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Opinion

Disentangling the Correlated Evolution of Monogamy and Cooperation

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Lifetime genetic monogamy, by increasing sibling relatedness, has been proposed as an important causal factor in the evolution of altruism. Monogamy, however, could influence the subsequent evolution of cooperation in other ways. We present several alternative, non-mutually exclusive, evolutionary processes that could explain the correlated evolution of monogamy and cooperation. Our analysis of these possibilities reveals that many ecological or social factors can affect all three variables of Hamilton's Rule simultaneously, thus calling for a more holistic, systems-level approach to studying the evolution of social traits. This perspective reveals novel dimensions to coevolutionary relationships and provides solutions for assigning causality in complex cases of correlated social trait evolution, such as the sequential evolution of monogamy and cooperation.

Monogamy and the Evolution of Cooperation

Lifetime monogamy has recently been invoked as a critical causal factor in the evolution and maintenance of cooperation in family-based social systems where helpers are offspring of the breeding individual or pair [1,2]. Lifetime genetic monogamy ensures that relatedness between helpers and the siblings they help rear is at least as high as the relatedness between helpers and their own offspring ($r_{sibling} = r_{offspring} = 0.5$). When the relatedness between the altruistic actor and the offspring of the recipient is equivalent to the relatedness between the actor and its own offspring, the relatedness terms in Hamilton's Rule ($r_{sibling}b > r_{offspring}c$) cancel out. Altruistic helping can then be favored when the benefits only marginally exceed the costs ($b > c$) [1,3]. Without genetic monogamy, $r_{sibling} < r_{offspring}$, and benefits must greatly exceed costs for cooperation to spread. Monogamy has thus been argued to provide a 'window' through which social organisms must pass before the evolution of sterile worker castes can occur [1,2]. Although this logic was initially used to explain the evolution of worker sterility in eusocial systems [1,4], genetic monogamy could also be an important factor in the evolution and maintenance of less permanent forms of cooperation such as cooperative breeding in family-based societies [5,6].

Correlations between monogamy and cooperation have been observed in several taxonomic groups. The evolution of sterile worker castes in eusocial hymenoptera is restricted to those lineages with ancestral lifetime monogamy, and polyandry appears to arise only after the loss of worker totipotency [4]. In birds, cooperative breeding appears more often in lineages with low promiscuity [5]. In addition, within cooperative bird species, helping frequency and promiscuity are negatively correlated [5]. In mammals, family-based cooperative breeding societies have also arisen only in socially monogamous lineages [7] (but see [8]). Furthermore, extra-pair paternity in socially monogamous mammals is rare and social bonds between males and females tend to be

Trends

Monogamy and cooperation tend to correlate in evolutionary time. Although traditionally attributed to increased sibling relatedness, a variety of factors could cause this correlation.

Monogamy and cooperation are favored by the same selective pressures and could be indirectly linked in certain environments.

Adaptations resulting from antecedent monogamy could create selective pressure for the subsequent evolution of cooperation. Ancestral adaptations to social monogamy could also provide variation in social traits that could be co-opted for cooperative traits, further contributing to the monogamy–cooperation correlation.

Coevolutionary dynamics between mating systems and social systems could yield correlations among terms in Hamilton's Rule, complicating the assignment of causality to any one term in the evolution of cooperation.

A holistic, systems-level approach is essential for understanding the correlated evolution of complicated behavioral traits, such as monogamy and cooperation.

Evolutionary path analyses should yield tractable methodological solutions for testing causality in complex evolutionary relationships such as that between monogamy and cooperation.

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long-lasting [7]. This results in genetic monogamy that could persist for several breeding cycles, allowing the opportunity for offspring helpers to assist in rearing full siblings [7,9]. Likewise, in birds extra-pair paternity and divorce rate are positively correlated, implying similarly long-lasting periods of high sibling relatedness in genetically monogamous species [10].

