Review Paper

Last lizard standing: The enigmatic persistence of the Komodo dragon

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A B S T R A C T

To understand why much of the world's terrestrial megafauna went extinct within the last 50,000 years, we can look at the exceptions: large-bodied species that avoided that fate. The Komodo dragon (*Varanus komodoensis*) is tenfold heavier than almost any other surviving lizard species, is currently restricted to small islands, and relies on scavenging as well as predation − attributes that doomed other megafaunal taxa to extinction. How did these giant reptiles persist? We suggest that the Komodo dragons' survival reflects general attributes of ectotherms (low energy demands; an ability to reduce mean adult body sizes during resource shortages) coupled with features of varanid biology (behavioural and ecological flexibility that allowed utilization of marine subsidies; salt tolerance), the habitat (a fragmented arid landscape better-suited to reptiles than to humans; and with substantial spatial and temporal variation in rainfall patterns and thus productivity), and the history of hominid colonization (when modern humans arrived, they brought with them novel prey [pigs] that blunted the impacts of hunting and habitat degradation). In short, the surprising persistence of the Komodo dragon is not due to any single unique attribute, but instead reflects a fortunate combination of factors relating to the species, the habitat, and the timeframe and nature of human colonization.

1. Introduction

Famously, the Earth's terrestrial fauna contained a diverse array of large-bodied taxa until about 50,000 years ago; but most of these so-called "megafauna" (species with adult body masses >44 kg: Martin, 1984) were extirpated soon after the arrival of modern humans (Burney and Flannery, 2005; Corlett, 2012; de Miranda, 2017). Island-living forms were at higher risk (Slavenko et al., 2016), especially if they relied upon both predation and scavenging (and thus, were dependent on carcasses of other megafauna: Fox-Dobbs et al., 2006; Meijer et al., 2015). Megafaunal extinctions occurred worldwide, albeit at different times (coincident with the spread of modern humans) and affected multiple lineages (mammals, birds, squamates, crocodilians, turtles) and organisms that spanned a variety of trophic roles (Miller et al., 2005). There has been considerable speculation about the causes of megafaunal extinctions, ranging from climate change to overhunting to introduced species to disease (e.g., Burney and Flannery, 2005; Wroe and Field, 2006). One way to gain insight into the

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extinctions is to look at the exceptions to the rule: giant terrestrial animals that have survived through to the present day, despite exhibiting characteristics associated with megafaunal extinction. The most spectacular reptilian examples of such exceptions-to-the-rule are the giant tortoises (*Aldabrachelys, Chelonoidis*) of the Galapagos and the Seychelles, and the Komodo dragon (*Varanus komodoensis*) of Indonesia.

With adults sometimes exceeding 85 kg (and occasionally, over 100 kg), Komodo dragons dwarf the maximum body mass of almost all other living lizard taxa by an order of magnitude (Auffenberg, 1981; Fry et al., 2009, Fig. 1a). Fossil evidence shows that *V. komodoensis* evolved around four million years ago and was widespread across mainland Australia (Hocknull et al., 2009). It had colonized the Wallacean islands of eastern Indonesia a million years ago, and remnant populations still persist in a few small arid islands in that region (Auffenberg, 1981; Murphy et al., 2015, Fig. 2). The species disappeared from its mainland Australian range about 50,000 years ago, coincident with widespread megafaunal extinctions in that continent (Roberts et al., 2001; Hocknull et al., 2009). Another, even larger congener (*V. priscus*) disappeared from Australia at around the same time (Molnar, 2004; Hocknull et al., 2009). Thus, Komodo dragons disappeared from most of their range soon after the arrival of modern humans, consistent with the broad scale of extinctions at that time. How, then, did the lizards persist in the westernmost part of their range, in the Wallacean islands, instead of suffering the same fate as their Australian conspecifics?

The enigma of the Komodo dragon's survival is exacerbated by the lack of large mammalian prey on those islands over the critical time period when other megafauna disappeared. Ecological studies on remnant populations of Komodo dragons show that adult lizards feed primarily on ungulates (deer, pigs, buffalo: Jessop et al., 2006) that were introduced to the islands about 7,000 to 10,000 years ago (Groves, 1984; van den Bergh et al., 2009; Sutikna et al., 2018, Fig. 1b). Any hypothesis to explain the Komodo dragon's persistence thus must explain their survival during two critical phases. First, how did populations of these massive animals remain viable for a million years on small islands that lacked large ungulate prey? Second, how did the Komodo dragons persist after modern humans arrived? Below, we explore those two questions.

