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of thinning depend on whether the erratics emerged from beneath through-flowing glacier ice at a time when the glaciers abutted the peaks directly or after the present pattern of skirting ice fields developed. In the first case, glacier axes must have stood higher than the erratics at the time of deglaciation. In the latter case, the elevations of the glacier axes may not have changed much since deglaciation. Although this makes it difficult to resolve very recent changes, it is a minor consideration for samples located hundreds of meters above the modern glaciers.

28. H. Conway, B. L. Hall, G. H. Denton, A. M. Gades, E. D. Waddington, *Science* **286**, 280 (1999).
29. R. A. Bindschadler, P. Vornberger, *Science* **279**, 689 (1998).
30. M. A. Fahenstock, T. A. Scambos, R. A. Bindschadler, G. Kvaran, *J. Glaciol.* **46**, 155 (2000).
31. I. Joughin, S. Tulaczyk, *Science* **295**, 476 (2002).
32. E. J. Rignot, *Science* **281**, 549 (1998).
33. A. Shepherd, D. J. Wingham, J. A. D. Mansley, H. F. J. Corr, *Science* **291**, 862 (2001).
34. M. Nakada, K. Lambeck, *Nature* **33**, 36 (1988).
35. Far from the ice sheets, relative sea level changes (i.e., changes in the relative height of land and sea causing coastlines to move landward or seaward) are strongly influenced by hydro-isostasy, a deepening of the ocean basins and tilting of continental margins in response to loading by meltwater. Modeled sea level changes in Africa, Australia, and other far-field sites assuming synchronous melting of ice sheets predict greater falls in relative sea level (~4 to 5 m) since 7000 years B.P. than those observed (1 to 3 m). The explanation for the difference, invoked by Nakada and Lambeck (*34*) but not substantiated until the recent discovery of late WAIS deglaciation, is continued meltwater addition to the oceans since 7000 years B.P.
36. I. D. Goodwin, *Quat. Sci. Rev.* **17**, 319 (1998).
37. K. Fleming *et al.*, *Earth Planet. Sci. Lett.* **163**, 327 (1998).
38. P. Johnston, *Geophys. J. Int.*, **114**, 615 (1993).
39. G. A. Milne, J. X. Mitrovica, *Geophys. J. Int.*, **126**, F13 (1996).
40. W. R. Peltier, *Rev. Geophys.* **36**, 603 (1998).
41. On the basis of the volume difference between the LGM reconstruction of Hughes *et al.* (*42*), which we take as a maximum estimate of the LGM ice sheet in West Antarctica, and the present-day ice sheet, in the sector draining across the coast from Thwaites Glacier (110°W) to Edward VII Peninsula (158°W). The volume of 5.1×10^5 km^3 (LGM to present) corresponds to ~1.4 m of esl, of which ~ 0.4 m would have been released since 10,000 years B.P. Glacier profiles interpolated between our elevation transects suggest that more than half of this volume (~0.2 to 0.3 m of esl) was released after 7000 years B.P. (fig. S1).
42. T. J. Hughes *et al.* in *The Last Great Ice Sheets*, G. H. Denton, T. J. Hughes, Eds. (Wiley, New York, 1981), pp. 263–317.
43. H. Liu, K. Jezek, B. Li, Z. Zhao, Radarsat Antarctic Mapping Project Digital Elevation Model Version 2 (National Snow and Ice Data Center, Boulder, CO, 2001); available at http://nsidc.org/data/nsidc-0082.html.
44. Scientific Committee on Antarctic Research, Antarctic Digital Database, Version 4.0 [cited 4 December 2002]; available at www.nerc-bas.ac.uk/public/magic/add_main.html.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/299/5603/99/DC1
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Orangutan Cultures and the Evolution of Material Culture

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Geographic variation in some aspects of chimpanzee behavior has been interpreted as evidence for culture. Here we document similar geographic variation in orangutan behaviors. Moreover, as expected under a cultural interpretation, we find a correlation between geographic distance and cultural difference, a correlation between the abundance of opportunities for social learning and the size of the local cultural repertoire, and no effect of habitat on the content of culture. Hence, great-ape cultures exist, and may have done so for at least 14 million years.

