

**IN ISLAND SYNDROME, DOES THE HORMONE PHENOTYPE OF FOUNDERS
DETERMINE LIFE HISTORY TRAITS AND BODY SIZE OF DESCENDANTS?**

revised June 2008

(reviewed by *Journal of Biogeography*, July 18, 2007, not accepted)

Cite as follows: Crockford, S. J. 2008. In island syndrome, does the hormone phenotype of founders determine life history traits and body size of descendants? Unpublished manuscript, on file at the Dept. of Anthropology, University of Victoria, British Columbia and available online at www.rhythmsoflife.ca

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In island syndrome, does the hormone phenotype of founders determine life history traits and body size of descendants?**S. J. Crockford****ABSTRACT**

Aim Here I apply a new theoretical model to explain island syndrome, the tendency for endemic island vertebrates to possess different body size and limb proportions compared to mainland ancestors. My goals here are to (1) summarize my new theoretical model, which was originally developed to explain rapid heterochronic speciation and animal domestication; (2) apply the model to speciation on islands to explain how and why recurring patterns of dwarfism, gigantism and flightlessness occur; (3) apply the model to a few specific examples of endemic island species, including extinct dwarf stegodons (*Stegodon sp.*), Haast's giant eagle (*Harpagornis moorei*), and the recently discovered putative dwarf hominin, *Homo floresiensis*.

Location Oceanic and near-shore archipelagos, and island-like ecosystems world-wide.

Methods Thyroid hormone (TH) is pivotal to the model used here to explain other examples of rapid heterochronic speciation (including animal domestication) because it regulates, in a time- and dose-dependant manner, such critical life history traits as behaviour in response to stress (including the stress of predation and competition) as well as the embryonic and postnatal growth rates that govern ultimate body size and age at sexual maturity. I contend that individual variation in these critical life history traits are linked in an evolutionarily significant manner by individual variation in species-specific rhythms of TH production.

Results TH rhythm theory explains why the extent and direction of heterochronic change in each instance of island colonization varies in a predictable manner. I contend that such changes not only reflect the particular TH rhythm phenotype of the founders but the circumstances of colonization (whether it is deliberate or accidental).

Main conclusions Although a number of suggestions have been offered to explain the phenomenon of altered growth rates amongst endemic island populations, no formula given so far fits all situations. This new and fully testable theory explains many diverse cases of the heterochronic changes characteristic of island syndrome, including flightlessness in birds, and suggests that the hormone phenotype of mainland founders determines life history traits and body size of island descendants.

Keywords: thyroid hormone, giants, dwarfs, flightlessness, heterochrony, stress, hormone rhythms, evolution, *Homo floresiensis*.

Running title: Hormone phenotypes & island syndrome

INTRODUCTION

Not all marine islands are equal: some lay relatively close to continental land masses and were connected to them for varying lengths of time during periods of lowered sea level, such as those off southern California and many of the islands in the Mediterranean. Other islands have always been remote and isolated, such as the islands of Hawaii. As a consequence, the ability of animals to colonize islands varies with the kind of island and its location, as well as the dispersal ability of the animal itself. Regardless of these differences, however, many animal populations on once-connected continental islands show similar trends over time as those on remote oceanic islands (Grant, 1998b), a pattern that certainly begs for an explanation. Animal species found on islands are often quite different in body size from their mainland counterparts, often so much so that determining their closest relatives was a challenge before DNA technology came along (e.g. Paxinos *et al.*, 2002; Poulakakis *et al.*, 2006; Shapiro *et al.*, 2002). Many island endemics are much larger or smaller than mainland counterparts, while birds often become flightless (Lomolino, 2005). Many examples are known only from fossils, including a recently discovered dwarf sauropod dinosaur (Sander *et al.*, 2006) and a fossil hominin from Indonesia designated a distinct dwarf species, *Homo floresiensis* (Brown *et al.*, 2004).

We know from experience that many extant island populations are especially vulnerable to rapid extinction in response to human hunting or disturbance (e.g. Gaskell, 2000; Quammen, 1996; Simmons, 1999), making them a special conservation concern. Most significantly, however, insular populations develop under such controlled conditions they come close to qualifying as natural experiments and as a consequence, in-depth studies of island endemics have been viewed as particularly applicable to answering questions of how adaptive evolutionary processes work in a variety of circumstances (Burness *et al.*, 2001; Grant, 1998a; Lomolino & Perault, in press; McClain *et al.*, 2006; Tikhonov & Vartanyan, 2001).

Many suggestions have been offered to explain the heterochronic changes in body size and proportion characteristic of island vertebrates, most of which contend that ecological conditions (such as size of island, density of the population, distance from land, lack of competition, lack of predation and/or dwindling food resources) must force these trends via natural selection, although no formula seems to fit all situations (e.g. Grant, 1998; Williamson, 1981; Lomolino, 2005). On-going debate regarding the taxonomic status of the putative dwarf *Homo floresiensis* (e.g. Balter, 2005; Nichols, 2006; Niven, 2007; Richards, 2006) have renewed calls to explain the dramatic differences in body size, proportion and behaviour characteristic of

island vertebrates compared to mainland ancestors (e.g. Lomolino, 2005; Meiri *et al.*, 2006; Millien, 2006; Raia & Meiri, 2006; White & Searle, 2006).

Here I address this issue for all island vertebrates by applying a newly-described biological mechanism for evolutionary change that considers thyroid hormone (TH) metabolism pivotal to domestication and other examples of rapid heterochronic speciation (Crockford, 2002, 2003, 2004, 2006). Island colonization considered in this light not only explains the parallels that have been noted previously between island endemics and domestic mammals (e.g. Grant, 1998a; Köhler & Moyà-Solà, 2004) but also the strong trend towards flightless gigantism and other anomalies of limbs and body shape common to endemic island birds and reptiles. Thyroid rhythm theory provides a more comprehensive explanation for island syndrome than previously proposed hypotheses because it describes a specific biological mechanism to account for rapid changes in life history traits that is widely applicable and testable.

ISLAND SYNDROME

Remote oceanic islands are difficult to colonize because of distance. Small terrestrial mammals and weak flying birds generally end up on oceanic islands by accident (so-called “sweepstakes dispersal”): rodents may become marooned on the vegetative flotsam (e.g. uprooted trees) generated by storms and small forest birds and bats can get blown far out to sea by fierce winds (Williamson, 1981). Migratory birds powerful enough to withstand storm winds may nevertheless colonize remote oceanic islands, perhaps due to navigational error. While large mammals are unable to colonize isolated oceanic islands by virtue of their size, islands just offshore from continents or island archipelagos connected in step-wise fashion to large land masses (such as Indonesia) are often close enough to allow strong swimming large mammals to establish successful island populations. In addition, some islands close to continents have been connected at various times in the past by falling sea levels or ice bridges, trapping large mammals on them.

Table 1. Examples of some insular birds and mammals, living and extinct.

