The ecology, behavior, and conservation of the Galápagos tortoises. Volume 10 1978

National Geographic Society (Estados Unidos)
Washington, D. C.: National Geographic Society, 1978

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The Ecology, Behavior, and Conservation of the Galápagos Tortoises

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Reprinted from: National Geographic Society Research Reports, 1969 Projects, pages 497-513, 3 figures

Washington, D. C.
1978

The Ecology, Behavior, and Conservation of the Galápagos Tortoises

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Grant No. 764: To study the distribution, ecology, and behavior of Galápagos tortoises.

From August 1969 to November 1971 a detailed study of the ecology and behavior of the Galápagos giant tortoises *(Geochelone elephantopus)* was carried out under the present grant. The primary goals of the investigation were threefold.

Firstly, we wished to conduct a long-term field study of the ecology and social behavior of the largest living terrestrial reptile. We proposed to include a consideration of population dynamics, seasonal migrations and daily movements, feeding ecology and habitat relations, and association of the tortoises with other animal species. The literature and unpublished research reports appearing before 1969 consisted almost entirely of anecdotal observations and affirmed that no detailed field studies had been conducted to that time.

Secondly, it was desired to determine the prospects for survival of all the extant subspecies and to provide basic information for the design of conservation-management programs by determining, for each race where possible, the present geographic distribution, population size and structure, reproductive cycle and reproductive potential, natural mortality rate, and the mortality rate and other negative effects caused by introduced mammalian predators and competitors.

Thirdly, and as an outgrowth of objectives one and two, it was proposed to collaborate extensively with the Galápagos National Park Service (part of the Ecuadorian Forestry Service) and the Charles Darwin Research Station in the design and execution of conservation-management programs for all the endangered subspecies. Through the decade of the 1960's, the Darwin Station, and later the Park Service, carried out surveys of the geographic distribution of some of the subspecies populations and made rough estimates of population sizes. Also, they began, for two subspecies, management programs that included nest protection to increase survival and the artificial incubation and raising of young for restocking on their respective native islands.

The following report covers those portions of the investigation supported by the National Geographic Society during the period 1969-1971. Results of part of the study have been published (see References); the remainder are presently in preparation. The studies and the conservation practices developed are being continued by the Galápagos National Park Service and one of us (MacFarland) in his present official capacity as director of the Charles Darwin Research Station, Santa Cruz, Galápagos.

Geographic Distribution and Population Biology

Numerous visits to and extensive surveys of the tortoise populations and their habitats resulted in accurate determination of which subspecies survive, detailed distributions of the populations on the various islands, and the population sizes and size class structures of almost all the subspecies. The permanent marking of tortoises for individual identification (by notching the marginal scutes in various combinations) was continued to the point that large percentages of the tortoises of the seven smallest, most endangered subspecies populations had been marked. The marking is required primarily for the continuing study of population dynamics, seasonal migrations, daily movements, reproductive biology, and growth and development, but it also allows some control of poaching and possible interisland transfers.

It is now known that 11 of the 15 tortoise subspecies originally described definitely survive (fig. 1); two became extinct in the latter part of the last century, and one probably never existed (the only individual ever seen and collected probably having been an artificial introduction). The fifteenth, that from Fernandina, is an enigmatic case. One individual was seen and collected there in 1906. In 1964, unmistakable large tortoise scats were found by Dr. John Hendrickson in a small meadow at 1,100 feet altitude on the west slope of the island. In full agreement with a request from the National Geographic Society, we made a special search of the best potential tortoise habitats on Fernandina (those lying on the western and southwestern slopes) including an extensive search of the same meadow and surrounding areas examined by Hendrickson. However, no tortoises or their sign were found in any of the areas, even though some would be excellent tortoise habitat. Since 1971 virtually all the remaining smaller vegetated areas on Fernandina

