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# The Galápagos Giant Tortoises (*Geochelone elephantopus*) Part II: Conservation Methods\*

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## ABSTRACT

Eight of the 11 surviving races of Galápagos tortoises are threatened due to decreased population sizes and predation and/or competition by introduced mammals. Systematic hunting has been effective for controlling and even eliminating goats on the less elevated, more sparsely vegetated, smaller islands and for controlling pigs, even on some of the larger islands. However, the method has been ineffective against dogs and cats and it is doubtful that it could be used to eliminate goats or pigs on the more elevated, larger islands which have a diversity of vegetation zones. Alternative control or extermination methods are being sought and tested for these feral mammals and black rats. In an attempt to increase yearly recruitment of hatchlings, lava corrals have been constructed around nests, resulting in almost 100 per cent success in preventing nest destruction by pigs; but the method was ineffective against dogs. While other control methods are being sought, young of the endangered races are being hatched and raised in captivity for restocking of endemic populations. During the past seven years, improved and highly successful techniques have been found for (1) establishment of breeding colonies and construction of artificial nesting sites, (2) transport of eggs from wild nests, (3) incubation of eggs, and (4) raising of young in captivity. By August 1972, 231 young of six races were being raised, and 71 4-5-6-5 year old captive raised tortoises released on Pinzón in 1970 and 1971 were in good condition and growing rapidly. The advantages of conducting the breeding/raising programme in the Galápagos rather than foreign locations are discussed.

## INTRODUCTION

Part I of this report (MacFarland *et al.*, 1974) summarized the status of the 11 surviving races of the Galápagos tortoise (*Geochelone elephantopus*). Briefly, although conditions vary considerably from race to race, eight are more or less severely threatened, 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. The other three races, each consisting of relatively large populations, are still poorly known, but they may be endangered due to predation by cats and black rats.

Three conservation methods have been and are being employed to preserve the tortoise races: (1) control, and extermination where possible, of introduced mammal populations; (2) protection of tortoise nests to prevent predation by pigs or dogs; (3) raising of young of the rarer races in captivity for restocking of endemic populations.

This paper evaluates these procedures, the results being based on cooperative research efforts of the Servicio del Parque Nacional Galápagos (SPNG; 1968-present), the Charles Darwin Research Station (1965-present), and the senior author and Dr W. G. Reeder of the University of Wisconsin, Madison (1969-present).

## CONTROL OF INTRODUCED MAMMALS

For most of the introduced mammals the only feasible control method now available is systematic hunting. Strong, effective poisons could be easily passed on in food chains, *e.g.*, to native carrion feeders and predators such as the Galápagos hawk and owls. Disease introduction could lead to infection of domestic animals or humans; even with adequate safeguards, it would be unwise politically at this time.

Systematic hunting requires frequent island visitation and large expenditures of manpower, time and funds. For example, it required over 1.5 years of concentrated effort, *i.e.*, 5-10 day hunting periods, by 3-6 men, every 6-8 weeks, to eliminate goats (approximately 560 animals) from comparatively small, low, and sparsely vegetated Santa Fe. Similar intensive hunting campaigns with .22 calibre rifles (and sometimes dogs) by the SPNG have resulted in other successes: (1) goats were apparently eliminated on Rábida in October, 1971; (2) goat populations have

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been reduced to less than 100 individuals on Marchena and less than 500 on Española; (3) over 18,000 goats, probably one-half of the population, were killed on Pinta during three visits between November 1971 and June 1972; and (4) pig populations have been greatly reduced on San Salvador and in the Tortoise Reserve on Santa Cruz.

It is unlikely that either goats or pigs could be exterminated by systematic hunting on the larger, more elevated islands which have a diversity of vegetation zones, e.g., San Salvador, Santa Cruz, Isabela. Both species become gun-shy and it is extremely difficult to cover adequately larger areas of broken terrain. Unless other methods are found, continual control will have to be practised.

Results on Cerro Azul (Isabela), San Cristóbal, and Santa Cruz have demonstrated that systematic hunting is not feasible for control of dog or cat populations. Both species are difficult to locate and approach. Other possibilities such as trapping or shooting at bait stations will be tested.

No attempts have been made yet to control donkeys or cattle.

The possibilities of controlling or exterminating black rats, especially on Pinzón, with anticoagulant poisons or sterilization agents are currently under investigation (Kramer, 1973).

#### PROTECTION OF TORTOISE NESTS

##### *Against Pigs*

Nests are protected by corrals constructed of large lava stones and measuring 1.5–2 m in diameter and 1 m high. Corrals of these dimensions prevent entry by pigs, yet do not block solar radiation from reaching the soil surface throughout almost all of the daylight hours.

The method was applied on a limited scale, i.e. 10–25 nests protected per year, to the Santa Cruz race (*porteri*) during the nesting seasons of 1964/65–1969/70. None of these nests were destroyed by pigs.

Beginning with the 1970/71 nesting season, corrals have been used much more extensively. The major nesting areas of the *porteri*, *vicina*, and *darwini* populations are visited every 1–4 weeks throughout the period when females are laying (June–December). Some nests are still destroyed, either because they are made in scattered sites outside of the main areas, or are made and subsequently found by pigs between visits; however, most are being protected. Of 262 nests of these three races protected in the 1970/71 and 1971/72 nesting seasons, only one was destroyed (Table I).

