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The Galápagos Giant Tortoises (*Geochelone elephantopus*) Part I: Status of the Surviving Populations*

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ABSTRACT

Eleven of the original 15 *races of Galápagos tortoises are known to survive. The populations of three of these may be self-replacing. The other eight are threatened with extinction, each by one or more of the following:* (1) *greatly decreased population size,* (2) *predation on nests and/or young by introduced pigs, dogs, cats, or black rats, and* (3) *competition for food resources with feral populations of goats or donkeys. Human exploitation of the tortoise populations has become relatively unimportant in the past few years for a number of reasons, including more widespread acceptance of protective laws and the increasing activity of the Servicio del Parque Nacional Galápagos and the Charles Darwin Research Station. Data on population sizes and sex structures, reproductive potential, and natural mortality rates suggest that all but two of the endangered populations could remain stable or even increase in size if the effects of introduced mammals were eliminated or greatly lessened.*

INTRODUCTION

Giant tortoises are the largest ecto-thermal terrestrial herbivores still in existence, making them extremely interesting for investigations of population dynamics, bioenergetics, and physiological and behavioural thermoregulation.

Unfortunately, they survive today only on the small atoll of Aldabra in the western Indian Ocean and in the Galápagos archipelago; and, although the Aldabra species (*Geochelone gigantea*) is not endangered (Gaymer, 1968; Grubb, 1971), most races of the Galápagos tortoise (*Geochelone elephantopus*) are threatened with extinction. The giant tortoises demonstrate in many ways the numerous actual and potential threats to the Galápagos ecosystem.

However, the seriousness of the situation in the Galápagos has been somewhat overstated. During the first six decades of this century, reports from scientific expeditions indicated that at least several, or perhaps most, of the tortoise races were extinct, and that most of the surviving populations were imminently in danger of the same fate (Van Denburgh, 1914; Townsend, 1925, 1931; Street, 1961(*a*) and (*b*); Hendrickson, 1965; Thornton, 1971). However, these reports were based mainly on visits to the smaller islands and only the coastal areas of the larger ones. Also, for several decades, it was widely accepted that the survival of the tortoises depended upon the establishment of breeding colonies outside of the Galápagos, and several expeditions in the 1920s and 1930s justified the collection of large numbers of tortoises for this purpose (Townsend, 1931; Meredith, 1939); these notions are still somewhat widespread (Street, 1961(*a*) and (*b*); Shaw, 1967), despite the total failure of most of these colonies to breed.

Field research over the past ten years by the Charles Darwin Research Station (CDRS) and the Servicio del Parque Nacional Galápagos (SPNG) and the senior author's investigations from August, 1969 to November, 1971 have significantly altered this bleak view of the status and survival potential of the tortoise populations. Extensive surveys, especially in the islands' interior regions, have resulted in the rediscovery of several races thought to be extinct, and the population sizes of most surviving races were found to be much larger than indicated by previous estimates (Van Denburgh, 1914; Bowman, 1960; Eibl-Eibesfeldt, 1959; Snow, 1964; Honegger, 1968; Thornton, 1971). This paper (Part I) briefly summarizes previous information and reports recent findings on (1) the sizes, sex and size-class structures, reproductive potential and mortality rates of the tortoise populations, and (2) the current threats to the tortoises posed by introduced mammals and human exploitation. Part II will evaluate the conservation methods currently being applied to the tortoise populations.

ORIGINAL DISTRIBUTION AND TAXONOMY

In the only major taxonomic treatment of the group, Van Denburgh (1914) assigned binomials to 13 of the

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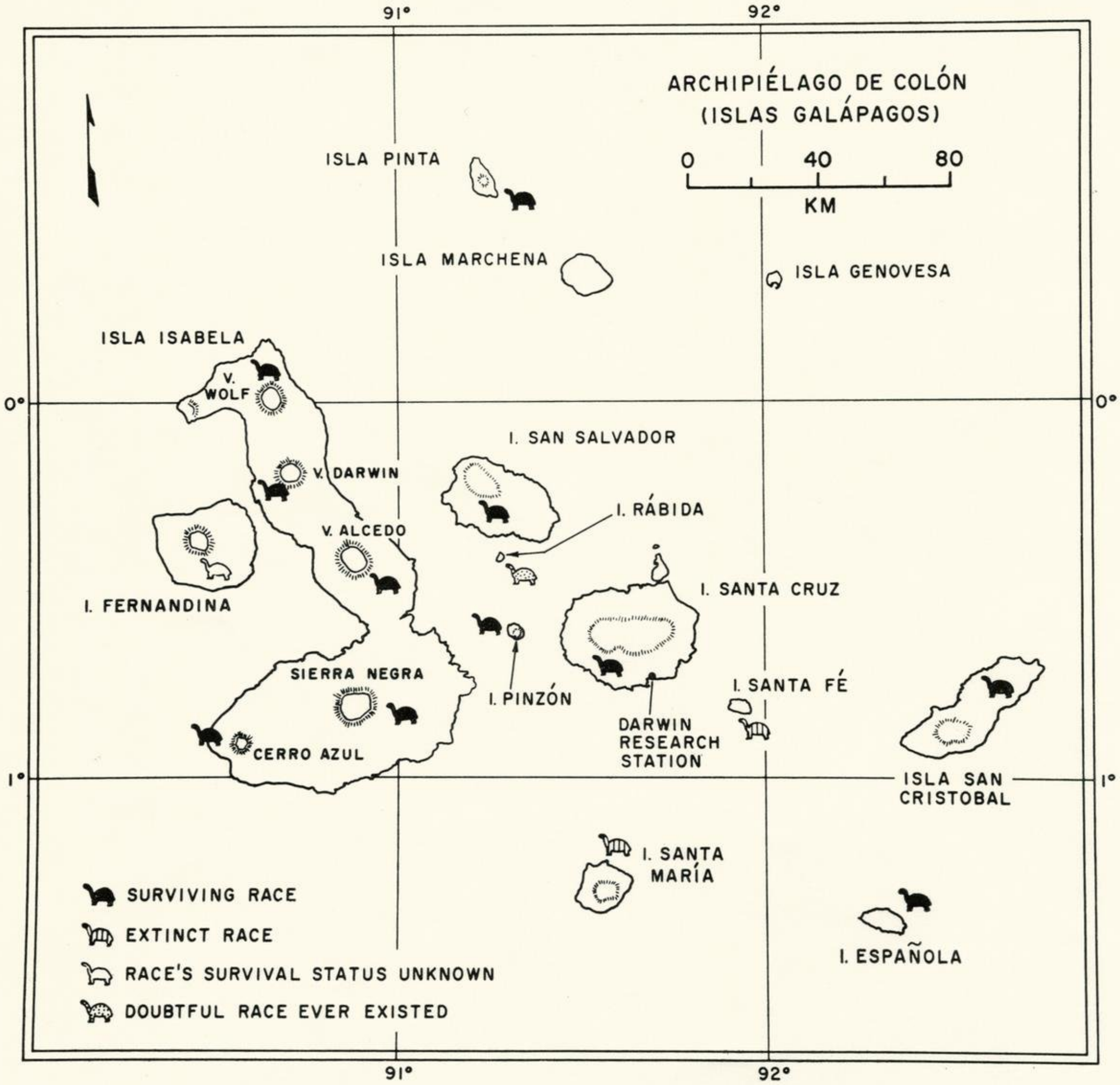

Fig. 1. *Distribution of the originally recognized* 15 *races of* G. elephantopus.

taxa, leaving those of Volcán Alcedo (Isabela) and Santa Fe unnamed because of insufficient material.* Ten of the 15 taxa were from separate islands, and one occurred on each of the five major volcanos of Isabela; eleven of these are known definitely to be surviving (Fig. 1, Table I).

