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# Privatization and Property in Biology

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1 Privatization and property in biology

2

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13

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15 **ABSTRACT**

16

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

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

41

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

44

45

46 INTRODUCTION

47

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

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

69

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

78

79           The second irony is that while biologists have expended great effort in  
80 understanding possible cooperative solutions to tragedies of the commons, they  
81 have tended to ignore the most obvious solution. The obvious, though not  
82 necessarily best, solution to Garrett Hardin's paradigmatic example of cattle

83 overgrazing a pasture owned in common is privatization of the pasture (Hardin  
84 1968).

85

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

96

## 97 **TERRITORIES**

98

99 Territoriality, which is widespread in animals (Maher & Lott 2000)(Burt  
100 1943; Klopfer 1969), is perhaps the best-recognized form of privatization, so we use  
101 it to introduce many points that may be more general.. It is an ancient concept.  
102 Around 300 BC, Aristotle realized that eagles need a large area for food and so  
103 exclude others (Lack 1944). In a review of the topic in birds, Nice traces  
104 territoriality to Olina's 1622 book, Uccelliera, that explicitly mentions male territory

105 invasion by nightingales (Nice 1941). It is no surprise that these earliest references  
106 are to birds since they are particularly active in their territorial defenses.

107

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

122

123         The early references and later discussions of territoriality make several  
124 important points (Klopfer 1969) that are relevant to privatization in general. First,  
125 the resource has to be sufficiently valuable to warrant the effort needed for  
126 privatization. Defense is frequently required because a resource that is valuable to  
127 its owner is likely to also be valuable to others. Defense can be viewed as what

128 distinguishes a territory from a home range. The requirement of defense is also  
129 what limits territory size. Territories can be only as large as is feasible for defense  
130 (Brown 1964). Either an exceptionally poor or rich territory may not be worth  
131 defending, the former for inadequate resources, the latter for too many invaders. A  
132 classic example is the golden-winged sunbird which only defends territories of  
133 flowers yielding sufficient nectar reward (Gill & Wolf 1975).

134

135 Ownership of territories can sometimes lead to investment in the protected  
136 resources. Beavers are perhaps the most famous example for their investments in  
137 dams and the water bodies they create (Bradt 1938). These dams change the  
138 landscape in ways that can even be viewed as geologic (Ruedemann & Schoonmaker  
139 1938), but it is unlikely beavers would evolve to build them if they could not keep  
140 the resource private. When territoriality privatizes partners, investments in those  
141 partners may be profitable. For example, at least two species of territorial  
142 damselfish weed their algal gardens and defend them against other damselfish and  
143 against sea urchins (Eakin 1987; Hata & Kato 2006). Social insects build elaborate  
144 nests to defend brood and stored resources (Hansell 1984).

145

## 146 **WHAT IS PROPERTY?**

147

148 We began with an analogy between preserving, protecting, controlling, and  
149 investing in bodies and doing likewise for entities outside of the body. Indeed, one's  
150 body is often regarded as property, the most fundamental property there is. There



151 are many adaptations that keep an organism entire and out of the digestive tracts of  
152 others, for example camouflage, hiding, distastefulness, weapons, shells,swiftness  
153 and selfish herds (Hamilton 1971). However, here we focus on privatization of  
154 resources other than self and kin. Our point here is not to nitpick what should and  
155 should not be considered property. Instead, the narrower focus serves to limit the  
156 scope of the review and to concentrate on the more novel aspects. Preserving,  
157 protecting and investing in survival and reproduction is expected, common, and  
158 well understood. What we want to understand is when and why this sensitivity to  
159 the future that applies to ordinary phenotypes also applies outside the body, to  
160 extended phenotypes (Dawkins 1982).

161

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

168

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

174 exchanges of property, and issues of privatization and owner control of the resource  
175 are often just as important here.

