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Contributed Paper

A framework to measure the wildness of managed large vertebrate populations

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Abstract: As landscapes continue to fall under human influence through habitat loss and fragmentation, fencing is increasingly being used to mitigate anthropogenic threats and enhance the commercial value of wildlife. Subsequent intensification of management potentially erodes wildness by disembodying populations from landscape-level processes, thereby disconnecting species from natural selection. Tools are needed to measure the degree to which populations of large vertebrate species in formally protected and privately owned wildlife areas are self-sustaining and free to adapt. We devised a framework to measure such wildness based on 6 attributes relating to the evolutionary and ecological dynamics of vertebrates (space, disease and parasite resistance, exposure to predation, exposure to limitations and fluctuations of food and water supply, and reproduction). For each attribute, we set empirical, species-specific thresholds between 5 wildness states based on quantifiable management interventions. We analysed data from 205 private wildlife properties with management objectives spanning ecotourism to consumptive utilization to test the framework on 6 herbivore species representing a range of conservation statuses and commercial values. Wildness scores among species differed significantly, and the proportion of populations identified as wild ranged from 12% to 84%, which indicates the tool detected site-scale differences both among populations of different species and populations of the same species under different management regimes. By quantifying wildness, this framework provides practitioners with standardized measurement units that link biodiversity with the sustainable use of wildlife. Applications include informing species management plans at local scales; standardizing the inclusion of managed populations in red-list assessments; and providing a platform for certification and regulation of wildlife-based economies. Applying this framework may help embed wildness as a normative value in policy and mitigate the shifting baseline of what it means to truly conserve a species.

Keywords: dynamics, indicator, management, policy, regulation, wildlife

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Un Marco de Trabajo para Medir el Estado Salvaje de Poblaciones de Vertebrados Mayores bajo Manejo

Resumen: Conforme los paisajes siguen cayendo bajo la influencia del humano por causa de la pérdida del hábitat y la fragmentación, cada vez se usa más el encercado para mitigar las amenazas antropogénicas o incrementar el valor comercial de la fauna. La intensificación subsecuente del manejo tiene el potencial para erosionar el estado salvaje al desincorporar a las poblaciones de los procesos a nivel de paisaje, desconectando así a las especies del proceso de selección natural. Por lo tanto, se necesitan herramientas para medir el grado al cual las poblaciones de especies de vertebrados mayores dentro de áreas de fauna protegidas y privadas son autosostenibles y libres de adaptarse. Diseñamos un marco de trabajo para medir dicho estado salvaje con base en seis atributos relacionados con las dinámicas evolutivas y ecológicas de los vertebrados (espacio, resistencia a las enfermedades y a los parásitos, exposición a la depredación, exposición a las limitaciones y fluctuaciones en las reservas de agua y alimentos, y reproducción). Para cada atributo, establecimos umbrales empíricos y específicos por especie entre cinco estados salvajes basados en las intervenciones de manejo cuantificables. Usamos datos de 205 propiedades privadas de fauna con objetivos de manejo que abarcan desde el ecoturismo hasta el uso para consumo para probar el marco de trabajo en seis especies de herbívoros con una gama de estados de conservación y valores comerciales. Los puntajes de estado salvaje entre las especies difirieron significativamente y la proporción de poblaciones identificadas como salvajes osciló del 12% al 84%, lo que indica que la herramienta detectó diferencias a escala de sitio entre las poblaciones de diferentes especies y las poblaciones de la misma especie bajo diferentes regímenes de manejo. Si cuantificamos el estado salvaje, este marco de trabajo les proporciona a los practicantes las unidades de medida estandarizadas que vinculan a la biodiversidad con el uso sostenible de la fauna. Las aplicaciones de este marco de trabajo incluyen informar a los planes de manejo de las especies a escalas locales; estandarizar la inclusión de las poblaciones manejadas en las evaluaciones de listas rojas; y proporcionar una plataforma para la certificación y regulación de las economías basadas en la fauna. La aplicación de este marco de trabajo puede ayudar a insertar a la fauna como un valor normativo dentro de la política y a mitigar la línea base cambiante de lo que significa conservar verdaderamente a una especie.

Palabras Clave: dinámicas, fauna, indicador, manejo, políticas, regulación

摘要: 人类活动引起的栖息地丧失和破碎化对景观造成了破坏, 为此, 越来越多的人使用围栏来减缓人为威胁的影响, 或提高野生动物的经济价值。这一举措带来的强化管理可能会使种群在景观尺度上脱离生物学过程, 不再受到自然选择而丧失野性。因此, 需要一套方法来评估保护地和私人领地中大型脊椎动物种群自我维持和适应环境的情况。我们设计了一个框架, 基于与脊椎动物的进化和生态动力学相关的六个属性 (空间、疾病和寄生虫抗性、被捕食风险、食物及水资源的限制和波动、繁殖) 来评估它们种群的野生性。我们根据可量化的管理干预措施, 对每个属性都设置了五种野生性等级之间物种特异的经验阈值。接下来, 我们收集了管理目标从生态旅游到消耗性利用的 205 个私有野生动物产业的数据, 用于检测这个框架在保护等级和经济价值各异的六种食草动物中的应用情况。结果表明, 不同物种的野生性指数差异显著, 被认为是野生的种群占比在 12%-84% 之间, 这说明我们的框架工具可以检测出相同或不同物种的种群在不同的管理制度下位点尺度的差异。通过对野生性的定量分析, 我们的框架为保护实践者提供了连接生物多样性与野生动物可持续利用的标准化计量单位, 可以应用于为当地的物种管理计划提供信息、在红色名录的评估标准中纳入人为管理种群, 以及为野生动物产业提供认证和监管平台等等。应用这一框架还有助于将野生性作为一种价值规范纳入政策体系, 并且在物种保护的定义变化时减缓影响。**【翻译:胡怡思; 审校: 聂永刚】**

