Ecological history and latent conservation potential: large and giant tortoises as a model for taxon substitutions

Dennis M. Hansen, C. Josh Donlan, Christine J. Griffiths and Karl J. Campbell

D. M. Hansen (dmhansen@stanford.edu), Dept of Biology, Stanford Univ., 371 Serra Mall, CA 94305, USA. – C. J. Donlan, Advanced Conservation Strategies, P.O. Box 1201, Midway, UT 84049, USA, and Copeland Fellow in Global Sustainability, Amherst College, Amherst, MA 01002, USA, and Dept of Ecology and Evolutionary Biology, Cornell Univ., Ithaca, NY 14853, USA. – C. J. Griffiths, School of Biological Sciences, Univ. of Bristol, Woodland Road, Bristol, BS8 1UG, UK, and Inst. of Environmental Sciences, Univ. of Zurich, 190 Winterthurerstrasse, CH-8057 Zurich, Switzerland. – K. J. Campbell, Island Conservation, LML, 100 Shaffer Road, Santa Cruz, CA 95060, USA, and School of Integrative Systems, Univ. of Queensland, Gatton, Queensland 4343, Australia.

Starting in the late 1970s, ecologists began unraveling the role of recently extinct large vertebrates in evolutionary ecology and ecosystem dynamics. Three decades later, practitioners are now considering the role of ecological history in conservation practice, and some have called for restoring missing ecological functions and evolutionary potential using taxon substitutes – extant, functionally similar taxa – to replace extinct species. This pro-active approach to biodiversity conservation has proved controversial. Yet, rewilding with taxon substitutes, or ecological analogues, is now being integrated into conservation and restoration programmes around the world. Empirical evidence is emerging that illustrates how taxon substitutions can restore missing ecological functions and evolutionary potential. However, a major roadblock to a broader evaluation and application of taxon substitution is the lack of practical guidelines within which they should be conducted. While the International Union for Conservation of Nature's reintroduction guidelines are an obvious choice, they are unsuitable in their current form. We recommend necessary amendments to these guidelines to explicitly address taxon substitutions. A second impediment to empirical evaluations of rewilding with taxon substitutions is the sheer scale of some proposed projects; the majority involves large mammals over large areas. We present and discuss evidence that large and giant tortoises (family Testudinidae) are a useful model to rapidly provide empirical assessments of the use of taxon substitutes on a comparatively smaller scale. Worldwide, at least 36 species of large and giant tortoises went extinct since the late Pleistocene, leaving 32 extant species. We examine the latent conservation potential, benefits, and risks of using tortoise taxon substitutes as a strategy for restoring dysfunctional ecosystems. We highlight how, especially on islands, conservation practitioners are starting to employ extant large tortoises in ecosystems to replace extinct tortoises that once played keystone roles.

Starting in the late 1970s, ecologists began unraveling the role of recently extinct large vertebrates in evolutionary ecology and ecosystem dynamics. For example, for the first time, the ecology of large-seeded fruits in the Americas and divaricating plants in New Zealand were viewed as anachronistic, due to the missing large vertebrates that once influenced their evolutionary ecology (Greenwood and Atkinson 1977, Janzen and Martin 1982). Such views based on ecological history came at a time when evidence was mounting that humans played a significant, if not the major, role in the extinctions of the late Pleistocene (Martin and Klein 1984).

Some three decades later, practitioners are now considering the role of ecological and evolutionary history in conservation practice. Some researchers have highlighted the underappreciated importance of evolutionary processes in effective biodiversity conservation planning (Erwin 1991, Atkinson 1998, Crandall et al. 2000, Ashley et al. 2003).

Others have gone further and called for restoring missing ecological functions and evolutionary potential with the introduction of related or sometimes unrelated taxa as analogues or substitutes for extinct species, often referred to as rewilding. While "rewilding" was originally coined by Soulé and Noss (1998), the term's meaning has been recently expanded in the scientific literature and media to include proposed reintroductions that incorporate ecological history back to the Pleistocene epoch (Atkinson 2001, Jones 2002, Steadman and Martin 2003, Galetti 2004, Donlan et al. 2005, 2006, Zimov 2005). We define taxon substitution as the replacement of extinct taxa by the introduction of analogue taxa – related or ecologically similar – to replace the ecological functions of the extinct species. Recently, empirical research has begun to illustrate how interactions of extinct species can be restored by using related or functionally similar taxa as taxon substitutes (Bond et al. 2004, Hansen et al. 2008, Griffiths et al.

2010). While the concept of rewilding remains a controversial means of restoring ecosystem processes (Caro 2007), taxon substitution projects are gaining acceptance within the public sector and a number of ambitious projects, firmly based on recent ecological history, are already underway (Zimov 2005, Curry 2008, Marris 2009). However, while some of these projects focused on taxon substitutions are based on sound science and justification, others may be misguided by bad historical information or dubious justifications. It is thus imperative that projects be judged on a case-by-case basis.

In this paper we first briefly discuss how existing guidelines and definitions fall short in providing an overall framework to help guide and inform taxon substitutions. The most suitable framework in which taxon substitutions should be addressed is the reintroduction guidelines of the International Union for the Conservation of Nature (IUCN 1998). Currently, those guidelines are limited to sub-species level substitutions (Soorae 2008). We propose that the IUCN reintroduction guidelines be revised to explicitly encompass taxon substitutions and promote a more holistic and dynamic approach to restoration. Revised guidelines are not only needed to provide a framework for how to implement well-thought-out taxon substitution projects, but are also particularly needed in order to discourage moving forward on projects when they are not justified scientifically, socio-politically, or pragmatically. In addition to guidelines, a second challenge to taxon substitutions is the sheer scale and accompanying controversy of many of the proposed projects (Galetti 2004, Donlan et al. 2005, Zimov 2005, Caro 2007). In response, we propose rewilding with large and giant tortoises (family Testudinidae) as a model to rapidly advance our understanding of taxon substitutions and provide much-needed empirical assessments of rewilding as a restoration tool.

Taxon substitutions and the IUCN reintroduction guidelines

Under the current IUCN guidelines for reintroductions, the aims of taxon substitutions fall within ''conservation or benign introductions'', defined as attempts to ''establish a species, for the purpose of conservation, outside its recorded distribution but within an appropriate habitat and ecogeographical area'' (IUCN 1998). However, the aims behind taxon substitutions and conservation introductions can differ. Conservation introductions deal exclusively with species that have ''become globally or locally extinct, or extirpated, in the wild'' (IUCN 1998), while taxon substitutions may involve species that may not be threatened within their native range. The IUCN guidelines would benefit from incorporating this distinction.

Reintroductions and translocations have historically been viewed in isolation from other conservation or restoration efforts, with a strong focus on avoiding extinction (Armstrong and Seddon 2008). The IUCN guidelines state that ''a conservation/benign introduction should be undertaken only as a last resort when no opportunities for reintroduction into the original site or range exist and only when a significant contribution to the conservation of the species will result'' (IUCN 1998). This inherently promotes a single-species approach, ignoring the potential for restoring lost or currently dysfunctional species interactions by using taxon substitutions. A recent review identified that the main goal of a majority of reintroduction projects was to increase the number of individuals or populations of the target species; in contrast, only two of 62 projects specifically listed restoration of species interactions as a goal (Soorae 2008). Reintroduction biology would benefit by incorporating the recent emphasis across conservation biology that focuses on ecological effectiveness and species interactions (Soulé et al. 2003, 2005, Ripple and Beschta 2007, Wright et al. 2007, Papanastasis 2009, Kaiser-Bunbury et al. 2010). With respect to restoring functional relationships within ecosystems, we propose that: 1) taxon substitutions, as defined above, are explicitly included as a stand-alone justification for a species introduction, and 2) reintroduction guidelines should include the use of taxa above the sub-species level under taxon substitutions, when it can be empirically demonstrated that the proposed substitute fulfills some ecological function(s) of the extinct taxon.

A vital role of conservation scientists is to inform policy and planning, while practitioners strive to implement action based on sound science. If empirical evidence exists that demonstrates how dysfunctional or lost species interactions and ecosystem processes can benefit from taxon substitutions – without negatively impacting human society, native biodiversity or ecosystem functions – it should be a clear goal to support such work. In order to contribute to biodiversity conservation, taxon substitutions must therefore be viewed and executed in a cost-benefit framework. Our proposed revision of the IUCN reintroduction guidelines would facilitate a much-needed transparent debate on the role of taxon substitutions in biodiversity conservation, and provide a framework to advance the science and application of taxon substitutions in restoration projects. Alternatively, a more all-inclusive set of introduction guidelines could be advanced by returning to the original definitions of translocations (IUCN 1987), along the lines recently suggested by Armstrong and Seddon (2008). In this case, taxon substitutions simply become a specialised case of introductions.

