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journal homepage: www.elsevier.com/locate/cbpaDigesta retention time in the Galápagos tortoise (*Chelonoidis nigra*)Elham Sadeghayobi^a, Stephen Blake^{b,c,d,e,f,*}, Martin Wikelski^b, James Gibbs^e, Roderick Mackie^g, Fredy Cabrera^d^a Department of Plant Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 D, SE-752 36 Uppsala, Sweden^b Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, D-78315 Radolfzell, Germany^c Whitney R. Harris, World Ecology Center, University of Missouri-St. Louis, B216 Benton Hall, One University Boulevard, St. Louis, MO 63121-4400, USA^d Charles Darwin Foundation, Puerto Ayora, Isla Santa Cruz, Galápagos, Ecuador^e 247 Illick Hall, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA^f Department of Biology, Washington University, Campus Box 1137, 1 Brookings Drive, St. Louis, MO 63130, USA^g Department of Animal Sciences, Division of Nutritional Sciences, University of Illinois, 1207 W. Gregory Drive, Urbana, IL 61801, USA

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ABSTRACT

The retention time of food in the digestive tract of animals has important implications for digestive physiology. Retention time impacts digestive efficiency and among herbivores affects plant–animal interactions including herbivory and seed dispersal. Poorly studied yet iconic Galápagos tortoises are large-bodied generalist herbivores and ecosystem engineers which migrate seasonally. Potentially variable digesta retention times due to strong seasonal and altitudinal temperature gradients may influence tortoise seed dispersal abilities and rates of herbivory. We fed captive adult tortoises living in semi-natural conditions on Galápagos with inert particles and seeds from locally available fruits to determine whether seed size and ambient temperature influenced retention time. Median retention time varied from 6 to 28 days, with a mode of 12 days. Seed size had no effect on any of our measures of retention time, but ambient temperature was inversely correlated with retention times. Long retention time facilitates long distance seed dispersal by Galápagos tortoises, which may improve effectiveness. The effect of temperature, which may double from hot lowlands to cold highlands through the seasonal cycle, on tortoise digesta retention time will strongly influence seed dispersal efficiency and may influence patterns of food selection and migration in this species.

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1. Introduction

The retention time of food in the digestive tract of animals is an important parameter in digestive ecology. Retention time impacts food intake rate and extraction of nutrients (Balch, 1950; Milton, 1981) and among herbivores may influence animal–plant interactions such as the volume of plant material consumed (grazing/browsing intensity) (Illius and Gordon, 1992) and seed dispersal (Pakeman, 2001). In a classic review paper of seed dispersal by animals, Eugene Schupp empirically defined seed dispersal effectiveness as the product of the quantity and quality of seeds dispersed (Schupp, 1993). Among factors that influence dispersal quality, digesta retention time may be of particular importance since it determines how long seeds are exposed to potentially advantageous and/or damaging digestive processes, and it influences the spatial scale and pattern of seed deposition. Trade-offs in seed dispersal effectiveness may exist among these effects of retention times; for example long retention time may increase the probability of long distance dispersal (Blake et al., 2009), a highly advantageous trait for

plants (Nathan and Muller-Landau, 2000), but may decrease seed viability (reviewed by Traveset (1998)). For example, on Aldabra Atoll in the Indian Ocean, giant tortoises (*Aldabrachelys gigantea*) have digesta retention times between 6 and 49 days (Coe et al., 1979) during which time they may travel considerable distances (Hnatiuk, 1978; Gibson and Hamilton, 1983). However Hansen et al. (2008) found that success of seed germination may decline with increasing digesta retention time in Aldabra tortoises, potentially reducing the advantage of tortoise-borne dispersal.

