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LARGE, PARTICULAR BOVIDS MAY REQUIRE LOCALISED CONSERVATION EFFORT TO PREVENT EXTINCTION

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ABSTRACT. — Given growing human populations, concomitant resource use, and habitat transformation, ungulates face the localised extinction of numerous populations. Among ungulates, bovids are particularly vulnerable as many species are harvested as bushmeat and have large home range requirements. Here we determined the extent of geographic distribution and species richness (extent of range overlap) for bovids (Order, Artiodactyla, Family, Bovidae, $n = 129$), and used the IUCN Redlist status of species to determine life history, ecological and anthropogenic correlates of decline (sourced through the PanTHERIA database). Based on the extent of range overlap, we found that bovid species richness is relatively high in the tropics, particularly across central and east Africa. We used generalised linear mixed models and multimodel inference to determine the parameters associated with extirpation, accounting for evolutionary relatedness (random effects). The best predictor of bovid extinction risk was body mass. Overall model deviance explained was low (3% for the global model), suggesting that localised correlates of population decline (not accounted for at a macro-ecological scale) may be key to conservation effort. Our work highlights the extraordinary diversity of bovid species in the tropics and provides insight into important correlates of decline across the family. We encourage the prioritisation of conservation resources toward tropical bovids, with emphasis on large and range-restricted species.

KEY WORDS. — Bovidae, extinction, generalised linear models, tropics, ungulates

INTRODUCTION

Future battlegrounds in species conservation will (mostly) be in the tropics (Lee & Jetz, 2008). At low latitudes, high levels of species richness and endemism (Lee & Jetz, 2008) are challenged by multiple factors such as growing human populations (Lutz & KC, 2010), concomitant habitat loss (Owens & Bennett, 2000; Kinnaird et al., 2003), increased human-wildlife conflict (Hoare & Du Toit, 1999) and harvest pressure (Cowlshaw et al., 2005). Furthermore, available funds for tropical biologists are relatively scarce (Sodhi, 2008), forcing conservation prioritisation in most instances (Wilson et al., 2011).

Indeed, recent studies across the tropics indicate large vertebrate decline in human-dominated landscapes. For example, Rajeev et al. (2011) noted a substantial decline

in mammal abundance and distribution attributed to habitat fragmentation and increased human presence in the Ghats region, India. Despite conservation efforts, Stoner et al. (2007) found that most East African ungulate species have declined in the past 30 years, and Cowlshaw et al. (2005) showed that slow-breeding and typically large mammals have been eradicated through the bushmeat trade in Ghana, West Africa.

These and other findings suggest that tropical, terrestrial mammal populations are now largely dependent on protected area networks (Fynn & Bonyongo, 2011). Although we note the deliberate disruption of conservation effort in Zimbabwe (Hughes, 2009; Lindsey et al., 2011), locally-funded protected area networks have the capacity to provide effective refuge. However, further complications can arise from projected shifts in temperature and rainfall regimes, triggering

latitudinal shifts in communities, such that protected areas are unable to provide refuge to some species' populations (McCarthy et al., 2011; Shoo et al., 2011).

Among tropical mammals, ungulates are one of the most vulnerable taxa to local extinction. Species within the taxa may have extensive range requirements (Armbruster & Lande, 1993), compete with humans for some food resources, particularly crops (Hoare & Du Toit, 1999) and are regularly harvested (Remis & Kpanou, 2011). Among ungulates, bovids are of particular interest. Species from this family play a central role in the bushmeat trade (Cowlshaw et al., 2005), and are important to the safari industry as trophy species (von Brandis & Reilly, 2008; Johnson et al., 2010). Further, some bovids are the cause of human-wildlife conflict (Dunham et al., 2010; Nyahongo & Rskaft, 2011), and bovids certainly play an important role in ecosystem function (Hobbs, 1996; Du Toit & Cumming, 1999; Fritz et al., 2002).

Given the threats faced by ungulates, and in particular bovids, it is useful to determine the extent of occurrence for species within the family, and further, using a surrogate of extinction risk, to attempt to tease-out important correlates of decline (such as Sodhi et al., 2008). Efforts to protect large or less fecund species can be made once these correlates are identified.