关键词: 野生动物, 指标, 政策, 规章, 动态, 管理

Introduction

Fragmentation from road construction, human settlement expansion, and a myriad of associated anthropogenic pressures is bringing wildlife species under human influence (Peterson et al. 2005; Laurance et al. 2014; Jones et al. 2018). Many protected area managers across the world, most notably in southern Africa, Australia, New Zealand, and the United States, are increasingly using fencing to respond to these threats (Hayward & Kerley 2009; Packer et al. 2013; Ringma et al. 2017), but there are concerns that such confinement undermines conservation value by stabilizing abundance at the expense of broader landscape connectivity (Woodroffe et al. 2014). Private landowners also use fences to reduce business risks and manage the commercial utilization of wildlife (Butler et al. 2005; Carruthers 2008; Mysterud 2010), which includes activities such as trophy hunting, selective breeding for live sales, meat production, and ecotourism (reviewed in Taylor et al. [2015]). Both conservation- and commerce-oriented paradigms can thus result in the intensification of management.

Management practices may convert selective pressures from natural to artificial by controlling breeding (e.g., mate pairing), mortality (e.g., disease control, hunting or predator removal), access to food and water (e.g., supplementary feeding and artificial waterpoint construction), and patterns of space use (e.g., perimeter fencing and the installation of enclosures) (Von Brandis & Reilly 2007; Hetem et al. 2009; Mysterud 2010; Taylor et al. 2015; Pitman et al. 2017), which undermines the fitness of the managed animals (Jule et al. 2008; Willoughby et al. 2017). Such practices may ultimately reduce natural variability in pattern and process and thus homogenize ecological communities (Clements & Cumming 2017). Because management strategies exist along a spectrum from captive-breeding to landscape-scale management, conservationists must determine at what point wildlife ceases to be wild so that biodiversity conservation and sustainable development can be balanced. Measuring wildness can be used to evaluate the effectiveness of interventions in conserving flourishing populations in functioning ecosystems (Redford et al. 2011) and may also assist policy makers to foster multifunctional landscapes that provide economic opportunities but retain biodiversity. Developing tools that help to quantify and visualize the potential trade-offs and synergies between these 2 goals will be crucial in bridging the gap between science and policy.

Wildness concerns the degree to which individuals exist autonomously in evolutionarily and ecologically functioning populations where genetic and phenotypic diversity enables natural selection to produce adaptation (Moritz et al. 2002; Redford et al. 2011; Mallon & Stanley Price 2013). The dynamic functional relationships between and within species sustain biodiversity by creating niches and generating landscape heterogeneity, thus establishing feedback loops between ecological and evolutionary processes (Erwin 2008; Laland & Boogert 2010; Odling-Smee et al. 2013). Cumulatively, these emergent properties of flux, dynamism, and autonomy can be called "wildness" (Evanoff 2005; Mallon & Stanley Price 2013; Pickett 2013), where interactive processing between organisms and their environment produces resilient systems (Cookson 2011). Thus, wildness is an integral property of ecosystem functioning and potentially ecosystem service delivery. Wildness, however, does not necessarily correspond to pristineness. Rather, they can be seen as orthogonal qualities where the apex of both is wilderness (Aplet et al. 2000). Specifically, Aplet et al.'s (2000) continuum of wildness distinguishes between naturalness, which describes the composition and structure of an ecosystem, and "freedom from human control," which describes the degree of biodiversity being self-willed. It is this latter quality, as applied to wildlife populations, that we aimed to describe here. Selective pressures may be different in human-modified landscapes ("novel ecosystems"; Hobbs et al. 2013), but degrees of wildness can still occur if species are provided with the opportunity to adapt to these pressures through natural selection and fulfill their functional roles within the landscape. Management that enables interaction between all components of the ecosystem will work to "produce wild things" (Cookson 2011) even within novel environments.

Biodiversity assessments should thus incorporate the capacity of populations (which we define as geographically distinct groups between which there is little demographic or genetic exchange), to be self-organized, self-sustaining, and integrated into an ecosystem. Currently, there is no standardized, measurable definition of wildness of a population. For example, the International Union for Conservation of Nature's (IUCN) Red List criteria define managed populations as wild if management aims to counteract human-induced threats or manage the overall habitat for the long-term persistence of the population. Conversely, populations dependent on direct intervention, where they would become locally extinct within 10 years without management, are not considered wild (IUCN 2017). These guidelines lack comprehensive empirical thresholds that can be used to standardize wildness evaluations. The vagueness of wildness as a concept prevents decision makers from establishing clear interventions and standards relating to species and land management and may lead to inflated estimates of conservation success. Given the global push to expand protected areas, and the simultaneous demands of conservation areas to contribute to sustainable development (Watson et al. 2014; Taylor et al. 2015), evaluating the effectiveness of these multifunctional landscapes in retaining conservation value is becoming a key policy issue.

