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# GALÁPAGOS TOMATOES AND TORTOISES

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One of the several unique features of tomatoes native to the Galápagos Islands—*Lycopersicon esculentum* var. *minor* (*L. cheesmanii* var. *minor*) and related forms—is seed dormancy. Less than one per cent of their seeds, which are notably smaller than those of other known tomatoes, will germinate without treatment. Germination of up to ten per cent can be obtained with var. *minor* if part of the seed coat is carefully excised (Rick, 1956). The present report deals with attempts to break the seed dormancy and, particularly, to find mechanisms in the native environment that might account for germination and establishment there of the Galápagos tomatoes.

Recently, improved germination of these forms was sought by trying methods that are familiar to horticulturists for their effectiveness in breaking seed dormancies of various plant species. We found that soaking seeds for various periods in stagnant or well-aerated water, subjection of dry or wet seeds to various temperatures or combinations of temperatures, and acid treatments were ineffective in raising emergence percentages. Following the discovery by Benedict and Robinson (1946) of the improved germination of guayule seeds effected by sodium hypochlorite treatments and successful applications of this method by Taylor (1949) to celery and by Laude (1951) to smilo grass, we tested its effectiveness on seeds of LA166, one of the most refractory of our Galápagos collections. Four lots were started: (1) control; (2) seed coats partly excised; (3) one-hour soaking in 2.6% sodium hypochlorite solution (half-strength household bleach); (4) soaking for two hours in the same strength solution. Seeds

of treatments 3 and 4 were thoroughly rinsed after exposure to hypochlorite. Germination was tested on moist blotting paper kept in plastic sandwich boxes. Treatment 3 removed most of the seed coat, partly exposing endosperm and embryo, while treatment 4 removed even more of the tissues. Most of the emergence occurred in the first eight days after sowing. After 15 days, the per cent germination in each lot was as follows: (1)—0, (2)—24, (3)—71, (4)—8. It is evident from these results and from the appearance of treated seeds that damage had resulted from the two-hour treatment (4). It has been our recent experience with certain other Galápagos accessions that seeds which fail to respond to a one-hour treatment may be induced to germinate by repeated treatments of half-hour and one-hour duration. Seedlings have been observed literally to pop out of the seed coats within minutes after these repeated treatments as if they had been simply unable to break through the seed coats. The one-hour treatment has become a standard procedure in our work and has continued to effect marked improvement in germination of the Galápagos accessions and also collections of the tomato species *L. peruvianum* and *L. chilense* as well as of the nightshades, *Solanum pennellii* and *S. lycopersicoides*.

Although the hypochlorite treatment provides a neat solution to the problem of germinating Galápagos tomato seeds, it does not solve the problem of establishment in nature. Various forms of these tomatoes exist in a wide distribution over the archipelago. Though not very abundant in most populations, their distribution extends to all of the larger islands and to several localities on each as verified by our observations and by earlier collections documented in herbarium specimens. We were not able to find them in certain areas (for example,

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James and Hood Islands) from which they had previously been taken, but their absence can readily be explained by the plague of feral goats that infest these islands.

In the course of these investigations it has been possible to test a number of mechanisms that might account for germination of the dormant seeds. Visits to the islands in 1952–53 and 1957 by RIB and in 1956 by CMR provided opportunity for making the following field observations. The great majority of the living plants are large, and it is evident from the extent of their growth that they are fairly long-lived perennials. Occasional small plants could be found in the crevices between the ubiquitous lava rocks, but their presence gave no clues as to the mode of their establishment.

The following two tomato accessions were selected for germination tests: LA166, *L. pimpinellifolium*, collected on Indefatigable Island ½ km from Academy Bay along the trail that leads from the coast to the farms in the highlands; LA317, *L. esculentum* var. *minor*, collected on Bartholomew Island about 200 m from the anchorage on the north shore. These collections, representing the two dominating biotypes in the archipelago, are described in detail by Rick (1956).

