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MacFarland, C. G.; Reeder, W. G.

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Breeding, Raising and Restocking of Giant Tortoises (*Geochelone elephantopus*) in the Galápagos Islands*

C. G. MacFarland and W. G. Reeder

INTRODUCTION

During the first six decades of this century, reports from scientific expeditions resulted in widespread acceptance of the idea that at least several, or perhaps most, races of the Galápagos Tortoise (*Geochelone elephantopus*) were extinct, and that virtually all surviving populations were imminently in danger of the same fate. It was also concluded that survival of the remaining races depended upon the establishment of breeding colonies outside of the Galápagos. Several expeditions in the 1920s and 1930s justified the collection of large numbers of tortoises for this purpose. Unfortunately, these notions are still widespread, especially among private collectors and even many zoo personnel, despite the total failure of most of these captive colonies to breed.

Field research conducted over the past ten years by the Charles Darwin Research Station and the Galápagos National Park Service, and the authors' investigations from August 1969 to November 1971, have significantly altered this bleak view of the status and survival potential of the tortoise populations. This paper briefly summarizes these findings and more extensively reports on the restocking programme now in operation in the Galápagos Islands. Except where noted, the data cover the period from 1965 to November 1971.

The value of attempting to preserve individual subspecies or races, rather than just the species, is frequently questioned. As is well known, the decision as to what constitutes a "species" or any of its sub-categories is very problematical (Mayr, 1963; chapters 2-4), especially when dealing with insular populations, where the test of natural reproductive isolation or compatibility cannot be made. As a minimum, the following types of information about a set of subspecies or races are required in order to determine whether they represent apparently incipient species or are but local variants within a larger interbreeding population comprising a single gene pool: (1) the extent of their geographical

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isolation; (2) the extent of natural gene flow among them; (3) the existence of isolating mechanisms that prevent or reduce the full success of intersubspecific or inter-racial crosses (Mayr, 1963; chapter 5). In any given case, some or most of this information is usually lacking. Even with extensive data, however, it is virtually never possible to predict the future evolutionary course of a set of subspecies or races. In our opinion, the safest method is to preserve the subspecies or races intact and not to interbreed them in captivity.

Geochelone elephantopus is a case in point. The various taxa (taxonomic categories) differ in shape, colour and thickness of carapace, maximum size attained, and lengths of neck and legs. However, variation within any taxon (taxonomic category) is great and the differences among taxa are only statistical, at best. Assigning an individual specimen to a definite taxon is extremely difficult, though the range of possibilities often can be reduced to three or four taxa.

In the only major taxonomic treatment of the group, Van Denburgh (1914) assigned binomials to 13 of the taxa, leaving two unnamed because of insufficient material.* However, he consistently used the term "races" in discussing the 15 taxa, clearly recognizing the large amount of intergradation of morphological characteristics. The more recent interpretations regard all the taxa as subspecies of the single species *Geochelone elephantopus* Harlan 1827 (Hendrickson, 1966).

Whether the taxa are considered races, subspecies, or even species is a moot point. All are geographically isolated populations on separate islands or volcanoes, except for *G.e. vicina* and *G.e. güntheri*, which occur together on southern Isabela.† There is no evidence of ethological isolating mechanisms for any of the taxa; whether interbreeding would result in reduced fertility remains to be tested. However, because of the geographic barriers, the probability of natural interbreeding is minute. Since the taxa have evolved differences and certainly have been physically separated for a long time period (biologically speaking), they should be preserved individually. The extinction of any one taxon would be an irreversible loss of a unique form of life.

We accordingly use the term "race" for each taxon, primarily because no marked differences in structure exist among them.

STATUS OF TORTOISE RACES

A detailed report has been published elsewhere (MacFarland, *et al.*, 1974a, 1974b). Since much new information has made the most recent reports (Snow,

* The subspecific name *vandenburghi* is commonly used and accepted for the tortoises of Volcan Alcedo, Isabela; we continue with this usage. However, we note that, on the basis of the described location, De Sola (1930) almost certainly mistakenly applied the name to specimens of *G.e. güntheri* from Sierra Negra, Isabela.

† Perhaps eventually the *vicina* and *güntheri* taxa will be combined. Van Denburgh (1914) was unable to clearly distinguish them. Until 1925, no known physical barriers separated the two volcanoes. An extensive lava flow in that year partially separated them, but a large area on the southern coast of Isabela still remains as a potential pathway for interchange. The question requires further study.

1964; Perry, 1970; Thornton, 1971) outdated, a brief summary is necessary for an understanding of current conservation practices.

Fifteen races of *G. elephantopus* were originally described (Van Denburgh, 1914), ten from separate islands and one from each of the five major volcanoes of Isabela (Fig. 1). The massive decimation of these large populations by human

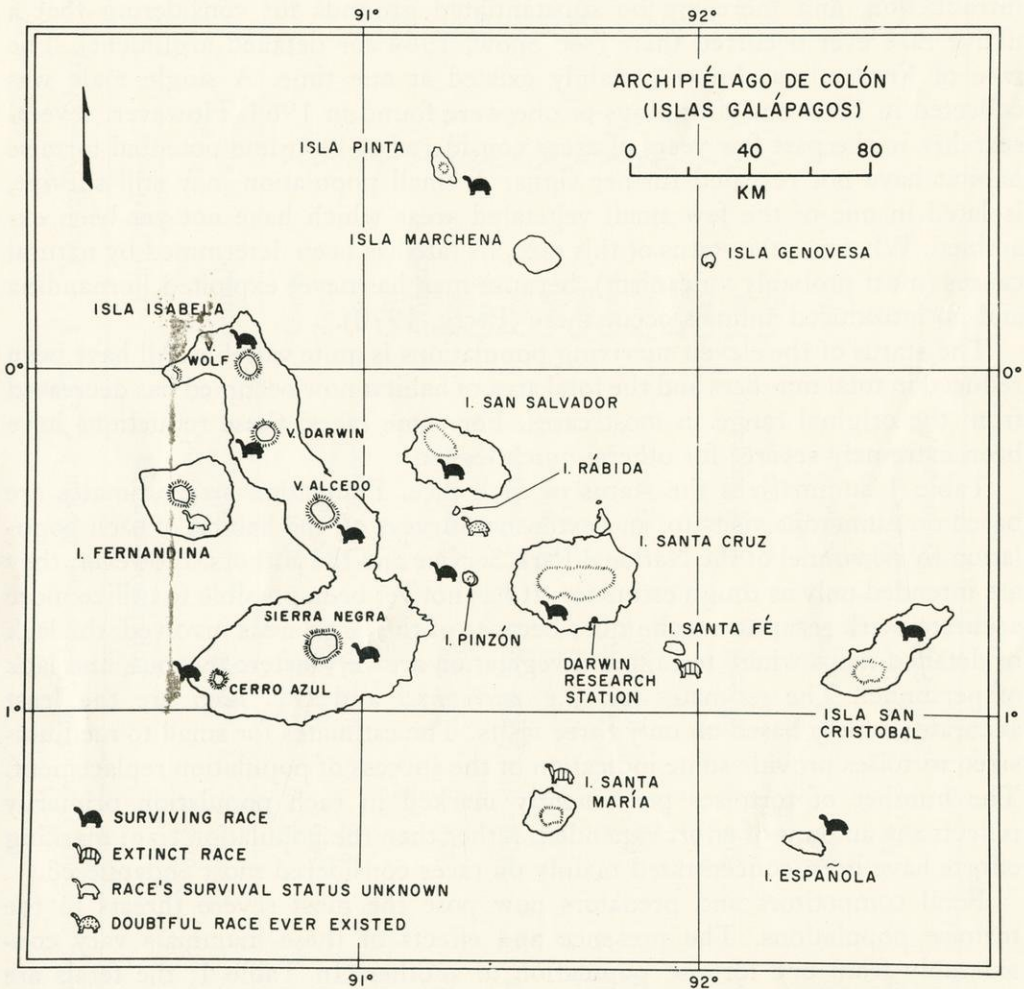


FIGURE 1. Map showing the distribution of the originally recognized 15 races of *G. elephantopus*.

exploitation has already been summarized in detail (Townsend, 1925; Slevin, 1959). During this century, various reports indicated that as few as two and perhaps many more races had been eliminated; the existence of some others was considered doubtful. However, these reports were based mainly on cursory visits to coastal areas. Extensive searches over the past ten years, especially in the islands' interior regions, have resulted in the rediscovery of several races thought to be extinct; the population sizes of most surviving races were found to be much

larger than indicated by all previous estimates in this century (Van Denburgh, 1914; Bowman 1960; Eibl-Eibesfeldt, 1959 and 1961; Snow, 1964).