The idea of genetic monogamy being an important prerequisite for the evolution of offspring helpers is both intuitively appealing and seemingly well supported in comparative analyses. However, genetic monogamy and cooperative breeding are both attributable to an array of ecological and social factors and are characterized by complex coevolutionary dynamics. Comparative studies that support the monogamy hypothesis have considered only a single link between monogamy and cooperation through sibling relatedness, and have thus ignored alternative explanations for this evolutionary correlation. Owing to the complex relationship between mating behavior and social behavior, a perspective that integrates the interactions that characterize these dynamic systems is necessary for evaluating the relationship between monogamy and cooperation. We adopt this systems-level perspective and use it to outline three alternative evolutionary processes that could account for the disproportionately high occurrence of cooperation in monogamous lineages (Figure 1). We present these alternative pathways not to question the role of relatedness in the evolution of cooperation but rather to highlight the potential complications faced when assessing causality in complex evolutionary relationships. By recognizing the codependence of mating systems and social systems in this way, we further demonstrate that some evolutionary or ecological factors could influence

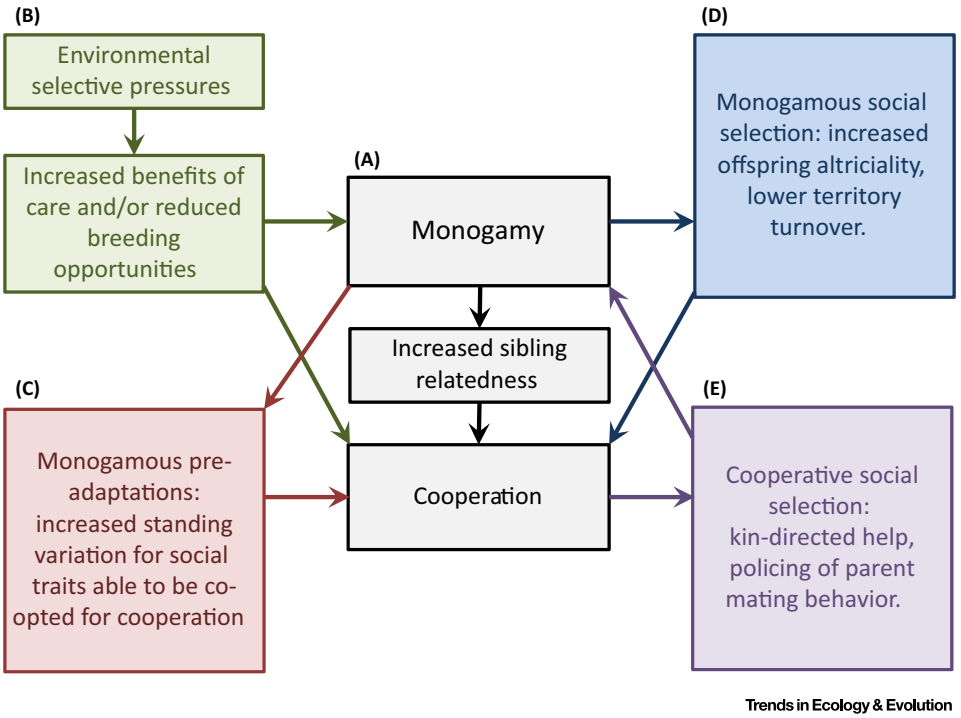

Figure 1. Schematic of the Alternative Hypotheses for the Correlation between Monogamy and Cooperation. Arrows indicate positive relationships. Gray boxes and black arrows (A) represent the classic view of the monogamy hypothesis, indicating a causal relationship between monogamy and cooperation through sibling relatedness. Green boxes and arrows (B) depict how common selective factors could favor monogamy and cooperation simultaneously. Red boxes and arrows (C) show how traits favored for pair cooperation and parental care could be co-opted for use in more complex social contexts. Blue boxes and arrows (D) depict how the evolution of monogamy influences the social environment such that cooperation is favored. Finally, purple boxes and arrows show (E) how cooperation could increase selective pressure for monogamy.