176

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

188

## 189 **HOW TO PRIVATIZE**

190

191         By privatization, we mean steps taken in the direction of gaining or  
192 protecting property. In humans, privatization often means moving resources from  
193 government control to private control, but in non-humans that lack governments it  
194 usually means taking resources out of public use. There are at several major  
195 methods of privatization. Physical force, or the threat of it, is perhaps the primary  
196 method of privatization. It is applicable not only to territories, but to more restricted

197 types of resources. Resources may be gathered from and moved into a defensible  
198 cache, as is the case with many rodents that store seeds in their burrows for winter,  
199 or burying beetles that move a carcass and defend it. Alternatively, individual items  
200 of property may be defended in place, such as a nest or a particularly rich food site.  
201 When other living organisms are the resource they themselves may be defended. A  
202 male may defend a harem of females from other males. Ants may defend a group of  
203 aphids and their rich honeydew.

204

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

213

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

220

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

232

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

242

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

258

259 A final solution to the dilemma of leaving property unprotected is to carry  
260 your property with you. Temporary carrying is common. A cheetah drags its kill up  
261 a tree, ants bring seeds back to the nest, birds ferry nuts to their caching locations.  
262 Others carry property with them during dispersal events, such as *Atta* ant queens  
263 carrying their mutualistic fungus to a new colony or *Dictyostelium* amoebas carrying  
264 bacterial prey to a new location (Brock et al. 2011; Mueller et al. 2005). But in these  
265 examples carrying serves only a brief subsidiary goal of putting the property in a

266 safer place or in a new place, rather than a direct privatizing function. Carrying  
267 property for longer periods is usually limited to property that is small and valuable.

268

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

276

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

282

283 In many symbioses one partner privatizes the other internally, with special  
284 cells like the bacteriocyte cells that aphids and many sap drinking insects have for  
285 their bacterial symbionts that process sugar rich plant sap into amino acids the host  
286 cannot produce (Moran & Telang 1998) Many other symbioses take this form  
287 (Douglas 1994). This form of carrying sometimes leads to vertical transmission,

288 which by tying together the reproductive fates of the partners, is particularly  
289 favorable to enhancing the evolution of intimate cooperation.

290

## 291 **THE ECONOMICS OF PRIVATIZATION**

292

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

305

306 A further advantage in some types of privatization is that the property can be  
307 enhanced. We have already mentioned beaver dams and weeding of algal gardens  
308 by damselfish. Such investment seems particularly likely to yield returns when the  
309 property is living, and can grow or propagate. Undesirable growths could be weeded  
310 out as in the damselfish (Eakin 1987). Fungus gardens can be fertilized by their ant

311 hosts(Martin 1970). Acacia are defended against large predators like elephants by  
312 ants(Goheen & Palmer 2010).

313

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

321

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

330

331 As a consequence, both durability and defensibility of the property are  
332 important because these, along with owner survival, determine whether the  
333 property will provide future benefits. A privatized resource has to be long-lasting



334 enough to be retain value, either because it is durable like a seed or a tree hollow, or  
335 because it is a source of continuing resource production, like a territory, or the  
336 zooxanthellae in coral, or the thorns and Beltian bodies of an ant acacia. Fruit and  
337 meat are difficult to store for later; seeds are much more easier to store because  
338 they have their own protections against microbes. Even if it is durable, a resource  
339 can lose value over time if it is insufficiently defensible, such that some one else  
340 ultimately reaps the gains.

341

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

354

355 **DETECTION AND RECOGNITION OF OWNERSHIP**

356

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

369

370           Animals sometimes act as if they recognize right of ownership; they will  
371 more readily fight as an owner than as an intruder. This is half explained by  
372 Maynard Smith's game theoretic analysis of the hawk, dove, and bourgeois  
373 strategies. When costs of fighting are sufficiently high, selection can favor a  
374 bourgeois strategy that fights when it is an owner and retreats when it is not  
375 (Maynard Smith & Parker 1976). It is only half an explanation because selection can  
376 equally favor the opposite strategy of fighting only as an intruder, which does not  
377 appear to be common in nature (Maynard Smith & Parker 1976). This has been  
378 explained, not fully satisfactorily, by assuming asymmetries in the payoffs such that  
379 incumbents have an some advantage in contests (Parker 1974). Another kind of

380 solution appears from incorporating eco-evolutionary feedbacks between selection  
381 on the trait and the payoffs (Kokko, López - Sepulcre & Morrell 2006; Gintis 2007).  
382 For example as fighting increases in the intruder class, more will die, making the  
383 wait for a territory shorter and diminishing the potential gains from fighting. In  
384 contrast, as the size of the population lacking territories decreases, fighting by  
385 owners becomes more profitable (Kokko et al. 2006). More work is needed on  
386 property recognition of property in animals.

