

Progress and priorities in research for the conservation of reptiles

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Introduction

The diverse and unique nature of many Galápagos reptiles, combined with a 150-year history of environmental challenges, has stimulated an intensive research and management effort to protect, recover, and preserve the native fauna and the ecosystems in which they occur. The attention afforded to various aspects of reptile conservation has been partially dictated by opportunity, expertise, human resources, funding, and technological capabilities, but many examples exist of past and present successes. Combined with current projects, those successes will contribute to the preservation of many components of the reptile diversity for which Galápagos is so well known throughout the world (CAYOT *et al.*, 1994; CAYOT and MORILLO, 1997).

Conservation and management of giant tortoises

As the primary centre of diversity of extant giant tortoises, a group that has suffered extinctions and range reductions in many other parts of the world, the Galápagos Islands are a true laboratory for tortoise conservation and management (MACFARLAND *et al.*, 1974a). Conservation programmes in Galápagos span a considerable scope of geography, complexity, and timing (MACFARLAND *et al.*, 1974b). Distinct taxa of giant tortoises exist on islands ranging from the southernmost island (Española), to the northern extremes (Pinta), through the central islands (Santa Cruz, Santiago, and Pinzón), to the western areas of the archipelago (Isabela). They occur on relatively small dry islands such as Pinzón and Española, and in quite mesic higher environments — on larger islands such as Isabela and Santiago. The occurrence of this taxonomic diversity with varying population sizes scattered in equally diverse environments presents special constraints on conservation activities. We will emphasize the diversity of problems and approaches in this overview.

Long-term recovery efforts with reduced tortoise populations

The tortoises on the islands of Española and Pinzón have been foci of dedicated recovery actions since 1964 and 1970 respectively. Española is a relatively low, arid island which was impacted by two distinct threats. Historically, whalers easily removed large numbers of tortoises due to the island's accessibility resulting from its low topography, overall arid vegetative cover, and secure anchorages. Introduced feral goats overran the island for many years and apparently competed with tortoises for forage. There were fewer than 20 giant tortoises on Española when conservation efforts started in the 1960s.

Goats were finally removed from Española by 1978 through the combined efforts of the Galápagos National Park Service and the Charles Darwin Research Station, but the tortoise population was judged to be in danger of extinction without an active captive breeding programme (CAYOT *et al.*, 1994; MACFARLAND *et al.*, 1974b). The programme was initiated with the transfer of 12 females and 2 males to captivity on the island of Santa Cruz. Subsequently a third individual was added when a large male was returned from the San Diego Zoological Society (FRITTS, 1978). Tortoises were maintained in captivity, artificial nest sites were provided, eggs were incubated in artificial chambers, and young were reared to the age of one or four years before being transferred back to their native island (MACFARLAND, 1974b; CAYOT and MORILLO, 1997).

Pinzón was similar to Española in being a small island of low elevation, arid habitats, and having been heavily used by whalers in search of tortoises. However, Pinzón's more difficult terrain and lack of secure anchorages for sailing ships resulted in less impact on adult tortoises by whalers and a larger number remained (>100 individuals). Goats were never established on Pinzón, but black rats were, sometime before the late 19th century. The introduced rats prey heavily on hatchling tortoises, and combined with native hawks have prevented recruitment of juvenile tortoises into the population for many years. It

Tortoises returned to Española Island through captive breeding

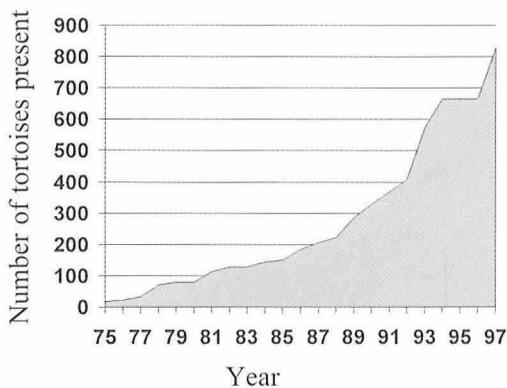


Figure 1. — Cumulative numbers of tortoises returned to Española Island as a result of captive breeding efforts by the Galápagos National Park Service and the Charles Darwin Research Station.