Most recent interpretations regard all the taxa as subspecies of the single species *G. elephantopus* Harlan 1827 (Hendrickson, 1966). Whether they are considered races, subspecies, or even species is a moot point at this time. The taxa differ in shape, colour and thickness of carapace, maximum size attained, and lengths of neck and legs. But variation within any taxon is great and the differences among taxa are, at best, statistical (Van Denburgh, 1914). Assigning an individual specimen to a definite taxon is extremely difficult, although the range of possibilities can often be reduced to three or four taxa. All are geographically isolated populations on separate islands or volcanos except for *G. e. vicina* and *G. e. güntheri* on southern Isabela. Limited evidence from zoos and the captive colonies at the CDRS indicates that no ethological isolating mechanisms exist among the taxa, but that interbreeding results in higher infertility of the eggs than normal. Because of the geographic barriers, the probability of natural interbreeding is minute. Since the taxa have evolved differences, and certainly have been separated for a long time period, we feel they should be regarded as unique and preserved individually. We use the term 'race' for each taxon, primarily because no marked structural differences exist among them.

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* For English equivalents of official Spanish names for islands see Wiggins & Porter (1971).

TABLE I

Co-distribution of Tortoise Populations and Wild Populations of Introduced Mammals

Race	*Location*	*Pigs*	*Dogs*	*Cats*	*Black rats*	*Goats*	*Donkeys*	*Cattle*
hoodensis	Española					×		
abingdoni	Pinta					×		
ephippium	Pinzón				×			
chathamensis	San Cristóbal							
	(northeastern part)		×	×		×*	×	
darwini	San Salvador	×			×	×	×	
vicina	Cerro Azul							
	south and SE	×	×	×	×			×
	east, west and NW		×	×	×			×
güntheri	Sierra Negra							
	east			×	×	×		
	south	×	×	×	×	×	×	×
	west			×	×			
vandenburghi	V. Alcedo			×	×		×	
microphyes	V. Darwin			×	×			
becki	V. Wolf			×	×			
porteri	Santa Cruz							
	east	×		×	×	×	×	×
	southwest	×		×	×	×	×	×*

* Extremely small population.

The following points sometimes cause confusion and will facilitate the remaining discussion:

(a) the subspecific name *vandenburghi* is used commonly and accepted for the population of Volcán Alcedo, Isabela. We continue with this usage, but note that, based on his described location, DeSola (1930) mistakenly applied the name to specimens of *G. e. güntheri* from Sierra Negra, Isabela.

(b) perhaps *vicina* (Cerro Azul, Isabela) and *güntheri* will eventually be combined. Van Denburgh (1914) was unable to distinguish them clearly. Until 1925 no known physical barriers separated the two volcanos. An extensive lava flow in that year partially separated them (J. Gordillo, 1971, pers. comm.), but a large area of the southern coast of Isabela still remains open as a potential pathway for interchange (Fig. 6).

(c) The single specimen of *G. e. wallacei* found on Rábida in 1906 (Van Denburgh, 1914) was probably an artificial introduction, and there are no substantiated grounds for considering that a native race ever occurred there (Fig. 1; also, *see* Snow, 1964 for detailed argument).

(d) The race of Fernandina (*G. e. phantastica*) probably existed at one time (Fig. 1). A single male was collected in 1906 (Van Denburgh, 1914), and droppings of one were found in 1964 (Hendrickson, 1965). Several searches in the past few years of areas considered to be prime potential tortoise habitat have not revealed further signs. A small population may still survive, isolated in one of the few small vegetated areas which have not been examined. Whatever the status of this race, its fate has been determined by natural causes (probably volcanism), because Man has never exploited Fernandina and no introduced mammals occur there.

HISTORICAL BACKGROUND

Reports from early mariners indicate that tortoises were widely distributed and extremely abundant on the various islands during the 1600s to early 1800s, even in the arid lowlands (*e.g.* Porter, 1815; summary in Van Denburgh, 1914). Additionally, their immobility, lack of defence, and capability of surviving for long periods without food or water made them easily obtainable and excellent ship's provender. As a result, the tortoise populations were severely decimated by seamen for two centuries, first by buccaneers in the late 1600s and 1700s, followed by whalers, fur sealers, merchantmen, and the crews of naval vessels from the late 1700s to the late 1900s (Townsend, 1925; Slevin, 1959). No exact calculation is possible, but one or two hundred thousand tortoises were probably removed by mariners during two centuries of plundering.

By the last two decades of the 19th century, the tortoise populations had been so reduced in the more accessible areas, that it was no longer possible to plan on provisioning ships with them. However, new threats had developed: (1) major settlements began on Santa María, southwestern San Cristóbal, and eastern Sierra Negra, in 1832, 1869, and 1895 respectively (Slevin, 1959; J. Gordillo, 1971, pers. comm.); (2) one or more of a variety of exotic mammals had been introduced to most of the areas inhabited by tortoises. Settlers slaughtered tortoises for meat and fat and modified huge areas of natural habitat by burning, fencing, and conversion of forest to pasture land. Probably most destructive of all was the flourishing business of exporting tortoise oil to continental Ecuador (Beck, 1903). Introduced mammals preyed on tortoise nests and young and competed for food resources.

The cumulative effects of these depredations were demonstrated by the results of a full year's collecting of tortoises in 1905–1906 (Van Denburgh, 1914): (1) the populations of Santa María and Santa Fe were extinct; they were probably eliminated sometime in the last half of the 19th century; (2) those of the small islands of Española and Pinta had been greatly reduced; (3) tortoises had been well cleaned out of the arid zones inland from accessible coastal landing sites on San Salvador, Pinzón, Santa Cruz, San Cristóbal, and the five major volcanos on Isabela; (4) most tortoises had been eliminated over wide areas surrounding the inland settlements on eastern Sierra Negra and southwestern San Cristóbal.

