# Effects of an exotic prey species on a native specialist: Example of the snail kite

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## ARTICLE INFO

## ABSTRACT

Despite acknowledging that exotic species can exhibit tremendous influence over native populations, few case studies have clearly demonstrated the effects of exotic prey species on native predators. We examined the effects of the recently introduced island apple snail (*Pomacea insularum*) on the foraging behavior and energetics of the endangered snail kite (*Rostrhamus sociabilis plumbeus*) in Florida. We conducted time-activity budgets: (i) on kites foraging for native Florida apple snails (*Pomacea paludosa*) in major wetland units within the kites' range that had not been invaded by the exotic island apple snail and (ii) on kites foraging for exotic apple snails in Lake Tohopekaliga, the only major wetland utilized by the snail kite that had suffered a serious invasion of *P. insularum*. When foraging for *P. insularum*, snail kites dropped a greater proportion of snails, and they experienced increased handling times and decreased consumption rates; however, kites foraging for *P. insularum* also spent a smaller proportion of the day in flight. Estimates of net daily energy balances between kites feeding on *P. insularum* versus *P. paludosa* were comparable for adults, but juveniles experienced energetic deficiencies when feeding on the exotic snail. Due to this discrepancy, we hypothesize that wetlands invaded by *P. insularum*, such as Lake Tohopekaliga, may function as ecological traps for the snail kite in Florida by attracting breeding adults but simultaneously depressing juvenile survival. This study highlights the conservation implications and importance of elucidating the effects that exotic species have on native specialists, especially those that are endangered, because subtle influences on behavior may have significant population consequences.

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## 1. Introduction

The increasing intensity of international commerce and travel, particularly over the last century, has exacerbated the spread of exotic species (Jenkins, 1996; Mooney and Cleland, 2001), which now pervade nearly every habitat on Earth (Vitousek et al., 1997). While many exotic species are considered innocuous transplants to their novel habitats, some exotics inevitably become invasive and can significantly impact native species (Mooney and Cleland, 2001; Strauss et al., 2006). Invasive exotic species may affect native animal populations in both positive and negative ways, ranging from facilitation (Schreiber et al., 2002) to extinction (Mooney and Cleland, 2001; Clavero and Garcia-Berthou, 2005); however, published examples of positive effects are far outnumbered by those of negative effects. In fact, exotic species invasions are perceived by most ecologists to be a leading cause of extinction among native species (Vitousek et al., 1997; Wilcove et al., 1998; Burbidge and Manly, 2002; Blackburn et al., 2004; Clavero and Garcia-Berthou, 2005).

Specialists, which are species that occupy a narrow niche, are more extinction-prone than generalists (Owens and Bennett, 2000; Purvis et al., 2000) and may be particularly vulnerable to invasions by exotics. In order to prevent the rapid extinction of many specialized species, it is critical to better understand the interactions between native specialists and invasive exotics. Exotic species can detrimentally affect native specialists through predation and competition (Fritts and Rodda, 1998; Wilcove et al., 1998), but sometimes exotic–native interactions can be more subtle. Unfortunately, studies clearly demonstrating the mechanistic responses of native specialists to invasions are not as common as one would think (Gurevitch and Padilla, 2004; Schreiber et al., 2002), and examples of exotic prey species (at least nonpoisonous ones) negatively affecting native predators are almost nonexistent (Vellend et al., 2007). Our study focuses on the interactions between an endangered predator and two prey species, one native and one exotic.

The snail kite (*Rostrhamus sociabilis plumbeus*) is an endangered raptor (Federal Register, 1967, 2007) whose range in the US is confined to the freshwater wetlands of central and southern Florida (Martin et al., 2006). This subspecies (*R.s. plumbeus*), which only occurs in Florida and Cuba, is genetically distinct from the other two snail kite subspecies (*Rostrhamus sociabilis sociabilis* and *Ros-*

*trhamus sociabilis major*), which occur in Mexico, and Central and South America (Haas et al., 2009). Although Haas et al. (2009) found a close genetic relationship between kites in Florida and Cuba, multiple studies of movement and population dynamics (e.g., Bennetts and Kitchens, 1997; Martin et al., 2006, 2007) suggest that the snail kite population in Florida is geographically isolated. Unless otherwise noted, we use the term *snail kite* in reference to the endangered population of *R.s. plumbeus* in Florida on which this study is focused.