Common name (*extinct)	Scientific name ¹⁻⁴	Change	Reference
Mammals			
Skomer bank vole (Skomer Is., Scotland)	<i>Clethrionomys glareolus skomerensis</i> ¹	giant	Adler & Levins, 1994
Coronation Island vole (SE Alaska)	<i>Microtus longicaudus coronarius</i> ¹	giant	Dawson <i>et al.</i> , 2007
Hutia (Bahaman islands)	<i>Geocapromys ingrahami</i> ⁴	giant	Burness <i>et al.</i> , 2001
Giant rat (Lesser Sunda Islands, Indonesia)*	<i>Hooijeromys nusatenggara</i> ⁴	giant	van den Bergh, 1999
Straight-tusked elephant (Sicily) *	<i>Elaphas falconeri</i> ²	dwarf	Palombo, 2001
Mammoth (Santa Rosa Is., CA)*	<i>Mammuthus exilis</i> ²	dwarf	Agenbroad, 2001
Mammoth (Wrangel Is., Siberia)*	<i>Mammuthus primigenius</i> ³	dwarf	Vartanyan <i>et al.</i> , 1993
Hippopotamus (Cyprus)*	<i>Phanourios minutes</i> ²	dwarf	Simmons, 1999
Cave goats (Majorca), five species*	<i>Myotragus spp</i> ²	dwarf	Kohler & Moyà-Solà, 2004
Red deer (Jersey, English Channel)*	<i>Cervus elaphus jerseyensis</i> ¹	dwarf	Lister, 1999, 2004
Water buffalo (Cebu, Philippines)*	<i>Bubalus sp. nov.</i> ⁵	dwarf	Croft <i>et al.</i> , 2006
Reindeer (Spitsbergen)	<i>Rangifer tarandus platyrhynchus</i> ¹	dwarf	Geist, 1998
Birds			
Dodo (Mauritius)*	<i>Raphus cucullatus</i> ⁴	flightless giant	Quammen, 1996
Giant goose (Hawaii, USA)*	<i>Branta sp. nov.</i> ⁵	flightless giant	Paxonos <i>et al.</i> , 2002
Laysan rail (Hawaii, USA)*	<i>Porzana palmeri</i> ²	flightless	Carlquist, 1965
South Island takahe (New Zealand)	<i>Porphyrio hochstetteri</i> ²	flightless	McNab & Ellis, 2006
Great auk (Newfoundland and Britain)*	<i>Pinguinus impennis</i> ⁴	flightless giant	Moum <i>et al.</i> , 2002
Auckland Island teal (New Zealand)	<i>Anas aucklandica</i> ²	flightless	Livezey, 1990
Haast's eagle (New Zealand)*	<i>Harpagornis moorei</i> ⁴	flighted giant	Bunce <i>et al.</i> , 2005

NOTES:

(1) inclusion of a subspecific designation indicates the island form is considered con-specific with mainland forms (if they still exist), not a unique species; (2) these are definitely considered distinct species from mainland ancestral forms; (3) these are considered con-specific with mainland forms but no sub-specific designation exists; (4) the ancestral species not known or only recently known, but the island form has a unique species name; (5) the island form is described but a scientific name has not been designated.

The most prominent trends in island syndrome have to do with size change, although changes in shape are also apparent in some lineages. Thus, small mammals generally get larger (as do some birds and many reptiles), large mammals get smaller (as do rabbits and hares, and some shrews, reptiles and birds), and many birds become flightless (Lomolino, 2005; Williamson, 1981). Many island-dwelling birds with reduced wing bones are also giants, with enlarged bills and well-developed hind limbs (e.g. Livesay 1989). Amongst island mammals, in addition to changes in size, pronounced differences are often observed in dentition, skeletal proportions, antler development, behaviour and life history characteristics such as age at sexual maturity (e.g. Adler & Levins, 1994; Cubo & Arthur, 2001; Raia *et al.*, 2003; Geist, 1998; Palkovacs, 2003).

A few examples of island syndrome are listed in Table 1, which also emphasizes the range of variation in scientific naming among them. Some island endemics, for example, are considered to belong to the same species as mainland forms but may be distinguished with a distinct subspecies name, while others are considered distinct species. However, there is no formal rule regarding scientific nomenclature of island forms.

Regardless of how they are named, several explanations have been offered over the years to account for trends among island-dwelling animals. These explanations hinge on one of three ecological factors (or combinations thereof) that differ between mainland and island environments: lack of competition between species, lack of predation, and either restricted or abundant food (Lomolino, 2005; Millien, 2006; Raia & Meire, 2006). A typical account suggests that an island founder population of large mammals will eventually become a small endemic form because they deplete limited food resources, allowing natural selection to favour smaller body sizes that require less food. Alternatively, founder populations of small mammals that colonize an island (such as rodents) often arrive to find not only abundant food but no predators or competitors: in this case, it is proposed that animals grow to larger and larger sizes until truly gigantic proportions are attained.

Some researchers (e.g. Palkovacs, 2003; Raia *et al.*, 2003) have suggested that selective factors alone are not adequate for explaining the phenomenal range of body size changes that have been documented for various populations of island-dwelling animals. They propose instead that shifts in life history traits, such as rates of mortality or the age when individuals reach sexual maturity, offer a better explanation for why island endemics change as they do. But while this

seems an eminently reasonable conclusion and probably correct (e.g. Bielby *et al.*, 2007; Day & Rowe, 2002), it does not address the question of how such changes are actually implemented biologically. Until this question is answered, we will not have a clear understanding of how and why the insular populations are so unique.

PARALLELS WITH DOMESTICATION

The most common and dramatic trend in island syndrome is size reduction of large animals. The dwarfing associated with island colonization is achieved by a shift in rates of growth, a phenomenon known as heterochrony. The particular type of heterochronic change associated with dwarfing is known as paedomorphosis or juvenilization, which results in individuals attaining smaller sizes at sexual maturity than their ancestors. Domestic animals are prime examples of this process, characterized as they are by distinctly juvenilized appearance and behaviour compared to their wild ancestors. Indeed, for decades, similar size and shape differences as documented between wild ancestors and domestic descendants have been noted between island endemics and their mainland ancestors (Geist, 1998; Köhler & Moyà-Solà, 2004; Palombo, 2001; Roth, 1996). In addition, many island endemics are also relatively tame or show markedly less aggression than mainland forms (Adler & Levins, 1994; Grant, 1998a).

I contend that the similarities between island-dwelling animals and domesticates are not coincidental but represent evidence that similar evolutionary processes are at work. The traditional view of domestication as deliberate human innovation is now considered untenable and in its place, I have proposed that domestication is simply a particular example of natural speciation (a process I call “protodomestication”). The common physical and behavioral changes seen in different domestic mammals can be effectively explained as the result of deliberate colonization of a particular habitat by stress-tolerant individuals of wild ancestors. As I have described in detail elsewhere (Crockford, 2002, 2003, 2004, 2006), this testable theory hinges on the fact that thyroid hormone (TH, which includes *triiodothyronine*, T₃ and/or *thyroxine*, T₄) regulates virtually all biological systems from the point of conception onward, including tooth enamel development (Noren & Alm, 1983). These multi-faceted influences come from a cascade of threshold-sensitive effects of TH on regulatory genes, basic cell functions, and other hormones (e.g. Anderson *et al.*, 2003; Bandyopadhyay *et al.*, 1996; Bassett & Williams, 2003; Brent, 2000; Chastel *et al.*, 2003; Farwell & Leonard, 2005; Flamant *et al.*, 2007; Gavlik *et al.*, 2002; Hadley, 2000; Hulbert, 2000; Liu & Brent, 2005; Shi & Barrel, 1992; Silva, 1995;

Yoshimura, 2006). T_3 is considered the more physiologically relevant form, especially in metabolism and gene regulation, but T_4 has critical effects on early growth and development (e.g. Forrest, 2004; Jones *et al.*, 2005; Lavado-Autric *et al.*, 2003; Poppe *et al.*, 2007).

THs are released in pulses from the thyroid gland, generating a rhythm of TH secretion that varies in intensity and frequency according to time of day, season, health, and age (e.g. Boelaert & Franklyn, 2005; Shi & Barrell, 1992; Tomasi & Mitchell, 1994). There is compelling evidence that TH rhythms are species-specific (but with individual variation) and that these coordinate the pulsatile release of other hormones (e.g. Duckett *et al.*, 1989; Gancedo *et al.*, 1997; Greenspan *et al.*, 1986; Lapsieritis & Hayssen, 2001; Wright *et al.*, 2003), although more comparative studies are desperately needed.

