PLANT ANIMAL INTERACTIONS

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Seed dispersal by the Florida box turtle (*Terrapene carolina bauri*) in pine rockland forests of the lower Florida Keys, United States

Abstract Seed dispersal by animals is one of the most important plant-animal mutualisms, but saurochory, the dispersal of seeds by reptiles, has received little attention. We investigated the role of the Florida box turtle (*Terrapene carolina bauri*) as a seed dispersal agent in pine rockland forests of the lower Florida Keys and examined the effect of turtle digestion on seed germination. We obtained seeds of 11 species with fleshy fruits and 2 species with non-fleshy fruits (a grass and legume) from the feces of 145 box turtles collected on Key Deer National Wildlife Refuge from 1999 to 2000. We planted the seeds of nine species and germination percentage (percentage of seeds that germinated during the experiment) varied from 10% to 80%. Comparative germination experiments were conducted with *Thrinax morrissii, Serenoa repens,* and *Byrsonima lucida.* We compared the germination percentage and germination rate (number of days from planting to seedling emergence) of seeds from three treatments (seeds recovered from feces, control seeds with pulp, and control seeds without pulp) and continued these experiments for up to 2 years. Passage through the box turtle digestive tract greatly enhanced the germination percentage and germination rate of *S. repens*, but decreased the germination percentage of *B. lucida* and *T. morrissii*, and decreased germination rate for *T. morrissii*. Subsequent destructive seed viability tests revealed that many ungerminated *T. morrissii* seeds remained viable, suggesting long-term seed dormancy may occur, even after passage through the turtle digestive system. In addition, the proportion of ungerminated seeds which remained viable was greater for seeds recovered from turtle feces than from control seeds with pulp. Furthermore, removal of fleshy pulp either manually or by the turtle digestive system may allow *T. morrissii* to escape insect predation.

Keywords *Byrsonima lucida* · Plant-animal interaction · Saurochory · *Serenoa repens* · *Thrinax morrissii*

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Introduction

Seed dispersal by animals is a critical plant-animal mutualism that plays an important role in the gene flow, demography, distribution, and evolution of plants (Howe and Smallwood 1982; van der Pijl 1982; Jordano 1992; Richardson et al. 2002). While seed dispersal by insects, birds, and mammals is well studied (Abrahamson 1989), saurochory, the dispersal of seeds by reptiles, has received comparatively little attention (Traveset 1998) despite recognition that early reptiles were a significant selective force in the evolution of modern fruit (van der Pijl 1982; Tiffney 1986; Moll and Jansen 1995). Although many reptiles are carnivorous and therefore unlikely to ingest fruits and disperse seeds, numerous partially or wholly herbivorous species are potential seed dispersal agents (Moll and Jansen 1995). Seed dispersal by aquatic and terrestrial chelonians (Moll and Jansen 1995 and review therein; Varela and Bucher 2002; Carlson et al. 2003), lizards (Iverson 1979; Whitaker 1987; Fialho 1990; Valido and Nogales 1994; Saez and Traveset 1995; Nogales et al. 1998; Castilla 1999), and one species of snake (Engel 1997) has been documented.

Previous studies of saurochory have several important limitations. Most notable is the paucity of germination experiments comparing seeds collected from reptile feces with those harvested directly from plants (Traveset 1998). Such experiments are necessary to quantify important components of dispersal effectiveness, such as germination rate, germination percentage, and the length of dormancy of ingested and uningested seeds, all of which have important ecological implications for plant establishment (Schupp 1993; Traveset et al. 2001a, 2001b). Furthermore, most comparative germination experiments have been conducted over brief periods (several months) in highly artificial settings (e.g., petri dishes and growth chambers), possibly masking differences in germination performance between ingested and uningested seeds (Traveset 1998). In addition, seeds that fail to germinate are generally assumed dead, but could merely be dormant (Traveset 1998). Finally, studies of saurochory have yet to explore the effect of fruit pulp removal on seed germination (Traveset 1998), although pulp removal by birds and mammals reportedly enhances germination (Temple 1977; Izhaki and Safriel 1990; Barnea et al. 1991; Bustamante et al. 1993; Traveset et al. 2001a, 2001b).