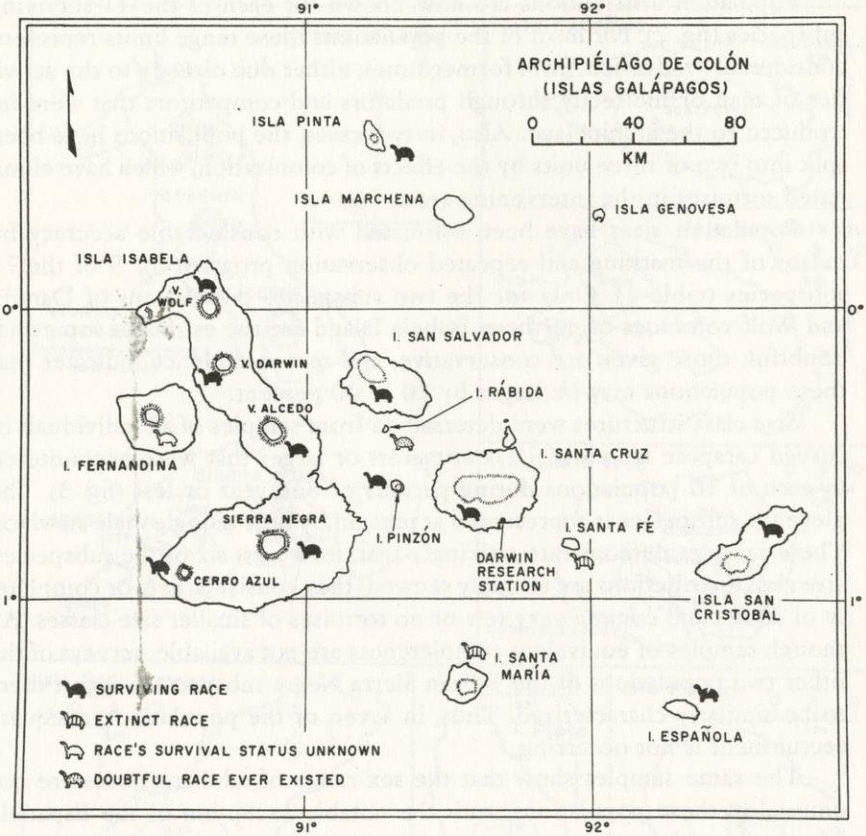


FIG. 1. Distribution of the 15 subspecies of Galápagos tortoises *(Geochelone elephantopus)* as originally recognized.

have been searched by the Park Service, but no tortoise sign has been located. Thus it is very probable that the 1906 and 1964 discoveries were of some of the very few remaining Fernandina tortoises. Perhaps the subspecies is now extinct. If so, it has probably been due largely to gradual reduction of available habitat on the island through volcanic activity, since no introduced mammals occur on Fernandina and man has never had notable influence there. The surface of Fernandina now consists of approximately 90 percent harsh, barren lava; only a few scattered strips of vegetation remain within which tortoises could survive. Further searches, especially in a few tiny vegetated areas not previously explored, are planned.

Population distributions are now known for each of the 11 surviving subspecies (fig. 2). For most of the populations these range limits represent considerable reduction from former times, either due directly to the activities of man or indirectly through predators and competitors that were introduced to the archipelago. Also, in two cases, the populations have been split into two or three units by the effects of colonization, which have eliminated tortoises in the intervening areas.

Population sizes have been estimated with considerable accuracy by means of the marking and repeated observation program for 9 of the 11 subspecies (table 1). Only for the two subspecies populations of Darwin and Wolf volcanoes of northern Isabela Island are the estimates somewhat doubtful; those given are conservative, and recent evidence indicates that these populations may be larger by 20 to 40 percent.

Size class structures were determined from samples of all individuals of curved carapace length of 10 centimeters or larger that were encountered in each of 10 populations during periods of one year or less (fig. 3). The eleventh subspecies is represented at present by only a single male survivor. These samples demonstrate strikingly that, in at least six of the subspecies, size class distributions are strongly skewed; they consist largely or completely of adults and contain very few or no tortoises of smaller size classes. Although samples of equivalent completeness are not available, surveys of the other two populations of the Volcán Sierra Negra subspecies suggest them to be similarly characterized. Thus, in seven of the populations, adequate recruitment is not occurring.

The same samples show that the sex ratios of adult tortoises are not unusual in these populations, with the notable exception of the Española Island subspecies.

Conservation: Status of the Populations and Management Program

A detailed analysis of the status of the giant-tortoise populations and an evaluation of the management program being conducted by the Park Service and the Darwin Station have been published (MacFarland, Villa, and Toro, 1974a; 1974b). In brief, the majority of the subspecies are definitely threatened, principally because of predation and/or competition by one or more species of introduced mammals. The most damaging of these exotic species are feral pigs, goats, dogs, cats, and the black or wharf rat. The tortoise subspecies and various populations can be divided into five groups based on their status (fig. 3; table 1).