To test the possibility that some substance or microorganism in the native soil might facilitate germination, the following test was made in 1956. In a single container of soil collected under plants at the site of the LA166 collection were planted 100 seeds each of (1) freshly extracted seeds of a large horticultural tomato (*L. esculentum*) grown in a nearby garden, (2) seeds immediately extracted from a plant of LA166, (3) seeds similarly obtained from another plant of LA166, and (4) seeds from the plant sampled in lot 2 that had been previously extracted and dried on paper. The soil was moistened by rain water previously collected in a cistern. For the 15 days of the test, the soil was maintained at various moisture levels. The only lot to germinate was No. 1, of which 38 seedlings had emerged by the sixth day. Mr. Alf Kastdalen, a farmer-

naturalist on Indefatigable Island, later made repeated unsuccessful attempts, some continuing over much longer periods, to start seeds from the same population. In view of these results it appears highly unlikely that any agent in the Galápagos soils stimulates germination.

#### RUMINATION TESTS

Attention was paid to any possible relationships between the Galápagos tomatoes and native animals in all the observed populations. In most of the colonies no evidence could be found of animals feeding on the fruits. Ripe fruits were retained on the plants indefinitely, eventually drying to the consistency of raisins. Various species of Darwin's finches (*Geospiza*), and particularly the Galápagos Mockingbird, *Nesomimus parvulus parvulus*, were seen frequently in the vicinity of the tomato populations. They were observed to visit the tomato plants, but in no instance did they display interest in the ripe fruits, which were always abundant. Seeds positively identified as those of Galápagos tomatoes were nevertheless found in crops and gizzards of *Geospiza fortis*, *G. fuliginosa*, *Camarhynchus psittacula*, *C. parvulus*, and *Platyspiza crassirostris* collected on Indefatigable Island.

Evidence of animal feedings on native tomatoes was encountered in two colonies—one on Chatham Island near Wreck Bay, the other on Bartholomew Island, the site of LA317. In both populations fragments of fruits and droppings containing seeds and pieces of fruit epidermis revealed that the tomatoes were being eaten by some species of rodent. Dr. Seth B. Benson of the Museum of Vertebrate Zoology, University of California, Berkeley, kindly examined the pellets and identified them as the excrement of a rat species, probably introduced *Rattus* and not likely the native rice rat, *Oryzomys*. Many of the seeds in the pellets were damaged, most likely as a result of mastication. Numerous intact seeds were extracted from the pellets, washed, and planted on blotting paper, but none germinated.

An exploratory test was conducted to

ascertain what effects bird digestion might have on viability of these seeds. Week-old chicks of the domestic fowl were fed counted lots of LA166 seeds, all droppings were subsequently collected, and seeds were extracted from the droppings. We are indebted to Dr. F. H. Kratzer of the Department of Poultry Husbandry, University of California, Davis, for handling the feeding and collection phases of this test. Somewhat less than five per cent of the seeds were recovered in an intact condition, the remaining being detected as empty seed coats, broken portions of endosperm and embryo, or fragments so completely demolished that they could not be identified. None of the intact seeds germinated. In view of these results and those of Roessler (1936; see discussion) with the California linnet, it is unlikely that species of *Geospiza* or any other bird with a gizzard plays a role in the inducement of germination or dispersal of Galápagos tomatoes.

Reptiles constitute a peculiarly large proportion of the Galápagos fauna. Of these the giant tortoises have been a dominant element in actuality as well as in reputation of the archipelago. Since tortoises are notoriously fond of fresh fruit and vegetables, it might logically be suspected that they play a role in the germination and dispersal of tomato seeds.

An opportunity for testing the effects of tortoise digestion arose when RIB returned from the islands in 1957 with two young specimens of *Testudo elephantopus porteri* from Indefatigable Island. In the subsequent two years they have grown rapidly in small compounds of lawn in Berkeley, California. Temperatures of this environment are generally lower than those of the native habitat. The specimens tend to remain under cover during cool periods and to emerge and become more active only in warmer weather. At the time of the following tests they weighed 11½ and 26 pounds apiece.