Large and giant tortoises: models for taxon substitutions

Tortoises of the family Testudinidae occur on most continents (except Antarctica and Australia) and on many isolated islands as a result of oceanic dispersal (Bonin et al. 2006, Crumly 2009). Many species, however, have gone extinct since the late Pleistocene. Within the last few millennia, the majority of tortoise extinctions occurred on islands. These recent tortoise extinctions present an opportunity to vet, implement, and evaluate the conservation potential of taxon substitutions. In that spirit, we provide an overview of extant and recently extinct large and giant tortoises, highlight the important roles of extant and extinct tortoises in some ecosystems, and argue that tortoises are a low-risk taxon for substitutions. Finally, we present and discuss several case stories that illustrate how extant tortoises can be suitable analogues for their recently extinct counterparts.

Global distribution and status of large tortoises

In general, we follow the taxonomy of Fritz and Havaš (2007), supplemented by recent findings in molecular studies (Austin et al. 2003, Le et al. 2006, Fritz and Bininda-Emonds 2007, Poulakakis et al. 2008). We include only tortoises with reported straight carapace or plastron lengths of >30 cm, which was chosen as our cut-off point because tortoises above this length are typically referred to as "large" and almost all known recently extinct tortoises are >30 cm.

At least 36 species of large and giant tortoises have gone extinct since the Pleistocene, with the majority occurring on islands and vanishing in the late Pleistocene (Table 1). At least 32 species are still extant, with the majority of higher-order taxa found on continents (Table 2). The only remaining species of giant tortoises growing to more than one meter carapace length are found on the isolated islands of Galápagos in the Pacific Ocean and the Aldabra Atoll in the Indian Ocean; *Geochelone* (*Centrochelys*) *sulcata* in the African Sahel belt comes close, with lengths of up to 83 cm.

Additional extinct tortoise species continue to come to light: sub-fossil specimens have been recently discovered both in the Mediterranean and Caribbean regions (Caloi et al. 1986, Meylan and Sterrer 2000, Chesi et al. 2007, Steadman et al. 2007).

Since the late Pleistocene, human predation and anthropogenic impacts have been major causes of tortoise extinction and endangerment. This is particularly well-documented for some of the recent extinctions on islands, including Madagascar, the Mascarenes, and the Galápagos (Van Denburgh 1914, Cheke and Hume 2008, Pedrono 2008). There is also ample evidence of early human tortoise-hunting in mainland habitats from the Paleolithic and onwards, including the Mediterranean Rim and southern Africa (Stiner et al. 1999, Klein and Cruz-Uribe 2000, Blasco 2008).

Some tortoise extinctions, however, occurred prior to human contact. For example, the Caribbean tortoise *Hesperotestudo bermudae* could have been lost due to partial submergence of its low-rise island home during recent interglacials (Meylan and Sterrer 2000, Olson et al. 2006).

Table 1. Extinct large and giant tortoises from the Pleistocene to Holocene.

Taxon	Distribution	Island/mainland	Last record	Maximum carapace length (cm)	References
Aldabrachelys abrupta	Madagascar	Island	Holocene	115	1, 2, 3
Aldabrachelys grandidieri	Madagascar	Island	Holocene	125	1, 2, 3, 4
Cheirogaster gymnesica	Minorca, Balearics	Island	Pleistocene		1, 5
Cheirogaster sp.	Pituysic Islands, Balearics	Island			5
Chelonoidis cubensis	Cuba, Brazil	Mainland and island	Pleistocene		1, 6
Chelonoidis elata	Cuba	Island	Pleistocene		1
Chelonoidis elephantopus	Floreana, Galápagos	Island	Holocene		7
Chelonoidis phantastica	Fernandina, Galápagos	Island	Holocene	86	7, 8
Chelonoidis? sellowi	Uruguay	Mainland	Pleistocene		1
Chelonoidis sombrerensis	Sombrero Island	Island	Late Pleistocene	100	1, 6, 9
Chelonoidis wallacei	Rabida, Galápagos	Island	Holocene	82	7, 10
Chelonoidis sp.	Santa Fe, Galápagos	Island	Holocene		7
Chelonoidis sp.	Great Abaco, Bahamas	Island	Holocene	46	11
Chelonoidis sp.	Dominican Republic	Island	Holocene	60	12, 13
*Chelonoidis? * sp.	Curaçao	Island	Pleistocene	80	14
Cylindraspis indica	Reunion, Mascarenes	Island	Holocene	60	2, 15
Cylindraspis inepta	Mauritius, Mascarenes	Island	Holocene	"Large"	2, 15
Cylindraspis peltates	Rodrigues, Mascarenes	Island	Holocene	42	2
Cylindraspis triserrata	Mauritius, Mascarenes	Island	Holocene	"Giant"	2, 15
Cylindraspis vosmaeri	Rodrigues, Mascarenes	Island	Holocene	110	15, 16
Geochelone burchardi	Canary Islands	Island	Pleistocene		1
Geochelone robusta	Malta	Island	Pleistocene	120	1, 17, 18
Geochelone sp.	Bahamas	Island		60	6
Geochelone sp.	Navassa Island	Island		40	6
Geochelone sp.	Barbados	Island	Late Pleistocene	60	19
Gopherus donlaloi	Mexico	Mainland	Pleistocene	54 (plastron)	20
Hesperotestudo crassiscutata	Southern USA, Central America	Mainland	Late Pleistocene	150	1, 13, 21
Hesperotestudo equicomes	Kansas, USA	Mainland	Pleistocene		1
Hesperotestudo incisa	Florida, USA	Mainland	Pleistocene		1
Hesperotestudo johnstoni	Texas, USA	Mainland	Pleistocene		1
Hesperotestudo wilsoni	Southern USA	Mainland	Holocene		1, 22
Manouria margae	Celebes, Indonesia	Island	Pleistocene	120–150	1, 23
Manouria oyamai	Ryukyu Islands, Japan	Island	Late Pleistocene	"Giant"	24
Megalochelys atlas	Java, India	Mainland and island	Pleistocene	180	1, 2
Megalochelys cautleyi	India	Mainland	Pleistocene		1
Monachelys monensis	Mona Island	Island	Pleistocene	50	1, 6

1: Auffenberg 1974, 2: Arnold 1979, 3: Pedrono 2008, 4: Bour 1984, 5: Sondaar and van der Geer 2005, 6: Auffenberg 1967, 7: MacFarland et al. 1974a, 8: Ernst and Barbour 1989, 9: Lazell 1993, 10: Steadman et al. 1991, 11: Steadman et al. 2007, 12: Franz and Woods 1983, 13: Meylan and Sterrer 2000, 14: Hoijer 1963, 15: Arnold 1980, 16: Stoddart and Peake 1979, 17: Caloi et al. 1986, 18: Hunt and Schembri 1999, 19: Ray 1964, 20: Reynoso and Montellano-Ballesteros 2004, 21: Cisneros 2005, 22: Moodie and Devender 1979, 23: Hoijer 1951, 24: Takahashi et al. 2003.

Table 2. Extant large and giant tortoises.

Species	Distribution	Island/mainland	Maximum carapace length (cm)	References
Aldabrachelys gigantea	Aldabra, Seychelles	Island	105	1
Astrochelys radiata	Southern Madagascar	Island	40	1
Astrochelys yniphora	Northwest Madagascar	Island	45	1, 2
Chelonoidis carbonaria	Northern South and Central America, introduced to Islands of Caribean	Mainland	70	1, 3
Chelonoidis chilensis	Southern South America	Mainland	43	1, 3
Chelonoidis denticulata	Northern South America and Trinidad	Mainland and island	82	1
Chelonoidis abingdoni	Pinta, Galápagos	Island	98	1, 4
Chelonoidis becki	Wolf volcano, Isabela, Galápagos	Island	104	1, 4
Chelonoidis chatamensis	San Cristobal, Galápagos	Island	90	1, 4
Chelonoidis darwini	Santiago, Galápagos	Island	102	1, 4
Chelonoidis ephyppium	Pinzon, Galápagos	Island	84	1, 4
Chelonoidis guntheri	Sierra Negra, Isabela, Galápagos	Island	102	1, 4
Chelonoidis hoodensis	Espanola, Galápagos	Island	75	1, 4
Chelonoidis microphyes	Darwin volcano, Isabela, Galápagos	Island	103	1, 4
Chelonoidis porteri	Santa Cruz, Galápagos	Island	105	1, 4
Chelonoidis vandenburghi	Alcedo volcano, Isabela, Galápagos	Island	125	1, 4
Chelonoidis vicina	Cerro Azul, Isabela, Galápagos	Island	110	1, 4
Chersina angulata	South Africa, southern Namibia	Mainland	30	5
Geochelone elegans	India, Pakistan, Sri Lanka	Mainland and island	38	1
Geochelone platynota	Burma	Mainland	30	1, 3
Geochelone (Centrochelys) sulcata	Central and North Africa, Sahel-belt	Mainland	83	1, 5
Gopherus flavomarginatus	North-central Mexico	Mainland	40 (fossils up to 100)	3
Gopherus agassizii	South-western USA, Mexico	Mainland	40	3
Gopherus polyphemus	South-eastern USA	Mainland	38	3
Indotestudo elongata	Asia (Nepal, India, China, Burma, Malaysia, Thailand, Cambodia, Vietnam)	Mainland	33	3, 6
Indotestudo travancorica	Western India	Mainland	30	3, 6
Kinixys erosa	Central West Africa	Mainland	40	3, 5
Manouria emys	Burma, Thailand, Malay Peninsula, Sumatra, Borneo	Mainland and island	60	3, 6
Manouria impressa	Burma, Thailand, Malay Peninsula, Vietnam	Mainland	33	3, 6
Stigmochelys pardalis	Eastern to southern Africa	Mainland	70	1, 3, 5
Testudo boettgeri	South-eastern Europe	Mainland	34	3
Testudo marginata	Greece, southern Balkan	Mainland	40	3