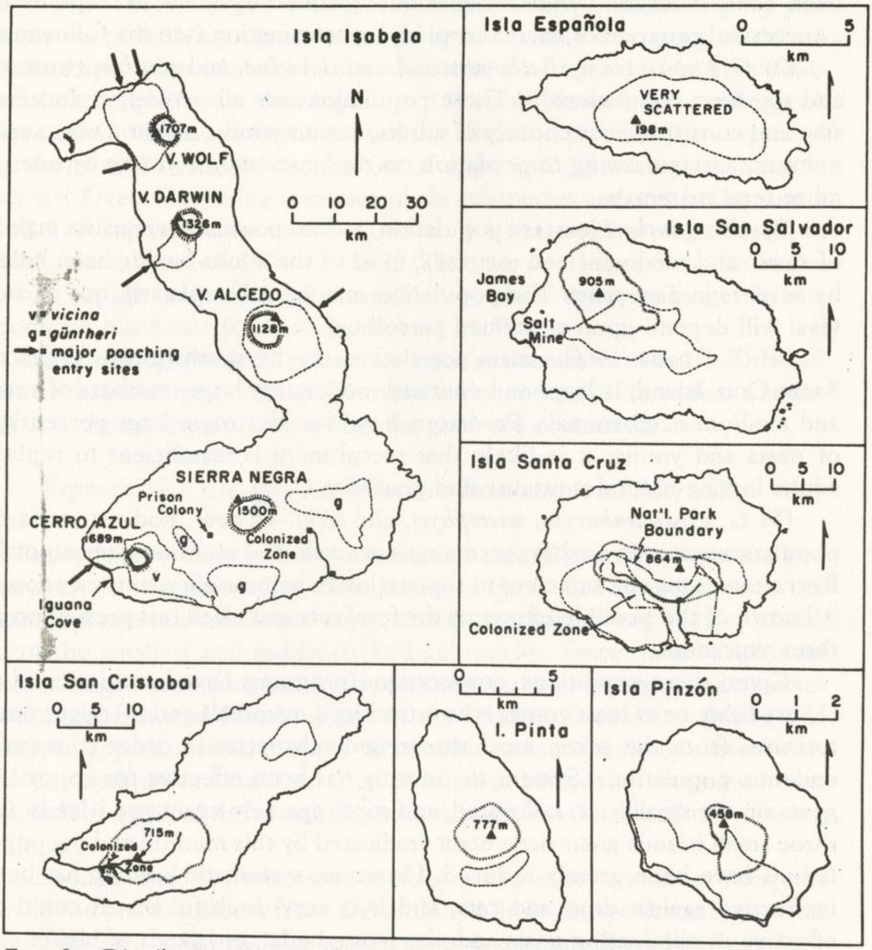


FIG. 2. Distributional limits (dotted lines) on individual islands and volcanoes of the 11 surviving subspecies of Galápagos tortoises.

(1) *Geochelone elephantopus hoodensis* and *G. e. abingdoni.*—These populations are extremely small. The density of the *hoodensis* population is so low and the sex ratio so skewed that the few adults still existing rarely, if ever, encounter one another and no reproduction occurs. The single Pinta Island male was discovered in November 1971 after several extensive searches indicated no sign of living tortoises. Thus there is still hope of finding a few additional individuals there. The vegetation of both islands had

been badly damaged by goats but is now recovering slowly in response to a successful program of goat control and extermination (see the following).

(2) *G. e. ephippium, chathamensis, darwini, vicina,* and *güntheri* (western and southern populations).—These populations are all severely reduced in size and consist almost entirely of adults, but no young, or but a very small number, survive, owing to predation on the nests and/or young by one or more feral mammals.

(3) *G. e. güntheri* (eastern population).—This population consists mainly of small- and medium-sized tortoises, most of the adults having been killed by settlers in past years. The population may be self-replacing, but its survival will depend upon continued patrolling.

(4) *G. e. porteri.*—The main population, on the southwestern slopes of Santa Cruz Island, is large and contains moderately large numbers of small and medium-sized animals. Predators, however, destroy a large percentage of nests and young; it is likely that recruitment is insufficient to replace adults lost by natural mortality and poaching.

(5) *G. e. vandenburghi, microphyes,* and *becki.*—These moderate to large populations contain sizable percentages of small- and medium-sized animals. Recruitment may be sufficient to replace losses by mortality, but not enough is known of the possible effects of the feral cats and black rats present on all three volcanoes.