The eastern box turtle (*Terrapene carolina*) is recognized as a potential seed dispersal agent for many understory shrubs and herbs in temperate forests of eastern North America (Martin et al. 1951; Klimstra and Newsome 1960; Rust and Roth 1981; Vuorisalo and Watson 1990), and experiments suggest that passage through the box turtle digestive tract enhances germinability for some species (Braun and Brooks 1987). The Florida box turtle (*T. carolina bauri*) has the southernmost distribution of the four *T. carolina* subspecies found in the United States, occurring throughout peninsular Florida and many of the Florida Keys (Dodd 2001).

In this study we address the following questions: (1) what plant species, if any, are dispersed by *T. carolina bauri*; (2) does passage through the turtle digestive system result in different seed germination behaviors (germination percentage and germination rate); (3) if so, are these differences caused by removal of the fruit pulp. To answer these questions we analyzed feces from wild box turtles, and then conducted two sets of germination trials: (1) germinability tests without controls and (2) comparative germination experiments with two control groups followed by viability tests on ungerminated seeds.

Materials and methods

This study was conducted on Key Deer National Wildlife Refuge (KDNWR; 24°42′N, 81°22′W), Big Pine Key, Monroe County, Florida, United States. KDNWR is characterized by extensive pine rockland forest, a fire-dependent ecosystem that occurs on limestone outcrops in extreme southern Florida (Snyder et al. 1990). This ecosystem is dominated by a relatively open canopy of slash pine (*Pinus elliottii*) with a diverse understory composed of shrubs, vines, herbs, and several species of palms (Snyder et al. 1990). The climate of this region is considered tropical with pronounced wet (May to October) and dry (November to April) seasons.

Seed recovery from feces

Box turtles were collected from June to October 1999, and July to November 2000. We searched for turtles during the morning (0730–1000 h) and late afternoon (1700–1930 h). In 1999 a trained dog was used to locate turtles, and during both years turtles were also opportunistically captured. We obtained feces by placing turtles overnight (12–18 h) in plastic buckets containing around 5 cm water to stimulate defecation (Thirakhupt and van Dijk 1994; Platt et al. 2001). Plant diaspores (seed dispersal units) and other items were then separated from feces using a sieve (2-mm mesh) and identified to the lowest possible taxonomic level. We planted a subset of diaspores in standard nursery pots within 1 week of recovery to verify species identification and determine if seeds would germinate after passage through the turtle digestive tract. Pots were placed in a semi-open shade house at KDNWR and watered as needed (see later).

Comparative germination experiments

Diaspores of two palms (*Thrinax morrissii* and *Serenoa repens*) and an understory shrub (*Byrsonima lucida*) were used in comparative germination experiments. All three species produce drupes (fleshy fruits); those of *T. morrissii* and *S. repens* are single seeded, while the stony endocarp of *B. lucida* contains three seeds. Hereafter, we refer to the latter as a diaspore as it comprises the natural dispersal unit (Allaby 1992). We selected these species because (1) their seeds occurred in the feces of at least five turtles and (2) sufficient mature seeds were available from local plants at the time of the experiments. We planted diaspores around 1 cm deep in standard nursery trays filled with a mixture of garden soil, sand, and mulch within 1 week of recovery. Germination experiments were conducted in a semi-open shade house at KDNWR where seed trays were exposed to partial sunlight and rain; supplemental watering was provided when trays became dry. Although our planting methods differed somewhat from natural conditions (e.g., garden soil, seeds buried rather than placed on surface, etc.), seeds of different treatments were subject to uniform germination conditions, which were appropriate to assess their relative performance.

We compared germination percentage (percentage of seeds that germinated during the experiment) and germination rate (number of days from planting to seedling emergence) of seeds from turtle feces with seeds collected directly from plants (hereafter referred to as controls). Turtles digested fleshy portions of fruits and we found only seeds without pulp in feces. We used two sets of controls to test the hypothesis that removal of fleshy pulp by turtle digestion causes differences in germination between seeds from feces and control seeds (van der Pijl 1982). Control groups consisted of (1) intact fruits and (2) seeds from which the fleshy pulp was removed by hand. The latter was accomplished by removing seeds from fruits and wiping them vigorously with a cloth to remove adhering bits of fleshy material. Control seeds were collected from ten randomly selected plants and pooled to generate random replicates for each species. The use of replicates for each treatment allowed us to assess variation in germination percentage within each treatment and provided a more robust statistical analysis. Unless indicated otherwise, germination trials for all treatment groups of the same species began on the same date and were terminated when no seed germinated for two (*T. morrissii* and *B. lucida*) or three (*S. repens*) consecutive weeks. At the conclusion of the germination trials, a random subset of ungerminated *T. morrissii* and *B. lucida* (2001 trials only) seeds and all ungerminated *S. repens* seeds were retrieved for viability tests.