Here we explore the extent of global species richness for bovids (Order Artiodactyla, Family Bovidae), a group whose members are mainly antelope and comprising ~130 species (Gatesy et al., 1992). We focus on bovids given the evolutionary history of these within the tropics (Bibi et al., 2009), and its importance to many human populations (Fa et al., 2005). Further, we use a database of known extinction correlates (Jones et al., 2009) and test for generalisations that predict extinction risk across bovids.

MATERIAL AND METHODS

Species richness. — We were interested in the spatial pattern of global bovid diversity. Species richness, or diversity may be simply defined as the number of genetically distinct species that occupy a pre-defined region (Magurran, 2004). Species diversity provides ecosystem resilience to change and disturbance (Walker & Salt, 2006), and is central to the practice of conservation biology (Myers et al., 2000).

To derive a measure of spatial diversity, we sourced bovid species' range maps through the International Union for the Conservation of Nature (IUCN) Redlist database (<http://www.iucnredlist.org>). Using ArcGIS (ARCMAP software, v.9.3, ESRI, Redlands, United States), a global map of bovid diversity was estimated by counting the number of species ranges present across a 0.5×0.5 arc-degree point grid. Thus areas of high diversity represent high range overlap, where numerous bovids co-exist, typically through resource partitioning (Traill, 2004). Of note, we excluded range for introduced bovids, such as banteng (*Bos javanicus*), introduced to tropical Australia (Bowman et al., 2010).

Correlate data. — We were interested in testing possible correlates of extinction in bovids. By correlates we mean parameters commonly linked to species extinction risk (O'Grady et al., 2004). As we lacked data on abundance, we relied on IUCN Red-listing as a proxy for predicted extinction (e.g., Keith et al., 2004).

We then compiled a list of all bovids' threat statuses from the IUCN Redlist. We developed a binary dependent variable from the listing, where Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), and Near Threatened (NT) were scored as 1, and Least Concern (LC) 0. Data Deficient species were discarded, as were those listed as Extinct. We also omitted domesticated bovids, and non-native populations (see Spear & Chown, 2009; Bowman et al., 2010). Our dataset ultimately consisted of 129 species.

Further, we developed a priori hypotheses (as per Burnham & Anderson, 2001) regarding possible correlates of species extinction (McKinney, 1997; O'Grady et al., 2004). The approach of multiple working hypotheses forced us to consider a set of candidate models that could be challenged with data (Burnham & Anderson, 2002). Following literature review, our candidate set included body mass (Gaston & Blackburn, 1995), diet breadth (sum of diet categories) or the number of food types eaten as a proxy for niche generalisation, mean human population density (persons per km²) and percent human population change (see Brashares et al., 2001). Correlate data were sourced through the publicly available database, PanTHERIA (Jones et al., 2009). A number of possible parameters were ultimately omitted as the life history and ecological data were simply unavailable for many species (see Jones et al., 2009). These included age-at-first-birth, longevity, habitat breadth, dispersal ability, abundance, and extent of population fragmentation (e.g., McKinney, 1997). We note that body mass is a useful proxy for age-at-parturition and social structure given allometric relationships in ungulates (Jarman, 1974).

Data were prepared in a spreadsheet and included taxonomic sub-families. These were Aepycerotinae, Alcelaphinae, Antilopinae, Bovinae, Caprinae, Cephalophinae, Hippotraginae, and Reduncinae.

Multi-model inference. — We used generalised linear mixed models (binomial distribution with logit link) using maximum likelihood estimation to fit the models (using the lme4 package). Information theoretic, multi-model inference metrics (Burnham & Anderson, 2001) were used to identify the suite of parameters (fixed effects) that best explained variation in bovid threatened status. The random effects error structure of the mixed models corrected for non-independence (evolutionary relatedness) of species, here taxonomic genus nested within sub-family (e.g., Blackburn & Duncan, 2001). We transformed (natural log) body mass and mean human population density as these data were not normally distributed.

RESULTS

Bovid species diversity, as measured by range overlap is notably highest across central and east Africa, with relatively moderate levels of diversity within western and southern Africa, and south Asia (Fig. 1). We noted relative low levels of diversity occur in southern Africa and south-east Asia, with practically no diversity across America and Europe. This pattern of diversity may be partly ecological, but is largely an artefact of bovid evolution during the Miocene (Bibi et al., 2009).