1.1. How did Komodo dragons persist without ungulate prey during the Pleistocene?

Before modern humans arrived, the Wallacean islands historically contained other types of large mammals (i.e., non-ungulates) that may have served as prey. For example, the Komodo dragons may have eaten or scavenged pygmy elephants (*Stegodon*) (Auffenberg, 1981; Diamond, 1987). However, *Stegodon* appears to have been extirpated about 50,000 years ago (van den Bergh et al., 2009; revised dating by Morley et al., 2017; Sutikna et al., 2016, 2018), leaving a long gap (from around 50,000 to 10,000 years ago) when the islands lacked large mammals. Scavenging birds in this region (giant maribou storks and vultures) went extinct when the *Stegodon* disappeared (Meijer et al., 2015; Sutikna et al., 2018); why didn't the same fate befall the lizards?

Several features of the biology of *V. komodoensis* may have facilitated its persistence:
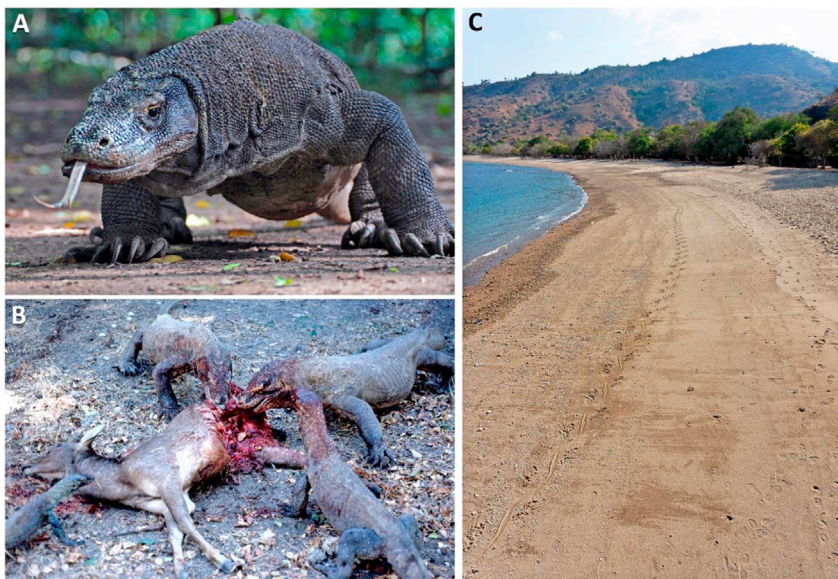