Eleven races have survived, in most cases due largely to the difficult terrain of the islands and the longevity of the tortoises. Two races are definitely extinct, and have been for more than a century. The other two races are enigmatic (see Fig. 1). The single specimen found on Rábida in 1906 was probably an artificial introduction, and there are no substantiated grounds for considering that a native race ever occurred there (see Snow, 1964 for detailed argument). The race of Fernandina almost certainly existed at one time. A single male was collected in 1906 and droppings of one were found in 1964. However, 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 yet been examined. Whatever the status of this race, its fate has been determined by natural causes (most probably vulcanism), because man has never exploited Fernandina and no introduced animals occur there (Perry, 1970).

The status of the eleven surviving populations is quite variable. All have been reduced in total numbers and the total area of habitat now occupied has decreased from the original range in most cases. For some races, these reductions have been extremely severe; for others, much less so.

Table 1 summarizes the status of each race. Population size estimates are based on numerous visits to, and extensive surveys of, the habitat of each population by personnel of the National Park Service and the authors. However, they are intended only as rough estimates. It has not yet been possible to utilize more accurate mark recapture techniques because of the large areas involved, the lack of detailed maps where terrain and vegetation are very heterogeneous, and lack of personnel. The estimates for *G.e. microphyes* and *G.e. becki* are the least accurate; each is based on only three visits. The estimates for small to medium-sized tortoises provide some indication of the success of population replacement. The number of tortoises permanently marked in each population primarily reflects the amount of effort expended, rather than the population size; marking efforts have been concentrated mainly on races considered most endangered.

Feral competitors and predators now pose the most severe threats to the tortoise populations. The presence and effects of these mammals vary considerably from one tortoise population to another. In Table 1, the ferals are divided into primary and secondary threats. The former are known either to destroy large numbers of tortoise eggs and/or young, or to limit severely the amount of available vegetation; the latter are either known to cause lesser amounts of similar damage, or are suspected of being predators or competitors. Black rats, cats, pigs and dogs all destroy hatchlings and very small tortoises. Pigs and dogs kill tortoises up to 25 lbs in weight and occasionally may destroy even larger ones. Pigs very efficiently destroy nests, and in some situations dogs do the same. Goats are the worst competitors, especially with young tortoises; donkeys and cattle may also compete for food.

TABLE 1. Status of 11 known, surviving races of *G. elephantopus*, November, 1971. Y = Young; N = Nests.

Race	Location	Number Marked	Population estimates		Primary threats		
			Total	Small-med. sized	Feral animals	Stages affected	Secondary and potential threats
<i>hoodensis</i>	Española	11	20-30	None	Goats	Y	—
<i>ephippium</i>	Pinzón	100	150-200	None	Rats	Y	—
<i>chathamensis</i>	San Cristóbal	213	500-700	Very rare	Dogs	N, Y	Rats
					Cats	Y	Goats
					Donkeys	Y	
<i>darwini</i>	San Salvador	389	500-700	Very rare	Pigs	N, Y	Rats
					Goats	Y	Donkeys
<i>porteri</i>	Santa Cruz	1460	2000-3000	Moderate numbers	Pigs	N, Y	Rats
					Cats	Y	Man
					Goats	Y	Donkeys
<i>abingdoni</i>	Pinta	0	Very Small	?	Goats	Y	—
<i>vicina</i>	Cerro Azul	196	400-600	Very rare	Pigs	N, Y	Rats
					Dogs	Y	Man
					Cats	Y	Cattle
<i>güntheri</i>	Sierra Negra	219	300-500	Rare except in one area (see text)	Pigs	N, Y	Cats, Rats,
					Dogs	Y	Man, Goats, Cattle, Donkeys
<i>vandenburghi</i>	V. Alcedo	403	3000-5000	Numerous	?	?	Cats, Rats, Man, Donkeys
<i>microphyes</i>	V. Darwin	65	500-1000?	Numerous	?	?	Cats, Rats, Man,
<i>becki</i>	V. Wolf	0	1000-2000?	Numerous	?	?	Cats, Rats, Man

Human exploitation is now a relatively minor problem. Settlers occasionally slaughter tortoises of the *porteri* and *güntheri* populations. Poaching, for meat and oil and of live tortoises for the international export market, occurs to a limited extent in certain coastal areas of the *vandenburghi*, *microphyes*, *becki*, *vicina* and *porteri* ranges.

The races can be divided into four groups based on their status, as follows (see Table 1).

(1) *hoodensis* and *abingdoni*. These two races have extremely small populations. The Española population has apparently not bred for years; the density is so low (ten females, two males found in the past 9 years) that the animals never meet. 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 and Weber, 1964). The Pinta race has just been rediscovered (November, 1971), after several extensive searches in recent years had indicated no signs of living tortoises. One animal and signs of several others were found. The status of this race will require further investigation, but it is almost certainly similar to that of *hoodensis*. The vegetation of both islands has been extensively damaged by goats (see Weber, 1971 for details).

(2) *ephippium*, *chathamensis*, *darwini*, *vicina*, and *güntheri*. 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 mammal species. For example, the *ephippium* population on Pinzón consists of approximately 150 old tortoises; 64 per cent are mature females. In the past 10 years this population has produced several thousand hatchlings. Despite extensive searches, only a single 1-year old tortoise was found in this period. The *ephippium* nesting areas are littered with fragmented remains of hatchlings eaten by black rats, *Rattus rattus*. Although *güntheri* fits generally into this category, it deserves special mention. One population of the race, isolated (by human settlement) on the eastern part of Sierra Negra from the remainder, consists mainly of small and medium-sized animals. Few adults survive there, most having been killed by settlers in recent years. The only feral mammals in this area are goats.

(3) *porteri*. The main population of this race, in a tortoise reserve on the southwestern slopes of Santa Cruz, is quite large and contains moderately large numbers of small and medium-sized animals. However, several 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, though slowly. The other small, isolated population of the race, in the eastern sector of the island (Snow, 1964) now consists of only a few dozen tortoises. Its survival remains doubtful due to occasional human predation.

(4) *vandenburghi*, *microphyes* and *becki*. These populations are of large size and contain 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. Black rats and cats are present on all three volcanoes; their effects are unknown. Although this has not yet been demonstrated, the numerous donkeys on Volcán Alcedo may cause some nest destruction; their trails and dust wallows are present in tortoise nesting area.

Human exploitation of the tortoise populations has been notably decreased in the past few years, due to increased patrolling by the Servicio del Parque Nacional Galápagos, and more widespread education within the archipelago. Recent Ecuadorian laws prohibit both poaching and export of the tortoises from either the islands or continental Ecuador (MacFarland and Black, 1971). Enforcement remains a problem and more effective patrolling is required, especially in certain coastal areas of Isabela where most of the poaching occurs.