The snail kite feeds almost exclusively on a single species of freshwater snail, the Florida apple snail (*Pomacea paludosa*) (Snyder and Snyder, 1969; Sykes, 1987), which is the only species of this genus native to Florida (Rawlings et al., 2007). Of the many morphological and physiological factors that can influence prey selection and suitability, prey size may be one of the most pertinent, especially for extreme dietary specialists (Stephens and Krebs, 1986). Sykes (1987) found that 98.5% of the snails selected by kites fell in the 30–60 mm size range (mean = 45.8) (measured linearly as the length of the snail shell along the spiral axis from the apex to the outer edge of the aperture lip). Several other authors have also noted that kites in Florida (Snyder and Snyder, 1969; Darby et al., 2007), as well as other snail kite subspecies in Costa Rica (Collett, 1977), Guyana (Beissinger, 1983; Bourne, 1993), Columbia (Snyder and Kale, 1983) and Venezuela (Beissinger et al., 1994) rarely consume snails greater than 60 mm in length. When feeding on native apple snails, kites follow a systematic behavioral procedure of negotiation, extraction, and consumption (detailed in Snyder and Snyder, 1969; Voous and Van Dijk, 1973; Sykes, 1987). The extreme form of dietary specialization observed in the snail kite has led some researchers (Darby et al., 2007; Rawlings et al., 2007) to question the ability of the kite to efficiently exploit the newly introduced island apple snail (*Pomacea insularum*), which commonly exceeds 90 mm and can reach 150 mm in length (Benson, 2007; Darby et al., 2007).

In addition to size considerations, learning and experience are also recognized as important factors contributing to foraging behavior, as animals develop search images and improve handling techniques for familiar prey types. Juveniles of most vertebrate species lack the experience accumulated by adults and thus may be more sensitive to environmental variation (Stephens and Krebs, 1986). Sykes et al. (1995) notes that compared to adults, recently fledged snail kites do not demonstrate the same adept negotiation skills when extracting native apple snails. Such foraging difficulties may be exaggerated when handling the larger exotic apple snails.

The island apple snail is native to Argentina, Brazil and Bolivia, and recently invaded several states in the US, including Florida (Rawlings et al., 2007); however the invasion history of *P. insularum* is somewhat unclear. Within the network of wetlands commonly utilized by the snail kite in Florida, high densities of *P. insularum* are currently confined to only one wetland fragment, Lake Tohopekaliga (Darby et al., 2007; Rawlings et al., 2007). The invasion of Lake Tohopekaliga likely occurred as early as 2001, but *P. insularum* may have been confined to a single cove and did not spread throughout the lake immediately (Darby, *personal communication*). However, shortly after a managed drawdown that was followed by extensive vegetation scraping and muck removal (conducted in 2003–2004), *P. insularum* established lake-wide distribution (Desa, 2008).

There is growing concern that this exotic species could invade other wetlands comprising the range of the snail kite (Rawlings et al., 2007). Conservation agencies are particularly concerned about the spread of *P. insularum* and its effects on the snail kite because the kite population has been drastically declining in recent years (Martin et al., 2007). The purpose of the present study was to provide an assessment of the impacts of *P. insularum* on snail kite behavior and energetics, and to identify any potential negative consequences that these impacts may have for the kite population.

We conducted behavioral observations of snail kites, from which we quantified foraging performance measures and time activity data, and then we estimated net daily energy balances. Four groups of kites were considered in our a priori hypotheses: (1) adults foraging for the native *P. paludosa*, (2) adults foraging for the exotic *P. insularum*, (3) juveniles foraging for *P. paludosa*, and (4) juveniles foraging for *P. insularum*. Based on our knowledge of snail kite ecology, we expect the exotic apple snail to have deleterious effects on kite foraging behavior, and we expect these effects to vary in magnitude between adult and juvenile kites relative to body weight and foraging experience.