Germination trials for *T. morrissii* included 216 seeds recovered from five turtles during September 2000. These were divided into 11 replicates of 20 seeds each, except for one that had only 16 seeds. Equal numbers of seeds per replicate were used for both control groups. Trials began in September 2000 and continued for 537 days (77 weeks).

Germination trials for *S. repens* included 24 seeds recovered from five turtles in October 2000. These were divided into four replicates of six seeds each. Due to the limited availability of seeds, only 18 and 17 seeds (three replicates each) were used for controls with- and without-pulp, respectively. Trials began in October 2000 and continued for 411 days (59 weeks).

Two comparative experiments were conducted for *B. lucida*. In the initial experiment, 144 diaspores recovered from 25 turtles during July 1999 were planted in 25 replicates of six diaspores each. Trials began in July 1999 and continued for 126 days (18 weeks). Ungerminated seeds from these trials were not retrieved for viability testing. We used only diaspores with the pulp removed as controls in this experiment, and intended to repeat the experiment with both sets of controls; however, in 2000 and 2001 *B. lucida* crops were small and we found insufficient numbers of diaspores in turtle feces. Thus, we conducted another experiment in 2001 and compared only the two sets of control diaspores (with- and without-pulp). Trials began in May 2001 and continued for 183 days (26 weeks). This combination of experiments allowed us to indirectly compare the germination behavior of seeds from feces with control seeds.

Tetrazolium seed viability tests

Ungerminated seeds were opened to expose the embryo and submerged in a 1% 2,3,5-triphenyl tetrazolium chloride solution for 2–4 h (Kearns and Inouye 1993). We classified embryos into five categories based on the extent of red staining: no staining, 1–25%, 25–50%, 50–75%, and 75–100%. Only embryos with >50% staining were considered viable. We also subjected mature seeds collected from wild plants to the staining solution as a positive control. The presence of unidentified insect larvae in seeds opened for viability testing was noted.

Statistical analysis

Data from different species were analyzed separately. All statistical analyses were performed with SPSS 10.0 (SPSS, Chicago). We used one-way ANOVAs to test for differences in germination percentage among the three treatments: seeds from turtle feces, control seeds with pulp, and control seeds without pulp. Germination trial replicates were used to generate variance within each treatment in the ANOVA. Germination percentages for *T. morrissii* were transformed using a square root arcsine transformation to meet the assumptions of parametric tests. Because transforming the germination percentage of *S. repens* and *B. lucida* did little to meet the parametric assumption of equal variance, we used non-transformed data in our analyses. Non-parametric tests (results not presented) on these variables were also used to verify parametric test results. We used post-hoc Tukey tests to detect differences between treatments. Kaplan-Meier (log rank) tests were used to detect differences in germination rates among and between treatments using pooled data from all replicates of the same treatment. Chi-square tests were used to test the distribution of ungerminated seed fates (viable vs dead) among and between treatments, and to compare the proportional distribution of different colored fruits available in pine rockland forests with those consumed by box turtles. Differences were considered significant at $P < 0.05$ and marginal at $P < 0.1$.

Results

We obtained feces from 145 box turtles and found that fleshy fruits and terrestrial snails (Mollusca) comprised the bulk of the diet. The seeds of fleshy fruited plants and snail remains occurred in the feces of 138 (95.1%) and 128 (88.2%) turtles, respectively. Leafy vegetation occurred in the feces of 33 (22.7%) turtles, while insects, fungi, and vertebrate remains (most likely consumed as carrion) were each found in the feces of 10 (6.8%) or fewer turtles. We recovered the seeds of 11 species of plants with brown, yellow, purple, blue, black, and white fruits, but the seeds of red-fruited species were absent from our sample (Tables 1, 2). There was no significant difference between the color of fruits available in pine rockland forest and