387

### 388 **SOCIALITY AND PRIVATIZATION: FRATERNAL ALLIANCES**

389

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

401

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

407

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

416

417           Here we are talking about privatization at the level of the colony, not the  
418 individual. Social insects have little or nothing that would be described as individual  
419 property. Of course, for social insects to benefit from group level privatization, they  
420 have to be collectivized at lower level through kin selection. Cooperation at the level  
421 of the colony is possible because benefits go to relatives, so genes for acquiring,  
422 protecting, and investing in colony property can proliferate (Hamilton 1964).  
423 Another way to think about it is that the colony goods are more analogous to the  
424 club goods of economists than true private goods. Club goods are excludable, like

425 private goods, but are non-rivalrous. In human economics non-rivalry means that  
426 consumption by one individual does not preclude consumption by another, as in  
427 cable television or a public park. Here, instead, the lack of rivalry and ability to share  
428 comes from a community of interests among the members of the club. Although one  
429 member of the colony may use the resource, reducing the pool available to others,  
430 that outcome can be perfectly acceptable to other colony members. Given this  
431 difference, it should be interesting to see how much of the economic theory of club  
432 goods is transferrable to non-human clubs.

433

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

439

440         Many solitary bees and wasps dig tunnels in the soil, provision them with  
441 pollen (bees) or insects (wasps), lay one or more eggs and then close the nest. This  
442 is a very risky process because others can steal the burrow, lay their own eggs in it,  
443 or remove prey. Even in the tiniest groups of two, cooperation can be hugely  
444 beneficial because one could guard while the other foraged. This would drastically  
445 reduce loss because the burrow would then never be undefended. Every report that  
446 we were able to find of these smallest groups indicated that one foraged while the  
447 other guarded the nest. For example, in 1969, Charles Michener reports that “In

448 halictines, burrows of solitary individuals are generally unguarded while burrows of  
449 the same species inhabited by two or more females are guarded much of the time..."  
450 p. 320 (Michener 1969).

451

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

458

459 Property in the form of a private nest is an important preadaptation for  
460 eusociality (Alexander 1974). At a minimum it constitutes a place where young can  
461 grow up and encounter their mother, providing the opportunity to help. In some  
462 social insects, the so-called fortress defenders (e.g. aphids, thrips, beetles, and  
463 termites), the nest played an additional important role as a private resource. Their  
464 ancestors lived, ate, and raised their young in enclosed spaces such as galls that  
465 provided the opportunity for some of the young to avoid the risks of dispersal and  
466 instead stay and use the resource of the natal structure. Indeed, the first castes in  
467 fortress defenders are typically soldiers that specialize to defend the property (and  
468 the young). The other major class of social insects, life insurers (ants, bees, and  
469 wasps), also have nests that they defend but the nests do not usually enclose a  
470 private food resource. But the privatization of the nest is still important in other

471 ways. The life-insurance advantage is the shadow-of-the-future advantage noted  
472 above. Investments in the nest (and the brood) can pay even if the investor dies. In  
473 addition, if the nest were not private – if it were a common resource used by many  
474 mothers – then relatedness in the incipient colony would be lower than the high  
475 levels that are necessary for the evolution of eusociality. Indeed there are bees and  
476 wasps that share nests communally, but these semisocial societies have not led to  
477 eusocial ones.

478

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

491

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

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

499

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

511

512         Another example of social privatization is demonstrated by many species of  
513 bacteria that produce bacteriocins (Riley & Gordon 1999; Riley & Wertz 2002).  
514 Recent authors have interpreted bacteriocins in the framework of social evolution  
515 (West et al. 2006; Kerr et al. 2002). Bacteriocins kill others that are not genetically  
516 identical to the actor, but are of the same species. In some cases, the cell that



517 releases the bacteriocins dies, so we could consider it to be a different caste from its  
518 clonemates. The clonemates are resistant to the toxin because they carry an antidote.  
519 Sensitive clones are killed. Thus, this is a way of privatizing the resources in the area  
520 for the killing clone (Inglis et al. 2009).