Decision makers need objective, standardized, and fine-scale frameworks to both measure wildness and determine at what point management intensity may negate wildness. The framework should provide information on wildness for a particular species at a local population scale, corresponding to the extent of the management regime or habitat island imposed by artificial barriers and identify wildness equitably across species, management regimes, and land-use types. This requires defining wildness states, mapping the relevant management attributes and actions applicable to each state, and delineating quantifiable thresholds between each state. Previous frameworks have categorized attributes fundamental to the wildness of populations but without determining fully quantitative thresholds. Those developed by Leader-Williams et al. (1997) and Mysterud (2010) distinguish between wild and nonwild populations and are congruent in their identification of breeding manipulation, space requirement, harvest selectivity, resource provision, and predation as key management interventions. Redford et al. (2011) defined 5 states of conservation success along a wildness spectrum. However, this classification also cannot be operationalized as a decision-making tool because the attributes are qualitative and do not provide species-specific, measurable thresholds to objectively distinguish between states. Additionally, they apply to the species overall and thus do not provide a platform for assessing the conservation value of local populations. We adapted Redford et al.'s (2011) framework to create a tool that both articulates and measures the wildness of populations by quantifying management interventions that impact on the evolutionary and ecological dynamics of species.

Methods

Building the Framework

To lay the foundation for a wildness framework, 2 expert workshops were convened by the South African National Biodiversity Institute (SANBI) at the Pretoria National Botanical Gardens in 2015. Thirty experts were invited, of whom 13 participated in one or more workshop and 3 others commented on draft versions of the framework. The participants had expertise across a broad spectrum of relevant wildlife management fields including population biology, conservation science, resource economics, evolutionary biology, natural resource management, and spatial ecology. Participants were drawn from organizations representative of wildlife management and policy development in South Africa. Iterative discussions at the first workshop produced the prototype framework. Participants identified attributes that influence short-term survival of populations and long-term adaptive potential of the population overall (reflecting functioning evolutionary processes); defined states along the wildness spectrum by adapting the Redford et al. (2011) classification to a local context and justified the boundary between wild and nonwild states; listed the potential management actions or characteristics that influence each attribute (drawn from field surveys, e.g., Taylor et al. [2015], and from the experience of the experts); and developed measurable thresholds for each attribute to discern between states. Species-specific threshold values (home range size, social group size, and social group composition) in each habitat type were gleaned from the literature (Supporting Information).

The prototype framework was then validated at the second workshop based on a training data set from a 2014 survey sent out to private landowners to support the revision of the Red List of Mammals of South Africa (Supporting Information). Additional indicator variables for some attributes were identified to give further empirical power in determining wildness states and the quantitative thresholds were recalibrated.

Piloting the Framework

We then piloted the revised framework on 6 herbivore species that are of conservation concern and have high value in the South African wildlife industry (breeding for live sale, trophy hunting and ecotourism); values ranged from US$1,200 to $38,000 at game auctions in 2014 (F. Cloete, personal communication): white rhinoceros (*Ceratotherium simum*); tsessebe (*Damaliscus lunatus*); bontebok (*Damaliscus pygargus pygargus*); mountain zebra (*Equus zebra*); roan antelope (*Hippotragus equinus*); and sable antelope (*Hippotragus niger*). The potential trade-off between conservation and commercial goals for these species thus provided an opportunity to test the efficacy of the framework in identifying wild populations across a range of management goals. We used a comprehensive data set on the management systems of 205 private wildlife areas (hereafter properties) comprising structured interviews conducted between 2014 and 2015 across South Africa (Taylor et al. 2015). These properties pertain to landowners utilizing wildlife on a commercial basis. Management regimes ranged from intensive breeding to extensive ecotourism and sizes ranged from 0.9 to 1030 km^2. Many properties have mixed economic portfolios with management regimes that vary according to the species (Taylor et al. 2015). Because all properties in the data set are fenced, we considered the property boundary to define a population of each species because movement is limited between properties aside from deliberate translocation. The data set included information relevant to all identified attributes, including property variables (size, location, land-use type, and fencing patterns); herbivore species composition and abundance; predator species composition; and management interventions, including veterinary care, supplementary feeding and water provision, predator control, intensive breeding, hunting, and habitat management practices.

Applying the Framework

Once we developed the framework, we applied the data from Taylor et al. (2015) to assess the wildness of populations belonging to the focal species. For each population, the attributes were scored by evaluating the data against the thresholds between wildness states. For each attribute, a score was assigned on an ordinal scale; the least wild state scored 1. The final wildness score for each population was calculated as the median value across attribute scores (details in Supporting Information). Interquartile ranges (IQR) were used to express the variation around wildness scores, both on a population and species level. We then tested whether the distribution of wildness scores across populations was significantly different between species with Mood's median test. The explanatory power of both population size and property size in determining the wildness status of a population was tested using ordered logistic regression. Species identity was included as a factor in the model to determine species-specific effects (details in Supporting Information). All analyses were performed in R version 3.4.2 (R Core Team 2014).

