
The property 'instinct'

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Evolutionary theory and empirical studies suggest that many animals, including humans, have a genetic predisposition to acquire and retain property. This is hardly surprising because survival is closely bound up with the acquisition of things: food, shelter, tools and territory. But the root of these general urges may also run to quite specific and detailed rules about property acquisition, retention and disposition. The great variation in property-related behaviours across species may mask some important commonalities grounded in adaptive utility. Experiments and observations in the field and laboratory suggest that the legal rules of temporal priority and possession are grounded in what were evolutionarily stable strategies in the ancestral environment. Moreover, the preferences that humans exhibit in disposing of their property on their deaths, both by dispositions made in wills and by the laws of intestacy, tend to advance reproductive success as a result of inclusive fitness pay-offs.

Keywords: extended phenotype; possession; intestate succession; endowment effect; inclusive fitness; paternity uncertainty

1. INTRODUCTION

People untrained in the law often think of 'property' as a relationship between a thing and a person. It is common for law professors to attempt to correct this lay notion by describing property as a relationship between people with respect to a thing. In denying the importance of the relationship between the person and his things, however, this professional view obscures the possibility that the institution of property rests in part on deep-seated connections to and attitudes toward things.

In the law, 'property' means rights in things. A woman has property when other persons share a respect for her relationship to some thing and are willing to enforce her rights. Embedded in the idea of property is the presumption that there are identifiable patterns in the resolutions of disputes over resources. In other words, there are criteria that determine how competing claims to assets will be resolved. It is possible that these factors, the determinants of property, are solely the product of laws and other conventions constructed by formal human organizations. Property, in such a view, rises and falls with human institutions. Bentham wrote (1914, pp. 145–147) 'there is no such thing as natural property: it is entirely the creature of the law. . . . Property and law were born together, and would die together. Before the laws property did not exist; take away the laws, and property will be no more'.

This article proposes an alternative possibility: basic components of property preceded formal institutions; fundamental principles of property are encoded in the human brain. There are obvious reasons to believe that a system for allocating rights in things could, at least in part, be hard-wired into animal brains. A scarcity of resources creates competition for them, and some forms of competition

result in harm to the competitors. Rivals can reduce the costs of competition by adopting strategies for determining the outcome of fights without physical damage. For example, many of nature's agonistic encounters between conspecifics are won by the larger contestant (Moretz 2003). If the larger rival is certain to win, competitors can save themselves the costs of battle by allowing the size asymmetry to settle the dispute before they actually engage in battle. Such strategies can be evolutionarily stable (Maynard Smith 1972; Maynard Smith & Parker 1976; Gibbard 1982). When an ESS is adopted by most members of a population, it cannot be invaded by the spread of any rare alternative strategy (Krebs & Davies 1997). Thus, a body is more likely to survive if its brain is equipped with rules of property incorporating ESSs for reducing the costs of allocating resources among competitors. Property is part of human biology.

This claim that legal rules are partly hard-wired might evoke the counter-argument that the sheer heterogeneity of those rules belies any significant genetic component. But that argument ignores the complex and continuous feedback loop between nature and nurture. ESSs can and do fine tune themselves in many different ways over time and across populations. They can also take on cultural superstructures, extending the human phenotype (Dawkins 1982) beyond our bodies. Just as humans share a universal grammar (Pinker 1994) despite wide differences in languages, humans may share a core property 'instinct' despite differences in property law. We may have an adaptation, an evolved mental mechanism, for dealing with several of the issues that arise repeatedly with regard to resources. Like our languages, our various legal systems may be extensions of our human phenotype. Our laws, including our property laws, are part of the niches we have constructed for ourselves.

One contribution of 16 to a Theme Issue 'Law and the brain'.

Our property instinct or mental adaptation might be nothing more than a natural inclination to learn the rules that other humans use to resolve the coordination problem inherent in resource disputes, much as we learn new words as toddlers to resolve the coordination problem inherent in communication. But it is also possible that the property instinct is more. An ability to recognize and, in appropriate contexts, adhere to specific conventions may be part of our behavioural repertoire.

For example, we may have an innate sense of alienability, a natural feeling that one person may transfer things to another. If such a tendency is heritable and adaptive, it is not difficult to imagine a more efficient and more adaptive version: in addition to transferring the thing itself, it should be possible to transfer the rights to the thing. For such alienation to be proper according to our adaptation, the transfer must be voluntary. Here, the property instinct connects with an instinct for equity in reciprocal exchanges (Brosnan & de Waal 2003) and thus can be seen as one part of a sense of fairness or justice.

Another component of our property instinct is an inclination for what to do with property. Instincts may tell us not only how to transfer property, but also to whom. These donative tendencies and the laws of inheritance that reflect them are discussed below.

A property instinct could combine a general inclination to acquire rules with some specific pre-wired options. For learning language, the human brain may be programmed to gather grammatical usage examples from the childhood environment (verbs preceding or following their objects and adjectives preceding or following their complements, etc.) and generalize from those examples to a conclusion that the language is 'head-first' or 'head-last' (Pinker 1994). Similarly, for learning property, the human brain might be endowed with an inclination to gather examples of resource allocation, and generalize from those examples to one of a range of available property rules. For example, humans might be programmed with three rules for initially allocating rights in a thing: to the first person to touch the thing, or to the older contestant, or to the dominant member of the group, all of which have the potential to seem 'natural'. Which of these three rules to apply would be determined by the culture in which the human grows up.

Whether evolutionary pressures acted precisely to create specific property rules or whether they created a probability distribution between sets of rules is not the focus here. It seems clear that there are certain rules of property that are recognized across a number of different species and have demonstrable adaptive value. These rules reflect what we could call a 'deep property structure' akin to the deep language structure. Recognizing this deep property structure may aid in understanding the rules of property and applying them to new situations.

2. FIRST IN TIME, FIRST IN RIGHT

Being first in time to capture or create a thing often creates some right to that thing. Historically, first discovery gave nations rights in foreign lands. The common law of property in England and the US has, as one of its cornerstones, the notion that the first person to possess a thing owns it. Could first-in-time be an ESS?

