

Original Article

The territorial foundations of human property^{☆,☆☆}Peter DeScioli^{*,1}, Bart J. Wilson*Economic Science Institute, Chapman University, Orange, CA 92866, USA*

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Abstract

Many animal species have morphological and cognitive adaptations for fighting with others to gain resources, but it remains unclear how humans make fighting decisions. Non-human animals adaptively calibrate fighting behavior to ecological variables such as resource quantity and resource distribution. Also, many species reduce fighting costs by resolving disputes based on power asymmetries or conventions. Here we show that humans apply an ownership convention in response to the problem of costly fighting. We designed a virtual environment where participants, acting as avatars, could forage and fight for electronic food items (convertible to cash). In two experimental conditions, resources were distributed uniformly or clustered in patches. In the patchy condition, we observed an ownership convention — the avatar who arrives first is more likely to win — but in the uniform condition, where costly fights are rare, the ownership convention is absent.

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1. Introduction

Many animals make nuanced and adaptive decisions about whether, and how intensely, to fight others to secure resources such as territory, food or mates (Brown, 1964; Kokko, Lopez-Sepulcre & Morrell, 2006; Maher & Lott, 2000; Maynard Smith, 1982; Parker, 1974). Research on territoriality has found that decisions about whether to fight are sensitive to as many as 20 ecological variables, including resource quantity, resource distribution, population density and predation levels (Maher & Lott, 2000). Research on animal contests has discovered that animals use strategies to reduce the costs of disputes such as fighting assessment (Parker, 1974) and conventions (Maynard Smith, 1982). However, despite a large literature on fighting in non-human

animals — including mammals, birds, fish and insects — little is known about how humans make fighting decisions.

Several scholars have applied theories from biology to understand how humans secure resources, deriving novel conclusions relevant to economics and property law (Gintis, 2007; Krier, 2009; Stake, 2004). These accounts particularly draw on Maynard Smith's (1982) concept of a fighting convention or an “uncorrelated asymmetry” in which animal fights are resolved based on an asymmetry that is uncorrelated with fighting ability. Maynard Smith's analysis led to the counterintuitive conclusion that animal fights can be more than battles of brawn: choosing whether to fight or flee based on a conventional asymmetry, such as prior possession, can be an evolutionarily stable strategy (ESS) because individuals thereby reduce fighting costs relative to others who ignore the convention (Maynard Smith, 1982). In humans, resource disputes are decided by more than sheer power and, hence, the strategic convention model could potentially explain the foundations of human property. However, no previous research has tested this hypothesis in humans using the standard experimental methods applied to non-human species.

The strategic convention model stands in contrast to traditional theories which claim that human property necessarily depends on verbal communication, individual reputation, productive labor, legal institutions, enforcement

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by authority or other complexities of human social life (Bentham, 1802; Grotius, 1625/1964; Hobbes, 1651; Hume, 1740; Kant, 1797/1991; Locke, 1689; Pufendorf, 1672/2005; Rousseau, 1762). If, instead, basic features of human property can arise from very simple pairwise conflicts, as in species with minimal social interaction, then ownership reflects a core human competency which does not depend on advanced social abilities such as language, reputation or third-party enforcement.

1.1. A virtual environment for disputes

We test whether human fighting decisions are sensitive to resource distribution (uniform or patchy), asymmetries in power and asymmetries in prior possession. We designed custom software to create a virtual environment for observing human resource disputes (see [Methods](#)). In each experimental session, 10 participants operate avatars in a virtual environment where they can forage and fight for food items which are convertible to cash ([Supplementary Video 1](#)). To secure resources, participants can “strike” other participants, which is costly for both players. Because strikes are implemented through avatars, they cause financial losses but not physical harm ([Fig. 1](#)). This allows us to use methods similar to those used in non-human animal studies where animals engage in actual fighting. In the environment, avatars can move to find shrubs, enter/exit shrubs and consume berries inside

shrubs. Avatars gain one “health point” for each berry consumed, increasing their health meter (0–100 points) and offsetting health losses from metabolism which occurs at a rate of −10 points per minute. Participants’ cash earnings accumulate continuously in proportion to the health of their avatars, providing financial incentives to maximize health. When two avatars enter the same shrub, they have an “interaction” in which each avatar can (1) *Leave*, allowing the other avatar to consume berries; (2) *Smile*, which produces a smile; or (3) *Strike*, which costs the striker one health point and imposes a greater cost (3 or 5 points) on the individual who is struck. Participants remain in the interaction, where they can smile or strike repeatedly, until one avatar leaves the shrub. Finally, we designed an experimenter’s monitor (not observed by participants) showing the movements and interactions of all 10 participants in the environment in real time and allowing experimental sessions to be replayed from complete records of participants’ actions ([Supplementary Videos 2 and 3](#)).