Most studies of zoochory and seed dispersal effectiveness have focused on birds and mammals which are often dispersers of prodigious volumes of seeds (Howe, 1990; Jordano, 2001), though other taxa including reptiles and fish may also be effective dispersers (Corlett, 1998). In terrestrial ecosystems, tortoises contribute to seed dispersal dynamics (Liu et al., 2004; Birkhead et al., 2005; Jerzolimski et al., 2009), particularly on oceanic islands where giant tortoises play a megafaunal role (Hansen et al., 2008; Blake et al., in second review). Tortoises are hindgut fermenters (Stevens and Hume, 1995) and can digest plant material as efficiently as mammalian herbivores (Bjorndal, 1997). They have anatomical, morphological and physiological features which are likely adaptations to herbivory. These characteristics include comparatively large body size and long digesta retention time (Barboza,

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1995). However, the rate at which food passes through the digestive tract is affected by body temperature, being slower at lower temperatures (Zimmerman and Tracy, 1989).

Despite its physiological and ecological importance, few studies on digesta retention time have been carried out on giant tortoises, especially on the iconic Galápagos tortoise (*Chelonoidis nigra*), the largest extant terrestrial reptile, a known seed disperser (Rick and Bowman, 1961; Blake et al., in second review) and an ecosystem engineer (Gibbs et al., 2010). A recent study demonstrated that mean retention time (MRT) scales to body mass (BM) among tortoise taxa by a factor of 0.17 (Franz et al., 2011), however this relationship was not significant when body mass exceeded 1 kg. Studies of captive tortoises in Europe have found MRT times between 267 and 317 hours (11–13 days) for particulate matter in four adult tortoises (Hatt et al., 2002), and 65–197 hours for juveniles (Franz et al., 2011).

As part of a study on the movement ecology of Galápagos tortoises and their potential as seed dispersers (Blake et al., in second review), we investigated digesta retention time in semi-natural conditions at the Charles Darwin Research Station on Santa Cruz Island, Galápagos. Here we evaluate two factors, particle size (which had no significant impact) and ambient temperature (which did) on digesta retention time and discuss the ecological implications of our results.

2. Materials and methods

Between November 2009 and March 2010, we determined digesta retention time (DRT) in Galápagos tortoises by feeding a sample of 19 adult males (Table 1) with seeds extracted from natural foods and inert rate of passage markers (RPMs). The tortoises were divided into four different groups and housed under semi-natural conditions in corrals in the Galápagos National Park (GNP) on Santa Cruz, Galápagos (Table 1). The GNP has a captive breeding facility in which young tortoises are raised in order to restock at risk wild populations. Adult tortoises that reside at the station are housed in outdoor facilities (corrals) bounded by tortoise-proof walls built from locally available lava, in which they are exposed to natural weather conditions. Two corrals were selected for this study (Table 1). The first was 8 × 13 m, contained a small artificial water pool for drinking and bathing and two small areas shaded with tin roofing. Along one side of the corral of saltbrush (*Cryptocarpus pyriformis*) bushes grew into the corral and were accessible to the tortoises. The corral floor was made of irregular volcanic rocks. The second corral was located ca. 200 m from the first and had an area of 22 × 45 m (Table 1). Vegetation was more abundant than in the small corral though was rarely consumed by the tortoises and consisted of saltbrush, yellow cordia (*Cordia lutea*) shrubs, and *Opuntia* cactus (*Opuntia echios*). The corral has an artificial water pool and a small concrete feeding platform. Throughout the study, tortoises were fed according to their usual schedule, i.e. three times a week, on Mondays, Wednesdays and Fridays. The tortoises were fed with plant species introduced to Galápagos; arrowleaf elephant ear (*Xanthosoma sagittifolium*) and swamp immortelle (*Erythrina corallodendron*). Food intake rates were not quantified for the tortoises used in our trials.

Table 1

Details of tortoise morphometrics and temperature at which DRT trials were conducted by group.