Ultimately, preservation of the tortoises, and the Galápagos environment in general, will require control, or elimination where possible, of the feral mammal populations. For most of these mammals, the only feasible method now available is systematic hunting. To date, the method has proved effective only with goats and pigs, and, for the former, only on the smaller islands. The National Park Service has eliminated goats from Santa Fé and markedly reduced their populations on Española, Marchena and Pinta. Similarly, pig populations have been reduced on San Salvador and Santa Cruz.

Where pigs are present, Park Service wardens protect tortoise nests with lava corrals, 1.5-2.0 m in diameter and 1 m high. The method has been almost 100 per cent successful in preventing nest destruction. Combined with effective control of pig populations by hunting, this method may prove to be sufficient for preserving certain races, e.g. *darwini* and *porteri*.

Systematic hunting requires frequent island visitation and great expenditures of manpower, time and funds. It is doubtful that the method could result in the elimination of either goats or pigs on the larger, more elevated islands with a diversity of vegetation zones. Judging from results on Cerro Azul, San Cristóbal, and Santa Cruz, the method is not feasible for controlling dogs or cats. Whether it would be effective against donkeys or cattle remains to be evaluated.

The possibilities of controlling or eliminating black rats, particularly on Pinzón, with anti-coagulant poisons or sterilization agents are currently under investigation.

BREEDING, RAISING, RESTOCKING PROGRAMMES

While additional control methods for feral mammals are being sought, the best interim preservation method is to raise young tortoises at the Darwin Research Station on Santa Cruz for eventual restocking of the native races.

The Darwin Station first initiated the programme in 1965, on a trial basis,

with the *ephippium* population. Since 1968 the programme has been a co-operative effort between the Darwin Station and the Servicio del Parque Nacional Galápagos (part of the Dirección de Desarrollo Forestal). Until very recently, the programme concentrated on only a few races because of lack of funds, personnel, and information concerning the status of some races; the data presented here reflect this concentration. Results from 1971 to 1972 are excluded, since data are currently being collected and analysed. Beginning with the 1972-73 breeding/nesting season, the programme will include all eight of the most endangered races, i.e., excluding only *vandenburghi*, *microphyes* and *becki*.

Two basic approaches are used. For the *hoodensis* population, which was reduced in size to the extent that mating was not occurring in the wild, a breeding colony was established at the Darwin Station. The same method is now being applied to *abingdoni*. For the races in which mating and nesting occur in the wild but feral predators destroy most of the nests and/or young (*ephippium*, *chathamensis*, *darwini*, *vicini*, *güntheri*), eggs are brought to the Station for incubation and raising of the hatchlings.

Since the *porteri* population is relatively large and therefore in less danger than most others, no concerted breeding and raising programme has been instituted. However, approximately 15-30 young per year-class are being raised in captivity for restocking of areas where poachers have depleted the population. These hatchlings derive from two sources: a small breeding colony at the Darwin Station (on display for visitors) and from nesting areas in the wild.

Breeding Colony Establishment

Over the past six years, one male and eight female *hoodensis* have been brought to the Darwin Station. The breeding enclosure is a large rectangular corral with lava walls measuring approximately 50 × 25 m; it is located in the typical coastal *Opuntia-fasminocereus* forest of Santa Cruz. It contains a large cement water pool and abundant natural shade; mud wallows are present occasionally after heavy rains. The tortoises are fed a combination of natural foods (*Opuntia* pads and fruits, *Commelina diffusa*, various grasses), introduced plants (otoy or *Xanthosoma* and grasses) and occasional fruits and vegetables.

As in most races in the wild, mating in the *hoodensis* group occurred from December to August, the peak period being February to June. It was not necessary to separate the male from the females for any period in order to produce successful matings.

One of the most important aspects of a breeding enclosure is the provision of proper nesting sites. On the basis of our observations of natural nesting areas of the *porteri*, *ephippium*, *darwini*, *microphyes*, *vicina*, *becki*, *güntheri* and *chathamensis* populations, it is considered that the sites should have the following characteristics:

- (1) The soil should be relatively fine and form an adhesive but workable mud when wetted by the copious urination of the female during excavation. The mud

facilitates digging, and results in a firm-walled and well-formed cavity, greatly reducing problems of cave-in. Sand or coarse, cloddy soils are improper substrates.

(2) Soil depth should be at least 25–40 cm and the surface area at least 3 sq. m in order to provide some freedom of movement for the female. Nest cavity depth is primarily determined by full extension of the female's rear legs, i.e., 25–35 cm depending upon racial and individual size variation.

(3) The soil should be rather vigorously tamped into place, layer by layer. This forms a solid working surface for the female, enhancing the excavation, and to some extent replicating natural sites.

The captive *hoodensis* females nested from late June to late November, approximately the same period as in wild populations of other races. Nesting

TABLE 2. Relationship of nesting success to soil type for and availability of artificial nesting sites for *G.e. hoodensis* in captivity at Darwin Station.

Year	Artificial nesting sites	No. of females	No. nights attempted nesting/clutch laid	No. clutches laid		
				On surface	Natural sites	Artificial sites
1967–68	None	1	20–30 ^a	2	0	—
1968–69	None	1	20–30 ^a	2	0	—
1969–70	3; soil coarse and cloddy	2	10–30	2	0	2
1970–71	4; soil fine and clay-like	3	1–4, rarely to 12	0	1	7
1971–72	4; soil fine and clay-like	6	1–4, rarely to 10	0	1	7

^a Not recorded accurately, approximate only.

attempts began in the late afternoon (1600–1800 h). Successful nesting required from 8 to 12 h. Except in rare instances, only one attempt per evening occurred.

During the 1967–68 and 1968–69 breeding seasons, the *hoodensis* females were not provided with artificial nesting sites; the few natural sites in the enclosure were small and surrounded by lava, lacking in depth and containing many obstructions (large stones); the soil was non-adhesive when wet. In 1969–70 three artificial sites were available, meeting the previously noted requirements, except that the soil was coarse and cloddy and thus had poor adhesiveness when wet. In 1970–71 four artificial sites were created using soil closely similar to that of natural nesting areas on Santa Cruz, and meeting all the previously noted requirements; the three 1969–70 sites were eliminated.

The lack of proper sites had marked effects (Table 2). During the first two breeding seasons, the females had great difficulty in excavating nest cavities.

They attempted to nest on successive evenings for long time periods, but obstructions and caving-in prevented nest completion; eventually the eggs were dropped on the lava surface of the enclosure. In 1969-70 almost all of the attempted nestings took place at the three artificial sites. However, caving-in was still a major problem resulting in long period of nesting attempts on successive evenings. Two nests were eventually made at these sites, but two clutches were also laid on the lava surface of the enclosure. During these first three nesting seasons, most eggs laid on the surface were destroyed by mockingbirds (*Nesomimus parvulus*) soon after being deposited. With the provision of proper soil type in the artificial sites (1970-71 and 1971-72), most nests were successfully

TABLE 3. Relationship of soil type of nesting sites to breakage or cracking of eggs during nesting, *G. elephantopus* (CDRS = Charles Darwin Research Station).