Introduced mammals and settlers continued to provide the main threats to the tortoises from the early 1900s to the mid-1960s. Human exploitation spread far beyond the three settled areas. As the local fishing industry grew, crews began regularly to visit numerous coastal landing spots on most of the islands, sometimes going inland for several kilometres to obtain tortoises and firewood. They also introduced goats in many places to provide an additional source of meat. Santa Cruz was colonized in the mid-1920s, followed by the establishment of feral populations of a variety of introduced mammals, much clearing, burning, and fencing of land in the interior, and extensive slaughtering of tortoises for local consumption; also, in the 1930s at least one to two thousand tortoises were killed on the island by oil hunters (A. Rambech, pers. comm.). Three temporary settlements caused considerable damage (Fig. 6): (1) from about 1924–1930 a salt mine existed at James Bay, San Salvador, and the workers conducted an extensive tortoise oil business in the western and southwestern interior of the island (A. Rambech, pers. comm.); (2) tortoises were almost completely eliminated from an area of approximately 120 km^2 in the southeastern, southern, and western parts of Sierra Negra by oil hunters from a prison colony located in the western interior of the volcano from 1946–1959; these operations even extended to eastern Cerro Azul; (3) tortoises were eliminated from an area of approximately 5 km^2 inland from Iguana Cove (southwestern Cerro Azul) by employees of cattle companies which operated from 1958–1960 and 1968–69. The latter two areas had been largely unaffected by previous human exploitation and reportedly contained huge tortoise populations (J. Gordillo, pers. comm.).

Overzealous and rather reckless collecting also took a heavy toll. The major expeditions from the 1880s to 1930 removed 661 tortoises from the Galápagos

TABLE II

Tortoises Removed from the Galápagos by Major Expeditions, 1880s–1930

Expedition	*Date*	*No. tortoises taken*	*Authority*
Albatross	1888 and 1891	15	Slevin, 1959
G. Baur	1891	21	Van Denburgh, 1914
Webster-Harris (for W. Rothschild)	1897	60	Slevin, 1959
Stanford Univ.	1898	21	Heller, 1903
Capt. Noyes	1900	23	Van Denburgh, 1914
R. Beck (for W. Rothschild)	1901	12	Van Denburgh, 1914
R. Beck (for W. Rothschild)	1901–1902	50	Van Denburgh, 1914
Calif. Acad. Sciences	1905–1906	256	Van Denburgh, 1914
Harrison-Williams	1923	1	Beebe, 1923
W. K. Vanderbilt	1928	5	Pinchot, 1930
New York Zoological Society	1928	180	Townsend, 1931
G. Pinchot	1929	7	Pinchot, 1930
Cornelius Crane Pacific Expedition	1929	2	Shurcliff, 1930
V. Astor	1930	8	Townsend, 1931

(Table II). Although this number was small relative to the tens of thousands of tortoises killed in other ways, the collections occurred at a time when the populations had already been badly decimated and were facing the threats of introduced predators and competitors. Paradoxically, the expedition accounts again and again bemoan the fact that most of the races were extinct, or nearly so, but then happily conclude that some of the last survivors had been collected and preserved.

PRESENT THREATS

Introduced Mammals

Exotic predators and competitors are now the greatest threat to the tortoise populations. It is difficult to quantify the population sizes of these species, but their distributions are now well known; one or more occurs in every area inhabited by tortoises (Table I). In most cases the populations of exotics appear to be very large; *e.g.*, 30,000–40,000 goats estimated to be on Pinta in November, 1971; 4,000–8,000 pigs estimated to be on San Salvador in August–September, 1970.

Those exotics which cause most of the damage and the stages of the life-cycle which they affect are known for most of the tortoise populations. The information given in Table III is based on observations of destroyed nests, remains of killed young and scats of the exotics (predators), and destruction of vegetation (competitors). Predators cause the most serious damage to most of the populations. Wherever present, pigs destroy the vast majority of nests (Fig. 2), and also kill large numbers of young tortoises, up to at least 35–40 cm in curved carapace length (*see* Van Denburgh, 1914, for definition) or approximately 4–6 years in age (Fig. 3). Dogs prey extensively on young tortoises, the largest recorded kill measuring 55 cm in curved carapace length or approximately 10–15 years old (September, 1971, Cerro Azul; Fig. 4). Dogs also destroy nests in some areas. Cats and black rats eat hatchlings, and probably kill young up to the age of 1–2 years (Fig. 5); neither species has been found to destroy nests.

It is not easy to demonstrate the direct effects of feral browsers and grazers on the tortoise populations. During most years the less elevated islands and the arid zones of the more elevated ones receive very little rainfall. Goats, and to some extent donkeys and cattle, devastate the vegetation in these areas (Weber, 1971), and the almost complete absence of food must affect smaller tortoises greatly. The nesting zones are located in these arid, lower areas and young tortoises do not begin migrating to higher elevations where food is more abundant until they are approximately 10–15 years old. Thus, competition probably has been —and is—a severe problem on Pinta, Española, the

TABLE III

Primary Threats to Tortoise Populations and Stages Affected; N = Nests, Y = Young (most severe ones capitalized)

Race	*Introduced mammals*	*Stages affected*
hoodensis	GOATS	*Y*
abingdoni	GOATS	*Y*
ephippium	BLACK RATS	*Y*
chathamensis	DOGS	*N, Y*
	donkeys	*Y*
darwini	PIGS	*N, Y*
	goats	*Y*
vicina		
south and SE	PIGS	*N, Y*
	dogs	*Y*
east, west, and NW	DOGS, CATS	*Y*
güntheri		
east	goats	*Y*
south	PIGS	*N, Y*
	dogs, cats	*Y*
west	cats	*Y*
vandenburghi	?	?
microphyes	?	?
becki	?	?
porteri	PIGS	*N, Y*
	cats, goats	*Y*

Fig. 2. Nest of G. e. porteri *destroyed by feral pig; Santa Cruz, August* 1969.