TABLE I  
*Results of Protecting Tortoise Nests with Lava Corrals to Prevent Predation by Pigs*

Location	Race	Nesting season	No. nests protected	No. protected nests destroyed
Santa Cruz	<i>porteri</i>	1970/71	46	1
		1971/72	115	0
San Salvador	<i>darwini</i>	1970/71	38	0
		1971/72	31	0
San Pedro area, Cerro Azul, Isabela	<i>vicina</i>	1971/72	32	0

In contrast, it was rare for an unprotected nest to last throughout the incubation period (3–8 months) without being destroyed by pigs. Results from one nesting area on Santa Cruz provide a striking example. Because no pig sign was evident, nests were marked but left unprotected during once a month visits over a six-month period in 1970. However, sometime between the sixth and seventh month visits, 23 of the 29 marked nests were destroyed. Signs in the area indicated that a single pair of pigs was responsible. They had apparently not passed by five of the unharmed nests which were located singly in scattered sites on the periphery of the nesting area; the sixth had been partially dug into, but not destroyed. Subsequently all nests encountered in this area have been protected; none of the 90 protected in the 1970/71 and 1971/72 nesting seasons were damaged, even though pigs frequented the area.

The corrals are utilized for two purposes. Eggs from some protected nests of the *vicina* and *darwini* populations are transported to the Darwin Station for hatching and raising of young. The corrals allow the nests to be protected soon after being made and then left undisturbed until late in the incubation period when transport results in only very low mortality of the well-developed embryos (see the following section). Additionally, the protected *porteri* nests and some from the *vicina* and *darwini* populations are left undisturbed and the young allowed to hatch and escape naturally. Many of the hatchlings are being marked in order to quantify survivorship. The predation rate on them by pigs will certainly be high, but hopefully the greatly increased recruitment of hatchlings will result in survival of larger numbers. This experiment began in 1971 and the data are insufficient to warrant conclusions.

Those populations of *güntheri* in which pigs are known to destroy nests have been insufficiently explored. Extensive examination of the habitat will

begin in 1972 in order to locate major nesting areas and protect nests.

#### Against Dogs

Four *chathamensis* nests were protected with lava corrals (dimensions as described above) in 1971. Unfortunately, dogs jumped into the corrals and destroyed the nests. Since it is desirable to transport eggs only late in their incubation period, other protection methods will be sought. In 1973/74 wire mesh cages placed over the nest and embedded in the soil will be tested as a preventative.

#### BREEDING, RAISING, AND RESTOCKING

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

Until recently the effort was concentrated on only a few races due to lack of funds, personnel and information concerning the status of some races. The data presented here reflect this concentration and cover the 1965/66–1970/71 breeding/nesting seasons, except where noted. Data for 1971/72 and 1972/73 are still being analyzed. Beginning with the 1973/74 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 for restocking of areas where poachers have depleted the population. These hatchlings are from a small breeding colony at the Darwin Station and from nesting areas in the wild.

#### Breeding Colony Establishment

Over the past seven years, one male (Fig. 1) and ten female *hoodensis* have been brought to the Darwin Station. The breeding enclosure is a large rectangular corral (50 × 25 m) with lava walls approximately

1.5 m high. It is located in the typical coastal *Opuntia-Jasminocereus* forest of Santa Cruz and 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.

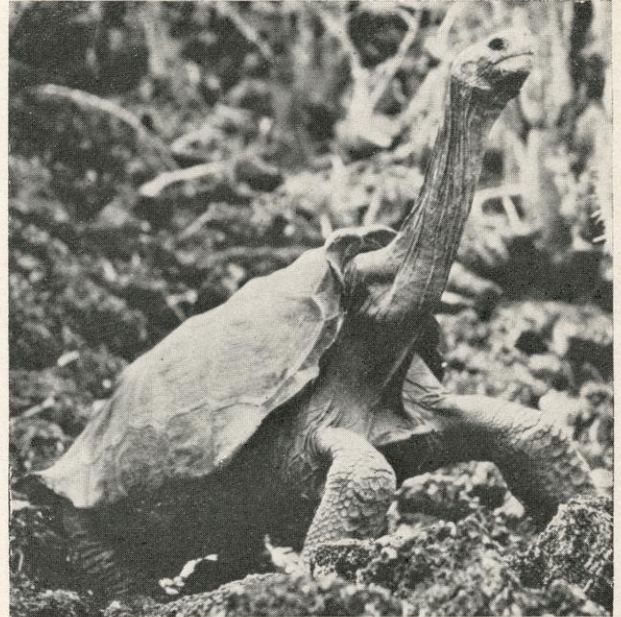


Fig. 1. Adult male *G. e. hoodensis* in breeding enclosure at Charles Darwin Research Station. Photo: National Geographic Society.

As in most races in the wild, mating in the *hoodensis* group occurred from December to August, the peak period being February to June. For captive *vicina* at the Honolulu Zoo, Throp (1969) reported that when the sexes were left together throughout the year, the females were unreceptive and clamped their bodies to the ground during mating attempts; but, after a six-month separation, the females reared up on their hind legs, allowing successful mating. We have observed scores of mating attempts in wild populations of *porteri*, *vandenburghi* and *ephippium* and in the *hoodensis* colony, but no instance of such 'rearing-up' behaviour by females was observed. In our experience, a female almost always tries to escape from the male, by swivelling or inching forward beneath him. If the male is persistent, the female most often eventually becomes passive and copulation is completed. No indication has been noted that females were more likely to become passive at certain times of the year. However, males generally sought females more actively and were more persistent during the peak period. It has not been necessary to separate the

captive *hoodensis* males and females in order to produce successful matings.