A first-in-time convention differs in an obvious way from the larger-wins convention mentioned above. The latter can be called a 'correlated' strategy because its winner is correlated to the winner in an actual physical fight (Maynard Smith & Parker 1976). Being first to possess, however, does not correlate as positively with winning the fight over a resource. Indeed, being first can be a disadvantage. A cheetah exhausted from the chase and with its kill in its mouth fights from a weaker position than a late-coming competitor that did not participate in the hunt.

First-in-time has both correlated and uncorrelated aspects: the first in time might be the fastest or smartest or otherwise possess a correlative adaptive advantage. But it is uncorrelated in that the first in time might also just be lucky. However, even if luck matters more, uncorrelated strategies can be evolutionarily stable (Maynard Smith & Parker 1976). Avoiding a physical fight by deference to the first in time is just as effective in preserving genes as avoiding a fight by deference to the larger body. An uncorrelated strategy can be evolutionarily stable even when there is a correlated strategy also available (Hammerstein 1981). Whether correlated or not, a first-in-time-wins convention built into competitors could reduce their losses from fighting over resources.

Therefore, it is theoretically possible for animals to be genetically programmed to be assertive in defending a resource they discover first and deferential when they come late (Maynard Smith & Parker 1976; Sugden 1986; Yee 2003). There is also empirical evidence that nature embedded a rule of temporal priority in our brains before culture codified it in our laws. First in time is the natural rule of sunspot ownership for speckled wood butterflies (Davies 1978; Epstein 1980), and it may be for swallowtail butterflies as well (Maynard Smith & Parker 1976). Unless we are to believe that butterflies communicate this strategy as a matter of culture, members of a species may share a genetic predisposition to be aggressive when first in time and to give up easily when the opposing conspecific was first.

It is important to stress that a first-in-time property convention, if there is one innate to humans, need not be a rigid routine that we follow in all contexts. Rather, like nearly all of our preferences, it takes the form of an inclination that sometimes predominates and at other times does not. Perhaps it plays a role only when the outcome of a fight does not matter very much (Grafen 1987). Nevertheless, just as our genes give us a taste for eating sweets and fats, our genes may incline us towards fighting harder or less hard for an item depending on whether we were first.

3. A NATURAL MEANING OF POSSESSION

We may share with butterflies an evolved strategy that favours those who are first. But first at what? The legal answer is often 'possession'. In the words of Justice Holmes, 'possession is the beginning of ownership' (*Missouri v. Holland* 1920 252 US 416–435, p. 434). Possession is the root of title (Epstein 1979; Megarry & Wade 1984; Rose 1985). But that does not really answer the question. If possession is the key, what does it take to establish possession? Property law breaks possession into two elements: physical control and intent to assert control.

The intent element seems natural in that it is closely related to, if not the same thing as, willingness to fight,

which in turn relates to the outcome of a physical contest over the resource. Willingness to fight may overcome inferior fighting ability. Smaller crickets defeated larger ones 30% of the time, possibly because they were more willing to fight (Hofmann & Schildberger 2001). If it matters to nature, it should not surprise us that intention matters to the law.

The other legal element of possession concerns the physical connection between the thing and its possessor. In a pair of nineteenth-century cases, *Young v. Hichens* (1844 12 Q. B. 518–520) and *Pierson v. Post* (1805 3 Caines 175–182, 2 Am. Dec. 264 (N.Y. 1886)), English and American courts confronted this question of defining the physical connection required to establish possession or occupancy. The judges hearing the cases decided that title in a wild animal belonged not to the person that first had a reasonable prospect of taking control but rather to the person that first had actual control. In *Young versus Hichens*, the plaintiff had nearly encircled some fish with a net when the defendant intruded. In his suit against the interloper, the plaintiff's claim rested on an assertion of possession. But the court was unwilling to find the requisite possession. Lord Denman stated (*Young v. Hichens*, p. 611), 'whatever the interpretation may be put upon such terms as "custody" and "possession", the question will be whether any custody or possession has been obtained here. I think it is impossible to say that it had, until the party had actual power over the fish'.

Although property teachers often treat this important legal line as arbitrary, evolutionary theory suggests deeper roots. A strategy can work for the benefit of both parties only when both parties respond to the same environmental trigger. Both need to know when to be assertive, when to be deferential. Humans with a miscalibrated cognitive module for recognizing possession by others would have found themselves trying to obtain what was fiercely defended, whereas those who did not recognize their own possession would have failed to keep track of things that could have been easily secured. The result is that most of us descended from beings who could correctly determine who was first according to the convention.

Evolutionary theory not only suggests that humans have a common sense of possession, it suggests two points about the content of that shared sense. First, the strategy must provide a single winner in a good number of situations; it can work only if it is based on some asymmetry. But different criteria harbour differing degrees of asymmetry. When the criterion serving as the basis for the convention has too little asymmetry, fights will occur. If fights occur often, the contestants employing that strategy will not survive as often as those employing an alternative, less symmetrical and thus more determinate strategy. The forces of selection probably defined our sense of possession to be highly asymmetrical, such that it would be exclusive in many cases.

Second, the criterion that determines possession must be observable (Maynard Smith & Parker 1976). Duels between resident damselflies are usually won by the fatter contestant but cannot be settled quickly on that basis because their reserves of fat are stored inside their skeletons, out of view (Marden & Rollins 1994; Mesterton-Gibbons & Adams 1998). Crickets whose antennae have been shortened fight longer perhaps because they are less able to determine their opponent's willingness to fight

(Hofmann & Schildberger 2001). For possession to work well as the hinge on which behaviour can pivot, possession has to depend on facts that can be perceived readily and reliably by the parties. Although it would help if both parties could observe whether the other is in possession, that is not strictly required. If the criterion is exclusive, it is enough that each party can tell whether he has satisfied the criterion. Conversely, the strategy of first-possession will have a hard time surviving as a strategy if a party cannot tell whether he himself has satisfied the criterion.

