complete. Take, for example, the LINE-1 transposable elements that are present in half a million copies – over 20% of the human genome. While the occasional transposon insertion will be maintained by purifying selection, the vast majority of them persist because of their selfish ability to self-replicate independently of the rest of the genome. Yanai and Lercher repeatedly emphasize that the citizens in the society of genes are involved in both cooperative and competitive interactions. Under this view of life, LINE-1 and other selfish genetic elements are easily accommodated.

In general, the original gene's-eye view and its vision of the history of life as a struggle of competing replicators helped make sense of longstanding evolutionary problems including the evolution of sex, altruism, and genetic conflicts. Moreover, like any conceptual framework worth its salt, it also introduced myriad new ones. One of these was the very existence of the genome itself. Why, given that each gene is looking out for itself, do genes come together in complex networks to construct organisms? Why do not selfish genetic elements, genetic entities promoting their own transmission at the expense of other genes and/organismal fitness, completely take over? How, as John Maynard Smith [2] put it, 'did it come about that most genes, most of the time, play fair, so that a gene's fitness depends only on the success of the individual that carries it?'

This is an area where the literature on major transitions in individuality has a lot to offer [3,4]. These transitions occurred when independently replicating individuals form collectives that can now reproduce only as a whole, thus forming a new level of individuality. Examples include the origin of multicellularity and eusocial societies. The first and most fundamental transition was the origin of the genome from cooperating replicators. Yanai and Lercher do not make use of the concept of major transitions, but several of their case studies could readily be incorporated. In addition to the cancer and transposable element examples mentioned above, I especially liked their discussion of the RNA World, a topic that, with a few notable exceptions [5], is largely absent from the mainstream study of conflict and cooperation. Similarly, their treatment of the origin and regulation of gene networks highlights another empirical goldmine to be approached with the tools of social evolution.

Genomes share many features with a complex society. Moreover, the origin of the genome was the first and only universal major transition and it has shaped all of life. Yet, its social evolution has typically received little attention. This book is a great contribution to the redressing of this balance.

The Society of Genes by Itai Yanai and Martin Lercher, Harvard University Press, 2016. US$27.95/£20.95, hbk (282 pp.) ISBN 978-0-674-42502-6

[1]Department of Molecular Biology and Genetics, Cornell University, Ithaca, NY 14853, USA

*Correspondence: arvid.agren@cornell.edu (J.A. Ågren).
@Twitter: @arvidagren

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Letter

Does Trophy Hunting Support Biodiversity? A Response to Di Minin *et al.*

William J. Ripple,[1,*] Thomas M. Newsome,[1,2,3] and Graham I.H. Kerley[4]

In their recent article 'Banning Trophy Hunting Will Exacerbate Biodiversity Loss' [1], Di Minin *et al.* presented a set of arguments in support of trophy hunting. They suggested that trophy hunting will benefit biodiversity (i.e., the number of plant and animal species in an area) through several main mechanisms, including (i) increased funding for conservation; (ii) a smaller carbon footprint compared with ecotourism; and (iii) the emphasis on maintaining large wildlife populations. Unfortunately, these justifications do not go deep enough into the direct and indirect mechanisms that affect native plant and animal species and ecosystems. In addition to potential social, economic, and ethical issues, we argue that greater consideration of the ecological and evolutionary effects of trophy hunting is required to fully evaluate it as a conservation tool.

For example, Di Minin *et al.* [1] stated that greenhouse gas emissions by ecotourists would be larger than those of trophy hunters because there are more ecotourists than trophy hunters. However, these ecotourists account for an extremely small fraction of total global greenhouse gas emissions, and these emissions cannot be linked to biodiversity at trophy hunting sites. Di Minin *et al.* [1] also emphasized that maintaining large wildlife populations for trophy hunting would aid biodiversity conservation. However, most of the individual animals that are hunted as trophies are large herbivores, and maintaining large populations of these high-demand species may not have any effect on the total number of plant and animals species in the area (i.e., biodiversity), or could cause biodiversity to decline due to potential impacts on plant communities from overgrazing and overbrowsing. This decline was the case in Yellowstone National Park, where the ecosystem was severely degraded after extensive hunting by humans and culling of large herbivores failed to take the predatory place of gray wolves as keystone species [2]. In addition, by maintaining high densities of a few select large herbivores inside game ranches (or in the absence of their predators), it could be detrimental where overgrazing or overbrowsing decreases foraging opportunities for coexisting native herbivores [3].