Ingestion of the seeds presented no difficulties since the tortoises proved to be veritably indiscriminate eaters. This objective

was attained simply by sprinkling the tomato seeds in the fashion of a condiment on lettuce and other items of their diet. In three of the feeding tests a liberal amount of carmine dye was fed simultaneously as a marker for identifying the feces that might contain seeds. The tortoises were maintained on a varied diet, the only items avoided being those that might be confused with the ingested tomato seeds. They were permitted to roam within their compound, where they could also feed on grass and soil materials. After the feedings the feces were collected at daily intervals, dried in the sun, and wrapped for temporary storage. Seed extractions were attempted after all feces of a single test had been collected. By a combination of washing, sedimentation, screening and flotation, the tomato seeds could be readily separated from other components. The effectiveness of this method is revealed by the rate of recovery of the seeds. The seeds were then counted, dried, and stored in packets for subsequent germination tests. For the emergence tests reported here the period of storage never exceeded one day.

Germination of the seeds was tested on blotting paper kept in plastic sandwich boxes. The paper was moistened with tap water and the boxes were placed in a well-lighted situation at room temperature, which varied from 25° to 30° C. The seeds were counted and removed as they sprouted. Numerous seedlings were later transferred to soil in greenhouse cultures, where nearly 100% survived and grew with normal vigor. In view of such successful establishment, the observed sprouting can be justifiably equated with germination.

For the first test a large lot of several thousand seeds of LA166 was fed to the tortoises in early April, 1960. No seeds were recovered from the feces, which had been collected for a two-week period following feeding. It was apparent from the remarkably intact condition of various ingested plant parts, including seeds of 12 different species, that such tortoise digestion would not likely damage the tomato seeds. Although two weeks is a remarkably long

TABLE 1. Seed recovery data for second tortoise feeding test

Days after feeding	Number of feces	Carmine in feces	Number recovered seeds		
			Normal	Damaged	Total
9	1	None detected			
11	4	Present	9		9
12	2	Present	2		2
13	3	Present	124		124
14	5	Present	714	7	721
15	1	Present			
16					
17	8	Present in few	76	2	78
18	7	Present in 2	86		86
20	4	None detected	13		13
		Total			1,133

Approximately 4,620 seeds of LA317 fed to tortoises June 18, 1960.

period for complete passage of a digestive tract, the only reasonable explanation for the failure of recovery was that a longer period was required and that feces containing the fed seeds would have been evacuated subsequent to the two-week period.

For the second test, seeds of LA317 were fed to the tortoises in late June, 1960. The seed number for this feeding was estimated by weight to be 4,620. Carmine was fed simultaneously as a means of marking the feces most likely to contain seeds. The dye did not appear in the feces until the 11th day after feeding, on which date tomato seeds also first appeared. As revealed in table 1, feces continued to be tinged with the dye until the fifteenth day; thereafter carmine was not in evidence in the feces or in the water in which they were soaked for seed extractions, but coats of some of the seeds appearing at later dates were strongly pigmented with carmine. Seeds continued to appear in the droppings until the 21st day—the final day of the collections. Judging from the rate of seed recoveries, a few more would probably have been obtained had collections been continued beyond that date. Less than one per cent of the recovered seeds showed any sign of damage detectable by

use of a low-power dissecting microscope. A total of 1,133 seeds, or 24.5% of the number fed, was recovered.

Other contents of the tortoise excrement should be mentioned here as they might be of general interest. In all the tests, a weird assortment of items was recovered. The dominant element was grass leaves, which, despite digestion, could readily be recognized. Pine needles were usually present, sometimes comprising most of the content of the droppings, and compressed into tight, fibrous pellets. A small proportion of sand and gravel with particles up to one centimeter in diameter was always present. A predilection for large, sharp, coarse objects was evident in the recovery of walnut shell fragments, acorns, and small pieces of wood. Rubber bands and safety pins were also ingested. The ability of the Galápagos tortoises to pass such items is not surprising in view of their diet of *Opuntia* pads, spines included, during the dry season in their native habitat.