Table 1. Definition of identified attributes relating to the evolutionary and ecological dynamics of managed populations and their key quantifiable indicator variables used to set threshold values between wildness states.

Attribute	*Definition*	*Reference**	*Indicator variables*
Space	facilitates coexistence and niche differentiation and adaptation through microhabitat use and habitat partitioning; allows populations to meet nutritional requirements across seasons; enables intraspecific interactions between social units (e.g., breeding and competition), interspecific interactions (e.g., predator-prey dynamics), and interactions with abiotic components of the landscape (e.g., ecological engineering)	Walker et al. 1987; Jule et al. 2008; Hayward & Kerley 2009; Jackson et al. 2014	home range size of species in specific biome or habitat dispersal capacity of species deduced by fence type and surrounding land use compatibility
Disease and parasite resistance	major role in regulating and creating biodiversity through coevolution; periodic disease outbreaks important population control mechanism; biodiversity loss exacerbates spread of infectious diseases	Altizer et al. 2003; Fincher & Thornhill 2008; Pongsiri et al. 2009	frequency, extent, and purpose of veterinary care (preventing all diseases versus preemptive vaccination against non-native diseases)
Exposure to natural predation	predation plays a top-down role in sustaining biodiversity. Predator-prey relationships are important drivers of evolution, creating trait diversity and new species, and enhance overall biodiversity through the creation of landscapes of fear. Intraguild competition within the predator community has large effects on predator population dynamics.	Linnell & Strand 2000; Creel 2001; Ripple et al. 2001; Yoshida et al. 2003; Thomson et al. 2006; Creel et al. 2007; Oro et al. 2013; Sandom et al. 2013; McArthur et al. 2014; Owen-Smith 2015; Terborgh 2015	presence or absence of predators functional composition of predator community frequency of exposure to predators
Exposure to natural food limitations and fluctuations	exposure to fluctuations in food availability, or resource pulses, influences evolution by driving diversity of life-history traits and thus facilitates the coexistence of ecological communities, especially when synergizing with the effects of predation. Limited food availability regulates population sizes and enhances community diversity.	Walker et al. 1987; Bond & Loffell 2001; Schmidt & Hoi 2002; Chesson et al. 2004; Peterson et al. 2005; Blanchong et al. 2006; Yang et al. 2008; Bishop et al. 2009	presence or absence of food provisioning frequency of food provision presence or absence of habitat modifications for production or ecosystem restoration population inside or outside native range
Exposure to natural water limitations and fluctuations	migrations and dispersals forced by water fluctuations are critical for ecosystem functioning as individuals will transport nutrients, energy, and other organisms between locations and enable ecological interactions between species in both space and time. Subsequent range expansions can feed back into evolutionary processes. Limited water availability regulates population sizes and enhances community diversity.	Walker et al. 1987; Owen-Smith 1996; Gaylard et al. 2003; Peterson et al. 2005; Smit et al. 2007; Bauer & Hoye 2014; Fronhofer & Altermatt 2015; Selebatso et al. 2018	even versus clumped distribution of water points, average interpoint distance frequency of water provision at artificial water points (pumped year-round or collects water seasonally)

Continued

Table 1. Continued.

Attribute	*Definition*	*Reference*[*]	*Indicator variable*
Reproduction	competition for mates determines what alleles are passed onto the next generation and at what frequencies, thus influencing evolutionary trajectories. Spatial and temporal variability in habitat and climate helps conserve genetic diversity because natural selection ensures individuals with the best chance to survive and reproduce in a particular setting will do so most successfully. This engenders adaptive capacity within the population and resilience to the population overall.	Jarman 1974; Price 1984; Allendorf et al. 2001; McPhee 2004; Olden et al. 2004; Von Brandis & Reilly 2007; Allendorf et al. 2008; Jule et al. 2008; Mysterud et al. 2008; Hetem et al. 2009; Champagnon et al. 2012; Willoughby et al. 2017	degree of breeding competition control degree of mate selection control off-take or augmentation strategy selective or nonselective

[*] *References are not exhaustive but rather emblematic of the research supporting the importance of the listed attributes.*

Results

The Framework

Six linked attributes relating to evolutionary and ecological dynamics were identified as contributing to the wildness of a population (Table 1). The attributes were then used to characterize 5 states along the wildness spectrum (Table 2): captive managed (CM), intensively managed (IM), simulated natural (SN), near natural (NN), and self-sustaining (SS). The quantifiable variables for each attribute from Table 1 were then converted into empirical thresholds (binary and continuous) to delineate between states (see framework summary in Table 3). The division between nonwild and wild states was drawn between IM and SN (Table 2), meaning that CM and IM states were nonwild and received a wildness score of 1 and 2, respectively, whereas SN, NN, and SS were defined as wild states and received scores of 3, 4, and 5, respectively. Thus, a population was considered wild if the median score across attributes was ≥3.