Among the numerous definitions of culture, the idea that it is a system of socially transmitted behavior is particularly useful for comparative purposes (*1*). Because the creation of culture under experimental conditions illuminates neither the extent of culture among wild animals nor its content, documenting culture's existence in nature remains essential. Unfortunately, this task is not easy; even if a study lasts long enough to show that a newly observed variant is an innovation, it remains difficult to demonstrate convincingly that the variant's acquisition by others is guided by social transmission. However, recent work on chimpanzees has shown geographic patterns in many behavioral variants that are consistent with the operation of cultural processes. A variant is considered cultural if it is customary (shown by most or all relevant individuals) or habitual (shown by at least several relevant individuals) in at least one site but is absent in at least one other ecologically similar site (*2*, *3*). Intraspecific genetic variation is almost certainly not responsible for these patterns (*4*).

Critics have stressed that the geographic approach may generate a type I error, spuriously leading us to conclude that cultures exist, when in fact unrecognized ecological differences between sites have produced within-population convergence and between-population divergence through individual learning (*5*–*7*). Hence, further tests are essential to increase our confidence in a cultural interpretation (*8*, *9*).

Orangutans (*Pongo pygmaeus*) showing variation in two forms of tool use consistent with culture (*10*, *11*) provide an opportunity for further testing. Here, we systematically apply the geographic approach to six different wild orangutan populations in Borneo and Sumatra (*12*) and test additional predictions derived from a cultural interpretation.

Table 1 lists three categories of geographic variants (*13*): (i) very likely cultural variants, which are behaviors present in at least one site at customary or habitual levels and absent elsewhere without clear ecological differences; (ii) likely cultural variants [as in (i) above] for which ecological explanations for absence, though unlikely, cannot be excluded; and (iii) rare variants that are unlikely to be maintained by social transmission. We shall refer to the first two as "putative cultural variants."

The list of putative cultural variants at the six sites (Fig. 1) contains 24 elements; an additional 12 local variants did not spread to customary or habitual level at any site. Data from additional sites would expand the list (*14*), as it does for chimpanzees (*3*). Of the putative cultural variants, 10 involve specialized feeding techniques, including tool use, and 6 are alternative forms of social signals, such as kiss-squeaks. As in chimpanzees (*2*, *3*), some variants may come close to reflecting shared meaning based on arbitrary symbols. In particular, the "raspberry" vocalizations, emitted in the

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final phase of nest building in Suaq Balimbing (*11*) and just before its start at Lower Kinabatangan (Table 1), seem to announce that the sender is bedding down for the night. Putatively cultural geographic variation in orangutans, therefore, is very similar to that in chimpanzees.

Human cultures show geographic patterning reflecting innovation and diffusion, and they incorporate more elements if they are open to influences from other societies (successful local innovation being comparatively rare), and within fairly broad limits show only a moderate effect of habitat on their content (*15*, *16*). If these generalizations also apply to orangutans and chimpanzees, it would increase our confidence in the cultural interpretation and the heuristic used here and elsewhere (*2*, *3*, *17*).

First, the innovation-and-diffusion hypothesis suggests that a behavioral variant often occurs at a site because it was brought there by animals dispersing from the site where it originated. We found the predicted correlation between geographic distance and cultural difference for the putative cultural variants (Fig. 2), i.e., those variants that spread well within at least one locality should therefore diffuse between localities as well. This relationship is unlikely to be an artifact because it is not found for the local variants that do not reach customary level at any site and therefore should diffuse poorly (Mantel tests: chimpanzees, $P = 871/5039 = 0.17$; orangutans, $P = 434/719 = 0.60$).

Second, the size of the local cultural repertoire is the balance between the rates of origination (due to innovation or diffusion from elsewhere) and extinction (due to failed social transmission). Thus, greater size of the local repertoire may reflect (i) higher rates of origination, which in turn reflect greater need for innovation due to marginal ecological conditions (necessity) or more opportunities for playful exploration (free time) (*18*); or (ii) higher rates of retention due to better conditions for diffusion between sites and social transmission within sites, caused by frequent tolerant proximity (*19*, *20*). Statistical power is insufficient to establish patterns if both influences are important, but if one predominates it should receive significant support. Across orangutan sites, no support exists for the necessity hypothesis (using percent of feeding time on tree cambium as an index of food scarcity and food-related local variants, cultural or not, as the response variable: $r = -0.812$, $n = 6$, $P < 0.05$, which is opposite to prediction), nor does statistical support exist for the free-time hypothesis (using total minutes in the day spent resting and total number of local variants, respectively: $r = -0.910$, $P < 0.05$, which is opposite to prediction). On the other hand, we did find support for the opportunities for social learning hypothesis as suggested by the pattern in humans: The number of customary and habitual variants in both orangutans (from Table 1) and chimpanzees [from table 1 in (*2*)] is predicted by the percentage of time that nondependent animals spend in association, which is used to index opportunities for learning from individuals other than the mother (*21*). Moreover, this relationship is stronger when limited to the customary and habitual variants that are related to feeding (Fig. 3), as expected, because acquisition of these variants should, on average, depend more on close-range socially biased learning than does acquisition of other variants. Hence, the size of the cultural repertoire at a given site is best predicted by the opportunities for oblique and horizontal social transmission during development.