The results in *Young v. Hichens* and *Pierson v. Post* are completely understandable on both these points. A first-in-time strategy based on an actual grabbing of the object satisfies the requirement of high asymmetry. It will be unusual for two claimants to have hold of an object at the same time. By contrast, it would be much more common for competitors to have a 'reasonable expectation' (*Young v. Hichens*) or a 'reasonable prospect' (*Pierson v. Post*) of securing the thing at the same time and thus be in simultaneous possession. Actual grabbing is also, of course, considerably more observable than the fleeting notion of a reasonable prospect of capture, the alternative rejected by the courts.

There is evidence supporting this claim that law's physical-control rule is of biological origin. Touching may be a key ingredient in animal possession. The male speckled wood butterflies in Davies's experiments fought 10 times as long when both had touched down on vegetation as when only one had done so. Being in close proximity or having a reasonable prospect of actual contact was apparently not enough for the butterfly to form the attachment needed to fight a protracted battle. It might not be a mere coincidence that physical touching is important to the law.

Not only is touching important to possession, but animals have a means of recognizing touching by themselves, obviously, and by others. A certain group of neurons fire when a monkey grasps a piece of food in a certain way (Rizzolatti *et al.* 1996). Moreover, when a monkey sees either another monkey or the human experimenter grasping the food, 'mirror neurons' fire in the subject monkey. Although there are 'mirror neurons' for many actions, the fact that there are neurons activated by grasping and by observing the act of grasping suggests that there are neurons associated with recognizing possession by ourselves and others.

Thus, we may be programmed to recognize when we have a certain proximate relationship to a physical object and, by mirroring, to recognize when others have a similar relationship to an object. Our brains may then determine 'ownership' by combining that relational data with information about previous relationships, such as information about who was first in time and what voluntary transfers have occurred. Certain combinations of information—'it is in my grasp' plus 'there is no previous owner'—may throw switches in our brains making us more willing to be assertive in excluding others from the thing. Such a neurological structure could provide part of the basis for a very natural law of property.

Maynard Smith (1982) referred to this strategy—defend aggressively when one is an owner and defer to the opponent when one is an intruder—as the 'bourgeois' strategy. Owners usually defeat intruders in a number of species, from baboons (Kummer *et al.* 1974) to damselflies (Waage 1988), and similar behaviour has been observed in

desert ants that mark their territories with pheromones and assert ownership when in territories marked by their colonies (Wenseleers *et al.* 2002), and in both sexes of Ozark zigzag salamanders (Mathis *et al.* 2000). In two species of colonial spider the larger conspecific wins, but if the contestants are of similar size, the resident usually defeats the intruder (Hodge & Uetz 1995).

This is not to say that all animals must follow the bourgeois strategy. One species of Mexican spider, for example, seems to follow an anti-bourgeois strategy, with the owners fleeing upon the arrival of intruders (Burgess 1976). Whether a population will evolve to bourgeois or anti-bourgeois may depend on resource-holding potential (Mesterton-Gibbons & Adams 1998). Indeed, no strategy will be an ESS in situations where it would make permanent reproductive losers of one group (Grafen 1987).

Landowners seem to follow the bourgeois strategy when they defend their lands with their lives rather than surrender them to invaders. Pape (2003) found that suicide attacks are carried out most often by persons who are trying to displace occupying invaders. 'In general, suicide terrorist campaigns seek to achieve specific territorial goals, most often the withdrawal of the target state's military forces from what the terrorists see as national homeland' (Pape 2003, p. 344).

Given the frequency of territorial behaviour in humans and other animals, it is reasonable to assume that there is some meaning of possession that is naturally shared among conspecifics. Even in the absence of law—*especially* in the absence of law—there are beneficial network externalities that arise from a common sense of ownership. When the nexus between a person and a thing becomes strong enough, he feels like the owner and others recognize him as the owner. The bourgeois strategy might have purely uncorrelated origins, or it might be based in part on an asymmetry in values. But whatever the origin, if a bourgeois strategy is part of our evolved psychological makeup, the necessary shared sense of when to be assertive and when to be deferential constitutes an innate sense of possession, and that common sense could be embodied in the common law's definition of possession. Because possession is, in turn, a block in the foundation of our law of property (Epstein 1979; Megarry & Wade 1984; Holmes, *Missouri v. Holland* 1920 252 US 416–435, p. 434), much of our property law could be built upon distinctions embedded in the structure of our brains.

4. LEGAL RECOGNITION OF THE WAXING AND WANING OF ATTACHMENTS

The rules that anchor the initial allocation of title in possession become easier to understand when we recognize that forming attachments may solve evolutionary problems. Clearly the ownership convention is more complicated for humans than for butterflies. Ownership, once established, can be transferred and does not evaporate as quickly. Humans keep track of earlier occupancies. However, even in societies recognizing potentially perpetual rights, ownership does not always last forever. Ownership in captured wild animals ends when they regain their natural liberty (*In re Oriental Republic Uruguay* 1993 821 F. Supp. 950–956 (D. Del.); *Mullett v. Bradley* 1898 53 N.Y.S. 781–783 (App. Div.)). 'In all these creatures,

reclaimed from the wildness of their nature, the property is not absolute, but defeasible: a property, that may be destroyed if they resume their antient wildness and are found at large' (Blackstone 1766, p. 393). Rights in personal property, in the US at least, end upon abandonment (*Eads v. Brazelton* 1861 22 Ark. 499, 79 Am. Dec. 88–102; *Erickson v. Sinykin* 1947 223 Minn. 232, 26 N.W. 2d 172–178; Blackstone 1766, p. 9; Pollock & Wright 1888) and easements may terminate by abandonment (*Crossley and Sons Ltd. v. Lightowler* 1867 2 Ch. App. 478–486; *R. v. Chorley* 1848 12 Q. B. 518–520; *Iowa State Highway Commission v. Dubuque Sand & Gravel Co.* 1977 258 N.W. 2d 153–154 (Iowa); *Megarry & Wade* 1984).