Framework Application

The wildness scores varied considerably for each species across the sampled properties. The distribution of wildness states between species yielded significant differences (Mood's median test, $\chi^2 = 89.7$, df = 5, $p < 0.05$) (Fig. 1). Three species had median scores of ≥3 (wild), and 3 species had median scores of <3 (nonwild). At the population level, 186 populations were analyzed across the 6 focal species; 63 (34%) populations were wild. Most populations (102, 55%) exhibited low variation across attribute scores (IQR <1), and 134 (72%) populations possessed a wildness score and IQR that fell entirely within either wild or nonwild states. The proportion of wild populations among species ranged from 12% (*Hippotragus equinus*) to 84% (*Ceratotherium simum*) (Fig. 1 & Supporting Information). Wildness states of species were not entrained by property identity: of 23 properties where 3 or more of the focal species co-occurred, 74% ($n = 17$) of the properties contained both wild and nonwild populations for different species, meaning the same property contained some species that were considered wild and some that were not. Wildness scores did not correlate with population size (ordered logistic regression model $p = 0.21$), but did correlate with property size across species ($p < 0.01$). Smaller areas generally had lower wildness scores, but the effect was species dependent (Supporting Information).

Discussion

We defined CM and IM states as nonwild because management influences reproduction, mortality, and resource requirements of all individuals directly. Conversely, SN, NN, and SS states were considered wild and characterized by management at the population or landscape scale. The division thus marked the difference between ensuring short-term survival of a population versus facilitating its long-term resilience. For natural selection to be the primary driver in managed ecosystems, animals must be allowed to die and thrive in spatially and temporally explicit cycles linked to nonequilibrium landscape-level processes (Pickett 2013). The attributes relate to the potential of a population to experience fluxes in landscape-level patterns and processes relating to resource distribution, intra- and interspecific competition, and environmental conditions. Populations characterized as wild are thus more likely to be functionally diverse and contribute to local ecosystem functioning (e.g., Gagic et al. 2015).

Although previous conceptual frameworks laid the foundations for assessing the wildness of populations (Leader-Williams et al. 1997; Mysterud 2010; Redford et al. 2011), ours is the first to set comprehensive

Table 2. A description of the wildness states adapted from Redford et al. (2011) during the expert workshops and a summary of the predicted effects on short-term survival and long-term resilience of a population.

Wildness state	*Definition*	*Effects on short-term survival*	*Effects on long-term resilience*
Captive managed	there is total control over individuals and populations in breeding camps. Animals will die at this location without continual management. Social dynamics and resource fluctuations negated by management.	population completely dependent on provisioning and veterinary care. Will die within days without intervention.	selective breeding negates adaptation and undermines the adaptive capacity of the population.
Intensively managed	direct human intervention at the individual or population levels or both. Social dynamics and resource requirements actively manipulated; thus, mate selection occurs in an artificial setting with limited opportunity for adaptation to the natural environment. Resource fluctuation negated by provisioning in times of nutritional stress. These populations may exist in semiextensive systems (as opposed to breeding camps) but with conditions controlled to benefit the focal species. This category includes captive breeding for conservation.	more individuals may be present than can naturally be supported. Veterinary care provided continuously and nonselectively in landscape. Population may be nonviable without provisioning and thus may become locally extinct within 10 years without human intervention.	only selected ecological interactions allowed, typically to maximize production of specific traits. Selective breeding or mate selection under nonnatural conditions dominates so population may not become adapted to the environment. Adaptation and adaptive capacity thus severely limited.
Simulated natural	limited but specific set of interventions to sustain populations and mitigate extrinsic factors (e.g., metapopulation management). Management aimed at reducing the impact of humans (i.e., habitat fragmentation, fences and illegal trade) at population level, rather than focusing on the individual. Inability to maintain viable and self-sustaining populations without long-term, periodic management of habitat and extrinsic factors. Social and resource requirements thus need punctuated intervention. No deliberate interference with mate selection although indirectly affected through harvesting or hunting of breeding individuals. Management is aimed at simulating natural processes through hunting, harvesting, and translocation.	no resource provisioning to individuals except under severe conditions where ordinarily animals would disperse. Veterinary care is in response to nonnative diseases. Number of individuals is close to what can be supported naturally (without intervention). Population likely to become extinct over time.	most ecological interactions are functional but links may be missing due to absence of certain species or habitats. Limited movement occurs across the landscape and there is limited dispersal between populations.
Near natural (NN)	very few interventions, all of which are directed at long-term ecosystem-process management and not at either specific individuals or populations. Social requirements of the population are met, but resource requirements may be altered in response to anthropogenically induced limitations. No deliberate interference with mate choice because management aims to sustain long-term ecosystem processes.	food provisioning is very occasional. Space is sufficient for the species to survive amidst environmental fluctuations (through die-offs if necessary). Major unnatural disturbances are mitigated periodically.	evolutionary process functioning in a near natural setting with mate choice unimpeded by human artifact. However, long-term resilience may still need assistance through periodic translocation between areas to ensure gene flow.

