

Diets of Two Nonnative Freshwater Turtle Species (*Trachemys scripta* and *Pelodiscus sinensis*) in Kawai Nui Marsh, Hawaii

Author(s): Aaron J. Works and Deanna H. Olson

Source: Journal of Herpetology, 52(4):444-452.

Published By: The Society for the Study of Amphibians and Reptiles

<https://doi.org/10.1670/17-137>

URL: <http://www.bioone.org/doi/full/10.1670/17-137>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Diets of Two Nonnative Freshwater Turtle Species (*Trachemys scripta* and *Pelodiscus sinensis*) in Kawai Nui Marsh, Hawaii

AARON J. WORKS^{1,2,4} AND DEANNA H. OLSON³

¹Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, Oregon 97331 USA

²Oahu Invasive Species Committee, Pacific Cooperative Studies Unit, University of Hawaii at Manoa, 743 Ulukahi Street, Kailua, Hawaii 96734 USA

³US Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, Oregon 97331 USA

ABSTRACT.—Island ecosystems provide habitat for many endemic species that may be threatened by nonnative species introductions. We examined nonnative freshwater turtle occurrences and diets to examine potential predation effects on native species in Kawai Nui Marsh, Oahu, Hawaii. No freshwater turtles are native to the Hawaiian Archipelago. The Pond Slider (*Trachemys scripta*) and Chinese Softshell (*Pelodiscus sinensis*) were the only turtles found in the marsh after 767 trap days. *Trachemys scripta* stomachs ($n = 50$) contained mostly the nonnative plant *Commelina diffusa* and nonnative snails (*Pomacea* sp.), whereas *Pelodiscus sinensis* stomachs ($n = 5$) contained mostly snails. Interspecific dietary overlap was low and intersexual dietary overlap in the sliders was high, with more diverse female diets. Small, medium, and large size classes of *T. scripta* stomachs contained different proportions of plant and animal matter, with the small size class containing less plant matter than the medium size class, and the large size class containing a greater volume of animal than plant matter. No native species were found in the stomach contents of the turtles sampled except a freshwater sponge (*Heteromyenia baileyi*). This lack of native species in their diets may have more to do with the degraded state of the marsh and lack of native taxa than with a preference for nonnative taxa. A potential concern could be nonnative freshwater turtle presence in pristine wetland habitats in Hawaii, because of the higher abundances of native species in those areas.

Studies of diet are important in nonnative species ecology to understand novel predator influences on ecosystems they invade, and specifically their interactions with native species (Vitousek, 1987). Nonnative herpetofauna can affect ecosystem dynamics through direct predation on native species (Savidge, 1988; Beard, 2007; Holland et al., 2010; Shine, 2010), competition for dietary and spatial resources (Sin et al., 2008; Wang et al., 2013; Doody et al., 2015; Rogers et al., 2017), and other indirect effects.

Diet studies of nonnative freshwater turtles have revealed effects on native fauna (Chen and Lue, 1998; Prevot-Julliard et al., 2007; Outerbridge, 2008; Perez-Santigosa et al., 2011) and can aid in the understanding of a species' trophic position within a food web. In a study by Marchetti and Engstrom (2016), the introduced Wattle-Necked Softshell (*Palea steindachneri*) in Hawaii either occupied the same position in the food web as native fishes or served as the top predator in the food web. In Hawaii, Newcomb's Snail (*Erinna newcombi*) is endemic to certain tributaries on Kauai, so risk of extinction to this species could be high (Marchetti and Engstrom, 2016). Fully understanding potential influences from nonnative freshwater turtles remains critical to aid in the conservation of Hawaii's unique wildlife.

Endemic wetland species in Hawaii include 4 fishes, 2 shrimps, 9 snails, and 31 dragonflies and damselflies (Yamamoto and Tagawa, 2000; Nishida, 2002; Christensen, 2015; Cowie et al., 2016a,b). In addition, Hawaii has four endemic and federally endangered wetland bird species that are of particular concern: the Hawaiian Duck (*Anas wyvilliana*), Hawaiian Coot (*Fulica alai*), Hawaiian Gallinule (*Gallinula galeata sandvicensis*), and Hawaiian Stilt (*Himantopus mexicanus knudseni*). Hawaii's native wetland biota may be at risk of direct or indirect influence from nonnative freshwater turtle presence, especially via trophic effects. Different freshwater turtle species have different feeding strategies and preferred food (Luiselli, 2008); because some turtle species are herbivorous and others

carnivorous, they directly influence specific taxa through consumption. Some turtle species have been documented preying on wetland birds (e.g., Pond Slider [*Trachemys scripta*]: Ligon, 2007; Ernst and Lovich, 2009; Colombian Slider [*T. callirostris*]: Pritchard and Trebbau, 1984), a particular concern in Hawaii.

Quantified diet studies can lead to a better understanding of freshwater turtle ecology, food-web dynamics, and ecosystem function (Vogt, 1981; Tucker et al., 1995; Platt et al., 2016; Eiseenberg et al., 2017). Identification of important food items for a species can contextualize interspecific interactions within a biological community. This information can be used to understand a nonnative species effect on a native species.

The aim of this study was to examine the diets of introduced freshwater turtles to better understand their ecology in a novel ecosystem, Kawai Nui Marsh, Oahu, Hawaii, a predominately degraded wetland that provides suitable habitat for endemic wetland birds and other native aquatic species. We wanted to know whether nonnative freshwater turtles consume native or nonnative prey, and therefore have potential to affect the novel ecosystem this wetland represents. In addition, we wanted to know if the species, sex, or size class of turtles determined amount of animal matter consumed. We hypothesized that nonnative turtles consume native invertebrates and vertebrates in the marsh and *Pelodiscus sinensis* (Chinese Softshell), female *T. scripta*, and larger *T. scripta* consume a larger proportion of animal matter, therefore having the potential to have more of an impact on native species. All stomach contents were quantitatively analyzed and intestinal tracts were qualitatively assessed for native prey remains. Diet comparisons were conducted between turtle species, and intraspecifically between sexes and among size classes.

MATERIALS AND METHODS

Study Site.—Turtles were collected within the waterways of Kawai Nui Marsh (21°23'41.8"N, 157°45'28.3"W [datum WGS