Table 1 Physical attributes, descriptive statistics, and the frequency of occurrence of diaspores found in the feces of 145 Florida box turtles from Key Deer National Wildlife Refuge, Florida. N = number of turtles from which a diaspore was recovered. Mean = mean number of diaspores per turtle; calculated using N rather than 145. Frequency of occurrence was calculated by dividing the number of turtles containing a particular diaspore by 145. Percentages do not sum to 100 because diaspores from multiple species were often found in the feces of a single turtle (*NA* not applicable)

Species	Growth form	Fruit color[c]	N	Mean (±1 SD)	Range	Frequency of occurrence (%)
Annona glabra[a, b]	Tree	Yellow	5	27.0 (30.4)	1 to 75	3.3
Brysonima lucida[a, b]	Shrub	Brown	78	27.9 (19.6)	1 to 80	52.0
Coccoloba uvifera[a, b]	Tree	Purple-black	2	1.5 (0.7)	1 to 2	1.3
Cocothrinax argentata[a, b]	Palm	Purple	11	4.3 (8.9)	1 to 31	7.3
Fabaceae	NA	NA	2	4.5 (0.7)	4 to 5	1.3
Ficus sp.[a, b]	Tree	Purple-black	1	NA	Ca. 250	0.6
Morinda royoc[a, b]	Vine	Yellow	24	55.0 (94.3)	1 to 414	16.0
Manilkara zapoda[a, b]	Tree	Brown	1	NA	NA	0.6
Paspalum spp.	Grass	NA	3	14.7 (11.5)	8 to 28	2.0
Psidium longipes[a]	Shrub	Dark purple	37	7.8 (16.2)	1 to 93	24.6
Serenoa repens[a, b]	Palm	Yellow	5	6.6 (5.3)	1 to 15	3.3
Smilax havenensis[a]	Vine	Blue-black	3	4.0 (3.6)	1 to 8	2.0
Thrinax morrissii[a, b]	Palm	White	37	51.0 (70.4)	1 to 330	24.6

[a]Species with fleshy fruit

[b]Seeds germinated successfully after recovery from turtle feces

[c]Based on Tomlinson (1986), Scurlock (1987), and personal observations

those consumed by box turtles (Chi-square =2.15, df =4, P =0.707). However, because box turtles consumed no red fruits, one cell in the analysis equaled zero and these results should therefore be interpreted with caution (Sokal and Rohlf 1981). Additionally we recovered a small number of intact grass and legume seeds (Table 1). We planted the seeds of nine fleshy fruited species and seeds of each germinated successfully (Table 1). Germination percentages of these seeds ranged from 10% to 80%. *B. lucida* fruits were available from June to August and seeds were recovered from 78 of 88 (91.5%) turtles captured during this period. *T. morrissii* fruits were available from July to October and seeds were recovered from 37 of 123 (30.0%) turtles captured during this period. Reproduction by *S. repens* is largely asexual (Clewell 1985; Nelson 1996), but we found small quantities of fruit from May to November (Koptur et al., unpublished data). *S. repens* seeds were found in the feces of 5 of 54 (9.2%) turtles captured from August to November.

Thrinax morrissii

The mean (±1 SD) germination percentage for seeds recovered from turtle feces, control seeds with pulp, and control seeds with pulp removed was 11.82 (±9.02), 15.34 (±9.55), and 19.43 (±7.57), respectively. Differences among treatments were only marginally significant (ANOVA, $F_{2,30}$ =2.82, P =0.071). Differences in germination rates among treatments were not significant (Fig. 1a; log rank statistic =4.47, df =2, P =0.10. Many ungerminated seeds remained viable when the experiment was terminated and the proportion of viable ungerminated seeds differed significantly among treatments (Fig. 2a; Chi-square =12.11, df =2, P =0.002). The proportion of dead seeds in feces was significantly less than in controls with pulp (Fig. 2a; Chi-square =12.12, df =1, P <0.001). The proportion of dead seeds in controls with pulp was greater than controls without pulp, but only marginally so (Chi-square =3.57, df =1, P =0.06). Most (98%) dead seeds contained unidentified insect larvae (Fig. 2a).