Continued

Table 2. Continued.

Wildness state	*Definition*	*Effects on short-term survival*	*Effects on long-term resilience*
Self-sustaining	no deliberate human interference to sustain or increase the population. However, there may be, or may have been, indirect human influence to which the population has adapted (.e.g., black-backed jackals [*Canis mesomelas*] on farmland in South Africa). Social and resource requirements are met.	no direct provisioning. Space is sufficient for the species to survive amidst environmental fluctuations (through die-offs if necessary). Population self-sustaining under current conditions.	ecological and evolutionary dynamics unimpeded. Dispersal and migration are possible such that natural selection is operating and adaptive capacity is sustained in the population.

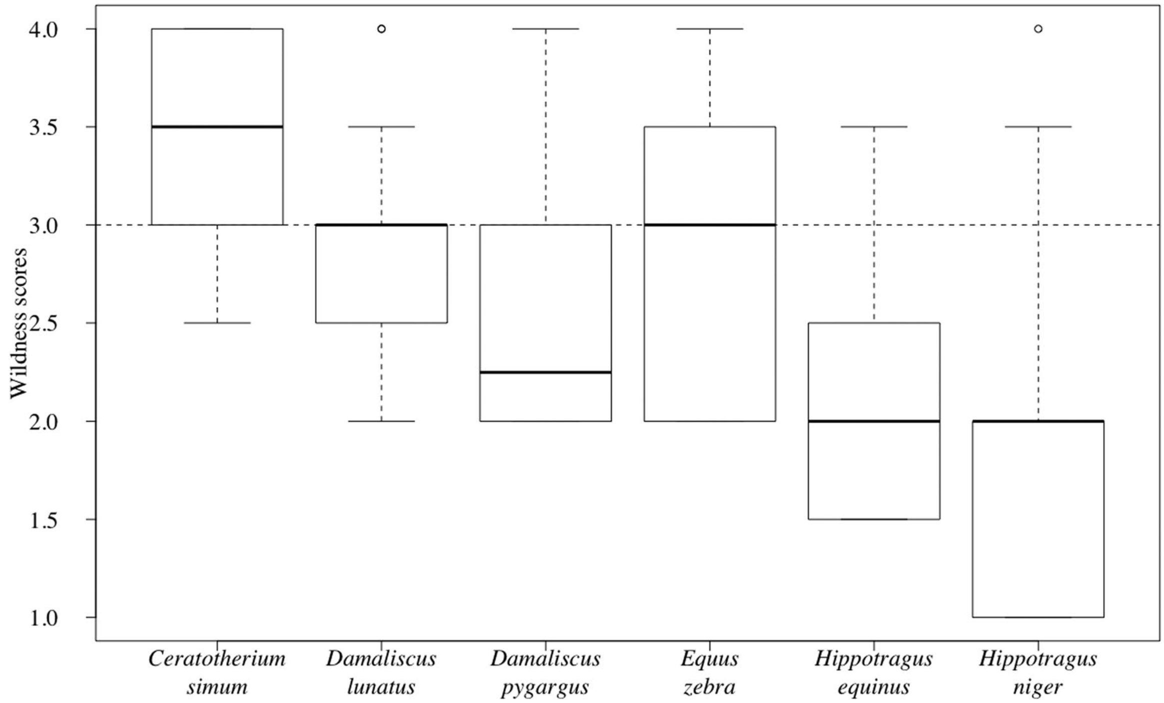

Figure 1. Distribution of wildness scores across properties for each species where the threshold for net wild populations is a median score of ≥3 (horizontal dotted line) (boxes, interquartile range (IQR); bold line, median; dotted lines, minima and maxima). The median wildness scores (and IQR) of each species are Ceratotherium simum *3.5 (3–4) (*n = *25);* Damaliscus lunatus *3 (2.5–3) (*n = *23);* Damaliscus pygargus pygargus *2.3 (2–3) (*n = *18);* Equus zebra *3 (2.1–3.5) (*n = *18);* Hippotragus equinus *2 (1.5–2.5) (*n = *26); and* Hippotragus niger *2 (1–2) (*n = *76).*

empirical thresholds between wildness states. We took these foundational frameworks a step further by testing whether their theoretical underpinnings had efficacy as a regulatory tool. We found significant differences in the median wildness scores of the 6 pilot species, possibly covarying negatively with commercial value (Dalerum & Miranda 2016; Supporting Information), which demonstrates the ability of the tool to delineate broad patterns between species under different management regimes. Each species exhibited both wild and nonwild populations (where the proportion of wild populations ranged from 12% to 84% across species) across a range of management systems, indicating that the tool can detect differences between populations of the same species on differently managed properties. Similarly, populations of different species co-occurring on the same property often spanned wild and nonwild states. These patterns indicate that wildness would be underestimated if deduced from the commercial value of species or top-down land-use classifications. Conversely, wildness would be overestimated if population size was used as a proxy because our preliminary results showed that local abundance did not necessarily correlate with wildness, which may be due to managers using intensive management to increase numbers for commercial goals. This framework thus enables a bottom-up quantification of wildness, avoiding the pitfalls of qualitative classifications, and can detect differences in wildness patterns between species overall; between

Table 3. Summary of the framework used to determine the wildness state of managed populations. Empirical thresholds between each wildness state are shown for each attribute.