⁴Corresponding author. E-mail: aaron.j.works@gmail.com
DOI: 10.1670/17-137

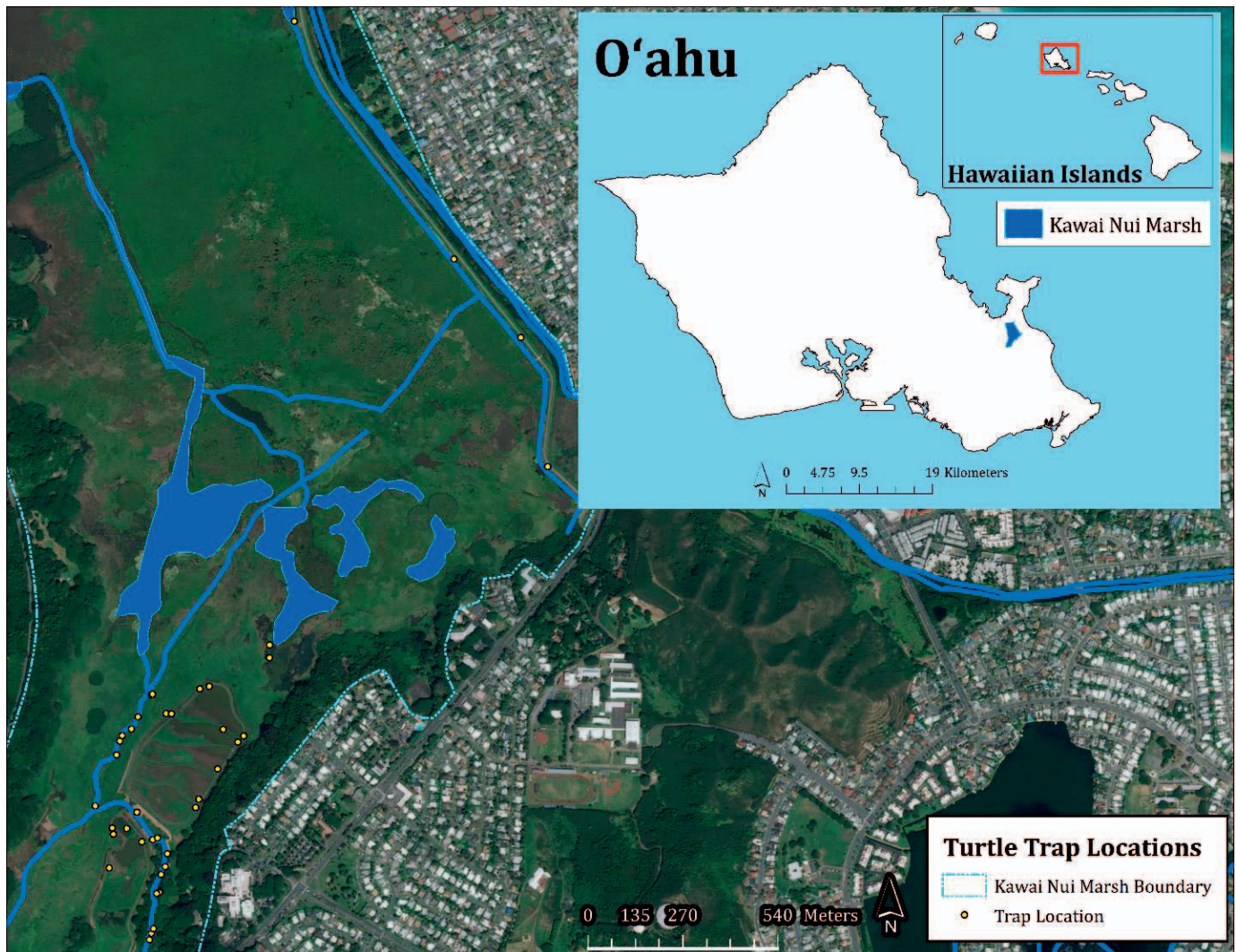


FIG. 1. Map showing the location of Kawai Nui Marsh on Oahu, Hawaii and the turtle trap locations throughout the marsh.

84]; ~390 ha), near Kailua, east of the Koolau Range (Fig. 1 [ArcGIS 10.2.2, ESRI, Redlands, California USA]). To assess the suite of turtle species present in the marsh, sites were chosen along Maunawili Stream and within natural and man-made ponds to encompass all available microhabitat types.

Trapping.—Turtles were trapped using 10 chimney traps baited with fish or chicken livers and hearts. Traps were placed throughout the natural and man-made ponds and Maunawili Stream at 40 locations (Fig. 1). The bottom portion of a trap was a collapsible commercial crab trap (dimensions: $81.3 \times 53.3 \times 20.3$ cm). The upper portion of the trap, or chimney, measured 198.1 cm in height, and provided a secondary chamber designed to minimize trap escape and allow an airspace for trapped turtles. The trap design allowed for extended trapping sessions, although a 24-h period was not exceeded. We usually left traps for several hours or overnight and checked them daily, or closed them if they could not be checked every day. We periodically moved traps to census different areas throughout the marsh; trapping effort per site ranged 0.7 to 82.4 d. We identified all captured turtles to species and weighed them to the nearest 1 g on an EK3550 kitchen scale (Etekcity, Inc., Anaheim, California USA). We measured the straight carapace length (SCL; nuchal to anal notch), straight

carapace width (at the widest point), and the straight plastron length of turtles with 01409A vernier calipers (Neiko Tools, Wenzhou, China) to the nearest 1 mm. All turtles were sexed using typical morphological characteristics specific to each sex (Reed and Tucker, 2012). *Trachemys scripta* males exhibit secondary sexual characteristics through elongated foreclaws and a cloaca positioned beyond the carapacial margin, whereas females do not show these characteristics (Cagle, 1948; Gibbons and Greene, 1990); *T. scripta* with <100 mm SCL, without sexual characteristics typical of a male, were designated as juveniles (Chen and Lue, 1998). *Pelodiscus sinensis* males differ from females by exhibiting longer tails with the cloaca positioned near the tip of the tail; tails in females barely extend beyond the rim of the carapace (Ernst and Lovich, 2009); *P. sinensis* with <180 mm SCL, without sexual characteristics typical of a male, were designated as juveniles (Ernst and Lovich, 2009). We calculated catch per unit effort (number of unique turtles captured per trap day) to estimate relative abundance of turtle species found in the marsh (House et al., 2011). We analyzed the first 50 *T. scripta* for diet, and all other *T. scripta* were uniquely marked for later identification using the coding system of Ernst et al. (1974). Turtles analyzed were humanely euthanized and dissected; gastrointestinal tracts

were removed and placed in a container and preserved by freezing for later analysis.

Diet Analyses.—Stomach contents were removed, washed with water, separated on a 0.5-mm-mesh sieve, sorted, and identified to the lowest identifiable taxonomic unit using a dissecting microscope ($\times 8$ – 35). We examined intestinal contents for the presence of native prey, but did not make measurements. We used the water displacement method to measure volume for each food item in the stomach to the nearest 0.1 mL using a graduated cylinder (Spencer et al., 1998; Perez-Santigosa et al., 2011; Selman and Lindeman, 2015). We determined occurrence percentage (%F) and volumetric percentage (%V) for each food category using the formulas derived from Colman et al. (2014): $\%F = (F_i / F_j) \times 100$, where F_i is the number of samples containing the item i and F_j is the total number of samples, and $\%V = (V_i / V_j) \times 100$, where V_i is the volume of the food item i and V_j is the total volume of all samples.

Food importance was determined for each food category using an index of relative importance (IRI). We calculated the IRI value for each food category i using percent total volume (% V_i) and percent frequency of occurrence (% F_i) using the formula derived from Bjorndal et al. (1997): $IRI_i = 100V_iF_i / \sum(V_iF_i)$. Values near zero equate to low importance and values closer to 100 are of high importance. We estimated dietary niche breadths using the Shannon index (Krebs, 1999): $H' = -\sum p_j \log p_j$, where p_j is the proportion of turtles found using food category j . We standardized the Shannon index using the formula (Krebs, 1999): $J' = H' / \log n$, where n is the total number of possible diet categories. Values near 0 indicate low diversity and values near 1 high diversity. We measured dietary niche overlap using the simplified Morisita index (Krebs, 1999): $C_H = 2\sum p_{ij} \cdot p_{ik} / (\sum p_{ij}^2 + \sum p_{ik}^2)$, where p_{ij} is the proportion that food category i is of the total food categories used by species j , and p_{ik} is the proportion that food category i is of the total food categories used by species k . Values near 0 indicate low overlap and values near 1 high overlap. We used frequency and volume proportions of food categories for measures of dietary diversity and overlap and used these measures to determine specialization and similarity in food use between sexes and species. Significant differences were evaluated with Pearson's chi-squared tests for the Shannon index comparisons. The simplified Morisita index for dietary overlap was considered minimal if values were <0.4 and of biological significance if values exceeded 0.6 (Tucker et al., 1995; Platt et al., 2016).