Fig. 1. (a) Sometimes exceeding 100 kg in weight, the Komodo dragon *Varanus komodoensis* is the largest species of lizard in the world (photo Ruchira Somaweera). (b) Large Komodo dragons in modern-day populations depend heavily upon introduced ungulates as prey. This Timor deer (*Rusa timorensis*) was actively hunted down by an adult Komodo dragon (photos W.K. Fletcher and Donna Baylis). (c) Komodo dragons frequently walk along the beaches at low tide scavenging beach-washed marine items (photo Richard Shine).
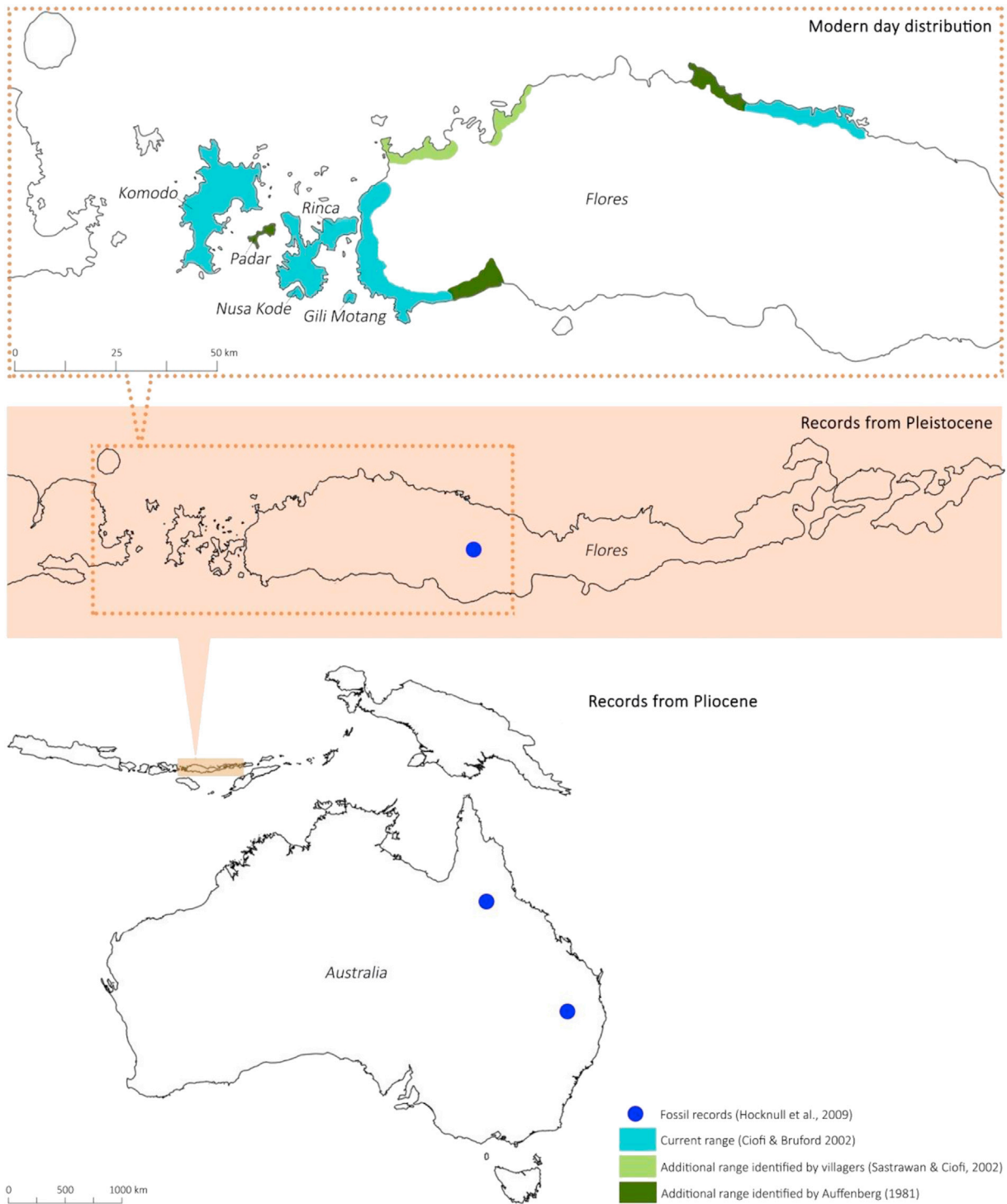
Fig. 2. Prehistoric fossil records and current known distribution of Komodo dragons (*Varanus komodoensis*).

(1) *Efficiency in energy use.* − As ectotherms, lizards require only around 10% of the food and water intake of a similar-sized endothermic predator (Pough, 1980, 1983). An island too small to support a viable population of mammalian predators (such as tigers) might well support a population of tiger-sized lizards.

(2) *Ability to utilize seasonal peaks in prey abundance.* − Unlike endotherms, ectotherms are able to subsist on food re-sources that are available only seasonally, rather than requiring year-round opportunities to feed (Pough, 1980; Bonnet

et al., 1998). Under the highly seasonal rainfall regimes of the Wallacean islands, some prey types may well have been available only for brief periods each year (e.g., during periods when birds or sea turtles were nesting).

(3) *Developmental flexibility.* — Squamate reptiles are capable of flexibly down-regulating growth at times of food scarcity; indeed, Galapagos marine iguanas (*Amblyrhynchus cristatus*) were reported to shrink by up to 20% when an El Nino event massively reduced their food supply (Wikelski and Thom, 2000). Likewise, Australian water pythons (*Liasis fuscus*) reduced growth rates, matured at smaller body sizes, and produced smaller clutches of eggs, after flooding eliminated their rodent prey (Ujvari et al., 2011). In spatial comparisons within snake species, the availability of prey drives geographic variation in mean and maximum body sizes (e.g., Pearson et al., 2002). Mean and maximum body sizes of *V. komodoensis* are far lower on islands where ungulate prey is scarce, than on nearby islands where ungulates are common (Jessop et al., 2006). That shift in adult body sizes likely reflects developmental plasticity rather than local adaptation, because some islands with small vs. large lizards are adjacent, with high rates of gene flow between them (Jessop et al., 2006).