1: Ernst and Babour 1989, 2: Pedrono 2008, 3: Bonin et al. 2006, 4: MacFarland et al. 1974a, 5: Branch 2008, 6: Auffenberg 1974.

Similarly, there is evidence that Aldabra was re-colonised by giant tortoises from Madagascar at least three times, following sea-level changes that caused temporal submergence (Taylor et al. 1979). Projected anthropogenic increases in sea level may thus threaten the world's largest remaining population of giant tortoises, *Aldabrachelys gigantea*, on Aldabra Atoll. Therefore, in some cases taxon substitution cannot be justified based on redressing past anthropogenic extinctions, but could be debated if the introduction of a generalised herbivore is deemed to be facilitating the desired trajectory of an ecosystem restoration project in such places. Indeed, this approach could be a good example of "restoring for the future" (Choi 2007, Macdonald 2009), e.g. maximising future ecosystem resilience.

Few extant tortoises have been studied in sufficient detail to assign an updated IUCN Red List Category. Researchers have argued, however, that almost all extant tortoises are declining, and that many species should be considered endangered (Bonin et al. 2006, Branch 2008). Current threats to tortoises include collection by humans, introduced predators, and climate change (Erasmus et al. 2002, Bonin et al. 2006).

Tortoises as ecological and evolutionary keystone species

True land tortoises (family Testudinidae) arose around 55 million years ago, and are part of the oldest surviving reptile lineage (Auffenberg 1974, Bonin et al. 2006). The slow metabolism of tortoises and their ability to withstand long periods without food or water have enabled them to colonise almost all continents and many islands, with most species found in subtropical and tropical regions. Tortoises are important components of many ecosystems, and often attain high densities and biomass (Iverson 1982). For example, *Astrochelys radiata* density estimates in Madagascar vary from 1250 to 5400 tortoises km^{-2} (Leuteritz et al. 2005). On Aldabra, biomass of *A. gigantea* has been estimated to be between 3.5 and 58 tonnes per square kilometer – more than the combined biomass of various species of large mammalian herbivores in any African wildlife area (Coe et al. 1979). In some African game parks, tortoise biomass outweighs that of several species of large mammalian herbivores (Iverson 1982, Branch 2008). Most extant tortoise species are highly generalised herbivores, frugivores or omnivores (Grubb 1971, Milton 1992, Bonin et al. 2006,

275

Branch 2008). Tortoises do not masticate their food, have a relatively simple digestive system, and many species have flexible digestive responses that are determined by diet (Guard 1980, Bjorndal 1989, Barboza 1995, Hailey 1997, McMaster and Downs 2008). It is likely that extinct tortoises had similarly broad diets.

In many ecosystems, tortoises are thus likely to be or have been keystone species; not in the classical sense as it pertains to ecosystem importance in relation to biomass (Paine 1969), but rather in relation to the topological position and importance of tortoises in interaction- and food webs (Jordán 2009). A good example is the gopher tortoise *Gopherus polyphemus*, which influences a number of key processes in North American long-leaf pine grasslands and forest ecosystems, including herbivory, seed dispersal, nutrient cycling, and creating and maintaining habitat heterogeneity via trampling or digging of burrows (Kaczor and Hartnett 1990, Carlson et al. 2003, Birkhead et al. 2005, van Lear et al. 2005, Means 2006). Oceanic island ecosystems also offer many examples; given tortoises' propensity for long-distance oceanic dispersal, they were likely often among the first large, non-volant vertebrates to colonise oceanic islands – thus shaping these isolated ecosystems from early on in their history (Hnatiuk 1978, Arnold 1979, Meylan and Sterrer 2000, Gerlach et al. 2006). The resulting long, shared ecological and evolutionary histories of island tortoises and their plant communities has shaped many plant-tortoise interactions, many of which have since been lost as a result of tortoise decline or extinction (Iverson 1987, Strasberg 1996, Eskildsen et al. 2004, Gibbs et al. 2008, Hansen et al. 2008, Hansen and Galetti 2009, Griffiths et al. 2010). For example, "tortoise turf", a plant community of endemic grass, herb and sedge species and engineered by continuous tortoise grazing and trampling, is thought to have been common on islands throughout the Indian Ocean before tortoises went extinct; it is now restricted to Aldabra (Merton et al. 1976, Cheke and Hume 2008).

Furthermore, evidence is mounting that tortoises are or were important seed dispersers on continents and islands in ecosystems ranging from coastal shrub and dry deserts to rainforests (Rick and Bowman 1961, Hnatiuk 1978, Milton 1992, Varela and Bucher 2002, Strong and Fragoso 2006, Hansen et al. 2008, Jerozolimski et al. 2009). Tortoises can eat large amounts of fruits and swallow relatively large fruits and seeds. For example, yellow-footed tortoises *Chelonoidis denticulata* in Brazil with average carapace lengths of only 25–30 cm defecated seeds up to 4.0×1.7 cm in size (Jerozolimski et al. 2009). Variable gut passage times have been reported for tortoises, with average values ranging from a few days to three weeks, allowing for mean dispersal distances of several hundred metres (Rick and Bowman 1961, Hansen et al. 2008, Jerozolimski et al. 2009).

Tortoises represent low-risk, high-impact taxon substitutions

On many islands, tortoise extinction has resulted in dysfunctional ecosystems with respect to seed dispersal and herbivory (Gibbs et al. 2008, Hansen et al. 2008, Hansen and Galetti 2009, Griffiths et al. 2010). On continents, the greater array of extant native herbivores and frugivores has likely helped buffer the ecological losses of tortoises (Hansen and Galetti 2009). Thus, tortoise taxon substitutions are arguably more imperative and appropriate on islands. Indeed, the impact and conservation value of tortoise taxon substitutions on islands is likely to be greater than suggested for mainland scenarios, due to the simpler ecosystems that have only recently been subjected to anthropogenic impacts (Kaiser-Bunbury et al. 2010).

Tortoises can be regarded as low-risk taxon substitutes (Griffiths et al. 2010). Due to their highly generalised diets and relatively minimal reintroduction requirements, it is likely that tortoises introduced as taxon substitutions would be able to reestablish some ecosystem functions of the extinct tortoises and become integral parts of their new ecosystems. We highlight five reasons for large tortoises being particularly well suited for taxon substitutions.

1) Populations of large tortoises have high intrinsic growth rates and are easy to breed or rear in captivity. If juveniles are headstarted in captivity, they have high survival rates even in the presence of introduced predators (MacFarland et al. 1974a).

2) Tortoises are easy and cheap to fence in. This is especially important for their use in the relatively small conservation management areas found on many oceanic islands. Moreover, within fenced areas, it is easy to up- and down-regulate tortoise numbers and size of individuals, even in large areas or on a seasonal basis. Excess individuals can be kept in holding pens elsewhere, or cordoned-off sections of the restoration area, and require comparatively little husbandry. Similar techniques are used for livestock – de facto taxon substitutes for extinct large mammalian herbivores – in large-scale continental grassland restoration projects (Papanastasis 2009).

3) Their versatility enables them to be introduced into a wide range of habitats of varying qualities including highly degraded areas, making tortoises an attractive option for early-stage restoration efforts. There is some evidence that native plant species and communities evolved to withstand tortoise herbivory on islands (Merton et al. 1976, Eskildsen et al. 2004). This can lead to tortoise taxon substitutes actively preferring introduced and invasive plant species, leading to competitive release for the native species and thus further facilitating habitat recovery (Griffiths et al. 2010).