Third, habitat may facilitate predictable individual learning and thus may facilitate convergent variant repertoires in separate localities, overriding the effects of the historical process of innovation and diffusion. No habitat effect is found, however, in orangutans, where pairs of sites with similar types of habitats do not have more similar variant repertoires than those with different types of habitats (sea-level floodplains versus mainly dryland forests) (Mantel test: $P = 503/719 = 0.70$; in chimpanzees, habitat effects are difficult to evaluate independently because they coincide with geographic differences).

These additional tests support a cultural interpretation of geographic variation in great-ape behavior and indicate fundamental similarities to human culture. However, because culture, as defined above, may be common among vertebrates (*1*, *17*, *22*), finer distinctions are needed for meaningful evolutionary reconstruction. Differences in cultures should reflect variation in the complexity of innovation and the mechanisms of socially biased learning. Thus, cultural elements may be (i) labels, where food preferences or predator recognition are socially induced (*5*, *7*, *23*) and which generally involve little innovation; (ii) signals, involving socially transmitted arbitrary innovations as variants on displays, such as kiss-squeaks on leaves or song

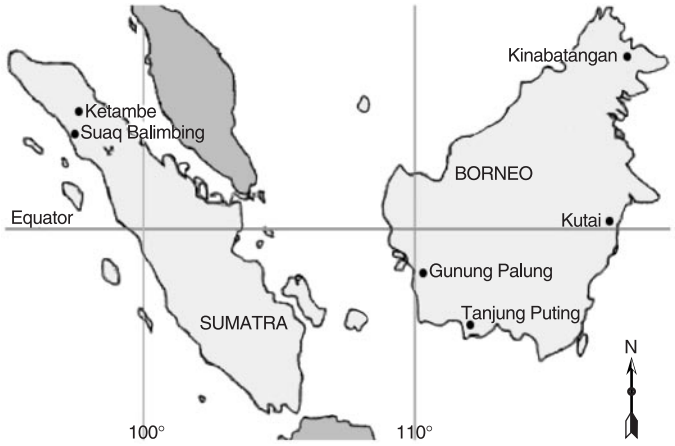


Fig. 1. Locations of the six study sites with long-term orangutan data included in this study.

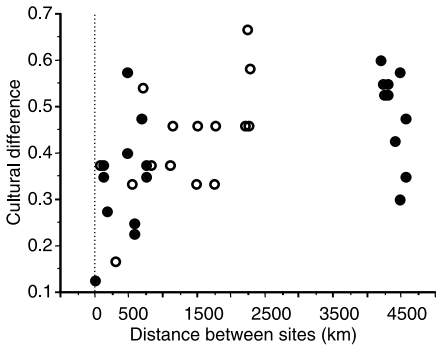


Fig. 2. The relationship between geographic distance (in kilometers) and cultural difference (as the percentage of difference over all habitual and customary local variants) in orangutans [open circles (from Table 1)] and chimpanzees {closed circles [from (*2*)]}. For orangutans, the relationship is significant [$r = +0.601$; Mantel test: a more extreme result in 21 of 719 possible permutations (*29*); $P = 0.029$]; for chimpanzees, it is marked ($r = +0.576$; Mantel test: $P = 334/5039 = 0.067$).