Race and location	Soil type of nesting sites	No. nests	No. eggs	% broken or cracked (No.)
Unspecified; San Diego Zoo (Shaw 1967)	sand	not stated, at least 3	44	66.0 (29)
<i>hoodnesis</i> (1969-70) CDRS	see Table 2	2	14	35.7 (5)
<i>hoodnesis</i> (1970-71, 1971-72) CDRS	see Table 2	19	112	4.5 (5)
<i>porteri</i> (1969-70, 1970-71) in wild	natural nesting areas	55	520	1.2 (6)
<i>ephippium</i> (1969-70, 1970-71) in wild	natural nesting areas	54	252 ^a	1.2 (3)

^a The 54 nests contained a total of 259 eggs; 7 were broken in 3 nests when a second female nested at a site where another nest already existed.

constructed at those sites and the number of evenings of attempted nesting per clutch laid decreased greatly. The females which had demonstrated great difficulty in nesting during the first 3 years, as well as females new to the enclosure in either of the latter two breeding seasons, constructed functional nests without difficulty.

Poor quality soil also results in a large proportion of eggs being broken or cracked during nesting. Provision of artificial sites with proper soil results in low percentages of breakage and cracking, comparable to those noted for nests of other races made in the wild (Table 3). Breakage and cracking of eggs by the *hoodnesis* females occurred during two parts of the nesting process: (1) just at the end of egg laying, when the females alternately inserted the rear feet, gently rearranging the eggs into more or less a single layer, and (2) during the first stages of covering the eggs with soil. When the soil was of poor quality, excessive caving-in resulted in insecure footing at these stages of the nesting process and

damage to many of the eggs occurred. In wild populations of *porteri* and *ephippium*, the same behaviour patterns occur during nesting, but egg breakage or cracking is extremely rare. Apparently the same factors resulted in a high percentage of breakage and cracking on a sand substrate at the San Diego Zoo, although Shaw (1967) attributed it partly to the laying process, i.e. the eggs striking one another during laying. However, in both the *hoodensis* colony and *porteri* and *ephippium* in the wild, this factor was unimportant. The eggs are encased in a thick, gelatinous fluid which maintains connection with the cloacal opening, thereby slowing their descent and cushioning them on impact. Breakage or cracking due to striking another egg or the cavity floor occur rarely.

Egg handling

Excavation of the nests in the Darwin Station breeding enclosure is essential because of the high probability of egg damage due to nest interference, i.e. more

TABLE 4. Relationship of age at handling to fertility and hatching success of six clutches, *G.e. hoodensis*, 1970-71, in captivity.

Time between laying and handling (h)	No. eggs in clutch	No. definitely fertile	No. dead embryos	No. hatched	No. added
9-12	6	2	1	1	4
15-18	5	4	0	4	1
15-18	1 ^a	1	0	1	0
15-18	7	6	2	4	1
87-90	6	6	1	5	0
109-112	7	5	0	5	2

^a 3 eggs in clutch, 2 broken.

than one nest being made at the same site. The surface of the enclosure consists primarily of lava, and only four artificial sites are available. In 1971-72, for example, seven of eleven nests were made at the same site.

Nests are usually excavated on the day following their construction. The eggs are weighed and measured in the laboratory and then placed in incubators. During these operations, the eggs are carried, in glass containers, a distance of approximately 200 m. The tops of the eggs are marked during excavation and they are carefully maintained in this same position throughout the handling process and incubation periods.

Fertility and hatching rates for six *hoodensis* nests, 1970-71, indicate no drastic damage to the eggs if they are excavated and handled during the first 109-112 h after being laid (Table 4). It seems unlikely that the handling process accounts for the four dead embryos; all were from several weeks to several months old at death. It is not possible to evaluate the 25 per cent (8) value for

addled eggs, because no data are available from the wild for *hoodensis*.* It thus remains possible that handling resulted in the destruction of a small percentage of fertile *hoodensis* eggs.

The same marking, weighing, and measuring procedures are applied to eggs brought from natural nesting sites. They are transported in metal cans, with sawdust packing. However, the eggs are subject to considerable tilting during transport, first for 1–6 h by backpack over rough trails and then for 5–14 h in fishing boats.

TABLE 5. Relationship of age of eggs at transport to fertility and hatching success, *G.e. ephippium* 1969–70 and 1970–71; data for undisturbed wild nests of *G.e. porteri*, 1969–70 and 1970–71 included for comparison.

Transport	No. nests	No. eggs	No. eggs excluded ^a	No. eggs incubated	% definitely fertile (No.)	% hatched (No.)	% dead embryos (No.)	% addled (No.)
<i>G.e. porteri</i>								
None	55	520	7	513	80.3 (412)	76.2 (391)	4.1 (21)	19.7 (101)
<i>G.e. ephippium</i>								
None	26	133	8	125	85.6 (107)	82.4 (103)	3.2 (4)	14.4 (18)
10–15 weeks old	16	71	13	58	82.8 (48)	74.1 (43)	8.6 (5)	17.2 (10)
7–9 weeks old	2	6	0	6	66.7 (4)	66.7 (4)	0 (0)	33.3 (2)
4–6 weeks old	6	29	3	26	50.0 (13)	19.2 (5)	30.8 (8)	50.0 (13)
0–2 weeks old	5	27	0	27	29.6 (8)	18.5 (5)	11.1 (3)	70.3 (19)

^a Excluded for various reasons, i.e. broken in laying or by nest interference, or (for transported clutches) broken by observer or found hatched in nest.

In order to evaluate the relationship of age at transport and addling, eggs from the *ephippium* population were brought to the Darwin Station for incubation at various ages (0–15 weeks). Transport was for 1–2 h by backpack and 5–6 h by boat. The younger the eggs at the time of transport, the greater the percentage of addling, or conversely, the lower the percentage which were definitely fertile (Table 5). Compared to the percentage addled for non-transported eggs in wild nests, these results strongly suggest that the transport process destroyed significant percentages of the younger eggs. Other possible factors, such as the time of laying during the nesting season (August–December) were eliminated by transporting eggs of varying ages at various times (October, December, January, February). When the eggs were transported at 10–15 weeks of age, at which time the embryos were well developed, the percentage definitely fertile

* Throughout this paper addled is defined as a liquified egg, i.e. either infertile or the embryo having died before attaining sufficient size to be detectable.

was little lower than for eggs left in the wild, and the percentage of dead embryos increased only slightly. Hatching occurred at 12–17 weeks of age, the variability being due to the time when the nests were made and the continually rising temperature of the macroclimate from August to March (see below).

This experiment with *ephippium* eggs demonstrates that it is feasible to maintain high fertility and hatching percentages if eggs are transported only late in their incubation period. This technique is now being applied to other tortoise races. Nesting areas are visited frequently (every 1 to 8 weeks); the age of a nest is determined in part by its degree of moistness, and by careful handling of eggs against sunlight.

Incubation

The incubators are constructed of wood, the interiors being cement-lined cavities measuring 58 × 58 × 50 cm depth. The bottom of the cavity is filled with fine soil to a depth of 12 cm. The eggs are slightly embedded in this soil. Level with the eggs are two insulated wooden doors, one with a glass panel behind it for viewing, the other for access to the cavity. Above the soil is a 15 cm air space, then a corrugated asbestos sheet 0.3 cm thick supporting 9 cm of soil, then a 13 cm air space. The chamber is topped by a metal sheet (0.1 cm thick) with its exterior painted dull black (Fig. 2).

The incubators are naturally heated and continual humidity control is practised. The soil is lightly sprinkled with water when the eggs are first placed in the chamber. Thereafter, a bowl of water is maintained in the chamber throughout incubation. Aeration occurs every 2 to 3 days when the access door is opened for a few minutes. A mercury thermometer, readable to 0.5°C through the glass panel, measures air temperature inside each chamber. Incubator temperatures are not checked on a precise schedule. However, they were recorded at least once (often 2–4 times) almost every day from early July to the end of March, 1969–70. During any given month, temperatures were checked on numerous occasions at all hours from 0500 to 2000 h. While permitting no precise evaluation of temperature cycling, the ranges of temperatures for each month were established. Daily maxima usually occurred between 1700–1900 h, minima between 0500–0800 h. During 1970–71, incubator temperatures were checked less often, but the same trends appeared as in 1969–70.