Seeds extracted from excrement collected 14, 17, and 19 days after feeding were subjected to germination tests. Untreated seeds, from the same source as those which were fed to the tortoises, served as controls. Also included were lots that had been soaked anaerobically in water for seven weeks and one that was treated for one hour in the dormancy-breaking hypochlorite solution. Each lot, except for the last mentioned, was subdivided into two equal groups, one being planted directly, the other being subjected to the hypochlorite solution for five minutes before planting. The latter treatment was applied as a sterilization precaution, which later tests revealed to be unnecessary.

Results of this germination test are presented in table 2. The point of primary interest is the very great improvement in germination wrought by tortoise digestion. Whereas one per cent germination was observed in the untreated control, comparable lots of recovered seeds germinated at the rates of 81, 80, and 60 per cent. The sterilization treatment generally increased the percentage emergence, but the differ-

TABLE 2. *Germination of seeds recovered in second tortoise feeding test and those of other treatments and control*

Treatment	Sterilization <sup>1</sup>	Total planted	Number of seeds															Germinated	
			Days after planting															Number	%
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		
Control		100				1												1	1
	treated	100		1		1		1		2	2	1		2				10	10
42 days in water		180										1						1	0.5
Hypochlorite <sup>2</sup>		142		6	22	8		24	28	5	5	3						101	81
14 days in tortoise		100		58	14	7	1				1							81	81
Same	treated	100	4	75	13			1		1			1					95	95
17 days in tortoise		39		10	15	3		1		1	1							31	80
Same	treated	38		14	6	1	1			1	1							24	63
18 days in tortoise		45		18	2			1		3	3							27	60
Same	treated	40	2	24	3	1	1											31	77

<sup>1</sup> 2.6% hypochlorite for 5 minutes.<sup>2</sup> 2.6% hypochlorite for 1 hour.

ence between control and digested lots is of the same remarkable magnitude. The seeds in the digested lots actually performed better than the ones which had their coats removed by hypochlorite solution. Table 2 reveals, furthermore, that seedlings emerged much earlier in the digested lots. Prolonged soaking in water did not improve germination. A trend toward lower germination percentages in lots that stayed for longer periods in the tortoise gut is suggested by the data, but the number of seeds is too small to establish this point.

A third test was conducted in August, 1960, utilizing LA166, the accession with greatest seed dormancy. For this experiment ripe fruits produced by plants grown in the greenhouse at Davis were fed to the tortoises in an effort to simulate the natural situation. A total of 487 fruits were fed to the two animals over a five-day period. Carmine was fed with the tomatoes on the first day. Both animals seemed rather indifferent to the tomatoes, possibly reflecting unfamiliarity, and it was necessary to mix the fruits with mashed bananas in order to achieve ingestion of the entire number. A few fruits were lost in the feeding process. By extracting and counting seeds from 86 fruits of the same batch it was estimated that about 17,400 seeds had been fed to the tortoises in this test.

Seeds were again successfully recovered from the droppings (table 3). In addition, it was possible to count the fruit pericarps, which were very little affected by digestion. The mildness of tortoise digestion is also reflected in the recovery of some 10% of the fruits in an essentially intact condition; such fruits were often broken at the stem end, but seeds and other contents were preserved in normal position. Seeds and carmine first appeared twelve days after the start of feeding. The dye could be detected

TABLE 3. *Seed recovery data for third tortoise feeding test*

Days after feeding	Number of feces	Carmine in feces	Number fruit skins		Number recovered seeds		
			Empty	In-tact	Free	In fruits	Total
8	5	None					
9	2	None					
10	1	None					
11	1	None					
12	2	Strong	27	1	642	11	653
13	3	None					
14	3	Strong	17		338		338
15	2	Moderate	18	4	331	78	409
16	3	Trace	119	16	1,350	290	1,640
17	3	None	56	5	611	105	716
18	3	None	16	3	259	71	330
Total			253	29	3,531	555	4,086

Approximately 17,400 seeds of LA166 fed to tortoises, starting on July 28, 1960.