	*Thresholds**				
Attribute	*captive managed*	*intensively managed*	*simulated natural*	*near natural*	*self-sustaining*
Space	single species camps camp (internal) fence: electrified or impermeable	area <1 home range unit electrified game perimeter fence	area ≥1 home range unit meshed or stranded perimeter fence with artificial passageways	area ≥2 home range units perimeter cattle fence with artificial passageways	home range units of area > no. social groups present no fence or perimeter cattle fence with artificial passageways
Disease and parasite resistance	veterinary care continuous direct to all individuals (including antibiotics) to mitigate native and non-native diseases	veterinary care permanent preventative measures in landscape (e.g., Duncan applicators and dips) to mitigate native and non-native diseases	veterinary care ad hoc, including preventative vaccination against native and non-native diseases	veterinary care ad hoc, including preventative vaccination against non-native diseases	no disease control
Exposure to natural predation	0 small-predator species (excluded or removed) 0 mesopredator species (excluded or removed) 0 apex predator species (excluded or removed)	≥1 small predator species, continual exposure ≥1 mesopredator species, occasional exposure (removed) 0 apex predator species (excluded or removed or absent)	≥3 small predator species, continual exposure ≥2 mesopredator species, continual exposure (removed ad hoc) ≥1 apex predator species, occasional exposure (removed ad hoc, controlled or absent)	≥3 small predator species, continual exposure ≥2 mesopredator species, continual exposure ≥1 apex predator species, continual exposure (removed ad hoc)	≥3 small predator species, continual exposure ≥2 mesopredator species, continual exposure ≥2 apex predator species, continual exposure
Exposure to natural food limitations and fluctuations	continuous food provision to all individuals in enclosures no access to natural habitat population outside indigenous range	>1 supplementary feeding events per year on average; salt licks ≥1 habitat modification for production population outside indigenous range	1 supplementary feeding event per year on average 1 habitat restoration intervention population inside or outside indigenous range	<1 supplementary feeding event per year on average 2 habitat restoration interventions population inside indigenous range	no supplementary feeding ≥3 habitat restoration interventions population inside indigenous range
Exposure to natural water and limitations and fluctuations	≥1 water point per encamped animal group	≥1 water point per home-range unit, even spacing	<1 water point per home range unit, even spacing	<0.5 water point per home range unit, asymmetrical spacing	<0.25 water point per home range unit, asymmetrical spacing

Continued

Table 3. Continued.

Attribute	Thresholds* captive managed	intensively managed	simulated natural	near natural	self-sustaining
	100% artificial water points, continuous availability	≥50% artificial water points, continuous availability	<50% artificial water points, mixed availability	<25% artificial water points, seasonal availability	100% natural water points, seasonal availability
Reproduction	1 breeding male per enclosure	population size <1 social unit (= 1 breeding male)	population size = 1 social unit (≥2 breeding males)	population size ≥2 social units (multiple breeding males)	population size ≥3 social units (multiple social groups)
	individuals matched and selected for specific traits (controlled breeding); presence of non-native subspecies or ecotypes	intensive breeding for production, periodically replacing breeding stock; presence of non-native subspecies or ecotypes	individuals not matched or selected, but limited mate choice de facto from small population size; absence of non-native subspecies or ecotypes	no breeding manipulation, mate choice uninhibited, but some demographic processes may be lacking; absence of non-native subspecies or ecotypes	no breeding manipulation, mate choice uninhibited, all demographic processes functioning, absence of non-native subspecies or ecotypes
	selective off-take or augmentation of individuals with specific genotypes (e.g. via stud books)	selective off-take or augmentation of individuals with specific traits	selective off-take or augmentation of individuals to simulate dispersal (e.g. as part of metapopulation strategy)	non-selective off-take or augmentation (based on postreproductive age where appropriate)	non-selective off-take (based on postreproductive age where appropriate); no augmentation following initial reintroduction

**The division between wild and nonwild populations is drawn between simulated natural and intensively managed, respectively. For each population, scores are assigned to each attribute based on the thresholds. The score corresponds to the wildness state on an ordinal scale (captive managed—1 to self-sustaining—5). Net wildness score of the focal population is calculated as the median of the attribute scores.*

populations on properties under different management regimes; and between populations of different species on the same property. This will enable policy makers to produce more meaningful national assessments and provide a fine-scale species management planning and auditing tool.

In line with species conservation guidelines (IUCN 2017), we consider wild populations within their indigenous range as possessing conservation value. The framework can be used to objectively identify populations that contribute to the conservation of the species and thus included in IUCN Red List assessments, thereby mitigating the often subjective interpretation of the guidelines by different assessors (Hayward et al. 2015). Captive-breeding programs for populations of threatened species managed outside their indigenous range (e.g., due to security threats or lack of natural habitat) may also have conservation value and here the framework can be applied to ensure the population remains as wild as possible to facilitate successful reintroduction. Populations outside their natural range, which are not considered of conservation value, can still benefit from the framework by using it to facilitate ecological land management for broader biodiversity benefits. Similarly, because this framework measures the viability of populations, it may also have utility in the newly developed IUCN Green List of species (Akçakaya et al. 2018), particularly in quantifying and standardizing the ecological functionality parameter.