We tested the hypothesis that resource distribution affects fighting behavior (defendability theory; [Brown, 1964](#)) by manipulating whether resources were distributed uniformly or clustered in patches, holding quantity constant. In the patchy condition, 10 brown shrubs produced five berries per minute and five green shrubs produced 20 berries per minute (total=150 berries per minute). In the uniform condition, 30 brown shrubs produced five berries per minute (total=150

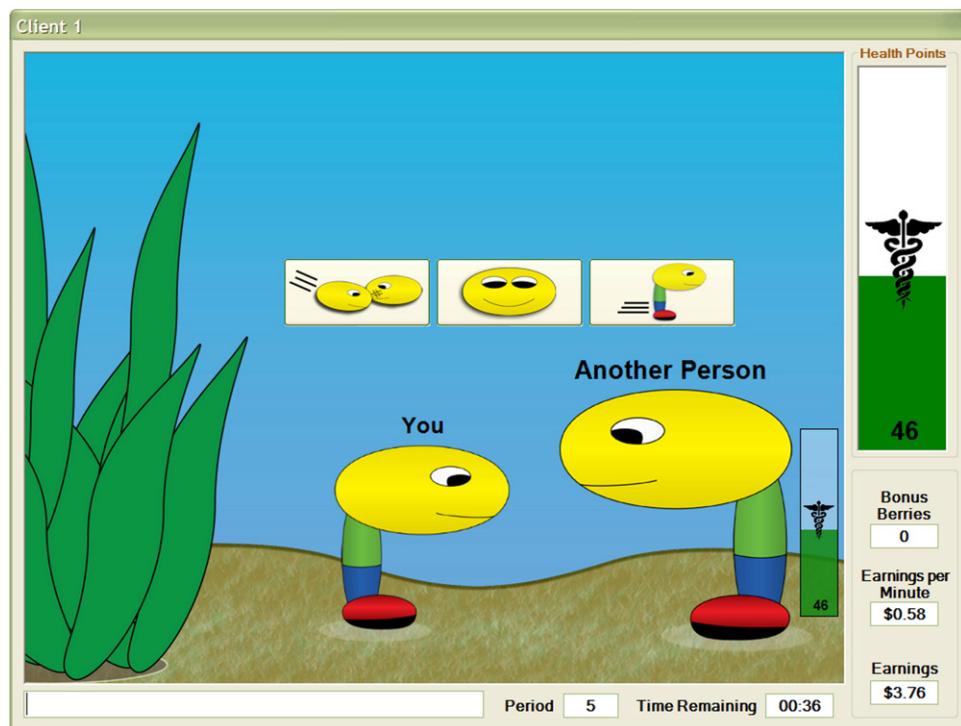


Fig. 1. Interaction between avatars. The screenshot shows the perspective of a Small resident who is having an interaction with a Large intruder. The participant controls the avatar by clicking on one of the three buttons showing strike, smile or leave.

berries per minute). We also tested whether participants could resolve resource disputes by using asymmetries in power (created by the experimenter) or asymmetries in prior residence. We manipulated power by randomly assigning half of participants to be Small avatars, whose strikes cause three health points of damage, and the other half to be Large avatars, whose strikes cause five health points of damage. The Large avatars appeared noticeably larger on the screen than the Small avatars (Fig. 1).

2. Methods

We recruited $N=120$ undergraduates to participate in an experiment in the laboratory of the Economic Science Institute at Chapman University. Participants were 50% female with a mean (S.D.) age of 20.6 (3.6) years. The reported ethnicities were 68% Caucasian, 8% Asian, 5% Hispanic and 19% others. Participants were recruited for an hour-long experiment, although the actual duration was less than 40 min. Participants were paid \$7 for showing up and they earned additional money as a result of their decisions in the experiment (mean=\$20.09, S.D.=\\$8.92).