One of the most common involuntary terminations of rights occurs by virtue of the doctrine of adverse possession. This doctrine wrests legal title from the person that is the current title holder according to the records and reallocates that title to the current possessor, without the consent of the record title holder. The law of adverse possession raises a profoundly difficult issue: how can the law divest a rightful owner of his property and transfer it to a mere squatter? The normative nature of the issue explains the prominence of adverse possession in the law-school curriculum. Over the years, legal scholars have constructed many rationales for the doctrine, none of which is very compelling today, however appropriate they might once have been (Stake 2001). Can evolutionary science provide any insight into the persistence of this odd exception to our ordinary rules of perpetual ownership? Yes.

(a) *Studies of birds*

Experiments performed with birds indicate that the attachment to territory and the trauma of losing possession of territory increases with the length of possession. Krebs (1982) removed pairs of resident great tits from their territories, kept them in captivity, and then released them after a replacement pair had settled in the vacated territories. The replacement birds that had been in possession for 3 h contested for ownership seven times longer than they did if they had just arrived, and they contested nearly twice again as long when they had been in possession for 10 h instead of 3 h. Beletsky & Orians (1989) found that replacement red-winged blackbirds that held territories for 6–7 days could usually defeat the original owners. Tobias (1997) removed European robins from their territories and then released them at varying periods after replacements had settled into those territories. The replacement robins defeated removed robins after the replacements had been in possession for 10 days in winter, and defeated removed robins for the bulk of the territory after only a single day in spring.

The authors of the experiments interpret their results as supporting the 'value-asymmetry hypothesis'. Over time, the value to the original bird declines, but declines slowly. The value to the replacement bird increases, and increases faster than the value to the original bird declines. Eventually, the value to the replacement exceeds the value to the original and the replacement will fight long and hard enough to fend off the original. If persistence and success in fighting for control of territory correlate with the pain of dispossession, that pain increases with the length of possession.

English law of territory ownership follows nature's lead. The adverse possession doctrine conforms to the principle reflected in the bird studies, that after the passage of time the value of the territory to the new claimant is greater than the value to the old claimant. To establish title by this passage of time, the squatter has to show that for the statutory period he had possession, that such possession was adverse to the owner, that it was continuous, that it was exclusive, and that the owner was out of possession (Megarry & Wade 1984; Smith 1996). The requirement of possession assures that the squatter had physical control and the intent to maintain it. If his possession was continuous, it was unbroken by his own abandonment or by the possession of others. Thus the doctrine asks whether the adverse possessor used the land as a true owner would, whether he showed the defensive, possessive attitudes one would expect of a true owner, and whether he formed the kind of attachment that leads to increased efforts in defence of territory. The requirements assure that the squatter did indeed form the strong ties that could be cut only with great pain. Conversely, the doctrinal inquiry also establishes that the record owner was not in possession and, therefore, does not feel like the typical owner of land and, hence, would not defend it to the same degree. As between the two claimants, the law allocates the loss to the non-possessor because the loss will hurt him less.

(b) *Studies of humans*

The doctrine of adverse possession also fits with what we are learning about the brain from experimental psychology and economics. People often demand more to give up some thing than they would be willing to pay for the exact same thing. Thaler (1980) called this pattern of underweighting of opportunity costs the 'endowment effect'. This anomaly is a manifestation of an asymmetry of value that Kahneman & Tversky (1984) dubbed 'loss aversion'. According to the theory of loss aversion, losses from one's endowment have more subjective impact than financially equivalent gains, and losses from endowment are more painful than losses of mere prospects (Kahneman *et al.* 1990, 1991; Korobkin 2003). This difference in impact is greater than would be expected from considering declining marginal utility alone.

In two experiments reported by Kahneman *et al.* (1990), the experimenters randomly divided subjects into three groups: buyers, choosers and sellers. The sellers were given coffee mugs, the choosers were given options to acquire coffee mugs and the buyers were given nothing. Sellers indicated the least they would take for their mugs, buyers indicated the most they would pay for mugs, and choosers indicated the price at which they would rather have cash than mugs. The experimenters found that subjects endowed with mugs placed a higher value on them than the choosers or the buyers. These experiments also support the conclusion that there is an endowment effect for cash, although the effect was smaller than for the corporeal coffee mugs (Stake 1995).

The studies of bird territoriality and human endowment effects lead to the conclusion that duration of actual possession and expectation of ownership make a difference to a person's attachment to a thing. The property doctrine of adverse possession conforms to this adaptation of the brain, implicitly recognizing that the claimant in recent, lengthy, exclusive possession has formed a greater

bond with the land and will fight harder for it. Property law resolves such disputes as they would be resolved in physical fights, without the need for combat.

5. GROUP PROTECTION OF INDIVIDUAL INTERESTS

The resemblance of non-human animal behaviours to human property institutions discussed so far should not be taken as sufficient to conclude that animals have what we call property. The human institution of property incorporates at least four elements. First, the owner must form some special relationship to the thing, such as being more willing to expend resources defending it. Second, conspecifics must in some way honour or respect the owner's relationship. Third, the owner must recognize that respect by others. Fourth, conspecifics as individuals or as members of the group must be willing to intervene on behalf of that owner, protecting the property from threats by challengers, whether they be conspecifics or others. On the third and fourth points, more research is needed.

Heinrich (1999) presents compelling evidence that ravens can gang together to protect their assets. He introduced a wild raven into a group of four ravens that had lived together nearly all of their lives. The four did not allow the wild raven to feed on the food pile in the aviary. With that access to food barred, the newcomer watched where the others cached emergency supplies from the food pile and tried to feed upon those caches. Although there was plenty of food to feed all five, the others killed the wild raven for her efforts to feed from their caches.