Serenoa repens

The mean (±1 SD) germination percentage for seeds recovered from turtle feces, control seeds with pulp, and control seeds with pulp removed was 79.17 (±15.96), 27.78 (±19.25), and 38.89 (±9.62), respectively. Differences among treatments were significant (ANOVA, $F_{2,7}$ =10.82, P =0.007). The germination percentage of seeds from turtle feces was significantly greater than seeds with and without pulp (Tukey, P =0.008 and 0.027, respectively), but differences between control groups were not significant (Tukey, P =0.671). Germination rates differed significantly among treatments (Fig. 1b; log rank statistic =16.98, df =2, P <0.001). Seeds from turtle feces germinated significantly faster than control seeds with (log rank statistic =10.52, df =1, P =0.001) and without pulp (log rank statistic =9.33, df =1, P =0.002). There were no significant differences in germination rates between control groups (log rank statistic =0.16, df =1, P =0.692). The proportion of viable ungerminated seeds was not significantly different among treatments (Fig. 2b; Chi-square =4.442, df =2, P =0.108). However, because two cells in the cross-tabulation have values less than five, these results should be interpreted with caution (Sokal and Rohlf 1981). None of the dead seeds contained insect larvae (Fig. 2b).
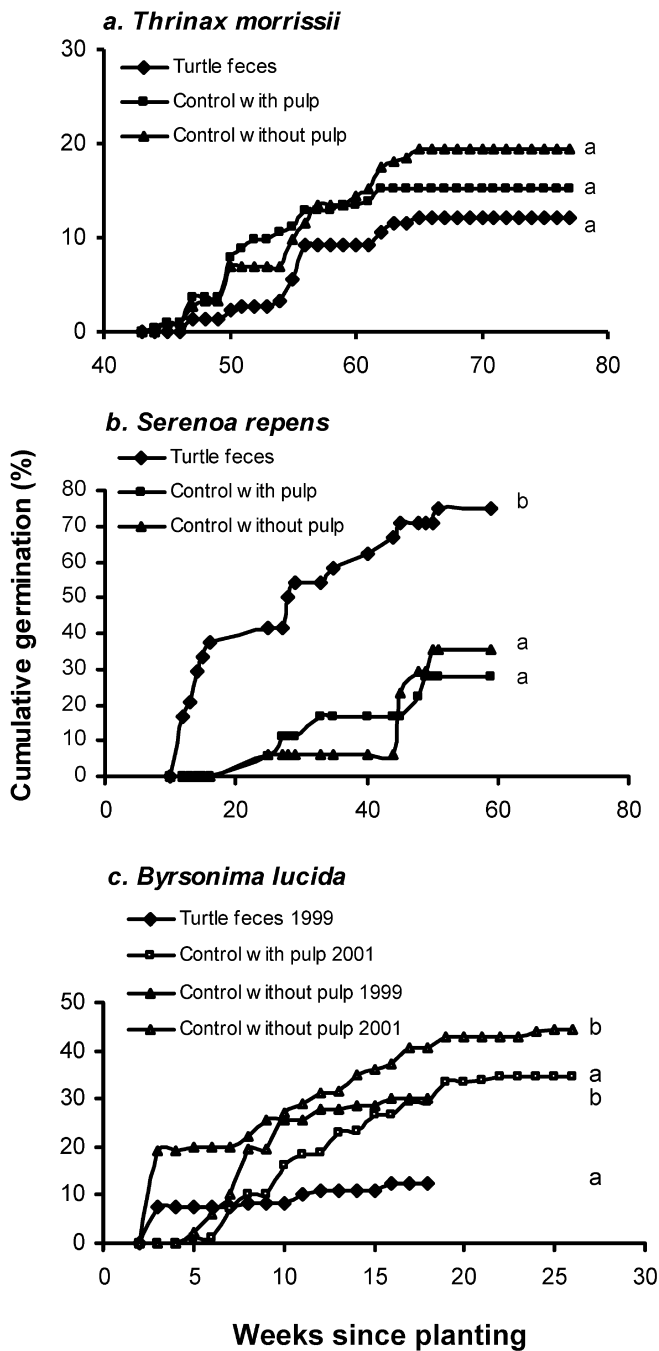
Byrsonima lucida