(4) *Ecological flexibility.* — Strong spatial and temporal shifts in diet show that varanid lizards can focus on locally available prey types (such as freshwater crabs, carcasses, or fish in drying ponds: e.g., Shine, 1986; Losos and Greene, 1988). On Rinca Island, Komodo dragons increased their consumption of macaques when growing numbers of tourists frightened away the ungulate prey (Imron et al., 2018); and the lizards also target scrubfowl eggs during the birds' nesting season (Lincoln, 1974).

(5) *Behavioural flexibility.* — Studies on captive Komodo dragons suggest that these lizards have better cognitive skills and more complex behavioural repertoires than do most other squamate species (e.g., Collins, 1956; Burghardt et al., 2002). Field studies on a large varanid species in tropical Australia have documented strong variation among individuals in "personality" types, linked to ecological traits such as habitat use (Ward-Fear et al., 2018). Such diversity is widespread in many organisms, but we are not aware of any other case where behavioural syndromes map so clearly onto ecological dimensions. If varanids are indeed unusual in exhibiting this level of variation among individuals in niche utilization, a population of these lizards may be able to exploit a wider range of foraging opportunities than would be accessible to many other reptile species.

(6) *Ontogenetic shifts in trophic niche.* — As in many ectotherms, Komodo dragons are ecologically independent over a wide range of body sizes (hatchling to adult) and forage on different prey types as they grow older and larger (e.g., Imansyah et al., 2008; Purwandana et al., 2016). For example, juvenile *V. komodoensis* are far more arboreal than are adults. That within-population variation in behavioural ecology means that a population can persist even if the trophic niche for the largest size classes is non-viable due to a lack of large prey. As long as sufficient prey are available to support individuals up to a size where reproduction is possible, the population can persist.

(7) *Parthenogenesis.* — Female Komodo dragons can produce viable offspring without mating (Watts et al., 2006). It is easy to imagine situations where males (by far the larger sex: Auffenberg, 1981) were eliminated by resource shortages (larger animals are the first to die, because of their greater energy needs: e.g., Ujvari et al., 2011), but with continued population-level reproductive output because of the capacity for parthenogenesis.

(8) *Salt tolerance.* — Komodo dragons (like other varanids) are physiologically able to concentrate and excrete excess salt (Dunson, 1984; King and Green, 1999). Thus, the salt load in a marine-based diet (from scavenging along beaches at low tide) would not be problematic for a Komodo dragon.

(9) *Cannibalism.* — In Auffenberg's (1981) analysis, conspecifics were the fifth most common prey type for adult Komodo dragons. In conditions of extreme food scarcity, a capacity for cannibalism might maintain population viability over the short term (van Kooten et al., 2007).

(10) *Inbreeding avoidance.* — The very small current population sizes of lizards on some islands — and also intermittently over evolutionary time, on many of the islands that harbour the species — mean that inbreeding could be devastating for population viability (O'Grady et al., 2006; Purwandana et al., 2014, 2015). However, studies on other lizard taxa suggest that even in the absence of kin-based recognition, females avoid inbreeding by selective use of sperm from distantly-related males to fertilize the eggs (Olsson et al., 1996). Such a mechanism would minimize the ill-effects of a small gene pool.

Habitat features of the Wallacean islands may have been important also:

(1) *Interconnectedness.* — The highly fragmented archipelago creates many semi-isolated islands, with low rates of genetic exchange between some islands (Auffenberg, 1981; Ciofi and Bruford, 1999a,b; Ciofi et al., 1999). Thus, any threatening process (such as a volcanic eruption, a change wrought by modern humans, or a crash in prey availability) would be spatially heterogeneous in its impact. A vulnerable species might find a refuge for long enough to survive the period of maximal risk.