Tortoises returned to Pinzón Island through captive rearing

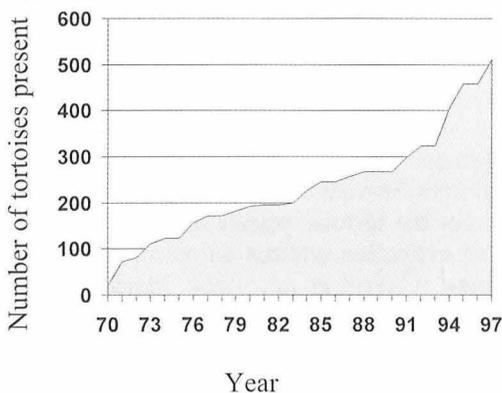


Figure 2. — Cumulative numbers of tortoises returned to Pinzón Island as a result of captive rearing efforts by the Galápagos National Park Service and the Charles Darwin Research Station. Numbers depicted are exclusive of resident adult tortoises that constituted the original breeding population.

was clear that without recruitment the future of the Pinzón tortoise was bleak

Removal of rats from Pinzón was not judged to be feasible in the 1960-70 period, and because the rats constituted no danger to adult tortoises or their eggs, a captive rearing programme was initiated that involved collection of eggs that were near to hatching, or hatchlings as they exited the nests. Hatchlings were transferred annually to the captive breeding facility on the island of

Santa Cruz, reared there to the age of 3-5 years, when they were judged to be large enough to resist predation by rats, and returned to their native island (MACFARLAND, 1974b).

The efforts directed at tortoises on Española and Pinzón have been underway for nearly 30 years and have resulted in hundreds of tortoises being returned to their native habitats (Figs 1 & 2) with documented high survival of the liberated individuals (CAYOT *et al.*, 1994; CAYOT and MORILLO, 1997). The programmes differed in that the programme for Española involved maintenance of all breeding stock in captivity, construction of artificial nesting areas, and incubation of eggs in artificial conditions, whereas the Pinzón programme left adults in their native habitats, allowed eggs to be deposited in nest sites selected by the females, and facilitated incubation under totally natural conditions. For Pinzón, only the juveniles were subjected to artificial rearing conditions during their first 3-5 years of life.

The costs and risks were greater for the Española effort but through continual refinement the programme can be judged to have been a success; it continues to this day. No mortality has occurred with adults from Española in captivity for more than 20 years; hatching rates have been continually improved with better handling practices; and distortion of sex ratios has been avoided even though incubation temperatures have been shown to determine the sex of hatchlings in this species, as in most species of chelonians. In part, this pitfall was avoided originally by the pragmatic necessity of using solar incubators that caused variable incubation temperatures from month to month and year to year, but in recent years it has been avoided by dividing most clutches into two treatment groups of eggs, with half incubated at low temperatures resulting in males, and half at higher temperatures resulting in females.

With several aspects of the Pinzón effort focused on free ranging adults, natural nests, and hence natural incubation conditions, the pitfall of unnaturally skewed sex ratios was avoided, but the numbers of eggs collected each year depended on the logistical mobilization of trained park wardens to find nests at the proper times and transfer the young tortoises to captivity. The young tortoises produced from this effort came from a much larger number of potential parents than the Española tortoises. The success of this project hinged on understanding the threat, assessing what activities were possible with available technologies and resources, and on maintenance of continuity over more than two decades to accomplish a significant improvement in the size and age-structure of the population. The possibility exists for future efforts to eradicate rats on Pinzón if the proper mix of control technologies and funding can be directed to the programme.

Considerable gains have been made with these two primary recovery efforts, and consideration is now being given to assessments of progress, determining what is the target population size for repatriation activity, what are the best alternatives for accomplishing that recovery, and

when to consider these populations to be at an evolutionarily resilient status capable of self-sufficiency with no or reduced management attention. At that point, effort should be shifted to other populations. Population models are currently being developed at the Charles Darwin Research Darwin Station that will facilitate such deliberations and support future decisions.

