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Privatization and property in biology

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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, although 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 that 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 nonrivalrous club goods of economics.

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 nonhumans. 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 nonkin end up harvesting the resources instead, the investment would not pay and so the act of investing would not evolve.

Table 1 gives definitions and examples of property and privatization. We expand on these below, but note now that property and privatization, although 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

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Table 1
Definitions and examples of property and privatization

	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

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 nonhuman 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 (Burt, 1943; Klopfer, 1969; Maher & Lott, 2000), 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 defences.

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 the paternity of the young that they care for (i.e. the privatization of a male's 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 that 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. Defence is frequently required because a resource that is valuable to its owner is likely to also be valuable to others. Defence can be viewed as what distinguishes a territory from a home range. The requirement of defence is also what limits territory size. Territories can be only as large as is feasible for defence (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, *Nectarinia reichenowi*, 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 that 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 whole 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 are 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

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