Participants were randomly assigned to one experimental condition, either the patchy condition or the uniform condition. There were six sessions per experimental condition with 10 participants each. Participants were taken into the laboratory and seated at computer stations separated by partitions to preserve anonymity. Participants were presented with a virtual environment on their computer screens. Ten participants were placed together in the same virtual environment. They read a set of experimental instructions describing the environment and the capabilities of their avatars during which they could practice moving around the environment, entering and exiting shrubs, and consuming berries (Supplementary Methods). Then the experiment began. The experiment lasted for 20 periods (1 min each) but participants did not know the number of periods in advance in order to eliminate potential end-game effects. After the experiment, participants were individually and anonymously paid their show-up payment plus experimental earnings and then dismissed.

2.1. Virtual environment software

We designed custom software which creates a virtual environment for observing human resource disputes (Supplementary Videos 1–3). The software is written in Visual Basic and is available from the authors upon request. In the environment, avatars can move to find shrubs, enter/exit shrubs and consume berries inside shrubs. Shrubs produce berries continuously during 1-min periods and berries that are not consumed disappear at the onset of the next period. Avatars have a health meter (0–100 points) which begins at 90 points, decreases through metabolism at a rate of –10 points per minute and increases when berries are consumed. Participants' cash

earnings accumulate continuously during the experiment in proportion to their avatar's health (Supplementary Methods). At maximum health, additional berries add "bonus points" which increase cash earnings but do not further increase health; this feature was designed to limit the health available for fighting to limit health asymmetries. If participants reach zero health, then their avatars die, participation in the experiment ends and they receive their accumulated earnings but cannot earn additional money.

Participants cannot see others' avatars unless two individuals enter the same shrub (for discussion, see Maher & Lott, 2000). In this case, the two participants are taken to an "interaction" screen. During an interaction, other avatars cannot enter the shrub; clicking causes a message indicating that the shrub is full. On the interaction screen, the prior occupant is in front of the shrub and the newcomer is shown approaching (Fig. 1). Each participant has three options: (1) *Leave*, which causes the avatar to exit the shrub, allowing the other avatar to pick berries; (2) *Smile*, which has no effects aside from causing the avatar to smile; and (3) *Strike*, which causes the avatar to hit the other avatar, costing the striker one health point and imposing a greater cost (3 or 5 points) on the other individual. After a strike, there is a 3-s delay before another strike can be delivered; this feature was designed to eliminate advantages based on clicking speed. The 3-s strike delay was also imposed at the outset of the interaction to eliminate the potential for surprise attacks. Similarly, after a participant exited a shrub, there was a 5-s delay before they could enter the same shrub.

The software allows the experimenter to control the number, location, color and productivity of the shrubs as well as the size and capabilities of the avatars. We manipulated resource distribution in two experimental conditions (six sessions each). In the patchy condition, there were 10 brown shrubs, which produced five berries per minute, and five green shrubs, which produced 20 berries per minute (total=150 berries per minute). After each period, one of the five green shrubs was randomly selected and changed to a brown shrub and a corresponding brown shrub changed to a green shrub. This feature was designed to increase turnover in residence in green shrubs. In the uniform condition, there were 30 brown shrubs which produced five berries per minute (total=150 berries per minute). We manipulated power by randomly assigning half of participants to be Small avatars, whose strikes cause 3 health points of damage, and the other half to be Large avatars, whose strikes cause 5 health points of damage. The Large avatars appeared considerably larger on the screen than the Small avatars (Fig. 1).

The software produces data files which record all of the participants' actions in the virtual environment. During the experiment, participants' actions are displayed on an experimenter's monitor showing all participants' avatars in the environment, and experimental sessions can be replayed from the data (Supplementary Videos 2 and 3).

3. Results

3.1. Overview of patchy and uniform environments

Table 1 reports statistics for session level data for the patchy condition ($n=6$ sessions) and the uniform condition ($n=6$ sessions). Participants were more efficient at foraging for berries in the patchy condition than in the uniform condition, extracting a greater proportion of the total available berries (3000 per session in both conditions). In both conditions, participants spent most of their time moving around the environment, but this proportion was greater in the uniform condition. Participants spent more time in shrubs and more time in interactions in the patchy condition relative to the uniform condition.