More noteworthy are three other raven stories that Heinrich (1999) presents anecdotally. At Cornell University, Kevin McGowan climbs trees to band ravens. Not only do ravens attack him when he comes into their territory, but neighbouring ravens join in the attack to defend the territory of the residents. In separate incidents, Lorenzo Russo and Chris Walsh each reported being attacked by resident pairs. When the attacks were unsuccessful, the pairs flew off, only to return shortly with three or five helpers, respectively, who joined in attacking the human interloper. This behaviour might be explained as instances of the helper ravens acting in anticipatory defence of their own territories, or the helpers may have been relatives acting in the interests of inclusive fitness. It could be the case, however, that the behaviour was not just nepotism or immediate self interest, but that it was an instance of reciprocal behaviour, neighbour ravens joining forces in group protection of a member's property. There is a lot more research to be done, but these stories hint that even the human institution of the group acting to protect the things of an individual may have ancient biological antecedents.

6. WHAT HUMANS DO WITH THEIR PROPERTY, AND THE LAWS OF INTESTACY

If humans have a property instinct, it ought to include not only respect for the possessions of others, protection of one's own possessions and helping in the defence of others', but also inclinations regarding what to do with those things that have been acquired. Obviously, people use assets to keep themselves alive, the evolutionary utility of which needs no discussion. It is worth noting, however, that the law recognizes this utility by allowing individuals great freedom in consuming assets as they please. Law

would undermine its own authority if it were to try to tell people how to use or not to use their things.

Very often, however, people do not consume their assets, but give them to others instead. If people have a property instinct, how do these gifts fit into that instinct? Evolutionary theory should allow us to predict donative behaviours as well as acquisitive and retentive behaviours. To whom do people give their property? In what ways does the law reflect those inclinations to make gifts? In other words, what is the phenotypical behaviour and in what way is the law an extension of that phenotype? Evolutionary analysis can parsimoniously explain several specific donative preferences and, in doing so, explain some of the basic contours in the laws that apply when someone dies without a will, the laws of intestate succession.

(a) *Benefactors' blood relatives*

Because a parent is just a gene's way of making another gene, selection should favour those genes that make good parents, parents who produce viable offspring and help those offspring to reproduce. There are a number of ways parents invest in their offspring (Trivers 1972). For example, female Belding's ground squirrels put themselves at risk by sounding alarms to warn other squirrels of predators. Sherman (1981) has found, however, that they are not indiscriminate in this risky warning behaviour. They make the alarm warnings more often when they have mothers, daughters or sisters nearby than when the surrounding squirrels are related less closely or not at all.

Another important means of increasing offspring survival and reproduction is the transfer of property, both tangible and intangible. Because property can be converted to food and shelter, parents, grandparents and more distant ancestors can enhance the chances that their offspring will survive by giving them property.

Actual giving conforms to the theory. Smith *et al.* (1987) found that 1000 randomly selected wills left 92.3% of the wealth to spouses and kin and only 7.7% to non-relatives. Gifts completed during the life of the donor follow a similar pattern. Anderson *et al.* (1999) studied parental investment by men. Their data indicate that children of the current mate of the donor were three times as likely to receive some money for college if they were the genetic children of the donor than if they were step-children of the donor. Children of a previous mate of the donor were four times as likely to receive some money for college if they were the genetic children of the donor than if they were step-children of the donor.

English and American laws of intestate succession follow this evolutionarily predictable pattern. The laws of descent and distribution allocate a large portion of a decedent's estate to surviving blood relatives. Indeed, if a decedent (deceased person) leaves no surviving spouse or relatives, the decedent's property escheats to the crown or state rather than going to in-laws, friends or other worthy recipients. We could explain the laws of intestacy on the theory that they were designed merely to mimic the testaments of persons who left wills. In this view, the law is simply being efficient. However, this efficiency explanation underestimates the degree to which it is important for laws of intestate succession to reflect what feels natural, or fair, or just, to those empowered to determine the rules. If the rules

favouring relatives do not seem fair at some basic level, they might not last long or garner much respect.

(i) *Genetic proximity*

The chances that a gene or allele is passed to a child are 50%, because half of each person's genes come from each parent. The chances that a gene will reach a grandchild are only one out of four, that odds diminishing by a factor of two with each succeeding generation. A selfish gene should be less interested in helping more distant family members. For this reason, we would expect decedents' gifts to be concentrated in closer relatives. This prediction is confirmed by both common experience and research by Smith *et al.* (1987), who found that decedents gave 46% of their wealth to relatives one-half related, 8% to relatives one-quarter related, and less than 1% to relatives one-eighth related. Evolution has selected in the human brain an inclination to give property to others, but that inclination is biased heavily towards persons who share a close genetic relationship.

Laws of intestate succession follow this preference by providing that closer relatives take before more distant relatives. Both the English statute (Megarry & Wade 1984) and section 2–103 of the Uniform Probate Code (Langbein & Waggoner 2003), which has been adopted in many of the United States, provide that siblings, cousins and more distant relatives of the decedent take nothing if children of the decedent survive. Thus, evolutionary theory explains the priority of closer relatives found in the laws of intestacy.

(ii) *Age of recipient*

Evolutionary theory also suggests that gifts to persons beyond reproductive years will generate no benefit for the donor's genes and, therefore, donors are less likely to give to elderly persons than to similarly related persons of child-bearing age. Adaptive giving would be expected to be biased towards donees who are most likely to have additional children. For example, a decedent is equally related to her children, siblings and parents, but in most cases she can do her genes more good by giving her property to her children rather than her parents because her children are more likely to reproduce. Moreover, a decedent's assets passed to parents or siblings are likely to end up in the hands of nephews and nieces, who are not as closely related to the decedent as her own children.

