

Research Summary

Of dwarfed buffaloes and conservation palaeobiology

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Islands are home to extraordinary biotas and have long been recognised as laboratories for the investigation of the fundamental biogeographical processes of colonization, evolution, and extinction (e.g., Darwin, 1860; Wallace, 1880; Whittaker et al., 2017). Bovids are intriguing elements of insular faunas and encompass several species that inhabited or are still living on islands located in different regions, from the Mediterranean to Southeast Asia. While the most popular insular endemic bovid is without doubt the extinct mouse-goat (*Myotragus balearicus*) from the Balearic Islands (e.g., Bover & Alcover, 2003; Köhler & Moyà-Solà, 2009; Bover et al., 2010; Palombo et al., 2013; Rozzi & Palombo, 2014), living examples of these wonders include three miniaturised buffalo species, which are of concern to the IUCN Asian Wild Cattle Specialist Group (AWCSG): the tamaraw (*Bubalus mindorensis*), endemic to Mindoro, the Philippines, and the anoas (*B. depressicornis* and *B. quarlesi*) from Sulawesi. Well over a century of studies by

evolutionary biologists, ecologists, palaeontologists, and biogeographers have identified particular traits and syndromes on which island forms repeatedly converge. The peculiar changes undergone by island bovids include body size reduction, increased molar crown height, transition towards a low-gear locomotion, and changes in brain size and morphology (e.g., Köhler & Moyà-Solà, 2004; Rozzi et al., 2013; Rozzi & Palombo, 2014; Rozzi & Lomolino, 2017; Rozzi, 2017, 2018).

Body size variation is a crucial aspect of the so-called island syndrome (sensu lato; see Lomolino et al., 2017). Large vertebrates, especially mammals, dwarf on islands in response to a combination of selective biotic and abiotic forces (e.g., characteristics of the islands and the species itself and release from ecological pressures of competition and predation; see e.g., Lomolino et al., 2012, 2013; Rozzi & Lomolino, 2017).

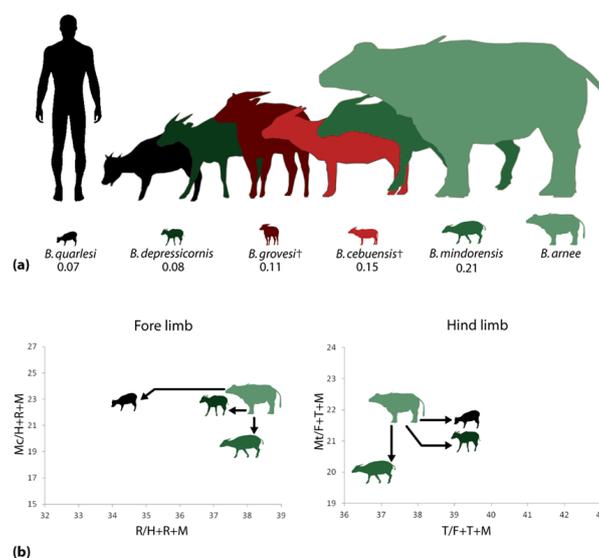


Figure 1. Body size divergence S_i values of selected living and extinct representatives of *Bubalus* (*Bubalus*) and *Bubalus* (*Anoa*). The dagger symbol (†) is used to designate extinct species. The scheme shows the focal buffaloes in proportion to a 1.8 m tall human. Modified from Rozzi, 2017 (a). Graphs comparing the ratio between metacarpal and radius length and ratio between metatarsal and tibia length, normalised with respect to the total length of the forelimb and hindlimb long bones. Black arrows highlight phyletic relationships among focal insular Bovini. Modified from Rozzi & Palombo, 2014 (b).

The island rule predicts this pattern and bovids are no exception, exhibiting body size reduction. To explore the size shift of focal species I calculated their body size divergence S_i (= mean body mass of individuals from an insular population or species divided by that of individuals of the mainland or ancestral form; see Rozzi, 2017, 2018). Values obtained for living and fossil dwarfed buffaloes are shown in Fig. 1a (for a comprehensive overview of their body masses see Rozzi, 2017, 2018). The estimate rests on the assumption that fossil water buffaloes would be the ancestors of the anoas and their Late Pleistocene/Holocene relative *B. grovesi* (see Rozzi, 2017), of *B. cebuensis* - the extinct buffalo from Cebu Island, and of *B. mindorensis*, and that the body masses of those putative ancestors would not differ significantly from that of their extant relative *B. arnee* (Rozzi, 2017). The relative size of *B. grovesi* indicates an average body size reduction of about 89% ($S_i = 0.11$) with respect to a typical water buffalo. *Bubalus depressicornis* and *B. quarlesi* exhibit even more extreme values, with a body size reduction of about 92% ($S_i = 0.08$) and 93% ($S_i = 0.07$), respectively (Fig. 1a).