Due to the relative size difference between native and exotic apple snails, we predict that within each age class (i.e., adults, juveniles), kites foraging for exotic snails will on average experience a significantly: (1) greater proportion of snails dropped, (2) longer handling time, (3) lower consumption rate, (4) lower net daily energy balance relative to kites foraging for native snails. Furthermore, due to the disparity in size and experience between adult and juvenile kites, we predict that when feeding on exotic snails, juvenile kites will on average have a significantly, (5) greater proportion of snails dropped, (6) longer handling time, (7) lower consumption rate, and (8) lower daily energy balance relative to adults.

## 2. Materials and methods

### 2.1. Study sites and study population

This study was conducted throughout the major remaining wetland fragments that comprise the range of the snail kite in Florida (for a detailed map of the study area see Fig. 1 in Martin et al., 2006). Sampling efforts were focused on Water Conservation Areas 3A (WCA3A) and 2B (WCA2B), Lake Kissimmee (Kiss), and Lake Tohopekaliga (Toho). Together, these wetlands represent much of the remaining core snail kite habitat in Florida, and during our study, these were the only wetlands that produced significant numbers of juveniles. As of 2007, only one of these wetlands, Toho, had suffered a major invasion of *P. insularum* (Rawlings et al., 2007; Darby et al., 2007), and since 2003 the exotic snail has been the most abundant, and nearly exclusive, apple snail in portions of the lake utilized by snail kites (Cattau, 2008; Desa, 2008).

Within Florida, the kite population is described as nomadic (Bennetts and Kitchens, 2000), and monthly movement probabilities range from 0.10 among isolated wetlands to 0.29 among contiguous wetland fragments (Martin et al., 2006). Studies of both
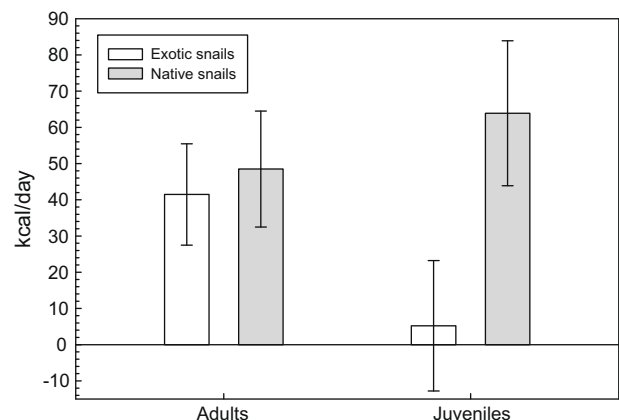


**Fig. 1.** Estimated net daily energy balances (kcal/day) for adult and juvenile snail kites feeding on exotic (*P. insularum*) versus native (*P. paludosa*) apple snails in Florida. Error bars represent 95% confidence intervals.

movement (Bennetts and Kitchens, 1997; Martin et al., 2006) and genetics (Rodgers and Stangel, 1996) confirm that the spatial distribution of kites in Florida shifts temporally and that sufficient individual movement among wetlands occurs, thus uniting the entire Florida population. The average annual population estimate for the period 2002–2005 was 1407 individuals (Martin et al., 2007). Over the 4 years duration of our study we repeatedly sampled in the most utilized wetland fragments within the range of the kite in Florida and obtained a large sample size relative to the total population size. Given that the kite population does not function as a metapopulation, inferences from our study are applicable to the entire kite population in Florida.

## 2.2. Data collection

### 2.2.1. Behavioral observations

Time-activity budget (TAB) observations were conducted on wild snail kites from 2003 to 2007 using continuous focal animal sampling (Altman, 1974). A total of 935 observation hours were accumulated during 742 individual TABs. A combination of hourly ($n = 721$) and day-long ($n = 21$) observations were conducted. The intended duration of the observation was determined prior to locating a focal individual; however, due to unpredictable weather events and equipment malfunctions, observations were sometimes stopped prematurely. Observations lasting atleast 8 h were classified as day-long observations, and those less than 30 min were censored from our analyses. Hourly observations ranged from 30 min to 3 h.

Individuals within each wetland were randomly selected for observation. Using a map of the wetland area that was overlaid with a numbered grid, a starting cell was randomly selected. Using an airboat and GPS unit for transportation and navigation, a TAB was conducted on the first individual detected within the chosen grid cell. If no snail kite was detected in the given cell, one of the eight surrounding cells was selected by blindly spinning a compass. When necessary, random compass directions guided subsequent grid cell selections until a snail kite was located. After completing a TAB, the random grid cell selection process was repeated.