One of the most important aspects of a breeding enclosure is the provision of proper nesting sites. Based on our observations of natural nesting areas of the *porteri*, *ephippium*, *darwini*, *microphyes*, *vicina*, *becki*, *güntheri* and *chathamensis* populations, 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 the excavation. The mud facilitates digging, greatly reduces problems of cave-in, and results in a firm-walled and well-formed cavity. Sand or coarse, cloddy soils are improper substrates.

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

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

The captive *hoodensis* females nested from late June to late November, approximately the same period as in wild populations of other races. Successful nesting required from 8–12 hours. Nesting attempts began in late afternoon (1600–1800 hours). If obstructions were present or excessive caving-in occurred, the female abandoned the attempt, usually after 2–4 hours of excavation. Except in rare instances, only one attempt per evening occurred. By the time the female ceased an attempt it was usually dark, and no attempts were ever begun after dark.

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 contained many obstructions (*e.g.* 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, cloddy, and had poor adhesiveness when wet. In 1970/71 four artificial sites were created using soil virtually identical to that of natural nesting areas on Santa Cruz, and meeting all the previously noted criteria; the three 1969/70 sites were eliminated.

The lack of proper sites had marked effects (Table II). During the first two breeding seasons, the females 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 time periods of nesting attempts on successive evenings. Two nests were eventually made at these sites, but two clutches were laid on the lava surface. During these first three nesting seasons, most eggs laid on the surface were destroyed by mockingbirds (*Nesomimus parvulus*) the morning after being deposited. With the provision of proper soil type in the artificial sites (1970/71 and 1971/72), most nests were successfully 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 three 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

TABLE II  
Relationship of Nesting Success to Soil Type and Availability of Artificial Nesting Sites; *G. e. hoodensis* in Captivity at Darwin Station

Year	Artificial nesting sites	No. ♀♀	No. nights attempted nesting/clutch laid	No. clutches laid		
				on surface	natural sites	artificial sites
1967/68	none	1	20–30*	2	0	—
1968/69	none	1	20–30*	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	10

\* Not recorded accurately, approximate only.

TABLE III  
*Relationship of Soil Type of Nesting Sites to Breakage or Cracking of Eggs During Nesting*

<i>Race and location</i>	<i>Soil type of nesting sites</i>	<i>No. nests</i>	<i>No. eggs</i>	<i>Percent broken or cracked (No.)</i>	
unspecified; San Diego Zoo (Shaw, 1967)	sand	not stated, at least 3	44	66	(29)
<i>hoodensis</i> (1969/70); Darwin Station	see Table II	2	14	35.7	(5)
<i>hoodensis</i> (1970/71, 1971/72); Darwin Station	see Table II	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*	1.2	(3)

\* 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.

in low percentages of breakage and cracking, comparable to those noted for nests of other races made in the wild (Table III). Breakage and cracking of eggs by the *hoodensis* 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 and damage to many eggs occurred. In wild populations of *porteri* and *ephippium*, the same behaviour patterns occur during nesting, but egg breakage and cracking are 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) also attributed it partly to the eggs striking one another during laying. However, in both the *hoodensis* colony and *porteri* and *ephippium* in the wild, breakage or cracking due to striking another egg or the cavity floor occur rarely. 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.

#### Egg Handling

Excavation of the nests in the breeding enclosure is essential because of the high probability of egg damage due to nest interference, *i.e.* more than one nest being made at the same site. In 1971/72, for example, 7 of 11 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 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 hours after being laid (Table IV). It seems unlikely that the handling process accounts for the four dead embryos; all were from several weeks to

TABLE IV  
*Relationship of Age at Handling to Fertility and Hatching Success of Six Clutches, hoodensis, 1970/71, in Captivity*

<i>Time between laying and handling (hrs)</i>	<i>No. eggs in clutch</i>	<i>No. definitely fertile</i>	<i>No. dead embryos</i>	<i>No. hatched</i>	<i>No. addled</i>
9–12	6	2	1	1	4
15–18	5	4	0	4	1
15–18	1*	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

\* 3 eggs in clutch, 2 broken.

several months old. 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*.<sup>†</sup> However, for unhandled eggs in wild nests of *ephippium* and *porteri*, 14.4 per cent and 19.7 per cent were addled, *i.e.*, probably mostly infertile, respectively (Table V). 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

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

TABLE V

Relationship of Age of Eggs at Transport to Fertility and Hatching Success, ephippium, 1969/70 and 1970/71; Data for Undisturbed Wild Nests of porteri, 1969/70 and 1970/71, included for Comparison

Transport	No. nests	No. eggs	No. eggs excluded*	No. eggs incubated	Per cent definitely fertile (No.)	Per cent hatched (No.)	Per cent dead embryos (No.)	Per cent 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 (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)

\* 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.

considerable tilting during transport, first for 1-6 hours by backpack over rough trails and then for 5-14 hours in fishing boats.