521

## 522 **EXCHANGES AND MARKETS: EGALITARIAN ALLIANCES**

523

524 In addition to societies based on kinship, sometimes called fraternal alliances,  
525 there are societies based on mutualistic exchange called egalitarian alliances often  
526 between members of different species (Queller 1997). The processes of exchange of  
527 property and services have some resemblances to markets (Noë & Hammerstein  
528 1995). A notable example of cooperation among non-relatives within species is  
529 mating, where genes and resources may be traded. When partners limit fitness,  
530 there is often an attempt to privatize them, for example through territories or mate  
531 guarding. Typically it is males attempting to privatize females, though it goes the  
532 other way in role-reversed species like jacanas (Owens 2002). In species where both  
533 parents provide resources to offspring, each may limit the others success, and both  
534 sexes may benefit from privatizing their partners (Emlen & Oring 1977;  
535 Wittenberger & Tilson 1980).

536

537 Egalitarian cooperation is more common between species, because partners  
538 are very different and each can trade for goods that it cannot produce itself. These  
539 interactions are called mutualisms. Because both parties benefit directly, mutualism

540 allows cooperation to evolve among non-kin (Sachs et al. 2004; Bronstein 1994).  
541 Examples of mutualisms include insect pollination of plants, fungus-alga  
542 collaboration in lichens, squid-bacteria light collaboration, plant-mycorrhiza carbon  
543 for nitrogen collaboration, aphid-bacteria carbon for nutrient collaboration, cleaner  
544 fish host collaboration, and many others. It is safe to say that no organism lacks  
545 obligate mutualists (Douglas 1994) and that all of these relationships must be at  
546 least partly private to be stable and this sometimes involves active privatization  
547 (Bronstein 2001).

548

549         As in mating systems, many mutualisms can viewed as markets in which  
550 partners are chosen for the exchange of property or services (Noë & Hammerstein  
551 1995). There are thus two levels of property involved in a mutualistic exchange. An  
552 interactant must first attempt control and privatize the disposition of its own  
553 resource, to donate its resources to a suitable partner – partner choice. In addition,  
554 it may need to take steps to privatize the partner, to ensure private use of the  
555 resources returned – partner fidelity feedback. Not all partner choice and partner  
556 fidelity feedback involves explicit privatization; for example, faithful feedback can  
557 sometimes occur simply because of simple proximity in immobile partners.

558

559         Exactly how mutualists ensure that the benefit goes to the correct partner  
560 depends on the kind of mutualism it is. Resource exchanges can be privatized for  
561 one partner when it houses the other, either temporarily or permanently. If one  
562 partner is inside the other, whatever benefit is provided generally goes

563 automatically to the host. *Vibrio* bacteria privatized by a squid produce light only for  
564 that squid, which the squid cannot do. Photosynthates provided by algae in a lichen  
565 go to the associated lichenizing fungus. Zooxanthellae do the same for their coral  
566 hosts. *Buchnera* bacteria are internally privatized by an aphid and produce vitamins  
567 and amino acids that the aphid cannot produce. The symbionts may be less able to  
568 privatize their hosts and instead rely on it being in the host's interest to provide for  
569 them, so they can return the favor.

570

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

580

## 581 **THE MAJOR TRANSITIONS AND PRIVATE CLUBS**

582

583 Maynard Smith and Szathmáry (Szathmáry & Maynard Smith 1995)  
584 emphasized that many of their major transitions in evolution required evolving new  
585 levels of cooperation. Our discussion in the last two sections suggests that

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

604

605         We began by noting how organisms preserve, protect, control, and invest in  
606 their own bodies. We then asked what kinds of extended phenotypes outside the  
607 body were subject to similar processes of privatization. We have now come back full  
608 circle, showing that the creation of bodies as we know them today required the

609 privatization of relationships at several levels. The collectivization seen in the major  
610 transitions depends critically on the new collectives being private clubs with limited  
611 membership.

612

613

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620

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792  
793

	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

794  
795 Table 1. Definitions and examples of property and privatization.  
796