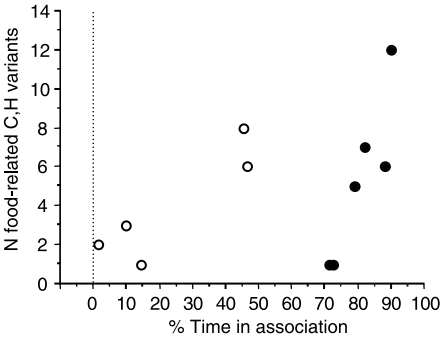


Fig. 3. The relationship between time spent in association (*30*–*32*) and the local repertoire of customary (C) and habitual (H) variants related to feeding in both chimpanzees (closed circles) (*2*, *3*) and orangutans (open circles). Association effect: $F[1,7] = 31.87$, $P < 0.001$; species effect: $F[1,7] = 18.29$, $P < 0.01$; interaction effect: $F[1,7] = 11.32$, $P < 0.05$. (No quantitative association estimate is available for Kutai orangutans, but the value would be low, supporting the trend).

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Table 1. Geographic variation in orangutan behavior patterns. C, customary; H, habitual; R, rare; P, present with unknown frequency, probably rare; E, absent for ecological reasons; A, absent; ?, unknown.

	Site and island					
	Gunung Palung (Borneo)	Tanjung Puting (Borneo)	Kutai (Borneo)	Lower Kinabatangan (Borneo)	Leuser, Ketambe (Sumatra)	Leuser, Suaq Balimbing (Sumatra)
Observation intensity (increasing ranks):	2	2	1	1	2	1
Very likely cultural variants						
1. Snag riding: Ride on pushed-over snag as it falls, then grab on to vegetation before it crashes on ground	A	C	A	A	A	A
2. Kiss-squeak with leaves: Using leaves on mouth to amplify sound, then drop leaf	C	A	H	A	A	A
3. Kiss-squeak with hands: Using fists (like trumpet) or flat hands on mouth to amplify sound	R	R	H	A	C	H
4. Leaf wipe: Wiping face with fistful of squashed leaves, then drop (in kiss-squeak context)	A	C	A	A	A	A
5. Play nests: Building nest for social play (no resting occurs)	C	C	P	A	C	H
6. Bunk nests: Build a nest a short distance above the nest used for resting (during rain)	A	P	A	H	A	A
7. Sun cover: Building cover on nest during bright sunshine (rather than rain)	A	?	C	C	H	A
8. Hide under nest: Seek shelter under nest for rain	A	R	C	P	R	A
9. Scratch stick: Using detached stick to scratch body parts	A	R	H	A	A	A
10. Autoerotic tool: Using tool for sexual stimulation (female and male)	A	A	P	A	C	A
11. Raspberry: Spluttering sounds associated with nest building	A	A	A	H	A	C
12. Symmetric scratch: Exaggerated, long, slow, symmetric scratching movements with both arms at same time	A	A	A	A	R	C
13. Twig biting: Systematically passing ends of twigs used for lining of nest past the mouth (sometimes including actual bite) during last phase of nest building	A	A	A	A	A	C
14. Leaf napkin: Using handful of leaves to wipe latex off chin	A	A	C	A	A	A
15. Branch as swatter: Using detached leafy branches to ward off bees/wasps attacking subject (who is usually raiding their nest)	R	R	H	H	H	H
16. Leaf gloves: Using leaf gloves to handle spiny fruits or spiny branch, or as seat cushions in trees with spines	A	R	A	A	H	E
17. Tree-hole tool use: Using tool to poke into tree holes to obtain social insects or their products	A	A	A	A	A	C
18. Seed extraction tool use: Using tool to extract seeds from the protected fruits of *Neesia* sp.	A	A	E	A	E	C
19. Branch scoop: Drinking water from deep tree hole using leafy branch (water dripping from leaves)	A	A	A	A	A	H
Likely cultural variants (ecological explanation not excluded)						
20. Snag crashing: Aimed pushing of dead standing trees	C	C	C	A	H	C
21. Bouquet feeding: Using lips to pick ants from fistful of dry, fresh, or rotting leaves (nests)	C	C	A	R	C	C
22. Nest destruction: Rummage through old orangutan nests for insects	H	C	P	A	H	H
23. Dead twig sucking: Breaking hollow (dead) twigs to suck ants from inside	A?	C	A?	A	C	C
24. Slow loris eating: Capture and eat slow loris hiding in dense vegetation	A	A	A	A	H	H
Rare behaviors						
1. Females rubbing their genitals together	R	R	A	A	A	R
2. Use leaf to clean body surface	R	A	A	A	A	A
3. Sneaky nest approach: Building series of nests, while approaching conspecific in fruit tree	R	A	A	A	A	A
4. Leaf bundle while sleeping ("doll")	R	R	A	A	A	A
5. Leaf scoop: Drinking water from the ground, using leaf as vessel (drinking straight from vessel)	R	A	A	A	A	A
6. Bridge nest: Build nest connecting two trees on opposite banks of river	A	R	A	A	A	A
7. Biting through vine to swing Tarzan-like across gap	A	R	A	A	A	R
8. Artistic pillows: Similar twigs lining nest	A	P	?	A	?	?
9. Branch dragging display on ground	A	A	?	R	A	A
10. Stick as chisel: To open termite nest in log on ground	A	A	A	A	R	A
11. Sponging: Drinking water using crumpled leaves	A	A	A	A	R	A
12. Hiding behind detached branch from predators or humans	A	R	P	R	R	A