Emerging tortoise conservation programmes on Isabela

Tortoise populations on other islands and individual volcanoes of Isabela, the largest island of Galápagos, are impacted by a variety of past and current threats ranging from historical reductions due to over-harvesting by whalers and colonists to competition and predation by introduced mammal species. These populations historically occupied much larger geographic areas than those on Española or Pinzón, and thus were more difficult to census, monitor, and protect. Some populations were difficult to access, occurring at high elevations, isolated by rough volcanic topography, and dispersed in densely vegetated areas. However, the discovery that several populations were severely reduced, failing to recruit new cohorts, or subject to continued predation, made it necessary to expand conservation efforts.

Over the last five years, an active captive-tortoise facility has been developed in the settlement of Villamil on the island of Isabela to deal with special problems on this island. The new facility has been supported by contributions from the Frankfurt Zoological Society, the World Wildlife Fund (USA), San Diego Zoological Society, the Ecuadorean Government, and other funding bodies. This facility includes the capability of using a variety of conservation measures (captive breeding and captive rearing) with associated opportunities to facilitate research and monitoring efforts for problematic populations. A secondary benefit of this centre results from increased activity by National Park personnel in the formerly isolated colonized area of southern Isabela. This programme provides obvious opportunities for the residents of Isabela to better understand the value of giant tortoises as important elements of Galápagos ecology, as part of the Ecuadorean natural heritage, and as touristic attractions of economic value to the region.

Tortoises of the southern volcanoes of Isabela - Sierra Negra and Cerro Azul

Southern Isabela was colonized in the late 1800s and consequently was exposed to major perturbations resulting from introductions of mammalian predators (cats, dogs, and pigs), feral ungulate populations (cows, burros, and goats), and over-exploitation of tortoises for meat and oil by visiting mariners and colonists alike. As a consequence, tortoises disappeared from vast areas of Sierra Negra, and to a lesser extent Cerro Azul, areas that were

formerly optimal habitat for exceedingly large populations of tortoises. Fragmented populations exist today in isolated patches of extreme eastern and southwestern Sierra Negra but these represent some of the driest and most marginal habitats for tortoises that originally occupied a much larger area. Ironically, the fragmentary populations on eastern Sierra Negra coincide with those sampled during the historical conservation effort of C. H. Townsend when tortoises were collected in 1928 for captive breeding in North American zoos (TOWNSEND, 1928).

The Townsend expedition was obviously on the lower slopes of Sierra Negra (DE SOLA, 1930) rather than Copley Mountain (= Volcan Alcedo), as most publications have erroneously reported, and this fact documents the origin of many captive tortoises residing in North American zoos today. A second sub-population exists on the western slopes of Sierra Negra, adjacent to the primary lava flow separating Sierra Negra from Cerro Azul in the area of Cerro Paloma. The only substantial population of tortoises on Sierra Negra exists in an area of extremely rough lava close to the coast near Caleta San Pedro near the middle of the southern coast of southern Isabela. Scattered individuals or clusters of individuals occur in other lowland areas, but the status of these tortoises is very hard to establish because of seasonal movements and the lack of dependable sightings throughout much of the area (FRITTS, 1984). Threats to these populations include: poaching by fishermen, wild fires, occasional harvesting by hunters, vulnerability during climatic extremes (such as drought), and predation by dogs and pigs (especially of young tortoises). These risks are aggravated by the small numbers of tortoises remaining and their localized distributions making them more vulnerable than if populations were more dispersed over the original and contiguous ecological range. Adults and juveniles from several sites are currently part of the captive reproduction programme based at the Isabela tortoise facility.

