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Do invertebrates have culture?

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A recent paper in *Current Biology*[1] showed for the first time that female invertebrates (*Drosophila melanogaster*) can perform mate choice copying. Here, we discuss how female mating preferences in this species may be transmitted culturally. If culture occurs in invertebrates, it may be a relatively ancient evolutionary process that may have contributed to the evolution of many different taxa. This would considerably broaden the taxonomic range of cultural processes, and suggest the need to include cultural inheritance in all animals into the general theory of evolution.[2-4]

From an evolutionary perspective, culture can be defined as the part of phenotypic variance that is inherited through social learning.[2] When defined in this way, cultural variation becomes part of inclusive heritability[2] and is thus open to evolution through natural selection in ways similar to genetic variation. In this context, cultural transmission may thus be viewed as an important process of evolution. The actual impact of culture, however, may be restricted by a limited prevalence across species with well developed cognitive abilities. Apart from humans, evidence of cultural variation has been reported in a restricted set of mammals, such as chimpanzees,[5-8] orangutans,[9] whales[10-12] and some songbirds.[13-17]

However, the paucity of evidence for cultural variance may result from the lack of methods to identify it. We have recently proposed four testable criteria on which to rely to demonstrate that a trait is at least partially culturally inherited.[2,4] The expression of the trait must first result from social learning, which is learning from others[18-22] (reviews in refs. 3 and 23–25). This is the essence of culture. Second, variation in the social information possessed by individuals must be socially transmitted across generations or at least from older to younger individuals.[7,26-29] This criterion establishes that the inheritance of behavioral variation across generations results from social learning. Third, social learning must modify the phenotype of the learning individual for sufficient time to allow other individuals to observe and learn its behavior.[30-32] The idea is that if a social influence only persists for a short period of time, it may be too labile to be transmitted to younger individuals. We only transmit attitudes to which we stick. Fourth, individuals should generalize socially learned information using it in new contexts.[1,31,33,34] This is because only general rules (such as preferences for large over small mates, or deciduous over coniferous forests), not specific situations, can be transmitted across generations.

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In our recent paper in *Current Biology*,[1] we studied the role of social learning in female mating preferences in an invertebrate, *Drosophila melanogaster*. Our results showed surprisingly that in an invertebrate, tactics of female mate choice fulfill three of the four criteria that demonstrate that a trait is transmitted culturally.

Our first two-choice experiment showed that social information can affect female preference for poor condition males. Females naturally tend to prefer good over poor condition males. However, that preference can be modified by manipulating the apparent mating success of the poor condition male. After having had the opportunity to witness a poor condition male mating with a model female, while a good condition male remained alone, 24 hours later virgin prospector females increase the proportion of time they spend near the poor condition male. Male mating success thus constitutes public information[35] that can influence a young prospector female's associative preference for a poor condition male. This social influence lasted for at least 24 hours, which comprises a substantial proportion of a fruit fly's life.

Our second experiment used artificial phenotypic variation whereby males were dusted with green or pink powder to study the role of social information on male mating success. We first presented green and pink males to a prospector virgin female and found no significant preference for copulating with males of either color. We then, through a glass partition, showed a prospector female a green male with a virgin female. Because virgin females rapidly copulate with the first male they encounter, this treatment provided positive public information about green males. Then in the next hour we showed a pink male with a recently mated female. Because recently mated females systematically reject males, this provided negative public information about the pink male. These trials were repeated with males of reversed male colors. We repeated this sequence three times and then presented the prospector female with a dyad of new green and pink males and recorded the male with which she copulated. When, during the demonstration, the glass partition was opaque so that the prospector female could not see the demonstration, the prospector female was equally likely to copulate with the green or pink male. However, when the glass partition was transparent, we found that the prospector female copulated significantly more often with the type of male she had seen copulating than with the type she had seen being rejected by other females.

Altogether our experiments provide the first evidence that female invertebrate can perform mate copying. More surprisingly, they also show that female mating preferences are at least partly socially learned (Criterion 1 of culture), that this influence lasts for a significant portion of a female's lifespan (Criterion 3), and that ~~Drosophila~~ females are able to extract general rules from the observation of specific situations (e.g., green are better than pink males; Criterion 4). Hence female sexual preference in Drosophila fulfills three of the four criteria of cultural transmission.