Given these conditions, conservation programs have been initiated to (1) eradicate or at least control the introduced mammals and (2) raise young tortoises from the seven most threatened subspecies in order to restock endemic populations. Systematic hunting has been effective for control of goats on the smaller, less elevated, and more sparsely vegetated islands. On three small islands goats have been eradicated by this method and pig populations have been greatly reduced. However, systematic hunting has been ineffective against dogs and cats, and it is very doubtful that it could be effective in eliminating goats and pigs from the larger islands of higher elevation with a diversity of vegetation zones. Alternative control or extermination methods are being sought and tested for these feral mammals as well as the black rat. Broad ecological studies of the latter species and feral goats are now under way.

In the interim, while new control methods are being investigated, management programs aimed at increasing the reproductive success of the populations and restocking of the endemic tortoise populations have been instituted. To increase yearly recruitment of hatchlings, lava corrals have been constructed around nests on several islands. This technique has resulted in almost total success in preventing nest destruction by pigs. During the past 9 years an extensive program of hatching and raising the young of endangered subspecies in captivity has been developed. Improved and highly successful techniques were developed for (1) establishment of breeding colonies and construction of artificial nesting sites in captivity, (2) transport of eggs from wild nests, (3) incubation of eggs, and (4) raising of young in captivity. Over 420 young tortoises of six subspecies are now being raised. In all, 122 captive-raised tortoises, 4.5 to 6.5 years old, were released on Pinzón Island between 1970 and 1973. They are now in good condition and growing rapidly and are large enough to be threatened no longer by the introduced black rats present in numbers on Pinzón.

These management programs are now so successful that 10 of the 11 extant subspecies will definitely survive if the control of introduced mammals and the raising and restocking program are continued.

Reproductive Biology, Reproductive Potential, and Mortality

Reproductive biology and potential and natural mortality were studied intensively in two subspecies: *G. e. porteri* of Santa Cruz Island, one of the largest and most dome-shaped races, and *G. e. ephippium* of Pinzón Island, one of the smallest and saddle-backed subspecies. Since Santa Cruz is an island of large size and high altitude, with vegetational diversity and relatively wet highlands, and Pinzón is one of the smaller, drier islands, these two situations approximate the range of conditions found among present tortoise populations and habitats. Similar but less complete information was obtained for eight of the remaining nine subspecies; these studies are being continued.

Although tortoises were seen mating during every month of the year, most of the activity occurs from December to June, the peak mating season being February to April. The nesting season extends from late June into mid-December. Females migrate from highland feeding zones to lower altitudes where they nest, then return to the highland zones one to three weeks later. When individual females nest sequentially in a single season, this same pattern occurs between nestings.

Based on estimated population sizes (table 1), censuses (fig. 3), and the known minimum size of females which nest, it was estimated that the Santa Cruz population contains 300-450 nesting females and that on Pinzón 99 to 132 nesting females. The Santa Cruz females lay one or two clutches each per year. The range of clutch number for Pinzón females has not been