Endemic buffaloes from the Philippines are larger than the anoas and their relative size indicates an average body size reduction of about 79% ($S_i = 0.21$) for *B. mindorensis* and of about 85% ($S_i = 0.15$) for *B. cebuensis* (Fig. 1a). Island dwarfing of bovids is more pronounced for species which have evolved on the focal islands for longer time periods (Rozzi, 2018). Moreover, while release from competitors appears to be the major force influencing dwarfing of other insular wonders (e.g., proboscideans), results of my research highlight the central role of predator diversity, or predatory release, in driving the body size evolution of insular bovids (Rozzi, 2018). This likely reflects differences in prey preferences. In fact, bovids and other ruminants (i.e., mesoherbivores) are among the most common prey of large carnivores both now and in the past. In contrast, large body size of megaherbivores, such as mammoths, stegodonts and elephants, renders their populations less susceptible to “top-down” limitation by predators.

A common feature in dwarfed island herbivores is a great shortening of the limbs, especially the distal limb elements. This has been explained as an adaptation for what Sondaar (1977) described as low-gear locomotion – a frequent phenomenon believed to be more adaptive, in the absence of predators, for climbing across rocky and/or uneven terrain than the ancestral (mediportal) bauplan (see e.g., Rozzi & Palombo, 2013, 2014). Limb bone shortening cannot be explained by a simple allometric downscaling of the animal, because the relative proportions of limb elements are drastically changed. Therefore, it is useful to compare the ratio of length of metacarpal/length of radius and length of metatarsal/length of tibia of extant insular species with that of their ancestors and with data available for the fossil species (Rozzi & Palombo, 2014). Results obtained for dwarfed buffaloes (Fig. 1b) indicate that all the extant species exhibit a shortening of limb length and metapodials, although each taxon shows peculiar relative proportions of limb elements. One of the most extreme cases is *B. mindorensis*, which strongly shortened the metapodials with respect to its closest mainland relative *B. arnee* (length of metapodials is less than 20% of the total length of the other limb elements) and only slightly reduced the lengths of radius and tibia (Fig. 1b). The variation of the limb shortening pattern in extant and fossil island herbivores can be explained in light of the predatory pressure that each focal species had/has to face in each insular community. For instance, bovids that evolved in a predator-free environment, such as the tamaraw, acquired morphological traits typical of low-gear locomotion (Rozzi & Palombo, 2014).

Several recent studies have illustrated how knowledge of the deep-time fossil record of ecological and evolutionary dynamics can contribute to the conservation of biodiversity (see e.g., Dietl & Flessa, 2009, 2011; Dietl et al., 2015; Dietl, 2016; Barnosky et al., 2017 and references in those papers).

***Conservation palaeobiology:** “the application of theories and analytical tools of paleontology to the solution of problems concerning the conservation of biodiversity” (Dietl & Flessa, 2009).

****Ecological naiveté:** “the tendency for long-term inhabitants of low diversity and disharmonic (unbalanced) islands to lose their capacities for detecting, avoiding or otherwise coping with competitors, predators and parasites from the mainland or otherwise more-balanced and species-rich assemblages - i.e., species at least initially absent from these islands” (Lomolino, 2016; Lomolino et al., 2017).

In particular the conservation palaeobiology* perspective (i.e., in the perspective provided by geohistorical data) is essential for the development of successful conservation strategies under current global change. Insular populations of large vertebrates, such as dwarfed buffaloes, often exhibit a trend towards ecological naiveté** and heightened vulnerability to extinctions - especially those at the hands of non-native species, including humans and their commensals (e.g., Lomolino, 2016). Investigating their evolutionary history and, in particular, how these endemics often lose or wane in those traits that allowed their mainland ancestors to survive in the face of intense ecological interactions can provide valuable information for conservation planning. Both taxon-based palaeontological methods - which rely on the presence, absence, or abundances of certain taxa and their underlying diversity - and taxon-free palaeontological methods - which use variables that reflect ecosystem function rather than structure - can provide critical data and insights (see Barnosky et al., 2017). For instance, delving into the phylogenetic relationships, timing of colonisation and mode of evolution of the anoa and tamaraw and of their extinct relatives is crucial to outline the range of taxonomic and relative abundance variation that characterises their ecosystems as they fluctuate over time. On the other hand, by focusing of their functional traits (i.e., ‘ecometrics’) - such as locomotor attributes, dental morphology and body size - it might be possible to infer the ability of these taxa to persist under particular scenarios of rapid environmental change or introduction of invasive species. All in all, palaeontological studies have the potential to inform conservation strategies for extant

miniaturised buffaloes and to produce detailed information on their uniqueness (i.e., ecological naiveté) and, thus, a better assessment of their conservation value.

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