4) The risk of negatively impacting disease dynamics of the native fauna is small. Reptile diseases and parasites are typically species-specific, with little risk of transfer to other reptiles or other vertebrates (Cooper and Jackson 1981). However, several tortoise species and populations are increasingly affected by within-species diseases (Flanagan 2000). Thus, disease screening and quarantine measures are essential before tortoise taxon substitutions, especially if sourcing individuals from several populations.

5) While there are naturalised populations of medium- and large-sized tortoises in several places around the world (e.g. Balearic Islands, Caribbean Islands, Lever 2003), the risk of tortoises becoming invasive pests is remote, given their life history traits. More importantly, the nature of tortoises facilitates management; the removal of a recently introduced population is feasible if deemed necessary.

There are important considerations and risks that will need mitigating before moving forward on any tortoise

taxon substitution program. Because of their highly general-ised diet, precautions must be taken to avoid tortoises assisting in the spread of invasive plant species via defecated seeds. Giant Aldabra tortoises released on Curieuse Island in the Seychelles have been observed feeding on fruits and seeds of several invasive plant species, and may be a contributing factor to their spread there (Hambler 1994). Similarly, tortoise taxon substitutions in the Galápagos could lead to an increased rate of invasion of some plant species, such as bramble *Rubus niveus* which tortoises consume (R. Atkinson pers. comm.). Proper quarantine measures that determine passage times for 100% of ingested seeds are critical. When *A. gigantea* tortoises were quar-antined before translocation to Round Island, Mauritius, some seeds took as long as three months to pass through the tortoises' guts (Griffiths unpubl.).

Another point to consider is the length of time required for tortoises to reach full size; while breeding and rearing large tortoises to use in rewilding projects may be straightforward, the time required may be a disadvantage in relation to projects that need a here-and-now capacity for restoring ecosystem function. In Galápagos, for example, there are plenty of small juvenile tortoises in the breeding centre that could be used immediately for taxon substitu-tion projects. Yet with respect to potentially controlling biomass of invasive plants, the impact of one adult tortoise would be much greater than that of dozens of small juveniles. To swiftly reach specific restoration goals it may therefore be preferable to also use translocated adults.

Selection of the taxon to be used for substitution must be strongly supported by ecological history, and balanced between phylogeny and natural history (Martin 1969, Donlan et al. 2006). For taxon substitutions whose goal centers on restoring species interactions or ecosystem func-tion, choosing the genetically closest extant tortoise as a substitute may in some cases not be an appropriate selection criterion (contrary to what the IUCN reintroduction guide-lines currently advise; IUCN 1998). This could be the case in an ecosystem where the closest relative of an extinct desert tortoise species is found in a rainforest, or in ecosystems where morphological divergence between species has led to more or less separate diets or feeding behaviours (see the Galápagos case story below for an illustrative example).

Lessons from tortoise reintroductions, translocations, and taxon substitutions

There have been several tortoise translocation projects worldwide, usually as part of single-species conservation projects rather than establishing new populations (Pedrono and Sarovy 2000, Atkinson 2001, Tuberville et al. 2005, 2008). These case studies, along with the abundant information on the ecology and conservation of North American tortoises (Bury and Germano 1994), are in-formative with respect to vetting potential tortoise taxon substitution programs. Bolson tortoises *Gopherus flavomar-ginatus* were recently reintroduced to New Mexico from Mexico after being absent in the United States for thousands of years (Truett and Phillips 2009). Whether one views this as an introduction or a reintroduction depends on which restoration benchmark is applied

(Donlan and Martin 2004). Within the conventional post-Columbian view, Bolson tortoises could be viewed as non-native species – which is indeed the status assigned to it by the US National Park Service (Houston and Schreiner 1995). In contrast, it can be viewed as a reintroduction from a prehistoric view that stretches back to the late Pleistocene, where this tortoise still roamed much of the southern USA (Morafka 1988, Truett and Phillips 2009).

Galápagos Islands

Giant tortoises are the flagship species of the Galápagos. Fifteen tortoise species are generally recognised, of which four are extinct and one is extinct in the wild (Table 1 and Table 2; for a recent discussion of taxonomic status of the Galápagos giant tortoises, see Russello et al. 2010). Species generally occur(ed) singly on separate islands, except for the largest island, Isabela, which has five species, each more or less separated by volcanic features. Two general carapace types exist, the rounded "domed" and the "saddleback" which rises sharply in the front (Van Denburgh 1914). The saddleback is considered an adaptation for browsing on elevated vegetation in dry habitats (Fig. 1A), while the domed is primarily found in wetter habitats where grazing is more common (Fig. 1B; Fritts 1984).

Human over-exploitation in the 1800s was the primary cause of the tortoise extinctions (Van Denburgh 1914), with invasive mammals impeding the conservation of many of the remaining species (MacFarland et al. 1974b, Fritts et al. 2000). Poaching by humans is still a significant threat to several tortoise populations (e.g. on southern portions of Isabela, Fritts et al. 2000). Populations of several endan-gered species have been supplemented with captive-bred or -reared tortoises (MacFarland et al. 1974a, Fritts 1984).

After a series of invasive mammal eradication campaigns (Campbell et al. 2004, Cruz et al. 2005, 2009), Galápagos restoration plans are considering taxon substitutions on two islands, Pinta and Floreana, where tortoise extinctions have occurred (Charles Darwin Foundation 2009, Galápagos Conservancy 2009). For Pinta Island tortoises *C. abingdoni*, the Espanola tortoise *C. hoodensis* is the prime candidate for taxon substitutions based on molecular data, along with sharing the same saddleback morphology (Poulakakis et al. 2008; Fig. 1C). Pinta Island restoration has been compli-cated by the fact that female tortoises from Isabela Island that are housed with Lonesome George (the sole remaining Pinta tortoise) recently laid eggs for the second time (although potentially infertile like the first batch from 2008). These events have led to speculation that George's genetics may be salvageable (Russello et al. 2007, Tran 2009). For the extinct Floreana tortoise *C. elephantopus* the closest relatives of the extinct tortoise are four of the species on Isabela (Poulakakis et al. 2008), but recent molecular studies have also uncovered several tortoises with a recent Floreana ancestry (Russello et al. 2010). These findings could lead to a conservation dilemma: repatriate Floreana with available extant tortoises to restore lost dynamics as soon as possible, or initiate a long-term breeding programme to create a lineage of tortoises with a genetical make-up very similar to the extinct species?
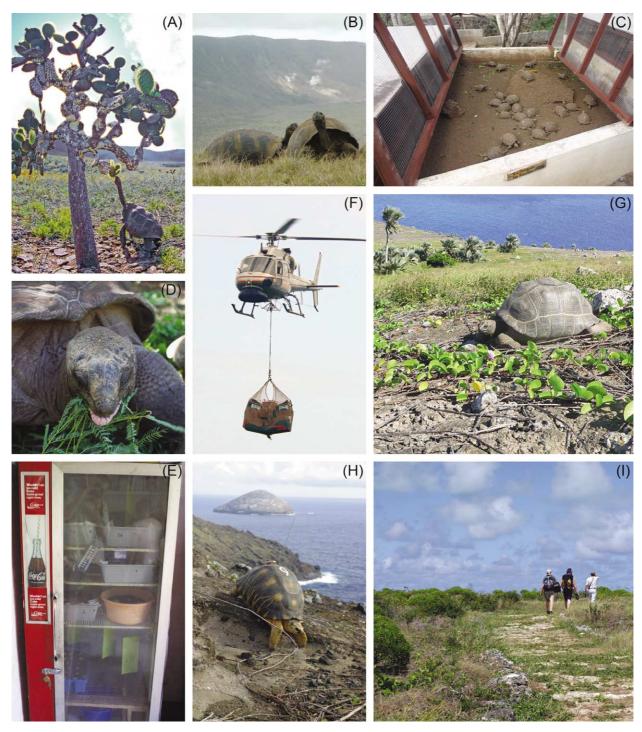
277

Figure 1. Large and giant tortoises and examples of potential and ongoing taxon substitution projects. In the Galápagos Islands there are two types of tortoises, reflecting adaptations to two main herbivory regimes: saddleback shells for browsing (A), and domed shells for grazing (B). Ideally, taxon substitutions should take such ecological information into consideration. For example, captive-bred juveniles of the saddleback *Chelonoidis hoodensis* from Espanola (C) could be used as taxon substitutes for the extinct saddleback *C. elephantopus* from Floreana (but see Galápagos case story in main text). In Mauritius, on the two small islands Ile aux Aigrettes and Round Island, ongoing tortoise taxon substitution projects aim to replace the recently extinct endemic species *Cylindraspis triserrata* and *C. inepta*. On Ile aux Aigrettes, giant Aldabra tortoises *Aldabrachelys gigantea* were introduced in 2000 and act as important seed dispersers and herbivores (D). Several tortoise nests have been found on the island and the eggs successfully reared in state-of-the-art incubators (E). On Round Island, *A. gigantea* and the smaller Madagascan radiated tortoise *Astrochelys radiata* were introduced in June 2007 (F–H). In a reserve created in 2007 in Rodrigues, practitioners wait for 100 000 native plants to grow large enough to allow several hundred *A. gigantea* and *A. radiata* to graze and browse freely (I). Photo credits: (A) by F. J. Sulloway, (B) by CJD, (C) by R. J. Hobbs, (D, E) by DMH, (F, G, H) by CJG, (I) by Matjaž Kuntner.