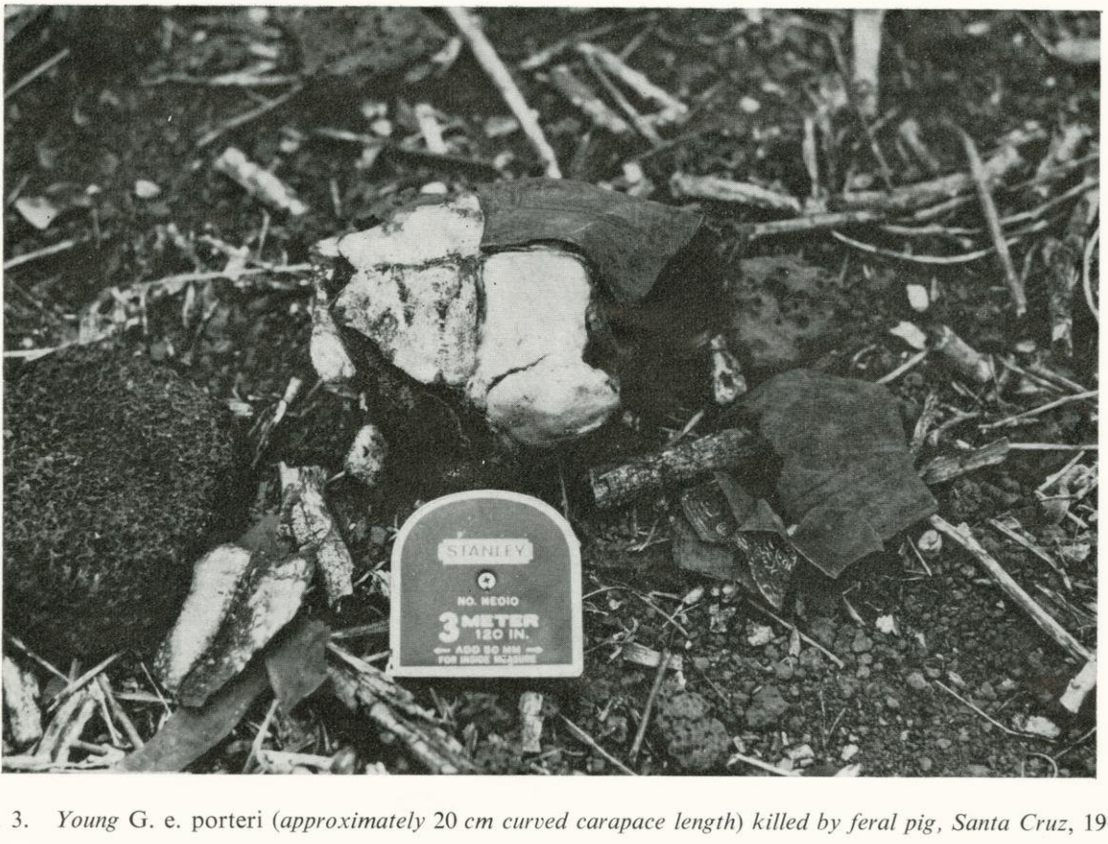

Fig. 3. Young G. e. porteri (*approximately* 20 *cm curved carapace length*) *killed by feral pig, Santa Cruz,* 1969.

Fig. 4. *Young* G. e. vicina (*approximately* 55 *cm curved carapace length*) *killed by feral dogs, Volcán Cerro Azul, Isabela,* 1971.

Fig. 5. *Hatchlings of* G. e. ephippium *killed by introduced black rats in tortoise nesting area, Pinzón,* 1970.

northeastern part of San Cristóbal (where tortoises survive), and in the arid zones of Isabela, Santa Cruz, and San Salvador. Subadults and adults apparently can co-exist with introduced competitors, because they spend most of the year in the higher, more humid areas.

It cannot be assumed that a given exotic species will have the same effect in the different habitats of the various islands and volcanos (Tables I and III). For example, dogs destroy most nests on San Cristóbal but do not even dig into them on Cerro Azul and Sierra Negra. On Pinzón, which is a very dry, relatively low island, black rats are distributed everywhere and kill virtually all hatchlings; however, in other locations we have found no evidence of the same behaviour and the rat populations are concentrated in the humid, densely vegetated, higher areas, but occur in extremely low densities in nesting zones.

In some locations the effects of some exotics has not been determined adequately, *e.g.* especially on volcanos Alcedo, Darwin, and Wolf.

Human Exploitation

There are three major problems at present:

(1) Fishermen occasionally go inland from certain coastal sites on Isabela to slaughter tortoises (Fig. 6). Evidence has been accumulated over the past few years indicating that poachers are taking live young tortoises from the nesting zones located

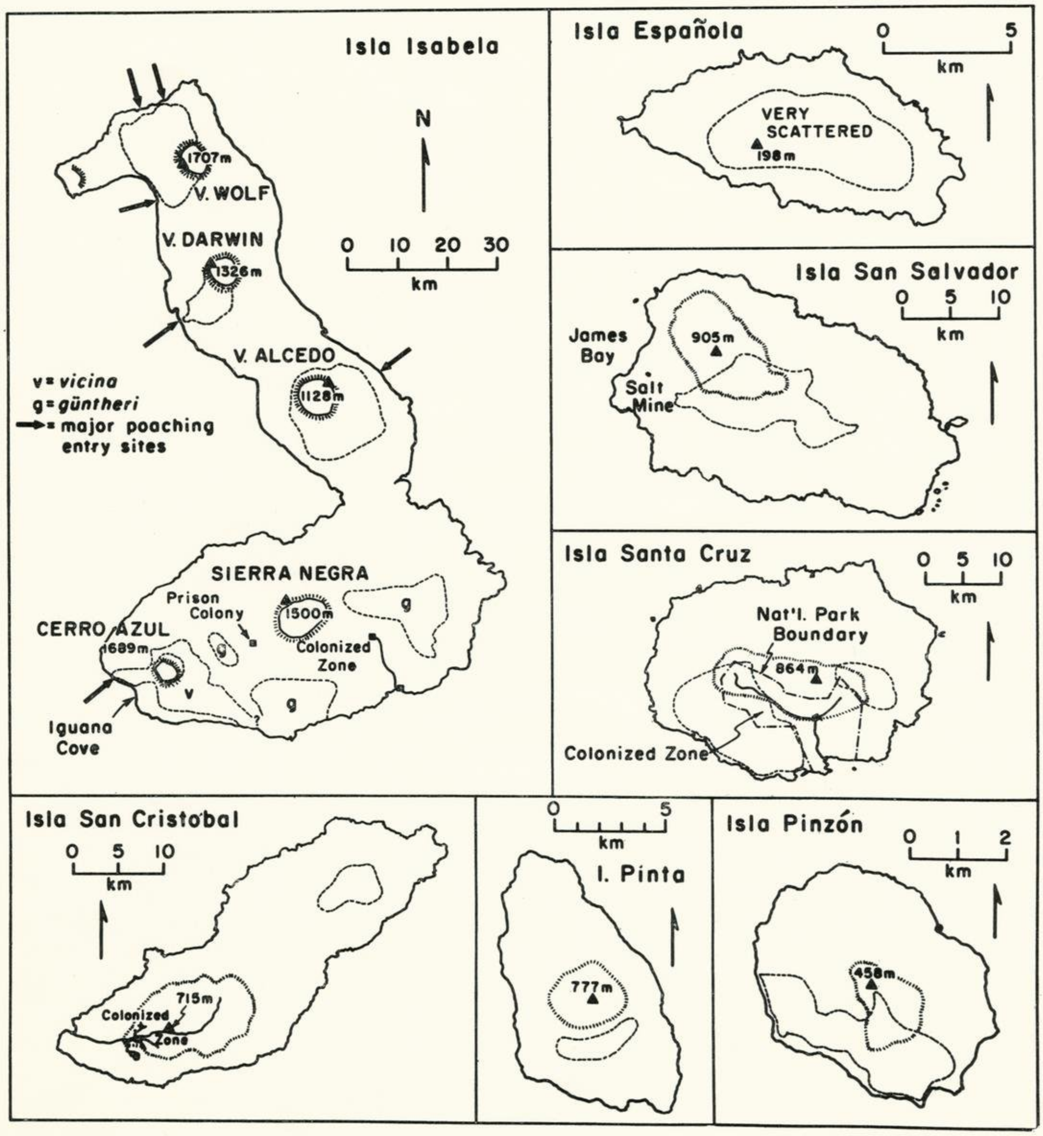

Fig. 6. Distributional limits (dotted lines) on individual islands and volcanos of 11 *surviving races of* G. e. elephantopus*; major locations mentioned in the text are indicated.*

in these same areas (excepting the Cerro Azul locality) in order to supply the international pet and collectors market (MacFarland & Black, 1971).

