Reichman 1984). A scattered cache relies on both concealment and memory or smell; these have been extensively studied (Brodin 2010). Scatter caching by mammals of a resource that can be relocated by smell is relatively safe from birds because they lack the sensitive smelling capabilities of mammals. Hiding may also occur via information limits. Flowers and fruits can use color to attract some kinds of mutualistic partners and partially hide from others.

Another way of making a resource private is to put it in a fortress or a structure that makes access more difficult. We consider structures fortresses only if the organism using them has in some way modified its environment into a structure that makes access for competitors more difficult. The fortress is typically a form of property itself, something that the owner invests in and defends. But it can also be a device to protect other property. Many mammals construct fortresses by digging burrows, often for their own shelter and protection, but sometimes also to protect property. A hoard of seeds hidden and defended in a burrow is one kind of fortress. Honeybees and stingless bees protect their honey and pollen resources in cavities that serve as fortresses. Microbes construct biofilms that help sequester resources. The commonest kinds of animal constructions are nests for rearing young and fortresses that limit access to resources (Hansell 1984). Putting property behind barriers can include elements of hiding. Intruders may know that there may be seeds in a burrow or honey in a hive, but they cannot know how much without first paying the price of breaching the fortress.

A final solution to the dilemma of leaving property unprotected is to carry your property with you. Temporary carrying is common. A cheetah drags its kill up a tree, ants bring seeds back to the nest, birds ferry nuts to their caching locations. Others carry property with them during dispersal events, such as *Atta* ant queens carrying their mutualistic fungus to a new colony or *Dictyostelium* amoebas carrying bacterial prey to a new location (Brock et al. 2011; Mueller et al. 2005). But in these examples carrying serves only a brief subsidiary goal of putting the property in a safer place or in a new place, rather than a direct privatizing function. Carrying property for longer periods is usually limited to property that is small and valuable.

Even when carrying is more permanent, the advantage may be bit different than some other forms of privatization. It may be less a matter of keeping a resource away from others than simply having it at hand. Hermit crabs provide an unusual example of permanently carrying large property (Bertness 1981). Carrying the shell that it has found does help privatize the shell from others who would take it, but the main reason for carrying the shell is the protection it affords its owner from predators. It needs to carry the shell to gain its benefits.

Perhaps the most common type of carrying is of mutualistic partners, which can be very small and easy to carry. The issue may be less keeping the resource from others than having it at hand to exploit. The bacteria that *Atta* ants carry on their surface are not being carried to prevent them from being stolen but to have them available to protect the colony's fungus (Cafaro et al. 2011).

In many symbioses one partner privatizes the other internally, with special cells like the bacteriocyte cells that aphids and many sap drinking insects have for their bacterial symbionts that process sugar rich plant sap into amino acids the host cannot produce (Moran & Telang 1998) Many other symbioses take this form (Douglas 1994). This form of carrying sometimes leads to vertical transmission, which by tying together the reproductive fates of the partners, is particularly favorable to enhancing the evolution of intimate cooperation.

THE ECONOMICS OF PRIVATIZATION

A private resource can increase immediate survival if it provides food or shelter. But the real point of privatizing a resource is that is makes it available for future use by the owner or others of the owner's choosing, such as offspring, other kin, or mutualistic partners. It also allows planning for the future based on the guaranteed resource. Prudent harvesting – taking less than is available so the resource is there for future use – becomes possible. Without privatization, prudence would be vulnerable to a tragedy of the commons; organisms that consumed as much as possible in the present would succeed more than those that held back. Privatization is a solution to the tragedy of the commons that might be more generally accessible to animals than are human solutions like negotiation. Other solutions to the commons tragedy in animals include high relatedness, policing, and the consequences of diminishing returns (Rankin, Bargum & Kokko 2007).

A further advantage in some types of privatization is that the property can be enhanced. We have already mentioned beaver dams and weeding of algal gardens by damselfish. Such investment seems particularly likely to yield returns when the property is living, and can grow or propagate. Undesirable growths could be weeded out as in the damselfish(Eakin 1987). Fungus gardens can be fertilized by their ant hosts(Martin 1970). Acacia are defended against large predators like elephants by ants(Goheen & Palmer 2010).

