EVOLUTIONARY BIOLOGY

Of war, tusks, and genes

Societal conflict leaves an evolutionary signature in wildlife

By **Chris T. Darimont**[1,2] *and* **Fanie Pelletier**[3]

Elephants have long been dragged into war. Referred to as "elephantry," military units rode into battle atop these giants over millennia. On page 483 of this issue, Campbell-Staton *et al.* (*1*) describe the evolutionary aftermath of a different type of wartime elephant use. Seeking ivory to finance a civil war in Mozambique, poachers relentlessly targeted specific African elephants (*Loxodonta africana*), individuals with tusks, sending the population—and the frequency of this important trait—into decline. The study reveals the consequence of this intense selective killing on the persistence of tusks and the genes associated, as well as for population dynamics. Campbell-Staton *et al.* also identify the simple genetic architecture underlying the presence of tusks. The findings bring new evidence to inform debates on the roles of environmental and selective forces underlying trait variation in populations subject to harvest.

Over and above the environmental variation to which populations are subject, selective killing of specific phenotypes can influence traits such as body or ornament (for example, horn, antler, or tusk) size. Through multiple analyses, Campbell-Staton *et al.* report how intensive selective killing of African elephants caused the rapid evolution of increased tusklessness in females. Field data revealed that the proportion of tuskless females increased by more than 30% as the population declined over 28 years, which included 15 years of civil war. The frequency of tuskless phenotypes among adult females born after the war was also higher than before the conflict, suggesting an evolutionary response. Simulations showed that the observed increase in tusklessness is extremely unlikely to have occurred without selective killing of tusked animals. Model outputs

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Elephants in Gorongosa National Park, Mozambique, declined by 90% during the 20-year civil war because of ivory poaching. This spurred the rapid evolution of tuskless females, such as this female *Loxodonta africana*.

estimated that the survival of tuskless individuals was five times higher than that of tusked individuals.

Campbell-Staton *et al*. also investigated whether these phenotypic changes were accompanied by a genetic signature. Analyses of whole-genome sequences from individuals with and without tusks supported the hypothesis of a more severe population decline among tusked compared with tuskless individuals. The authors then looked for a pattern of inheritance that could explain the variation in tusk morphology observed in the field. Using data on mother-offspring phenotypic associations, they found that for ~9 out of 10 offspring, the phenotype of the offspring was consistent with a single-locus X-linked dominant model of inheritance. The observed sex bias in the offspring produced by tuskless mothers suggest that tuskless male offspring were nonviable. Using a candidate gene approach, they then identified two genes involved in tusk presence that explain a large amount of variation: *AMELX* (*X-linked isoform of amelogenin*) and *MEP1a (meprin A subunit alpha*), which are known to have functional associations with the development of mammalian teeth. Physical linkage between *AMELX* and male-lethal loci nearby on the X chromosome may explain lethality among males inheriting the trait.

Campbell-Staton *et al*.'s elegant approach is among the rare studies to document a genetic response to harvest selection, informing debate about the potential for selective harvests to lead to evolutionary responses. Work on trophy hunting of bighorn sheep (*Ovis canadensis*) in Canada, for example, has shown that size-selective regulations with no harvest quotas can lead to the evolution of smaller horns (*2*), although the genetic mechanism remains to be elucidated. The lack of evidence linking observed phenotypic trends to changes in the genetic composition of harvested populations more broadly, however, has been used by wildlife and fisheries managers and scientists to argue against the likelihood or importance of potential evolutionary changes in harvest systems (*3*). The comprehensive work by Campbell-Staton *et al*. has clearly satisfied the burden of evidence, showing that selective killing can indeed leave a strong evolutionary signature. Restoration of the trait and its associated ecosystem function might therefore require longer time scales than those for phenotypic changes not associated with genetic changes, an important implication relevant to other systems.

Generalization of the findings on African elephants is constrained by the relatively simple genetic basis underlying tusklessness. Although other studies have shown that ornament traits can be influenced by a single gene [such as horn size in Soay sheep, *Ovis aries* (*4*)], it is more commonly observed that traits involved in response to environmental changes, including selective mortality, are affected by both many small-effect genes and in some cases one or a few genes of major effect (*5*). Accordingly, a quantitative understanding of whether and how much the phenotypic changes observed in myriad animal populations subject to harvesting (*6*) are associated with genetic changes remains a complex challenge (*7*).

More broadly, even perfect knowledge of underlying genetic contributions do not address social-evolutionary processes that influence nonhuman life in today's world. An extreme social event (a war, in this case) that triggered intense, selective exploitation of elephants crisply illustrates the pronounced coupling between human societies and evolutionary processes in other life forms. Through humanity's cultures, economies, medicines, built environments, and more, societies have set in motion selective landscapes never before experienced by the world's biota (*8*). Moreover, and often related to ecological changes imposed by humans, societies must commonly respond to the evolution of other organisms, a reality brought into painful relief during this extended COVID-19 pandemic. Recently, such complex relationships among society, ecology, and evolution have been well examined in perhaps the most radically changed of all landscapes, cities (*9*). The conceptual advances gained in urban systems can inform work in other contexts in which humanity's hand in, and response to, evolution will likely also be observed. Future work could also draw upon the well-developed theoretical basis for understanding sustainability in what has been referred to as "social-ecological systems" (*10*), which could be adapted to consider evolutionary interactions and outcomes.

Progress in understanding these complex relationships will require more interdisciplinary research. Until recently, natural and social sciences have largely been independent enterprises. In the context of harvest selection, evolutionary ecologists could team up with social scientists. They may ask, for example, how hunters and fishers would trade-off, personally and economically, the ability to target the largest phenotypes now with the specter of losing those phenotypes in the future. As noted in the context of ecology (*10*), past and current societies and the institutions that govern them might have considered similar trade-offs and sought solutions from which researchers and managers can potentially learn. ■

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REFERENCES AND NOTES

1. S. C. Campbell-Staton *et al*., *Science* **374**, 483 (2021).
2. G. Pigeon, M. Festa-Bianchet, D. W. Coltman, F. Pelletier, *Evol. Apps* **9**, 521 (2016).
3. A. Kuparinen, M. Festa-Bianchet, *Philos. Trans. R. Soc. Lond. B Biol. Sci*. **372**, 20160036 (2017).
4. S. E. Johnston *et al*., *Nature* **502**, 93 (2013).
5. R. A. Bay *et al*., *Am. Nat*. **189**, 463 (2017).
6. C. T. Darimont *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **106**, 952 (2009).
7. F. Pelletier, D. W. Coltman, *BMC Biol*. **16**, 7 (2018).
8. S. R. Palumbi, *Science* **293**, 1786 (2001).
9. S. Des Roches *et al*., *Evol. Apps* **14**, 248 (2020).
10. E. Ostrom, *Science* **325**, 419 (2009).

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