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 hours by backpack and 5-6 hours by boat. The younger the eggs at the time of transport, the greater the percentage of addling (Table V). 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 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 in age, the variability being due to the time when the nests were made and the continually warming macroclimate from August to March (*see* the following).

In order to maintain high fertility and hatching percentages, the technique of transporting eggs only late in their incubation period 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 candling 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 exterior painted dull black.

The incubators are naturally heated and continual humidity control is practised. The soil is lightly sprinkled when the eggs are first placed in the chamber. Thereafter a bowl of water is maintained in the chamber throughout incubation. Aeration occurs every two to three 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 0500-2000 hours. While permitting no precise evaluation of temperature cycling, the range of

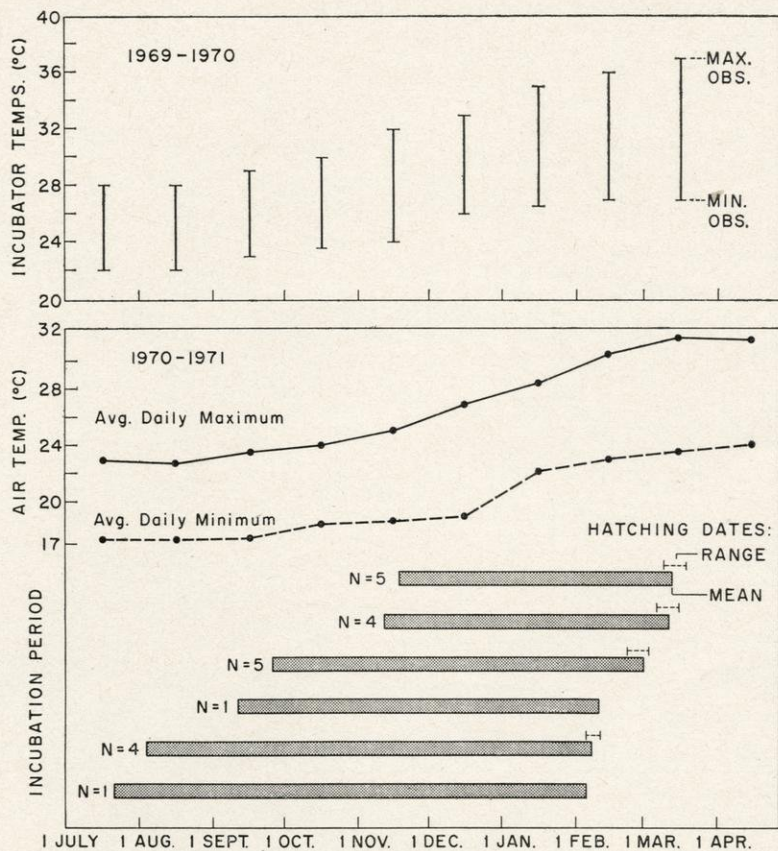


Fig. 2. Dependence of length of incubation period on time during nesting season when nest is made; data for six *G. e. hoodensis* nests in incubators at Darwin Station;  $N =$  no. eggs hatched. Average daily maxima and minima taken at 2 m in standard weather shield; monthly range for incubator temperatures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

temperatures for each month was established. Daily maxima usually occurred between 1700–1900 hours, minima between 0500–0800 hours. 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. 2) 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.

As expected, incubation periods in the wild demon-

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

Temperatures from 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. 3). 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.

#### Hatching and Early Post-hatching Care

In 1969/70 and 1970/71, hatching dates, for eggs of *ephippium*, *hoodensis*, *darwini*, *chathamensis*, and

\* 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*).



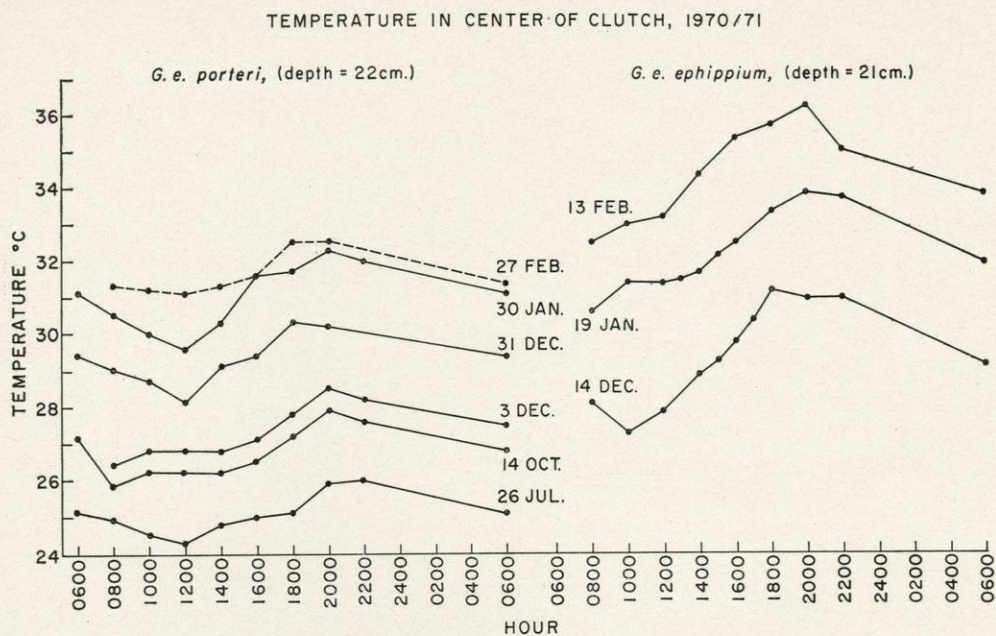


Fig. 3. Temperatures, recorded by thermocouples, from within nests in the wild. *G. e. porteri* nest made 20–21 June 1970; *G. e. ephippium* nest made approximately 30–31 October 1970.