Participants entered shrubs less frequently in the patchy condition than in the uniform condition. When inside a shrub (including foraging and interactions), participants collected less berries per second in the patchy condition than in the uniform condition (0.34 vs. 0.49). The time that it took to move from one shrub to the next was somewhat longer in the patchy condition than in the uniform condition (9.50 vs. 7.15 s). In terms of berries per second in shrubs, these transit times equal 3.24 and 3.51 berries (points), respectively. These amounts provide an estimate of the opportunity cost of leaving a shrub to find another one. We can compare the opportunity cost of leaving a shrub to the average costs of staying to fight, which we defined as staying longer than 3 s. In the patchy condition, the average strike costs per interaction (>3 s), across sessions, were mean=3.01, S.D.=0.82 points and the time costs were mean=8.74, S.D.=0.69 s. In the uniform condition, the strike costs per interaction were mean=1.38, S.D.=0.93 and the time costs were mean=6.14, S.D.=0.45 s.

Table 1
Session summary statistics by condition

	Patchy		Uniform		<i>t</i>	<i>p</i>
	Mean	S.D.	Mean	S.D.		
% of berries extracted ^a	74	3	57	2	11.99	<.001
% time moving	46	4	71	2	14.19	<.001
% time in shrubs	40	4	25	2	8.57	<.001
% time in interactions	14	2	4	1	15.76	<.001
No. of shrub entrances	593	114	1189	48	11.78	<.001
Time between shrubs (s)	9.50	1.34	7.15	0.21	4.25	.0017
Berries/second in shrub	0.34	0.03	0.49	0.04	7.11	<.001
No. of interactions	208	34	98	13	7.46	<.001
Time/interaction (s)	4.24	0.90	2.33	0.34	4.89	<.001
Smiles/interaction	2.23	0.84	1.20	0.37	2.75	.021
Strikes/interaction	0.43	0.15	0.11	0.09	4.56	.001
Total strike costs (points)	451	139	52	35	6.80	<.001
Total strike costs (\$)	53.80	20.21	7.12	6.44	5.39	<.001
Total earnings (\$)	226.86	32.73	174.91	9.75	3.73	.0039

Mean (S.D.) values for six sessions in each condition. Each of the 12 sessions had 10 participants.

^a Percentage of the total (3000) available berries extracted by participants.

3.2. Fighting in the patchy and uniform conditions

We observed more intense fighting in the patchy condition than in the uniform condition (**Table 1**). Participants' interactions lasted longer and they involved more strikes in the patchy condition than in the uniform condition. Participants' strikes reduced their aggregate cash payoffs by an average of \$53.80 for (10-participant) sessions in the patchy condition vs. \$7.12 for sessions in the uniform condition. We also observed more smiles per interaction in the patchy condition. The *Smile* option was originally included so participants would not be encouraged to strike by the options available to them. Surprisingly, participants frequently used the “cheap talk” smiles and often in extended bouts, suggesting use as a low-cost threat display. Last, we observed more deaths in the patchy condition (11/60) than in the uniform condition (0/60) ($p<.001$, Fisher's Exact Test).

3.3. The effects of asymmetries on disputes

We analyzed whether asymmetries predicted the winner, defined as the avatar who remained in the shrub after the other individual exited. In the patchy condition, the prior resident defeated the intruder in 71.39% of cases ($n=1248$), significantly greater than chance ($p<.001$, binomial test). When there was a size difference, Large avatars tended to defeat Small avatars (66.76%, $n=719$, $p<.001$). When there was a health difference, more healthy avatars tended to defeat less healthy avatars (66.37%, $n=1219$, $p<.001$). This initial analysis suggests that humans are able to use several asymmetries to resolve disputes. We observed a different pattern of results in the uniform condition. The residence effect was not only reduced, but significant in the opposite direction: prior residents were slightly more likely to exit first (44.31%, $n=589$, $p=.006$). Similarly, we observed no size effect (54.84%, $n=341$, $p=.08$) and no health effect (49.91%, $n=559$, $p=1.00$). These proportions differed significantly from the patchy condition (all χ^2 's >14.09 , all p 's $<.001$). These results show that, in the uniform condition, where costly fights were rare, participants did not generally use asymmetries to decide conflicts. Hence, we focused further analysis on disputes in the patchy condition.

For the patchy condition, we tested whether fighting behavior differed for interactions in brown shrubs and green shrubs (**Table 2**). Disputes over green shrubs lasted more than twice as long as brown shrubs and they involved more smiles and strikes. Looking at the influence of asymmetries, in green shrubs we observed a residence effect, size effect and health effect. These effects did not occur in brown shrubs. These results show that, consistent with theories about resource distribution, fighting is more severe for resource clusters. Furthermore, participants selectively used asymmetries to resolve disputes over highly contested resources but not for less contested resources.