Once again, research by Smith *et al.* (1987) confirms the prediction of evolutionary theory with regard to the behaviour of testators (persons who died with wills). The decedents in the study gave 38% to their children compared with only 8% to their siblings and nothing to their parents. Of course, there are other explanations: older relatives might also tend to be less needy because they have had more time to accrue resources. Turning from testate to intestate succession, when the law distributes assets on behalf of a decedent who has not executed a will, it tracks the general preference for younger persons, allocating the estate to the living children or their issue, if there are any, rather than to the decedent's parents or siblings (Megarry & Wade 1984; Uniform Probate Code section 2–103 (Langbein & Waggoner 2003)).

The optimal evolutionary strategy gets more complicated when there are no children and the choice of

beneficiaries is between parents and siblings. When a childless person is old enough to have children, his parents are unlikely to produce many more children and it makes sense to send his assets to his siblings rather than his parents, the younger generation being generally more likely to convert resources into additional copies of the donor's genes. At about the same time that people gain the physical capacity to have children, they gain the legal capacity to execute a will, and as just noted those wills tend to allocate assets to fecund siblings over ageing parents.

However, when a person is too young to have children, it is likely that some of her siblings are also too young to have children and that her parents are still young enough to produce additional children. In such situations, it makes biological sense for her to send her assets to her parents, who may still be able to have children and in any case will be likely to spend some of the assets supporting their other children, the decedent's siblings. Indeed, if the siblings are minors, the parents will probably spend the assets more wisely and effectively on behalf of the siblings than the siblings would do themselves. Furthermore, the parents are better able to tell who in the family would benefit most from the assets and are likely to allocate the assets efficiently, allocating them to one child or spreading them around as needs be. Allocating the decedent's assets to all her siblings might spread the assets too thinly, for example. If the decedent does not have children, her genetic interests are the same as her parent's interests, and they might be better at furthering the family genes by focused giving than an automatic allocation of equal portions to all siblings.

Most Anglo-American laws of descent and distribution conform to this biological priority by giving to parents before turning to siblings of the decedent. If the parents are dead, however, the assets will pass to the siblings. Thus the law makes a rough cut, favouring children when there are some, and then going next to parents if there are no children, which makes sense when the decedents are too young to write a will.

(iii) *Paternity uncertainty and maternity certainty*

An efficient gene, one designed to make the most of its resources, would build a brain that avoids wasting resources on persons who are less likely to carry that gene. Half of all parents, the male half, cannot be completely confident that their children are indeed the product of their gametes. To the extent that a man is uncertain a child is his, we should expect him to be less inclined to allocate property to that child. Conversely, we should expect to see greater giving when certainty of parenthood is higher. Once again, the pattern of actual giving tracks the evolutionary theory. Buss (1999) reports that Anderson *et al.* (1999) found that children of the few men who expressed uncertainty in their paternity were much less likely than the children of confident fathers to receive money for college from those fathers.

Older versions of the Uniform Probate Code expressly recognized the uncertainty surrounding paternity and the preference of men for not giving to the children of other men. Before 1990, section 2-109 provided that 'a person born out of wedlock is . . . a child of the father, if . . . the paternity is established by an adjudication before the death of the father or is established thereafter by clear and convincing proof . . .' (Langbein & Waggoner 2003). The same

section also recognized that men were more likely than women to deny support to their children by its provision that mothers could inherit from their illegitimate children but fathers could do so only if they had not refused to support them. These provisions were changed to be sex-neutral in the 1990 reforms.

Despite hospital errors, human mothers, like other mammalian mothers, are nearly certain of their maternity. Given their greater confidence, evolutionary theory predicts that if all else is equal mothers will give more property to offspring than will fathers. Furthermore, evolutionary theory predicts that grandparents of either gender will give more to children of daughters than to children of sons. There are two links from a grandparent to a grandchild. Father-child links are less certain than mother-child links. Therefore, a brain built by rational, selfish genes would devote the most property to grandchildren connected by two maternal links, less to grandchildren connected by one maternal link and one paternal link, and the least to grandchildren connected by two paternal links.

This prediction was confirmed by DeKay (1995). The subjects reported getting the most in gifts from their maternal grandmother and the least from their paternal grandfather. This result is probably not a result of the general tendency of women to give more than men because, on average, the mother's father gave more property than the father's mother. Gaulin *et al.* (1997) similarly found a matrilineal bias in the investment by aunts and uncles. Both aunts and uncles showed more concern for their sisters' children than for their brothers' children. One way for genes to favour the children of sisters is to generate a stronger tie to sisters. Thus it is not surprising that Salmon & Daly (1996) found that both male and female college students were more likely to name a sister than a brother as the sibling to whom they felt closest. The warmth for sisters' offspring reflects back upon the sisters themselves.

Of course these findings reveal a lot about our attitudes towards other people. But they also reveal something about property. If the donative urge is millennia old, the sense of control over assets must stem from an even earlier date for it is hard to have a sense of how to allocate assets without first having a sense of what things are one's assets. It is a risky move for a parent to give his child property to which someone else feels attached.

(iv) *Wealth of the beneficiary*

In addition to age and genetic relatedness, there are other criteria that a well-adapted brain might use to determine how to allocate property within its control. Donor behaviour ought to depend on the behaviour expected of donees. Donees can use resources for a number of purposes: to survive, to attract mates and provide for offspring. In pre-modern societies, wealth is indeed associated with reproductive success (Borgerhoff Mulder 1998); the relationship is less clear in developing and developed societies (Judge & Hrdy 1992; Low 2000). However, although any donee can make use of additional resources, they are not all equally likely to convert parental gifts of property into offspring.

Evolutionary pressure could have shaped brains to send property where it will be most efficiently deployed. One factor that affects the ability of the donee to benefit from a

gift is the level of resources already available to that donee. That is, when instructing its body to shift resources to others, an efficient brain would take into account the resource level of the various potential donees.