Separate statistical tests were conducted for the 1999 and 2001 trials because differences in the number of days to seedling emergence suggest germination conditions varied between years. We therefore performed our analyses on both pooled and unpooled data from 1999 and 2001. In 1999 the mean (±1 SD) germination percentage for seeds recovered from turtle feces and control seeds with pulp removed was 14.44 (±18.22) and 32.33 (±24.97), respectively. In 2001 the mean (±1 SD) germination percentage for control seeds with pulp and with pulp removed was 34.44 (±20.50) and 44.44 (±20.22), respectively. Significant differences in germination percentage among the four treatments were noted after we pooled 1999 and 2001 data (ANOVA; $F_{3,105}$ =9.17, P <0.001); germination percentage of seeds from feces was

Table 2 Color of fleshy fruits occurring in pine rockland forests and consumed by box turtles at Key Deer National Wildlife Refuge, Big Pine Key, Florida, United States. Fruit color from Tomlinson (1986), Scurlock (1987), and personal observations

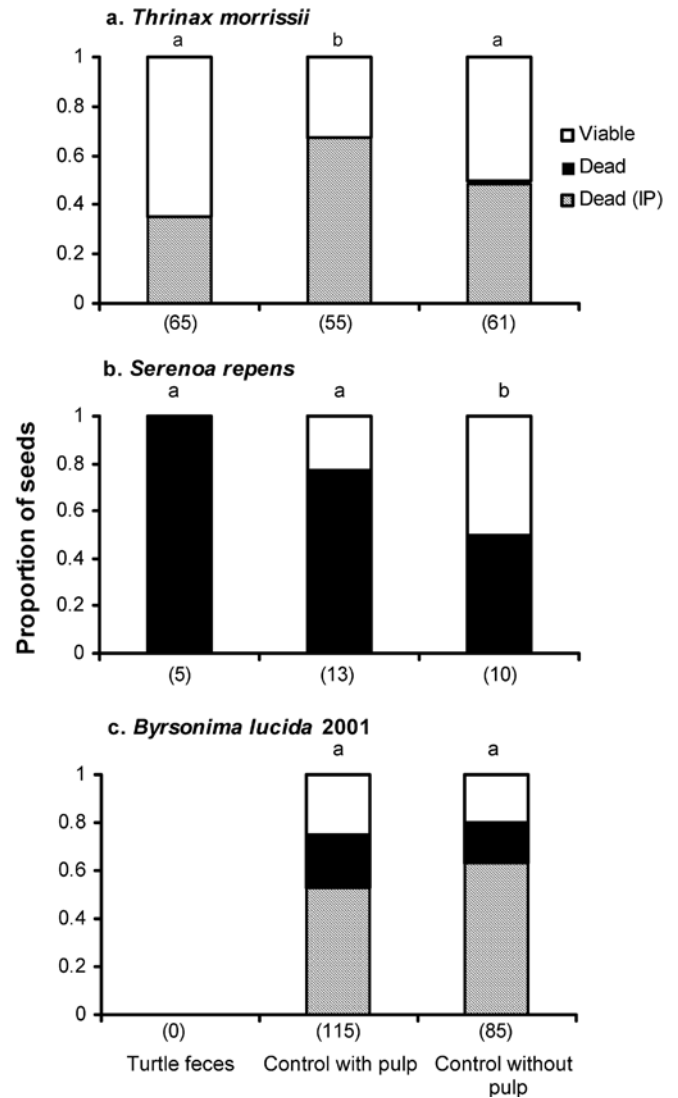| Fruit color	No. of species occurring in pine rockland forests	No. of species consumed by box turtles
Brown	2 (6%)	2 (18%)
Blue/purple/black[a]	16 (49%)	6 (55%)
Red	4 (12%)	0 (0%)
White	5 (15%)	1 (9%)
Yellow	6 (18%)	2 (18%)
Total	33	11

[a]Published descriptions of color are vague for dark-fruited species (i.e., blue-black or purple-black)

Fig. 1 Cumulative germination percentage curves for *Thrinax morrissii* (**a**), *Serenoa repens* (**b**), and *Byrsonima lucida* (**c**) seeds from three treatments (seeds recovered from box turtle feces, controls with pulp, and controls without pulp). *Different letters within each species indicate significant differences (P <0.05) in germination rate. Note that pair-wise comparisons for B. lucida were between treatments of the same year only (1999 or 2001)*