To better understand the relative effects of prior residence and fighting assessment, we concentrated on disputes over

Table 2

Patchy condition: green vs. brown shrubs

	Green		Brown		<i>t</i>	<i>p</i>
	Mean	S.D.	Mean	S.D.		
Time/interaction (s)	4.60	5.56	2.10	1.99	6.78	<.001
Smiles/interaction	2.43	4.61	0.93	1.60	4.89	<.001
Strikes/interaction	0.50	1.25	0.11	0.05	5.48	<.001
	%	<i>p</i> ^a	%	<i>p</i> ^a	χ^2	<i>p</i>
Resident wins	75.54	<.001	53.42	.33	45.57	<.001
Larger wins ^b	68.66	<.001	58.52	.06	5.09	.024
Healthier wins ^c	69.35	<.001	53.13	.39	21.55	<.001

In the patchy condition, statistics for interactions in green ($n=1014$) and brown ($n=234$) shrubs.

^a The *p* value for the hypothesis test against 50% chance levels.

^b There was a size difference in $n=584$ interactions in green shrubs and $n=178$ in brown shrubs.

^c There was a health difference in $n=995$ interactions in green shrubs and $n=224$ in brown shrubs.

green shrubs. We examined whether the residence effect was a byproduct of a tendency for more powerful Large avatars to be residents (e.g., see Kemp & Wiklund, 2004; Pryke & Andersson, 2003). Fig. 2 shows the resident effect by the sizes of resident and intruder (“Small–Large” indicates Small resident and Large intruder). When sizes are matched in Small–Small and Large–Large interactions, we observed strong residence effects, 76% and 83%, respectively, showing that the residence effect cannot be reduced to a size/power effect. Additionally, when size differs (Small–Large and Large–Small), residence significantly affects the frequency of wins for Large avatars (46% vs. 84%) [$\chi^2(1,$

$n=584)=97.85$, $p<.001$]. The relative strengths of residence and size effects can be compared by considering the Small–Large conflicts in which these two asymmetries are opposed. In our environment, neither effect dominated: when Small residents faced Large intruders there was no statistical difference in frequencies of victory. To account for individual and session level variation, we conducted probit analyses with and without random effects for resident subject and session (Supplementary Table S1). The session level random effects were small and insignificant. For individual level random effects, we found no qualitative differences. Moving from a Small–Small to a Large–Small interaction increases the likelihood that the resident wins by 9 percentage points, and moving from a Small–Small to a Small–Large interaction decreases the likelihood that the resident wins by 18 percentage points.

Further, we predicted that conflicts between Small residents and Large intruders would be the most severe fights precisely because size and residence asymmetries are opposed. Indeed, disputes lasted longer for Small–Large interactions (mean=6.36, S.D.=5.90) than for other types (mean=4.08, S.D.=5.35) [$F(1, 1010)=27.04$, $p<.001$], disputes had more smiles for Small–Large interactions (mean=3.08, S.D.=4.30) than for other types (mean=2.23, S.D.=4.68) [$F(1, 1010)=4.93$, $p=.027$] and disputes had more hits for Small–Large interactions (mean=0.87, S.D.=1.57) than for other types (mean=0.39, S.D.=1.11) [$F(1, 1010)=24.44$, $p<.001$].

We looked more closely at the mechanics of the residence effect. In non-humans, individuals of some species do not contest residence, whereas in other species residents win because they fight harder (see Kokko et al., 2006). We tested whether the residence effect occurred not only in shorter interactions but also in escalated conflicts. We categorized interactions as escalated disputes with durations in the top quartile, duration >5 s ($n=282$), or as non-escalated disputes with duration ≤ 5 s ($n=732$). We observed residence effects in escalated disputes (71.99%, $p<.001$) and in non-escalated disputes (76.91%, $p<.001$), and the difference between these proportions was not significant [$\chi^2(1, n=1014)=2.67$, $p=.10$]. We examined whether residents were willing to incur more costs than intruders before giving up a fight over a green shrub. For fight duration, participants waited significantly longer before giving up when they were residents (mean=5.31, S.D.=6.15) than when they were intruders (mean=4.37, S.D.=5.34) [$t(1,012)=2.31$, $p=.021$]. For strike costs, participants withheld greater damage in health points before giving up when they were residents (mean=2.71, S.D.=5.35) than when they were intruders (mean=1.30, S.D.=3.46) [$t(1,012)=4.82$, $p<.001$]. Together, these results show that the residence effect reflects more than a tendency for intruders to yield, without contest, to prior residents. Prior residence shapes not only whether fights escalate but also how hard each side fights during an escalated conflict.