TABLE 4. Germination of seeds recovered in third tortoise feeding test and those of hypochlorite treatment and control

Treatment	Total planted	Number of seeds																Germinated	
		Days after planting																Number	%
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	17–20			
Control	100																	0	0
Hypochlorite <sup>1</sup>	100	11	15	13	3	1					1			1	7			52	52
12 days in tortoise free seeds	100		5	2	6	5	1											19	19
15 days in tortoise free seeds	100					2												2	2
15 days in tortoise seeds from intact fruits	78						1											1	1.3
18 days in tortoise	100																	0	0

<sup>1</sup> 2.6% hypochlorite for 1 hour.

until the 16th day and seeds were still appearing on the 20th day, the last day of collections. The absence of seeds on the 13th day and other irregularities, we suspect, reflects a slower passage through the smaller tortoise, whose feces alone were collected on that date. A total of 4,086, or 23.5% of the ingested seeds, was recovered.

Germination tests were made without sterilization treatment and included the usual control and lot with seed coats removed. The response was slower and very much smaller than with LA317 (table 4). The best germination—52%—was recorded for the hypochlorite treatment. Next highest was 19% found in free seeds recovered 12 days after feeding. Germination in later recoveries dropped to very low levels. Thus, although digestion did not induce high germination percentages, it permitted *some* germination—a response that was never obtained in controls of LA166. The decrease in germination of the later recovered lots, together with a similar trend observed in the second test, suggest that prolonged retention in the tortoise digestive tract might have an unfavorable effect on seed viability.

A fourth test was conducted to see what effects, if any, tortoise digestion might have on viability of garden tomato (*L. esculentum*) seeds, which do not require special aids for germination at any time after harvest. Several workers have reported (see

Discussion) that digestion by domestic animals tends to lower the germination percentage of non-dormant seeds. For this purpose approximately 1,200 seeds of a freshly extracted batch of a large-fruited tomato were fed to the larger tortoise of the pair used in these tests; feces were collected, seeds extracted, and germination tested in the same fashion as for the preceding tests. Seeds first appeared in the excrement seven days after feeding and continued until the 17th day—the last day of collecting. A total of 449 seeds, or 42% of the total fed, was recovered. Samples of 50 seeds each were tested for germination from batches that were recovered 7, 10, 12, and 16 days after feeding. Control germination was perfect; the digested lots germinated 82, 70, 84, and 80 per cent respectively, and their seedlings emerged much earlier than those of the controls. The mean germination of all digested lots was  $79 \pm 3$  per cent, revealing a significant reduction below that of the control level. Despite the general reduction, the data do not show any trend toward lower germination in the lots retained in the tortoise gut for longer periods.

#### DISCUSSION

The literature reveals numerous examples of the effects of animal digestion upon the viability of seeds of various plant species. Such experiments were conducted as early as the 19th century by Kerner (1902) to settle

contemporary disputes about the possible role of animals in dispersing plant seeds. He ascertained that seeds of a few plant species passed undamaged through the pig, but that the seeds of the majority of plant species tested lost their viability after passage through the digestive tracts of several mammals. Finches, gallinaceous birds, and other species with gizzards destroyed most seeds that had been fed to them. With certain other bird species (blackbird, thrushes, European robin) seeds retained good viability; germination of most seeds was generally retarded, but in the case of *Berberis*, *Ribes*, and *Lonicera*—genera prone to seed dormancy—it was accelerated. The damage that may be inflicted upon seeds by bird digestion is well illustrated by Roessler's (1936) experiment, in which she obtained germination of only 7 of 40,025 seeds from various plant species fed to California linnets.

Rumination effects on seed germination have also interested agronomists, particularly in respect to problems of the spread of weeds in pastures. A complete review of the literature will not be attempted here; instead attention will be called to several well-documented experiments. Harman and Keim (1934) tested the percentage and viability of seeds of six weed species recovered in the feces of calves, horses, sheep, hogs, and chickens. No seeds were recovered from the chickens except 1.9% of velvetweed (*Abutilon abutilon*). For the remaining animals a mean of about 20% of the seeds were recovered. Germination percentages of all except *Rumex acetosella* were improved by passage. Seeds of all tested species lost their ability to germinate after being retained in manure for two months. In similar experiments Burton and Andrews (1948) demonstrated that passage through the bovine digestive tract reduced the viability of certain grass and lespedeza seeds, but actually induced an increased germination of Bermuda grass.