I propose that individual variation in species-specific rhythms of TH production (TH rhythms) link individual variation in a wide variety of selectable life history traits in vertebrates, including morphological, physiological, reproductive and behavioural characteristics, especially the behavioural response to stress. In protodomestication, I suggest that human-dominated environments attracted a few individuals with stress-tolerant TH phenotypes as founders, which set the stage for developmental changes associated with heterochronic speciation in their descendants. In other words, because wild founders of early domesticates (whether wolves, wild boar or aurochs) possessed a similar TH rhythm variant, their descendants possessed predictable and consistent differences. This plausible and testable hypothesis explains protodomestication not as human innovation but as a natural speciation process with parallels in many other lineages, including island colonists.

I maintain that animals who consciously and deliberately colonize islands are a hormonally-similar, non-random subset of the original population—that if we were to measure TH secretion patterns of colonizers, we would find particular TH rhythms associated with stress-tolerant behavior of that species. As a consequence, similar trends in outcome are inevitable every time an island is deliberately colonized. Stress-intolerant animals simply choose not to participate in deliberate colonization events. Why choose to colonize an island in the first place? Large herbivorous mammals can probably smell vegetation on offshore islands. Stress-tolerant individuals of species that are good swimmers (such as deer, elephants, and hippopotamus) may occasionally cross long stretches of water to explore such offshore resources and simply decide to stay. Although colonization of islands must happen only rarely, once undertaken, it seems not

to be reversed – which means that once a few colonizers occupy an island, the ocean becomes as effective as a fence in confining them.

All new habitats are associated with novel stressors and islands are no exception. Island colonization presents both limitations and opportunities, which are not only potentially stressful but require behavioural responses: 1) predator vigilance is still required, since even if predators are not present, this can never be assumed; 2) decisions are required regarding the many unoccupied habitats available for use (as suggested by Carlquist, 1965), especially if there are no competitors; 3) former seasonal movements between resource areas (e.g. Raia *et al.*, 2003) are often no longer possible—movement is restricted by the small physical space and oceanic boundary; 4) the small number of initial founders severely restricts mate choice for many generations; 5) there is, or at least appears to be, no escape.

To initial stress-tolerant founders, these factors (predator vigilance, opportunities that require decision-making, restricted movements, limited mate choice, and virtual imprisonment) may not be especially disturbing, but may prove very stressful for individuals born in subsequent generations who by chance inherit a thyroid rhythm that is less stress-tolerant. In contrast to protodomestication and other examples of colonization, on islands such stress-intolerant descendants are not free to leave. This inability to leave the new colony presents the largest difference between island colonization and protodomestication. *Even if there is still a navigable distance between a continental island and the mainland, a stress-intolerant individual is as unlikely to attempt an escape from an island as to have chosen to swim there from the mainland in the first place.* This is one reason I suggest original founders must be particularly stress-tolerant, at least when colonization is by deliberate choice.

What happens when one of these less stress tolerant second or third generation founders becomes pregnant while trapped on an island? During pregnancy, we know that absolute levels of TH rise significantly, often to double pre-pregnancy levels (Chan & Kilby, 2000; Forrest, 2004; Poppe *et al.*, 2007), because T₄ is essential for fetal development and growth at all stages. Studies in humans as well as experimental animals have shown that when T₄ levels do not rise to appropriate levels during pregnancy, premature birth or reduced uterine growth are almost inevitable and smaller than usual newborns are the result (Chan *et al.*, 2005; Kilby *et al.*, 1998; Stagnaro-Green *et al.*, 2004). Because we also know that stress of any kind reduces T₄ production immediately and often profoundly (Hadley, 2000), I suggest that this relationship

between maternal stress, TH, and fetal growth becomes paramount to understanding island syndrome (see also Badyaev *et al.*, 2005; Partecke *et al.*, 2006).

RESTRICTED FETAL GROWTH AND ISLAND DWARFS

Reduction of available T₄ due to maternal stress from any cause will impact fetal growth. It has been shown that small offspring produced because of reduced fetal growth seldom re-coop this loss: even if growth is not restricted afterward, premature and low-birth-weight individuals not only remain small throughout life but produce smaller than average offspring themselves (Forchhammer, 2000; Luo *et al.*, 1998; Roff, 2000). Reduced fetal growth resulting from maternal stress can thus have population-level impacts over time.

It has also been demonstrated that small individuals of large mammals mature earlier on average than larger ones (e.g Fedoseev, 1975; Finley *et al.*, 1983; Palkovacs, 2003). For late maturing large animals such as elephants, this disparity can amount to several years difference, and significantly, a small female elephant who matures at 11 years may be capable of producing several more offspring over her lifetime than a female who matures at 15 years—and so will all of her small, early-maturing daughters. An extreme example of this phenomenon is seen in the extremely dwarf, ca. one m. tall, straight-tusked elephant (*Elaphas falconeri*) that lived on Sicily during the Pleistocene, which has been estimated to have reached sexual maturity as early as three to four years of age (Palkovacs, 2003).

For smaller animals, especially those that first breed at one year of age or less, early maturation will be much more subtle. For example, in an experimental population of Siberian silver foxes, the earliest breeding females every season were advanced by only a few weeks but were always stress-tolerant (“less fearful”) individuals (Belyaev, 1979; Trut, 1999). Smallish, early-breeding animals may be the most stress-tolerant individuals within many large-bodied mammalian populations, although this trend has not been documented (for small mammals the reverse *has* been documented, as discussed below).

I propose that deliberate colonization (including protodomestication) bring early maturing individuals together within founding populations because only stress-tolerant individuals participate in these events. Due to the fact that the only growth programs available among these founders are governed by the specific TH rhythm patterns that produce stress-tolerant early breeders, most offspring will inherit similar stress-tolerance along with other

behavioral and morphological traits associated with those specific growth programs. However, a few offspring of these original colonizers will invariably have somewhat less stress-tolerance than their founder parents, a phenomenon that may re-occur in subsequent generations. Under circumstances of protodomestication and mainland colonization, individuals with reduced stress-tolerance are free to leave the stressful habitat and return to the original population: in island colonization, such freedom to emigrate doesn't exist.

A short aside is called for here to discuss the different effects on growth precipitated by food limitations vs. maternal stress, since food limitation is often suggested as precipitating island dwarfing (e.g. Carlquist, 1965; Raia *et al.*, 2003; Sondaar, 1977). In a pregnant female, food deprivation (fasting) primarily affects the condition of the dam: reduced food intake reduces the amount of T_3 available for her cellular and tissue functions due to reduced conversion of T_4 to T_3 , which causes a reduction in basal metabolic rate (Franklyn, 2000; Hulbert, 2000). Since production of T_4 continues as normal, and because the fetus can utilize unconverted T_4 , the fetus is protected from direct metabolic effects of fasting unless it becomes prolonged (e.g. Armario *et al.*, 1987; Chan *et al.*, 2005; Schew *et al.*, 1996). In contrast, even short-term psychological stress caused by competition for food, or panic induced by futile searches for food (especially for females with underlying stress intolerance), will result in profound reduction in T_4 secretion from the thyroid gland and an immediate effect on the developing fetus. Therefore, I contend it is primarily the stress experienced by the dam that negatively affects the developing fetus, not the reduced maternal basal metabolic rate resulting from any short-term food shortages. After birth, food shortages may restrict the growth of juveniles but such growth-restricted youngsters may eventually catch up on growth if conditions improve. In contrast, the effects of maternal stress on fetal growth are not only more profound but appear to be irreversible (cf., Badyaev *et al.*, 2005).