(v) *Interaction of wealth and sex of recipient*

Another factor in the ability of the donees to make use of gifts in some situations might be their sex. Males and females do not have the same capacity for creating children (Low 2000). To take human examples, no woman on record has had even one-tenth as many children as Morocco's Emperor Moulay Ismail The Bloodthirsty, who claimed to have fathered more than 700 sons, and received credit for 888 children in The Guinness Book of World Records (Pinker 1997). As Pinker (1997, p. 478) puts it, '[u]nder polygyny, men vie for extraordinary Darwinian stakes—many wives versus none—and the competition is literally cutthroat'. By necessity, the high reproductive success of some males ties up the reproductive capacities of multiple females, leaving other males with no opportunities to reproduce. The result is that the variation in number of offspring is greater for males than for females. In their study of 1500 Californians who died leaving wills, Judge & Hrdy (1992) found a variance of 3.45 for women, as compared with 4.34 for men.

Any gender difference in the variance in reproduction creates the potential for a difference in the reproductive pay-off from resources. For example, Judge & Hrdy (1992) found that men whose estates were above the median value left more surviving children than did men whose estates were smaller. The same was not true, however, of women; those who left more wealth did not also leave more surviving children.

Trivers & Willard (1973) deduced that there could be an interactive effect between sex and resource level. The Trivers–Willard hypothesis says that the condition of animals will influence whether they invest more resources in male or female offspring. The pay-off to additional resources is nonlinear and differs by sex. Parents who cannot endow a son with enough resources to get him a mate should invest their resources in their female children if they are to maximize their reproductive success (Hartung 1982). Parents who can put sons in a position to have more than one mate should direct more resources towards sons, or in some circumstances even concentrate them in a single son. There is evidence supporting this conjecture in the behaviour of mice (Rivers & Crawford 1974), spider monkeys (McFarland Symington 1987) and red deer (Clutton-Brock *et al.* 1986). Evolution could have tailored the human brain to discriminate between sons and daughters in allocating the property within its control and to determine that allocation differently depending on a number of factors, including the available resources.

The Trivers–Willard hypothesis seems to dovetail with the ancient law of primogeniture (Boone 1986). Under primogeniture, a decedent's land passed to a single son, thereby maximizing that son's chances of becoming an alpha male and, hence, his reproductive opportunities. If the decedent had no son, his assets passed equally to his daughters, as might be adaptive according to Trivers and Willard.

One problem with this explanation of the law of descent is that it does not explain why modern lawmakers have forsaken primogeniture in favour of equal distribution among children. The older and newer rules might be reconciled by focusing on the fact that primogeniture fits the needs of wealthier decedents, whereas egalitarian, modern law fits the needs of poorer decedents. If through the ages the law has come to incorporate more of the values and sentiments of people of modest means, this might help explain why the law has shifted from the rules of primogeniture to the modern rules of more equal distribution. More likely, modern norms of equality have simply overridden the sentiments favouring a single male heir.

Studies of individually directed giving are mixed on this issue of whether humans behave as predicted by Trivers and Willard. In support of the hypothesis, Smith *et al.* (1987) found that while the proportion of estates given to females did not vary much according to wealth, the proportion given to males shifted from about half that of females for poor families to twice that of females for wealthy families. Other support for Trivers–Willard has been found in fifteenth and sixteenth century Portuguese families (Boone 1986), the Yomut of Turkmenistan (Irons 2000), and the Mukogodo of Kenya (Cronk 2000). However, while Judge & Hrdy (1992) did find that parents showed more favouritism among sons than among daughters, their study of California wills failed to find the other predicted interactive effect, that of greater giving to sons when there is greater wealth to give. Freese & Powell (1999) also failed to find the predicted interaction when they studied parental investment in adolescents. Borgerhoff Mulder (1998) found that survival rates in the Kipsigis of Kenya do not support Trivers–Willard, but parental investment in education does track the Trivers–Willard pattern, and increasingly so in recent years.

The Trivers–Willard hypothesis might lead to an explanation of recently heralded findings regarding likelihood of divorce (Morgan *et al.* 1988; Dahl & Moretti 2004). Dahl & Moretti examined 60 years of US Census Bureau data and found that families with one girl were 1–7% more likely to divorce than families with one boy, with the effect increasing with family size, but decreasing to zero over recent decades. Similarly, Morgan *et al.* (1988) had earlier found that sons reduce the risk of marital disruption by 9% more than daughters. There are a number of conceivable explanations for these findings, including the possibilities that men want sons and keep marrying until they get one or that men become more involved in the family when they have a son. However, Trivers–Willard offers an explanation that is not rooted in a preference for sons or traditional gender roles. Because divorce is costly, it decreases family assets. Investing effort to keep a marriage together increases family assets available to the children, and thus could be seen as an investment in the children. Couples, or at least one of the partners, make a greater investment when they have a male child than when they have females. This difference in investment makes biological sense if inherited wealth is more important to a son's reproductive success than to a daughter's, which Trivers–Willard argues would be the case when the parents are rich in resources. What remains to be determined is whether the divorce rate is a function of the interaction of wealth and sex of the child.

The Trivers–Willard theory might explain the divorce data in another, somewhat backwards and as yet incompletely explained, way. Because mothers can invest less in male offspring by bearing fewer of them, the theory suggests that mothers poor in resources might produce relatively more female offspring, whereas mothers rich in resources might produce more males. This prediction was borne out in an experimental field study in which female opossums given supplemental provisions produced more male offspring than did controls (Austad & Sunquist 1986), and it has been observed that female red deer (Clutton-Brock *et al.* 1986) and spider monkeys (McFarland Symington 1987) produce a higher ratio of males if they are high in rank. For human examples, consider that wives of American Presidents have borne 86 male and 58 female children (Betzig & Weber 1995), and white American mothers, who are statistically richer, have relatively more male children than black American mothers (National Center for Health Statistics 1999). Some women can anticipate divorce, certainly if they are contemplating initiating proceedings but maybe also if they sense such an inclination on the part of their husbands. Married women sensing an unmarried future are also sensing a lower level of support, and for that reason would be predicted by the Trivers–Willard theory to have more female children, although the physiological mechanism for this is unclear (McFarland Symington 1987). Also, such women, who have the sense that they might be unmarried at a later date, might indeed be more likely to be unmarried at a later date. Viewed after the divorce, it looks like the daughters helped cause the divorce, but instead the impending divorce helped cause the daughters.