A similar phenomenon is appreciated and exploited by the Ecuadorians. One of us (CMR) learned in conversation with hacen-

deros near Quito that seeds of certain edible species of *Carica* and *Passiflora* are difficult to sprout. This problem is customarily circumvented and plants established by feeding the fruits to workers, who are subsequently instructed to defecate in assigned pits in the fields.

Dr. Herbert G. Baker, Director of the Botanical Garden, University of California, Berkeley, recently informed us of some observations that are pertinent to this discussion. With his kind permission we cite briefly his experiences in Ghana with seed germination of the baobab tree (*Adansonia digitata*) and the sausage tree (*Kigelia africana*). Without treatment these seeds are very difficult to germinate, yet he observed that numerous seedlings were becoming established in rocky areas considerably distant from trees of either species. It became evident that these places were favorite roosts of the baboons, and remains of fruits revealed that they were being devoured by these simians. The extremely strong jaws of the baboons are adequate to crush the very hard, indehiscent fruits of these trees, and, without such aid, the seeds would have no opportunity for dispersal. The germination rate of seeds removed from baboon dung found at these sites was much improved.

Various observations and experiments have therefore established that seeds may retain their viability despite animal digestion and that the seeds of a few species actually germinate better as a result of this process. Plant species showing the latter reaction are naturally prone to seed dormancies. Of all examples known to us, the response in LA317 of the Galápagos tomato accessions is the most dramatic, changing from practically nil to as much as 80% as a result of tortoise digestion. In the examples cited from the literature the greatest improvement did not exceed 20% germination. In the latter cases no net gain was realized because seed recovery from the animal feces was low.

Several questions are raised by the discovery of improved germination of Galápa-



gos tomato seeds by tortoise digestion. One of these is the problem of what physiological mechanism in animal digestion is responsible for the improvement. Three mechanisms might be considered: (1) elimination of a substance that chemically inhibits germination; (2) removal of an obstacle to exchange of substances essential for germination; (3) release of a mechanical barrier to emergence of the seedling. The first proposal is rendered unlikely by the slight, though consistent, improvement of emergence wrought by the seed coat excision treatments. Since this method removes only a small fraction of the seed coat, it would be ineffective in counteracting an inhibiting substance. The interpretation offered by the second proposal is consistent with most of the treatments that improve germination: mechanical removal of part of the seed coat, total removal by hypochlorite, and tortoise digestion. Water and oxygen are the two substances ordinarily absorbed by seeds and essential to germination. Of these, water can be ruled out of consideration because moistening seeds of all Galápagos accessions results in rapid imbibition and swelling. Improved gas exchange would more likely be the factor involved here, as it also is in instances of improved germination effected by hypochlorite, which have been reported in the literature. The third proposal is suggested by the phenomenally rapid emergence of seedlings from seeds requiring repeated treatments with hypochlorite. It has been our experience with the latter that each exposure to the chemical, which erodes away the seed coat, is followed within minutes by the rapid emergence of seedlings from a portion of the seeds, no further germination occurring until immediately after the next treatment. A facilitation of chemical interaction, as proposed in the preceding alternative, could scarcely account for such a rapid response. This concept would also explain the low frequency response to mechanical excision. Here the chance removal of a segment of the seed coat covering the radicle of the embryo would account for emergence. Tortoise digestion does not result in any

changes of the seed coat that are visible externally, yet might soften critical layers sufficiently to permit seedlings to emerge. Although our data are not sufficiently critical, the bulk of evidence favors the explanation based simply on seed coat mechanics.

If tortoise digestion improves germination by permitting gas exchange or by relieving mechanical confinement, how is this accomplished? It is beyond the scope of this project to test extensively the various processes of tortoise digestion *in vitro*. Such an approach would furthermore be largely empirical because very little is known about digestion of chelonians in general, let alone Galápagos tortoises in particular. It is nonetheless clear from our tests with the latter and with chickens that mechanical abrasion is not likely the critical part of digestion. It is more likely one of the wide variety of enzymatic reactions that are part of gastric and intestinal digestion. Also, the fermentation of carbohydrates that is promoted by the microflora of the colon should not be overlooked.