Therefore, pregnant females of large animals born during the early generations of island colonization who have reduced stress-tolerance (and thus react more profoundly to any stressor) are likely to produce smaller, earlier maturing offspring. Because founding populations have so few members, smaller, earlier maturing individuals will quickly outnumber large individuals simply because of their faster generation times. Large individuals don't disappear entirely, they just become increasingly rare. Indeed, one of the characteristics of island populations seldom mentioned is the pronounced variation in size and morphology relative to mainland forms. For example, the population of extinct mammoths on Santa Rosa Island off California, although

usually described as “dwarfed,” has been estimated to have had one large mammoth for every 10 dwarf ones (Caloi *et al.*, 1996; Grant, 1998a).

In other words, shortage of food due to rapid population growth (habitat saturation) is unlikely to be a driving force in the early stages of island colonization. On the contrary, unless an island is extremely small there should be enough resources for many generations before the equilibrium point between population size and available food is surpassed (Raia *et al.*, 2003). Evidence of dwarfing often occurs long before this point is reached, as discussed below. This is not to say that food supply is never a limiting factor, however, since once the equilibrium point between number of animals and available food is surpassed, animals clearly must compete for food. Juveniles may not get enough for optimum growth in their first year; pregnant females may experience competitive stress over available food and produce smaller offspring, who subsequently produce small offspring themselves. Thus, a trend toward small size may also take place among island populations if conditions of prolonged competition for food exists, as has been proposed for Spitsbergen reindeer (Table 1, also Klein *et al.*, 1987).

To summarize: 1) in protodomestication, stress-tolerant individuals of large mammals interbreed exclusively within a small founder population where escape – i.e. *emigration* - is possible. These founders produce slightly dwarfed (“juvenilized”) offspring due to the reduced variation in growth programs available among founders; emigration of stress-intolerant individuals born in early generations keep the changes from being extreme; 2) in island colonization, stress-intolerant individuals born in the early generations of this environment produce much more profoundly dwarfed offspring because it is emigration-proof—if island founders include a few stress-intolerant individuals from the very beginning, as may happen when once-connected islands populated during times of lower sea levels suddenly become cut off by rapidly rising seas, even more profound dwarfing can occur (Fig. 1).

Both moderate and extreme dwarfing can occur on the same island at different times due to repeated colonization events by the same ancestral species (e.g. such as seen on the island of Sicily during the Pleistocene: here the extremely dwarfed elephant, one metre tall *Elaphas falconeri* came first and the moderately dwarfed form, *E. mnaidriensis*, came later). Remains of extremely dwarfed individuals have been recorded on islands within 4,000 to 6,000 years after initial colonization events in extinct large mammals although the process almost certainly begins soon after arrival and proceeds rapidly (Lister, 1989, 2004; Lomolino & Perault, in press; Tikhonov & Vartanyan, 2001; Vartanyan *et al.*, 1993).

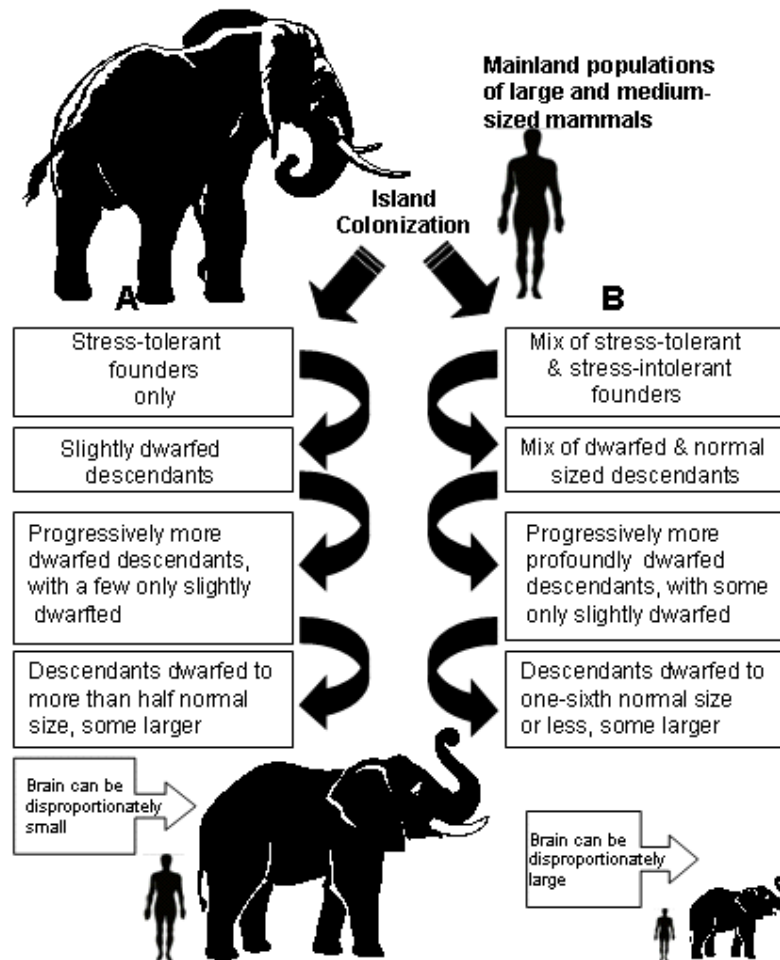


Figure 1 A model for insular dwarfing in large to medium-sized mammals.

DWARF STEGODONS IN INDONESIA—AN EXAMPLE

The above generalities can be used to explain the fossil record of the primitive Southeast Asian elephants known as stegodons on Flores Island, one of the larger islands of the Lesser Sunda archipelago that lies east of Java. Flores was never connected to the islands on either side, isolated by deep channels that narrowed just enough (to ca. 25 km) during times of extremely low sea levels to allow deliberate colonization by *Stegodon trigonocephalus* from Java (via the islands of Bali and Lombok to the west).

Colonization of Flores by stegodons from Java occurred at least twice: once at about 1,500,000 ya and another at about 800,000 ya. The first colonization resulted in the generation of *S. sondaari*, the smallest of all Indonesian stegodon species. This dwarf stegodon had an estimated weight of about 300 kg (vs. 1000-1700 kg for ancestral forms) and molar teeth with more complex cusp patterns than its ancestor (van den Bergh 1999). The most recent well-documented remains of this dwarfed form date to about 900,000 ya but the species appears to have become extinct shortly after, suggesting it survived on Flores for about half a million years (van den Bergh *et al.*, 2001).

At about 800,000 ya, a second *Stegodon* colonization of Flores occurred, associated with yet another major drop in sea level. This group of stegodon colonizers evolved into *S. florensis* and flourished until it became extinct due to a major volcanic eruption just before 12,000 ya (Morwood *et al.*, 2004; van den Bergh *et al.*, 2001). *S. florensis* is estimated to have weighed about 850 kg and thus was only moderately dwarfed compared to mainland forms (van den Bergh 1999). Van den Bergh and colleagues (2008) have recently described the latest Plesistocene population, which lived from ca. 95,000-12,000 ya, as a distinct subspecies, *S. f. insularus*, intermediate in size between early and mid-Pleistocene forms (cf. Rolland & Crockford 2005).

As mentioned previously, most examples of extremely dwarfed large mammals are associated with islands that were once connected to other land masses, thus presenting an opportunity for a small colony of both stress-tolerant and stress-intolerant individuals (a hormonally heterogeneous mix) to become stranded together. This pattern suggests that if early Flores stegodons were extremely dwarfed, they should be descendants of a hormonally heterogeneous founding population. But how could a hormonally heterogeneous group of

stegodons get to Flores, when it was never connected to other islands in the archipelago? Turned around this way, the really significant question is not why Late Pleistocene stegodons on Flores did not become extremely dwarfed but why the earlier population did.