*porteri*, extended from early November to the first week of April.

It was especially important to allow adequate time for hatching among sibling eggs. The first signs of hatching, pips in the shell, were usually visible in all eggs of a single clutch within 0–6 days (based on 16 *ephippium* clutches, 1969/70 and 1970/71, 1 *porteri* clutch, 1970/71, and 3 *hoodensis* clutches, 1970/71). However, in some exceptional *ephippium* clutches, hatching of the first and last egg began up to 25 days apart (e.g., clutch of 5 eggs, 13 days; clutch of 2 eggs, 16 days; clutch of 2 eggs, 22 days; clutch of 3 eggs, 25 days).

The time required for the hatching process was also quite variable, both within and among clutches (Table VI). Although the data were collected for only a limited number of clutches, it is clear that 4–7 days may often be required for the hatching process. Occasionally, it was obvious after 9–12 days that a

hatchling was having great difficulty escaping from the egg. In 1969/70, in five such instances (all *ephippium*) the shell was carefully removed; three of the hatchlings appeared premature, i.e., notably smaller than normal, but from eggs of average size. Only one of the five (premature) has since died.

After hatching, the young were kept in a dark chamber in the laboratory for 4–10 days while the large, exposed, somewhat fragile yolk sac was regressing. When it was no longer visible, they were transferred to raising pens.

#### Hatching and Fertility Rates

Fertility and hatching rates were high for eggs left *in situ* in wild nests of *ephippium* and *porteri* (Table V). 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 eggs incubated at the Station,

TABLE VI  
Time Required for Hatching Process (first pip to emergence) in Incubators at Darwin Station

Race	No. clutches	No. eggs	Hatching dates	Hatching time (days)		
				$\bar{X}$	Range	Greatest range for sibling eggs
<i>ephippium</i> 1969/70 and 1970/71	13	30	31 Dec.–20 Mar.	3.5	0.8–7.5	2.5–7.4
<i>hoodensis</i> 1970/71	3	9	20 Feb.–15 Mar.	4.2	3–6	3–6

TABLE VII  
Results of Incubation at Darwin Station, 1966/67–1970/71

Race	Breeding/nesting seasons	No. eggs incubated	Per cent definitely fertile (No.)	Per cent hatched (No.)	Per cent dead embryos (No.)	Per cent addled (No.)
<i>ephippium</i>	1966/67–1970/71	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)	23.7 (28)	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 (0)
	Totals	482	71.8 (346)	47.9 (231)	23.9 (115)	28.2 (136)

1966/67–1970/71,\* demonstrate notably lower fertility and hatching rates and higher percentages of dead embryos and addled eggs (Table VII) than for nests of *porteri* and *ephippium* in the wild (Table V). However, transport damage almost certainly accounted for a large proportion of the addled eggs and dead embryos: the eggs of *darwini* and *ephippium*, 1966/67–1968/69 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.

Fertility and hatching rates from breeding colonies in zoos have been much lower than at the Darwin Station. For 258 eggs (race unspecified) 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, 1972). The reasons for these low rates are unknown. Throp (1972) notes that fertility rates were high in viable clutches but were zero in many others.

Complete infertility or low fertility were rare for individual clutches of *ephippium* and *porteri* left *in situ* in the wild (Table VIII).

Limited data are available on the fertility of multiple clutches laid by a single female in one nesting season (Table IX). For undisturbed *porteri* nests in the wild, both clutches laid by a single female in one nesting season were at least partly fertile. For *hoodensis* clutches laid in captivity and handled as previously described, each female laid one clutch of very abnormal (thin shelled, oversized, ovoid in shape), completely infertile eggs; their other clutches (normal-sized, nearly spherical eggs) all showed at least partial fertility.

\* Data excluded for *ephippium*, 1965/66 because 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.

#### Raising, Mortality and Growth

Young *G. e. ephippium* from the year classes 1965/66–1967/68 were raised, until January, 1970, in large chicken-wire cages located just above sea level and 25 m inland from the high tide line. Due to 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 hours/day by two 60–100 watt tungsten light bulbs, and no exposure 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 (*see* Perry 1970, photographs), and all year classes of 1969/70 and later, of all races, have been raised entirely within it. There is no exposure to sea breezes, and a battery of six 100-watt tungsten light bulbs provides heat and light 10 hours/day in one corner of each pen. Water is provided *ad libitum* two 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 were due to accidents, *e.g.*, killed by rats.

Most natural deaths, regardless of race or year class, occurred during the first 9 months of life (Table X). 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 winds at the earlier used seaside pens, increased the frequency of such digestive problems.