In this connection it should be mentioned that we have conducted preliminary tests of the effects of standard laboratory peptic and pancreatic enzymes upon germination of seeds of LA317. The tests were too brief and the results insufficiently consistent to merit complete presentation here. They would justify solely the statement that germination was substantially improved only by pancreatic enzyme treatment. The subject obviously deserves thorough investigation.

The tests reported in this paper suggest that the giant tortoises of the Galápagos Islands might play a role in the germination and dispersal of native tomato species. They do not prove the case. A number of points should be considered in relation to this speculation. In the first place it is the only known natural means of breaking the tomato seed dormancy. Other animals of the rather restricted fauna of the archipelago that might be suspected to play a similar role are the land iguana, *Conolophus subscristatus*, and species of Galápagos mockingbird, *Nesomimus*. The former, en-

tirely herbivorous, is known from the lower elevations where native tomatoes frequent. Being a reptile and herbivorous, its digestive system might be similar to that of the tortoises and might act similarly on tomato seeds. The mocker is likewise largely herbivorous and is found in the areas of the tomato populations. As previously revealed, however, it was observed in nature not to display any interest in the wild tomato fruits. The effects of its digestion are unknown, but it might logically be suspected that the period of bird digestion in general is too short to be effective.

Another consideration is the very long period required for passage through the tortoise gut. According to our results with carmine and tomato seeds, from one to three weeks are required, and it follows from the retrieval of seeds continuing up to the 21st day in the third test that they would have likely continued to appear for several more days. It is also reasonable to suspect that in the warmer climate of their native habitat the tortoises are more active and digestion would take place more rapidly, yet it is clear that a period unusually long for vertebrates is involved. The advantages for dispersal of seeds inherent in such long passages are obvious. According to many observers on the islands, the tortoises roam considerably while feeding and mating. Their agency could therefore be exceedingly effective not only in breaking the seed dormancy but also in providing an effective means of distribution.

We might speculate even further about the distributional role of the tortoises. As just mentioned, they could be highly effective in spreading the native tomatoes within islands. It is also within the realm of possibility that they could play a limited role in the spread from island to island. The problem of such migrations has been treated by several authorities. The Galápagos tortoises will naturally float in seawater, and, with the coincidence of favorable currents, they might rarely drift from one island to another. The distances are short and the viability of the tortoises—for example, their

ability to survive long fasts—is known to be enormous. Van Denburgh (1914) discounts the possibility of any such migrations on the basis of the helplessness of the tortoises in water, the risk of injury on treacherous reefs and rocky shores, and the extreme endemism of the island populations. Beebe (1924), on the other hand, who captured a tortoise on Duncan Island and found it adept at swimming in seawater, considers migrations between islands possible.

The distribution of tomato biotypes discloses a very effective means of dispersal. The most abundant type is *L. esculentum* var. *minor*, represented in our tests by LA317. It occurs on at least eight of the major islands and in widely separated loci on each of the two larger islands, James and Albemarle (Rick, 1956). The phenotype of var. *minor* is remarkably stable throughout this range as judged from herbarium specimens and from living cultures. Such a distribution stands in marked contrast to the extreme endemism exhibited by the genus *Scalesia*, for which Howell (1941) lists 19 species native only to the Galápagos and of which only two species occur on more than one island. Such differences in distribution must logically reflect marked differences in effectiveness of dispersal. The interrelationship with the tortoises would provide a very simple and effective means of explaining the widespread distribution of the tomato biotypes.

The possibility of other native animals assisting in the germination and distribution of Galápagos tomatoes has already been discussed. The advent of man on the Galápagos has unfortunately resulted in severe depletion and even extinction of the giant tortoises from some of the islands. Since some of these very islands (Bartholomew, Seymour) still have native tomato populations, obviously some other agent must be responsible for their presence. The land iguana and mockingbird have been previously suggested as other agents. The herds of feral animals, particularly goats, that exist on several islands might also be suspected. Their digestion bears resemblances

to that of the tortoises in respect to their vegetable diet and relatively long digestion period. Examples from the literature have been cited of recovery of weed seeds and improvement of germination of certain species thereof following digestion by domestic ruminants.