Incubation periods in these chambers were quite variable, the length depending upon the time of nesting. Two major seasons occur in the Galápagos (see Bowman, 1961 for details): the *garúa* season (June–December) with frequent cloud cover and misty rain, and the hot season (January–May) with infrequent cloud cover, occasional heavy showers (only in some years), and intense solar radiation. A general warming trend occurs from August through March, the sharpest rise in temperatures occurring from mid-December through late March.

The data resulting from incubation of six *hoodensis* clutches in 1970–71 (Fig. 3) show that the earlier a nest is laid during the nesting season, the longer

the incubation period. Changes in macroclimatic temperatures from July to March correlate well with these results; temperatures within the incubator chambers follow the same upward trend.



FIGURE 2. Front view of the naturally heated incubators at the Darwin Station.

As expected, incubation periods in the wild demonstrated the same relationship. For *porteri*, they varied from 250 to 110 days, for nests ($N = 15$) made from late June to early December; for *ephippium*, from 120 to 85 days for nests ($N = 6$) made from late September to mid-November.

Temperatures from natural nests of *porteri* and *ephippium* in the wild fell within the range of those measured in the Station incubators, but were much less

variable (Fig. 4). The *porteri* eggs in the wild were subjected to temperatures near the incubator minimum, but no high temperatures; the reverse occurred for the *ephippium* eggs.* No evidence exists that the wider range of incubator temperatures causes egg damage, but more data are needed to evaluate this possibility.

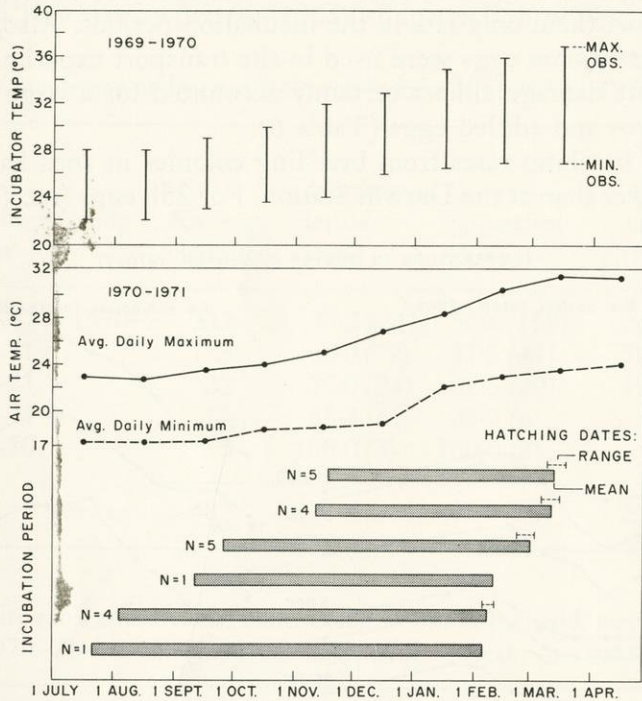


FIGURE 3. Dependence of length of incubation period on time during nesting season when nest is made; data for six *G.e. hoodensis* nests in incubators at Darwin Station; N = no. eggs hatched. Average daily temperature maxima and minima were taken at 2 m in a standard weather shield; monthly range for incubator temperatures (1969-70) established as indicated in the text.

Hatching and fertility rates

Fertility and hatching rates were high for eggs left *in situ* in wild nests of *ephippium* and *porteri* (Table 5). Since the eggs had not been disturbed, these percentages of added eggs can be used as rough estimates of natural infertility rates.

Combined results for all eggs incubated at the Station, for the years 1966-67 to 1970-71,† demonstrate notably lower fertility and hatching rates and higher

* The *porteri* and *ephippium* nesting situations are considered typical of the range of conditions found among the tortoise races: The Santa Cruz nesting areas (*porteri*) have more total daily cloud cover at any given time of year than those on Pinzón (*ephippium*). Santa Cruz is one of the larger, wetter, more elevated islands; Pinzón is representative of the smaller, lower, drier islands.

† Data excluded for *ephippium*, 1965-66, because the number of eggs incubated was not recorded, and for two *hoodensis* nests, 1969-70, and two *hoodensis* nests, 1970-71, because eggs were clearly abnormal and infertile; i.e. very thin-shelled, ovoid in shape and enlarged.

percentages of dead embryos and addled eggs (Table 6) than for nests of *porteri* and *ephippium* in the wild (Table 5). However, most of the eggs incubated at the Station were those transported by boat from the *ephippium* and *darwini* populations. The eggs of *darwini*, and *ephippium* 1966–67 to 1968–69, were of unknown, but greatly variable, ages when transported; no special care was taken to transport them only late in the incubation periods. Also, the 1969–70 and 1970–71 *ephippium* eggs were used in the transport experiments described above. Transport damage almost certainly accounted for a large proportion of the dead embryos and addled eggs (Table 6).

Fertility and hatching rates from breeding colonies in zoos have been quite variable, but lower than at the Darwin Station. For 258 eggs (race(s) unspecified)

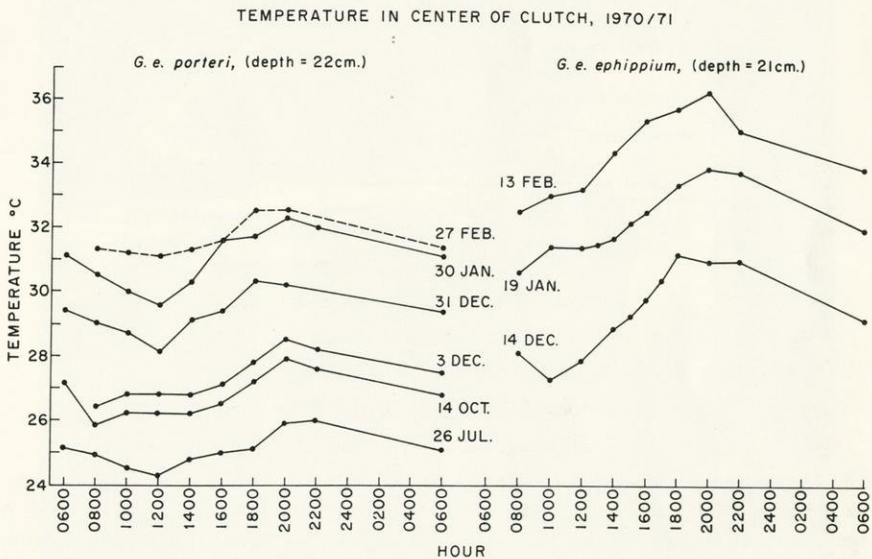


FIGURE 4. Temperatures, recorded by thermocouples, within nests in the wild. *G.e. porteri* nest made 20–21 June, 1970; *G.e. ephippium* nest made approximately 30–31 October, 1970.

at the San Diego Zoo, 10.42 per cent were fertile and 6.97 per cent hatched (Shaw, 1967); for 191 eggs of *vicina* at the Honolulu Zoo, 32.46 per cent were fertile, 31.10 per cent hatched (Throp, 1969). The reasons for these low rates are unknown. Throp notes that fertility rates were high in viable clutches but were zero in many others.

On the Galápagos, complete infertility or low fertility rates were rare for individual clutches of *ephippium* and *porteri* left *in situ* in the wild (Table 7).