While recent genetic information may be seen to complicate the management decision of the actual selection of the appropriate tortoise species for the potential repatriation onto Floreana and Pinta Island, such information is nonetheless informative. When combined with ecological knowledge, managers are positioned to proceed with a taxon substitution program based on sound science if deemed appropriate. Given that the invasive mammal populations – the main driver of biodiversity loss and ecosystem degradation – have been eliminated or are in the process of being eliminated, ecosystem restoration via taxon substitution is a logical next step in the conservation of the Galápagos Islands.

Mascarene Islands

The premier examples of the use of taxon substitutes to replace extinct tortoises in rewilding projects come from two of the Mascarene Islands in the Indian Ocean: Mauritius and Rodrigues. These islands were each home to two of the five species of giant tortoises from the endemic Mascarene genus *Cylindraspis* that went extinct between the early 1700s and mid 1800s (Table 1, Arnold 1979, Austin and Arnold 2001).

Mauritius and its offshore islets were home to the two endemic species *Cylindraspis inepta* and *C. triserrata*. Remnants of coastal tortoise habitat are today restricted to offshore islets, most notably Ile aux Aigrettes and Round Island. Both islands are regarded as showcases for restoration as their degraded states are being reversed with a suite of well-planned restoration projects, including intensive systematic weeding programs and the eradication of introduced predators and herbivores prior to the introduction of endangered endemic plants and animals (Jones 2008). Both islands once harboured *Cylindraspis* tortoises (Cheke and Hume 2008). To advance the restoration of these islands, several individuals of *Aldabrachelys gigantea* from captive herds in Mauritius were introduced to Ile aux Aigrettes in 2000 and Round Island in 2007 (Jones 2002; Fig. 1D, F and G). Several Madagascan radiated tortoises *Astrochelys radiata* from captive-bred stocks were also introduced to Round Island, to examine which extant tortoise species is a more suitable substitute for the extinct *Cylindraspis* tortoises (Griffiths et al. 2010) (Fig. 1F and H). A major goal of these taxon substitutions is to restore lost grazing and seed dispersal functions. Preliminary results are encouraging on both islands: tortoises are dispersing seeds of several native plants and are selectively grazing exotic plant species, such as the highly invasive *Leucena leucocephala* (Fabaceae) on Ile aux Aigrettes (Fig. 1D). With proper management, tortoise grazing and browsing is likely to replace ongoing intensive manual weeding. The *A. gigantea* tortoises on Ile aux Aigrettes are already breeding, with some eggs hatching in situ and others collected for rearing in an incubator, providing the next generation of taxon substitutes for further restoration projects (Fig. 1E).

Rodrigues was once home to the two giant tortoise species *C. peltastes* and *C. vosmaeri* (Arnold 1979). Rodrigues has suffered the extinction of most of its terrestrial vertebrates and was considered one of the most degraded island ecosystems worldwide (Gade 1985). Several integrated restoration projects have been initiated since the late 1990s. In 2007, a nature reserve was created, which aims to recreate a large tract of a Rodrigues ecosystem as it is thought to have been 400 yr ago. Around 100 000 native and endemic shrubs and trees have been planted (Fig. 1I), and introduced *A. gigantea* and *A. radiata* tortoises are already grazing and browsing in parts of the reserve (Weaver and Griffiths 2008).

Seychelles

Before human arrival, many islands in the Seychelles housed giant tortoises. After human settlement in the mid 1700s, over-exploitation combined with depredation by introduced predators lead to the extinction of most populations of Seychelles tortoises by the early 1800s (Arnold 1979, Stoddart and Peake 1979). Molecular evidence from living tortoises and museum specimens strongly suggests that all Seychelles *Aldabrachelys* tortoises form one species, *A. gigantea* (Austin et al. 2003, Palkovacs et al. 2003). Today, *A. gigantea* is only found in the wild on Aldabra. However, there are claims of several extant *Aldabrachelys* species (Gerlach 2004, but see Frazier 2006). Whatever the eventual outcome of these taxonomical deliberations, the Seychelles have provided some valuable lessons in giant tortoise translocation – be they taxon substitutions or re-introductions – and offer much potential for future rewilding projects involving tortoises.

For example, there was a large-scale translocation of a total of 250 tortoises, from Aldabra to Curieuse between 1978 and 1982 (Stoddart et al. 1982, Hambler 1994). Even though tortoises have been stolen from the island, or have died, this project is partly a success from a tourism point of view, but the effects on the ecosystem have been little studied (Stoddart et al. 1982, Samour et al. 1987, Hambler 1994), and worryingly include the dispersal by tortoises of invasive plants (Hambler 1994). On Cousine, introduced tortoises have been credited with restoring large-herbivore grazing, seed dispersal, and creating or maintaining habitat for endangered invertebrates (Samways et al. 2010). Several other islands harbour (re)introduced *A. gigantea* tortoises, including Bird, Denis, Silhouette, and Moyenne (Gerlach 2004, Hansen unpubl.). Many of these islands are privately owned tourist destinations, and the giant tortoises are often portrayed as a major attraction, highlighting the potential for economical as well as ecological justification for tortoise taxon substitutions on islands.

Madagascar

Madagascar was home to two species of giant tortoises, *Aldabrachelys grandidieri* and *A. abrupta*. They went extinct in pre-European times, but likely as recently as 1250 and 750 yr ago, respectively (Burleigh and Arnold 1986). They occurred over large parts of the island, from coastal habitats to the central highlands, and often in sympatry (Arnold 1979, Pedrono 2008). Even though both species had dome-shaped shells, isotope analyses of subfossil remains suggest some niche-differentiation in diet, with the larger *A. grandidieri* perhaps mostly a grazer confined to open areas,

and the slightly smaller *A. abrupta* preferring to browse in more shrubby or forested habitats (Burleigh and Arnold 1986, Pedrono 2008). Many Madagascan plants possess seemingly anachronistic anti-herbivory traits (Grubb 2003), which may well be a result of selective pressures once exerted not only by extinct elephant birds (Bond and Silander 2007), but also by the extinct giant tortoises.

The paleoecology of Madagascar was evoked by Burney (2003), who lamented the recent loss of all the large Madagascan vertebrates – and then looked into a feasible future, where some of the functional ghosts could be resurrected with taxon substitutions. Madagascar may, in fact, provide large-scale restoration experiments in the near future. Several scientists have suggested using *A. gigantea* from Aldabra or from captive or rewilded stock elsewhere as taxon substitutes (D. A. Burney, C. J. Raxworthy and O. L. Griffiths pers. comm.). Captive *A. gigantea* in Madagascar seem to do well, even under severe neglect, so chances for successful introductions with minimum population management are quite high. Current efforts to model the likely distribution of *A. abrupta*, based on plentiful subfossil remains, could serve as a template for where in Madagascar *A. gigantea* could be used as a taxon substitute (C. J. Raxworthy pers. comm.).

The Caribbean

Given the number of islands, their geological history, and their proximity to continental regions with large tortoises, there are relatively few known extinct tortoises from this region (ten species; Table 1). However, some fossil remains have only been discovered recently (Meylan and Sterrer 2000, Steadman et al. 2007), and it is likely that future work will increase the tally.

The South American red-footed tortoise *Chelonoidis carbonaria* (and possibly *C. denticulata*) has been introduced to many islands in the Caribbean (Lever 2003). *Chelonoidis carbonaria* has been present in a naturalised state on some of the islands for decades, and perhaps several hundred years (Lever 2003). Future studies of Caribbean *C. carbonaria* populations could be compared to our knowledge about the species in its native continental South America (Bjorndal 1989, Moskovits and Bjorndal 1990, Jerozolimski et al. 2009), and provide valuable information for potential tortoise rewilding projects in the Caribbean. Interestingly, the naturalised *C. carbonaria* tortoises reported on Barbados are already de facto taxon substitutes for an extinct giant tortoise species ("*Geochelone*"; genus indet.) that occurred on the island (Table 1, Ray 1964, Lazell 1993).

Conservation problems in the endangered Caribbean dry forests include invasive plants and a lack of seed dispersal services, and restoration here relies heavily on human intervention (Ray and Brown 1995). Building on the preliminary successful tortoise taxon substitutions in Mauritius (see above), we suggest that tortoise rewilding may well be a cost-effective way to facilitate even large-scale dry forest restoration in the Caribbean, with the tortoises acting as seed dispersers and herbivores.