We calculated Mann–Whitney U -tests to identify differences in proportions of vegetation and animal foods contained within the stomachs of turtles by species and sexes. To identify foods that contribute significantly more to the diets of males than to those of females, we calculated Fisher's exact test of independence for each food using %F and %V. A two-sample t -test was used to check whether SCL was different in males and females. We corrected all statistical analyses for multiple comparisons for false discovery rate using the method of Benjamini and Hochberg (1995). In addition, we performed a one-way analysis of variance (ANOVA) to assess differences in plant and animal volume contained within the stomachs of different turtle size classes. Afterward, a Tukey–Kramer test was calculated to search for pairwise significance between the size classes. Last, we computed a two-way ANOVA to identify an interaction effect between size class and sex. All statistical analyses were performed in program R (vers. 3.3.1; R Core Team, 2016) with an α of 0.05 to indicate significance.

RESULTS

Trapping occurred from April to November 2016 when air temperatures ranged between 18.1 and 30.8°C and rainfall was not extreme. Two nonnative turtle species were captured in 767 trap days (no. of traps $\times$ no. of days) in Kawai Nui Marsh: *T. scripta* ($n = 116$ total, 111 unique) and *P. sinensis* ($n = 6$). Catch per unit effort for *T. scripta* and *P. sinensis* was 0.145 and 0.008 unique turtles per day, respectively. Turtle captures increased over accumulating trap days (Fig. 2). The *T. scripta* analyzed were captured in April through June and all *P. sinensis* were captured in July and August.

The SCL and mass ($x \pm SD$ [range]) were 172 ± 37 mm (88–236 mm) and 891 ± 525 g (119–1,956 g), respectively, for *T. scripta*, and 166 ± 71 mm (24–248 mm) and 817 ± 543 g (4–1,731 g), respectively, for *P. sinensis*. We obtained stomach contents of 50 *T. scripta* (29 females, 19 males, and 2 juveniles), and 5 *P. sinensis* (3 males, 2 females, and 1 juvenile [empty stomach]; Appendix 1). The *T. scripta* diet contained 18 categories, and hence had a wider array of food items than found in *P. sinensis* (with 5 food categories; Appendix 1). The most important items in the diet of *T. scripta* were *Commelina diffusa* (IRI = 85.4), *Pomacea* sp. (IRI = 7.7), crayfish (IRI = 2.9), thiarid snails (IRI = 1.6), and *Corbicula fluminea* (IRI = 1.0; Appendix 1). The intestinal contents of *T. scripta* did not contain native prey.

The most important items in the diet of *P. sinensis* were *Pomacea* sp. (IRI = 88.2), thiarid snails (IRI = 5.9), and *C. fluminea* (IRI = 2.0; Fig. 3 and Appendix 1). Only animal foods were found in the stomachs of *P. sinensis*. The intestinal contents of *P. sinensis* did not contain native prey.

In the following text, P -values with asterisks indicate comparisons that were statistically significant after application of false discovery rate corrections. *Trachemys scripta* fed on more food categories (mode, range: 2, 1–5) per turtle than *P. sinensis* (1, 0–2; $W = 246.5$, $P = 0.01^*$). *Trachemys scripta* stomachs contained a mean food volume of 6.00 cm³ (range 0.60–13.25 cm³), whereas *P. sinensis* stomachs contained a mean prey volume of 1.75 cm³ (range 0.00–4.00 cm³). Dietary niche breadth of *T. scripta* for frequency and volume of food (Shannon index, $J' = 0.80$ and 0.47, respectively) was wider than that of *P. sinensis* (Shannon index, $J' = 0.45$ and 0.23, respectively; $\chi^2 = 24.66$, $df = 1$, $P < 0.01^*$ and $\chi^2 = 11.63$, $df = 1$, $P < 0.01^*$, respectively). Dietary overlap was moderate and low for frequency and volume according to the simplified Morisita index ($C_H = 0.50$ and 0.19, respectively). The low *P. sinensis* sample size may not fully represent *P. sinensis* prey in this system and precluded diet analyses by sex and size class.

In *T. scripta*, dietary patterns with sex and size were detected. Female *T. scripta* ate from all 18 food categories, whereas male *T. scripta* food came from 10 categories. Also, females fed on more food categories per turtle than males (mode and range for females: 4, 1–5; for males: 1, 1–4; $W = 157$, $P = 0.01^*$). The most important items in the diet of females were *Commelina diffusa* (IRI = 80.8), crayfish (IRI = 5.9), *Pomacea* sp. (IRI = 5.4), thiarid snails (IRI = 4.2), and *Corbicula fluminea* (IRI = 2.7; Fig. 4 and Appendix 1). For males, the most important items in the diet were *Commelina diffusa* (IRI = 84.7), *Pomacea* sp. (IRI = 12.1), and fishes (IRI = 1.3; Fig. 4 and Appendix 1). Female and male stomachs contained a similar mean food volume per turtle ($W = 239$, $P = 0.45$); in particular, the volumes and frequencies of both plant and vertebrate food were the same between males and females (plant volume: $W = 260.5$, $P = 0.76$; plant frequency: $W = 269.5$, $P = 0.88$; vertebrate volume: $W = 334.5$, $P = 0.13$; vertebrate frequency: $W = 315.5$, $P = 0.31$). In contrast, female