Further experiments are needed to demonstrate that this form of social learning fulfills the second criterion, i.e., that it can lead to the transmission of sexual preferences from older to younger individuals. If this were the case, it would mean that female mating preferences in this invertebrate are at least partly transmitted culturally. This seems surprising because ~~Drosophila~~ have a ~~minute~~ brain and are not usually considered to possess cognitive abilities compatible with cultural transmission (reviewed in refs. 25 and 36). However, this may not be so surprising in view of the pervasive occurrence of social learning, social and sexual imprinting, imitation, copying and teaching[3,4,8] (review in refs. 23, 24, 29 and 37–39) in many different contexts and in taxa as varied as birds,[31,40-43] mammals,[44] fish[32,45,46] and insects.[1,47] Even plants[48] show characteristics akin to social learning. These results suggest that more species may possess the cognitive abilities necessary to transmit social information across generations.

In conclusion, evidence for culture in invertebrates should encourage further research to test the generality of our results. Subsequently, a study of *Drosophila serrata* found no evidence for social learning in a mate choice context.[49] However, that study differed from ours in many important ways that potentially may have hampered the detection of social learning. For instance, in that study, attractor females were of another species (*D. birchii* "of similar age"). It may well be that prospector females detected that these females were not conspecifics and they thus may have not considered the demonstration as providing useful information about male attractiveness. We now need to test multiple species with reliable designs. We also need to determine whether the second criterion of transmission across generations is fulfilled in *Drosophila melanogaster*. In case of a positive result, as suggested by Ellouise Leadbeater, it would introduce "a mainstream model species to the study of how animals use social information"[50] and how such cultural transmission may affect evolution in general. This would also suggest that cultural evolution may be a relatively ancient evolutionary process that may have contributed to the evolution of many different taxa. This would considerably broaden the taxonomic range of cultural processes, and beg for the inclusion of cultural inheritance into the general theory of evolution, and not only for human evolution.[2-4]

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References

1. Mery F, et al. Public versus personal information for mate copying in an invertebrate. Curr Biol 2009; 19:730-4.
2. Danchin É, Wagner RH. "Inclusive Heritability": combining genetic and nongenetic information to study animal culture. Oikos 2010; 119:210-8.
3. Danchin É, Giraldeau LA, Valone TJ, Wagner RH. Public information: from nosy neighbors to cultural evolution. Science 2004; 305:487-91.
4. Danchin É, Wagner RH. In: Behavioural Ecology. Danchin É, Giraldeau L-A, Cézilly F, (eds.,) Oxford University Press, Oxford 2008; 693-726.
5. Whiten A. The second inheritance system of chimpanzees and humans. Nature 2006; 437:52-5.
6. Lycett SJ, Collard M, McGrew WC. Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. Proc Natl Acad Sci USA 2007; 104:17588-92.
7. Whiten A, Mesoudi A. An experimental science of culture: Animal social diffusion experiments. Phil Transact Royal Soc London B Biol Sci 2008; 363:3477-88.
8. Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. Phil Transact Royal Soc B Biol Sci 2009; 364:2417-28.
9. Vogel G. Orangutans, like chimps, heed the cultural call of the collective. Science 2003; 299:27-8.
10. Whitehead H, Rendell L. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. J Anim Ecol 2004; 73:190-6.
11. Whitehead H. Cultural selection and genetic diversity in matrilineal whales. Science 1998; 282:1708-11.
12. Rosenbaum HC, et al. The effect of differential reproductive success on population genetic structure: correlations of life history with matrilines in humpback whales of the gulf of Maine. J Hered 2002; 93:389-99.
13. Slabbekoorn H, Smith TB. Bird song, ecology and speciation. Phil Transact Royal Soc London B Biol Sci 2002; 357:493-503.
14. Beecher MD, Brenowitz EA. Functional aspects of song learning in songbirds. Trends Ecol Evol 2005; 20:143-9.
15. Brenowitz EA, Beecher MD. Song learning in birds: diversity and plasticity, opportunities and challenges. Trends Neurosci 2005; 28:127-32.
16. Putland DA, Nicholls JA, Noad MJ, Goldizen AW. Imitating the neighbours: vocal dialect matching in a mimic-model system. Biol Lett 2006; 2:367-70.
17. Fitch WT. Birdsong normalized by culture. Nature 2009; 459:519-20.
18. Boyd R, Richerson PJ. In Social-learning. Psychological and Biological Perspectives (Zentall TR, Galef BGJ, eds.) 29–48 (Lawrence Erlbaum Associates, Publishers, Hillsdale, New Jersey, Hove and London, 1988).
19. Henrich J, McElreath R. The wvolution of cultural evolution. Evol Anthropol 2003; 12:123-35.
20. Richerson PJ, Boyd R. Not by Genes Alone. University of Chicago Press, Chicago 2005.
21. Henrich J, Boyd R, Richerson PJ. Five misunderstandings about cultural evolution. Hum Nat 2008; 19:119-37.
22. McElreath R, Henrich J. In: Oxford Handbook of Evolutionary Psychology. Dunbar R, Barrett L, (eds), Oxford Univ Press, Oxford 2009; 571-85.
23. Heyes CM, Galef BGJ. Social learning and Imitation: the Roots of Culture. Academic Press, New York 1996.
24. Galef BG, Giraldeau LA. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav 2001; 51:3-15.
25. Leadbeater E, Chittka L. Social learning in insects—From miniature brains to consensus building. Curr Biol 2007; 17:703-13.
26. Lefebvre L. The opening of milk bottles by birds—evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission. Behav Proc 1995; 34:43-53.
27. Avital E, Jablonka E. Animal Traditions. Behavioural Inheritance in Evolution. Cambridge University Press, Cambridge 2000.
28. Hirata S, Watanabe K, Kawai M. In: Primate Origins of Human Cognition and Behavior. Matsuzawa T, (ed), Springer Verlag Japan, Tokyo 2001; 487-508.
29. Horner V, Whiten A, Flynn E, de Waal FBM. Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. Proc Natl Acad Sci USA 2006; 103:13878-83.
30. Brooks R. The importance of mate copying and cultural inheritance of mating preferences. Trends Ecol Evol 1998; 13:45-6.
31. White DJ, Galef BG. 'Culture' in quail: social influences on mate choices of female Coturnix coturnix. Anim Behav 2000; 59:975-9.
32. Witte K, Noltemeier B. The role of information in mate-choice copying in female sailfin mollies (*Poecilia latipinna*). Behav Ecol Sociobiol 2002; 52:194-202.
33. White BN, Galef BG. Differences between the sexes in direction and duration of response to seeing a potential sex partner mate with another. Anim Behav 2000; 59:1235-40.
34. Godin J-GJ, Herdman EJE, Dugatkin LA. Social influences on female mate choice in the guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. Anim Behav 2005; 69:999-1005.