Focal individuals were assigned to age classes based on plumage characteristics. Snail kites are sexually dichromatic, and mature adults (>36 months) of each sex have very distinct plumage coloration (Sykes et al., 1995). While reversed size dimorphism does occur in snail kites, it is weakly pronounced relative to other raptors, and much size overlap exists between the sexes (Sykes et al., 1995). Preliminary analyses revealed no significant differences in foraging behaviors or daily activity patterns between adult males and adult females (Cattau, 2008); therefore, they were pooled into a single adult age class. Juvenile kites (<6 months), which constituted the second age class, have distinct plumage and eye coloration, although the sexes cannot be distinguished (Sykes et al., 1995). Kites between 6 and 36 months old are hard to age with visual cues and were classified as subadults during field observations. However, juvenile survivorship parallels that of adults by 5 months of age (Bennetts and Kitchens, 1999), and preliminary analyses found no significant differences in foraging behaviors or daily activity patterns between adults and subadults (Cattau, 2008); therefore, individuals that were originally classified as subadults in the field because of their ambiguous plumage were included in the adult age class for our analyses.

Snail kites are not easily disturbed by the presence of humans or airboats from distances greater than 49 ± 18 m (Rodgers and Schwikert, 2003; Bennetts et al., 2006). To avoid potential observer effects on behavior, kites were monitored from at least 70 m away using 10× binoculars and a 15×–60× spotting scope. The focal kite was observed continuously, and two observers were always pres-

ent so that observation and data recording could occur simultaneously. The time of day to the second was recorded whenever the focal kite engaged in a pertinent behavior (e.g., started flying, captured a snail, returned to a perch, finished eating a snail, dropped a snail), and the number of snails captured and subsequently consumed (successful captures), as well as the number captured and subsequently dropped (unsuccessful captures) were tallied. Note that visual cues (e.g., the splash on the water; the lag time before sinking; Darby et al., 2007) were used to distinguish between whole snails that were dropped and empty shells that may have been inadvertently picked up but were subsequently rejected. The latter were not counted as unsuccessful captures and were not included in our analysis.

For each TAB observation, the following behaviors were quantified: proportion of snails dropped, search time, handling time, consumption rate, and proportion of time in flight. The proportion of snails dropped was defined as the number of unsuccessful captures divided by the total number of captures (i.e., successful plus unsuccessful captures). Search time for each successful capture was measured as the elapsed time from taking flight to capturing a snail. Occasionally, the exact time for capturing a snail could not be recorded due to visual obstruction, and these instances were censored from our analysis. The handling time for each successful capture was measured as the elapsed time from landing on a perch with a snail to the end of consumption (as in Sykes, 1987; Bourne, 1985). Instances in which the exact beginning and/or ending time of a handling bout was not observed were censored from our analysis. Consumption rate was defined as the number of successful captures (snails that were captured and subsequently consumed, not dropped) divided by the total observation time in seconds (later converted to hours). Note that capture rate is defined differently among authors studying the foraging ecology of the snail kite (Cary, 1985; Sykes, 1987; Bennetts and Kitchens, 2000). Our definition of consumption rate is synonymous with the definition of capture rate in Cary (1985) and Sykes (1987); however, since our study also deals with snails that were captured then dropped, a more concise definition was justified, so we use the term consumption rate instead. The proportion of time in flight was calculated as the total amount of time spent flying during a TAB divided by the total observation time.

### 2.2.2. Snail sampling

Apple snail shells often accumulate beneath frequently used feeding perches, and snails consumed by kites can be distinguished from those consumed by other predators (Snyder and Snyder, 1969; Tanaka et al., 2006). After the completion of a TAB, empty snail shells were collected from the feeding perches used by the focal kite. Only fresh shells, as determined by coloration and smell (Bourne, 1993), were collected. However, it was impossible to identify and link individual shells to specific handling times without severely disrupting the behavior of the focal individual; therefore, handling time could not be regressed directly on shell length.

Snail shells were identified to species (Rawlings et al., 2007). The length of each shell was measured to the nearest millimeter using vernier calipers. Shell length was measured linearly along the spiral axis from the apex to the outer edge of the aperture lip. Note that the diameter measurement in Sykes (1987) and the height measurement in Darby et al. (2007) are both equivalent to our length measurement, and they are relabeled as length throughout this text (for a discussion of Pomacea snail shell measurements see Youens and Burks, 2007).