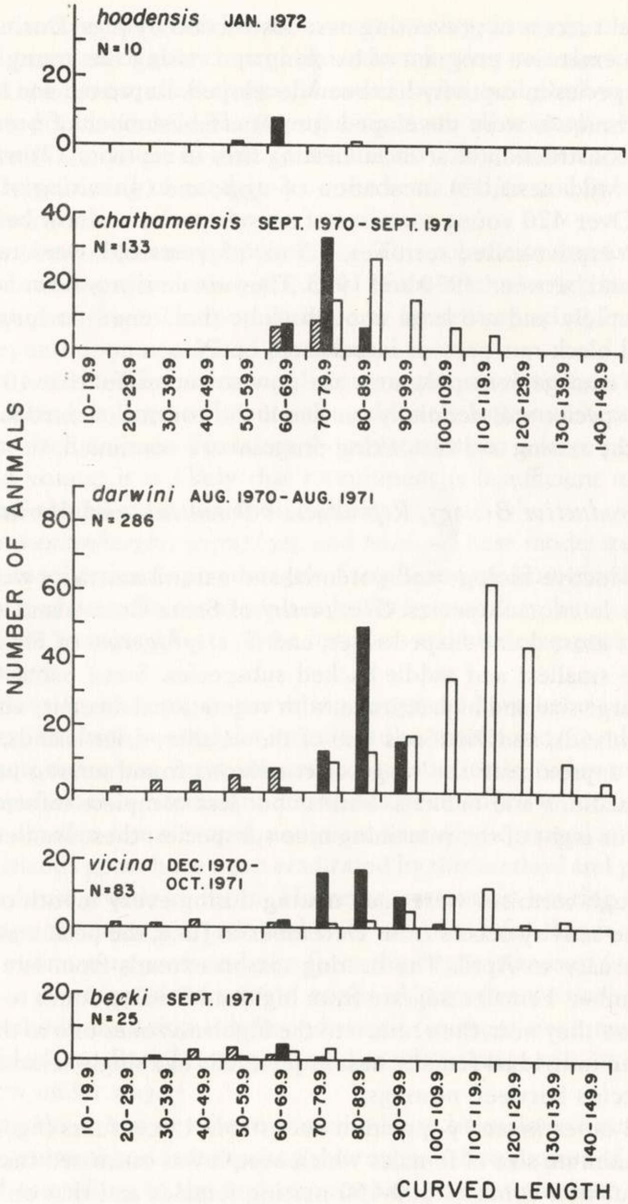
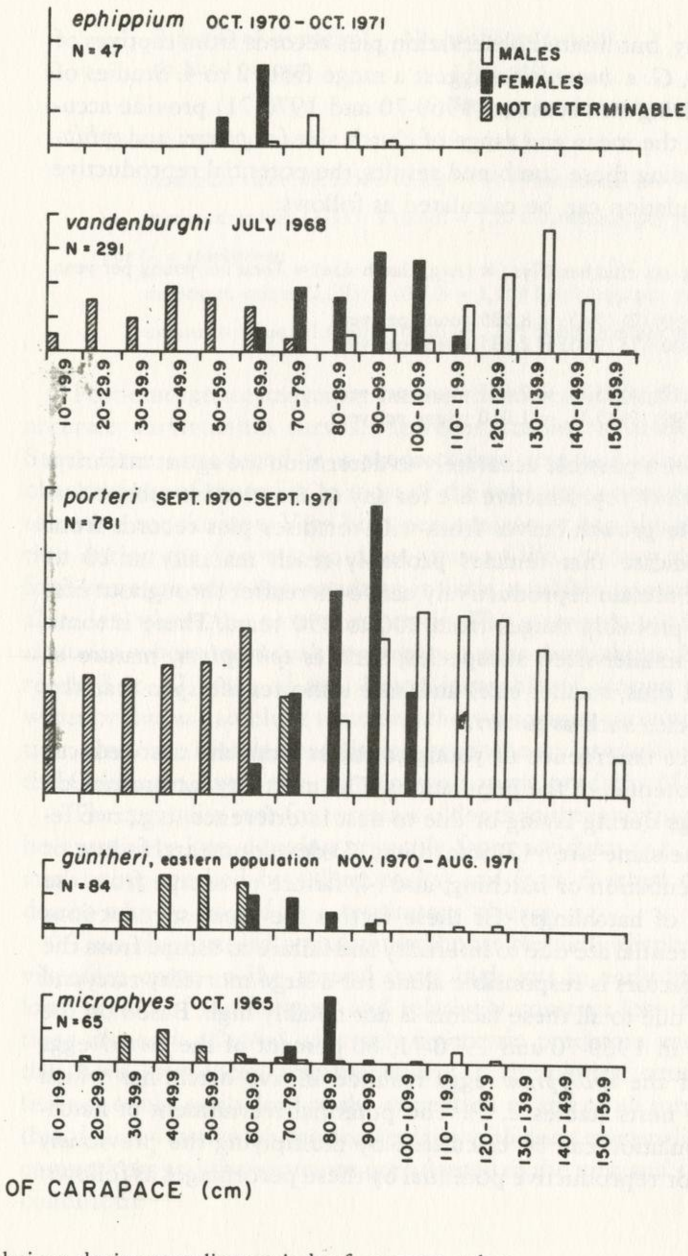


FIG. 3. Size class distributions of all tortoises encountered in the various



populations during sampling periods of one year or less.

determined precisely, but limited observation plus records from captives of a similar subspecies, *G. e. hoodensis,* suggest a range from 2 to 4. Studies of nests in the wild during two seasons (1969-70 and 1970-71) provide accurate values for both the mean and range of clutch size for *porteri* and *ephippium* (table 2). By using these combined results, the potential reproductive output of each population can be calculated as follows:

(No. nesting ♀♀) × (Avg. no. clutches/♂/yr.) × (Avg. clutch size) = Total no. young per year.
Thus, for *G. e. porteri:*
  maximum value: (450) (2) (9.45) = 8,505 young per year
  minimum value: (300) (1) (9.45) = 2,835 young per year
For *G. e. ephippium:*
  maximum value: (132) (4) (5.1) = 2,693 young per year
  minimum value: (99) (2) (5.1) = 1,010 young per year

It has not yet been possible accurately to determine the age at maturity, longevity, and length of reproductive life for any of the tortoise subspecies. However, composite growth curves from wild tortoises plus records from captive animals indicate that females probably reach maturity at 20 to 35 years of age and remain reproductively active thereafter throughout life, and that longevity probably ranges from 100 to 150 years. There is some evidence that the smaller-sized subspecies, such as *ephippium,* mature at a younger age (and thus, smaller size) and have a shorter life span than the larger-sized subspecies such as *porteri.*

Mortality before emergence of young tortoises from the nest reduces the reproductive potential of the populations. The mortality factors include (1) breakage of eggs during laying or due to nest interference (e.g., two females nesting in the same site); (2) infertility; (3) developmental failure or anomaly during incubation or hatching; and (4) failure to escape from the nest (entombment of hatchlings). Of these factors the greatest reductions in reproductive potential are due to infertility and failure to escape from the nest. None of the factors is responsible alone for a large mortality rate, and the total mortality due to all these factors is not notably high. Based on the wild nests studied in 1969-70 and 1970-71, 66 percent of the *porteri* eggs and 72 percent of the *ephippium* eggs resulted in live hatchlings which emerged from the nests (tables 2, 3). The potential recruitment of hatchlings for each population can be calculated by multiplying the previously calculated values for reproductive potential by these percentages as follows:

$$\left(\frac{\text{Potential no. young/yr.}}{\text{i.e., total no. eggs}}\right) \times \left(\frac{\text{No. hatchlings escaped}}{\text{No. eggs}}\right) = \text{Total no. hatchlings recruited per year.}$$

Thus, for *G. e. porteri:*

maximum value: (8,505) x (0.66) = 5,613 hatchlings per year

minimum value: (2,835) x (0.66) = 1,871 hatchlings per year

For *G. e. ephippium:*

maximum value: (2,693) x (0.72) = 1,950 hatchlings per year

minimum value: (1,010) x (0.72) = 731 hatchlings per year

Post-emergence mortality has not been studied sufficiently to provide accurate survivorship curves. However, studies of marked hatchlings on Santa Cruz introduced in a predator-free area and censuses and general observations of mortality in most of the subspecies populations allow a few tentative conclusions. Very high percentages of hatchlings die from starvation during the first two to three years of life. At least three out of every four years are very dry, resulting in little available vegetation in the lower altitudes, where the nesting zones lie. The young do not migrate to higher altitudes, where more lush vegetation occurs throughout the year, until they reach 8 to 12 years of age. Being incapable of storing large amounts of water or fats as can older tortoises, the very young succumb easily to starvation. On some islands, there is apparently heavy predation on hatchlings by the Galápagos hawk, the only known natural predator of the tortoise.

The mortality rate for tortoises older than three to four years appears to be extremely low, deriving primarily from accidents *(e.g.,* falling into crevices, being crushed by falling rocks) and from thermal stress. Occasional deaths may be caused by a respiratory disease.

Thus the tortoise populations almost certainly display a Type III survivorship curve in the natural state: high loss in early life, followed by a long period of much lower and relatively constant loss. But most populations are now affected adversely by exotic predators and/or competitors that have introduced artificial effects to the natural situation. This interference could easily lead to the extinction of any or all tortoise populations that did not evolve on the archipelago with such mammalian predators and competitors and therefore are not adapted to the new and suddenly changed conditions.

Seasonal and Daily Movements

Analyses of data on seasonal migrations, daily movements, and home range size in relation to habitat quality and social behavior are now being completed for the Santa Cruz population. A few general conclusions can be made.