(2) Settlers still slaughter tortoises in the interior regions of Santa Cruz and eastern Sierra Negra.

(3) The human population is growing rapidly on Santa Cruz and Sierra Negra; for example, it increased from approximately 600 to 2,000 on Santa Cruz between 1964 and 1971. The increase has been due to both a high birth rate and continuing immigration from continental Ecuador. As a result, the demand for clearing uninhabited land continues to increase.

Legislation applicable to these problems exists (MacFarland & Black, 1971). In 1959 all uninhabited areas of the Galápagos were declared as a national park (Ecuador, 1959), thus making it illegal to colonize or modify unsettled areas; the law also expressly prohibited the capture or removal of many animals, including tortoises and their eggs. A 1970 law (Ecuador, 1970) aimed at stopping the international pet trade, makes it illegal to export many animals from Ecuador (including Galápagos tortoises), regardless of whether they are in captivity or from the wild, or on the continent or the Galápagos. A 1971 decree (Ecuador, 1971) establishes very strict guidelines for the conduct of visitors while on National Park land: essentially everything is protected and nothing must be altered or removed. Two actions in other countries are related to these laws: in 1967, the American Association of Zoological Parks and Aquariums and the International Union of Directors of Zoological Gardens agreed to boycott the illegal giant tortoise trade (Honegger, 1968); and it is prohibited to import Galápagos tortoises or their parts or products into the United States under the Endangered Species Conservation Act (United States, 1969).

The critical problems have been detection and apprehension of lawbreakers and enforcement of the laws. These require adequate funds and personnel for widespread and frequent patrolling, and cooperation of political authorities (civilian and/or naval). The SPNG was established in 1968 as part of the Forest Service, and has grown to the present force of a director, two conservation officials and nine wardens; two wardens are stationed semi-permanently on Santa Cruz and two on Sierra Negra. In addition, visits are made frequently throughout the year to most of the islands. There have been several significant accomplishments:

(1) Examination of the remains of slaughtered tortoises at the entry areas on Isabela (Fig. 6) indicate that poaching has decreased greatly in the past few years. For example, on Cerro Azul in an area of 0·9 km^2 (September, 1971), only eight of 60 slaughtered tortoises had been killed in the previous 1–2 years; the remainder appeared to be 2–5 years old. This apparently has been due to more widespread knowledge and acceptance of the law, limited patrolling by the SPNG, a decrease in the number of tortoises available, and the changing economic base of many boat-owners from fishing to chartering for scientists, the CDRS and SPNG, and tourists.

(2) Poaching in the interior regions of south-western Santa Cruz and eastern Sierra Negra has also decreased greatly in the past few years (Table IV), primarily due to almost continuous patrolling and acceptance of the law.

TABLE IV

Slaughtering of G. e. porteri *on Santa Cruz by Settlers in Recent Years*

Year	*No. tortoises found slaughtered*
1965–1968	approx. 15–25 per year
1969	15
1970	6
1971	2

(3) A border separating the colonized zone from National Park land was constructed, clearly marked and mapped, on Santa Cruz in 1969–1970. Similar plans are being prepared for Sierra Negra. Between 1969 and 1971, approximately 15 families moved into National Park land on the north side of Santa Cruz and began clearing, fencing, and burning. This important first test case was resolved favourably in 1972 by a government agency, the Ecuadorian Institute of Agrarian Reform and Colonization: all the settlers moved out of National Park territory. Some were resettled in the islands and the others returned to continental Ecuador. Hopefully, this definite action will help discourage the further flow of colonists to the islands. However, similar problems will certainly continue to arise as the human population increases, unless improvements in land-use patterns and agricultural techniques become widespread in colonized areas and alternative types of economic activity develop. At present the same governmental agency is developing plans for redistribution of land within the colonized zones in order to divide large single-family holdings and accommodate more small farms. It will be of paramount importance to develop local involvement in the rapidly-growing tourist industry in the near future.

The most immediate problem is to stop the poaching of live tortoises on Isabela. The SPNG and CDRS are planning to station two wardens with a boat permanently in the canal between Fernandina and Isabela, from which they can regularly patrol these critical coastal areas. This station and several others will combine conservation surveillance with ecological, meteorological, and geological monitoring (Simkin, Reeder, & MacFarland, 1973; Kramer, 1973).

Initial action in continental Ecuador has been successful: the Forest Service has forced two wild animal export businesses to cease operation, both of which exported many Galápagos tortoises in the past.

TORTOISE POPULATIONS AT PRESENT

Distribution

Except for the three northern volcanos of Isabela, the present distribution of the tortoise populations shows the marked effects of past human exploitation (Fig. 6). They have been nearly, or completely, eliminated from most coastal areas and from much of their range in the interior of several islands, *e.g.* San Cristóbal, Pinta, Española, Pinzón, and San Salvador. On Santa Cruz and Sierra Negra, the populations have been divided into widely-separated portions by settlement.

Size, Sex Structure, and Size Class Structure

It has not been possible to use accurate mark/recapture techniques to determine population sizes because of the large areas involved, the lack of detailed maps where the terrain and vegetation are heterogeneous, and the lack of personnel. However, rough estimates have been calculated on the basis of numerous samples and extensive habitat surveys of all the populations except *G. e. becki* and *G. e. microphyes* (Table V). The latter two populations have been sampled only three times each and the estimates are tentative.

During most of the samples of the definitely endangered populations, *i.e.* excluding only *G. e. becki*, *G. e. microphyes*, and *G. e. vandenburghi*, tortoises of 15–20 cm curved carapace length and larger have been marked individually (notches cut in the marginal scutes). Tortoises of less than 15–20 cm curved carapace length (approximately 0–1–1/2 years old) cannot be permanently marked because the carapace is too fragile; these small-sized tortoises were marked individually with paint or scratches on the scutes. Marking will provide information on population structure and aid in tracing the source of poached animals and detecting inter-island transfers.