In order to estimate the weight and caloric content of exotic snails consumed by kites during our study, live exotic snails ($n = 889$) were captured in funnel traps (for trap design see Darby et al., 2001) on Toho. The shell lengths were measured, and the whole wet weight of each snail (i.e., whole snail with shell and

operculum) was recorded to the nearest tenth of a gram using a digital scale. Each snail then had its shell, operculum, and in the case of female snails, its albumen gland (the only internal tissue commonly discarded by kites prior to consumption; Snyder and Snyder, 1969; Sykes, 1987) removed. The wet weight of edible tissues from each snail was then weighed to the nearest tenth of a gram and regressed on shell length. The proportion of wet weight of edible tissues to whole wet weight was also calculated (see Section 2.3.3).

Three random pooled samples ($n_1 = 20$, $n_2 = 30$, $n_3 = 30$) of edible snail tissues from these exotic snails were packed on dry ice and shipped overnight to Silliker Laboratory in Chicago, IL for biochemical analysis. Each sample was homogenized with a laboratory blender. As was done for native snails by Sykes (1987), the percent moisture was obtained and the caloric content (kcal/g dry edible tissues) was determined via bomb calorimetry (see Table 1).

### 2.3. Data analysis

#### 2.3.1. Data considerations
An obvious assumption of observational studies is that the behaviors observed during TABs are representative of normal daily behavior. Breeding status (Sykes et al., 1995) and weather conditions (Bennetts and Kitchens, 2000) both have effects on snail kite behavior. To avoid confounding effects of behavioral variation during different stages of the reproductive process, TABs were only conducted on non-breeding kites. Kites that engaged in any behavior indicative of breeding (e.g., courtship displays, snail delivery to a mate, nest building, nest defense, provisioning of young) were not included in our analyses. Juvenile kites that were observed being fed by an adult were also excluded from our analyses. Thus, our inferences are limited to snail kites that are foraging independently and cannot necessarily be extrapolated to kites that are provisioning offspring or a mate. Given the low number of independent juveniles and high number of breeding adults during the period January–April, most of our observations were conducted during May–December of each year.

To avoid potential confounding effects of inclement weather conditions on kite behavior, observations were not made during times of rain or heavy wind (Cary, 1985; Bennetts and Kitchens, 2000). Furthermore, temperature can affect snail availability, which may alter foraging behavior. Water temperature is negatively correlated with the frequency at which apple snails visit the surface of the water (Stevens et al., 2002), and in turn, a negative correlation has been shown between ambient air temperature and the capture rate achieved by foraging kites in Florida (Sykes et al., 1995). Ambient air temperature was measured at the beginning and end of each observation using a digital thermometer. The average temperature from each observation was used to place TABs into the following four categories: <10 °C, 11–20 °C, 21–

30 °C, or > 30 °C (see Sykes et al., 1995). Controlling for age, snail species, and time-of-day, we conducted a preliminary analysis using hourly TAB observations to test for the effects of temperature on consumption rate. We found that temperature had a significant effect on consumption rate, but after model simplification following Crawley (2007, pp. 374–377), only two temperature categories (<21 °C and ⩾21 °C) were justified (unpublished data). Given that most observations took place during the period May–December and that the average monthly temperature during this period was 24 ± 1 °C (SFWMD, 2008), ninety percent of our observations fell in the ⩾21 °C category. To avoid the confounding effects of unusually cold temperatures, observations from the <21 °C category were censored from our analyses.

Since it was not logistically feasible to observe an individual from sunrise to sunset, we examined diurnal activity patterns in order to address potential biases that could arise if kite behavior changed systematically throughout the day. Previous studies found that time-of-day does not significantly affect capture rate or the proportion of time in flight for snail kites in Florida (Cary, 1985; Sykes, 1987); however, these same authors go onto suggest that there seems to be a reduction in activity during midday. Our observations were distributed over all daylight hours and assigned to one of three time-of-day categories: morning (sunrise plus 3 h), evening (sunset minus 3 h), and afternoon (everything in between). Our preliminary analyses confirmed that time-of-day did not significantly affect consumption rate or the proportion of time in flight (unpublished data); therefore, time-of-day was not included in further analyses.