During most of the year the great majority of adult and subadult tortoises are concentrated in the higher, more moist, and densely vegetated areas from 450 to 1,000 feet in elevation on the southwestern slope of the island. In contrast, the juveniles are distributed mainly at elevations between 200 and 450 feet in drier transitional zone vegetation, and the youngest animals (up to 10-15 years of age) are confined throughout the year to the arid lowland nesting areas between the coast and about 200 feet elevation. Despite this general distributional pattern, juveniles can be found in other zones extending all the way from the coast up to 550 or 600 feet and adults and subadults in all zones from the coast to 1,400 or 1,500 feet in elevation.

Two periods of more concentrated migratory movement are observed. (1) Between June and December the very large-sized females move to the nesting areas. (2) On the average, in three out of four years, a large percentage of adults and subadults move to the arid lowlands (coast to 200 feet elevation) during the later two to three months of the hot season (January to May). This is apparently due to the fact that little or no rainfall occurs during the period, vegetation at the higher altitudes dries severely, and the tortoises move to lowland *Opuntia* forests for food.

During the *garúa* season (misty rain; from June to December, when the vegetation is relatively lush and standing water is normally available above 300 feet altitude) and during rainy hot seasons (about one out of every four), the daily movements and home range size of all tortoises are more limited (based on observations of one to two weeks of individual tortoises). The home-range size is generally positively correlated with tortoise size, ranging from 200 to 400 square meters for small juveniles of 25 to 35 centimeters curved carapace length to 1,000 to 1,500 square meters for large adult males and females. During those hot seasons with little or no rain, when the vegetation dries and standing water becomes unavailable, home-range size increases dramatically for all size classes, becoming 5 to 10 times the area of activity during the wetter seasons.

Social Behavior

Detailed quantitative as well as descriptive data were gathered on mating and agonistic behavior patterns by direct observation and still and motion-picture photography. This information is still to be analyzed and will be published later. A few general conclusions follow.

(1) Adult males have a definite rut period, whereas adult females never display any period of special receptiveness. The females attempt to avoid copulation throughout the year.

(2) "Courtship" is relatively simple; the males appear to select adult females by visual and/or olfactory inspection. Most of the male-female interaction consists of male behavior patterns designed to threaten the female to passivity and acceptance of copulation.

(3) The tortoises are definitely not territorial. However, specific feeding sites, resting sites in areas with limited shade, and mud or water wallowing sites are defended for short periods (a few hours up to one to three days) by all size classes. The larger of two tortoises in such encounters almost invariably dominates in the interaction. Similar aggressive fights occur between adult males over access to adult females during the mating season.

(4) Although not enough data yet exist to make an unequivocal statement, dominance hierarchies appear not to exist in the tortoise populations. Rather, the largest individuals almost always are dominant in any given interaction. There is no evidence for the occurrence of individual recognition and some against it.

Association with Other Species

A number of associations with other animal species were studied. The most thoroughly investigated, both descriptively and quantitatively, is that of a cleaning symbiosis in which the small ground finch removes ticks from the tortoise subspecies of Volcán Alcedo and Pinzón and Santa Cruz Islands. The finches initiate a cleaning sequence by approaching and sometimes performing a presentation display to the tortoise. After perceiving either or both the approach and display, the tortoise responds by assuming a motionless, fully raised posture with the legs and neck fully extended. The posture appears to serve at least two functions: (1) It increases to a maximum the exposure of skin surface area, especially those portions that are mostly unavailable when the tortoise is in a resting or inactive posture; (2) it minimizes flightiness of the finches and the danger that they will be injured. Both the ticks eaten *(Amblyomma)* and the cleaning activity are most concentrated on those skin areas that are least exposed—the leg and neck pockets and the basal area of the neck. The finches only rarely cleaned or initiated the approach display with inactive tortoises, and the latter were