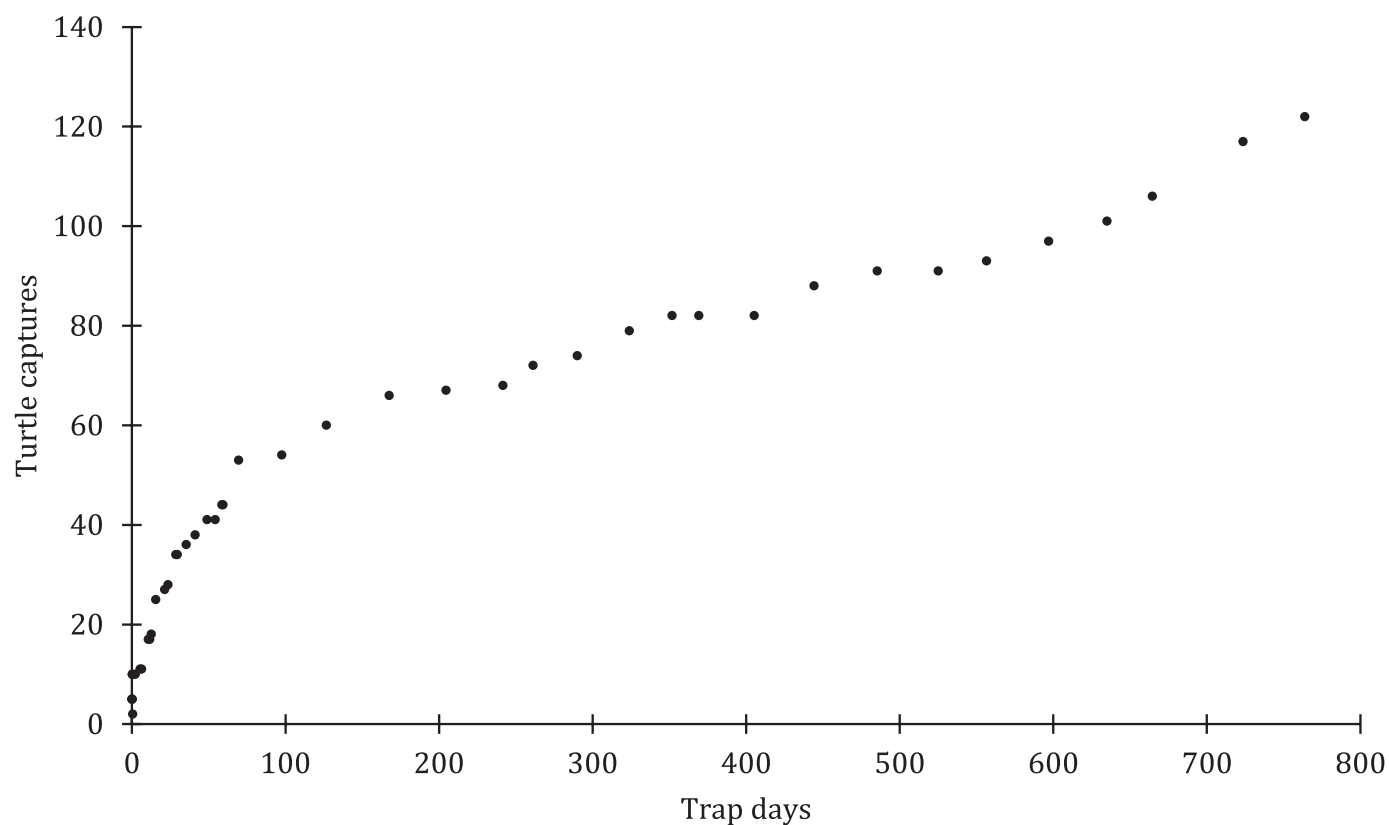


FIG. 2. Accumulation of turtle captures with trap days in Kawai Nui Marsh on Oahu, Hawaii.

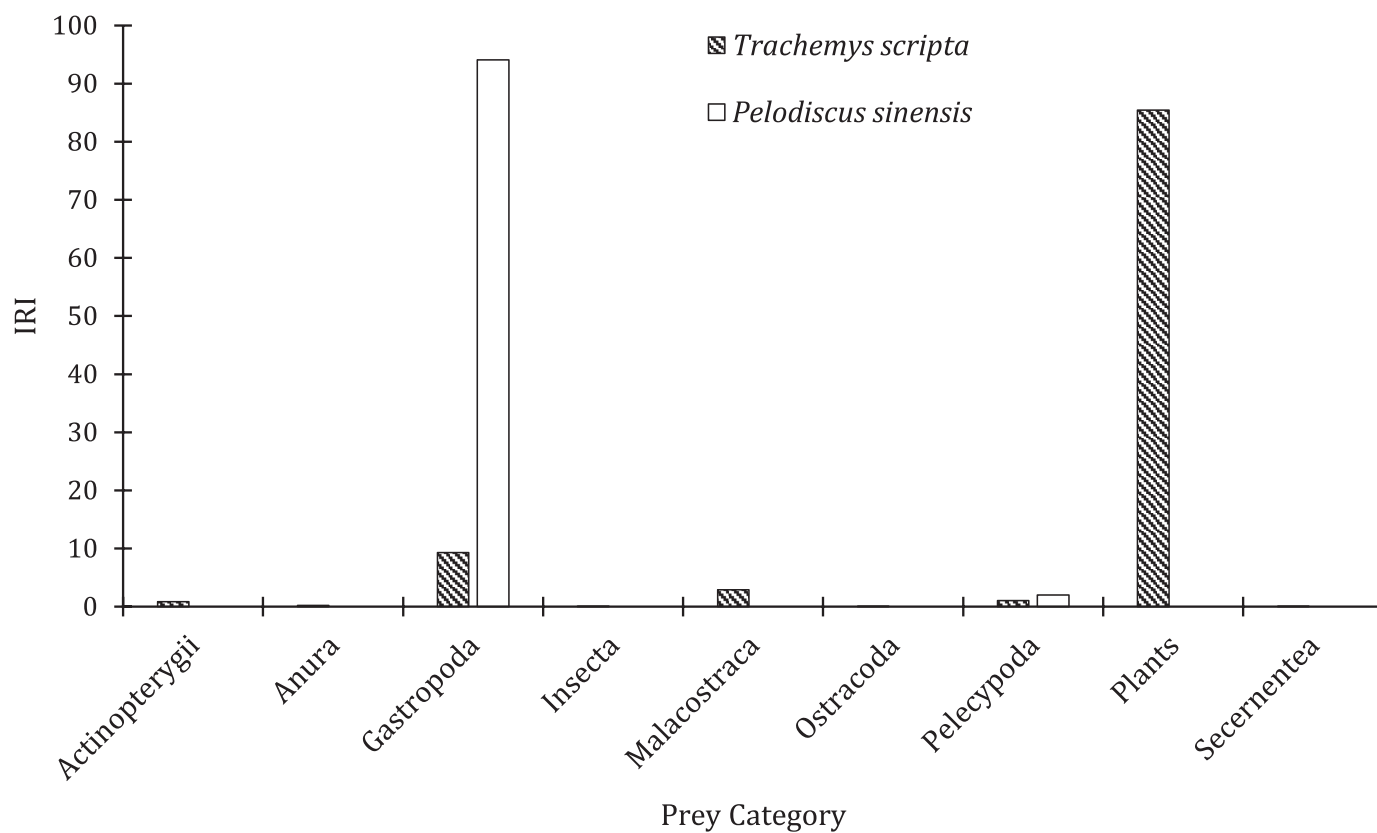


FIG. 3. Index of relative importance for taxa in stomach contents of *Trachemys scripta* and *Pelodiscus sinensis* in Kawai Nui Marsh on Oahu, Hawaii.