Not all kites encountered in the field could be identified individually (Martin et al., 2006, 2007). Therefore, it was impossible to determine if and how often unmarked individuals were observed more than once. To minimize the potential departure from independence, which is a basic assumption of multivariate statistical analysis, individuals within each wetland were randomly selected for observation (see Section 2.2.1). However, 16 of the 122 marked individuals that were observed during our study were randomly encountered more than once. Thus, approximately 13% of the 747 individual TABs conducted during our study may include individuals that had already been observed. Since these individuals could not be identified in all cases, quantified behaviors (proportion of snails dropped, search time, handling time, consumption rate, proportion of time in flight) from each observation were treated as independent samples in our analyses. Since it was possible to have multiple search times and handling times from the same individual during an observation, the average search time and the average handling time per TAB were used as response variables to avoid pseudoreplication (Crawley, 2007).

#### 2.3.2. Modeling foraging behavior
Following Crawley (2007), a generalized linear model (GLM) was constructed for each response variable based on the distribution of the data, and goodness of fit was assessed by visually inspecting diagnostic plots. The proportion of snails dropped was modeled using a GLM with a logit link and binomial error. Both search time and handling time were log-transformed to meet assumptions of normality and homoscedasticity, and each was modeled using a GLM with an identity link and Gaussian error. Consumption rate was modeled using a GLM with a log link and poisson error by treating the number of snails consumed as the dependent variable and incorporating total observation time as an offset.

A starting model for each response variable was constructed based on our a priori predictions. Explanatory variables were categorical and included age (adult, juvenile) and snail species (native, exotic). Given the unbalanced nature of the data, the GLM for each response variable was used to perform an analysis of deviance

**Table 1**
Nutritional content of exotic (*P. insularum*) and native (*P. paludosa*) apple snails reported as percent dry weight of edible tissue.

| | Snail species | | |
| --- | --- | --- | --- |
| | *P. insularum* This study | *P. paludosa* Sykes (1987) | *P. paludosa* Beissinger (1984) |
| kcal/g | 3.25 ± 0.11 | 4.60 ± 0.18 | 4.52 ± 0.25 |
| Fat (%) | 2.87 ± 0.21 | 3.4 | 3.11 ± 0.49 |
| Carbohydrate (%) | 11.05 ± 5.63 | 27.4 | NA |
| Protein (%) | 63.63 ± 6.28 | 36.3 | 61.5 ± 5.2 |
| Moisture (%) | 13.37 ± 2.40 | 14.5 | NA |
| Ash (%) | 22.48 ± 2.50 | 32.1 | 9.59 ± 1.16 |

Values shown are mean ± s.d.

(analogous to Type III ANOVA) to test for the effects of age, snail species and the age by snail species interaction (McCullagh and Nelder, 1989; Crawley, 2007). All statistical analyses were conducted in Program R, version 2.8.1 (R Development Core Team, 2008). All descriptive statistics are reported as mean ± SE unless otherwise noted. Significance is reported at $\alpha = 0.05$.

### 2.3.3. Estimating average snail weights and caloric contents

Sykes (1987) predicted the wet weight of edible tissues of *P. paludosa* as a function of shell length using the following equation: *wet weight of edible tissues* = 0.6769 ∗ *shell length* – 20.3448. From this model he derived whole wet weights and caloric values by employing the following relationships: (1) the wet weight of edible tissues accounts for 0.49 of the whole wet weight, (2) the proportion of dry weight to wet weight of edible tissues is 0.145, and (3) the caloric value of edible tissues by dry weight is 4.60 kcal/g. Applying the model and relationships in Sykes (1987), we used the lengths of native snail shells measured in our study to estimate the average whole wet weight and average caloric content of native snails handled and consumed by kites.

Following the approach in Sykes (1987), we created the following regression model for *P. insularum*: *wet weight of edible tissues* = 0.8465 ∗ *shell length* – 19.0461, ($r^2$ = 0.75, $P < 0.001$). Our model and its respective coefficient of determination were comparable to that in Sykes (1987). Applying this model, we used the lengths of exotic snail shells to estimate the average whole wet weight and average caloric content of exotic snails handled and consumed by kites during our study using the following relationships: (1) the wet weight of edible tissues accounts for 0.58 (SE = 0.01) of the total wet weight of exotic snails, (2) the proportion of dry weight to wet weight of edible tissues is 0.13 (SE = 0.01), and (3) the caloric value of edible tissues by dry weight is 3.25 kcal/g (SE = 0.06).