Resources most worth privatizing are often rare, expensive, durable, clumped, and defendable. Resources that are abundant, or of low value are often not worth the effort of privatizing. Grazers will not usually defend grass. A tree in fruit may be worth privatizing if it is the only such tree in the area, but perhaps not if such trees are abundant. Males more often attempt to privatize females than vice versa, because females and the investment they put into their young are more often the limiting resource (Wilson & Daly 1992).

In these respects, the economics of privatization resemble those for contests for immediate resources, but they differ in one important respect. Potential property owners should be selected to discount the future payoffs if they (or their kin) might not be around to enjoy the property later and also if the property might not be around later. Indeed, because future benefits are discounted, property must actually be more valuable when used in the future than it would be if used today. The chief reason this might be so is future scarcity, either predicable (like winter) or unpredictable.

As a consequence, both durability and defensibility of the property are important because these, along with owner survival, determine whether the property will provide future benefits. A privatized resource has to be long-lasting enough to be retain value, either because it is durable like a seed or a tree hollow, or because it is a source of continuing resource production, like a territory, or the zooxanthellae in coral, or the thorns and Beltian bodies of an ant acacia. Fruit and meat are difficult to store for later; seeds are much more easier to store because they have their own protections against microbes. Even if it is durable, a resource can lose value over time if it is insufficiently defensible, such that some one else ultimately reaps the gains.

These various conditions may explain why property is less common for most organisms than it is for humans. Perhaps few resources have sufficiently high value, defensibility, and durability. But another factor may be equally important. Human societies usually have some higher-level sanction of property rights through customs, laws, and enforcement although, especially where institutions are weak, people also defend their own property. Non-humans do not generally have the higher-level institutions and each individual must therefore rely on itself or its kin group (but see "Recognition of ownership" below). This usually means that the owner must be sufficiently near its property resource to defend it. For animals that must move around to make a living, this is a strong limitation. Either they must carry the resource with them, check on it frequently, or exclude competitors from a territory that includes all the property to be defended.

DETECTION AND RECOGNITION OF OWNERSHIP

Although only humans have higher-level social institutions that protect property, other organisms may sometimes have evolved recognition of ownership and hesitation to challenge it. That is, they often modify their behavior depending on whether they are an owner or intruder. First, ownership is often advertised. Birds sing on their territories and mammals mark them chemically(Klopfer 1969). Although there is no institutional enforcement, advertising does at least tell a potential intruder that there is an owner present and there is likely to be a cost to intruding, so it might be better to move on. If the advertisements are individually recognizable, they can also provide additional information to regular neighbors that this particular owner who has fought them in the past is still present. Advertising will not generally work in the absence of the threat of force, but it is sometimes a useful adjunct to force.

Animals sometimes act as if they recognize right of ownership; they will more readily fight as an owner than as an intruder. This is half explained by Maynard Smith's game theoretic analysis of the hawk, dove, and bourgeois strategies. When costs of fighting are sufficiently high, selection can favor a bourgeois strategy that fights when it is an owner and retreats when it is not (Maynard Smith & Parker 1976). It is only half an explanation because selection can equally favor the opposite strategy of fighting only as an intruder, which does not appear to be common in nature (Maynard Smith & Parker 1976). This has been explained, not fully satisfactorily, by assuming asymmetries in the payoffs such that incumbents have an some advantage in contests (Parker 1974). Another kind of solution appears from incorporating eco-evolutionary feedbacks between selection on the trait and the payoffs (Kokko, López ‐ Sepulcre & Morrell 2006; Gintis 2007). For example as fighting increases in the intruder class, more will die, making the wait for a territory shorter and diminishing the potential gains from fighting. In contrast, as the size of the population lacking territories decreases, fighting by owners becomes more profitable (Kokko et al. 2006). More work is needed on property recognition of property in animals.