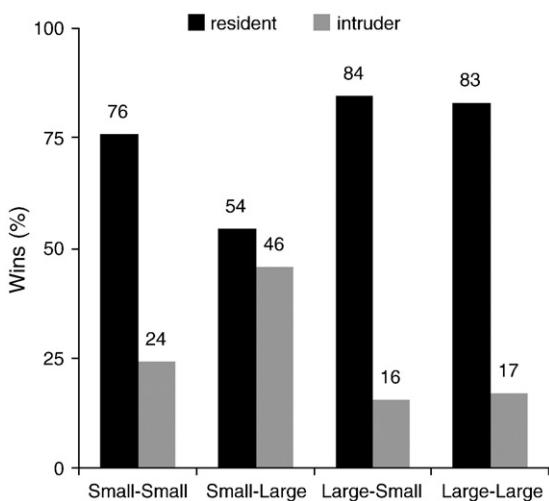


Fig. 2. Resident and intruder wins by resident–intruder sizes for disputes over green shrubs in the patchy condition. Residents have significantly more wins in fights that are Large–Large ($n=240$, $p<.001$, binomial test), Large–Small ($n=352$, $p<.001$) and Small–Small ($n=190$, $p<.001$). For Small–Large fights, the difference between Small residents and Large intruders is not significant ($n=232$, $p=.21$).

3.4. Logit model of resident wins

We used a logit analysis to examine how our experimental manipulation of resource distribution affected the residence convention. To estimate how much of the resident effect in the patchy condition vis-à-vis the uniform condition can and cannot be explained by differences in size, hits and health of the participants, we conducted a Blinder–Oaxaca decomposition on a logit model of resident wins (Fairlie, 2005). This technique quantifies the separate contributions of treatment differences in the measurable characteristics of our experiment (size, hits, health and gender of the participants) to the observed gap in the likelihood that the resident wins an interaction in the patchy condition vis-à-vis the uniform condition. The percentage of the residence effect that *cannot* be explained by the observable characteristics of the interactions can be attributed to different social processes caused by the experimental manipulation of resource distribution, i.e., the residence convention of property we observe in the patchy condition but not in the uniform condition.

For each interaction, either the resident remains in the shrub and the intruder leaves ($Y=1$) or vice versa ($Y=0$). We assume that a set of observable factors \mathbf{x} listed in Table 2 explain the decision, so that $\text{Prob}(Y=1)=\Lambda(\beta' \mathbf{x})$, where $\Lambda(\cdot)$ is the logistic distribution. The standard Blinder–Oaxaca decomposition of the patchy (P)/uniform (U) gap in the average value of Y can be expressed as:

$$\bar{Y}^P - \bar{Y}^U = [\hat{\beta}^{P'} (\bar{x}^P - \bar{x}^U)] + [(\hat{\beta}^P - \hat{\beta}^U)' \bar{x}^U], \quad (1)$$

where $\hat{\beta}^i$ is a vector of estimated coefficients for condition i . The first term in brackets is the explained difference in resident wins due to the difference in observed characteristics in the two conditions ($\bar{x}^P - \bar{x}^U$). The second term in brackets is the unexplained difference due to differences in residence conventions ($\hat{\beta}^P - \hat{\beta}^U$). Following Fairlie (2005), the logit decomposition can be written as:

$$\begin{aligned} \bar{Y}^P - \bar{Y}^U &= \overbrace{\sum_{j=1}^{n^P} \frac{\Lambda(\hat{\beta}^{P'} x_j^P)}{n^P}}^a - \overbrace{\sum_{j=1}^{n^U} \frac{\Lambda(\hat{\beta}^{P'} x_j^U)}{n^U}}^b \\ &\quad + \overbrace{\sum_{j=1}^{n^U} \frac{\Lambda(\hat{\beta}^{P'} x_j^U)}{n^U}}^c - \overbrace{\sum_{j=1}^{n^U} \frac{\Lambda(\hat{\beta}^{U'} x_j^U)}{n^U}}^d, \end{aligned} \quad (2)$$

where n^i is the number of observations for condition i .² Like those of any nonlinear regression model, the estimated coefficients are not necessarily the marginal effects. Hence, we computed the partial derivatives for the patchy condition (Table 3) and the uniform condition (Supplementary Table S2).