At least three possible scenarios can be suggested. The first possibility is that the ancestral populations were different: while both early and middle Pleistocene ancestors technically belonged to the same species of *Stegodon*, they may not have been precisely equivalent. Colonizing founders from the two time periods may have differed enough to generate distinct descendants. This is precisely what has been suggested by researchers trying to assign appropriate scientific names to the many Pleistocene populations of elephants on islands in the Mediterranean, which all appear to have descended from a mainland straight-tusked elephant (*Elephas antiquus*) (Palombo & Ferretti, 2005; see also Poulakakis *et al.*, 2006).

Another, perhaps equally likely, explanation to account for extreme dwarfing in the earlier Flores population is that the extended social bonds of elephant mothers and offspring, which most other large mammals do not have, encouraged a more physiologically and behaviourally heterogeneous mix of *Stegodon* to swim offshore than usually occurs. The prolonged mother/calf bond characteristic of elephants and perhaps to a lesser degree in hippos (as for modern *Hippopotamus amphibious* described by Hanken & Wake, 1993), might induce stress-intolerant offspring, even as adults, to accompany stress-tolerant mothers on an offshore swim they would not undertake alone. This would explain why primitive elephants and their relatives, as well as hippos, often (but not always) became extremely dwarfed even when deliberate colonization events were involved.

Thus, during the mid-Pleistocene, the second wave of stegodon colonizers to Flores may have been only moderately dwarfed because the population derived on this occasion from a deliberate colonization event by a few stress-tolerant individuals only, generating less extreme changes in growth programs. However, the possibility also exists that the second colonization event was different from the first because low sea levels during that period also brought a predator to Flores: *Homo erectus*. A viable population of near-normal sized stegodons may have survived longer than the previous extremely dwarfed population because hunting by *H. erectus* kept the animals relatively large and late maturing. Hunting would also have kept population density low enough to prevent habitat saturation and subsequent dwarfing due to food shortages. A similar pattern of early colonizers becoming extremely dwarfed while later ones did not is also documented for the Pleistocene straight-tusked elephants (*Elephas antiquus*) that colonized the

Mediterranean island of Sicily: in this case, the presumed predators on the later population were large carnivores whose remains are found in same-age deposits (Caloi *et al.*, 1996; Palombo, 2001b; Palombo & Ferretti, 2005). Similarly, there is evidence for late Pleistocene predation of stegodons on Flores by hominins: age profiles of *Stegodon* remains suggest that juvenile animals were preferentially targeted by late Pleistocene hunters, although in earlier times very small adults (if they existed) may also have been taken (Morwood *et al.*, 2004).

DWARF *HOMO* ON FLORES ISLAND?

Adult stegodons seem to have been avoided by late Pleistocene *Homo* hunters on Flores, although adult mammoths were hunted successfully in other regions (Fisher, 1996). A possible explanation for this lies in evidence that late Pleistocene *Homo* on Flores was an island dwarf itself. Flores appears to have been colonized by *H. erectus* from Java, with finds of simple flaked stone tools dating their arrival at about 840,000 ya (van den Bergh, 1999, 2001).

Skeletal remains of this small species, designated *H. floresiensis*, suggest it stood only about 1.0 m. tall (Lahr & Foley, 2004). With features strongly indicative of a *H. erectus* ancestor but with an unusually small brain, the remains nevertheless date to a period between 35,000 and 14,000 ya (average about 18,000 yr), perhaps extending back to about 74,000 yr (Brown *et al.*, 2004). While a continuous link between the earliest and latest finds has not yet been demonstrated (i.e. no skeletal remains of hominins, dwarf or otherwise, have been found in the oldest deposits, only tools), like other large mammals that colonized islands, *H. erectus* on Flores appears to have become a dwarf endemic species.

Stress-tolerant *H. erectus* individuals may have colonized Flores by swimming or via constructed or naturally-occurring rafts. It is the deliberate nature of the journey, however, that makes this scenario equivalent to colonization by other large mammals. It is unlikely *H. erectus* was capable of constructing advanced watercraft as *H. sapiens* later did, but eminently reasonable to assume it had discovered the floating characteristics of bamboo and mangrove logs. It is also unreasonable to assume *H. erectus* was incapable of swimming moderate distances in warm seas, given that such a journey could be assisted by a floatation device as simple as a bundle of bamboo sticks.

Note that *H. floresiensis*, while small, is more than one-half ancestral size (Lahr & Foley, 2004 give a range of 1.55 to 1.78 m for *H. erectus*), similar to the moderate dwarfing seen in *Stegodon* of the same time period on Flores. Although surprisingly petite, the small brain relative

to body size reported for *H. floresiensis* (ca. 380 cm³ vs. 650-1,260 cm³ for *H. erectus*, see Lahr and Foley, 2004) is not unique among medium-sized dwarfed mammals: Majorcan cave goats, for example, also had disproportionately small brains (Köhler & Moyà-Solà, 2004; Niven, 2007). In contrast, severely dwarfed elephants (reduced to one sixth ancestral size or less), such as *E. falconeri* from Sicily, had relatively large brains for their body size (Palombo, 2001a).

Debate continues regarding the status of this hominin and is not likely to end soon (e.g. Niven, 2007; Richards, 2006), with recent analysis of wrist bone shapes bolstering a *H. erectus* ancestor and taxonomic distinction for *H. floresiensis* (Gibbons, 2007). There is no particular reason, besides non-scientific anthropocentrism, why a colonizing *H. erectus* would be exempt from the natural dwarfing processes that affected other island mammals. It is both plausible and biologically sound to consider *H. floresiensis* as an endemic island dwarf descended from a *H. erectus* ancestor, via the same juvenilizing effects of deliberate island colonization as other medium- and large-sized mammals; whether it deserves a unique species name is debatable.

If this hominin is indeed an endemic island dwarf, we should anticipate that subsequent finds will show the marked size variation characteristic of all island dwarfs: a few large specimens as well as dwarf ones should be present and do not constitute evidence that dwarf individuals were pathological. We should also recognize that evolutionary change undoubtedly continued in *H. floresiensis*, perhaps along the same trajectory as the transformation of *H. erectus* to *H. sapiens*, and that these might produce characteristics vaguely reminiscent of anatomically modern humans. While TH rhythm theory does not prove that *H. floresiensis* was an endemic dwarf of *H. erectus*, it does provide a plausible and testable mechanism to explain such an outcome.

However, the dwarfing characteristic of large mammals is only one type of change associated with island colonization and in the next section I address the phenomenon of small animals that become giants and birds that lose the ability to fly.

GIGANTIC RODENTS AND FLIGHTLESS BIRDS

We cannot say that domestication and island colonization always produce dwarf individuals because in rodents and some birds the opposite appears to be true: island endemics are most often larger than mainland forms (Adler & Levins, 1994; Lomolino, 2005; White & Searle, 2006) and early forms of domestic rodents and birds are larger than ancestral forms (e.g. Clark & Price, 1981; Macdonald *et al.*, 1993; Stuermer *et al.*, 2003). Giant Indonesian rats and

the Caribbean hutia (Table 1) are but two extinct examples. I suggest that this reversal of the dwarfing phenomenon reflects basic differences in the correlation between stress tolerance, growth, and reproduction in small animals, since it has been demonstrated that stress-tolerant rodents are larger, more fecund, and mature earlier than stress-intolerant individuals (Miller *et al.*, 2002).

Understanding why gigantism is the norm among island populations of small mammals is a matter of following the reasoning outlined above for island colonization in large mammals. Colonization of islands by rodents usually occurs by chance, often via rafting on storm wreckage, and because these are not deliberately initiated events, founding populations of rodents are more likely to contain a mix of stress-tolerant and stress-intolerant individuals (even if only one of each, or a single pregnant individual). Since larger-than-average individuals of small mammals are not only more stress-tolerant but earlier to mature than smaller individuals, large individuals will soon outnumber smaller ones within an expanding population. Large individuals become the norm not because there are plentiful resources or lack of predators but because they reproduce faster. Offspring born to any stress-intolerant rodent dams in the population will be smaller and mature later: small individuals do not necessarily cease to exist, they simply become very rare.