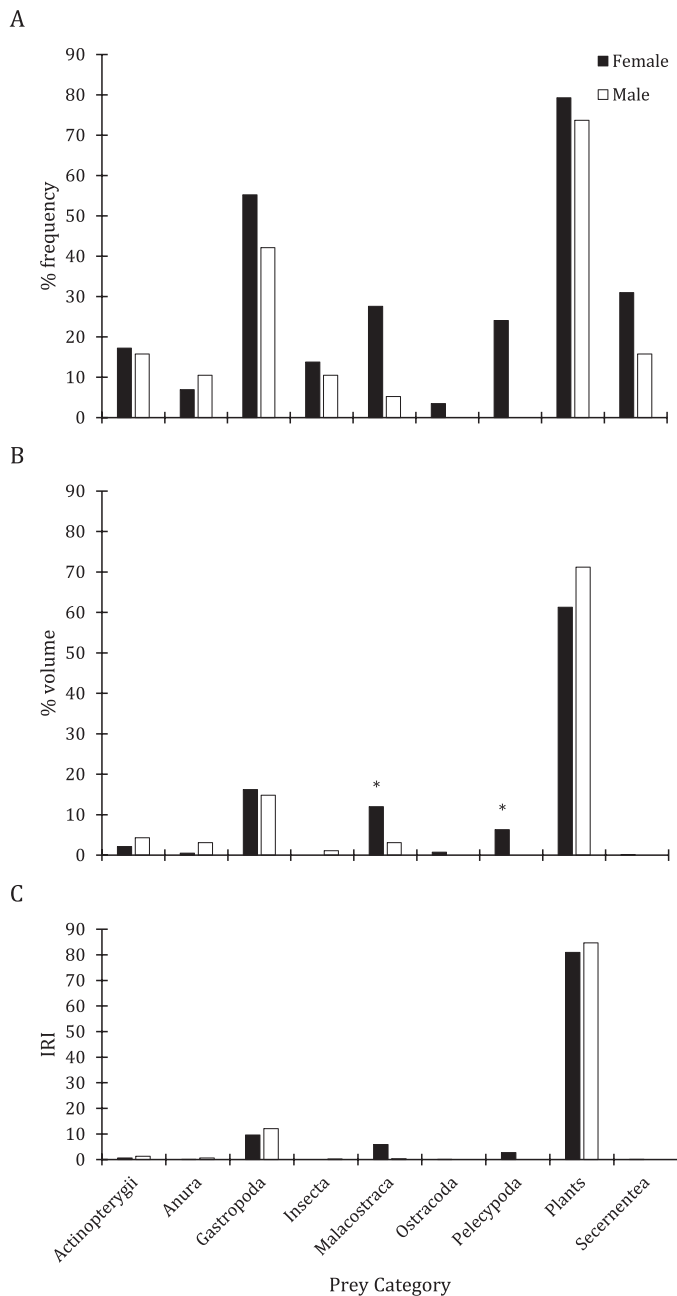


FIG. 4. Percent frequency (A), percent volume (B), and index of relative importance (C) of food items by category contained in stomachs of female and male *Trachemys scripta* in Kawai Nui Marsh on Oahu, Hawaii. Asterisk designates statistically significant difference after false discovery rate correction, $P < 0.05$.

stomachs contained more invertebrate prey than males, by both volume ($W = 103$, $P < 0.01^*$) and frequency ($W = 164$, $P < 0.01^*$). Fisher's exact test of independence revealed differences in the frequency and volume of *Corbicula fluminea* ($P = 0.03$ and $P = 0.01^*$, respectively) and thiarid snails ($P < 0.01^*$ and $P = 0.01^*$, respectively) contained in stomachs, and in the volume of crayfish ($P = 0.01^*$) ingested, with females containing larger proportions than males. Fisher's exact test of independence suggested that fish, apple snails, insects, plants, anurans, ostracods, and nematodes contained within stomachs were not different for percent frequency or volume between males

and females. Dietary niche breadth of females for frequency and volume (Shannon index, $J' = 0.83$ and 0.50 , respectively) were wider than that of males (Shannon index, $J' = 0.65$ and 0.33 , respectively; $\chi^2 = 5.85$, $df = 1$, $P = 0.02^*$ and $\chi^2 = 5.27$, $df = 1$, $P = 0.02^*$, respectively). Dietary overlap was biologically significant according to the simplified Morisita index for frequency and volume ($C_H = 0.84$ and 0.96 , respectively).

As noted in other systems, *T. scripta* captured in our study were sexually dimorphic in size. The mean SCL ($x \pm SD$ [range]) for females ($n = 29$) was 190 ± 27 mm (129 – 236 mm) and for males ($n = 19$) was 153 ± 33 mm (107 – 235 mm). Female carapace length was longer than male carapace length ($t_{33.36} = 4.051$, $P < 0.01$) and the mean mass for females was $1,139 \pm 455$ g (372 – $2,058$ g) and for males was 592 ± 406 g (187 – $1,887$ g).

The plant and animal matter contained in stomachs differed across small, medium, and large size classes of *T. scripta* (SCL = 100 – 150 [$n = 14$], 151 – 200 [$n = 21$], and 201 – 250 mm [$n = 13$], respectively). For plant matter, there was a difference in the mean volume (cm^3) contained within stomachs among small (2.23 cm^3), medium (5.95 cm^3), and large (2.88 cm^3) size classes ($F_{2,45} = 5.27$, $P = 0.01$). A Tukey–Kramer test suggested an increase in mean plant matter in stomachs between the small and medium size classes ($P = 0.01$), a close-to-significant decrease of mean plant matter in stomachs from the medium to large size classes ($P = 0.06$), and a similar amount of mean plant matter in stomachs between the small and large size classes ($P = 0.89$; Fig. 5).

Mean volume (cm^3) of animal matter contained within stomachs differed among small (1.16 cm^3), medium (1.66 cm^3), and large (4.16 cm^3) size classes of *T. scripta* ($F_{2,45} = 6.53$, $P < 0.01$). A Tukey–Kramer test suggested that a similar amount of animal matter by mean volume was found in stomachs between the small and medium size classes ($P = 0.80$), an increase was found from the medium to large size classes ($P = 0.01$), and an increase was found between the small and large size classes ($P < 0.01$) for *T. scripta* (Fig. 5). Female *T. scripta* in the small, medium, and large size classes exhibited different gravidity percentages: 0 , 47 , and 100% , respectively.

Last, there was not an interaction between *T. scripta* size class and sex for mean plant ($F_{2,42} = 0.27$, $P = 0.77$) and animal volume contained in stomachs ($F_{2,42} = 1.74$, $P = 0.19$). The two-way ANOVA for the effect of sex on mean plant ($F_{1,42} = 0.59$, $P = 0.45$) and animal ($F_{1,42} = 0.03$, $P = 0.86$) matter contained in stomachs revealed that there was no support for a significant sex effect. The two-way ANOVA revealed a significant effect of size class on mean plant ($F_{2,42} = 5.04$, $P = 0.01$) and animal ($F_{2,42} = 7.22$, $P < 0.01$) volume contained in stomachs.

DISCUSSION

The baited chimney traps used for turtle capture in this study were likely biased for capture of omnivorous and carnivorous turtles; trapping methods failed to account for strictly herbivorous turtle species. Also, *Graptemys* sp. are highly carnivorous, but do not enter traps in proportion to their abundance because they are mollusc specialists (Ernst and Lovich, 2009). *Graptemys* sp. are sold in local pet stores, so their presence in the marsh is possible.

Trachemys scripta was much more abundant than *P. sinensis*. Trapping efforts yielded an increasing accumulation of turtle captures even with permanently removing 56 turtles from the trapping area. The capture rate of turtles seems to suggest low densities of *T. scripta* and very low densities of *P. sinensis*. A