GNP ID	Morphology	Carapace length	Carapace width	Group	Corral	Mean temp (°C) during DRT
17	Saddlebacked	76	84	1	1	23.3
19	Domed	118.9	114.4	1	1	23.3
29	Saddlebacked	92.7	89.3	1	1	23.3
15	Domed	114.2	113	1	1	23.3
36	Domed	122.3	143.7	2	2	25.6
53	Domed	145.2	140	2	2	25.6
56	Domed	137.3	152.8	2	2	25.6
57	Domed	116.3	124.7	2	2	25.6
58	Domed	144.7	144.7	2	2	25.6
59	Domed	146.8	143.1	2	2	25.6
2	Domed	114	115.4	3	1	26.7
5	Domed	122	119.5	3	1	26.7
22	Domed	110.7	110.4	3	1	26.7
37	Intermediate	105.5	101.1	3	1	26.7
47	Saddlebacked	89	91.6	3	1	26.7
1	Domed	103	103.5	4	1	28.1
16	Domed	88.3	92.5	4	1	28.1
30	Domed	107.1	108	4	1	28.1
15	Domed	114.2	113	4	1	28.1

The tortoises were divided into four groups of four or six individuals (Table 1), and each group was used for a separate trial over successive months during which time the mean ambient temperature during each trial increased as the hot wet season progressed (23.3, 25.6, 26.7, and 28.1 °C) (Table 1). Mean temperature values reflect the mean daily shade temperature from hourly measurements during the period from RPM ingestion until complete recovery.

Each tortoise was given a mix of up to three species of seeds and six different types of inert plastic beads. Seeds were from fruits which tortoises consume naturally on Santa Cruz including papaya (*Carica papaya*), passion fruit (*Passiflora edulis*) and common guava (*Psidium guajava*) which are all introduced species but which are heavily preferred tortoise foods. Plastic beads were either circular of 5.5, 3.5 and 1.8 mm in diameter, or rods of 10, 5 and 1 mm in length and 1 mm diameter, all selected to be within the size range of seeds dispersed by wild Galápagos tortoises (Blake, pers. obs.). For the rest of this paper, both natural seeds and plastic beads are collectively referred to as rate of passage markers (RPMs). Usually, 200 of each RPM type were fed to each tortoise though limited supplies of RPMs on Galápagos meant that not all tortoises received all RPM types. Rate of passage markers were uniquely color coded for each individual tortoise so that RPMs could later be associated with a particular tortoise when found in dung piles of unknown origin. Each tortoise was fed its full complement of RPMs once at the beginning of the trial and thereafter monitored frequently (usually every two hours) from dawn until dusk for the presence of dung in its corral. Each new dung pile was recovered immediately, washed using a fine sieve, and all RPMs were identified and counted. Each trial was terminated when no new RPMs were recovered for a period of five days.

Three estimates of retention time in days were defined for each RPM type for each tortoise: Time to the appearance of the first RPM,

Table 2

Mean digesta retention times of rate of passage markers recorded over the range of mean ambient temperatures encountered during the study.

Temperature (Celsius)	23.3			25.5			26.7			28.1		
	Mean (SD)	Min.	Max.	Mean (SD)	Min.	Max.	Mean (SD)	Min.	Max.	Mean (SD)	Min.	Max.
Time to first appearance	11.9 (1.58)	11	13	11.1 (2.26)	10	13	9.53 (1.92)	8	12	6.57 (2.55)	6	9
Median retention time	12.7 (2.75)	11	17	12.9 (2.16)	11	20	10.7 (2.14)	9	14	7.5 (2.16)	6	11
Time to longest retention	14.3 (4.50)	12	22	17.3 (3.04)	13	27	12.6 (2.16)	10	15	9.39 (3.87)	7	13

Table 3
The effects of rate of passage marker size and ambient temperature on mean digesta retention times.