Birds that colonize islands and subsequently generate giant descendants with altered limb and beak proportions are also explainable by this concept because in birds stress-tolerant individuals appear to be larger than stress-intolerant ones, as is true for rodents (Miller *et al.*, 2002), complicated by the fact that the TH required for embryonic development in birds is deposited by the hen into egg yolk (Dawson *et al.*, 1994; Hulbert, 2000; Lien & Siopes, 1990; Sotherland & Rahn, 1986; McNabb, 2006). Species-specific rhythms of maternal TH in bird females almost certainly generate a species-specific yolk characterized by regions of different TH concentrations but because each egg is produced separately, there will be slight individual differences that affect growth rates of the developing embryo. While the existence of species-specific layering of TH in yolks has not yet been demonstrated, it has been shown for steroid hormones (Bowden *et al.*, 2001; Gil *et al.*, 2007); all hormones, including TH, have been shown to decline as the embryo develops (Bowden *et al.*, 2002; Wilson & McNabb, 1997). I contend that some kind of concentration gradient of TH must exist that allows the yolk to reflect maternal TH rhythms, since we know that timing and amount of hormone delivered to TH-dependent genes in the developing embryo (such as *Sonic hedgehog*, fibroblast growth factor and bone

morphogenic protein genes) are as critical to birds in a threshold-dependant manner as for other vertebrates (Blache *et al.*, 2001; Bucher *et al.*, 1986; McNabb, 2006; Tickle 2003).

Differences in timely availability of TH to developing chicks, caused by slight differences in maternal provisioning of TH to yolk, is more likely to produce flightless descendants in precocious species (who, like chickens and ducks, are well developed at birth and feed independently within a few days) than in species with altricial young (who, like the starling and other small forest birds, hatch at a much less developed stage). Faster embryonic growth in precocious young is apt to disrupt body part symmetry, since limb and beak regions do not grow synchronously (Riddle & Tabin, 1999). Elements of the pectoral girdle (wings and sternum) may be under-developed (paedomorphic) while hind limbs and beaks develop normally. Growth rate reductions in the pectoral girdle may be a consequence of depleted TH stores due to growth rate increases earlier in the embryonic period (Cubo & Arthur, 2001; Livezey, 1988, 1989, 1990). Once these changes occur, however, they will be heritable over many generations. As for body size reductions in large mammals, heritability of body size and limb proportion in birds is primarily controlled by maternally-provided TH. Maternal control over growth and development shapes the cellular architecture and nerve connections within the hypothalamus tissues of the embryonic brain that will be responsible for generating hormone rhythms after hatching (Lavado-Autric *et al.*, 2003): alter the TH pattern from maternal sources during embryonic development and not only do body size and limb proportion change but so does the cellular architecture of the hormone-controlling portions of its brain, perpetuating an altered TH rhythm during post-natal growth and for all subsequent generations of offspring.

For example, Ricklefs & Marks (1985) used precocious Japanese quail *Coturnix coturnix japonica* to demonstrate how selection can alter body proportions in a descendant population. Over 47 generations, only the heaviest individuals (measured at 4 weeks of age) were selected for further breeding. At the end of the selection period, adult birds were not only twice the size of birds from a control (unselected) population but were differently proportioned, with relatively larger pectoral muscles, reduced wings and smaller brains.

As for rodents, large stress-tolerant female birds appear to produce somewhat larger offspring. Offspring that grow faster than usual during early development will mature early at a large size. However, I propose that past a certain threshold, accelerated growth can disrupt development of wing and sternal elements, generating large offspring incapable of flight. In addition, large flightless offspring that mature early should produce more offspring over a

lifetime than small ones: small offspring with well-developed wings should become increasingly rare until they no longer exist. When no predators are present, as is usual for remote oceanic islands, reduced wings and ground-dwelling habits are not particularly disadvantageous. I content that although flightlessness cannot be caused by lack of predators (or generated simply because flightlessness requires less energy, as suggested by McNab & Ellis, 2006), development of flightlessness does require lack of predation to be perpetuated. Consequently, completely flightless birds tend to survive over time only on remote islands, even if they are generated in other circumstances.

Due to the rather strict requirements necessary for generating altered wing proportions and greatly increased body size, large flightless birds tend to descend from ancestral species that are migratory and have relatively precocious development, since extended incubation exposes developing chicks to disruption of maternal provisioning of TH to yolk. Consequently, most flightless or nearly-flightless island species have descended from relatively few bird families: they derive almost exclusively from pigeons, rails, alcids, ducks and geese (Carlquist, 1965; Gaskell, 2000; Livezey, 1989, 1990; McNab & Ellis, 2006). Some examples include the extinct giant dodo of Mauritius and the large flightless solitaires of two small islands north of Mauritius, Rodrigues and Réunion, which all descend from pigeon-like species (Shapiro *et al.*, 2002): note that while the common rock dove and domestic pigeon (the best known members of this family), are anomalous in producing altricial young, most other species produce precocious young and are strongly migratory.

Rails, geese and ducks have many flightless or near-flightless members (Table 1). Hawaii once sported a giant flightless goose recently shown by genetic analysis to have descended from the common Canada goose (*Branta canadensis*) (Paxinos *et al.*, 2002). Ducks and geese are not only precocious (although slightly less so than gallinaceous birds like quail) but most are strongly migratory (Ricklefs & Marks, 1985; Sedinger, 1986). The now extinct great auk of North Atlantic islands was a very large flightless member of a little-known marine bird family, the Alcidae, which are migratory sea birds that produce chicks as precocious as ducks and geese (Gaskell, 2000; Livezey, 1988; Moum *et al.*, 2002; Sotherland & Rahn, 2001).

A number of flightless island species exist that do not at first glance appear to fit the above profile. However, in most cases, consideration of their particular life-history traits explains their susceptibility to growth disturbances during island colonization. One such example is the giant Galápagos cormorant (*Compsohalieu harrisi*). Cormorants are large coastal sea

birds and although most are non-migratory and relatively altricial, they have large eggs that generate large chicks at hatching. Large eggs and large hatchlings suggests that quite a lot of growth is going on inside the egg rather than after hatching (Carey *et al.*, 1980; Dunn, 1975; Sotherland & Rahn, 2001). Another example is the kakapo (*Strigops habroptilus*) of New Zealand, a flightless parrot: although parrots are altricial, they nevertheless produce relatively large eggs and chicks, and most are also strongly migratory (Vendramin-Gallo *et al.*, 2001).

GIGANTISM IN RETILES AND BIRDS

Most reptile families tend to generate enlarged island endemics, such as giant island tortoises and the enormous Komodo dragon, a varanid lizard that still lives on a few islands in Indonesia (Carlquist, 1965; Quammen, 1996). In reptiles, where growth does not stop with sexual maturation, rapid early growth can generate much larger sizes than usual, even if growth slows after maturation; in some species, relatively faster growth rates may also continue after sexual maturation.

For reptiles and birds that colonize islands, as for small mammals, the critical feature appears to be individual variation in early growth rates, because rapid early growth allows individuals to reach larger sizes before sexual maturity is attained. In contrast, dwarfing of large mammals is associated with marked individual variation in timing of sexual maturation because early maturation stops growth before maximum sizes are reached. Also, in reptiles, amphibians, fish and some birds, fecundity increases with increased size (e.g. Berkeley *et al.*, 2004; Elinson, 1987): larger individuals produce more offspring. Over time in an isolated island population, larger animals of such egg-layers will become the most common form. Small individuals do not cess to exist but become very rare.