² The results are largely unaffected if we use a probit specification. Eq. (2) holds exactly for the logit model with a constant term and, hence, our choice in reporting that model's estimates.

Table 3
Patchy condition: logit analysis of resident wins

Variable	Marginal effect	Standard error	p
Hits by resident	0.0995	0.0312	.001
Smiles by resident	-0.0047	0.0063	.451
Health of resident	0.0020	0.0005	<.001
Hits by Large resident	0.1357	0.0516	.009
Hits by intruder	-0.1037	0.0313	.001
Hits by Large intruder	-0.1219	0.0387	.002
Smiles by intruder	0.0103	0.0067	.125
Health of intruder	-0.0016	0.0005	.001
Time in shrub by resident	0.0021	0.0002	<.001
Marginal effect for dummy variable is $P 1-P 0$			
Large resident	0.0381	0.0271	.160
Large intruder	-0.0279	0.0272	.306
Large resident*Large intruder	0.0247	0.0350	.480
Female resident	0.0319	0.0274	.244
Female intruder	-0.0235	0.0262	.369
Female resident*Female intruder	-0.0385	0.0418	.358
Period1	-0.1011	0.0946	.285
Period2	-0.0972	0.0926	.294
Period3	-0.1710	0.1107	.123
Period4	-0.1092	0.0911	.231
Period5	0.0339	0.0505	.501
Period6	-0.0497	0.0729	.496
Period7	-0.0629	0.0752	.403
Period8	-0.0307	0.0675	.649
Period9	0.0533	0.0451	.237
Period10	0.0632	0.0437	.148
Period11	0.0648	0.0414	.117
Period12	0.0247	0.0537	.646
Period13	0.0761	0.0354	.032
Period14	0.0114	0.0537	.832
Period15	0.0371	0.0488	.448
Period16	-0.0626	0.0814	.442
Period17	0.0204	0.0589	.729
Period18	0.0741	0.0397	.062
Period19	0.0965	0.0345	.005

Partial derivatives of probabilities with respect to the vector of characteristics for patchy condition. Values are computed at the means of the continuous variables and at zero for all dummy variables ($n=1248$).

Residents in the patchy condition maintain ownership of the shrub 71.4% of the time ($a=.714$), whereas only 44.3% of uniform residents retain the shrub ($c=.443$). Of particular interest is how much of this difference can be explained by hits, health and size. We find that nearly half of this difference, $a-b=.136$ to be precise, can be explained by the different observed tendencies and characteristics of the residents and intruders. That leaves a rather large amount of the resident effect ($b-c=.135$) to attribute to different social processes caused by the experimental manipulation of resource distribution.³ When a valuable resource was concentrated, participants quickly (within a 20-min experiment) adopted a convention of prior residence and that explains half of the difference in resident wins between the two treatment conditions.

³ With a probit specification the estimate of $b-c$ is 53.1% of $a-c$.

Focusing on the patchy condition, the logit model can also show how different variables affected fight outcomes (Table 3). Looking at the size effect, the model shows that it is not size per se which affects outcomes, but rather, it is the greater impact of Large individuals' strikes. Neither resident size nor intruder size affects the likelihood that the resident wins ($p=.160$ and .306, respectively). However, hits by a Large resident and Large intruder have large effects on the likelihood of winning, 14 ($p=.009$) and -12 ($p=.002$) percentage points, respectively. In comparison, Small hits have smaller effects. Hits by a Small resident and Small intruder increase the likelihood of winning by 10 ($p<.001$) and -10 ($p<.001$) percentage points, respectively.

Resident and intruder health have expected signs and similar offsetting marginal effects. Also, time in residence (prior to an interaction) predicts victory: For every 10 s in residence the likelihood of winning increases by 2 percentage points ($p<.001$), a result which has also been found in non-human species (Alcock & Bailey, 1997; Haley, 1994). Finally, gender and the number of smiles for both residents and intruders have no significant effect. All but three of the fixed effects for periods are insignificantly different from the baseline of period 20.