35. Wagner RH, Danchin É. A taxonomy of biological information. Oikos 2010; 119:203-9.
36. Chittka L, Niven J. Are bigger brians better? Curr Biol 2010; In press (DOI 10.1016/j.cub.2009.08.023.
37. Franks NR, Richardson T. Teaching in tandem-running ants. Nature 2006; 439:153.
38. Thornton A, McAuliffe K. Teaching in wild Meerkats. Science 2006; 313:227-9.
39. Boesch C. Teaching among wild chimpanzees. Anim Behav 1991; 41:530-2.
40. Galef BGJ, White DJ. Evidence of social effects on mate choice in vertebrates. Behav Process 2000; 51:167-75.
41. Galef BGJ, Whikin EE. Interaction of social and individual learning in food preferences of Norway rats. Anim Behav 2001; 62:41-6.
42. Ophir AG, Galef BGJ. Female Japanese quail affiliate with live males that they have seen mate on video. Anim Behav 2003; 66:369-75.
43. Galef BG, Lim TCW, Gilbert GS. Evidence of mate choice copying in Norway rats, *Rattus norvegicus*. Anim Behav 2008; 75:1117-23.
44. Deutsch JC, Nefdt RJC. Olfactory cues influence female choice in two lek-breeding antelopes. Nature 1992; 356:596-8.
45. van Bergen Y, Coolen I, Laland KN. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. Proc Royal Soc London B 2003; 271:957-62.
46. Coolen I, Ward AJW, Hart PJB, Laland KN. Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. Behav Ecol 2005; 16:865-70.
47. Coolen I, Dangles O, Casas J. Social learning in noncolonial insects? Curr Biol 2005; 15:1931-5.
48. Karban R, Maron J. The fitness consequences of interspecific eavesdropping between plants. Ecology 2000; 83:1209-13.
49. Auld HL, Punzalan D, Godin J-GJ, Rundle HD. Do female fruit flies (*Drosophila serrata*) copy the mate choice of others? Behav Proc 2009; In press.
50. Leadbeater E. Social learning: what do Drosophila have to offer? Curr Biol 2009; 19:378-80.