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Evolution: The rise and fall of island dwarfs and giants

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Islands are arenas for a range of striking evolutionary phenomena, including the island rule — the tendency for larger animals to shrink and smaller animals to enlarge. A new study of insular mammals finds such body size shifts predispose these evolutionary marvels to greater extinction risk.

Islands are often referred to as natural laboratories, providing inspiration and testbeds for the development of numerous ecological and evolutionary theories[1,2]; and of course, the theory of evolution by natural selection itself owes its formulation in no small part to the study of the biota of islands. While true, the label masks the fact that today very few islands can be considered entirely natural. Indeed, several of the classic archipelagos used in island biology studies have seen such substantial anthropogenic changes that almost their entire complement of specific taxonomic groups has been lost[3,4]. Over 70% of recorded extinctions in the last 500 years have been island endemics, despite islands only representing ~7% of the global land surface area[5]. If we extend the time window back before 1500 CE — a period when most islands were first colonised by humans — the loss of species is even greater. For example, recent work has shown that almost half of island endemic birds known to be present ~100,000 years ago are either extinct or currently threatened with extinction[6,7]. Certain archipelagos have fared worse than others, with New Zealand, the Mascarenes, the Caribbean, Hawaii, and several other Pacific archipelagos being particularly hard hit in terms of their bird communities[4,7,8]. Insular extinctions are by no means unique to the birds, however, with many taxonomic groups having suffered large numbers of island extinctions[3,5,9,10]. A new study by Roberto Rozzi and colleagues[10] now provides the most up-to-date synthesis of island extinctions with regard to mammals, finding evidence of hundreds of insular mammalian extinction events (both natural and anthropogenic extinctions).

Given the above, it is evident that humans have had severe impacts on island biodiversity, resulting in the extinction of hundreds (probably thousands) of species. What is needed then is to better understand the causes of such substantial loss. These causes can be lumped into two coarse groups: the anthropogenic drivers of extinction, such as invasive species, habitat destruction, and hunting[11]; and the characteristics of island species themselves[1,12]. In regard to the latter, the distinctive nature of island environments has led to a range of evolutionary changes in different taxonomic groups — collectively termed 'island syndromes'. Perhaps the most famous example of an island syndrome is the often observed change in body size of insular organisms: the island (body size) rule[13–15]. While island rule studies have been undertaken for numerous taxonomic groups[16], the pattern was initially explored for mammals, and was concisely described[13] as a "graded trend from gigantism in the smaller species of insular mammals to dwarfism in the larger species" (Figure 1). Numerous hypotheses have been proposed to explain the island (body size) rule in mammals, including resource limitation in insular environments[1] and ecological release from competition and predation pressure relative to the ancestral mainland area[14,15]. As with almost all ecological patterns, however, the island (body size) rule is not universal, and its generality has been questioned for several reasons[17].

Despite the large amount of research previously undertaken on the island (body size) rule and the knowledge that body mass is an established predictor of extinction likelihood (larger species within a given taxon typically being more at risk of extinction) across many groups[3,7], the relationship between the magnitude of mammalian body size evolution on

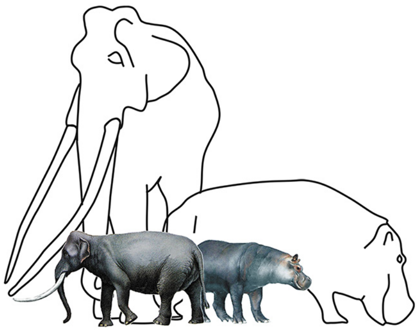

Figure 1. Examples of extinct island dwarf species from the Pleistocene.
Two island dwarf species: the Sicilian dwarf elephant (*Palaeoloxodon falconeri*) and the Cypriot dwarf hippopotamus (*Hippopotamus minor*). These species — both of which are believed to have been the smallest of their kind (<10% of their ancestral mainland body mass[14,20]) — are presented relative to their mainland ancestor/close relative. Drawings are roughly to scale. Figure from Lyras[20] and used with permission of George Lyras.

islands and extinction risk was not fully understood. The study by Rozzi and colleagues[10] set out to evaluate how evolution toward gigantism and dwarfism has affected the extinction risk of island mammals — in terms of natural and anthropogenic extinctions. To this end, the authors analysed body mass data from 1231 extant (threatened and non-threatened) and 350 extinct insular mammal species. For each species, body size change was calculated using island–mainland comparisons of populations or, in the case of island endemics, of sister species. Using these data, Rozzi and colleagues[10] found that there was a strong relationship between the magnitude of body size change (i.e., the extent to which the body mass of an island species increased or decreased relative to its mainland ancestor), in addition to body mass, and extinction risk. Put succinctly, the likelihood of extinction, or of being threatened with extinction, is highest in the "most extreme island dwarfs and giants", as well as being higher in those with larger body mass in general[10]. Many of these spectacular examples of island evolution have thus unfortunately been lost (e.g. the Cypriot dwarf hippopotamus; Figure 1), with most of those that remain being at risk of extinction in the near future (e.g., the Critically Endangered dwarf tamaraw of Mindoro). While some of these extinctions were likely to be due to natural causes, Rozzi and colleagues[10] calculate that insular extinction rates increased 10-fold following the arrival of modern humans. It is a similar story with birds, with many of the most extreme examples of insular avian giants and dwarfs having joined their mammalian counterparts in the abyss of extinction. These include the giant moa of New Zealand, along with their predator the Haast's eagle, the elephant birds of Madagascar (the largest being around 3 meters tall), and the dwarf King Island emu — all believed to have been driven extinct at least in part by human actions.