Most populations of tortoises on Cerro Azul are less threatened than those on Sierra Negra, but one area of particular concern is an elevational zone where both *Geochelone vicina* and *G. guntheri* occur. In this area, reproductive success is limited by pig predation on nests (FRITTS, 1984) and by a recently introduced ant, *Solenopsis geminata*, which scavenges eggs and may prey upon nestling tortoises (TAPIA, 1997). Current studies of nest survivorship, basic reproductive parameters, and specifics of temperature determination of sex will facilitate conservation of these tortoise populations. Other areas of Cerro Azul are priorities for monitoring nesting success, potential damages due to predators, and overall population characteristics.

Volcan Alcedo - a pending environmental crisis for giant tortoises

The realization within recent years that an invasion of

goats from southern Isabela onto the slopes of Volcan Alcedo has justified a major effort to protect the largest population of giant tortoises left in Galápagos. As the goat population has soared on Alcedo, damage to the vegetation, major erosion, and conflicts with tortoises have become apparent. A concerted effort has been launched to control goats on Alcedo (first, to initially reduce the expansion, and secondarily to reduce the population to less threatening levels) and fulfill a plan to ultimately eliminate them from northern Isabela.

This programme is unprecedented, both in size and complexity, but the results of an international workshop involving a multi-disciplinary team of conservation experts will guide the effort over the next few years. Factors that contribute to the potential for success are the extremely large size and ecological complexity of Alcedo, the tenacity and long life-span of giant tortoises, and the dedication and competence of the Galápagos National Park Service in dealing with introduced populations of mammals. Most at risk are the juvenile tortoises and reproductive females that occupy the lower elevations where food and water are most limited during dry periods. Some damage may have been forestalled in 1998 due to extremely wet conditions related to the El Niño event, but an intensive and continuing effort will be essential to prevent major declines of the tortoise population in the drier periods likely to follow the current mesic period. Beyond protection of critical trees and other plant species, it may be necessary as an interim measure to protect large areas that serve as important nesting areas and juvenile tortoise habitats.

Northern Isabela - tortoises on Volcan Wolf and Volcan Darwin

Tortoise populations on these volcanoes are less threatened than those on southern Isabela, but monitoring programmes are essential to protect critical habitats. Goats have now been seen across all of northern Isabela, but their density remains very low on Volcan Wolf and Cerro Ecuador. On Volcan Darwin, just north of Volcan Alcedo, their density has reached a level where impacts on the vegetation were noticeable prior to the 1997-98 El Niño. However, the ecological diversity of habitats occupied by tortoises on these volcanoes, the poor knowledge of their distribution and status, and the logistical problems of working in these topographically complex regions warrant special efforts involving both research and management teams to document, assess, and address problems before irreversible damage occurs. Access to geographic positioning technology (GPS) — a relatively new tool — will be important in facilitating research and management efforts on the large volcanoes of Alcedo, Darwin, and Wolf, and funding must be sought for sufficient equipment to support adequate numbers of Galápagos National Park Service personnel and biologists of the Charles Darwin Research Station.

Historically problematic tortoise populations

The status of tortoises on the islands of Fernandina and Pinta warrants special consideration. Tortoises have not been sighted on Fernandina since Rollo Beck removed a single adult male for scientific purposes in 1906. This island is one of the most active volcanoes in the Galápagos Archipelago, making it tempting to conclude that tortoises may have been extirpated or reduced to evolutionarily precarious numbers by volcanic activity (MACFARLAND *et al.*, 1974a). However, many disjunct habitat patches exist on this large and complex volcanic island; exploratory work has been limited; and occasional reports of large scats that could be those of very large land iguanas, or tortoises, have provided some basis for further work to determine if a remnant tortoise population exists. Additional surveys may be justified before declaring the tortoises of Fernandina definitely extinct.