Trophy hunting can also distort community structure and function on game ranches, where less valuable species are replaced by more valuable species [4], or where predators are persecuted to protect valuable large herbivores, which are considered trophy species [5]. In addition, species are frequently introduced to broaden the range of hunted species, and these carry risks of becoming invasive, competing, or hybridizing with indigenous species, and spreading diseases and parasites [6]. Fencing on game ranches can fragment wildlife populations [7], leading to the disruption of dispersal and migratory movements, inbreeding and loss of heterozygosity. If trophy hunting dramatically distorts community structure and function, other potential ecological consequences include changes to predator–prey dynamics, herbivore–plant interactions, and density or behaviorally mediated trophic cascades [8]. These changes could result in 'trophic downgrading' of ecosystems, putting additional pressure on biodiversity [9].

There are also evolutionary-scale consequences of the selective harvesting of trophy animals with particular heritable phenotypic traits [10,11]. This artificial selection typically leads to a rapid decline (within a few generations) in the desired trophy attributes within the hunted population. Such traits, including features such as body size, may be linked to other fitness-related attributes, such as physiological tolerances or disease resistance [10] and, thus, would lead to a decline in fitness. These selective pressures, which amount to domestication, vary as a function of hunting intensity, duration, and population size, and, thus, fluctuate among species [11]. Another form of domestication emerging from trophy hunting is the selective breeding for desirable traits in individuals, such as large manes in lions [12] or, in extreme cases, artificially selected color variants maintained by inbreeding [6].

Di Minin *et al.* [1] are correct in stating that trophy hunting can increase funding for conservation (this is well known), but they have failed to address the effects of trophy hunting on the suite of mechanisms driving species interactions, plant community dynamics, natural selection, trophic cascades, and ecosystem structure and function. While there are many issues relating to the pros and cons of trophy hunting, we suggest that the ecological and evolutionary discussion should focus on relevant variables and interactions that can be linked to trophy hunting. This discussion would then help drive the research that is needed to further the important debate on the ecological consequences of trophy hunting. Moreover, this would alert the trophy-hunting industry to areas of research that need to be funded and supported by the industry itself.

[1]Global Trophic Cascades Program, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA
[2]Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, VIC 3125, Australia
[3]Desert Ecology Research Group, School of Biological Sciences, University of Sydney, NSW 2006, Australia
[4]Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela Metropolitan University, Port Elizabeth, 6031, South Africa

*Correspondence: bill.ripple@oregonstate.edu (W.J. Ripple).

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Letter

Trophy Hunting Does and Will Support Biodiversity: A Reply to Ripple *et al.*

Enrico Di Minin,[1,2,*] Nigel Leader-Williams,[3] and Corey J.A. Bradshaw[4,5]

In our paper [1] we discussed the importance of trophy hunting as a conservation tool provided it can be done in a controlled manner to benefit biodiversity conservation and local people. To address some of the concerns about trophy hunting, we proposed adopting 12 new recommendations that embrace the guiding principles on trophy hunting promoted by the International Union for the Conservation of Nature. Ripple *et al.*'s comment [2] on our paper argues that greater consideration needs to be given to the ecological and evolutionary effects of trophy hunting to evaluate it fully as a conservation tool. Most of the concerns that they raise have already been raised and are not restricted to trophy hunting. In fact, these same concerns also apply to conservation areas where ecotourism is the primary land use. In addition, their reply is limited in scope because their concerns apply