Body mass was the best predictor of bovid extinction (Table 1), based on Akaike’s corrected information criterion (AICc). We derived Evidence Ratios (ER; as a measure of comparative support) for the mass and diet breadth models (Burnham & Anderson, 2002). These were calculated by summing the weighted AICc values for body mass parameters (Table 1) and dividing the sum of these by the diet breadth model (thus the ratio for evidence between models that contained these parameters). From the data, body mass showed three times as much support as diet breadth (ER = 3.3).

Despite having 129 data points, the highest number of parameters (K) was 7 (for the global model) given the requirements to include random effects in the model. Thus there were ~18 data points per parameter. This could perhaps explain the low deviance explained by all models, including the global (Table 1).

Nonetheless, despite a lack of goodness-of-fit, we note empirical support, based on $\Delta AICc$ values (Burnham & Anderson, 2002) for body mass (Table 1), and partly for

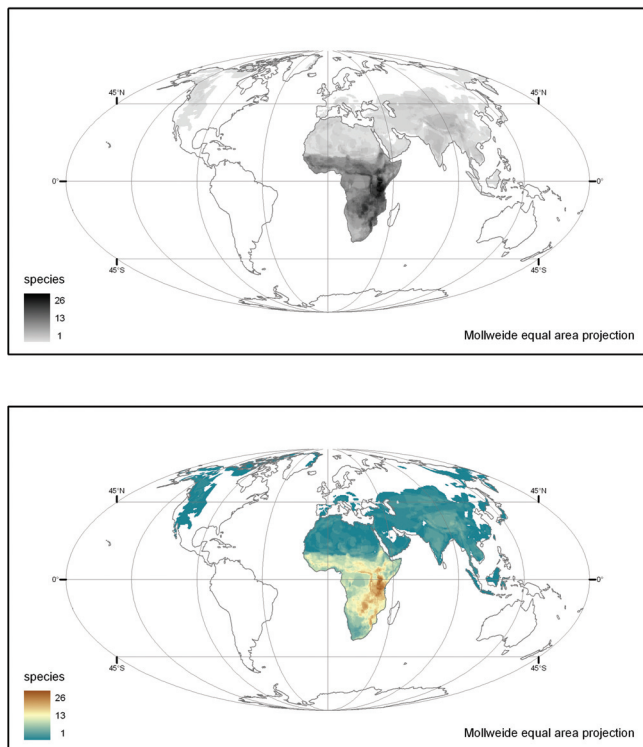


Fig. 1. Global diversity for Bovidae, as measured by range overlap.

diet breadth. This suggests that large-bodied ungulates (see Fig. 2), with limited diet breadth (Fig. 3) are vulnerable to extirpation.

With relatively few bovid species weighing over 100 kg (Fig. 4), it appears that conservation effort should focus on large bovinds (the intercept for the (logit) model was -4.92 and the slope 0.4362). Indeed, body mass is strongly skewed in bovinds (Fig. 4), with the median body mass at 54 kg despite a maximum adult mass of 930 kg (data ranged from 2.9–930 kg). This is similar to most mammal groups (Gardezi & da Silva, 1999).

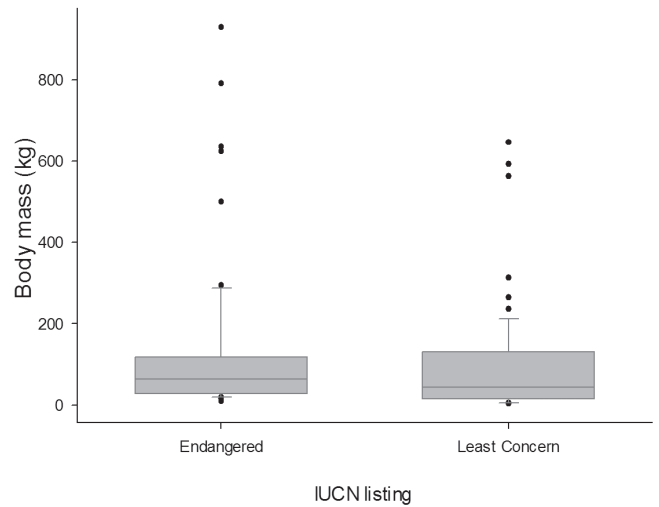


Fig. 2. Boxplot display of body mass (kg) for Bovidae, categorised by IUCN listing. For listing, Endangered pools Critically Endangered, Extinct in the Wild, Endangered, Vulnerable, and Near Threatened (n = 62) and Least Concern (n = 67) as listed. Boxes represent median values, upper and lower quartiles, whiskers represent the 10th and 90th percentile with outliers displayed outside of these.