The future survival of the tortoises of Pinta Island is also problematic, with only a single living male known. The Pinta tortoise population fell victim to periodic hunting by fishermen who apparently tired of a diet restricted to fish during long excursions to the northern waters of Galápagos; and also to competition from a goat population originally introduced in the late 1950s. Goats have now been largely removed from Pinta through intensive control campaigns over a period of more than two decades, but despite thousands of man-days on the island, only one male tortoise (popularly known as “Lonesome George”) has been discovered. However, due to the success of the major hunting campaigns in the 1971-1982 period, goats were reduced to extremely small numbers, trips to the island have been much less frequent, vegetative recovery has been significant, and a re-survey of the island is necessary. Juvenile tortoises are extremely difficult to find, and any juveniles that might have been present, but overlooked two decades ago, are likely to have survived. They, or their sign, would be more detectable at present than before due their subsequent growth to a larger size.

While the probability of additional tortoises surviving on Pinta is low, the consequences of extinction of the Pinta tortoise are sufficiently serious in terms of the conservation of biodiversity and ecosystem values to justify this conservation effort. Recent molecular genetic studies of tortoises from all known populations in Galápagos, and of Galápagos tortoises of unknown origin in zoos, furnishes another, admittedly small, chance of identifying living tortoises from Pinta that may have gone undetected. The single living Pinta male is held at the Tortoise Conservation Centre on Santa Cruz Island and the discovery of any female of the Pinta population would provide an additional opportunity to use the captive breeding and rearing technology for recovery of this population. By using experienced tortoise searchers, and potentially even trained dogs, every effort should be made to investigate the possible existence of additional individuals as potential mates for the single known

male. Only after this possibility is eliminated should other more extreme conservation strategies be considered, such as cloning or cross-breeding.

Marine iguanas

The conservation of marine iguanas presents a similar array of problems, needs, and approaches as does the programme for tortoises. Significant diversity is known to exist, with major differences in size, coloration, and seasonality among populations on various islands. Genetic studies have recently attempted to clarify relationships among populations and with evolutionary outgroups (RASSMAN *et al.*, 1997, SITES *et al.*, 1996). Populations of marine iguanas show greater variation in DNA from mitochondria than from the cell nucleus, suggesting differential migratory patterns of males and females. While predictable patterns of size exist among populations apparently related to energetic constraints (WIKELSKI *et al.*, 1997), the molecular analyses support the conclusion that marine iguanas represent a single variable species. Apart from sea turtles, marine iguanas have the greatest potential of natural inter-island dispersal of any native reptile and their low levels of variability apparently reflect a fair amount of gene flow among populations (RASSMAN *et al.*, 1997).

In the late 1970s alarming levels of predation on adult marine iguanas by feral dogs (KRUUK and SNELL, 1981) combined with a similar situation in land iguanas, prompted a successful campaign greatly reducing the numbers and impacts of feral dogs (SNELL *et al.*, 1984). Some populations currently lack juveniles, potential evidence of poor recruitment likely to be due to predation on the young iguanas by cats. (CAYOT *et al.*, 1994a; YACELGA, 1995). Many populations are free of predation from introduced mammals, but may still oscillate greatly due to variations in ocean conditions during and between El Niño phenomena (LAURIE, 1990; LAURIE and BROWN, 1990).

The combination of large natural fluctuations in population size and relatively high ability to disperse among islands (at least compared to other reptiles within Galápagos) indicate that Galápagos marine iguanas could have a meta-population structure. In that situation the populations of individual islands would be isolated for evolutionarily short periods of time and experience exchanges of individuals more frequently than more terrestrial species. It would be likely that small populations would frequently go extinct and perhaps be recolonized by dispersal from nearby members of the meta-population. Under continued natural conditions such a dynamic system would be persistent within the archipelago even though a particular island might lack marine iguanas at various times in its history.

However, with the introduction into the system of new predators, like the dogs and cats mentioned above, the effects of the natural population declines could be amplified. Within Galápagos, introduced mammalian predators

are more common on the larger islands and impacts are greatest there. It is likely that those are the primary islands which would serve as source populations for recolonization and recuperation after a severe natural decline. However, if introduced predators lower those populations then the meta-population itself might lose its dynamic ability to respond and wide-ranging extinction could become a problem.