In some lineages of reptiles, such as tortoises, stress slows early grow and delays maturation, generating larger size at maturity. For example, in at least one tortoise, slow growth and delayed maturation resulting in larger body size has been shown to be a response to the stress of low temperatures (Lagarde *et al.*, 2001; see also O'Steen & Janzen, 1999 on hatchling snapping turtles). In other groups, such as pythons, more rapid early growth without changing the age at maturity also leads to larger sizes. While such growth increases in pythons are assumed to be the result of more abundant or larger prey (e.g. Madson & Shine, 2000), another interpretation is also possible.

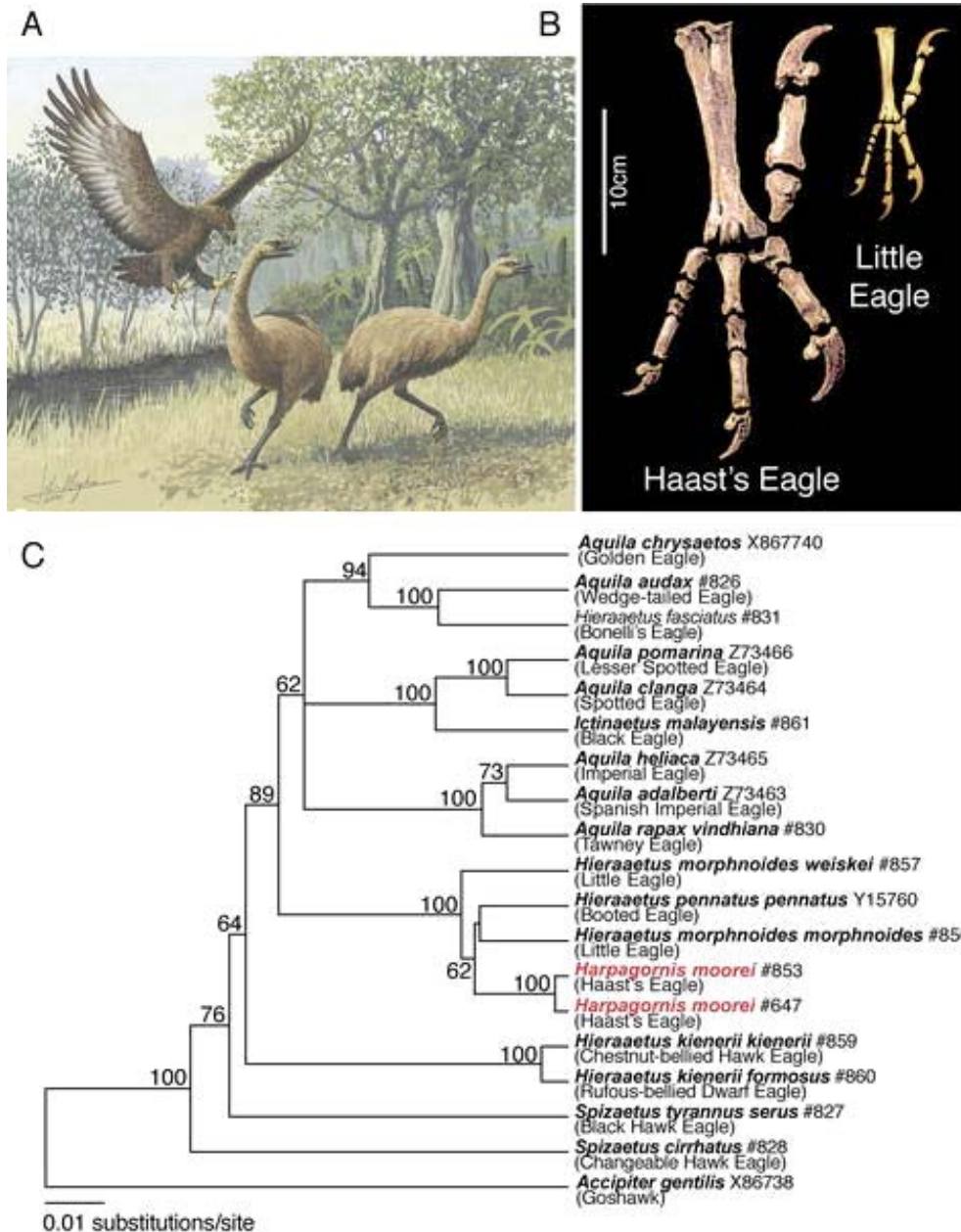


Figure 2 Artistic representation, bones and phylogenetic analysis of New Zealand's extinct Haast's giant eagle (*H. moorei*). (A) An artist's impression of *H. moorei* attacking the extinct New Zealand moa (by John Megahan). (B) Comparison of the huge claws of *H. moorei* with those of its close relative, the "little" eagle (*Hieraaetus morphnoides*). (C) Maximum-likelihood tree based on *cyt b* data (circa 1 kb), depicting phylogenetic relationships within the "booted eagle" group. *Harpagornis moorei* (red) groups exclusively with the small *Hieraaetus* eagles, and genetic distances suggest a recent common ancestor about 0.7–1.8 million years ago. Reproduced with permission, from Bunce *et al.*, 2005.

For snakes that colonize islands, dietary change may have a significant impact on descendant populations, if one takes age as well as size of prey into account. One good example of this is demonstrated by the giant tiger snakes that inhabit some islands off southern Australia (Keogh *et al.*, 2005). These big snakes eat mainly seasonally available shearwater (“muttonbird”) chicks because for much of the year there is little else available. Shearwater chicks are considerably larger than the prey consumed by small tiger snakes on the nearby coastal mainland, where shearwater rookeries do not exist. As a consequence, Keogh *et al.* conclude that absolute size of prey item is the controlling factor: large prey makes for large snakes.

I suggest, however, that all prey items are not equal, gram for gram. A rapidly growing bird chick of any species has higher relative concentrations of TH than an adult (Blache *et al.*, 2001; Hulbert, 2000; Schew *et al.*, 1996; Wilson & McNabb, 1997). Carnivorous bird and reptile species that colonize any new habitat (including islands) and consequently shift from eating adult prey animals, such as rodents, to young animals or even eggs, would almost certainly experience significant increases to their own early growth, and the early growth of their offspring, due to the increased consumption of TH because unique among hormones, TH can be absorbed from ingested food and used as readily as self-produced TH (Hulbert, 2000). Increases in juvenile growth rates without a delay in age at maturity would lead to larger adult sizes. And because large adults produce more eggs, large individuals would soon dominate the population. Several other island populations of snakes with markedly larger body sizes are known to eat primarily unfledged seabird chicks (e.g. Boback, 2003), as do some giant island rodents (e.g. Gough Island mice, which feed on unfledged albatross chicks).

Another example is equally illustrative, although it involves a carnivorous bird rather than a reptile. The giant Haast’s eagle of New Zealand (*Harpagornis moorei*), now extinct, grew to tremendous size: it probably weighed more than 16 kg, larger than any living eagle (Fig. 2). Although it has been assumed that its ancestor was a somewhat smaller eagle from Australia, ancient DNA analysis of Haast’s eagle bones have shown that its closest relative is very small indeed, an Indonesian eagle weighing only about one kg. The authors of this study imply that Haast’s eagle got big because it preyed on the adults of large flightless moas, a group of birds unique to New Zealand. In other words, as for snakes, they assume that larger prey generates larger predators, which I suggest is too simplistic.