(2) *Marine subsidies.* — Although terrestrial productivity is reduced by low rainfall over much of the year, combined with porous limestone soils (Monk and de Fretes, 2012), the oceans surrounding Komodo are rich in marine life (Allen, 2008). Komodo dragons frequently walk along the beach at low tide (Fig. 1c), scavenging items that have been washed ashore (Auffenberg, 1981) as well as in shallow waters. Burden (1928) reported that on a small island (Padar) supposedly lacking ungulate prey, Komodo dragons fed entirely on turtle eggs. Large varanids in Australia (*V. panoptes*

and *V. varius*) likewise depredate on sea-turtle nests (Lei and Booth, 2017, 2018). Marine subsidies are key to the ecology of other large terrestrial predators in insular ecosystems also (e.g., bears − Aguss et al., 2007; Flynn et al., 2007).

In combination, these ideas suggest the following scenario. Komodo dragons evolved their gigantic size as an adaptation to feeding on the Australian mesofauna. When fluctuating sea levels provided land bridges, the lizards expanded their range westward into the Wallacean islands, where the presence of pygmy elephants enabled *V. komodoensis* to continue its role as a predator and scavenger of large mammals. As energy-efficient ectotherms, the lizards were able to maintain viable population sizes even on small islands − facilitated by an ability to switch rapidly between alternative prey types as opportunities arose. Thus, small islands could serve as refugia, and as sources for recolonization of larger islands in a metapopulation structure. After *Stegodon* disappeared, many of the feeding opportunities for lizards (such as seasonal availability of sea-turtle eggs) were marine-derived. Their low metabolic rates and large body sizes enabled Komodo dragons to deal with long periods of water and food scarcity, and high loads of salt in the marine resources they could find. During periods when food supplies were limited, growth rates declined and maximum body sizes shrunk (as occurs in modern-day populations of Komodo dragons if ungulates are rare: Jessop et al., 2006). Thus, part of the reason for the continuing survival of these giant lizards was that over long periods of time, they were not giants − or at least, nowhere near as large as they are today (due to the current abundance of feral ungulate prey).

In keeping with the "intermittent dwarfing" hypothesis, the sizes of fossil teeth found on Flores suggest that most lizards during the Pleistocene may have been smaller than those currently alive (Hocknull et al., 2009). Although sample sizes are small, the modal tooth base lengths from fossil sites at Tangi Talo (n = 4) and Ling Bua (n = 5) were both 4 mm, whereas the modal base length for teeth from 168 living specimens was 6 mm (Figure S1 in Hocknull et al., 2009).

1.2. How did the Komodo dragon withstand human-imposed pressures during the Holocene?

Early hominids (*Homo floresiensis*) coexisted with Komodo dragons for much of the Pleistocene, and ate the lizards (via predation and/or scavenging: van den Bergh et al., 2009). Regardless, the worldwide history of megafaunal extinctions correlates more closely with arrival of modern humans at a site rather than with the presence of other hominid species (Lorenzen et al., 2011; Sandom et al., 2014). Debates still rage about the role of modern humans in killing off the megafauna (e.g., Wroe and Field, 2006), but that high temporal correlation suggests a causal connection (Burney and Flannery, 2005).

Homo floresiensis disappeared from the Wallacean islands about 50,000 years ago (recalibration of fossil dates by Sutikna et al., (2016, 2018) indicates a much older disappearance than inferred by van den Bergh et al., (2009)). Modern humans may have arrived on Flores and Komodo at around the same time. Initial estimates of a later arrival time (about 11,000 years ago) have been falsified by the discovery of fossil remains of modern humans in Sumatra, Borneo, Flores, and Timor from about 40,000 years ago (O'Connor, 2007; Morley et al., 2017; Sutikna et al., 2018; Westaway et al., 2017). However, hominids probably were uncommon in the Komodo dragon's current range during the period when megafaunal extinctions were occurring in nearby Australia (Roberts et al., 2001; Barnosky et al., 2004; Miller et al., 2005; Barnosky and Lindsey, 2010).