Discerning between wild and nonwild populations will allow policy makers to create multifunctional landscapes where wildlife can both provide socioeconomic opportunity and sustain ecological processes. For example, there is increasing pressure on the hunting industry to demonstrate that the quarry is free-roaming and that hunting contributes to maintenance of wild populations of indigenous species and their habitats, which has resulted in the proposal of a certification scheme for informing consumer choice (Wanger et al. 2017). Evaluating wildness could thus contribute to the green economy because the framework provides a mechanism to deliver market information to consumers of ecotourism or trophy hunting who are concerned about the sustainability and authenticity of their experience. Additionally, nonwild populations provide economic value in their contribution to the rural economy and food security through game meat markets and associated services (Mysterud 2010; Taylor et al. 2015). Although a property owner may be specializing in intensive breeding for a certain species, the rest of the property may be extensive and provide conservation benefits for other species. Quantifying the possible trade-offs between biodiversity and economic activity on landscape scales can help decision makers design incentives and landowner regulations.

Although our framework does not explicitly link to indices of natural habitat, intactness, or productivity, the wildness scores can be aggregated for each property or protected area (if a standardized set of species is assessed) and incorporated into broader biodiversity assessments at landscape scales. For example, the wildness scores can be incorporated into landscape-scale indicators that measure wilderness characteristics (Carver et al. 2013) to prioritize areas for protected-area expansion or corridor creation.

This framework is currently most applicable to populations of large vertebrate species that may be directly affected by management activities (smaller species with high mobility and small home ranges would likely be classified as self-sustaining). Large vertebrates possess economic value (both consumptive and nonconsumptive use) and are thus most often the focal points of management plans and conservation strategies. The way in which they are managed is likely to have ramifications for other species and the ecosystem as a whole (i.e., umbrella species). The attribute scores provide a diagnostic to design appropriate conservation-oriented management plans. For example, protected area managers may use the framework to modify management effectiveness templates so that the data more accurately incorporate the possible effects of management on species. Although our data set included private protected areas, future work will survey statutory protected areas to provide baseline wildness evaluations and management effectiveness indicators.

The framework can also be modified to suit user needs. For it to be widely applied across geographic regions and land management systems around the world, it must become less data intensive. Once a larger sample size has been obtained, attributes that covary can be identified and redundant variables removed in favor of the covariate that is easier to measure to produce a data-light version of the framework. For example, intensive breeding and veterinary care may covary because both are used by managers to produce disease-free Cape buffalo (*Syncerus caffer caffer*) (Laubscher & Hoffman 2012), meaning data on either reproduction or veterinary care may be used as a proxy for the other.

Similar to reducing the attribute load of the framework, the relative explanatory power of each management variable should be explored through statistical modeling and weighted accordingly because some may be more important in determining wildness. For example, as one of the main mechanisms of natural selection is competition for scarce resources, supplementary feeding may more directly influence the evolutionary dynamics of species than other attributes (reviewed in Oro et al. 2013). Space is also likely to be more influential because wildness scores are negatively correlated with decreasing property size, which is expected because smaller areas require more intensive management. Determining property size thresholds for species of varying body sizes, below which all populations of a particular species can be considered nonwild, will reduce processing time in applying the framework.

A major theme for future research must focus on ground-truthing the wildness states quantified through the framework. Current evidence demonstrates that captive-bred animals have reduced fitness in unmanaged landscapes (McPhee 2004; Jule et al. 2008; Willoughby et al. 2017), but much work remains to measure the long-term effects of various management intensities on the survival and adaptive capacity of populations across species. One approach is measuring population-level indicators of evolutionary and ecological functioning, such as genetic and trait diversity, and the persistence probability of the population when management interventions are removed or when animals originating from various wildness states are reintroduced into unmanaged areas. We expect animals at the lower end of the wildness spectrum to have lower chance of long-term persistence, whereas animals at the higher end should have increasingly higher probabilities of survival and persistence over time because these populations should have retained relatively more adaptive capacity. Collecting these data would enable calibration of the threshold values, which could lead to collapsing or expanding the number of wildness states.

Because wildlife is increasingly brought under human influence, embedding an empirical evaluation of wildness into regulatory processes becomes paramount to counteract the shifting baseline syndrome of the conservation ideal: evolutionary and ecologically dynamic species integrated into functioning ecosystems. Our framework standardizes the measurement of the wildness of managed large vertebrate populations at the property scale and conceptually aligns management with the overarching goal of sustaining biodiversity and ecosystem functioning. The quantification of wildness also has importance beyond technical measurement for policy and assessment purposes because it represents a more positive and creative conservation agenda. If conservation ideals are not articulated, measured, and mainstreamed, the world will be composed of little more than megalopolises, technogardens, and zoos bereft of the wildness needed to sustain human imagination.

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Supporting Information

An explanation of wildness scoring system (Appendix S1) and ordered logistic regression results (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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