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dialects (*17*); (iii) skills, involving rare innovations (including tool use), whose complexity depends on the nature of socially biased learning [which affects the degree of ratcheting (*6*)]; and (iv) symbols, probably derived from signal variants that became membership badges of the social unit or population (*6*, *15*).

Species are expected to vary in the kinds of cultural elements they display. Only humans have all four kinds of cultural elements, whereas, unique among nonhuman primates, chimpanzees and orangutans show the first three (*2*, *3*, *8*–*11*), which are made possible by innovative abilities and sophisticated forms of socially biased learning (*24*–*26*). Human cultures, therefore, differ from those of great apes in having unambiguously symbolic elements (*6*, *27*), far more complex skills, and far greater repertoire sizes, made possible by cognitive differences affecting innovation or observational learning (*1*, *5*, *6*). The presence in orangutans of humanlike skill (material) culture pushes back its origin in the hominoid lineage to about 14 million years ago, when the orangutan and African ape clades last shared a common ancestor (*28*), rather than to the last common ancestor of chimpanzees and humans.

Important tasks for the future include documenting the possible interdependence among these different kinds of cultural elements, identifying the conditions favoring their evolution, and assessing whether they all show the geographic and social correlates known for humans and demonstrated here for great apes.

References and Notes

1. R. Boyd, P. J. Richerson, *Proc. Br. Acad.* **88**, 77 (1996).
2. A. Whiten *et al.*, *Nature* **399**, 682 (1999).
3. A. Whiten *et al.*, *Behaviour* **138**, 1481 (2001).
4. F. B. M. de Waal, *Nature* **399**, 635 (1999).
5. B. G. Galef Jr., *Hum. Nat.* **3**, 157 (1992).
6. M. Tomasello, *The Cultural Origins of Human Cognition* (Harvard Univ. Press, Cambridge, MA, 1999).
7. B. G. Galef Jr., in *The Biology of Animal Traditions*, D. M. Fragaszy, S. Perry, Eds. (Cambridge Univ. Press, Cambridge, in press).
8. C. Boesch, P. Marchesi, N. Marchesi, B. Fruth, F. Joulian, *J. Hum. Evol.* **26**, 325 (1994).
9. W. C. McGrew, R. M. Ham, L. J. T. White, C. E. G. Tutin, M. Fernandez, *Intern. J. Primatol.* **18**, 353 (1997).
10. C. P. van Schaik, C. D. Knott, *Am. J. Phys. Anthropol.* **114**, 331 (2001).
11. C. P. van Schaik, in *The Biology of Animal Traditions*, D. M. Fragaszy, S. Perry, Eds. (Cambridge Univ. Press, Cambridge, in press).
12. After compiling a preliminary list of candidate cultural variants, representatives of all sites with long-term data on wild orangutans convened in San Anselmo, California, from 14 to 17 February 2002 to discuss these variants and to identify new ones through plenary discussion of site descriptions and video footage from multiple sites. We used the same criteria as employed in the chimpanzee comparison, including those for prevalence at a given site (*2*, *3*).
13. Included sites had more than 4 years of intensive observations of at least 25 individual orangutans and 10,000 contact hours. Observation intensity is based on numbers of observation hours and total duration of the study as (i) less than 25,000 hours or (ii) more than 25,000 hours. We excluded (i) universals, which are behavior patterns that were found at all sites or were absent for obvious ecological reasons; (ii) variant feeding techniques on the same species of fruit (unless one involved tools), because different morphologies and subtle ecological influences producing independent convergence within sites are difficult to exclude without detailed examination; and (iii) variants with localized distributions that most likely reflect ecological conditions (e.g., lathering of fruit pulp or seeds in the fur of arms, drinking water from natural containers such as pitcher plants, making ground nests, wading through standing water, etc.).