In keeping with a role for modern humans in megafaunal decline, *V. komodoensis* was eradicated from its mainland Australian range soon after *Homo sapiens* arrived there 50,000 years ago (Hocknull et al., 2009); and has declined substantially over its range in Flores since humans arrived there (especially in areas with high population densities of humans: van den Bergh et al., 2009; Sutikna et al., 2018). A lack of *V. komodoensis* fossils in sites such as Timor suggest early extirpation of large terrestrial species soon after the arrival of modern humans (O'Connor, 2007). In contrast to other megafaunal species, however, *V. komodoensis* has not been extirpated − it persists in a small part of its former range. Why have these megafaunal remnants survived? The timespan of sympatry between modern humans and Komodo dragons (at sites where the species still persists) is far longer than humans required to extirpate megafauna on other islands (e.g., New Zealand − Duncan and Blackburn, 2004; Vanuatu − White et al., 2010). Importantly, molecular-clock analyses suggest that populations of *V. komodoensis* on Komodo Island have been separate from those on all other islands for round 80,0000 years whereas the other populations exchanged genetic material with Flores until around 10,000 years ago (Ciofi and Bruford, 1999a,b; Ciofi et al., 1999). Thus, the lizards on Komodo had to deal with the impacts of modern humans separately from the lizards in other parts of the species' range. Strikingly, both of these subpopulations persisted.

As is the case for the species' persistence through the Pleistocene, we attribute the continued survival of the Komodo dragon throughout the Holocene to multiple factors:

(1) *The introduction of ungulates.* − Modern-day populations of Komodo dragons depend heavily upon deer, pigs and buffalo, which provide prey suitable for large adult dragons (Jessop et al., 2006). Pigs were brought in about 7,000 to 10,000 years ago (van den Bergh et al., 2009; Sutikna et al., 2018); their high fecundity likely created an abundant food source for the lizards at the same time as populations of modern humans were increasing. Deer and buffalo are more recent introductions (e.g., Groves, 2006; Sutikna et al., 2018). Coincidentally, then, the ungulate most likely to rapidly establish dense feral populations (the pig) was also the first to arrive. The massive addition to the prey base from feral pigs may have buffered any impact from other threats (due to hunting, habitat degradation, etc.) imposed by modern humans.

(2) *Seasonal aridity.* — The virtual lack of permanent waterbodies on islands with porous soil (like Rinca) must have discouraged human habitation. The lack of rainfall over most of the year renders agriculture almost impossible (Pet and Yeager, 2000). Early populations of modern humans in this region may have relied heavily upon freshwater shellfish for food (Sutikna et al., 2018), a resource unavailable on the more arid Wallacean islands. By reducing densities of people living on the islands, aridity may have mitigated the intensity of conflict between humans and lizards. In keeping with that idea, the relatively well-watered island of Flores has supported denser populations of humans, and hence greater habitat degradation, than have the smaller more arid islands that also support *V. komodoensis* (Forth, 2010). As a result, populations of Komodo dragons have undergone greater declines on Flores than on some of the smaller islands (Ciofi and de Boer, 2004; Ariefiandy et al., 2015).

(3) *Harsh and variable conditions.* — The fossil record at Liang Bua in Flores reveals major volcanic eruptions at around 50,000 and 12,000 years ago, at times when faunal composition shifted significantly (Sutikna et al., 2018). Also, climatic reconstructions suggest that Flores experienced variable climatic regimes throughout the time when modern humans have been present in the area (Westaway et al., 2009). An early period of wetter conditions (49,000 to 39,000 years ago) was followed by an arid phase, then a return to monsoonal conditions about 15,000 years ago (Westaway et al., 2009). The low energy demands of ectothermy may have enabled varanid lizards to endure that stochasticity more easily than could endotherms such as modern humans (see above).

(4) *Risk-avoidance by lizards.* — As noted above, some populations of varanids contain individuals with a wide range of "personality" types (Ward-Fear et al., 2018). The existence of "shy" individuals may have enabled survival of a subset of lizards (disproportionately females (Ward-Fear et al., 2018), the more critical sex for population viability (Caughley and Sinclair, 1994)). Any factor increasing survival rates of females would be especially important in *V. komodoensis*, where adult sex ratios are highly biased towards males (Laver et al., 2012).

In summary, populations of Komodo dragons were severely affected by the arrival of modern humans, but ecologically-enforced low densities of humans, plus the mitigating impact of other factors (especially, abundant new prey types) enabled the giant lizards to avoid extinction.