Accurate size class structures cannot be determined from the data on all marked tortoises, because, for almost all populations, the marking period covers several years or more. However, analysis of all marked animals (Table V), based on the first encounter of each individual, does demonstrate that most of the definitely endangered populations consist mainly of adults, indicating low rates of population recruitment. Except for *G. e. hoodensis* and *G. e. abingdoni*, the

TABLE V

Population Size Estimates and Breakdown of Marked Tortoises for Races of G. elephantopus

Race	*Marked tortoises*								*Estimated population size*
	Marking period	*Total No.*	*Adults*		*Medium sized*			*Small sized*	
			♂♂	♀♀	♂♂	♀♀	*Non-sexed*		
hoodensis	8/63–6/72	13	2	11	0	0	0	0	20–30
abingdoni	11/71–6/72	1	1	0	0	0	0	0	very small
ephippium	4/63–3/69	100	35	63	1	1	0	0	150–200
chathamensis	12/65–9/71	213	94	63	54	2	0	0	500–700
darwini	6/65–10/71	389	224	97	27	6	27	8	500–700
vicina	4/66–10/71	196	77	85	11	12	9	2	400–600
güntheri									
east	7/66–7/71	178	7	19	4	26	21	101	200–300
south and west	7/66–8/71	41	14	20	3	1	0	3	100–200
vandenburghi	5/65 and 7/68	402	135	117	13	26	39	72	3,000–5,000
microphyes	10/65	65	6	26	2	1	8	22	500–1,000?
becki	—	0	—	—	—	—	—	—	1,000–2,000?
porteri									
southwest	4/62–10/71	1,368	284	245	150	98	161	430	2,000–3,000
east	5/62–11/71	92	17	18	25	9	7	16	50–100

populations apparently consist of adequate numbers of adults of both sexes for successful reproduction in the wild, assuming no predation or competition by exotics.

Size class structures were determined from samples of all individuals of 10 cm curved carapace length and larger which were encountered in each population during periods of one year or less (Fig. 7). Special attention in sampling was given to the nesting zones and surrounding arid areas to which tortoises of the smaller size classes are confined. Hatchlings (6–9 cm curved carapace length) are secretive during the first few months of life and are difficult to detect; they were rarely seen, certainly not adequately sampled, and were excluded from this analysis. The complete absence or very small numbers of tortoises in the medium and smaller size classes demonstrates that replacement is not occurring in many of the populations (Fig. 7; *see* Appendix for explanation of sex and size class criteria and difficulty of ageing tortoises).

The races and various populations can be divided into five groups, based on their status:

(1) *hoodensis* and *abingdoni*—these populations are extremely small. The density of the *hoodensis* population is apparently so low that the animals

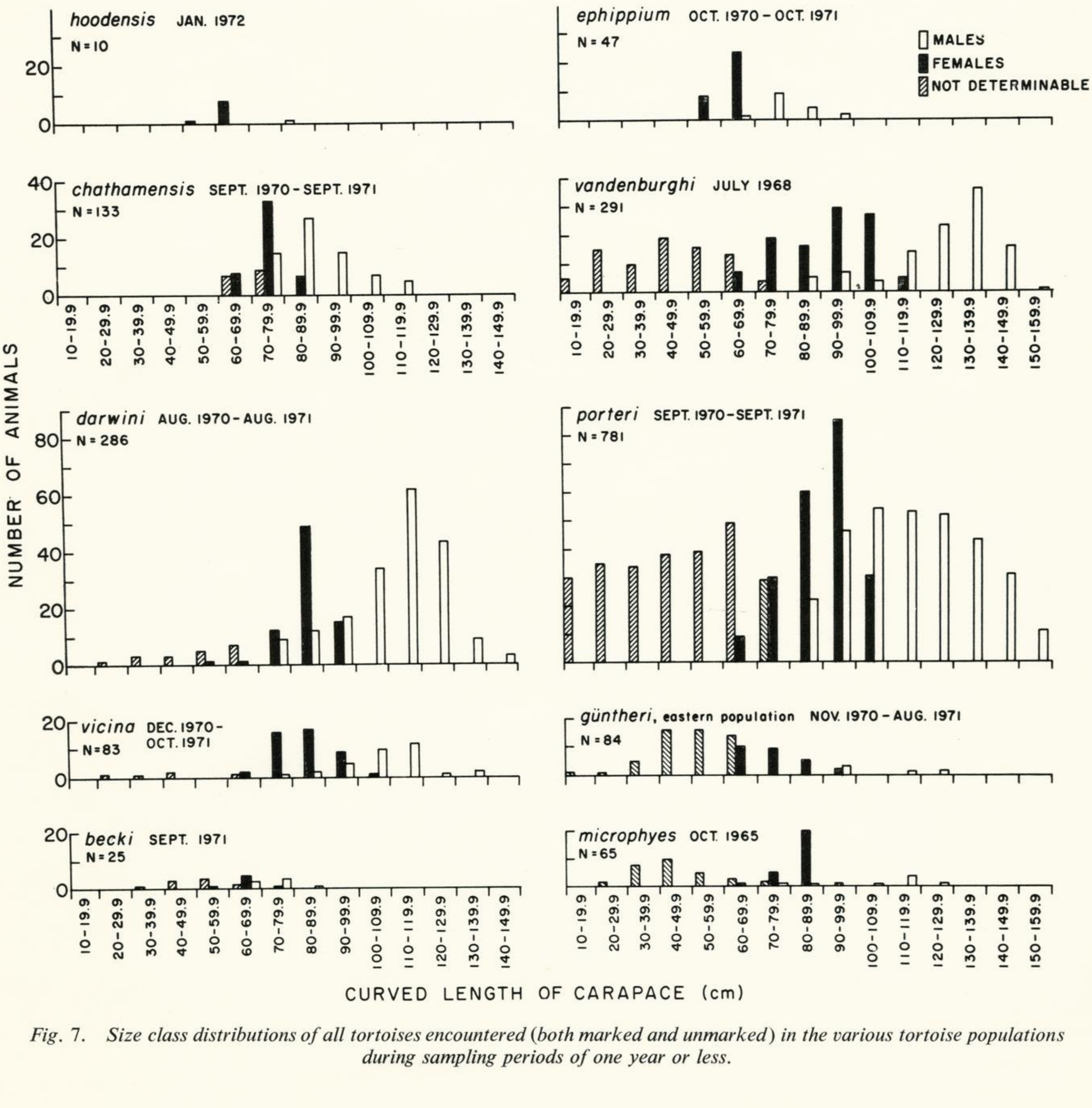

Fig. 7. Size class distributions of all tortoises encountered (both marked and unmarked) in the various tortoise populations during sampling periods of one year or less.

do not encounter one another. All tortoises found were old adults and the females had extensive lichen growth on the upper-rear portion of the carapace, an indication that no recent mating attempts had occurred (Hendrickson & Weber, 1964). The Pinta race was recently rediscovered (November, 1971) after several extensive searches in recent years indicated no signs of living tortoises. Two animals and signs of a few others were found. The status of this race will require further investigation but it is certainly similar to that of *hoodensis*. The vegetation of both islands has been badly damaged by goats (Weber, 1971).