14. E. A. Fox, I. bin'Muhammad, *Am. J. Phys. Anthropol.*, in press.
15. F. M. Keesing, *Cultural Anthropology: The Science of Custom* (Holt, Rinehart, and Winston, New York, 1958).
16. J. C. Hudson, *Geographical Diffusion Theory* (Northwestern University Studies in Geography No. 19, Northwestern Univ., Evanston, IL, 1972).
17. L. Rendell, H. Whitehead, *Behav. Brain Sci.* **24**, 309 (2001).
18. H. Kummer, J. Goodall, *Philos. Trans. R. Soc. London Ser. B* **308**, 203 (1985).
19. S. Coussi-Korbel, D. M. Fragaszy, *Anim. Behav.* **50**, 1441 (1995).
20. C. P. van Schaik, R. O. Deaner, M. Merrill, *J. Hum. Evol.* **36**, 719 (1999).
21. In an analysis of covariance (ANCOVA), the effect of association time is significant (ANCOVA: $F[1,7] = 9.74$, $P < 0.05$), whereas the effects of species and the interaction are not.
22. T. Nishida, in *Primate Societies*, B. B. Smuts *et al.*, Eds. (Chicago Univ. Press, Chicago, 1987), pp. 462–474.
23. E. Curio, in *Social Learning: Psychological and Biological Perspectives*, T. R. Zentall, B. G. Galef Jr., Eds. (Erlbaum, Hillsdale, NJ, 1988), pp. 75–97.
24. A. Whiten, *Cogn. Sci.* **24**, 477 (2000).
25. M. Myowa-Yamakoshi, in *Primate Origins of Human Cognition and Behavior*, T. Matsuzawa, Ed. (Springer, Tokyo, 2001), pp. 349–367.
26. T. Stoinski, A. Whiten, *J. Comp. Psychol.*, in press.
27. R. Tuttle, *Curr. Anthropol.* **42**, 407 (2001).
28. M. Goodman *et al.*, *Mol. Phylogenet. Evol.* **9**, 585 (1998).
29. N. Mantel, *Cancer Res.* **27**, 209 (1967).
30. C. Boesch, in *Great Ape Societies*, W. C. McGrew, L. F. Marchant, T. Nishida, Eds. (Cambridge Univ. Press, Cambridge, 1996), pp. 101–113.
31. Y. Sugiyama, *Primates* **9**, 225 (1968).
32. Y. Sugiyama, *Primates* **22**, 435 (1981).

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Single-Gene Greenbeard Effects in the Social Amoeba *Dictyostelium discoideum*

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Selection can favor reproductive altruism if an altruism allele aids copies of itself by helping relatives. The alternative "greenbeard" mechanism, in which an allele directly recognizes and aids copies of itself in others, is generally thought to be too complex for a single gene to carry out. The *csA* gene in *Dictyostelium discoideum* acts as a single-gene greenbeard. When wild-type cells are mixed with *csA*-knockout cells, the wild type is more altruistic, but is also able preferentially to direct the benefits to other wild-type cells. Both properties derive directly from homophilic cell adhesion of the protein encoded by *csA*.

Selection can favor an allele that causes self-sacrifice if it enhances the fitness of others who bear the allele (*1*). Generally, individuals recognize other bearers—relatives—by some combination of social context and learning (*2*). Alternatively, alleles might directly recognize copies of themselves, regardless of average relatedness (*3*). These so-called greenbeard alleles, the term originally coined by Dawkins (*4*), are generally thought to be rare because they must cause a complex of three effects: a perceptible trait (the hypothetical green beard), recognition of this trait in others, and preferential treatment of those recognized (*3*, *4*). The few known examples—poison-antidote systems like bacteriocins (*5*, *6*) and the fire ant gp9 locus (*7*, *8*)—involve or are thought to involve multiple tightly linked genes. However, Haig has suggested that a single homophilic cell adhesion gene could cause all three effects (*9*). Here, we show that this is true for the *csA* (*contact site A*) gene of the slime mold, *Dictyostelium discoideum*.

D. discoideum is a highly social eukaryotic microorganism (*10*). Most of the time,

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