Digesta retention time	ANOVA summary	
	Seed size	Ambient temperature
Time to first appearance	$F_{(11,147)} = 0.51, P = 0.892$	$F_{(3,147)} = 190.95, P < 0.001$
Median retention time	$F_{(11,147)} = 1.36, P = 0.206$	$F_{(3,147)} = 79.29, P < 0.001$
Time to longest retention	$F_{(11,147)} = 6.13, P < 0.001$	$F_{(3,147)} = 68.39, P < 0.001$

the median retention time (MRT, when half of the RPMs were recovered), and time to longest retention (recovery of the last RPM). In total 86% of the 22,000 RPMs fed to the tortoises were recovered.

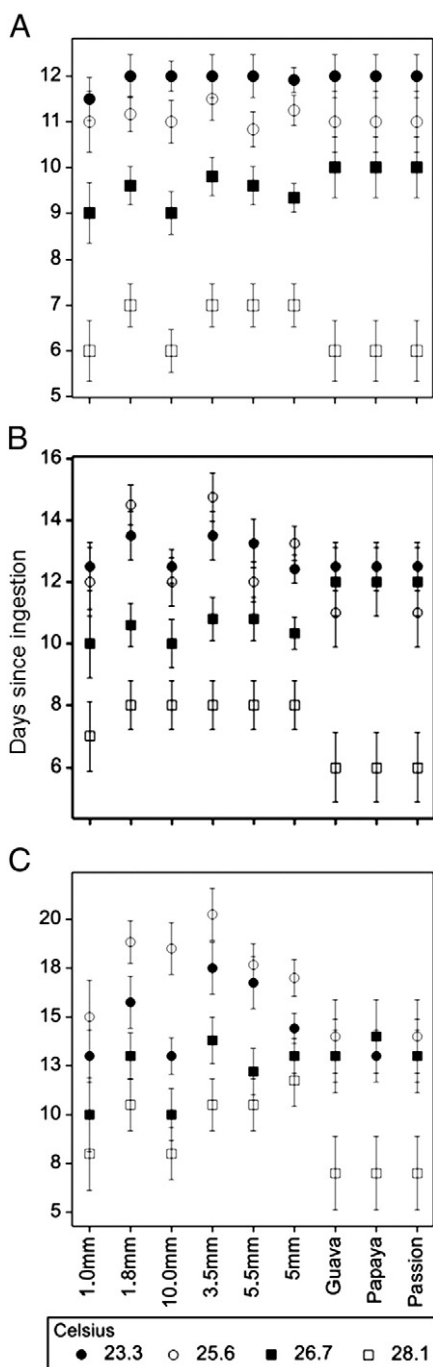


Fig. 1. Mean digesta retention times by rate of passage marker type and ambient temperature: A) time to first appearance, B) median retention time, C) time to last appearance.

All statistical tests used below were carried out using Genstat 13 (VSN International LTD).

3. Results

3.1. Impact of RPM type and ambient temperature on digesta retention time

Rate of passage markers remained in the gut for a range of 6 to 28 days across the 19 tortoises, with a mode of 12 days. Increasing ambient temperature significantly decreased all three estimates of digesta retention (Tables 2 and 3, Fig. 1). Regression analysis of MRT against temperature showed a significant positive relationship ($F_{(1,147)} = 27.95, P < 0.001$; CI intercept = 20.51–31.58, CI slope = -0.72 to -0.36). An analysis of variance (Table 3) indicated that RPM size did not influence the time to first appearance or median retention time. Rate of passage marker size did influence longest retention time (Table 3), but there was no obvious trend between these variables.

3.2. Patterns of RPM recovery over time

The pattern of excretion of RPMs with time varied considerably between tortoises (Fig. 2). Some tortoises passed a small number of RPMs at or shortly after first appearance, followed by a short burst of rapid output, while others showed a consistent output of RPMs over several days, followed by a gradual reduction with a relatively long tail. Still others showed peak production early followed by a long tail of low output. Overall patterns varied between individual animals and there was no clear relationship with carapace length (a measure of body size). A generalized linear model with a Poisson distribution and a log link function of the proportion of seeds recovered per day by temperature supported the hypothesis that DRT decreases as temperature increases ($F_{(4,147)} = 36.1, P < 0.001$) (Fig. 3).

