Monogamy with a purpose

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Humans are fascinated by animal monogamy. In the 1960s, Konrad Lorenz idealized the lifelong pair-bonds of geese until one of his students pointed out some infidelities and suggested that geese may be “only human” (1), and Desmond Morris (2) speculated about the advantages of the pair-bond for early humans. Even though many theories have since been proposed, human monogamous inclinations have also been questioned, including the pervasive idea that it all boils down to provisioning by fathers.

Biologists prefer to place monogamy in a broad comparative perspective to determine what factors may have promoted its evolution. Why is monogamy ten-times more common in birds than mammals? Additionally, even though relatively common in primates, why are there no primates—other than humans—in which multiple reproductive pairs live together? Primate monogamy generally entails territoriality, with both the male and the female repelling outsiders of their own sex.

Recently, two independent British teams have addressed these issues by analyzing variation in candidate traits that may have pushed species toward monogamy. Both studies used Bayesian and maximum-likelihood statistics to explore three traits: (*i*) paternal care, (*ii*) female sociality, and (*iii*) infanticide. The researchers used different databases, however. Kit Opie’s University College London team compared data on 230 primate species (3), whereas Dieter Lukas and Tim Clutton-Brock of Cambridge University covered no less than 2,545 mammalian species, including 330 primates (4). The teams further classified mating systems differently, with one team criticizing the classification of the other (4).

The teams agreed on one crucial point, though, which is that paternal care is more likely a consequence of monogamy—an evolutionary afterthought with benefits—than the key to its existence. This conclusion left the other two factors, female sociality and infanticide, as possible drivers, and it is here that the teams parted ways. Opie at al. (3) were so convinced that infanticide was the primary cause that they put it in their title. That males kill youngsters sired by other males is known of many species, and widely viewed as a way of speeding up a female’s reproduction to the advantage of the infanticidal male (5, 6). The primate literature is rife with theories about how the need to curb infanticide shaped social organization, including a tendency of males to accompany and protect a female carrying their progeny (7). The low infanticide rate in monogamous species noted by both research teams appears to fit this idea, but does not necessarily imply a causal connection. Is monogamy effective at preventing infanticide or was there perhaps never much infanticide in these species to begin with?

The Cambridge team (4) points out that most monogamous animals do not fit the typical mold of infanticidal species. It is only when the duration of lactation exceeds that of gestation that the killing of another male’s offspring benefits males. However, this is hardly a common characteristic of monogamous animals. The Cambridge team argues against infanticide as a cause, therefore, and concludes that monogamy likely began as a way for males to monopolize isolated females. Whenever food competition drove females apart, males ended up defending one female at a time because they could not claim several females at once. Once a male had settled on guarding a single female, the defense of her offspring and provisioning of food were logical extensions.

The contrast in conclusions by both teams is disturbing given the tight statistical connection between monogamy and discrete female ranges. Both teams found this connection to exceed the one between monogamy and infanticide (table T1 in ref. 3 and table S2 in ref. 4). So, why did Opie et al. (3) place so much emphasis on infanticide? Were the authors swayed by prior theorizing (7) or by sound statistical arguments? Opie et al. estimated transition rates in three stochastic models, each including a mating system and one other factor; their results show that transitions from polygyny to pair-bonding can happen at similar rates whether female ranges overlap or not (figure 1*B* in ref. 3). Estimated transition rates further suggested that to move to pair-bonding required passing through a stage with high infanticide (figure 1*C* in ref. 3). However, data on infanticide is notoriously hard to obtain, and when the authors restricted their analysis to the subset of studies with the most reliable data, the connection with infanticide fell away (figure S2 in ref. 3). To us, the results are entirely consistent with an emphasis on female ranges, hence in line with the

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conclusions of Lukas and Clutton-Brock (4). The latter authors stress that 60 of 61 mammalian transitions to monogamy (including five of six primate transitions) went through a stage in which females lived solitary lives.

