ecological context (Pena-Castillo & Hughes 2007). This undoubtedly extends to all model organisms. Ecological genomics shows how connections between fields of research that have been traditionally separated can answer fundamental questions that neither field could have offered on its own.

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doi: 10.1111/j.1365-294X.2007.03504.x

PERSPECTIVE

Phenotype matching and inbreeding avoidance in African elephants

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Abstract

Perhaps the most important 'decision' made by any animal (or plant) is whether to disperse — leave kith and kin, or remain with the familiar and related. The benefits of staying at home are obvious, so dispersal requires an explanation — and the most popular is that dispersal functions to avoid inbreeding depression. Strong support comes from the observation that dispersal is so often sex biased. Simply put, all else being equal members of both sexes should prefer to remain philopatric, but this would lead to inbreeding depression so members of one sex have to disperse. In principle, this link between inbreeding depression and sex-biased dispersal could be broken if individuals recognize close kin and avoid mating with them. Archie *et al.* (2007) provide one of the most compelling analyses to date of the interaction among inbreeding avoidance, kin recognition and mating strategies in any mammal, clearly showing that elephants recognize even close *paternal* kin and avoid mating with them. Their important results illuminate the subtleties of elephant inbreeding avoidance as well as illustrate the difficulty of arriving at definitive answers to questions about the evolution of dispersal behaviour.

Keywords: dispersal, elephants, inbreeding avoidance, mate choice

Received 11 August 2007; revision accepted 24 August 2007

The authors combine over 35 years of behavioural and demographic observation on the elephants of Amboseli National Park and environs with genotyping of 545 individuals at 11 microsatellite loci. Using these data, they examine the relative incidence of three levels of sexual behaviour (male following, guarding and copulating with oestrus females) across four categories of potential mates: relative to non-'close kin' members of other social groups, how often were those behaviours directed at females of their natal group, close kin irrespective of natal group, and close kin related only paternally. In all comparisons, males directed less reproductive behaviours towards females of these three categories, and in all cases, the avoidance was greater for behaviours more likely to result in conception (although 2 of 10 assigned fathers with known natal group sired offspring with a natal female — not significantly different from non-natal group females).

Do these results demonstrate that elephants avoid inbreeding? It depends on the definition of kin. For this study, close kin are defined as showing pairwise genetic distance significantly > 0.25, 'most parents and offspring, many (but not all) siblings, and relatively few less-closely related pairs'. Historically, some analyses have attributed dispersal to avoidance of individuals with $r \approx 0.1$, while others have shown mating preferences for cousins; the varying definitions of 'kin' obscure what may well be nonlinear patterns of mate choice regarding relatedness (Moore 1993). Thankfully, Archie *et al*. carefully define 'close kin'; it is up to the reader to remember that whether elephants prefer or abhor mating with cousins remains to be seen. Although there are good logistical reasons for dichotomizing 'kinship', one hopes that future research will attempt to analytically differentiate among degrees of relatedness ≥ 0.0625, and avoid using the phrase 'non-kin' for individuals with $r \geq 0.125$.

Which elephants avoid close inbreeding? The article is framed around male decision-making, and the authors suggest that the very high costs of competition (death and injury occur) devalue the benefit of an inbred offspring to males. The alternative is that female avoidance of inbreeding increases the cost to males of courting and mating with close relatives. Because of the high costs of gestating and nursing infants, female mammals are expected — and observed — to be more averse to close inbreeding than are males (Waser *et al*. 1986; Moore 1993; Höner *et al*. 2007). It is indicative of the difficulty of studying breeding behaviour in long-lived and slow-reproducing animals that after 30+ years, 'it is unknown exactly how much control females have' (Archie *et al*. 2007). They may not need much: elephants' size allows them largely to escape the two principal dangers of dispersal, predation and starvation. With dispersal nearly 'free' for males and competition costly, even slight female preference for less-related males could favour male dispersal without the males themselves being averse to inbreeding per se. Since dispersal costs are typically high for smaller animals, elephants are problematic exemplars and the debate continues, theory outstripping data (Lawson Handley & Perrin 2007). With more studies like this one and that of Höner *et al*. (2007), though, data will catch up.

The authors found that 3.29% of 152 calves were born to closely related parents, which they note is on the low side compared with some other mammals. However, their estimate may be too low: if inbreeding depression occurs in this population (it might not; see Crnokrak & Barrett 2002), early (including prenatal) mortality would remove inbred calves from the population before their faeces could be sampled. To the extent that inbreeding depression is a factor, they unavoidably are less likely to detect inbreeding. This is just one of the complexities involved in testing functional explanations for dispersal (see Fig. 1 for another).

That elephants can identify paternal kin via phenotype matching is intriguing. If the mechanism is olfactory (as seems likely), it lends support to the idea that elephants can recognize the bones and ivory of deceased relatives. McComb *et al*. (2006) found no evidence of such post-mortem kin recognition, but they washed their experimental skulls. The possibility that a sense of kinship extends beyond the natal family and after death should be remembered when culling is considered.

