

indicated that the extinction rate was below that for speciation, and far too low to produce an apparent pattern of increased speciation rate on large islands. Moreover, they showed that, on large islands, higher proportions of the lizard communities were comprised of morphologically and ecologically similar species (i.e. 'superspecies complexes'). If speciation rates were comparable among islands, the proportion of species represented by superspecies complexes should arguably be similar.

Losos and Schluter's study shows that the impact of history on species distributions extends beyond that of chance

or accidents of ancestry, but instead, is consistent with evolutionary theory. They also demonstrate that historical effects reflect themselves in patterns of ecomorphology. The proportion of species in superspecies complexes implies that allopatric speciation was common on the largest islands, but became less frequent with decreasing island area, thereby generating a positive species–area relationship. An explanation based on a link between habitat diversity and speciation rate was insufficient because some lineages from old, topographically and climatically diverse islands had not speciated. This suggests that the spatial context of

speciation, rather than ecological selection pressures, was more important in producing the positive species–area relationship in Caribbean *Anolis* lizards. Thus, historical approaches not only complement ecological studies of diversity patterns, but an evolutionary perspective is also essential for understanding community structure.

1 Losos, J.B. and Schluter, D. (2000) Analysis of an evolutionary species–area relationship. *Nature* 408, 847–850

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Infidelity as a transaction between social mates

Why are some females faithful to their mates, whereas others are promiscuous, and why do males tolerate cuckoldry, raising both their own and the young of another male? Determining these answers is central to our understanding of mating systems and sexual selection. The past decade has been marked by an infusion of molecular analyses of paternity, revealing enormous variation in cuckoldry rates across species, populations and even individuals. Arguments have been waged about the underlying determinants of the levels of cuckoldry and female infidelity. In many species, females might be largely in control of which male or males they mate with. Understanding promiscuous behaviour might, therefore, be achieved best by examining the costs and benefits of cuckoldry to females. Until now, however, no formal framework existed that simultaneously took into account both female and male interests to provide a comprehensive explanation of how these costs and benefits might interact to shape the evolution of infidelity.

Janet Shellman-Reeve and H. Kern Reeve¹ have now developed a mathematical model similar to transactional (optimal skew or concession) models in which cuckoldry in broods receiving biparental care is viewed as emerging from a transaction between the mated pair. The model assumes that a female can obtain good genes (i.e. better genes than from her current mate) by mating with a second male. The model also assumes that males can assess their potential risk of being cuckolded, but might not be able to

recognize their own young within the brood. If they suspect, however, that their paternity is sufficiently low, they might choose to abandon both their mate and the brood. Conversely, a female can choose to divorce her mate and raise a brood comprised entirely of cuckolded young on her own. This elegant model provides the first formal framework for evaluating how good genes can tradeoff with good care in determining the frequency of cuckoldry. The model shows that a female is expected to become more promiscuous when the value of the care of her mate (in terms of offspring survivorship) becomes lower or when the genetic quality of a potential cuckold male becomes higher relative to that of the current mate of the female. Given such circumstances, a paired male can only demand the small amount of paternity that a female is willing to give him before she discounts his value altogether and chooses to raise cuckolded young on her own.

Cuckoldry and parental care is perhaps best studied in birds, and the transactional model of Shellman-Reeve and Reeve provides a remarkably unified explanation for all of the major empirically observed predictors of cuckoldry rates in birds that provide biparental care. Perhaps most importantly, the model makes an important connection between the extensive theory of transactions and theory of mate choice and parental investment. It is probable that, given the depth of transactional theory, many more insights will arise from this new association. For example, 'tug-of-war' models might be amendable to address

cuckoldry and parental care in mating systems in which males have more control of paternity, such as might be the case in external fertilizers, or systems where males are larger than females. Nevertheless, it appears that transactional theory might provide the basis for a truly unifying theory of social interactions.

1 Shellman-Reeve, J.S. and H.K. Reeve (2000) Extra-pair paternity as the result of reproductive transactions between paired mates. *Proc. R. Soc. London B Biol. Sci.* 267, 2543–2546

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