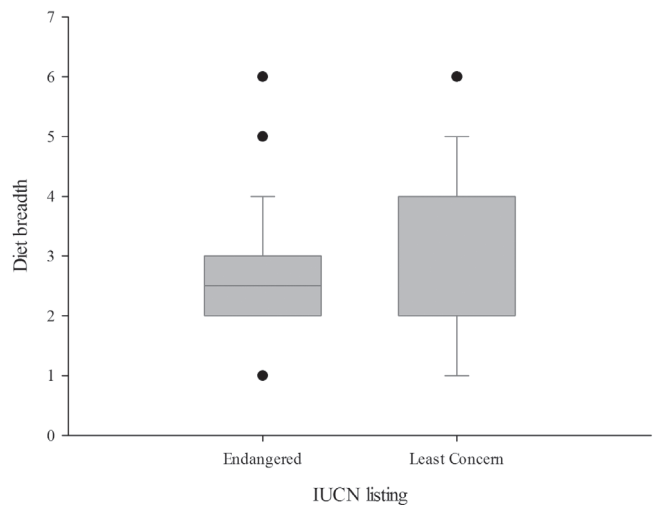


Fig. 3. Boxplot display of diet breadth for Bovidae, categorised by IUCN listing. Diet breadth values represent the number of diet categories, defined for herbivores as fruit, flowers/nectar/pollen, leaves/branches/bark, seeds, grass and roots/tubers (see Jones et al., 2009). Boxes represent median values, upper and lower quartiles, whiskers represent the 10th and 90th percentile with outliers displayed outside of these.

Table 1. Results from generalised linear mixed-effect models of global bovid IUCN listing to environmental and anthropogenic effects. All models include subfamily as a random effect. Shown are the number of model parameters, including random effect variance decomposition (k), Akaike's corrected information criterion (AIC_c), distance from best model (ΔAIC_c), Akaike weight ($wAIC_c$) scaled relative to a total sum of 1, and percent deviance explained (% DE) as a measure of goodness-of-fit.

Candidate models where response is IUCN listing (0=LC, 1=NT+VU+EN+CR+EW)	k	AIC_c	ΔAIC_c	$wAIC_c$	% DE
Body mass	4	178	0.000	0.44	2.10
Null	3	179.4	1.433	0.22	0.00
Diet breadth	4	180.4	2.415	0.13	3.3
Human population change	4	181.2	3.237	0.09	0.66
Human population density	4	181.3	3.357	0.08	0.19
Global model	7	182.9	4.961	0.04	3.0

Candidate models where response is IUCN listing (0=LC, 1=NT+VU+EN+CR+EW)	k	AIC_c	ΔAIC_c	$wAIC_c$	% DE
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DISCUSSION

The high diversity of bovids across Africa, and to a lesser extent Asia, is an evolutionary artefact. Since the Miocene ~20 mya, Bovidae have undergone rapid radiation and is unparalleled in mammals of similar body size (Gatesy et al., 1992). This diversification has resulted in more than 120 extant species and ~300 extinct species, distributed across Africa, Eurasia, and North America (Gatesy et al., 1992). An Old World post-Miocene radiation explains the lack of native bovids in Australia and South America. Indeed continental separation appears to have contributed towards the first major split in Bovidae, with Bovinae remaining in Eurasia and Antilopinae developing in Africa (Hassanin & Douzery, 1999). Subsequent radiation during the middle Miocene gave rise to most extant Bovinae and Antilophinae tribes (Hassanin & Douzery, 1999). A third radiation event, at the Miocene-Pliocene boundary occurred during the spread of grasslands—with the evolution of bovids adapted to savanna-type habitats (Gatesy et al., 1992; Hassanin & Douzery, 1999), thus the emergence of highly specialised grassland antelopes represented by Reduncinae, Alcelaphinae, and Hippotraginae (Matthee & Davis, 2001).