TABLE VIII

Fertility Rates of Individual Clutches Left in situ in the Wild, 1969/70 and 1970/71 Data Combined: cf. Table V;  
 $\bar{X}$  = mean,  $s$  = standard deviation

Race	No. eggs incubated/clutch			No. clutches with per cent definitely fertile of					
	$\bar{X}$	range	$s$	0	1-24	25-49	50-74	75-99	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

TABLE IX

Fertility of Multiple Clutches Laid by Single Females in One Nesting Season, 1970/71; Undisturbed *porteri* Clutches in Wild, *hoodensis* Clutches Laid in Captivity

♀ No.	Nest No.	Date laid (1970)	No. eggs	No. damaged in laying	No. definitely fertile	No. hatched	No. dead embryos	No. added
<i>porteri</i>								
127	1	21 June	11	0	10	10	0	1
	10	30 Aug.*	10	0	8	7	1	2
131	3	12 Aug.	6	0	1	1	0	5
	50	26 Oct.*	11	1	10	10	0	0
787	2	1 Aug.	9	0	8	8	0	1
	16	16 Sept.	9	0	6	6	0	3
<i>hoodensis</i>								
14,001	1	12 July	7	0	0	0	0	7
	3	3 Aug.	5	0	4	4	0	1
	5	25 Sept.	7	0	5	5	0	2
	8	14 Nov.	6	0	6	5	1	0
14,006	2	31 July	6	0	2	1	1	4
	4	21 Sept.	7	0	0	0	0	7
	7	12 Nov.	7	0	6	4	2	1

\* Approximate dates,  $\pm 2$  days.

TABLE X

Natural Mortality Rates and Age and Mortality Relationships for the Breeding and Raising Programme, 1965/66–August 1972. Hatchlings which Died Accidentally are Excluded

Race and year class	No. hatchlings	Per cent mortality (No.)	Number died (months)					
			0-3	>3-6	>6-9	>9-12	>12-18	>18
<i>G. e. ephippium</i>								
SEASIDE PENS								
1965/66	35	17.1 (6)			Not recorded			
1966/67	43	51.2 (22)	9	9	3	1	0	0
1967/68	46	50.0 (23)	9	2	4	0	8	0
TORTOISE HOUSE OR LABORATORY								
1968/69	12	25.0 (4)	0	4	0	0	0	0
1969/70	38	21.1 (8)	4	3	0	0	1	0
1970/71	21	28.9 (6)	4	0	1	1	0	0
<i>G. e. hoodensis</i>								
1970/71	20	5.0 (1)	1	0	0	0	0	0
<i>G. e. porteri</i>								
1970/71	20	10.0 (2)	0	1	1	0	0	0
<i>G. e. darwini</i>								
1970/71	61	18.0 (11)	3	8	0	0	0	0
	296	27.7 (82)						

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 X).

Figure 4 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 three-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.

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 would 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 instituted, and exterior balconies, where solar radiation is more available, have been 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 11 December 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

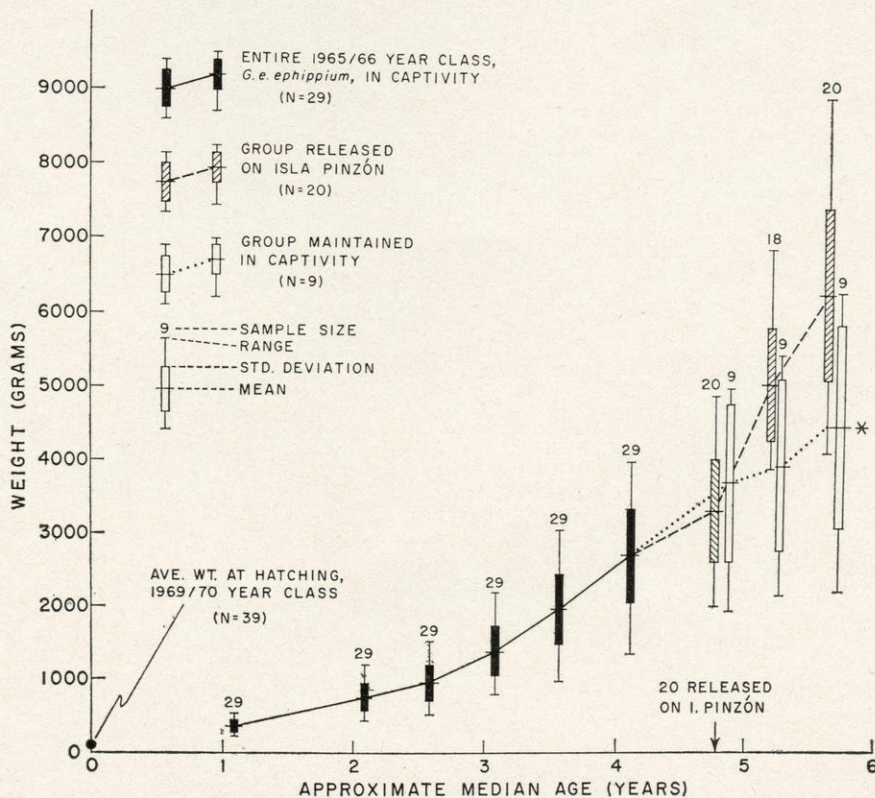


Fig. 4. Growth curve for 1965/66 year class *G. e. ephippium* raised in captivity at Darwin Station; \* symbols for range and standard deviation shifted slightly to the right for clarity.