SOCIALITY AND PRIVATIZATION: FRATERNAL ALLIANCES

Sociality has a special relationship with privatization. At a broad scale there are two main kinds of sociality within a species: those of unrelated individuals, herds or flocks, and those of related individuals, clones or families, though the line may be blurry (Hatchwell 2010). Groups of unrelated individuals make it nearly impossible to privatize a resource because so many individuals are competing for the same resource at the same time and place. This is the case for herds of zebras or schools of fish. They may gain the benefit of protection from predation by being in a group, but will face exceptional competition for resources since they are surrounded by others needing exactly the same resource (Hamilton 1971). This kind of group is most common in areas where predation is a threat and resources are not distributed in ways that make them easy to privatize.

Social organisms that live in groups of relatives face a very different situation that makes them much more likely to be able to privatize resources. These kinds of social organisms include families of birds, social insects, colonial invertebrates, and some kinds of biofilms of bacteria. Sociality in kin groups is particularly favorable to privatization and property for two reasons.

First, when groups privatize resources the benefit need not pay back to the actor, but can pay back to relatives. This can include relatives that are not yet born when the resource is first privatized. This reduces future discounting, to the point where the shadow of the future may be longer for investments in property than for investments in self. Inheritance of territories is a common feature in perennial territorial organisms, for example, in cooperatively breeding birds (Woolfenden & Fitzpatrick 1978). An ant worker that invests in nest building may benefit relatives that are born many years later.

Here we are talking about privatization at the level of the colony, not the individual. Social insects have little or nothing that would be described as individual property. Of course, for social insects to benefit from group level privatization, they have to be collectivized at lower level through kin selection. Cooperation at the level of the colony is possible because benefits go to relatives, so genes for acquiring, protecting, and investing in colony property can proliferate (Hamilton 1964). Another way to think about it is that the colony goods are more analogous to the club goods of economists than true private goods. Club goods are excludable, like private goods, but are non-rivalrous. In human economics non-rivalry means that consumption by one individual does not preclude consumption by another, as in cable television or a public park. Here, instead, the lack of rivalry and ability to share comes from a community of interests among the members of the club. Although one member of the colony may use the resource, reducing the pool available to others, that outcome can be perfectly acceptable to other colony members. Given this difference, it should be interesting to see how much of the economic theory of club goods is transferrable to non-human clubs.

The second special feature of kin groups is that they have the potential to provide a solution to what may often the biggest barrier to property. When a solitary individual moves about, for example to forage, it must either bring its property with it, or leave it behind undefended. Social groups can solve this dilemma by having some individuals guard while others forage.

Many solitary bees and wasps dig tunnels in the soil, provision them with pollen (bees) or insects (wasps), lay one or more eggs and then close the nest. This is a very risky process because others can steal the burrow, lay their own eggs in it, or remove prey. Even in the tiniest groups of two, cooperation can be hugely beneficial because one could guard while the other foraged. This would drastically reduce loss because the burrow would then never be undefended. Every report that we were able to find of these smallest groups indicated that one foraged while the other guarded the nest. For example, in 1969, Charles Michener reports that “In halictines, burrows of solitary individuals are generally unguarded while burrows of the same species inhabited by two or more females are guarded much of the time…" p. 320 (Michener 1969).

Resources can be even more effectively defended if there are castes that have evolved for the primary function of defense. Gall forming aphids like *Pemphigus spyrothecae* have soldiers with thick legs that successfully deterred intruders (Foster 1990). Ants have many striking defensive castes (Hölldobler & Wilson 1990). One of the most impressive is the *Colobopsis* subgenus of *Camponotus* which has soldiers with flattened heads that act like stoppers that block the nest entrance.

Property in the form of a private nest is an important preadaptation for eusociality (Alexander 1974). At a minimum it constitutes a place where young can grow up and encounter their mother, providing the opportunity to help. In some social insects, the so-called fortress defenders (e.g. aphids, thrips, beetles, and termites), the nest played an additional important role as a private resource. Their ancestors lived, ate, and raised their young in enclosed spaces such as galls that provided the opportunity for some of the young to avoid the risks of dispersal and instead stay and use the resource of the natal structure. Indeed, the first castes in fortress defenders are typically soldiers that specialize to defend the property (and the young). The other major class of social insects, life insurers (ants, bees, and wasps), also have nests that they defend but the nests do not usually enclose a private food resource. But the privatization of the nest is still important in other ways. The life-insurance advantage is the shadow-of-the-future advantage noted above. Investments in the nest (and the brood) can pay even if the investor dies. In addition, if the nest were not private – if it were a common resource used by many mothers – then relatedness in the incipient colony would be lower than the high levels that are necessary for the evolution of eusociality. Indeed there are bees and wasps that share nests communally, but these semisocial societies have not led to eusocial ones.