Land iguanas

The land iguanas of Galápagos are more diverse than reflected by current taxonomic treatments which recognize two nominate species. Morphological comparisons among all extant populations identify three distinct populations or groups, two of which represent named species and a third distinct evolutionary lineage that may warrant specific status (SNELL *et al.*, 1984). Current biochemical studies of molecular morphology may provide tests of hypotheses drawn from macromorphological analyses upon their completion (Rassman pers. com.). Of the currently recognized species, *Conolophus pallidus* is limited to a single island (Santa Fé) while *C. subcristatus* naturally occurred on Fernandina, Isabela, Santa Cruz, Plaza Sur, Baltra, and Santiago within the last 170 years.

Land iguanas have been extirpated from Santiago, Baltra, and vast areas of southern Isabela. Feral dogs have caused much of the decimation, but feral pigs and humans have played significant roles as well (SNELL *et al.*, 1984). Because the damaging populations of feral dogs have largely been reduced, the most significant threat to current land iguana populations appears to be feral cats that prey upon hatchlings and very young juveniles.

Populations of land iguanas can be more quickly decimated by introduced predators than populations of tortoises simply because adult iguanas are susceptible as well as juveniles. Thus, some of the population crashes observed have been alarmingly rapid. Between 1975 and 1977 feral dogs extirpated all but a few iguanas from northwestern Santa Cruz and the area around Bahia Cartago, Isabela. In the face of such rapidly developing threats, the primary conservation action was immediate removal and protection of the adults. Following protection of the adults in captivity at the CDRS, research led to successful reproduction and rearing in captivity between 1977 and 1981 (SNELL, 1985; CAYOT *et al.*, 1994).

The land iguana population from the island of Baltra has a different history. Iguanas had vanished from Baltra by 1954 after the island suffered the construction and operation of an American airbase during the Second World War. Some combination of habitat destruction, human predation, and feral animals proved fatal to the iguana population (WORAM, 1991). Luckily, a few adults transferred to a nearby island from Baltra in the 1930s remained, and served as the basis for

the captive rearing programme of the 1980s and 1990s (BANNING, 1933, SNELL *et al.*, 1984, CAYOT and MENOSCAL, 1992).

Like Galápagos tortoises, some populations of land iguanas have responded well to restoration programmes of the CDRS and the GNPS. Since the first formal repatriations to Bahía Cartago, Isabela Island, in 1982 (REYNOLDS, 1983), a total of 737 land iguanas have been repatriated (390 to Bahía Cartago, Isabela; 257 to Cerro Dragon, Isabela; and 94 to Baltra). Survival of the repatriates to adult size exceeds an average of 40% for these three populations. Reproduction by repatriated individuals occurs at all three sites.

In addition to further control of feral mammals, future activities for the conservation of land iguanas will include continuing the restoration programmes, investigating the magnitude of impacts caused by cats, especially on northern Isabela, and evaluating the potential for a restoration programme on southern Isabela where only a few scattered populations remain.

Other reptiles of Galápagos

Lava lizards, snakes, and geckos are less famous residents of Galápagos than giant tortoises and the iguanas, and at least geckos and lava lizards may be more resilient. We know of no extirpated populations of either lava lizards or geckos. However, both groups have shown behavioural shifts in response to various introduced vertebrates (STONE *et al.*, 1994; OLMEDA and CAYOT, 1994) and some of their populations on smaller islands may be threatened.

Snakes are the rarest reptiles of Galápagos on inhabited islands, but are relatively common on others where they occur. Predation by cats is the most likely cause of their decline, but rats may also contribute. If we are unable to control introduced populations of cats and rats in the near future, it may become necessary to establish programmes for the conservation of snakes, at least on Santa Cruz. It is probably too late for Floreana Island, where they appear to be extinct (GREENE and REYNOLDS, in prep.).

There are two other species of reptiles naturally occurring in the islands. Yellow-bellied sea snakes are a pelagic species observed in low numbers every few years. Their occurrence may vary with water temperatures (REYNOLDS and PICKWELL, 1984) and probably has little to do with human activity within the archipelago. Green sea turtles are numerous, and nest in varying numbers on the beaches of almost every island. Fortunately, green turtles have not been popular direct targets of human predation to date, although recent increases in fishing activity within the Galápagos have led to increased numbers of carapaces found around fishing camps. Sea turtle nests are destroyed and most eggs are eaten by feral pigs on several islands, lending yet more support to the view that feral pigs must be controlled as soon as is possible.