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 temporarily fill. 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 young tortoises.

At release, the tortoises were almost five 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 hours per day. Their behaviour did not differ apparently 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 re-located, weighed, measured, and examined one, two, five and ten months after release. No sign of rat attacks or injury was detected. After ten months in the wild, every individual had approximately doubled in weight.

Their growth rate was markedly higher than for the nine in captivity (Fig. 4). The mean weights for the two groups were not significantly different near the release date, but were so at five and ten 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 ten months after release (Fig. 5). Although the total area of distribution was greater at each re-mapping period, little difference existed between two, five,

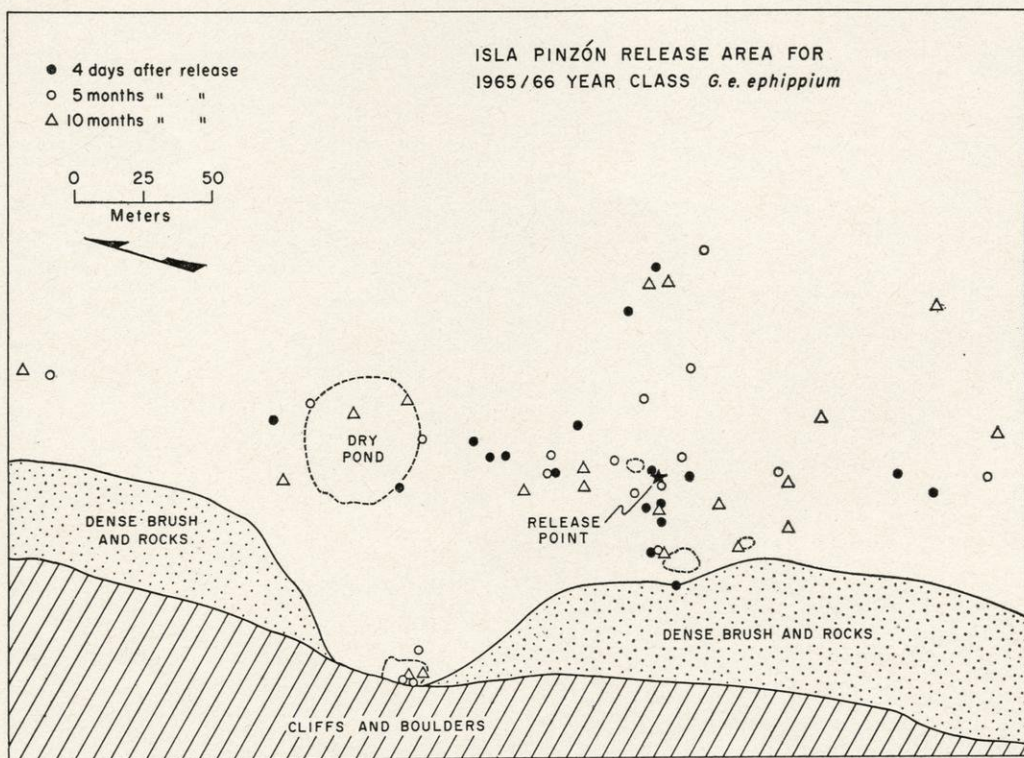


Fig. 5. Distribution of 1965/66 *G. e. ephippium* young at four days, five months, and ten months after release on Pinzón;  $N = 18, 18$  and  $20$  respectively.

and ten months. In fact, after only four days, much of the dispersal had occurred. After one month, the distribution pattern was more or less mid-way between that at four 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 one, two, five, and ten month visits. The daily movements of individuals observed during these visits were usually restricted to an area of 400 m<sup>2</sup> 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 1,000 m<sup>2</sup> 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 ten 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.

Twelve of these young were located during a brief reconnaissance of this area 17 months after their release in May 1972. They had all gained substantially in weight and size and were in fine physical condition.

In October 1971, 51 additional young were released in three groups on Pinzón. Two groups, the 9 remaining 1965/66 and the 1966/67 (N = 19) 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 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.

Initial results from these releases are encouraging. During a brief visit to the areas in May 1972, the following numbers were located, measured, weighed and examined: 2 of the 1965/66 group of 9; 4 of the 1966/67 year class; 12 of the 1967/68 year class. They had all increased greatly in size and weight and had no signs of injury or ill health.

#### DISCUSSION

The preceding results emphatically demonstrate that (1) it is possible to establish functional breeding colonies of *Geochelone elephantopus* in the Galápagos

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 'nursemaid' procedures will have to be continued indefinitely. Estimates of the carrying capacity of the various islands or volcanos 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 restocking 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. For six of the eight endangered Galápagos tortoise races, these problems are avoided by obtaining eggs and/or hatchlings 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 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 1973, 5,000–6,000 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 SPNG, and that the effort is being aided by the internationally supported Darwin 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 reclaim some that has been lost or altered in the Galápagos.

We do, of course, assert that every 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. Captive-bred tortoises could help eliminate the illegal international trade which still exists.

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 & Duplaix-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 unknown 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 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. Jack Throp, Chairman of the Giant Tortoise Committee of the Wild Animal Propagation Trust, is currently coordinating

such a programme among zoos in the United States, and has had considerable success in breeding and raising *G. e. vicina* at the Honolulu Zoo (Throp, 1972). 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.