Conclusion

Despite global potential for resurrecting lost species interactions and restore degraded ecosystem functions, taxon substitutions remain controversial. We suggest that a healthy debate on the applicability of taxon substitutions could be facilitated by including guidelines for them within an expanded IUCN species translocation framework. This would have the added benefit of promoting species interactions and functional integrity of ecosystems as integral parts of all translocation projects. Furthermore, conducting taxon substitutions and reintroductions within a proper experimental framework will facilitate the interpretation of ecosystem responses, providing direction and insight for future management actions, as well as providing ideal templates for studies in community ecology (Armstrong and Seddon 2008).

Due to their controversial nature, taxon substitution projects will likely be attracting closer scientific scrutiny than comparable taxon reintroductions. This extra scrutiny is justified due to the potential for unwanted consequences brought on by novel species interactions (Ricciardi and Simberloff 2009). Taxon substitutions are often advocated on grounds of reviving lost or dysfunctional ecosystem dynamics (Hamann 1993, Galetti 2004, Donlan et al. 2006, Gibbs et al. 2008, Hansen et al. 2008, Griffiths et al. 2010). These process-oriented hypotheses lend themselves toward an experimental a priori approach that is often lacking in re-introduction projects with a strict species conservation focus (Armstrong and Seddon 2008). Additionally, projects that use non-threatened species as taxon substitutions are useful to experimentally explore factors affecting translocation success, a luxury that translocation projects with endangered species can ill afford. Hypothesis-driven and explicit guidelines for taxon substitutions would also help discourage and prevent programs that are not justified on scientific, historical, or socio-political grounds.

We have highlighted how the extinction biogeography of tortoises offers a model to provide much-needed empirical evaluation of taxon substitutions and rewilding efforts. For endangered tortoise species, we believe in situ conservation should take priority over their use in taxon substitution projects. But even in these cases, translocation or captive breeding could provide animals for taxon substitution projects elsewhere, affording the species one or several additional refuges from possible extinction. Considering how few extant species of large and particularly giant tortoises remain globally and how many of these have rapidly dwindling populations, heeding Aldo Leopold's advice from an ecological, evolutionary, and historical perspective, is likely wise and doing so in the wild via taxon substitutions is – perhaps ironic to some – abiding by the precautionary principle: "the first rule of intelligent tinkering is to save all the pieces".

References

Armstrong, D. P. and Seddon, P. J. 2008. Directions in reintroduction biology. – Trends Ecol. Evol. 23: 20–25.

Arnold, E. N. 1979. Indian Ocean giant tortoises: their systematics and island adaptations. – Phil. Trans. R. Soc. B 286: 127–145.

Arnold, E. N. 1980. Recently extinct reptile populations from Mauritius and Réunion, Indian Ocean. – J. Zool. 191: 33–47.

Ashley, M. V. et al. 2003. Evolutionarily enlightened management. – Biol. Conserv. 111: 115–123.

Atkinson, I. A. E. 1998. Conserving plants as evolutionary entities: successes and unanswered questions from New Zealand and elsewhere. – Aliso 16: 103–112.

Atkinson, I. A. E. 2001. Introduced mammals and models for restoration. – Biol. Conserv. 99: 81–96.

Auffenberg, W. 1967. Notes on West Indian tortoises. – Herpetologica 23: 34–44.

Auffenberg, W. 1974. Checklist of fossil tortoises (Testudinidae). – Bull. Florida State Mus. 18: 121–251.

Austin, J. J. and Arnold, E. N. 2001. Ancient mitochondrial DNA and morphology elucidate an extinct island radiation of Indian Ocean giant tortoises (*Cylindraspis*). – Proc. R. Soc. B 268: 2515–2523.

Austin, J. J. et al. 2003. Was there a second adaptive radiation of giant tortoises in the Indian Ocean? Using mitochondrial DNA to investigate speciation and biogeography of *Aldabrachelys* (Reptilia, Testudinidae). – Mol. Ecol. 12: 1415–1424.

Barboza, P. S. 1995. Digesta passage and functional anatomy of the digestive tract in the desert tortoise (*Xerobates agassizii*). – J. Comp. Phys. B 165: 193–202.

Birkhead, R. D. et al. 2005. Patterns of folivory and seed ingestion by gopher tortoises (*Gopherus polyphemus*) in a southeastern pine savanna. – Am. Midl. Nat. 154: 143–151.

Bjorndal, K. A. 1989. Flexibility of digestive responses in two generalist herbivores, the tortoises *Gechelone carbonaria* and *Geochelone denticulata*. – Oecologia 78: 317–321.

Blasco, R. 2008. Human consumption of tortoises at Level IV of Bolomor Cave (Valencia, Spain). – J. Archaeol. Sci. 35: 2839–2848.

Bond, W. J. and Silander, J. A. 2007. Springs and wire plants: anachronistic defences against Madagascar's extinct elephant birds. – Proc. R. Soc. B 274: 1985–1992.

Bond, W. J. et al. 2004. Plant structural defences against browsing birds: a legacy of New Zealand's extinct moas. – Oikos 104: 500–508.

Bonin, F. et al. 2006. Turtles of the World. – Johns Hopkins Univ. Press.

Bour, R. 1984. Taxonomy, history and geography of Seychelles land tortoises and fresh-water turtles. – In: Stoddart, D. R. (ed.), Biogeography and ecology of the Seychelles Islands. Dr W. Junk, pp. 281–307.

Branch, B. 2008. Tortoises, terrapins & turtles of Africa. – Struik Publ., South Africa.

Burleigh, R. and Arnold, E. N. 1986. Age and dietary differences of recently extinct Indian Ocean tortoises (*Geochelone* s. lat.) revealed by carbon isotype analysis. – Proc. R. Soc. B 227: 137–144.

Burney, D. A. 2003. Madagascar's prehistoric ecosystems. – In: Goodman, S. M. and Benstead, J. (eds), The natural history of Madagascar. Univ. of Chigaco Press, pp. 47–51.

Bury, R. B. and Germano, D. J. (eds) 1994. Biology of North American tortoises. – Fish and Wildlife Research 13. United States Dept of the Interior, National Biological Survey, Washington, DC, USA.

Caloi, L. et al. 1986. La fauna a vertebrati terrestri del Pleistocene delle isole del Mediterraneo. – Geol. Rom. 25: 235–256.

Campbell, K. et al. 2004. Eradication of feral goats *Capra hircus* from Pinta Island, Galápagos. – Oryx 38: 328–333.

Carlson, J. E. et al. 2003. Seed dispersal by *Gopherus polyphemus* at Archbold Biological Station, Florida. – Florida Sci. 66: 147–154.

Caro, T. 2007. The Pleistocene re-wilding gambit. – Trends Ecol. Evol. 22: 281–283.

Charles Darwin Foundation 2009. – <www.darwinfoundation.org/>, accessed 27 August 2009.

Cheke, A. S. and Hume, J. P. 2008. Lost land of the Dodo. – Christopher Helm.

Chesi, F. et al. 2007. Middle Pleistocene giant tortoises from Sicily. – In: Tintori, A. and Boccaletti, M. (eds), VII Giornate di Paleontologia della Società Paleontologica Italiana, p. 19.

Choi, Y. D. 2007. Restoration ecology to the future: a call for new paradigm. – Restor. Ecol. 15: 351–353.

Cisneros, J. C. 2005. New Pleistocene vertebrate fauna from El Salvador. – Rev. Brasileira Paleontol. 8: 239–255.

Coe, M. J. et al. 1979. The biomass, production and carrying capacity of giant tortoises on Aldabra. – Phil. Trans. R. Soc. B 286: 163–176.

Cooper, J. E. and Jackson, O. F. 1981. Diseases of Reptilia. – Academic Press.

Crandall, K. A. et al. 2000. Considering evolutionary processes in conservation biology. – Trends Ecol. Evol. 15: 290–295.

Crumly, C. R. 2009. Totoises. – In: Gillespie, R. G. and Clague, D. A. (eds), Encyclopedia of islands. Univ. of California Press, pp. 921–926.

Cruz, F. et al. 2005. Conservation action in the Galápagos: feral pig (*Sus scrofa*) eradication from Santiago Island. – Biol. Conserv. 121: 473–478.

Cruz, F. et al. 2009. Bio-economics of large-scale eradication of feral goats from Santiago Island, Galápagos. – J. Wildl. Manage. 73: 191–200.

Curry, A. 2008. Pleistocene park: where the auroxen roam. – Wired Magazine September 22.

Donlan, C. J. and Martin, P. S. 2004. Role of ecological history in invasive species management and conservation. – Conserv. Biol. 18: 267–269.