It should perhaps be no surprise then that the social insects provide some of the best examples of privatization and property. Beyond the nest, many ants are territorial (Hölldobler & Lumsden 1980). These territories can last as long as the colony exists. Some ant species increase their ability to privatize a resource like extrafloral nectaries by building multiple nests, as in the case of *Crematogaster opuntiae* which maintained similar territories for the three years of the study (Lanan & Bronstein 2013). The harvester ant *Pogonomyrmex occidentalis* maintains territories that exclude conspecifics (Cole & Wiernasz 2002). Social insects often store food resources in their nests, for example honey in bees and seeds in harvester ants. Finally, social insects provide the most elaborate examples of agriculture outside of humans, with farming of fungi by termites and ants, as well has herding of aphids and scale insects (Mueller et al. 2005).

Once a sterile worker caste evolves, it too can become a form of property. Honey-filled repletes of *Myrmecocystus* are stolen in colony raids(Hölldobler 1981;

Kronauer, Miller & Hölldobler 2003). More generally, stealing of worker brood is common because ants generally learn their colony identity after they eclose as adults, so stolen brood mistakenly work for the stealers (Carlin 1988). This can occur facultatively within species. There are also obligate slave-making species that can obtain workers only in this way (D'Ettorre & Heinze 2001).

The spectacular success of social insects, especially ants, in dominating many terrestrial ecosystems (Wilson 1987) may be due in part to their ability to collectively privatize resources. However, the advantages of property and privatization also apply in a variety of social groups other than social insects. Red-cockaded woodpeckers nest in cavities in living trees, a scarce resource whose presence enhances the territory (Walters, Copeyon & Carter III 1992). Acorn woodpeckers laboriously construct granary trees with a separate hole for each acorn, considerably enhancing the territory in the process and creating a resource that can last for generations (Koenig et al. 2000; Koenig 1987). Naked mole rats invest in elaborate tunnel systems that provide defense for their underground tuber food resources (Sherman, Jarvis & Alexander 1991).

Another example of social privatization is demonstrated by many species of bacteria that produce bacteriocins (Riley & Gordon 1999; Riley & Wertz 2002). Recent authors have interpreted bacteriocins in the framework of social evolution (West et al. 2006; Kerr et al. 2002). Bacteriocins kill others that are not genetically identical to the actor, but are of the same species. In some cases, the cell that releases the bacteriocins dies, so we could consider it to be a different caste from its clonemates. The clonemates are resistant to the toxin because they carry an antidote. Sensitive clones are killed. Thus, this is a way of privatizing the resources in the area for the killing clone (Inglis et al. 2009).

EXCHANGES AND MARKETS: EGALITARIAN ALLIANCES

In addition to societies based on kinship, sometimes called fraternal alliances, there are societies based on mutualistic exchange called egalitarian alliances often between members of different species (Queller 1997). The processes of exchange of property and services have some resemblances to markets (Noë & Hammerstein 1995). A notable example of cooperation among non-relatives within species is mating, where genes and resources may be traded. When partners limit fitness, there is often an attempt to privatize them, for example through territories or mate guarding. Typically it is males attempting to privatize females, though it goes the other way in role-reversed species like jacanas (Owens 2002). In species where both parents provide resources to offspring, each may limit the others success, and both sexes may benefit from privatizing their partners (Emlen & Oring 1977; Wittenberger & Tilson 1980).

Egalitarian cooperation is more common between species, because partners are very different and each can trade for goods that it cannot produce itself. These interactions are called mutualisms. Because both parties benefit directly, mutualism allows cooperation to evolve among non-kin (Sachs et al. 2004; Bronstein 1994). Examples of mutualisms include insect pollination of plants, fungus-alga collaboration in lichens, squid-bacteria light collaboration, plant-mycorrhiza carbon for nitrogen collaboration, aphid-bacteria carbon for nutrient collaboration, cleaner fish host collaboration, and many others. It is safe to say that no organism lacks obligate mutualists (Douglas 1994) and that all of these relationships must be at least partly private to be stable and this sometimes involves active privatization (Bronstein 2001).