#### ACKNOWLEDGEMENTS

Funding for the work performed by the SPNG and Darwin Station came from many organizations, in particular the Government of Ecuador, the World Wildlife Fund, the Smithsonian Institution, the New York Zoological Society, the San Diego Zoological Society, the Frankfurter Zoologische Gesellschaft, and the California Academy of Sciences. Many individuals contributed funds which made conservation efforts much more effective. The senior author's research was supported by grants to W. G. Reeder from the National Science Foundation, Grant No. GB-12256, and the National Geographic Society. Many individuals contributed much time and effort to these conservation programmes; in particular, we thank former conservation official Juan Black and the wardens of the SPNG, the personnel of the Darwin Station, and Jan MacFarland and Tjitte DeVries. William G. Reeder and Peter Kramer offered many helpful suggestions concerning the manuscript. Cheryle Hughes prepared the drawings and Don Chandler processed photographic materials.

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#### Dr David L. Lack, FRS

As Professor Niko Tinbergen has commented, 'Oxford without David Lack; the [Edward Grey Institute of Field Ornithology] without its stimulating leader—is hard to accept. The full significance of his untimely death will only gradually be realised, but the magnitude of his achievement is clear.' Born in London in July 1910, the oldest of the four children of a leading surgeon, David Lack was educated principally at Gresham's School, Holt, Norfolk ('chosen', he himself wrote, 'for its modern approach to science and its encouragement of hobbies'), where his contemporaries included several others who were to make their mark later in life, and at Magdalene College, Cambridge, where he read principally zoology but could not rise above the second class. Yet he became a shining example of how little such gradings matter for the real enthusiast who, endowed with good ability and sufficient persistence, knows precisely what he wants to do—in his case, ornithology. In this his field-work ranged from the Arctic to the tropics, and his main books were concerned with bird populations and regulation of numbers, ecological adaptation and the effects of isolation, and other aspects which were not without their conservational implications.

In 1945, at the age of 35, Lack became that *rara avis*, a professional ornithologist with a salary of £500 pa on taking over the directorship of the Edward Grey Institute at Oxford, remaining in that position for the rest of his life—and gracing it in many notable ways. Somewhat incongruously the Institute was housed with Charles Elton's Bureau of Animal Population in part of the former main building of the University Department of Botany in the ancient Botanic Garden, which it was always a nostalgic pleasure to revisit, and where Lack seemed to be in his element—when not in the field—with the passages rambling and birds twittering outside. His qualities and attainments are well brought out in the tributes paid in the obituary columns of *Ibis* (Vol. **115**, pp. 431–41, 1973), by Alan L. Hodgkin, L. S. V. VENABLES, Ernst Mayr, Alister C. Hardy, W. H. Thorpe, and Niko Tinbergen, to which it would be presumptuous on our part to try to add. Although his books and papers were not

primarily conservational in emphasis, his feeling for our subject made him a valued Consulting Editor of *Biological Conservation*, always ready to referee a paper, give needed advice, or answer a query promptly and meticulously. His early death is a grievous loss to us all.

The accompanying photograph (Fig. 1) shows Dr Lack in a jovial mood not so long ago, and makes it difficult for colleagues to realize that he is no longer with us. It is therefore gratifying to note that the Council of the British Ornithologists' Union 'has decided to commemorate his life and works by raising a fund for studentships in field ornithology bearing his name', for which generous contributions are sought. They should be sent to the British Ornithologists' Union (David Lack Studentships), c/o Zoological Society of London, Regent's Park, London NW1, England.

N. POLUNIN

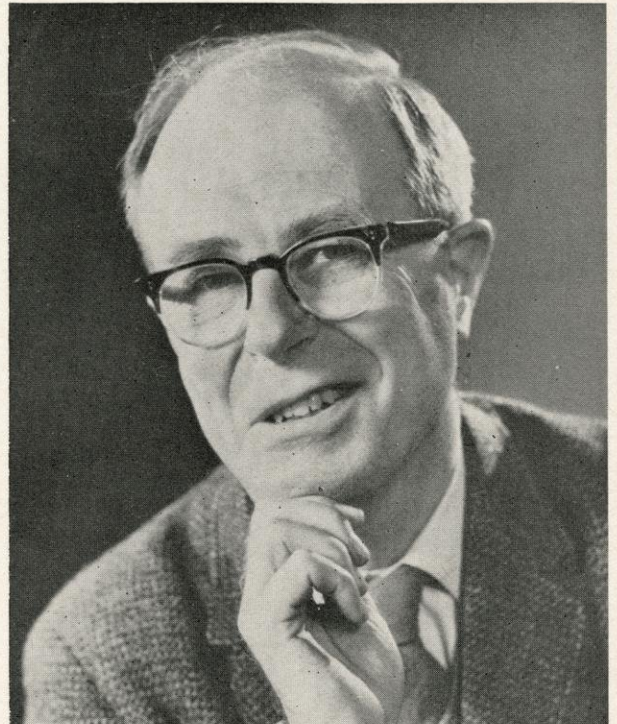


Fig. 1. Dr David L. Lack, FRS. Photo: Ramsay & Muspratt, Oxford.