Donlan, C. J. et al. 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. – Am. Nat. 168: 660–681.

Donlan, J. et al. 2005. Re-wilding North America. – Nature 436: 913–914.

Erasmus, B. F. N. et al. 2002. Vulnerability of South African animal taxa to climate change. – Global Change Biol. 8: 679–693.

Ernst, C. H. and Barbour, R. W. 1989. Turtles of the world. – Smithsonian Inst. Press.

Erwin, T. L. 1991. An evolutionary basis for conservation strategies. – Science 253: 750–752.

Eskildsen, L. I. et al. 2004. Feeding response of the Aldabra giant tortoise (*Geochelone gigantea*) to island plants showing heterophylly. – J. Biogeogr. 31: 1785–1790.

Flanagan, J. 2000. Disease and health considerations. – In: Klemens, M. W. (ed.), Turtle conservation. Smithsonian Inst. Press, pp. 85–95.

Franz, R. and Woods, C. A. 1983. A fossil tortoise from Hispaniola. – J. Herpetol. 17: 79–81.

Frazier, J. 2006. Giant tortoises of the Indian Ocean. – Herpetol. Rev. 37: 368–373.

Fritts, T. H. 1984. Evolutionary divergence of giant tortoises in Galápagos. – Biol. J. Linn. Soc. 21: 165–176.

Fritts, T. H. et al. 2000. Progress and priorities in research for the conservation of reptiles. – In: Sitwell, N. et al. (eds), Science

for conservation in Galápagos. Bulletin de'l Inst. Royal des Siences Naturalles de Belgique, pp. 39–45.

Fritz, U. and Bininda-Emonds, O. R. P. 2007. When genes meet nomenclature: tortoise phylogeny and the shifting generic concepts of *Testudo* and *Geochelone*. – Zoology 110: 298–307.

Fritz, U. and Havaš, P. 2007. Checklist of chelonians of the world. – Vertebr. Zool. 57: 149–368.

Gade, D. W. 1985. Man and nature on Rodrigues: tragedy of an island common. – Environ. Conserv. 12: 207–215.

Galápagos Conservancy 2009. – <www.Galápagos.org>, accessed 27 August 2009.

Galetti, M. 2004. Parks of the Pleistocene: recreating the Cerrado and the Pantanal with megafauna. – Natureza and Conservação 2: 93–100.

Gerlach, J. 2004. Giant tortoises of the Indian Ocean. – Chimaira, Frankfurt.

Gerlach, J. et al. 2006. The first substantiated case of trans-oceanic tortoise dispersal. – J. Nat. Hist. 40: 2403–2408.

Gibbs, J. P. et al. 2008. The role of endangered species reintroduction in ecosystem restoration: tortoise-cactus interactions on Espanola island, Galápagos. – Rest. Ecol. 16: 88–93.

Greenwood, R. M. and Atkinson, I. A. E. 1977. Evolution of divaricating plants in New Zealand in relation to moa browsing. – Proc. N. Z. Ecol. Soc. 24: 21–33.

Griffiths, C. J. et al. 2010. The use of extant non-indigenous tortoises to replace extinct ecosystem engineers: a restoration tool. – Rest. Ecol. 18: 1–7.

Grubb, P. 1971. The growth, ecology and population structure of giant tortoises on Aldabra. – Phil. Trans. R. Soc. B 260: 327–372.

Grubb, P. J. 2003. Interpreting some outstanding features of the flora and vegetation of Madagascar. – Perspect. Plant Ecol. Evol. Syst. 6: 125–146.

Guard, C. L. 1980. The reptilian digestive system: general characteristics. – In: Schmidt-Nielsen, K. et al. (eds), Comparative physiology: primitive mammals. Cambridge Univ. Press, pp. 43–51.

Hailey, A. 1997. Digestive efficiency and gut morphology of omnivorous and herbivorous African tortoises. – Can. J. Zool. 75: 787–794.

Hamann, O. 1993. On vegetation recovery, goats and giant tortoises on Pinta Island, Galápagos, Ecuador. – Biodivers. Conserv. 2: 138–152.

Hambler, C. 1994. Giant tortoise *Geochelone gigantea* translocation to Curieuse Island (Seychelles): success or failure? – Biol. Conserv. 69: 293–299.

Hansen, D. M. and Galetti, M. 2009. The forgotten megafauna. – Science 324: 42–43.

Hansen, D. M. et al. 2008. Seed dispersal and establishment of endangered plants on oceanic Islands: the Janzen-Connell model, and the use of ecological analogues. – PLoS One 3: e2111, doi: 10.1371/journal.pone.0002111.

Hnatiuk, S. H. 1978. Plant dispersal by the Aldabran giant tortoise, *Geochelone gigantea* (Schweigger). – Oecologia 36: 345–350.

Hoijer, D. A. 1951. Pygmy elephant and giant tortoise. – Sci. Monthly 72: 3–8.

Hoijer, D. A. 1963. *Geochelone* from the Pleistocene of Curaçao, Netherlands Antilles. – Copeia 1963: 579–580.

Houston, D. B. and Schreiner, E. G. 1995. Alien species in national parks: drawing lines in space and time. – Conserv. Biol. 9: 204–209.

Hunt, C. O. and Schembri, P. J. 1999. Quaternary environments and biogeography of the Maltese Islands. – In: Mifsud, A. and Savona Ventura, C. (eds), Facets of Maltese prehistory. The Prehistoric Society of Malta, p. 243.

IUCN 1987. IUCN position statement on the translocation of living organisms: introductions, re-introductions, and re-stocking. – Prepared by the Species Survival Commission in collaboration with the Commission on Ecology and the Commission on Environmental Policy, Law and Administration.

IUCN 1998. Guidelines for re-introductions. – IUCN/SSC Re-introduction Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK.

Iverson, J. B. 1982. Biomass in turtle populations: a neglected subject. – Oecologia 55: 69–76.

Iverson, J. B. 1987. Tortoises, not dodos, and the Tambalacoque tree. – J. Herpetol. 21: 229–230.

Janzen, D. H. and Martin, P. S. 1982. Neoptropical anachronisms: the fruits the Gomphoteres ate. – Science 215: 19–27.

Jerozolimski, A. et al. 2009. Are tortoises important seed dispersers in Amazonian forests? – Oecologia 161: 517–528.

Jones, C. G. 2002. Reptiles and amphibians. – In: Perrow, M. R. and Davy, A. J. (eds), Handbook of ecological restoration. – Cambridge Univ. Press, pp. 355–375.

Jones, C. G. 2008. Practical conservation on Mauritius and Rodrigues: steps towards the restoration of devastated ecosystems. – In: Cheke, A. S. and Hume, J. P. (eds), Lost land of the Dodo. Christopher Helm, pp. 226–259.

Jordán, F. 2009. Keystone species and food webs. – Phil. Trans. R. Soc. B 364: 1733–1741.

Kaczor, S. and Hartnett, D. 1990. Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida USA sandhill community. – Am. Midl. Nat. 123: 100–111.

Kaiser-Bunbury, C. N. et al. 2010. Conservation and restoration of plant–animal mutualisms on oceanic islands. – Perspect. Plant Ecol. Evol. Syst. 12: 131–143.

Klein, R. D. and Cruz-Uribe, K. 2000. Stone age population numbers and the average tortoise size at Byneskranskop Cave 1 and Die Kelders Cave 1, Southern Cape Province, South Africa. – S. Afr. Archaeol. Bull. 38: 26–30.

Lazell, J. D. J. 1993. Tortoise, cf. *Geochelone carbonaria*, from the Pleistocene of Anguilla, northern Lesser Antilles. – J. Herpetol. 27: 485–486.

Le, M. et al. 2006. A molecular phylogeny of tortoises (Testudines: Testudinidae) based on mitochondrial and nuclear genes. – Mol. Phylogenet. Evol. 40: 517–531.

Leuteritz, T. E. J. et al. 2005. Distribution, status, and conservation of radiated tortoises (*Geochelone radiata*) in Madagascar. – Biol. Conserv. 124: 451–461.

Lever, C. 2003. Naturalized reptiles and amphibians of the world. – Oxford Univ. Press.

Macdonald, D. W. 2009. Lessons learnt and plans laid: seven awkward questions for the future of reintroductions. – In: Hayward, M. W. and Somers, M. J. (eds), Reintroduction of top-order predators. Wiley-Blackwell, pp. 411–448.

MacFarland, C. et al. 1974a. The Galápagos giant tortoises (*Geochelone elephantopus*) part II: conservation methods. – Biol. Conserv. 6: 198–212.

MacFarland, C. G. et al. 1974b. The Galápagos giant tortoises (*Geochelone elephantopus*) part I: status of the surviving populations. – Biol. Conserv. 6: 118–133.