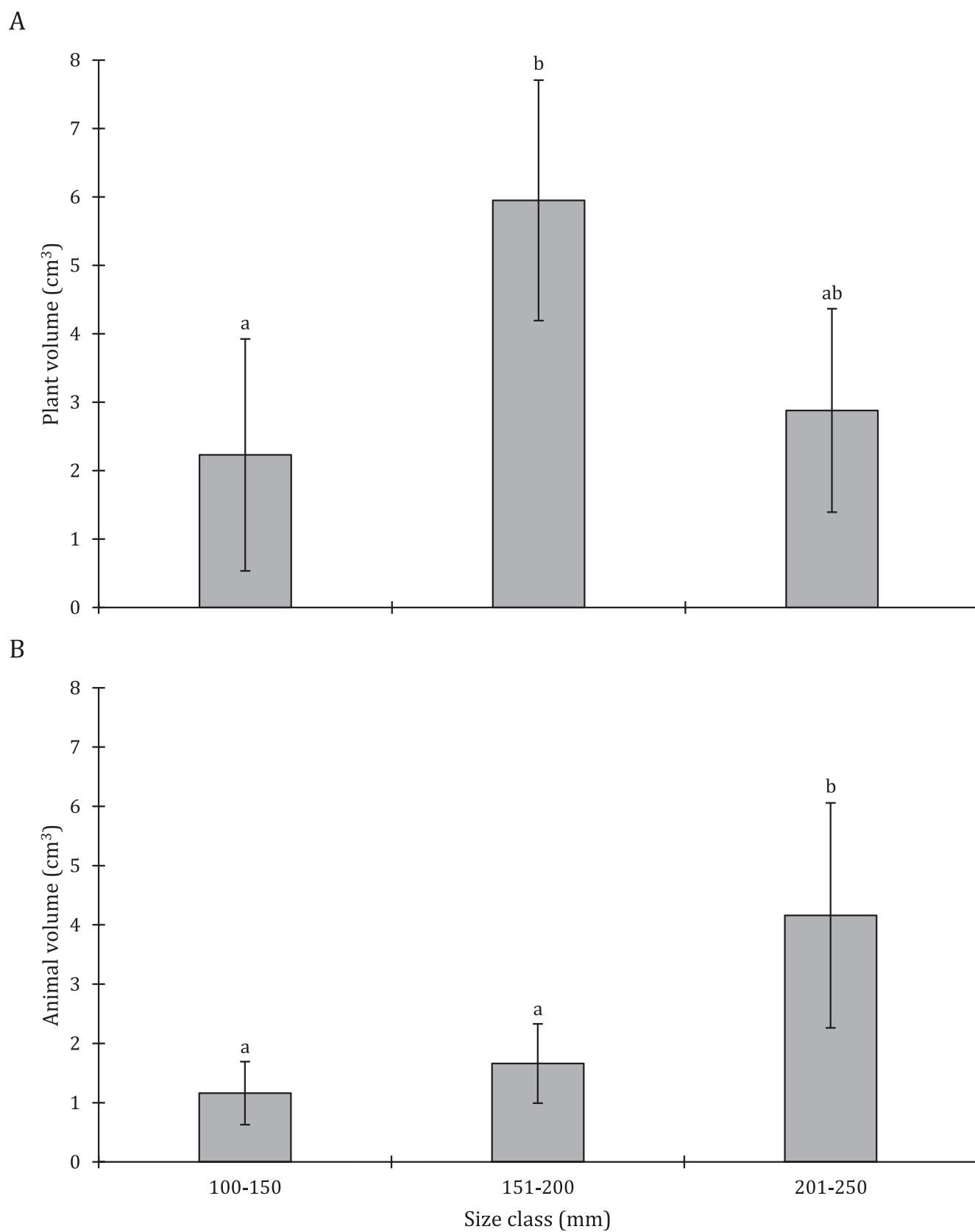


FIG. 5. Plant (A) and animal (B) volume (mean, 95% confidence limits) contained in stomachs of small, medium, and large size classes of *Trachemys scripta*. Bars sharing the same letter are not significantly different ($P < 0.05$).

comparable study of *T. scripta* capture rates by Hays and McBee (2010) revealed one *T. scripta* captured every 0.6 trap days. This capture rate is 11 times greater than the capture rate in our study, suggesting a low density of turtles in the marsh.

Although nonnative species introduced to novel ecosystems can result in direct predation of native prey to the point of extinction (Rodda and Savidge, 2007), this seems to be the exception and not the rule. No freshwater turtles are native to the Hawaiian Islands, so their presence in Hawaii warranted further analysis of their diet. The stomach contents of *T. scripta* and *P. sinensis* indicated that these turtles were omnivorous and carnivorous, respectively, with diets primarily composed of nonnative foods. These turtles had similar diets to what has been previously reported in other studies (Ernst and Lovich, 2009). In this study, *P. sinensis* were dietary specialists, consuming mostly molluscs, and *T. scripta* were dietary generalists, with larger turtles consuming mostly animal matter. These turtles may have a greater impact on native aquatic fauna if they occur in other Hawaiian wetlands containing more native species; however, nonnative freshwater turtle survival in Hawaii may possibly depend on the presence of nonnative foods. The lack of native prey in our findings may have more to do with prey availability as *T. scripta* and *P. sinensis* are known to be opportunistic feeders (Ernst and Lovich, 2009) and Kawai Nui Marsh contains nonnative aquatic organisms (DOFAW, 2011; MacKenzie and Bruland, 2012). The only native organism identified was a sponge, *Heteromyenia baileyi*, that may have been incidentally ingested when the single *T. scripta* that contained *H. baileyi* was feeding on plant matter.

Only female *T. scripta* stomachs contained clams. The clams may have been preferred by females because of their high nutrient content, especially protein and calcium, which would be needed for egg production. Calcium is critical for egg production and sources of calcium have been found more frequently in gravid turtles than in nongravid turtles (Moore and Dornburg, 2014). Female *T. scripta* could have a greater impact on native aquatic species in more pristine wetlands in the Hawaiian Islands because of the increased volume of animal matter found in their stomachs.

Large *T. scripta* stomachs contained a significantly greater amount of animal prey than the smaller size classes. Future diet impact studies might focus on capturing large *T. scripta* (e.g., >200 mm SCL) to further examine potential predation on native species. Medium-sized *T. scripta* ate more vegetation, and the smallest sliders ate more animal than plant matter, which parallels other *T. scripta* diet studies (Hart, 1983; Parmenter and Avery, 1990); *T. scripta* tends to undergo an ontogenetic shift from a mostly carnivorous diet in small size classes to mostly herbivorous in larger size classes. A higher protein content in animal prey in the diet of juveniles likely allows for greater growth (Bouchard and Bjorndal, 2006). Interestingly, *T. scripta* in the large size class shifted again to less plant and more animal food. The females in the large size class were 100% gravid compared with only 47% gravid in the medium size class. The higher proportion of protein from animal prey seems to be necessary for egg production. Large *T. scripta* may possess the size and strength necessary to consume largely hard-shelled prey as seen with the Venezuelan Slider (*Trachemys callirostris chichiriviche*; Pritchard and Trebbau, 1984).

Trachemys scripta has a 61-h digestive turnover rate (Parmenter, 1981), so prey discovered in the gastrointestinal tracts likely covered about 2 d of eating. Trapped turtles could have occupied the traps for a maximum of 24 h. This delay likely

caused a decrease in the overall contents retained in the gastrointestinal tract, although for this study only one turtle had an empty gastrointestinal tract. The lack of evidence of native species remains in *T. scripta* or *P. sinensis* stomachs rules out dietary specialization on native fauna; however, our analysis would likely miss the occasional predation of native taxa. In this study, we did not assess prey availability and hence predator electivity of prey. Further research is warranted to elucidate electivity of prey of nonnative freshwater turtles in Kawai Nui Marsh to further understand direct impacts on native aquatic species.

Acknowledgments.—Research was conducted under University of Hawaii at Manoa Institutional Animal Care and Use Committee protocol 16-2329. We thank the Oahu Invasive Species Committee field personnel for their assistance with fieldwork.