(2) *ephippium, chathamensis, darwini, vicina*, and *güntheri* (western and southern populations)—these populations are all reduced in size, and consist almost entirely of adults. Mating and nesting occur unimpeded. However, virtually none —or only extremely small numbers—of the young survive, due to predation on the young and/or nests by one or more feral mammals. For example, the *ephippium* population on Pinzón has produced approximately 7,000–19,000 hatchlings during the past 10 years. Despite frequent and extensive searches in the nesting zones only a single one-year-old tortoise was found in this time period, and the nesting areas are littered with fragmented remains of hatchlings eaten by black rats.

(3) *güntheri* (eastern population)—this population consists mainly of small and medium-sized animals and appears to be self-replacing. However, few adults remain, most having been killed by settlers in past years; continued patrolling will be necessary to protect the population.

(4) *porteri*—the main population of this race, which inhabits the southwestern slopes of Santa Cruz, is quite large, and contains moderately large numbers of small and medium-sized animals. However, predators destroy large numbers of nests and young. Although not proven, it seems likely that recruitment is too low to replace adults lost by natural mortality and poaching. Probably the population size is declining continually, although slowly. The other small, isolated population of the race, in the infrequently-patrolled eastern sector of the island, consists now of only a few dozen tortoises. Its survival remains doubtful due to occasional human predation.

(5) *vandenburghi, microphyes* and *becki*—these populations are of moderate to large size and contain rather large numbers of small and medium-sized tortoises. Recruitment may be sufficient to maintain them as stable populations. However, present information is inadequate to provide conclusions regarding their status because black rats and cats may destroy young on all three volcanos. Although not yet demonstrated, the numerous donkeys on Volcán Alcedo may cause some nest destruction; their trails and dust wallows are present in tortoise nesting areas.

Reproductive Potential

Detailed information on reproductive potential was obtained for *G. e. porteri*, one of the races which attains greatest size and is dome-shaped, and *G. e. ephippium*, one of the smallest-sized and saddle-backed races (Van Denburgh, 1914). Santa Cruz is one of the larger, wetter, more elevated islands with maximum diversity of vegetation zones; Pinzón, one of the smaller, drier islands (Bowman, 1961). Thus, these two situations somewhat approximate the range of conditions found among the tortoise populations and habitats.

In order to determine fertility and hatching rates and the percentages of hatchlings which escape from nests, frequent visits were made to the major nesting areas on both islands during the laying period (June–December); nests were marked, left *in situ*, and their surfaces examined frequently during the hatching and emergence period (December–early April). Hendrickson (1965) noted the very hard, dried-mud cap which forms the top of the tortoise nest, and suggested that, in most years, the hatchlings must die entombed because of inability to dig through the cap; he hypothesized that the hatchlings escape in large numbers only in those occasional years when heavy rains occur during the wet and hot season (January–May). Therefore, almost all nests were left completely undisturbed until the hatchlings' exit holes appeared, or until well after the end of the projected incubation period if no such holes appeared. A few nests were opened late in the projected incubation period in order to determine hatching dates; eggs in most of these were found to have hatched or were in the process of hatching. These hatchlings were released in the area and unhatched eggs were recovered and allowed to incubate.

Based on all the marked nests, fertility and hatching rates were high and mortality rates during incubation were low for both populations (Table VI).

Escape rates of hatchlings from completely undisturbed nests were high in both populations (Table VII). All the hatchlings which escaped did so when the nest caps were still dry and hard, and almost all the exit holes were made directly up through the cap rather than through the soil to the side of it. In nine nests in which hatchlings were entombed, only a single individual from one of the bottommost eggs was trapped; they apparently hatched later than others in

TABLE VI

Fertility and Hatching Results from Nests in the Wild

Race and nesting season	*No. nests*	*No. eggs*	*Clutch size*		*Per cent definitely fertile (No.)*	*Per cent hatched (No.)*	*Per cent dead embryos (No.)*	*Per cent addled* (No.)*	*Per cent broken† (No.)*
			Average	*Range*					
porteri									
1969/70	10	91	9·1	6–11	85·7 (78)	84·6 (77)	1·1 (1)	12·1 (11)	2·2 (2)
1970/71	45	429	9·5	3–16	77·9 (334)	73·2 (314)	4·7 (20)	21·0 (90)	1·1 (5)
1971/72	113	1,047	9·3	3–16	—	75·6 (792)	- - - - - -	24·4 (255)	- - - - - -
ephippium									
1969/70	13	65	5·0	2–7	78·5 (51)	75·4 (49)	3·1 (2)	20·0 (13)	1·5 (1)
1970/71	13	68	5·2	4–8	82·4 (56)	79·4 (54)	2·9 (2)	7·4 (5)	10·3 (7)

* A liquefied egg, *i.e.*, infertile or the embryo having died before attaining sufficient size to be detected.

† Broken during laying or due to nesting interference, *i.e.*, two females nesting at same site.

the same nests and became trapped under rocks in the sides of the nests or soil loosened by their escaping siblings. Entire groups of hatchlings were entombed in eight nests. The January–May period in 1970 was dry, but heavy rains in March, 1971 did saturate and soften the nest caps of six of these nests; however, the trapped hatchlings were still unable to escape.

On Santa Cruz, only the larger, older females (approximately 90 cm curved carapace length and larger) were found to nest. The population contains an estimated 300–450 females of this size range, based on an estimated total population size of 2,000–3,000 individuals (Table V) and only 15 per cent of them are nesting sized females (Fig. 7). These females lay one or two clutches each per year. On Pinzón, all females encountered were of nesting size, and similar calculations give an estimated 99–132 females in the population. The number of nests laid per female per year on Pinzón is not known, but limited results from a *G. e. hoodensis* colony in captivity at the CDRS suggests a range of values of two to four.