I contend that Haast's eagle got very large without losing its ability to fly because its ancestors that colonized New Zealand had a unique and very different prey item to subsist on: the newly-hatched chicks of a variety of moa species. Some of these moa species were very large indeed (Anderson, 1989; Bunce *et al.*, 2003) and produced very large chicks. As for the shearwater chicks mentioned in the tiger snake scenario, newly-hatched moa chicks would have had much higher levels of TH than prey items like adult rodents or even adult birds that are the usual prey of many small eagles. Ingestion of prey items with higher than usual levels of TH does not usually disrupt reproduction in carnivorous animals but it could increase growth rates for developing embryos and newly hatched altricial chicks.

Living eagle species are altricial: they grow rapidly over a period of several months but are totally dependent on their parents for food (Bortolotti, 1984; Lyons & Mosher, 1987). If fed TH-laden foods, such as newly-hatched moa chicks, during this time of rapid growth, the size of colonizing Haast's eagle ancestors would almost certainly have been enhanced. At maturity, given the same diet of moa chicks, new eagle founders would have produced egg yolks with relatively higher than ancestral levels of TH but without a marked disorganization or disruption of hormone deposition as in non-carnivorous species. Female offspring of such founders, as adults eating the same diet of moa chicks, would have produced egg yolks with TH levels conducive to more rapid fetal growth and then rapid hatchling growth, leading to rapid attainment of gigantic size in descendants without loss of flight ability.

Bunce and colleagues include in their report an illustration of a Haast's giant eagle attacking a full grown moa of one of the largest species (see Fig. 2, based on skeletal evidence of injuries on moa remains held in museum collections which are consistent with such an attack). However, I suggest that such injuries to adult moa are more likely to have arisen as a result of a hen defending her victimized chicks and not because Haast's eagle consumed such large adults.

SELECTION ON ISLANDS

As in domestication, as soon as shifts in TH metabolism generate distinct growth patterns and other life history traits among island colonizers, selective forces (e.g. differential predation or access to resources) can shape the trajectory of the population. For example, some researchers have suggested that dwarf elephantoids (true elephants, mastodons, mammoths and stegodons) may be capable of negotiating steeper slopes than normal sized individuals, allowing them increased access to available resources (Agenbroad, 2001; Sondaar, 1977). The same may be

true for other large mammals that habitually colonize continental islands, such as hippopotamus and deer. Given such an advantage and without predation, very small individuals on mountainous islands might indeed be more reproductively successful than larger individuals. If predators exist, however, small individuals of large taxa may be at risk of being picked off as fast as they can be produced. With selective predation on small individuals only, a founding population would increase much more slowly over time and the average size would stay relatively close to that of the original founders or be only somewhat smaller.

SUMMARY AND DISCUSSION

TH theory defines a biological mechanism capable of generating growth program changes in island colonizers fast enough to be effective in ecological time (*sensu* Gould 1977). Based on experimental selection experiments, such changes would have begun within only a few generations. If individual differences in TH rhythms account for virtually all evolutionarily significant differences in life-history traits, as I maintain must be the case, the particular TH rhythms of individuals within small founding populations should modify life history traits of descendants in a few predictable ways. In other words, the particular TH rhythms possessed by founders profoundly effects the outcome of colonization events.

I contend that it is the particular combination of stresses unique to islands plus the TH rhythms possessed by the individuals in the founding population that interact to shape island colonizers so consistently. Many stresses correlated with island habitats are similar to those associated with protodomestication, where deliberate colonization leads to rapid but consistently moderate changes in growth programs and size at sexual maturity. Over time, the stresses unique to island environments, especially lack of emigration potential for stress-intolerant individuals born in subsequent generations, drives further size reduction or enhancement. When chance or tight-knit social bonds between individuals result in islands being colonized by a small group with variable stress-tolerance, changes in growth programs can reach extremes.

Deliberate colonization by stress-tolerant individuals is required to explain why island syndrome is moderate in some instances and extreme in others, although predation may explain a few cases of less extreme size reduction. Disparity in relative size of stress-tolerant individuals among different mammalian orders accounts for the disparity in direction of growth rate change; in birds, differences in developmental stage and size at hatching explains disparities in shape change, summarized as follows: 1) Large mammals get smaller with protodomestication and

island colonization (via paedomorphosis or juvenilization) because colonizers are usually stress-tolerant phenotypes, with TH rhythms (and associated growth patterns) that typically generate early maturation at smaller sizes. Stress-intolerant phenotypes born in any generation, or included by chance with the original founders, respond to stress by producing even smaller offspring (i.e. very extreme dwarfing). The greater the number of stress-intolerant individuals present among founders, or born in early generations, the greater the degree of dwarfing likely to occur. Small individuals soon outnumber large ones because they have faster generation times (a process equally applicable to *Homo erectus* colonizers), even when plenty of food is available; 2) Small mammals and precocious birds get larger with protodomestication and island colonization (peramorphosis or gigantism) because stress-tolerant individuals, by virtue of their particular thyroid rhythms, are relatively large, mature early and have increased fecundity. Large individuals soon outnumber small ones because they have faster generation times, not because there is a lack of predators or especially plentiful food supplies; 3) Maternal stress can affect fetal development unevenly in stress-intolerant precocious birds, resulting in stunting of some traits (paedomorphic change) and over-development of others (peramorphic change), due to differences in the precise timing of stress-induced disruption of maternal provisioning of thyroid hormone to yolk combined with differential timing in development of various body parts. Perpetuation of traits that impart a flightless lifestyle, however, occurs primarily on remote islands where natural predators are absent.

TH rhythm theory provides a more comprehensive explanation for the patterns of dwarfing, gigantism and flightlessness documented for island mammals and birds than previously proposed hypotheses because it describes a testable biological mechanism to account for observed trends in behavioral and morphological change as well as critical life history traits. However, TH rhythms are not easy to measure: they require automated, surgically-implanted blood sampling devices and assays accurate for minute quantities of hormone (as per Windle *et al.*, 1998 for corticosterone). The fact that both rodents and birds are common island colonizers and have long been used as laboratory models (e.g. Dawson *et al.*, 1994; Dmitriev *et al.*, 2001; McNabb, 2006; Ricklefs & Marks, 1985) means they should be suitable for testing of TH rhythm theory as it applies to island syndrome.

Life history traits are certainly important in bringing about the changes in morphology, behaviour and reproductive physiology associated with island syndrome but recognizing that these factors affect populations over time does not address the issue of how such changes are

initiated, coordinated or controlled in founder populations (cf. Day & Rowe, 2002; Dufty *et al.*, 2002; Gluckman & Hanson, 2006; West-Eberhard, 2005). I contend that unique TH rhythms may account for all individual differences in life history traits and that few, if any, of these traits are actually controlled in any evolutionarily significant way by independently inherited genes. A small founder population has little TH rhythm variation to pass along to offspring: inheritance of only a few similar TH rhythms among descendants shifts all TH-controlled traits simultaneously as the population establishes a new mean pattern. This process can generate permanent transformations in island populations over a very short period of time but the outcome in each case depends on precisely which individuals become founders, a conclusion Lomolino (2005) reached even without a mechanism to explain how it would be implemented.

If island syndrome is to fulfill its promise as a window on evolutionary processes, we simply must have a theoretical concept that links individual variation in critical life history traits and gene expression with changes in habitat. While TH rhythm theory may not, upon testing, turn out to be the best answer, I contend we need something similar if we truly want to understand the mechanism that consistently causes small populations of animals who invade islands to transform rapidly into astonishing new forms.

ACKNOWLEDGEMENTS

I thank Pasquale Raia, Nicolas Rolland, and Josephine Joordens for critical comments on an earlier draft of this paper, and am grateful to the anonymous reviewers of this manuscript and the journal editor for providing useful suggestions. A copy of my Ph.D. dissertation, which explains thyroid rhythm theory in full, is available to any reader on request, from scrock@uvic.ca.

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BIOSKETCH

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