Common elements for reptile conservation

The overall objective of reptile conservation programmes in Galápagos has been to preserve diversity. Thus, each population is considered a separate evolutionary unit and a suitable focus of preservation. In each case, comprehensive ecological, population, and reproductive research was needed to guide management efforts. Control or elimination of threats was attempted concurrent with efforts to increase population sizes and return progeny to natural conditions. Understanding dietary, reproductive, and thermal needs, normal growth and maturation patterns, and habitat use by native reptiles at individual sites was essential to the enhancement of conservation programmes and important for their success (SNELL 1985, CAYOT *et al.*, 1994).

Reptile conservation successes in Galápagos have been well documented, and these efforts stand as examples for programmes in other parts of the world. In most cases, the level of funding was modest, the approaches were pragmatic, and the technologies used were as simple as possible. Considerable benefits have been conferred on these programmes by conducting them all within the Galápagos Islands, taking advantage of natural climates, native food species, and the isolation from foreign diseases, etc. The provision of adequate funding, the continued involvement of adequately trained and dedicated biologists in research and management efforts, and continued diligent analysis of problems and potential solutions are all critical to the future progress of these important activities.

Acknowledgments

These programmes have extended over thirty years. The list of people crucial to their success is immense, and impossible to detail here. However, without the personnel, consultants, and volunteers associated with the GNPS and the CDRS, several populations now roaming free would be extinct. Likewise, it is impossible to give adequate appreciation to all the private individuals, conservation and research funding agencies, and government bodies which have contributed the funds necessary to carry out the programmes briefly described here, but that support has been and continues to be vital for the preservation of Galápagos reptiles. We thank Robert Reynolds for providing comments on the manuscript.

References

- BANNING, G. H., 1933. Hancock expedition to the Galápagos Islands, 1933. General Report. *Bulletin Zoological Society of San Diego*, 10: 1-30.
- CAYOT, L. J. & R. MENOSCAL, 1992. Land iguanas return to Baltra. *Noticias de Galápagos*, 51: 11-13.
- CAYOT, L. J., K. RASSMANN, & F. TRILLMICH, 1994. Are marine iguanas endangered on islands with introduced predators? *Noticias de Galápagos*, 53: 13-15.
- CAYOT, L. J., H. L. SNELL, W. LLERENA, & H. M. SNELL, 1994. Conservation biology of Galápagos reptiles: Twenty-five years