While the observation that larger species are more at risk of extinction matches the findings of previous studies, the results of Rozzi and colleagues[10] indicate that this increase in extinction risk is evident in both directions with respect to body size shifts, with insular dwarfs also being disproportionately vulnerable. Overall, these results indicate that many of the evolutionary adaptations of species in response to the distinct environments they encounter when they arrive on islands (i.e., island syndromes) have increased their susceptibility to extinction[10,12,15]. For example, one explanation for body size shifts in insular mammals is a release from predation pressure. However, this then means that these species are ill-prepared for the subsequent introduction of novel predators, such as cats, rats and mice, to islands by humans[15]. A similar scenario can be seen with the reduction in dispersal ability observed in many insular birds, plants and insects — an evolutionary response to the reduced need for strong dispersal ability on islands — which predisposes these species to greater extinction risk[1,6].

The results of Rozzi and colleagues[10] also provide additional confirmation of the general vulnerability of island species compared to their continental cousins. For example, while the probability of mammals becoming extinct was found to be similar for large-bodied species on both islands and continents, there were found to be substantially higher proportions of threatened and extinct small and intermediate-sized mammals on islands compared to continents. When combined with the observations of earlier studies[3,6,7], these findings indicate that, while several traits are indicators of extinction risk (e.g. body size, dispersal ability, generation length), one of the most important predictors of the likelihood of extinction is simply whether or not a species is an island endemic. Lastly, Rozzi and colleagues[10] have provided further evidence that the scale of anthropogenic extinctions on islands has influenced our perception of 'natural' island biological patterns[18,19], a fact that has already been noted with respect to the island rule[15]. This issue is by no means exclusive to islands and going forward it is imperative that more is done to fully understand how the past impacts of humans have shaped our understanding of the natural world.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Mosquito biology: Scents and selectability

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Malaria-transmitting mosquitoes are skilled human hunters, selectively choosing their prey based on a complex array of sensory cues. A new study unveils a distinct pattern of preference for human-associated olfactory cues that underlies the selective behavior of these mosquitoes.

It's a warm summer night, and you are sitting outside with your friends, sipping cold drinks and enjoying the gentle breeze. Suddenly, you hear that tell-tale buzzing sound. It is a mosquito on a search for its next victim. You try to swat it away, but it's too late. You feel the sharp sting of its proboscis piercing your skin. As you scratch at the itchy welt on your arm, you can't help but wonder — why do mosquitoes always seem to find you, no matter how much bug spray you use or how much skin you cover? While their uncanny ability to locate exposed human flesh might seem like magic, in reality, mosquitoes use several factors, including visual cues, body heat, humidity, carbon dioxide (CO_2), and chemicals emitted by the skin, to select their target[1]. In a new study published in this issue of *Current Biology*, Giraldo, Rankin-Turner, and colleagues[2] investigate the dynamic interplay of these sensory cues that drive the attraction of *Anopheles gambiae*, a species of African mosquito known for transmitting malaria, toward a human host.

Previous laboratory studies have suggested that when female *Anopheles* mosquitoes go hunting for a blood meal at night, they use multiple sensory cues to detect and locate humans in the vicinity[3,4]. The first cue they pick up on is the CO_2 we exhale, which causes them to fly upwind in search of a host[5,6]. As they get closer to a potential host, they sense other scents emanating from our bodies and breath[7,8], which also trigger their visual search for a target[4,9]. Once they are within close proximity, they rely on additional cues, such as body heat and moisture, to zero in on their target[10,11] (Figure 1A,B). However, the relative importance of these cues and how mosquitoes use them to navigate and select a human host in their naturally complex environments is not fully understood.

To bridge this gap in knowledge, Giraldo, Rankin-Turner, and colleagues conducted large-scale multi-choice assays in a large outdoor flight cage in Zambia, Africa. For these choice assays, they placed eight dark-colored heated disks — serving as visual and thermal targets for mosquito landings — in an octagonal pattern at the center of the cage, each equipped with an air duct for olfactory stimulus delivery and an infrared camera for visualizing mosquito landings. The disks were set to 35°C to mimic human skin temperature and were baited with different olfactory cues to measure the innate olfactory preferences of mosquitoes as they search for a human target over a naturalistic range of distances. The authors based this setup on their laboratory experiments, which showed that a combination of visual, thermal, and olfactory cues is most effective at evoking landing behavior in *Anopheles* mosquitoes, at least at close range (Figure 1C).

In a series of multi-choice experiments conducted in semi-outdoor conditions, the authors first mapped out the relative importance of sensory cues that attract mosquitoes toward a warm visual target. They found that a combination of thermal and visual cues alone was insufficient to attract mosquitoes flying over a range of