Raising, mortality and growth

Young *G.e. ephippium* from the year-classes 1965–66 to 1967–68 were raised, until January, 1970 in large chicken-wire cages located just above sea level and 25 m inland from the high tide line. Because of the cage structure and surrounding vegetation, the pens received very limited solar radiation. At night

throughout the year and during part of most days of the garúa season, the pens were exposed to strong, cool breezes. Water was provided *ad libitum*. Food consisted of green roughage, native grasses, *Commelina diffusa*, introduced grasses, and occasionally, partially-dried *Opuntia* fruits.

The 1968–69 *ephippium* year-class was raised in the laboratory; heat and light were provided 10 h/day by two 60–100W tungsten light bulbs, and no exposure

TABLE 6. Results of incubation at Darwin Research Station 1966–67 to 1970–71.

Race	Breeding/Nesting seasons	No. eggs incubated	% definitely fertile (No.)	% hatched (No.)	% dead embryos (No.)	% added (No.)
<i>ephippium</i>	1966–67 to 1970–7	312	77.2 (241)	50.6 (158)	26.6 (83)	22.8 (71)
<i>darwini</i>	1970–71	118	61.0 (72)	37.3 (44)	37.3 (44)	39.0 (46)
<i>hoodensis</i>	1970–71	32	75.0 (24)	62.5 (20)	12.5 (4)	25.0 (8)
<i>porteri</i>	1970–71	17	35.3 (6)	35.3 (6)	0 (0)	64.7 (11)
<i>chathamensis</i>	1969–70	3	100.0 (3)	100.0 (3)	0 (0)	0 (9)
TOTALS		482	71.8 (346)	47.9 (231)	23.9 (115)	28.2 (136)

TABLE 7. Fertility rates of individual clutches left *in situ* in the wild, *porteri* and *ephippium*, 1969–70 and 1970–71 data combined; cf. Table 5; \bar{x} = mean, s = standard deviation.

Race	No. eggs incubated/clutch			No. clutches with % definitely fertile					
	\bar{x}	range	s	0	1–24	25–49	75–50	99–74	100
<i>porteri</i>	9.3	5–16	2.6	2	2	3	11	18	19
<i>ephippium</i>	4.8	2–8	1.6	1	0	0	4	6	15

to cool breezes occurred. Food and water conditions were as for the previous groups.

In January 1970 all year-classes were moved to a new tortoise raising centre, constructed mainly with funds provided by the San Diego Zoological Society. All year-classes of 1969–70 and later, of all races, have been raised entirely within this centre. Each year-class of each race is maintained unexposed to sea breezes; a battery of six 100W tungsten light bulbs provides heat and light 10 h/day in one corner of each pen. Water is provided *ad libitum* 2 days/week; food is as previously described.

Between early 1966 and November 1971, 266 tortoises were hatched at the Station and 67 hatchlings were brought there from nests in the wild. Of the 333

young tortoises, 104 (31.2 per cent) had died by August, 1972. However, 3 per cent of the deaths resulted from accidents, e.g. killed by rats.

Most natural deaths, regardless of race or year-class, occurred during the first 9 months of life (Table 8). Mortality was apparently caused by digestive difficulties; food accumulated in the intestines, eventually resulting in infection and degeneration of the intestinal lining. Infrequent solar radiation and the cool

TABLE 8. Natural mortality rates and age and mortality relationships for the breeding and raising programme, CDRS, 1965-66 to August 1972; hatchlings which died accidentally are excluded.

Race and year class	No. hatchlings	% mortality (No.)	Number died						> 18 mth	
			0-3 mth	3-6 mth	6-9 mth	9-12 mth	12-18 mth			
<i>G.e. ephippium</i>										
1965-66	35	17.1 (6)	N/R	N/R	N/R	N/R	N/R	N/R	N/R	Seaside pens
1966-67	43	51.2 (22)	9	9	3	1	0	0	0	
1967-68	46	50.0 (23)	9	2	4	0	8	0	0	
1968-69	12	25.0 (4)	0	4	0	0	0	0	0	Tortoise house or laboratory
1969-70	38	21.1 (8)	4	3	0	0	1	0	0	
1970-71	21	29.9 (6)	4	0	1	1	0	0	0	
<i>G.e. hoodensis</i>										
1970-71	20	5.0 (1)	1	0	0	0	0	0	0	Tortoise house or laboratory
<i>G.e. porteri</i>										
1970-71	20	10.0 (2)	0	1	1	0	0	0	0	
<i>G.e. darwini</i>										
1970-71	61	18.0 (11)	3	8	0	0	0	0	0	Tortoise house or laboratory
TOTAL	296	27.7 (82)								

N/R = not recorded

winds at the seaside pens used earlier increased the frequency of such digestive problems.

In general, survival rates were markedly higher for those year-classes, regardless of race, raised from hatching in the tortoise centre or laboratory as compared to those raised in the seaside pens during the first 18 months or more of life (Table 8). Excluded from Table 8 are data from three races (6 year-classes) with extremely small sample sizes (3-7 hatchlings).

Figure 5 illustrates the growth rate for the first year-class of tortoises raised at the Station, *G.e. ephippium* 1965-66. Age was determined as the approximate median, because hatching occurred over a 3-month period from late December to late March. Unfortunately, the tortoises were not weighed at hatching. However, the average weight at hatching (79.7 g.; range, 56.8-101.8; $s = 9.3$)

of the 1969–70 *ephippium* year class is given as an approximation. Curves for the other races and year classes raised in captivity are very similar.

Data on growth rates of young tortoises in the wild are very limited. During the first 8 months of life in 1971, two sets of wild young *porteri*, each consisting of four siblings, had average growth rates approximately 1.6 and 1.4 times greater than hatchlings of the same and other races raised at the Station.

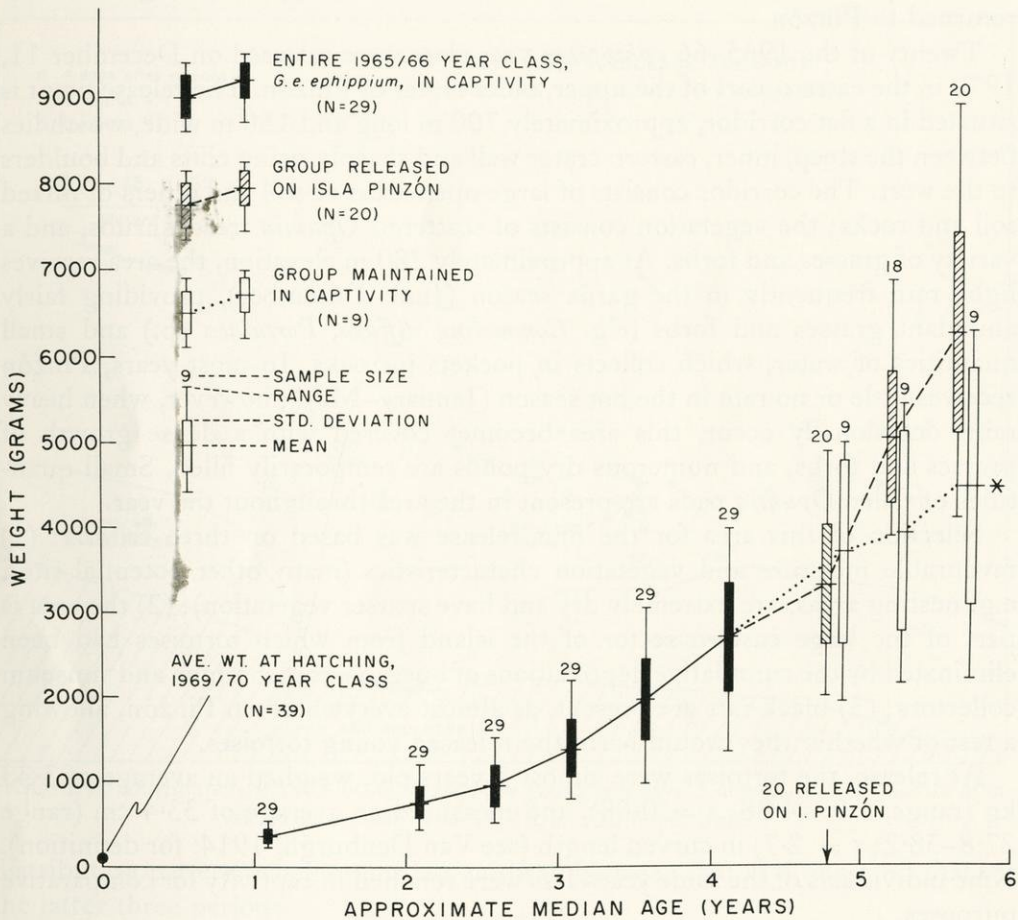


FIGURE 5. Growth curve for 1965–66 year-class, *G.e. ephippium* raised in captivity at Darwin Station. * Symbols for range and standard deviation shifted slightly to the right for clarity.