Undeniably, the consequence of sex-biased dispersal in animals is that inbreeding is reduced. Concluding that it functions to avoid inbreeding is complicated for three interrelated but distinct classes of reason: first, there are a number of genetical and behavioural reasons to stay close to home (Waser *et al*. 1986); second, the cost of inbreeding may be determined by dispersal patterns rather than drive them (cf. Crnokrak & Barrett 2002); and third, alternative functions (e.g. avoiding intrasexual competition) may be sufficient to explain most (but not all) observed sex-biased dispersal (Moore 1993). The theory suggests that only one sex should disperse, but dispersal by both males and females is reasonably common (Moore 1984; Lawson Handley & Perrin 2007). The theory is severely strained by nondispersal. While rare (perhaps unexpectedly so, cf. Kokko & Ots 2006), examples of animals in which many/most members of both sexes remain geographically or socially philopatric do exist, with (Thunken *et al*. 2007) or without (Keane *et al*. 1996; Winters & Waser 2003) close inbreeding. Intriguingly, sympatric groups of killer whales show either total bisexual natal philopatry or a mix of philopatric and dispersing individuals of both sexes, depending on foraging ecology (Baird & Whitehead 2000).

Fig. 1 'He's not my father!' — no full siblings were detected by Archie *et al*. It is too soon to tell whether this was due to avoidance of repeat breeding (which would be both curious and relevant to analyses of dispersal) or (more likely) small sample size. Photo by Petter Granli.

The authors' attention to the implications of their findings for elephant management is welcome; inbreeding (and outbreeding) effects must be considered when designing protected areas (Edmands 2007). However, elephants are long-lived, capable of long-distance dispersal through inhospitable habitat, and we now know that they can behaviourally avoid inbreeding. Although their long-term survival requires attention to genetic considerations, they should be relatively slow to suffer genetically from habitat fragmentation. By contrast, fragmentation can facilitate illegal hunting for bushmeat and ivory, both immediate and pressing concerns (Fig. 2; see www.bushmeat.org). Molecular biologists make important contributions to population monitoring and protected area design, but in far too many places gangs of poachers with AK-47 s are a more urgent problem.

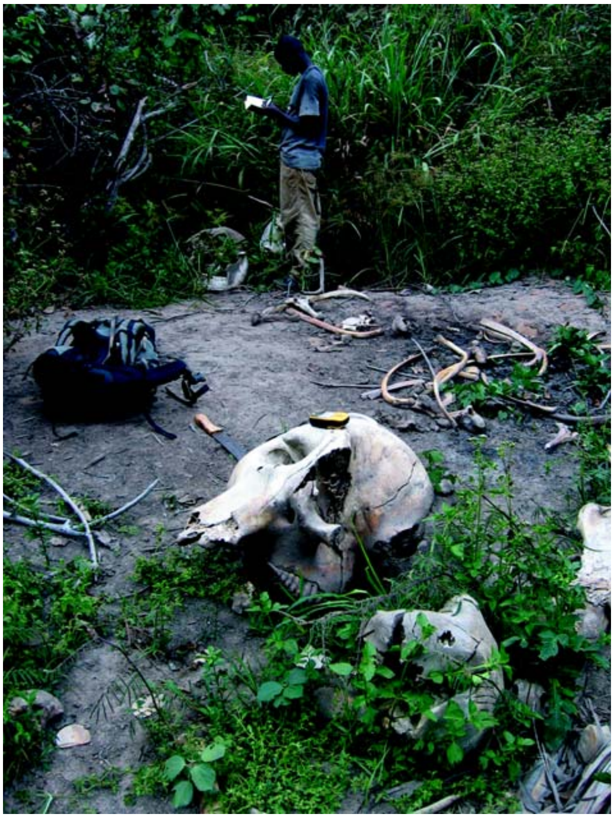

Fig. 2 The tuskless adult may be a sign of genetic drift due to population fragmentation rather than adaptive response to ivory hunting (Whitehouse 2002), but inbreeding didn't kill the calf (foreground) or four adults found in a Forest Reserve in Tanzania. Photo by the author.

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doi: 10.1111/j.1365-294X.2007.03560.x

PERSPECTIVE

The origins of weedy rice

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Abstract

Where do weeds come from? How do they evolve from non-weedy ancestors? In this issue of *Molecular Ecology*, Londo and Schaal examine the origin of weedy rice (*Oryza sativa*) populations in the USA. Analysing nuclear DNA sequence and microsatellite data, they show the importance of parallel evolution, hybridization, gene flow, and migration in the evolution of these weeds.

Keywords: crops, evolution, gene flow, hybridization, rice, weeds

Weedy rice infests rice fields worldwide. It is a particularly insidious weed due to its similarity to the domesticated varieties. Many of the easiest ways to kill weedy rice are likely to also harm the crop, so weed management is problematic. Moreover, if even a small fraction of the weedy plants survive and reproduce, weedy rice is so productive that it can spread and cause major economic damage (Ferrero 2003). There are some barriers to gene flow between domesticated *Oryza sativa* and its wild ancestor, *Oryza rufipogon* and other species of weedy rice, but gene flow can still occur (Chu & Oka 1970; Chen *et al*. 2004). Thus, one factor that may make this weed particularly problematic is that improvements introduced into domesticated rice can also spread into its weedy relatives

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