Further research could examine the Trivers–Willard proposition in the context of both lifetime and testamentary human altruism. A study of lifetime giving might, for example, investigate whether wealthier parents in industrialized societies offer their male children disproportionately better opportunities for college educations. Inequality in such a domain would be less obvious to the donors and, hence, be less likely to be purposively overcome by persons ordinarily attentive to the social norm of equality. It also could be the case that the adaptation itself is sensitive to the perceived connection between reproductive success and wealth. In other words, if people do not see wealthier men having substantially higher numbers of children, they do not perceive a winner-take-all race and they might not feel any urge to give more to their sons. Another possibility is that modern egalitarian social norms have overcome a Trivers–Willard discriminatory adaptation, even if humans are born with one.

(b) *Attracting mates*

The instinct to care for one's children has no application until there are children to care for. An even more basic instinct, then, is to perform the steps needed to create offspring. One of those steps is attracting a mate, and being generous might advance that cause. A woman who sees a man being generous has some reason to believe that the man will be generous to her, helping her to survive. He might also be generous to his children (Buss 1999), helping them to survive, and helping them to attract mates (if they are generous in turn), all of which redounds to the genetic benefit of their mother. Thus, to a female brain evolved to

respond to the potential benefits of charity, the generous male looks like a better prospect than the skinflint. Because generosity attracts persons who expect to be beneficiaries, generosity towards mates and potential mates brings sexual opportunities. Therefore, such giving should be expected and is consistent with the theory that people are selfish reproducers. Anderson *et al.* (1999) offer some evidence that men use their charity to impress potential partners. They found that a child was nearly three times as likely to receive money for college from its father or stepfather if he was living with the mother at the time the child entered college.

Gifts that become effective at the death of the donor can do little to improve the dead person's sexual opportunities. Nevertheless, Fellows *et al.* (1978) found that the desire to give to mates continues to the end of life. It could be that giving to spouses at death is just a vestige of the habit of giving during life. But another way to look at testamentary gifts to spouses is that, because a will is made during life, the charitable value of the will is actually enjoyed during life. Thus, testamentary giving may still be an act of courtship.

There is another biological explanation for testamentary gifts to spouses. Decedents can reasonably expect their surviving spouses to pass a portion of the gifts on to their children. Judge (1995) found that men often expressed confidence that their wives would provide for, or pass property along to, their common children. Among those estates studied by Judge & Hrdy (1992), when men died they left nearly 70% of their assets to their spouses. That men ordinarily expected a portion of these assets to reach their children is indicated by the fact that in one-quarter of the cases in which they took the unusual step of leaving less than half of their assets to their surviving spouse, they did so to leave the large bulk of their estate to children from previous marriages. When women died, they left less of their assets to their surviving spouses than did men, perhaps in part because their husbands might remarry and devote some of those resources to children of that new marriage. Indeed, when couples marry at an older age, having already produced children with previous mates, they often make premarital agreements designed to direct assets to their own children rather than to their spouses or their spouses' children.

In their basic approach, modern English and American laws of intestacy track the preference for generosity towards mates by allocating a substantial portion of the decedent's estate to the surviving spouse (Megarry & Wade 1984; Uniform Probate Code section 2–103 (Langbein & Waggoner 2003)). Some variants track the evolutionary model a bit more closely by paying attention to whether the surviving children were children of both the decedent and the surviving spouse or just one of them. Section 2–102 of the Uniform Probate Code (Langbein & Waggoner 2003) provides that more assets go to the surviving children and fewer go to the surviving spouse when the decedent leaves children whose other parent is not the surviving spouse. When the survivor was not the parent of all of the decedent's children, the decedent cannot count on as much generosity from the survivor to the decedent's children by other parents. To achieve the same balance of giving between children and spouse when the surviving spouse is less likely to give to the decedent's children, the decedent has to give more to them directly rather than relying on the

survivor to be a conduit. Similarly, when the decedent was the parent of only some of the survivor's children, the decedent might not wish to support those other children as fully as the decedent's own children and so must give assets directly to the decedent's children rather than to the spouse as a proxy because the spouse will not distinguish between the children as the decedent would have wished.

There have long been limitations on the minimum that a decedent could leave to his or her surviving spouse. According to Geddes & Zak (2002) many legal systems have assured the wife one-third of the husband's estate upon the husband's death. They argue that the 'rule of one-third' increases the mother's investment in their children. If she were not guaranteed such a share, the wife would expend too little effort on mothering their children and too much effort acquiring resources for herself. If she were assured more than one-third, she would invest more in the children, but that would leave less for the men, which would not be favoured in a patriarchal legal system.

The various arguments here should not be read to contend that the law was written expressly to achieve biological goals. Some laws of intestate succession have been drafted to mimic what people would do on their own (Fellows *et al.* 1978; Beckstrom 1985), to achieve decedents' desires without need for any action by the decedents. Other normative goals include justice. But no matter which, our biology is involved. The laws of intestacy extend the human phenotype.

7. CONCLUSION

Property is more than a social invention; it is set of feelings built into our brains to solve survival problems confronting our ancestors. There are many dimensions to the property instinct, ranging from what constitutes property to what to do with property. Doubtless, these dimensions of the property instinct will be developed further, corrected and clarified, and other dimensions will be discovered as the science of behaviour progresses. Exploration and improved understanding of the property instinct should help us to place the various property laws on a more scientific footing than is possible today.

The author thanks Val Nolan Jr, Owen Jones, Jeremy Freese, Nicholas Georgakopoulos, Mitu Gulati, Erik Lillquist, Karen Parker, Sarah Brosnan, David Snyder, the anonymous reviewers and especially Oliver Goodenough for their considerable help in improving this paper. I could not have completed the project without research support from Indiana University School of Law-Bloomington.

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GLOSSARY

ESS: evolutionarily stable strategy