The low growth rates in captivity at the Station may be due primarily to the lack of natural solar radiation in the raising pens. Water is available in greater quantities than in the wild. Although the young receive primarily natural foods, a greater variety could certainly improve growth rates and probably reduce mortality. Very low mortality rates and high growth rates have been achieved at the Honolulu Zoo with young *vicina* which are fed lettuce, fruit, and Gaine's Dog Meal (Throp, 1972; personal communication). At present, dietary changes

are being considered, and exterior balconies, where solar radiation will be available, are being added to each pen of the tortoise raising centre.

Return to the wild

Through August, 1972, a total of 302 young tortoises had been or were being raised at the Station, as follows: 148 *ephippium*, 25 *hoodensis*, 28 *porteri*, 71 *darwini*, 29 *vicina* and 1 *chathamensis*. Of these, 71 *ephippium* young have been returned to Pinzón.

Twenty of the 1965–66 *ephippium* year-class were released on December 11, 1970 in the eastern part of the upper, older crater of Pinzón. The release point is situated in a flat corridor, approximately 700 m long and 150 m wide, which lies between the steep, inner, eastern crater wall and sharply rising cliffs and boulders to the west. The corridor consists of large open areas of soil and others of mixed soil and rocks; the vegetation consists of scattered *Opuntia* trees, shrubs, and a variety of grasses and forbs. At approximately 280 m elevation, the area receives light rain frequently in the garúa season (June–December), providing fairly abundant grasses and forbs (e.g. *Commelina diffusa*, *Portulaca* sp.) and small quantities of water, which collects in pockets in rocks. In most years, Pinzón receives little or no rain in the hot season (January–May); however, when heavy rains occasionally occur, this area becomes covered with a dense growth of grasses and forbs, and numerous dry ponds are temporarily filled. Small quantities of fallen *Opuntia* pads are present in the area throughout the year.

Selection of this area for the first release was based on three criteria: (1) favourable moisture and vegetation characteristics (many other potential sites, e.g. nesting areas, are extremely dry and have sparser vegetation); (2) the area is part of the large eastern sector of the island from which tortoises had been eliminated by the cumulative depredations of buccaneers, fishermen and museum collectors; (3) black rats are present, as almost everywhere on Pinzón, allowing a test of whether they would harm the released young tortoises.

At release, the tortoises were almost 5 years old, weighed an average of 3.33 kg (range, 1.99–4.88; $s = 0.68$), and measured an average of 33.4 cm (range 27.8–38.2; $s = 2.7$) in curved length (see Van Denburgh, 1914, for definition). Nine individuals of the same year-class were retained in captivity for comparative purposes.

The young were watched for several hours immediately after release and for several days thereafter for 2–4 h per day. Their behaviour did not apparently differ from that of young wild *porteri*. Within a few minutes of release, they were feeding on several species of forbs, engaging in agonistic displays, and generally wandering over the area. Beginning with the first evening, they constructed the typical shallow night-time burrows under small shrubs or grass clumps in loose soil.

They were relocated, weighed, measured, and examined 1, 2, 5 and 10 months after release. No sign of rat attack or injury was detected. After 10 months in the wild, every individual had approximately doubled in weight.

Their growth rate was markedly higher than for the nine in captivity (see

Fig. 5). The mean weights for the two groups were not significantly different near the release date, but were so for the weights taken at 5 and 10 months after release (two-tailed t -test, $p < 0.4$, $p < 0.05$, $p < 0.01$, respectively).

Overall dispersal of the group was not great during the 10 months after release (Fig. 6). Although the total area of distribution was greater at each re-mapping period, little difference existed between 2, 5, and 10 months. In fact, after only 4 days, much of the dispersal had occurred. After 1 month, the

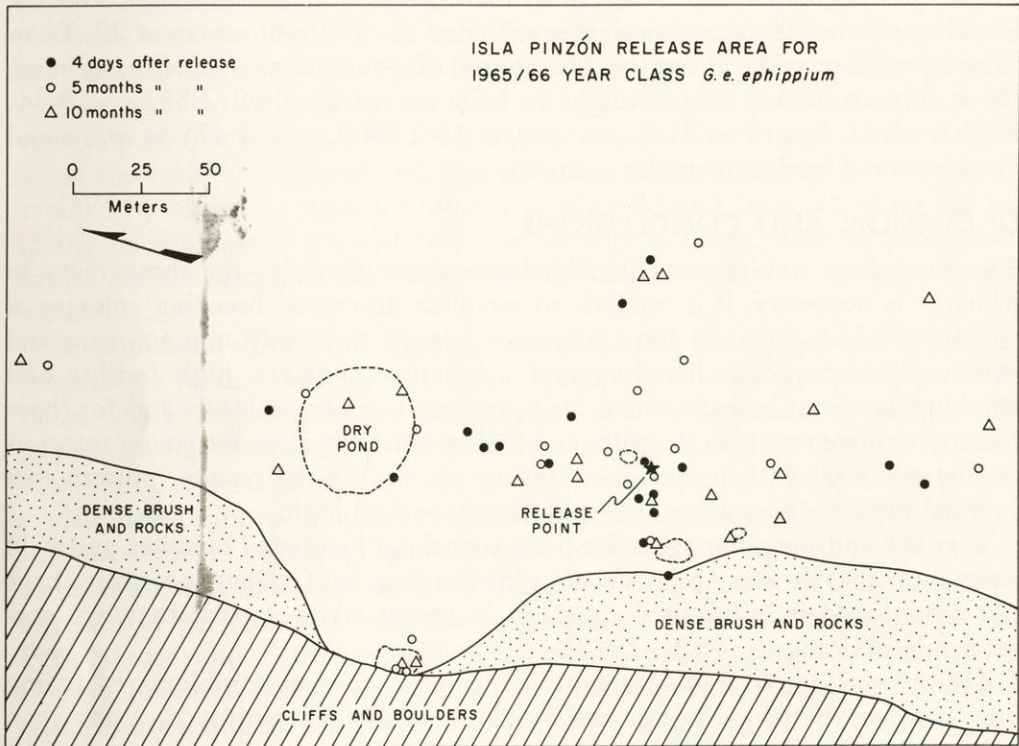


FIGURE 6. Distribution of 1965-66 *G. e. ephippium* young at 4 days, 5 months, and 10 months after release on Pinzón; N = 18, 18, and 20 respectively.

distribution pattern was more or less midway between that at 4 days and that of the latter three periods.

In general, the same individuals were found in the same part of the release area at the 1, 2, 5 and 10 month visits. The daily movements of individuals observed during these visits were usually restricted to an area of 400 sq. m or less.