Possibly, the outcomes of these kinds of analyses are not transparent enough, or the computational methods not powerful enough. The factors studied seem to interact to such a degree that analysis of just one factor at a time is not very informative. One solution would be to analyze multiple factors simultaneously, which might allow us to identify interactions that remain “hidden” in simple binary analyses. It would be good to move toward such a multidimensional approach.

For infanticide to play a key role, it would need to be relatively frequent and males would need to be quite effective at preventing it. Males would need to mate-guard (i.e., prevent females from mating with other males) as well as offspring-guard (i.e., prevent infanticide), because in evolutionary terms the prevention of infanticide makes sense only by males assured of their paternity. This is a rather costly proposition as it would tie males down in terms of movement and extrapair mating opportunities. Such a strategy would become even more problematic in groups with multiple males and females. Under those circumstances, which probably prevailed during human prehistory, the evolution of monogamy faces many serious obstacles (8). In large game hunters, for example, men often spend time away from their community, leaving women and children unattended.

Nevertheless, many human societies know monogamy, imperfect as the institution may be. This is one of the most important differences between human social organization and that of our closest relatives, the African apes, which lack nuclear families that draw males into offspring care (9, 10). Human monogamy may have evolved for different reasons and under different circumstances than monogamy in the majority of birds and mammals, however. Perhaps monogamy did not evolve in the genetic sense at all, but rather in a cultural sense, because even though some fossils have been interpreted as evidence for monogamy during human prehistory (11), humans and their ancestors are too sexually dimorphic in size to be considered naturally monogamous (12). Because human monogamy is unlikely to have arisen in the context of mutually exclusive female ranges, it appears fundamentally different from, say, the well-known monogamy of gibbons or marmosets, which live in isolated pairs. Several scenarios try to explain the advantages of monogamy within a larger society, one of which harks back to Morris’ (2) proposal that by sexually and reproductively equalizing the men within a community, pair-bonding fosters cooperation (13, 14).

Even if the origins of monogamy in humans are unique, the two analyses discussed here offer a first hint of the conditions favoring the evolution of monogamy, which may help us understand how the human case compares with that of other animals, and which natural tendencies (e.g., bonding, caring) it recruited to arrive at a similar arrangement.

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1 Lorenz K (1966) *On Aggression* (Routledge, London); reprinted (2002).

2 Morris D (1967) *The Naked Ape* (Delta, New York); reprinted (1999).

3 Opie C, Atkinson QD, Dunbar RI, Shultz S (2013) Male infanticide leads to social monogamy in primates. *Proc Natl Acad Sci USA* 110(33):13328–13332.

4 Lukas D, Clutton-Brock TH (2013) The evolution of social monogamy in mammals. *Science* 341(6145):526–530.

5 Sugiyama Y (1965) On the social change of Hanuman langurs (*Presbytis entellus*) in their natural condition. *Primates* 6:381–418.

6 Hrdy SB (1974) Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol (Basel)* 22(1):19–58.

7 van Schaik CP, Dunbar RIM (1990) The evolution of monogamy in large primates: A new hypothesis and some crucial tests. *Behaviour* 115:30–62.

8 Gavrilets S (2012) Human origins and the transition from promiscuity to pair-bonding. *Proc Natl Acad Sci USA* 109(25): 9923–9928.

9 de Waal FBM (2005) *Our Inner Ape* (Riverhead, New York).

10 Chapais B (2008) *Primeval Kinship: How Pair-Bonding Gave Birth to Human Society* (Harvard Univ Press, Cambridge, MA).

11 Lovejoy CO (2009) Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326(5949):74e-1–74e-8.

12 Rogers AR, Mukherjee A (1992) Quantitative genetics of sexual dimorphism in human body size. *Evolution* 46:226–234.

13 Boehm C (2012) *Moral Origins: Social Selection and the Evolution of Virtue, Altruism, and Shame* (Basic Books, New York).

14 Gavrilets S (2012) On the evolutionary origins of the egalitarian syndrome. *Proc Natl Acad Sci USA* 109(35): 14069–14074.