4. Discussion

4.1. Methodological constraints

Ideally, we would have estimated digesta retention time over the full range of ecological, environmental, and physiological conditions experienced by wild Galápagos tortoises. This would require the ability to dose RPMs, follow tortoises over long periods and reliably recover feces from tortoises ranging over large areas (Blake et al., in second review). It would be very difficult to carry out these studies on digestive physiology in the natural environment. Instead, our tortoises were housed in corrals under natural lowland vegetation conditions, with regular feeding on introduced plant species. This differs from the wild state, where food resources are highly variable in abundance and quality (Cayot, 1987), and temperature varies considerably through the year (Trueman and d'Ozouville, 2010). Therefore our results should be considered as reliable estimates of digesta retention time under our experimental conditions. Further work is needed to assess the impact variation in diet, feed intake, body size and temperature on free living populations of tortoises.

4.2. Ecological implications of digesta retention time

The digesta retention times we recorded are consistent with those previously estimated for Galápagos tortoises (Rick and Bowman, 1961; Hatt et al., 2002; Franz et al., 2011) and for Aldabra tortoises (Coe et al., 1979; Hamilton and Coe, 1982; Franz et al., 2011), though the latter showed longer mean retention times of up to 49 days. Patterns of excretion of RPMs were consistent to those reported by Franz et al. (2011), who discuss potential causes of these patterns at length. Long retention times provide plants the seeds of which are