Present-day bovid diversity in tropical regions, particularly Africa, provides a unique conservation opportunity. Tropical Africa and parts of Asia maintain a remnant of a lineage that evolved long before humans, and indeed played a part in hominid evolution (Bibi et al., 2009). This diversity needs to be protected. One step towards preventing extirpation is to understand the parameters associated with species' population decline (see Caughley, 1994), and our results here have addressed this to some extent. Although our hypothesized extinction correlates explained very little model deviance (Table 1), our finding that body mass predicts possible extirpation is similar to numerous studies across taxa (McKinney, 1997; Fagan et al., 2001; Cardillo et al., 2005), though some authors regard body size as unimportant (Johnson, 2002). Large body size can make species vulnerable to hunting pressure (Cowlshaw et al., 2005), and further large ungulates tend to forage over extensive areas (Armbruster & Lande, 1993), with subsequent human-wildlife conflict (Hoare & Du Toit, 1999).

The lack of statistical power for our models (see Burnham & Anderson, 2002) prevented us from predicting species-specific extirpation, but we can draw some useful inference. For example, heavier bovids are more likely to be IUCN-listed and therefore, more likely to face localised extinction. We don't suggest that conservation funds target large-bodied bovids only, but rather that biologists working in the tropics, especially central Africa are aware that large antelope are relatively vulnerable.

Our finding on diet breadth, or the sum of diet categories, is interesting. Bovids with a broad feeding strategy are less likely to be IUCN Red-listed. These included mixed feeders, such as impala (*Aepyceros melampus*) and some duiker species that are insect foragers. Bovids with a narrow diet breadth included specialised grazers, such as hartebeest species and Cape buffalo (*Syncerus caffer*), and specialised browsers such as nyala species.

Asian water buffalo (*Bubalus bubalis*), introduced to tropical Australia, have been shown to be relatively more successful than another introduced ungulate in Australia: the banteng (*Bos javanicus*)—through a broader feeding niche (Bowman

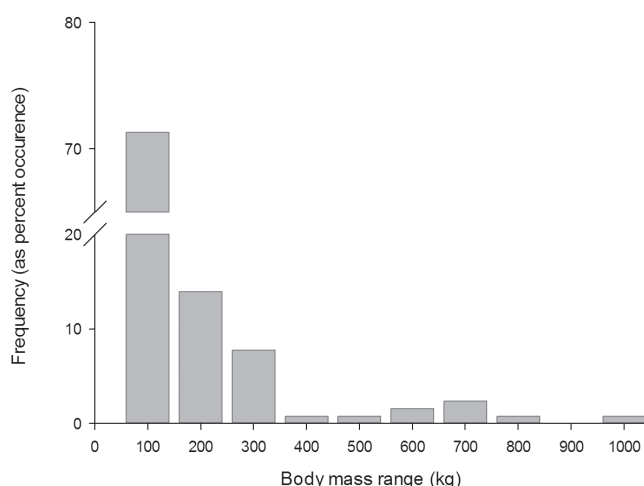


Fig. 4. Frequency distribution body mass (kg) for Bovidae ($n = 129$), scaled to percent. Body mass data are categorised from 0–100, through to 900–1000 kg. Minimum mass = 2.9 kg, maximum = 929.5 kg, mean = 110.5 kg, and median = 54.3 kg.

et al., 2010). The likelihood of specialised feeders being IUCN Red-listed extends beyond ungulates, with similar findings for bats (Boyles & Storm, 2007). Again although there was some support for the diet-breadth model based on Akaike's Information Criterion (Table 1), the overall deviance explained was low, suggesting too few data points to draw strong conclusions.

Of further interest is our finding that, by including species range size as provided through PanTHERIA (Jones et al., 2009), we explain 50% model deviance. Range retraction is a key criterion for IUCN Red-listing, so testing for range size is 'circular', however it does imply that bovids with small ranges are more likely to face localised extinction. This is of particular concern based on projections of community-level shifts due to climatic change, where protected areas do not change with shifting ranges (see McCarthy et al., 2011).

The lack of conclusive evidence for our hypotheses suggests that correlates associated with bovid decline are localised. While body mass and diet breadth do determine the probability of bovid species' population decline, there are other parameters that we did not measure due to lack of data. These include longevity, dispersal, abundance, genetic variation, and behaviour (see McKinney, 1997).

Together with the knowledge provided here, ongoing conservation effort can focus on collating data on population trends and localised threats. Particular attention needs to be paid to tropical regions, where high levels of species diversity still persist, especially across central Africa. These data, together with spatial data on the extent of habitat fragmentation, are critical to conservation plans.

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