- of successful research and management. In: J. B. MURPHY, K. ADLER, & J. T. COLLINS (Editors), *Captive Management and Conservation of Amphibians and Reptiles*. Society for the Study of Amphibians and Reptiles, Ithaca (New York). Contributions to Herpetology, Volume 11, pp. 297-305.
- CAYOT, L. J. & G. E. MORILLO, 1997. Rearing and repatriation of Galápagos tortoises: *Geochelone nigra hoodensis*, a case study. In: P. VAN ABBEMA, J. (Editor). *Proceedings: Conservation and Management of Tortoises and Turtles - An International Conference*. 11-16 July 1993, State Univ. of New York, pp. 178-183.
- DE SOLA, C. R., 1930. The liebespiel of *Testudo vandenburghi*, a new name for the Mid-Albemarle Island Galápagos Tortoise. *Copeia*, 1930: 79-80.
- FRITTS, T. H., 1978. Española tortoise returns. *Noticias de Galápagos*, 28: 17-18.
- FRITTS, T. H., 1984. Evolutionary divergence of giant tortoises in Galápagos. In: R. J. BERRY (Editor), *Evolution in the Galápagos Islands*. Academic Press, London, UK, pp. 165-176.
- KRUUK, H. & H. L. SNELL, 1981. Prey selection by feral dogs from a population of marine Iguanas (*Amblyrhynchus cristatus*). *Journal of Applied Ecology*, 18: 197-204.
- LAURIE, W. A., 1990. Population biology of marine iguanas (*Amblyrhynchus cristatus*). I. Changes in fecundity related to a population crash. *Journal of Animal Ecology*, 59 (2): 515-528.
- LAURIE, W. A., & D. BROWN, 1990. Population biology of marine iguanas (*Amblyrhynchus cristatus*). II. Changes in annual survival rates and the effects of size, sex, age and fecundity in a population crash. *Journal of Animal Ecology*, 59 (2): 529-544.
- MACFARLAND, C., G. J. VILLA, & B. TORO, 1974a. The Galápagos giant tortoises (*Geochelone elephantopus*) I. Status of the surviving populations. *Biological Conservation*, 6 (2): 118-133.
- MACFARLAND, C., G. J. VILLA, & B. TORO, 1974b. The Galápagos giant tortoises (*Geochelone elephantopus*) II. Conservation Methods. *Biological Conservation*, 6 (2): 198-212.
- OLMEDO, J. and L. J. CAYOT, 1994. Introduced geckos in the towns of Santa Cruz, San Cristóbal, and Isabela. *Noticias de Galápagos*, 53: 7-13.
- RASSMANN, K., D. TAUTZ, F. TRILLMICH, & C. GLIDDON, 1997. The microevolution of the Galápagos marine iguana *Amblyrhynchus cristatus* assessed by nuclear and mitochondrial genetic analyses. *Molecular Ecology*, 6: 437-452.
- REYNOLDS, R. P., 1983. Experimental repatriation of captive-reared land iguanas (*Conolophus subcristatus*) at Cartago Bay, Isabela. *Ambio*, 12 (3-4): 189.
- REYNOLDS, R. P. & G. V. PICKWELL, 1984. Records of the yellow-bellied sea snake, *Pelamis platurus*, from the Galápagos Islands. *Copeia*, 1984: 786-789.
- SITES, J. W., S. K. DAVIS, T. GUERRA, J. B. IVERSON, & H. L. SNELL, 1996. Character congruence and phylogenetic signal in molecular and morphological data sets: A case-study in the living iguanas (Squamata; Iguanidae). *Molecular Biology and Evolution*, 13: 1087-1105.
- SNELL, H. L., 1985. Behavioural and morphological adaptations by Galápagos land iguanas (*Conolophus subcristatus*) to water and energy requirements of eggs and neonates. *American Zoologist*, 25: 1009-1018.
- SNELL, H. L., H. M. SNELL, & C. R. TRACY, 1984. Variation among populations of Galápagos land iguanas *Conolophus* contrasts of phylogeny and ecology. *Biological Journal, Linnean Society*, 21 (1-2): 185-208.
- STONE, P. A., H. L. SNELL, & H. M. SNELL, 1994. Behavioural diversity as biological diversity: introduced cats and lava lizard wariness. *Conservation Biology*, 8: 569-573.
- TAPIA A., W., 1997. Aesthete actual y distribución estacional de las tortugas gigantes (*Geochelone elephantopus spp.*) de Cinco Cerros, Volcan Cerro Azul, Isla Isabela, Galápagos, Ecuador. Tesis de Grado, Universidad Tecnico del Norte, Ibarra, Ecuador.
- TOWNSEND, C. H., 1928. The Galápagos Islands revisited. *Bulletin New York Zoological Society*, 31(5): 148-169.
- WIKELSKI, M., V. CARRILLO, & F. TRILLMICH, 1997. Energy limits to body-size in a grazing reptile; the Galápagos marine iguana. *Ecology*, 78: 2204-2217.
- WORAM, J. M., 1991. Who killed the iguanas? *Noticias de Galápagos*, 50:2-17.
- YACELGA, M., 1995. Metodologías para mejorar la sobrevivencia de iguanas marinas en poblaciones amenazadas. Tesis de grado, Universidad Central de Ecuador, Quito, Ecuador.

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