This contrasted notably with the daily and longer term movements of wild *porteri* individuals of the same size in lowland nesting zones on Santa Cruz during the extremely dry hot season of 1970. They covered areas of up to 1000 sq. m daily while foraging and were found at locations up to 500 m apart from one month to the next.

The limited dispersal of *ephippium* young was possibly due to climatic conditions and the resultant abundance of vegetation on Pinzón during the 10

months. Heavy rains in early March provided a lush growth of forbs and grasses which were present from mid-March to late May. Forbs were moderately abundant during other months.

In October 1971, 51 additional young were released in three groups on Pinzón. Two groups, the nine remaining 1965-66 and the entire 1966-67 year-classes, were placed in dry nesting zones on the island's outer flanks. Dispersal and daily and seasonal movements of these groups will be compared to the 1965-66 group of 20. The entire 1967-68 year-class was released on the island's eastern side in an area similar to that of the 1965-66 group of 20. Their survival will provide a test of the ability of younger and smaller tortoises ($N = 23$; at release mean weight = 1.54 kg, range 0.90-2.35, $s = 0.34$; mean curved length = 21.2 cm, range 18.2-24.0, $s = 1.47$) to withstand black rats and environmental conditions.

DISCUSSION AND CONCLUSIONS

The preceding results emphatically demonstrate that, (1) for those races in which it is necessary, it is possible to establish functional breeding colonies of *Geochelone elephantopus* in the Galápagos Islands with only minimal care and effort; (2) with proper handling and incubation methods, high fertility and hatching rates can be maintained for eggs from breeding colonies and for those transported from nests in the wild, and (3) low mortality rates for young tortoises can be achieved with proper care during raising. Initial results indicate that survival rates of the young, after restocking, will be high.

Fertility and hatching rates for both artificially incubated clutches and wild nests show that there is no justification for the idea that Galápagos tortoises have not reproduced in substantial numbers in recent times or that they are now incapable of doing so (Shaw, 1967).

However, the programme faces numerous future tests and problems. Hatching rates and survivorship during raising can certainly be improved. Long-term survival rates and reproductive success of restocked tortoises remain to be evaluated. It may be necessary to raise the young of those races threatened by pigs or dogs to a relatively large size before releasing them in the wild. Complete elimination or substantial control of feral animals will be required, otherwise the current "nursemaiding" procedures for most or all of the endangered races will be required indefinitely. Estimates of the carrying capacity of the various islands or volcanoes and reproductive potential and mortality rates for the tortoise populations must be made in order to avoid overstocking.

There are numerous advantages to conducting such breeding, raising and restocking programmes in the Galápagos rather than establishing breeding colonies in North America, Europe or other locations. Natural climatic conditions and easily available natural habitat, food species, and nesting soils eliminate most of the reproductive, veterinary, dietary and special housing problems encountered in foreign locations. Costs are low and efficiency high: no long-distance transport of adults for breeding colonies and young for re-

stocking is required; food and housing expenses are minimal. Since eggs for most endangered races can be brought in large numbers from the wild, total production of young is high for the time, effort and funds invested.

Inbreeding and genetic drift pose great potential problems for almost all breeding programmes with captive species, because the original parental generation usually consists of only a small number of individuals. Even the building up of a large colony of apparently "normal", interbreeding individuals from a small number of parents is not *prima facie* evidence that such genetic problems have not occurred. In such situations, the variability of the gene pool has certainly been reduced. Such individuals, though healthy and reproductive in the controlled artificial environment of a zoo, may have low or reduced survivorship and/or reproductive success after return to their native habitat.* For six of the eight endangered Galápagos tortoise races, these problems are being avoided by obtaining eggs from nests in the wild and then returning the offspring to their native populations. The attempt is being made to locate more adults for the *hoodensis* and *abingdoni* breeding colonies to increase genetic variability.

An additional significant advantage of conducting the raising and restocking programme in the Galápagos is its potential educational and public relations value. Guides demonstrate the various stages of the programme to visitors in the tortoise raising centre and at the breeding enclosures and incubators. In 1972, 4000–5000 tourists (approximately 15–20 per cent Ecuadorians) were expected to visit these facilities. A number of local inhabitants work within the programme, and many others visit the Darwin Station to observe its operation. Visitors are made aware that conservation of the Galápagos environment in general, and the tortoises in particular, is now the responsibility of the Ecuadorian National Park Service, and that the effort is being aided by the internationally supported Darwin Research Station, research by scientists, and the funds and interest of organizations and individuals from many parts of the world. The tortoise conservation programme thus serves as a prime example of what needs to be done to preserve what remains and to reclaim some of what has been lost or altered in the Galápagos.

We suggest that, perhaps in the majority of cases, such advantages would make it far more effective to invest most time, manpower, and funds in the establishment of education programmes, habitat and population status studies and breeding/raising centres for endangered species in or near their native habitats rather than in other locations. Of course, in some cases other factors make this impossible, e.g. warfare, other political problems, or virtual total habitat destruction. In such cases, a viable breeding nucleus in a safer location may be the main hope for preserving a species. However, we question whether

* Experiments testing survivorship and reproductive success in native habitats, of populations bred and raised in captivity from a small parental generation, are of immediate importance. A wide variety of vertebrate species should be tested and non-endangered species should be used.

the alternatives are seriously considered for many endangered species when breeding colonies are planned and established and funds raised, especially in North America and Europe. Whether some environmentalists, zoo personnel and animal suppliers like it or not, the survival of most endangered species and their habitats ultimately depends upon the interest and involvement of the people and governments of the native areas, albeit with international aid and cooperation in most cases. We suggest that more zoos and their sponsoring societies should follow the lead of the few, e.g. the San Diego and New York Zoological Societies, and begin expending a substantial proportion of their funds on the preservation of endangered species in their native habitats. Vast opportunities exist for sponsoring status surveys, ecological and ethological field studies, educational programmes, establishment of reserves, training of native personnel, and the construction of breeding/raising facilities for endangered species.

We do, of course, assert that effort should be made to establish successful breeding colonies with Galápagos tortoises already captive in zoos and private collections. They could serve the primary function of supplying tortoises to other zoos and private collectors on a world-wide basis. Although most zoos no longer attempt to obtain Galápagos tortoises from the islands or continental Ecuador, some private collectors still provide a market for illegal poaching and export activities. Captive-bred tortoises could help eliminate this market.

Unfortunately no completely accurate census of Galápagos tortoises in zoos and other collections exists. For 1971, the *International Zoo Yearbook* reported a total of 278 in 61 collections (Lucas and Duplax-Hall, 1972). However, most collections contain only one to a few individuals and the race of most specimens is unknown. Cooperative exchange among collections will be necessary and racial lines should be kept pure, even if it requires excluding large numbers of unidentified specimens from breeding programmes. It would be most advantageous to return specimens of the extremely rare races, i.e. *hoodensis* and *abingdoni*, to the breeding colonies in the Galápagos in order to increase genetic variability. If only one or a few specimens of a less rare race exist in captivity, it would be most useful to return these to the natural populations in the Galápagos. The New York Zoological Society returned an adult *G.e. ephippium* female in 1971, an act which resulted in much publicity and goodwill both on the Galápagos Islands and in continental Ecuador.

Whenever breeding colonies can be formed with reasonably large numbers of captive adults of single races, such should be supported. As reported elsewhere in this volume, Jack Throp, Chairman of the Giant Tortoise Committee of the Wild Animal Propagation Trust is currently coordinating such a programme, and has had considerable success in breeding and raising *G.e. vicina* at the Honolulu Zoo. Of course, whenever significant numbers of tortoises are produced by breeding colonies of endangered races, such as the Honolulu *vicina* group, they could be used both for supplying collections and restocking of Galápagos populations.

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