TABLE 1. POPULATION SIZE ESTIMATES AND NUMBER OF MARKED TORTOISES FOR SUBSPECIES OF *GEOCHELONE ELEPHANTOPUS*

Race	*Location*	*Marking period*	*Marked tortoises*							*Estimated population size*
			Total No.	*Adults* ♂	*Adults* ♀	*Medium sized* ♂	*Medium sized* ♀	*Medium sized Non-sexed*	*Small sized*	
Geochelone elephantus										
hoodensis	Española	8/63-6/72	13	2	11	0	0	0	0	20-30
abingdoni	Pinta	11/71-6/72	1	1	0	0	0	0	0	very small
ephippium	Pinzón	4/63-3/69	100	35	63	1	1	0	0	150-200
chathamensis	San Cristóbal (northeastern part)	12/65-9/71	213	94	63	54	2	0	0	500-700
darwini	San Salvador	6/65-10/71	389	224	97	27	6	27	8	500-700
vicina	Cerro Azul	4/66-10/71	196	77	85	11	12	9	2	400-600
güntheri	Sierra Negra:									
	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	Volcán Alcedo	5/65 and 7/68	402	135	117	13	26	39	72	3,000-5,000
microphyes	Volcán Darwin	10/65	65	6	26	2	1	8	22	500-1,000?
becki	Volcán Wolf	–	0	–	–	–	–	–	–	1,000-2,000?
porteri	Santa Cruz:									
	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

unlikely to respond to such attempts. Most initiation attempts occurred with active tortoises, which almost always responded. The results suggest that feeding efficiency has determined the finches' preference for active tortoises. Quantitative details of the symbiosis and related factors have been published elsewhere (MacFarland and Reeder, 1974).

A number of other associations were noted, as follow:

(1) The vermillion flycatcher, the endemic Galápagos flycatcher, and the Galápagos hawk all use the tortoise as a "beater," capturing insects that the tortoise stirs up while walking.

(2) The yellow warbler, lava lizards, and geckoes all capture small insects that fly very near to and land on the tortoises.

(3) The Galápagos dove, the Galápagos mockingbirds, and several

TABLE 2. FERTILITY AND HATCHING RESULTS FROM NESTS IN THE WILD

Race and nesting season	No. nests	No. eggs	Clutch size Average	Clutch size Range	Percent definitely fertile (No.)	Percent hatched (No.)	Percent dead embryos (No.)	Percent addled* (No.)	Percent broken† (No.)
Geochelone elephantopus 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)
Geochelone e. 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 time.

TABLE 3. ESCAPE OF HATCHLINGS FROM COMPLETELY UNDISTURBED NESTS IN THE WILD

Race and nesting season	No. nests	No. hatched	Percent hatchlings escaped (No.)	No. hatchlings escaped / No. eggs
Geochelone elephantopus porteri				
1969/70	10	77	80.5 (62)	0.681
1970/71	39	272	89.9 (249)	0.665
Geochelone e. ephippium				
1969/70	12	46	95.7 (44)	0.721
1970/71	11	46	87.0 (40)	0.727

species of Darwin's finches were seen to search or pick through tortoise scats for food (seeds, insects, or snails living within the scats).

(4) The tortoises on almost all islands were found to have ticks of at least one, in some cases two, species. Careful collections of these ectoparasites were made from tortoises of most subspecies. These specimens and data have provided the major source of information for reports on the taxonomy of the ticks and their co-distribution with the tortoises (Hoogstraal,

Clifford, and Keirans, 1973; Keirans, Hoogstraal, and Clifford, 1973).

(5) Tortoises of almost all subspecies were found commonly to have algae, fungi, and lichens growing on the carapace. The lichens are particularly interesting, for it appears that at least six or seven species, commonly found on rocks in the Galápagos, grow also on those carapace surfaces that are protected from abrasion. Such relationships are extremely rare, the only other known case being that of lichens apparently growing on the elytra of certain beetles in New Guinea.

These relationships will be described at greater length in a series of short publications.

Environment of the Tortoise Reserve, Santa Cruz

A preliminary quantitative study of the vegetation was made along a transect from the sea to the upper boundary of the Tortoise Reserve (ca. 200 meters elevation; Santa Cruz Island) along a gradually ascending distance of 12,900 meters. The purpose of the separate study was (1) to establish suitable methods by which the herb and shrub cover, of importance to tortoises as shade and food, could be quantitatively described, and (2) to study the character of vegetation change along such a gradual ascent. This transect passes from the upper margin of the Mangrove or Littoral Zone through the *Cryptocarpus,* Arid, and Transition Zones.

Stand organization, comments on species replacement, and several methods of data analysis are discussed in the paper of Reeder and Riechert (1975).

At the same time, using the vegetation sampling areas along the same transect, we made initial quantitative collections of arthropods. The long-term intent is to relate in detail arthropod and vegetational distributions, with the view of studying their interdependencies.

Thus it has been that not only is the tortoise program, established under National Geographic Society sponsorship, continuing to the present, but also other ecological studies have been undertaken as logical extensions and have themselves become full-fledged research programs.

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