LITERATURE CITED

- BEARD, K. H. 2007. Diet of the invasive frog, *Eleutherodactylus coqui*, in Hawaii. *Copeia* 2007:281–291.
- BENJAMINI, Y., AND Y. HOCHBERG. 1995. Controlling the false discovery rate—a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B—Methodological* 57:289–300.
- BJORNDAL, K. A., A. B. BOLTON, C. J. LAGUEUX, AND D. R. JACKSON. 1997. Dietary overlap in three sympatric congeneric freshwater turtles (*Pseudemys*) in Florida. *Chelonian Conservation and Biology* 2:430–433.
- BOUCHARD, S. S., AND K. A. BJORNDAL. 2006. Ontogenetic diet shifts and digestive constraints in the omnivorous freshwater turtle *Trachemys scripta*. *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches* 79:150–158.
- CAGLE, F. R. 1948. Sexual maturity in the male, *Pseudemys scripta troostii*. *Copeia* 1948:108–111.
- CHEN, T. H., AND K. Y. LUE. 1998. Ecological notes on feral populations of *Trachemys scripta elegans* in northern Taiwan. *Chelonian Conservation and Biology* 3:87–90.
- CHRISTENSEN, C. C. 2015. Type species designation for *Pelagolimnaea* Germain, 1928, and a correction regarding the type species of *Pseudisidora* Thiele, 1931 (Gastropoda: Basommatophora: Lymnaeidae). *Bishop Museum Occasional Papers* 116:53–56.
- COLMAN, L. P., C. L. S. SAMPAIO, M. I. WEBER, AND J. C. DE CASTILHOS. 2014. Diet of olive Ridley sea turtles, *Lepidochelys olivacea*, in the waters of Sergipe, Brazil. *Chelonian Conservation and Biology* 13:266–271.
- COWIE, R. H., V. HÉROS, N. R. YEUNG, AND K. A. HAYES. 2016a. Annotated catalogue of types of Hawaiian land and freshwater snails (Mollusca: Gastropoda) in the Muséum national d'Histoire naturelle, Paris, with lectotype designations. *Zoosystema* 38:245–266.
- COWIE, R. H., V. HÉROS, N. R. YEUNG, AND K. A. HAYES. 2016b. Annotated catalogue of types of Hawaiian land and freshwater snails (Mollusca: Gastropoda) in the Muséum national d'Histoire naturelle, Paris, with lectotype designations. Addendum: lectotype designation for *Lymnaea affinis* Souleyet, 1852. *Zoosystema* 38:389–391.
- DOFAW (DIVISION OF FORESTRY AND WILDLIFE). 2011. Wetland restoration and habitat enhancement plan, Kawai Nui Marsh, Kailua, Oahu. Department of Land and Natural Resources, State of Hawaii, USA.
- DOODY, J. S., R. SOANES, C. M. CASTELLANO, D. RHIND, B. GREEN, C. R. MCHENRY, AND S. CLULOW. 2015. Invasive toads shift predator-prey densities in animal communities by removing top predators. *Ecology* 96:2544–2554.
- EISEMBERG, C. C., S. J. REYNOLDS, K. A. CHRISTIAN, AND R. C. VOGT. 2017. Diet of Amazon river turtles (Podocnemididae): a review of the effects of body size, phylogeny, season and habitat. *Zoology* 120:92–100.
- ERNST, C. H., M. F. HERSHEY, AND R. W. BARBOUR. 1974. A new coding system for hard-shelled turtles. *Transactions of the Kentucky Academy of Sciences* 35:27–28.
- ERNST, C. H., AND J. E. LOVICH. 2009. *Turtles of the United States and Canada*. 2nd ed. John Hopkins University Press, USA.

- GIBBONS, J. W., AND J. L. GREENE. 1990. Chapter 9: reproduction in the slider and other species of turtles. Pp. 124–134 in J. W. Gibbons (ed.), *Life History and Ecology of the Slider Turtle*. Smithsonian Institution Press, USA.
- HART, D. R. 1983. Dietary and habitat shift with size of red-eared turtles (*Pseudemys scripta*) in a southern Louisiana population. *Herpetologica* 39:285–290.
- HAYS, K. A., AND K. MCBEE. 2010. Population demographics of red-eared slider turtles (*Trachemys scripta*) from Tar Creek Superfund Site. *Journal of Herpetology* 44:441–446.
- HOLLAND, B. S., S. L. MONTGOMERY, AND V. COSTELLO. 2010. A reptilian smoking gun: first record of invasive Jackson's chameleon (*Chamaeleo jacksonii*) predation on native Hawaiian species. *Biodiversity Conservation* 19:1437–1441.
- HOUSE, W. J., I. M. NALL, AND R. B. THOMAS. 2011. Selected aspects of semi-aquatic turtle assemblages in east-central Kansas ponds. *Transaction of the Kansas Academy of Science* 114:239–244.
- KREBS, C. 1999. *Ecological Methodology*. 2nd ed. Addison-Wesley Educational Publishers, Inc., USA.
- LIGON, D. B. 2007. *Trachemys scripta elegans* (red-eared slider) predation. *Herpetological Review* 38:201–202.
- LUISELLI, L. 2008. Resource partitioning in freshwater turtle communities: a null model meta-analysis of available data. *Acta Oecologia* 34:80–88.
- MACKENZIE, R. A., AND G. L. BRULAND. 2012. Nekton communities in Hawaiian coastal wetlands: the distribution and abundance of introduced fish species. *Estuaries and Coasts* 35:212–226.
- MARCHETTI, M. P., AND T. ENGSTROM. 2016. The conservation paradox of endangered and invasive species. *Conservation Biology* 30:434–437.
- MOORE, J. A., AND A. DORNBERG. 2014. Ingestion of fossil seashells, stones and small mammal bones by gravid gopher tortoises (*Gopherus polyphemus*) in south Florida. *Bulletin of the Peabody Museum of Natural History* 55:55–63.
- NISHIDA, G. M. (ed.) 2002. *Hawaiian Terrestrial Arthropod Checklist*. 4th ed. Hawaii Biological Survey, Bishop Museum, USA.
- OUTERBRIDGE, M. E. 2008. Ecological notes on feral populations of *Trachemys scripta elegans* in Bermuda. *Chelonian Conservation and Biology* 7:265–269.
- PARMENTER, R. R. 1981. Digestive turnover rates in freshwater turtles: the influence of temperature and body size. *Comparative Biochemistry and Physiology Part A: Physiology* 70:235–238.
- PARMENTER, R. R., AND H. W. AVERY. 1990. Chapter 20: the feeding ecology of the slider turtle. Pp. 257–266 in J. W. Gibbons (ed.), *Life History and Ecology of the Slider Turtle*. Smithsonian Institution Press, USA.
- PEREZ-SANTIGOSA, N., M. FLORENCIO, J. HIDALGO-VILA, AND C. DIAZ-PANIAGUA. 2011. Does the exotic invader turtle, *Trachemys scripta elegans*, compete for food with coexisting native turtles? *Amphibia-Reptilia* 32:167–175.
- PLATT, S. G., A. R. BEREZIN, D. J. MILLER, AND T. R. RAINWATER. 2016. Dietary study of the rough-footed mud turtle (*Kinosternon hirtipes*) in Texas, USA. *Herpetological Conservation and Biology* 11:142–149. http://www.herpconbio.org/Volume_11/Issue_1/Platt_etal_2016.pdf.
- PREVOT-JULLIARD, A. C., E. GOUSSET, C. ARCHINARD, A. CADI, AND M. GIRONDOT. 2007. Pets and invasion risks: is the slider turtle strictly carnivorous? *Amphibia-Reptilia* 28:139–143.
- PRITCHARD, P. C. H., AND P. TREBBAU. 1984. *The Turtles of Venezuela*. Miami University, USA.
- R CORE TEAM. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <https://www.R-project.org/>.
- REED, R. N., AND A. D. TUCKER. 2012. Determining age, sex, and reproductive condition. Pp. 151–163 in R. W. McDiarmid, M. S. Foster, C. Guyer, J. W. Gibbons, and N. Chernoff (eds.), *Reptile Biodiversity: Standard Methods for Inventory and Monitoring*. University of California Press, USA.
- RODDA, G. H., AND J. A. SAVIDGE. 2007. Biology and impacts of Pacific Island invasive species, 2. *Boiga irregularis*, the brown treesnake (Reptilia: Colubridae). *Pacific Science* 61:307–324.
- ROGERS, H. S., E. R. BUHLE, J. HILLERISLAMBERS, E. C. FRICKE, R. H. MILLER, AND J. J. TEWKSBURY. 2017. Effects of an invasive predator cascade to plants via mutualism disruption. *Nature Communications* 8:14557.
- SAVIDGE, J. A. 1988. Food habits of *Boiga irregularis*, an introduced predator on Guam. *Journal of Herpetology* 22:275–282.
- SELMAN, W., AND P. V. LINDEMAN. 2015. Life history and ecology of the Pascagoula map turtle (*Graptemys gibbonsi*). *Herpetological Conservation and Biology* 10:781–800.
- SHINE, R. 2010. The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Quarterly Review of Biology* 85:253–291.
- SIN, H., K. H. BEARD, AND W. C. PITT. 2008. An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii. *Biological Invasions* 10:335–345.
- SPENCER, R. J., M. B. THOMPSON, AND I. D. HUME. 1998. The diet and digestive energetics of an Australian short-necked turtle, *Emydura macquarii*. *Comparative Biochemistry and Physiology* 121:341–349.
- TUCKER, A. D., N. N. FITZSIMMONS, AND J. W. GIBBONS. 1995. Resource partitioning by the estuarine turtle *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. *Herpetologica* 51:167–181.
- VITOUSEK, P. M. 1987. Introduced species in Hawaii: biological effects and opportunities for ecological research. *Trends in Ecology & Evolution* 2:224–227.
- VOGT, R. C. 1981. Food partitioning in three sympatric species of map turtle, genus *Graptemys* (Testudinata, Emydidae). *American Midland Naturalist* 105:102–111.
- WANG, J., H. SHI, S. HU, K. MA, AND C. LI. 2013. Interspecific differences in diet between introduced red-eared sliders and native turtles in China. *Asian Herpetological Research* 4:190–196.
- YAMAMOTO, M. N., AND A. W. TAGAWA. 2000. *Hawaii's Native and Exotic Freshwater Animals*. Mutual Publishing, USA.