4. Discussion

We report experimental evidence showing that human fighting decisions are sensitive to resource distribution, asymmetries in power and asymmetries in prior residence. The human residence effect shown here is of particular importance given centuries of debate about the foundations of human property. We observed an ownership convention in an experimental environment which allowed minimal social behavior — dyadic hitting and smiling — without language use, reputation or third-party intervention. Ownership did not go uncontested, but rather, residents tended to fight harder than intruders, and, further, participants applied the convention selectively for (high value) green shrubs but not for (low value) brown shrubs. This evidence supports recent proposals that the foundation of human property is the ability to apply strategic conventions, or “uncorrelated asymmetries” (Maynard Smith, 1982), to reduce the costs of fighting (Gintis, 2007; Krier, 2009; Stake, 2004).

Numerous animals — ranging from caterpillars (Yack, Smith & Weatherhead, 2001) to songbirds (Carpenter & MacMillen, 1976) to elephant seals (Haley, 1994) — have evolved cognitive mechanisms which adaptively manage resource disputes. Importantly, these regulatory mechanisms are not generally well described as “fixed instincts” or as “hardwired,” but oppositely, the empirical evidence reveals sophisticated computational control systems which process information about ecological variables and specific adversaries to adaptively deploy offensive, defensive and evasive maneuvers (reviewed by Kokko et al., 2006; Maher & Lott, 2000). These discoveries raise questions about the mental

competencies that humans bring to bear on resource disputes. Ethnographic studies have investigated the sensitivity of human territoriality to key ecological variables (Baker, 2003; Cashdan, 1983; Dyson-Hudson & Smith, 1978). Also, recent laboratory studies indicate that humans are able to assess fighting ability by accurately estimating others’ strength from pictures of their bodies and faces (Sell et al., 2009). Further, these cues of formidability regulate anger toward antagonists (Sell, Tooby & Cosmides, 2009). The experiment reported here is the first to use standard experimental methods from the non-human literature to investigate human fighting decisions.

The virtual environment developed here can be used in future research to address a number of questions about human property. By labeling participants with unique colors, we can observe how reputation affects fighting and ownership conventions. By adding the ability for electronic discussion, we can observe the effects of communication and relate outcomes to the content of conversations. By allowing third-party intervention, we can test whether enforcement by authorities can reduce fighting costs. By allowing participants to invest effort to improve shrub output, we can examine the influence of productive labor on disputes and property. These and other manipulations can help us untangle the complex relationships between ownership cognition, different human social abilities and the efficiency of resource allocations.

A particularly challenging problem will be understanding the diversity of ownership conventions both within and between cultures. In many species, cognitive mechanisms for fighting seem to operate over a relatively limited domain, e.g., caterpillars fight over leaves but not over twigs (Yack et al., 2001). Humans are extreme in the wide variety of resources which they extract and create in their environments. The diversity of human resources might have selected for cognitive mechanisms which not only use ownership conventions but also create new property conventions for novel resource disputes. Consistent with this idea, our data show that humans are able to use ownership conventions in a novel virtual environment. Our experiment also suggests that ecological variables are one source of variability in ownership conventions. The same resource distributed differently in one human group vs. another (or at different times in the same group) can be subject to different property conventions. Finally, variation in property rules can be explained in terms of multiple equilibria. Resource disputes are coordination games typically modeled by the Hawk–Dove game (Maynard Smith, 1982), and these games often have many stable equilibria. For example, if multiple uncorrelated asymmetries are available, such as prior possession vs. current usage, then recognizing any of these asymmetries could be a stable equilibrium, and different human groups might vary in which asymmetry is used. This potential for variation creates a daunting challenge, but cognitive approaches might help limit the theoretical possibilities by considering how the human mind operates to locate these equilibria.

Many scholars have argued for the fundamental importance of property in human societies (Alchian & Demsetz, 1973;

De Soto, 2000; Demsetz, 1967; Ellickson, 1991; North, 1981; Ostrom, 1990). If humans have specialized cognitive abilities for managing resource disputes, then these computational systems shape individual behavior and population-level patterns (e.g., Lopez-Sepulcre & Kokko, 2005) like in non-human species (Mougeot, Redpath, Leckie & Hudson, 2003). This puts a high priority on understanding the cognitive competencies behind ownership and how they interact with the complexities of human social life.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.evolhumbehav.2010.10.003.

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