Marris, E. 2009. Reflecting the past. – Nature 462: 30–32.

Martin, P. S. 1969. Wanted: a suitable herbivore. – Nat. Hist. 78: 35–39.

Martin, P. S. and Klein, R. G. 1984. Quaternary extinctions: a prehistoric revolution. – Univ. of Arizona Press.

McMaster, M. K. and Downs, C. T. 2008. Digestive parameters and water turnover of the leopard tortoise. – Comp. Biochem. Physiol. A 151: 114–125.

Means, D. B. 2006. Vertebrate faunal diversity of longleaf pine ecosystems. – In: Jose, S. et al. (eds), The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, pp. 157–213.

Merton, L. F. H. et al. 1976. Giant tortoise and vegetation interactions on Aldabra Atoll – part 1: inland. – Biol. Conserv. 9: 293–304.

Meylan, P. A. and Sterrer, W. 2000. *Hesperotestudo* (Testudines: Testudinidae) from the Pleistocene of Bermuda, with comments on the phylogenetic position of the genus. – Zool. J. Linn. Soc. 128: 51–76.

Milton, S. J. 1992. Plants eaten and dispersed by adult leopard tortoises *Geochelone pardalis* (Reptilia, Testudinae) in the southern Karoo. – S. Afr. J. Zool. 27: 45–49.

Moodie, K. B. and Devender, T. R. V. 1979. Extinction and extirpation in the herpetofauna of the Southern High Plains with emphasis on *Geochelone wilsonii* (Testudinidae). – Herpetologica 35: 198–206.

Morafka, D. J. 1988. Historical biogeography of the bolson tortoise. – Ann. Carnegie Mus. 57: 47–72.

Moskovits, D. K. and Bjorndal, K. A. 1990. Diet and food preferences of the tortoises *Geochelone carbonaria* and *Geochelone denticulata* in northwestern Brazil. – Herpetologica 46: 207–218.

Olson, S. L. et al. 2006. Geological constraints on evolution and survival in endemic reptiles on Bermuda. – J. Herpetol. 40: 394–398.

Paine, R. T. 1969. A note on trophic complexity and community stability. – Am. Nat. 103: 91–93.

Palkovacs, E. P. et al. 2003. Are the native giant tortoises from the Seychelles really extinct? A genetic perspective based on mtDNA and microsatellite data. – Mol. Ecol. 12: 1403–1413.

Papanastasis, V. P. 2009. Restoration of degraded grazing lands through grazing management: can it work? – Restor. Ecol. 17: 441–445.

Pedrono, M. 2008. The tortoises and turtles of Madagascar. – Natural History Publications (Borneo).

Pedrono, M. and Sarovy, A. 2000. Trial release of the world's rarest tortoise *Geochelone yniphora* in Madagascar. – Biol. Conserv. 95: 333–342.

Poulakakis, N. et al. 2008. Historical DNA analysis reveals living descendants of an extinct species of Galápagos tortoise. – Proc. Nat. Acad. Sci. USA 105: 15464–15469.

Ray, C. E. 1964. A small assemblage of vertebrate fossils from Spring Bay, Barbados. – J. Barbados Mus. Hist. Soc. 31: 11–22.

Ray, G. J. and Brown, B. J. 1995. Restoring Caribbean dry forests: evaluation of tree propagation techniques. – Restor. Ecol. 3: 86–94.

Reynoso, V.-H. and Montellano-Ballesteros, M. 2004. A new giant turtle of the genus *Gopherus* (Chelonia: Testudinidae) from the Pleistocene of Tamaulipas, Mexico, and a review of the phylogeny and biogeography of gopher tortoises. – J. Vertebr. Paleontol. 24: 822–837.

Ricciardi, A. and Simberloff, D. 2009. Assisted colonization is not a viable conservation strategy. – Trends Ecol. Evol. 24: 248–253.

Rick, C. M. and Bowman, R. I. 1961. Galápagos tomatoes and tortoises. – Evolution 15: 407–417.

Ripple, W. J. and Beschta, R. L. 2007. Restoring Yellowstone's aspen with wolves. – Biol. Conserv. 138: 514–519.

Russello, M. A. et al. 2007. Lonesome George is not alone among Galápagos tortoises. – Curr. Biol. 17: 317–318.

Russello, M. A. et al. 2010. DNA from the past informs ex situ conservation for the future: an ''extinct'' species of Galapagos tortoise identified in captivity. – PLoS One 5: e8683, doi: 8610.1371/journal.pone.0008683.

Samour, H. J. et al. 1987. A survey of the Aldabra giant tortoise population introduced on Curieuse Island, Seychelles. – Biol. Conserv. 41: 147–158.

Samways, M. J. et al. 2010. Restoration of a tropical island: Cousine Island, Seychelles. – Biodivers. Conserv. 19: 425–434.

Sondaar, P. Y. and van der Geer, A. A. E. 2005. Evolution and extinction of Plio-Pleistocene island ungulates. – Quaternaire 2: 241–256.

Soorae, P. S. 2008. Global re-introduction perspectives: re-introduction case-studies from around the globe. – IUCN/SSC Re-introduction Specialist Group, Abu Dhabi, UAE.

Soulé, M. and Noss, R. 1998. Rewilding and biodiversity: complementary goals for continental conservation. – Wild Earth 8: 18–28.

Soulé, M. E. et al. 2003. Ecological effectiveness: conservation goals for interactive species. – Conserv. Biol. 17: 1238–1250.

Soulé, M. E. et al. 2005. Strongly interacting species: conservation policy, management, and ethics. – Bioscience 55: 168–176.

Steadman, D. W. and Martin, P. S. 2003. The late Quaternary extinction and future resurrection of birds on Pacific islands. – Earth-Sci. Rev. 61: 133–147.

Steadman, D. W. et al. 1991. Chronology of Holocene vertebrate extinction in the Galápagos Islands. – Quat. Res. 36: 126–133.

Steadman, D. W. et al. 2007. Exceptionally well preserved late Quaternary plant and vertebrate fossils from a blue hole on Abaco, The Bahamas. – Proc. Nat. Acad. Sci. USA 104: 19897–19902.

Stiner, M. C. et al. 1999. Paleolithic population growth pulses evidenced by small animal exploitation. – Science 283: 190–194.

Stoddart, D. R. and Peake, J. F. 1979. Historical records of Indian Ocean giant tortoise populations. – Phil. Trans. R. Soc. B 286: 147–158.

Stoddart, D. R. et al. 1982. Tortoises and tourists in the western Indian Ocean: the Curieuse experiment. – Biol. Conserv. 24: 67–80.

Strasberg, D. 1996. Diversity, size composition and spatial aggregation among trees on a 1-ha rain forest plot at La Reunion. – Biodivers. Conserv. 5: 825–840.

Strong, J. N. and Fragoso, J. M. V. 2006. Seed dispersal by *Geochelone carbonaria* and *Geochelone denticulata* in north-western Brazil. – Biotropica 38: 683–686.

Takahashi, A. et al. 2003. A new species of the genus *Manouria* (Testudines: Testudinidae) from the Upper Pleistocene of the Ryukyu Islands, Japan. – Paleontol. Res. 7: 195–217.

Taylor, J. D. et al. 1979. Terrestrial faunas and habitats of Aldabra during the late Pleistocene. – Phil. Trans. R. Soc. B 286: 47–66.

Tran, M. 2009. Lonesome George, the last Galápagos giant tortoise, may become a dad. – <http://guardian.co.uk>, accessed 28 August 2009.

Truett, J. and Phillips, M. 2009. Beyond historic baselines: restoring bolson tortoises to Pleistocene range. – Ecol. Restor. 27: 145–151.

Tuberville, T. D. et al. 2005. Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). – Anim. Conserv. 8: 349–358.

Tuberville, T. D. et al. 2008. Long-term apparent survival of translocated gopher tortoises: a comparison of newly released and previously established animals. – Biol. Conserv. 141: 2690–2697.

Van Denburgh, J. 1914. Expedition of the California Academy of Sciences to the Galápagos Islands 1905–1906. – Proc. Cal. Acad. Sci. 2: 203–374.

Van Lear, D. H. et al. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. – For. Ecol. Manage. 211: 150.

Varela, R. O. and Bucher, E. H. 2002. Seed dispersal by *Chelonoidis chilensis* in the Chaco dry woodland of Argentina. – J. Herpetol. 36: 137–140.

Weaver, E. A. and Griffiths, O. L. 2008. A guide to La Vanille Réserve des Mascareignes. – Bioculture Press, Rivière des Anguilles, Mauritius.

Wright, S. J. et al. 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. – Biotropica 39: 289–291.

Zimov, S. A. 2005. Pleistocene park: return of the mammoth's ecosystem. – Science 308: 796–798.