Fig. 2 Outcome of viability tests on ungerminated seeds of *Thrinax morrissii* (**a**), *Serenoa repens* (**b**), and *Byrsonima lucida* (**c**) from three treatments (seed recovered from box turtle feces, controls with pulp, and controls without pulp). Note that no dead *T. morrissii* seeds were found without insect predation (*IP*) in turtle feces or controls with pulp, hence solid bars are not shown for these treatments. There was no insect predation of *S. repens* seeds. *Different letters within each species indicate a significant difference in categories of seed viability between treatments (P <0.05). Numbers below the histograms indicate the sample size*

significantly less than control seeds without pulp (1999), control seeds with pulp (2001), and control seeds without pulp (2001) (Tukey, P =0.019, 0.004, and 0.001, respectively). Independent sample t-tests indicated that germination percentage of control seeds without pulp was greater than seeds from turtle feces in 1999 (t_{49} =−2.85, P =0.006). Marginal differences in germination percentage

were found between control seeds with pulp and without pulp in 2001 (t_{58} =−1.90, P =0.062).

There were significant differences in germination rate among all treatments when we pooled data from 1999 and 2001 (Fig. 1c; log rank statistic =25.82, df =3, P <0.001). Control seeds without pulp germinated significantly faster than seeds from turtle feces in 1999 (Fig. 1c, log rank statistic =12.79; df =1; P <0.001). Likewise, control seeds without pulp germinated significantly faster than control seeds with pulp in 2001 (log rank statistic =4.65, df =1, P =0.031). There was no significant difference between the proportion of viable vs dead ungerminated seeds in the two control treatments in 2001 (Fig. 2c; Chi-square =0.75,

$df =1$, $P =0.386$). More than 80% of the dead seeds contained insect larvae (Fig. 2c).

Discussion

Box turtles consumed and probably disperse 13 of 33 (39%) species with fleshy fruits that occur in pine rockland forests of KDNWR, including dominant components of the shrub (*B. lucida, T. morrissii, S. repens, Coccothrinax argentata*) and herbaceous (*Morinda royoc*) layers (Snyder et al. 1990). Moreover, the presence of legume and grass seeds in feces suggests that box turtles disperse the seeds of non-fleshy fruits as well. Although box turtles are omnivorous (Dodd 2001; this study), we found nothing to suggest that the seeds recovered from turtle feces were secondarily acquired by ingesting animals; terrestrial snails were the principal animal prey of box turtles and the remains of vertebrates potentially capable of consuming fruit were recovered from only a small number of turtles. Furthermore, we frequently observed turtles consuming fruits in the field and often found them beneath fruiting plants.

Dispersal of *T. morrissii*, *S. repens*, and *C. argentata* seeds by box turtles are among the few documented cases of palm seed dispersal by a reptile. Previous studies concluded that reptile mediated dispersal of palm seeds is rare and identified only one species of lizard (*Cyclura carinata*) as an important dispersal agent (Zona and Henderson 1989; Zona 2002).

Box turtles may be significant seed dispersal agents in the pine rockland forests of the Florida Keys as they occur at high densities (up to 14.9 turtles/ha on other islands in south Florida; Langtimm et al. 1996) and the pool of potential bird and mammal seed dispersers is less diverse relative to the Florida mainland (Lazell 1989). Furthermore, seeds require from 2 to 20 days to pass through the digestive tract (Braun and Brooks 1987), during which time turtles can move several hundred meters within a home range as large as 5 ha (Stickel 1950; Schwartz and Schwartz 1974; Strang 1983; Dodd 2001).