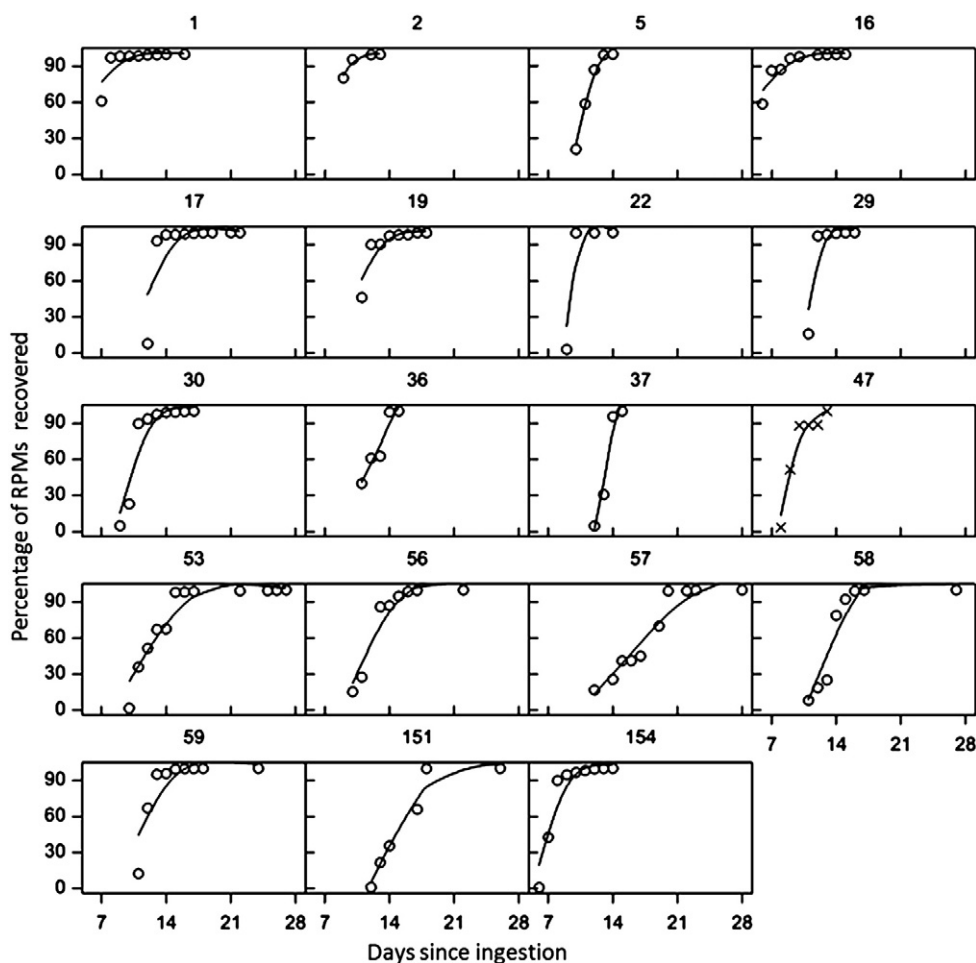


Fig. 2. Temporal pattern of rate of passage marker recovery by tortoise ID (with fitted exponential curves).

consumed and excreted in viable form by tortoises with an excellent long distance dispersal mechanism. During the 12 day median retention time, a Galápagos tortoise may move over 3 km linear distance, and up to 4.4 km over a 28 day retention time (Blake et al., in second review). Recent work indicates that Galápagos tortoises

disperse intact seeds from at least 44 plant species (Blake et al., in second review). Since there are few other large-bodied vertebrate dispersers found on Galápagos, tortoise mediated seed dispersal may be an important factor in determining patterns of distribution of numerous plant species both within and between islands in the Galápagos archipelago (Blake et al., in second review).

Thermal constraints on digesta passage time are common among reptiles (Waldschmidt et al., 1986; Lichtenbelt, 1992) which may behaviorally select ambient temperature to optimize digestion of plant cell walls and energy expenditure (Tracy et al., 2005). However tortoises also show flexibility in digestive processes in response to dietary variability such as fiber content and cell wall digestibility (Bjorndal, 1989). For example, desert tortoises may adjust their mean retention time in order to extract sufficient nitrogen from different food species (Bjorndal, 1989). We can discount such responses from our study since our study animals were fed a consistent diet in terms of species composition, volume and frequency.

In a parallel study, we found that mean monthly temperature in 2009–2010 within tortoise range on Santa Cruz varied from 17.2 to 27.9 °C (Blake et al. unpub. data). Adult tortoises migrate from the highlands during the cool season to lowlands in the hot season (Cayot, 1987; Blake et al., in second review), maximizing the range of ambient temperatures to which they are exposed. Our regression line of MRT against temperature (linear in this case through the true relationship is likely curvilinear (Lichtenbelt, 1992) would predict a doubling of MRT over this range, from 9 days at 27.9 °C in lowlands during the hot wet season to 19 days at 17.2 °C in the highlands during the cool dry season. Given that energy extracted from food during digestion is a

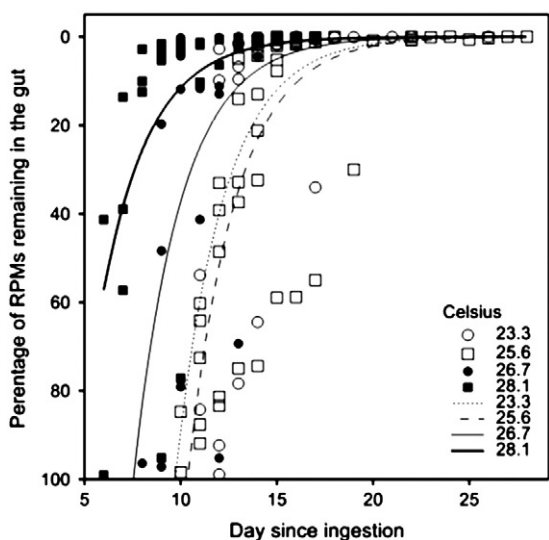


Fig. 3. Temporal pattern of rate of passage marker recovery by ambient temperature.

function of the time that food is retained in the gut (Sibley, 1981; Tracy et al., 2006), we suggest that that tortoises may migrate across the altitudinal temperature gradient on Galápagos at least in part to maximize energy gained from food resources.

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