2. Discussion

Our speculative scenario identifies two timeframes over which extinction of the Komodo dragon might have been expected, given general ecological principles and declines in other megafaunal taxa. For example, the analysis by Slavenko et al. (2016) identified large body size and insularity as key factors predicting extinction of lizard species in the late Quaternary. Komodo dragons likely survived the Pleistocene via ecological flexibility. The challenge of supporting a viable population of gigantic predators on small low-productivity islands is eased if the predator in question can operate over a wide range of body sizes rather than only above the size used as the cutoff for defining "megafauna" (e.g., >44 kg: Martin, 1984). In practice, most adult female Komodo dragons fall below this criterion even in present-day populations, where abundant ungulates allow rapid growth and large maximal body sizes (e.g., in Auffenberg's (1981) study, no female *V. komodoensis* weighed >30 kg). All that is required for population persistence is that some subset of the size range of adults is ecologically viable. Even in times of resource scarcity, when mean and maximum body sizes decreased, small Komodo dragons could find enough prey to survive. Thus, we speculate that this megafaunal species was able to avoid extinction because a population of ectotherms contains ecologically independent individuals that span a wide range of sizes (Pough, 1980). At least some of those body sizes (the smaller ones) remained ecologically viable (and able to reproduce) even when local conditions rendered larger sizes unsustainable. Additionally, the fragmented insular habitat created spatial variation in traits (such as mean body sizes and diets) both in traits that influenced vulnerability, and in the intensity of threatening processes (both stochastically and as a function of island size).

Although far briefer, the second timeframe — Holocene coexistence with modern humans — would have posed a greater threat to Komodo dragon populations. All across the world, megafaunal species rapidly went extinct in this situation (Burney and Flannery, 2005). But on the Wallacean islands, habitats were more suited to an ectotherm with low requirements for energy and water and a high tolerance of salt loads, than to hominids with their much higher metabolic needs. Periodic volcanic eruptions and shifts in climate may have further reduced the numbers of colonizing humans. And critically, the proliferation of edible large ungulates coincident with colonization by modern humans meant that although Komodo dragons were suddenly under threat from diverse processes (including hunting, habitat degradation, and changed fire regimes: Ciofi, 1999; Jessop et al., 2006) the lizards were simultaneously provisioned with a new source of prey (Forth, 2010). The two factors may have offset each other, with higher mortality but increased energy availability and thus, higher rates of reproduction. The niche that Komodo dragons evolved to fill — predation on the Pleistocene Australian mesofauna — had provided them with the weapons (including venom: Fry et al., 2009) and foraging tactics needed to bring down large mammals. After millenia of functioning in a different trophic niche — exploitation of diverse smaller prey, often marine-derived — the Komodo dragon reverted to the ecological role in which it had originally evolved.

According to the scenario we have outlined, the persistence of the Komodo dragon is a result of interacting factors that encompass the biology of the lizards, the landscape in which they have survived, and the timeframe, nature and history of colonization of the area by modern humans. Stochastics have been important, with the fragmented archipelago creating

multiple near-independent populations that were more resilient to overall extirpation than any single population would have been. None of the factors that we have identified as facilitating the survival of the Komodo dragon is unique; but the combination of factors, and their interaction, may be shared by few if any other megafaunal taxa.

What do these ideas tell us about management of the Komodo dragon into the future? At first sight the relevance is low because the commercial benefits of a booming tourism industry have transformed human attitudes towards these giant lizards (Walpole and Goodwin, 2000; Walpole, 2001). They are a source of income rather than a threat to livelihoods. However, experiences in other parts of the world tell us that bureaucratic protection may mean little if megafauna impose a risk or commercial cost to human inhabitants of the region (as for lions in some parts of Africa: Kerbis Peterhans and Gnoske, 2001) or even if local residents resent the government's emphasis on wildlife rather than people (e.g., the antagonism of Galapagos fishermen towards giant tortoises: Nicholls, 2010) (see also Forth, 2010). In a landscape at increasing risk from climate change and human overpopulation, the continued survival of these giant lizards will require committed efforts by local authorities (Rodriguez, 2014; Ardiantiono et al., 2015). Komodo dragons escaped the fate of most megafauna — extinction during the Pleistocene or Holocene — but are now subject to novel challenges (including, paradoxically, the increased tourism attracted by the lizards' iconic status: Walpole and Goodwin, 2000; Endo, 2013).

Conflicts of interest

The authors have no competing interest to declare.

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Appendix A. Supplementary data

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