

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.

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Letter

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

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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

mainly to a single country – South Africa – and have been discussed in detail elsewhere [3].

In this reply, we restate the importance of trophy hunting to create incentives for biodiversity conservation, preventing habitat loss, and highlight how improvements in conservation policy can be used to address some of the concerns raised. Ripple *et al.* [2] state that 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’. However, not only did they neglect to quantify this fraction but they also overlooked the problem that the contribution of emissions from tourism to climate change sets a potentially major challenge for the sustainability of international tourism. Indeed, tourism transport, accommodation, and associated activities contributed an estimated 5% of global anthropogenic CO₂ emissions in 2005 [4]. Climate change is already threatening the persistence of biodiversity at trophy-hunting sites, as demonstrated by the increasing frequency of extreme El Niño events (e.g., the current drought threatening southern Africa) [5]. Ripple *et al.* [2] also mentioned how maintaining large populations of targeted species, especially large herbivores, can affect biodiversity via overgrazing/browsing, but this issue is not restricted to areas where trophy hunting is the main land use; rather, it is common to most small, fenced conservation areas where ecotourism is the dominant activity [6].

Despite already raising the issue in our paper and providing recommendations to avoid such consequences [1], Ripple *et al.* [2] stated how trophy hunting can disrupt community structure and functioning, with evolutionary-scale consequences when ‘... less [economically] valuable species are replaced by more [economically] valuable species, or where predators are persecuted to protect [economically] valuable large herbivores’. However, this concern is

mainly limited to South Africa where many wildlife populations are artificially managed within fenced reserves. The full range of species needed to create a functional ecosystem might not be available at trophy hunting sites (this is also the case of conservation areas where ecotourism is the main land use and where many species have been historically extirpated). The main weakness of this critique is that unless harvest is intensive and affects a large proportion of the adult population (i.e., decidedly not the case for most trophy-hunted species in Africa), negative evolutionary consequences of harvest are unlikely. Our recommendation for population viability analyses [1] that include the evolutionary consequences of harvest are certainly advisable in cases where rare or small-population species are trophy-hunted. Additionally, species richness and community structure are higher in these intensively managed sites compared with agricultural and other competing land uses [7]. Predator persecution is indeed an issue in South Africa, although national and local conservation authorities are responding to this problem by implementing evidence-based conservation actions (e.g., [8]). Additionally, a year-long ban on leopard hunting has been imposed in 2016 to gather more evidence on the size of South Africa's leopard population [9].

Even though the problem applies equally to ecotourism, the issue with managed species derived from elsewhere in South Africa can be addressed by improving current policies (e.g., the Biodiversity Act in South Africa) to prevent introductions of such *ex situ* species. However, there is considerable debate globally regarding what constitutes a species' ‘previous’ range, and whether this should be the dominant consideration when deciding whether to assist migration in light of shifting climates [10]. Furthermore, the South African Hunters and Game Conservation Association have strongly denounced selective and intensive game breeding practices (e.g., enhancing or altering genetic characteristics of game

species for commercial purposes, including artificial and unnatural manipulation to achieve unusual coat colors and excessive horn lengths), and they have called upon the South African government to implement conservation strategies in the interest of protecting the country's biodiversity [11].

In conclusion, we reiterate how the lack of incentives generated from trophy hunting will worsen biodiversity loss, but that compared with ecotourism, trophy hunting can provide much greater area-based returns to funding conservation and have fewer negative impacts in terms of emissions and ecosystem functioning. Our recommendations [1] require that resources generated from trophy hunting are used to monitor targeted (and even non-targeted) species and ecosystems. Without doubt, there is a need to improve and enforce national policies that consider the ecological, social, and economic issues around trophy hunting. Furthermore, we support the notion that the conservation community would benefit from a better understanding of the ethics of trophy hunting [12].

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Letter

Bolder Takes All and the Role of Epigenetics. A Comment on Canestrelli *et al.*

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In a recent article in *TREE*, Canestrelli *et al.* [1] make a case for the role of animal personality in biogeography through historical colonisation processes, by arguing that personality as a heritable trait affects dispersal propensity and population structure. They propose focussing on the use of genomic tools to investigate the genetic architecture of animal personality, after which spatial and temporal variation in personality can be studied to test their hypothesis. Here we want to broaden this discussion by expanding on the contribution of heritable epigenetic variation to personality phenotypes, which may have important consequences for the

maintenance of personality variation in time and thereby the methods suitable for testing the hypothesis proposed by Canestrelli *et al.* [1].

The importance of animal personality in dispersal and colonisation processes is undebated (e.g., [2,3]). The underlying proximate mechanisms of variation in personality traits, however, are a continuous subject of discussion. Animal personality traits have a heritable component and much of the research attention has been focussed on the association between novelty-seeking behaviour and genomic variants at the *DRD4* gene. With recent increased research efforts, it is becoming clear that consistent patterns linking *DRD4* polymorphisms with behavioural traits are not obvious [4–6]. In addition, existing associations can be lost over time as a result of changing environments, with the consequence that the original associations with specific genotypes cannot be retrieved.

Several recent studies have argued that behavioural variation is partly mediated by epigenetic mechanisms [7], and variation in DNA methylation in, for example, *DRD4* has also been shown to be linked to heritable variation in both human [8] and animal [9] studies. Although evidence is accumulating that DNA methylation patterns are heritable for at least some generations, the nature of such epigenetic marks is that they are more plastic than the underlying genes. Whereas genomic variation, regardless of the association with the phenotypes, will be maintained and can therefore be investigated for many generations, we must assume at this stage that methylation patterns are faster to erode with time. Returning to Canestrelli *et al.* [1], we therefore face the challenge of investigating the role of personality in historical colonisation processes while the variation in and heritability of personality that can be attributed to DNA methylation is likely to be absent in contemporary populations.

To circumvent such issues of signal erosion, we here propose to first focus on current range expansions or metapopulation processes to obtain a mechanistic understanding of the role of DNA methylation in the link between personality and colonisation. While there is a strong focus on the role of personality in contemporary colonisation processes as reviewed by Canestrelli *et al.* [1], DNA methylation has thus far received little research attention. This is unsurprising as there are three questions to be answered about the link between personality and DNA methylation before we can proceed to the importance of this link in colonisations. First, which part of the variation in and heritability of personality traits in wild populations can be attributed to DNA methylation and which genes are involved? Second, are personality–methylation associations dependent on the environment? If personality-dependent methylation is purely environmentally driven, this will contribute only to the plasticity in behaviour rather than in the consistent nature of personality traits. Third, what is the transgenerational inheritance of personality-related methylation patterns?

Only when these questions are answered we can investigate the importance of personality-associated DNA methylation by integrating methylation measures into current research on personality effects on colonisation. This will require observations on temporal and spatial variation in methylation patterns across populations. As such data will be hard to retrieve, individual-based and spatially explicit simulation models are a good tool to extrapolate any observed relationships in space and time to further the generation of testable hypotheses. Returning to historical processes, there is recent evidence that methylated parts of the genome have an increased mutation rate [10]. As techniques improve, this information can be used to expose past methylation patterns that are related to colonisation–behaviour associations. Alternatively, the use of ancient DNA