As in mating systems, many mutualisms can viewed as markets in which partners are chosen for the exchange of property or services (Noë & Hammerstein 1995). There are thus two levels of property involved in a mutualistic exchange. An interactant must first attempt control and privatize the disposition of its own resource, to donate its resources to a suitable partner – partner choice. In addition, it may need to take steps to privatize the partner, to ensure private use of the resources returned – partner fidelity feedback. Not all partner choice and partner fidelity feedback involves explicit privatization; for example, faithful feedback can sometimes occur simply because of simple proximity in immobile partners.

Exactly how mutualists ensure that the benefit goes to the correct partner depends on the kind of mutualism it is. Resource exchanges can be privatized for one partner when it houses the other, either temporarily or permanently. If one partner is inside the other, whatever benefit is provided generally goes automatically to the host. *Vibrio* bacteria privatized by a squid produce light only for that squid, which the squid cannot do. Photosynthates provided by algae in a lichen go to the associated lichenizing fungus. Zooxanthellae do the same for their coral hosts. *Buchnera* bacteria are internally privatized by an aphid and produce vitamins and amino acids that the aphid cannot produce. The symbionts may be less able to privatize their hosts and instead rely on it being in the host's interest to provide for them, so they can return the favor.

External mutualisms are harder to privatize. Even rhizobia in nodules may cheat (Kiers et al. 2003). Pollination is an external mutualism that exchanges a resource, typically nectar, for pollen transport. Many floral characteristics have evolved to restrict the resource to the appropriate pollinator, but the restrictions often do not fully exclude others (Maloof & Inouye 2000). Much of the richness and diversity of this and other mutualisms probably comes from incomplete attempts at privatization and avoiding parasites on the interaction. Much of the work on the privatization of mutualisms has concentrated on when privatization is foiled and benefits go to someone other than the intended partner (Bronstein 2001).

THE MAJOR TRANSITIONS AND PRIVATE CLUBS

Maynard Smith and Szathmáry (Szathmáry & Maynard Smith 1995) emphasized that many of their major transitions in evolution required evolving new levels of cooperation. Our discussion in the last two sections suggests that cooperation is often intimately tied with privatization. However, the most consistent similarity across the major transitions is the privatization of partners or the building of clubs. The transition to eusociality involves a switch to sharing of club goods and the same is true for other transitions. In the evolution of multicellularity, the club is a group of cells of the same species. In the eukaryotic transition, it is a set of cells from different species, some of which become organelles. The first step in Szathmáry and Maynard Smith's major transition cascade is compartmentalization of replicating molecules (Szathmáry & Maynard Smith 1995), with the compartment defining the club and privatizing interactions among the molecules. In every case, it is a key attribute of an organism that its component parts be private, sharing within but excluding outsiders (Strassmann & Queller 2010; Queller & Strassmann 2009). Methods for keeping the club private include a mix a physical and chemical force, as well as barriers. The kin recognition in social insects and the tissue incompatability in multicellular organisms are usually coupled with attacks on outsiders. Organelles in eukaryotic cells are privatized by enclosure in their host cell but also by mechanisms that kill one organelle lineage when two merge in sexual reproduction. Similarly, the compartmentalized genes in cells are protected by the cell membrane as well as by mechanisms that target foreign DNA, such as restriction endonucleases.

We began by noting how organisms preserve, protect, control, and invest in their own bodies. We then asked what kinds of extended phenotypes outside the body were subject to similar processes of privatization. We have now come back full circle, showing that the creation of bodies as we know them today required the privatization of relationships at several levels. The collectivization seen in the major transitions depends critically on the new collectives being private clubs with limited membership.

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	Property	Privatization
Definition	Resources outside the body that an individual (or group) preserves, protects, and controls.	An attempt to acquire or keep property
Examples	Territories, domiciles, food sources and caches, traded resources, some mates and trading partners,	Physical force, chemical means, concealment, fortresses, carrying, enclosure

Table 1. Definitions and examples of property and privatization.