Accepted: 6 August 2018.

Published online: 27 November 2018.

APPENDIX 1. Frequency (*F*, %) of food items, volume (*V*; cm³; %) of food items, and index of relative importance (IRI) of each food category in the diet of *Trachemys scripta*, *Pelodiscus sinensis*, and female and male *Trachemys scripta* collected from Kawai Nui Marsh, Oahu, Hawaii, based on stomach content analysis.

Food category	<i>Trachemys scripta</i> (<i>n</i> = 50)			<i>Pelodiscus sinensis</i> (<i>n</i> = 5)			Female <i>T. scripta</i> (<i>n</i> = 29)			Male <i>T. scripta</i> (<i>n</i> = 19)		
	<i>F</i>	<i>V</i>	IRI	<i>F</i>	<i>V</i>	IRI	<i>F</i>	<i>V</i>	IRI	<i>F</i>	<i>V</i>	IRI
Plants	37 (74)	194.5 (64.7)	85.44				22 (79.3)	119.35 (61.3)	80.92	14 (73.7)	74.15 (71.2)	84.71
Filamentous algae	3 (6)	0.1 (0.03)	0.00				2 (6.9)	0.1 (0.05)	0.01	1 (5.3)	0 (0)	0
<i>Commelina diffusa</i> (leaves and stems)	37 (74)	191.4 (63.64)	85.40				22 (75.9)	116.25 (59.7)	80.84	14 (73.7)	74.15 (71.2)	84.71
<i>Albizia samani</i> (seeds)	1 (2)	2 (0.67)	0.02				1 (3.5)	2 (1.0)	0.06			
<i>Schoenoplectus</i> sp. (seeds)	1 (2)	1 (0.33)	0.01				1 (3.5)	1 (0.5)	0.01			
Invertebrates												
Gastropoda	40 (80)	89.2 (29.7)	13.28	5 (83.3)	9.5 (90.5)	96.1	27 (93.1)	68.7 (35.3)	18.32	10 (52.6)	19.7 (18.9)	12.61
Planorbidae	26 (52)	47.75 (15.9)	9.27	4 (80)	9 (85.7)	94.1	17 (55.2)	31.5 (16.2)	9.61	8 (42.1)	15.5 (14.8)	12.09
Thiaridae	1 (2)	0.4 (0.13)	0.01				1 (3.5)	0.4 (0.2)	0.01			
Ampullariidae (<i>Pomacea</i> sp.)	11 (22)	12 (3.99)	1.59	1 (20)	1.5 (14.3)	5.89	11 (37.9)	12 (6.2)	4.17			
Haplosclerida	18 (36)	35.35 (11.75)	7.67	3 (60)	7.5 (71.4)	88.2	9 (31.0)	19.1 (9.8)	5.43	8 (42.1)	15.5 (14.8)	12.09
Spongillidae (<i>Heteromyenia baileyi</i>)	1 (2)	0 (0)	0				1 (3.5)	0 (0)	0			
Insecta	6 (12)	1 (0.3)	0.04				4 (13.8)	0 (0)	0			
Diptera	2 (4)	0.5 (0.17)	0.01				1 (3.5)	0 (0)	0	2 (10.5)	1 (1.1)	0.2
Hymenoptera	1 (2)	0 (0)	0				1 (3.5)	0 (0)	0	2 (10.5)	0.5 (0.5)	0.10
Formicidae (<i>Pheidole megacephala</i>)	4 (8)	0.5 (0.17)	0.03				2 (6.9)	0 (0)	0	2 (10.5)	0.5 (0.5)	0.10
Malacostraca												
Decapoda												
Cambaridae (<i>Procambarus clarkii</i>)	9 (18)	26.55 (8.83)	2.88				8 (27.6)	23.3 (12.0)	5.89	1 (5.3)	3.25 (3.1)	0.32
Ostracoda	1 (2)	1.4 (0.47)	0.02				1 (3.5)	1.4 (0.7)	0.04			
Pelecypoda												
Corbiculidae												
Veneroida (<i>Corbicula fluminea</i>)	7 (14)	12.25 (4.07)	1.03	1 (20)	0.5 (4.8)	1.98	7 (24.1)	12.25 (6.3)	2.71			
Secernentea												
Camallanida												
Vertebrates	13 (26)	0.25 (0.08)	0.04	1 (20)	0 (0)	0	9 (31.0)	0.25 (0.1)	0.07	3 (15.8)	0 (0)	0
Actinopterygii (flesh and bone)	17 (34)	17.05 (5.7)	1.29	1 (20)	1 (9.5)	3.9	8 (27.6)	6.6 (3.4)	0.76	8 (42.1)	10.25 (9.9)	2.69
Amphibia	8 (16)	8.6 (2.86)	0.83				5 (17.2)	4.1 (2.1)	0.65	3 (15.8)	4.5 (4.3)	1.32
Anura (flesh and bone)	4 (8)	4.25 (1.41)	0.21				2 (6.9)	1 (0.5)	0.06	2 (10.5)	3.25 (3.1)	0.64
Unknown animal flesh	5 (10)	4.2 (1.4)	0.25	1 (20)	1 (9.5)	3.91	1 (3.5)	1.5 (0.77)	0.05	3 (15.8)	2.5 (2.4)	0.73
Miscellaneous objects												
Small pebble	1 (2)	0 (0)	0				1 (3.5)	0 (0)	0			