Experimental studies indicate that box turtles readily discern color and preferentially select orange and red while disregarding green and blue, although their reaction to other colors has not been tested (Dodd 2001). However, the majority of fruits consumed by box turtles on KDNWR were dark (blue/purple/black) and the seeds of red-fruited species were absent from fecal samples. We attribute this to the rarity and fruiting habits of red-fruited species on our study area. Only four red-fruited species occur on KDNWR and three (*Crossopetalum rhacoma*, *C. ilicifolium*, and *Guapira discolor*) are extremely rare (Koptur et al., unpublished data). The fourth (*Guettarda scabra*) is somewhat more abundant, but ripened fruits rarely fall to the ground, instead being retained on branches and probably consumed by birds (Koptur et al., unpublished data). It is possible that olfactory cues, while poorly understood, may also play a role in fruit selection by box turtles (Fitch 1965; Dodd 2001). It is clear, however that fruits consumed by box turtles either occurred on plants with prostrate growth forms (e.g., *M. royoc*, *Smilax havanensis*, and *S. repens*) or readily dropped to the ground at maturity (e.g., *B. lucida*, *C. argentata*, and *T. morrissii*).

Some abundant low-growing species that produce fleshy fruits (*Ernodea littoralis* and *Randia aculeate*) were surprisingly absent in the feces we examined. Seeds of these fruits could have been completely digested along with the fleshy parts, in which case box turtles act as seed predators. Another possibility is that box turtles simply do not consume these fruits. Furthermore, it is likely that we underestimated the number of species dispersed by box turtles as sampling occurred only during summer and early fall, and species that fruit at other times were undetected by this sampling regime. Finally, the mesh size (2 mm) of the sieve we used for separating fecal material may have allowed small seeds (*Bletia purpurea*, *Tillandsia* spp. and some grasses) to pass through undetected.

The effects of digestion on the germination performance of seeds varied among species. The germination percentage and rate of *S. repens* seeds recovered from feces was greater than control seeds, while the reverse was true for *B. lucida* and *T. morrissii*. Variable effects of digestion on germination performance among plant species have likewise been noted in other studies of mammals, birds, and a few reptiles (Traveset 1998). In addition, our results are consistent with the observation that larger seeds are more likely than small seeds to be affected positively (greater germination percentage of ingested vs uningested seeds) by digestion (Traveset and Verdu 2001). *S. repens* has the largest seed of the three species tested, and it was the only one to respond positively to turtle digestion. In other studies of reptile-mediated seed dispersal, there were no differences in germination percentage or rate between seeds from feces and controls (Moll and Jansen 1995; Castilla 2000; Hartley et al. 2000).

Differences in germination performance between seeds from turtle feces and control seeds with pulp removed suggest that the effects of digestion on seed germination is unlikely due solely to pulp removal. Nevertheless, when compared to control seeds with pulp, manual pulp removal improved, though not significantly, germination percentage in all three species. Furthermore, germination rate increased in *B. lucida*, but decreased in *T. morrissii* and *S. repens* in response to pulp removal. Although the mechanism for the latter is unclear, pulp removal (either manually or by digestion) possibly triggered secondary seed dormancy (Traveset 1998).

Likewise, the low germination percentage of *T. morrissii* and *B. lucida* seeds recovered from feces is not due to mortality resulting from passage through the digestive tract as tetrazolium tests indicate that most ungerminated seeds remain viable. Instead these results further suggest that digestion initiates seed dormancy (Traveset 1998). Although prolonged seed dormancy has demographic costs, it allows seeds to disperse through time and serves as a propagule and genetic reservoir

(Baker 1989; Baskin and Baskin 1989; Silvertown and Lovett-Doust 1993).

While dissecting seeds for viability tests we noted that the majority of dead *T. morrissii* seeds suffered from insect predation, and the percentage of dead seeds was greatest among control seeds with pulp. Thus, pulp removal, either manually or by digestion appears to provide an escape from insect predation. Fleshy pulp is a potential source of infection by fungal or other pathogens (Traveset 1998), but to our knowledge, this is the first report of a reduction in insect seed predation by pulp removal.

In summary, our study demonstrates that box turtles consume large numbers of fleshy fruits from a number of plant species in pine rockland forests, and many of these seeds survive passage through the digestive tract. However, the benefits to plants from this interaction vary, in part due to the differential effects of digestion on seed germination behaviors. Although high mortality rates (up to 99%) are common in plant seeds dispersed by animals, the benefits of being transported away from the parent plant likely outweigh the costs of this interaction (Janzen 1984). Furthermore, plants may derive additional benefits when box turtles move into recently burned areas to forage on new regrowth (Borg and Liu, personal observations). Seeds dispersed into these areas are likely to encounter favorable microsites for seedling establishment (Daubenmire 1968; Menges 1995).

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