The putative relationship between tortoise digestion and tomato seed germination suggests that species which are related to the Galápagos tomatoes and have similar dormancies might also rely to some extent upon animal vectors for germination and dispersal. As revealed by our work, seed dormancies exist, and they can be broken by hypochlorite treatment in some accessions of two other tomato species, and in two related nightshade species. We have no experimental evidence for such animal interrelationships with these species, but in their habitat in western Peru and Chile, a much greater variety of animals exists that might play such a role.

This relationship might have a much wider significance among species of higher plants. Heretofore the adaptive significance of seed dormancies has been explained in various ways. Some dormancies are known that undoubtedly prevent germination under conditions that would be disadvantageous to the growth of the particular species. Others promote survival by preventing immediate germination of all of the seeds. But the effects of animal digestion on germination of a wide variety of higher plant species suggest that the dormancies might have evolved as a special device to promote dispersal. The dormancy devices among these examples are different; to wit, in the Galápagos tomatoes it appears likely to be a mechanical obstruction to germination; impermeability of the seed coat is the factor in at least some of the species tested by Harman and Keim (1934); the after-ripening phenomenon is characteristic of the genera that showed improved germination in Kerner's (1902) tests; the processes concerned with other examples may still be unknown. Animal digestion is therefore effective in breaking seed dormancies of several different types. Thus the

various seed dormancies might have evolved not only to prevent germination under unfavorable conditions but also to facilitate dispersal by animal agents.

Finally, the origin of such relationships between animal digestion and seed germination presents a serious problem. Passage through the animal gut can be readily visualized as an effective means of dispersal, but its role in germination is another matter. According to all evidence, seeds of these native tomatoes will not germinate unless exposed to such treatment. The tomatoes would then presumably be entirely dependent upon the animal vector for completion of their life cycle. Although such a relationship is completely effective in guaranteeing a dispersal commensurate with the wanderings of the responsible animal, the fate of the plant hinges entirely on the vagaries of the animal. The fate of the forms which mutated from a free-germinating to the dormant-seeded condition would seem to have been even more precarious. If indeed this happened, the premium gained in dispersal must have outweighed the risks involved in developing the dormant condition. This problem is certainly no more serious than the one posed by the origin of the interdependence of *Yucca* species and species of the *Tegiticula* (*Pronuba*) moths that pollinate them.

#### SUMMARY

Seeds of tomato species native to the Galápagos Islands are subject to extreme seed dormancy of indefinite duration. The dormancy is alleviated by treating the seeds with a strong solution of sodium hypochlorite, which erodes the seed coat. In a search for natural dormancy-breaking devices, the following treatments proved ineffective: soaking in stagnant or well-aerated water, various temperatures applied to wet or dry seeds, application of acids, planting in native soil, and passage through the gut of immature chickens. Additionally, seeds collected from rat droppings found under plants in their native habitat did not germinate. On the other hand, digestion by the native giant tortoise results in marked

improvement in speed and percentage of germination, the degree of response varying with the tomato biotype. Passage through the tortoise gut required from one to three weeks and probably longer. In all tests a minimum of one-quarter of the ingested seeds was recovered, and the seeds revealed no macroscopic effects of digestion. The dormancy mechanism most likely responsible is one of simple mechanical obstruction of emergence by the seed coat. These results suggest that the giant tortoise might be an important natural agent not only in breaking the dormancy but also in effectively dispersing the tomato seeds. Following tortoise digestion, seeds of the garden tomato, which are not prone to dormancy, germinated but at a lower percentage than that of untreated seeds. The digestive reaction that is most likely responsible for alleviating dormancy, the possible role of other animal agents on the Galápagos Islands, and evolutionary aspects of animal digestion as a promoter of germination and of dispersal of plant seeds are discussed.

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