The potential recruitment of hatchlings per year for each population can be calculated by using the values

TABLE VII

Escape of Hatchlings from Completely Undisturbed Nests in the Wild

Race and nesting season	*No. nests*	*No. hatched*	*Per cent hatchlings escaped (No.)*	*No. hatchlings escaped / No. eggs*	*No. nests with:**			
					No entombed hatchlings	*One entombed hatchling*	*Entire group entombed*	*Other*
porteri								
1969/70	10	77	80·5 (62)	0·681	5	3	1	1
1970/71	39	272	89·9 (249)	0·655	23	5	5	3
ephippium								
1969/70	12	46	95·7 (44)	0·721	10	0	1	0
1970/71	11	46	87·0 (40)	0·727	8	1	1	1
				Total	46	9	8	5

* In three *porteri* nests (1970/71) and one *ephippium* nest (1969/70) none of the eggs hatched.

presented above and values for the combined data of 1969/70 and 1970/71 (Tables VI and VII), as follows:

$$\begin{aligned} &(\text{No. nesting } ♀♀ \text{ in population})\\ &\quad\times (\text{Avg. no. clutches}/♀/\text{year})\\ &\quad\times (\text{Avg. clutch size})\\ &\quad\times \left(\frac{\text{No. hatchlings escaped}}{\text{No. eggs}}\right)\\ &\qquad\qquad = \text{Total no. hatchlings recruited per year}\end{aligned}$$

Thus, for *G. e. porteri*:

maximum value: (450) (2) (9·45) (0·66)
= 5,613 hatchlings/year
minimum value: (300) (1) (9·45) (0·66)
= 1,871 hatchlings/year
For *G. e. ephippium*:
maximum value: (132) (4) (5·1) (0·724)
= 1,950 hatchlings/year
minimum value: (99) (2) (5·1) (0·724)
= 731 hatchlings/year

It has not yet been possible to determine accurately age at maturity, longevity, and length of reproductive life for any of the Galápagos tortoise races in the wild. At the Honolulu Zoo, a *G. e. vicina* female began nesting at approximately 25 years of age (Throp, in press). However, since Galápagos tortoises usually grow more rapidly in zoos, maturity in the wild may not be reached until later, perhaps at 30–40 years of age.

Natural Mortality

Darwin (1845) stated that the Galápagos hawk preyed heavily on tortoise hatchlings and many present-day inhabitants suggest the same. However, although the hawk is a likely predator, no substantial observations of such behaviour have been reported. One of us (MacF.) observed several instances on Pinzón in which hawks landed near and inspected young tortoises as small as 27 cm curved carapace length, but made no attempt to attack them. There are no other known natural predators of tortoises or their eggs. Mortality of tortoises older than 2–3 years is largely due to accidents such as falling into crevices, being crushed by falling rocks, etc. and to thermal stress. Deaths may be caused occasionally by respiratory infections.

Approximations of natural mortality rates were obtained by counting the number of tortoises which had died of apparently natural causes within the census periods reported in Fig. 7. The time since death can be determined approximately by the degree of deterioration and breaking-up of the carapace and plastron; but the method is adequate only for tortoises of 30–35 cm curved carapace length, *i.e.* approximately 3–4 years old, and larger because the bones of smaller animals deteriorate too rapidly.

The numbers of natural deaths were as follows: *ephippium*, 0; *chathamensis*, 2 adult males, 1 adult female; *darwini*, 1 adult male; *vicina*, 1 adult male, 1 adult female; *güntheri* (east), 0; *porteri*, 2 adult males, 1 adult female, 1 small one. Thus, natural mortality rates of tortoises of 3–4 years of age and older are apparently very low, when based on the population censuses (Fig. 7).

Observational problems and the effects of introduced mammals make it difficult to determine natural mortality rates for smaller tortoises. Mortality is probably very great for younger animals, especially hatchlings, during those years when forage is very scarce in the lowland nesting zones, due to a lack of heavy rains during the wet season. Limited data are available for a small (approximately 2 ha) nesting zone on Santa Cruz which is devoid of pigs and black rats, and only rarely visited by a few goats or cats. In 1970 this area received only 26·6 mm of rainfall during the wet season and forage at ground level was almost non-existent; in 1971 rainfall during the same period was 255 mm and the area became covered with a dense growth of herbs which lasted from late March until August. During the January–March period in 1970, 57 hatchlings emerged from nests in this area and 20 were marked individually with paint; in 1971, 47 emerged in the area and 21 were similarly marked. The nesting zone and an additional area of 2 ha surrounding it were searched at least once a month from January, 1970 to November, 1971. Three hatchlings (one marked, two unmarked) were found in March and April, 1970, and all were emaciated and apparently starving; no others were found after that period. In 1971 hatchlings were found frequently and were healthy and growing rapidly; for example, 10 of the marked ones located on 12 November, 1971, weighed 3–4 times more than at emergence in March, 1971.

Rainfall data recorded since 1950 (Alpert, 1963; Charles Darwin Research Station, 1965–1972) indicate that heavy rains occur on the average in only one out of every four years.

CONCLUSIONS

Of the 11 surviving races, only *becki, microphyes*, and *vandenburghi* can be considered as comparatively unendangered at present. All the others are threatened with extinction, primarily due to introduced mammals.

The data on population sizes, sex and size class structures, reproductive potential and natural mortality suggest that all but two of the threatened races could probably maintain stable populations or even increase in numbers if these introduced predators and competitors were eliminated. Population stability or increase in size would probably occur even if natural mortality rates were high for hatchlings and very small tortoises. The absence of natural predators, great longevity, and low adult mortality rates would mean that only a tiny fraction of the eggs laid would have to survive to adulthood to replace natural losses. Conservation of these races will ultimately depend upon eliminating or controlling introduced mammal populations; while these methods are being developed it will be necessary to maintain these populations at a reasonably stable size by raising of young and restocking.

The *hoodensis* and *abingdoni* populations are so reduced that males and females will have to be brought together in captive breeding colonies in order to produce young and restock the native habitats.

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APPENDIX

Ageing

There is no known method for accurately ageing Galápagos tortoises. Annuli on the carapace scutes cannot be used because climatic conditions and the corresponding growth of tortoises vary considerably from year to year. Ages given in the text are based on data from young raised in captivity at the CDRS and from wild young marked as hatchlings and periodically re-encountered.

Sex and Size Classes

The secondary sexual characteristics and ease of distinguishing adult males and females and the difficulties of sexing smaller tortoises are essentially the same for the Galápagos races as Grubb (1971) described for the Aldabra species. Moreover, since the maximum size attained differs for the various Galápagos races, the minimum size at which tortoises can be sexed differs considerably for the races. Table VIII presents the size class ranges found to be accurate in the field and used in the analysis of all marked tortoises (Table V). Adult males and females and small-sized, non-sexable tortoises are easily distinguished in the field; however, medium-sized animals were often not sexable.

Table VIII

Size Class Ranges in Marked Tortoises

	Size class ranges (curved carapace length in cm)					
	Adults		*Medium-sized*			*Small-sized*
	♂♂	♀♀	♂♂	♀♀	*Not sexable*	
hoodensis and *ephippium*	70+	55+	55 to <70	45 to <55	45 to <55	<45
chathamensis	80+	60+	60 to <80	50 to <60	50 to <60	<50
darwini	90+	70+	70 to <90	55 to <70	55 to <70	<55
vicina and *güntheri*	90+	75+	70 to <90	55 to <75	55 to <75	<55
microphyes	85+	70+	65 to <85	55 to <70	55 to <75	<55
vandenburghi and *porteri*	95+	80+	80 to <95	65 to <80	65 to <80	<65