### 2.3.4. Estimating daily energy balances

As has been done for snail kites in Venezuela by Beissinger (1983), daily energetic expenditures were calculated using Eq. (10) from Koplin et al. (1980), which calls for the following: (1) average temperature, (2) photoperiod, (3) proportion of diurnal activity time spent in flight, (4) flight coefficient, and (5) body mass. The average monthly temperature in the snail kite's range for the period May–December is 24 ± 1 °C (SFWMD, 2008), and the average photoperiod is 12.3 h (NOAA, 2008). The weighted mean proportion of time in flight (weights were assigned based on total observation time for each TAB) was calculated for each group of kites (Table 2). A flight coefficient of 7 was assumed. Varying the flight coefficient between 5 and 9 did not significantly affect our results. Mean body masses for adult (427 ± 4 g) and juvenile (389 ± 6 g) kites were derived from Valentine-Darby et al. (1997).

Gross daily energetic intakes were calculated using the consumption rate for each group of kites (Table 2) and the caloric content of the respective prey species (see Section 3.1). A 12.3-h photoperiod and an assimilation coefficient of 0.9 were assumed (Beissinger, 1983). Net daily energy balances were obtained by subtracting expenditures from intakes. Standard errors and confidence intervals for all derived estimates were approximated using the delta method (Rice, 1995).

## 3. Results

### 3.1. Diet

Snails of the genus *Pomacea* accounted for 99.4% of the snail kite's diet during our study. Out of the 2712 prey captures observed, only 15 included non-snail prey items, all of which were small unidentified turtles.

Empty snail shells were collected from snail kite feeding perches in the following areas: WCA3A, WCA3B, WCA2B, ENP, Okee, GW, SJM, Kiss, and Toho (see Fig. 1 in Martin et al., 2006). Toho was the only wetland in which shells from *P. insularum* were found. The mean shell length of exotic snails consumed by kites was 63.5 ± 0.4 mm ($n$ = 1486), and the mean length for native snails was 40.7 ± 0.1 mm ($n$ = 6421). Exotics were significantly larger than natives (one-sided Welch *t*-test, $t_{.05,7905}$ = 95.5, $P < 0.001$). Our linear models indicated that the mean whole wet weight of exotic snails handled by kites was 59.8 ± 0.7 g, while the mean whole wet weight for native snails was 15.0 ± 0.1 g.

Exotic snails store significantly fewer calories per gram of dry weight than do native snails but other nutritional measures for the exotic fall within the range of reported values for the native snail (Table 1). Our linear models indicated that the mean energetic content of exotic apple snails consumed by kites was 11.33 ± 0.33 kcal/snail, while the mean energetic content for native snails was 3.93 ± 0.09 kcal/snail.

### 3.2. Effects of the exotic snail on foraging behavior

Both age ($\chi^2$ = 21.1, $df$ = 1, $P < 0.001$) and snail species ($\chi^2$ = 132.9, $df$ = 1, $P < 0.001$) significantly affected the proportion of snails dropped, but there was no significant interaction ($\chi^2$ = 0.2, $df$ = 1, $P$ = 0.6). Within age classes, the proportion of snails dropped was significantly greater when handling exotic snails than it was when handling natives (Table 2), which supports *Prediction* 1. When handling exotic snails, juveniles dropped a significantly greater proportion of snails than did adults (Table 2), which supports *Prediction* 5.

Both age ($F$ = 7.8, $df$ = 1, $P$ = 0.005) and snail species ($F$ = 411.3, $df$ = 1, $P < 0.001$) significantly affected handling time, but there was no significant interaction ($F$ = 0.4, $df$ = 1, $P$ = 0.5). Within age classes, handling times were significantly longer for exotic snails than for natives (Table 2), which supports *Prediction* 2. When feeding on exotic snails, juveniles had a significantly longer handling time than did adults (Table 2), which supports *Prediction* 6.

**Table 2**
Mean (95% confidence interval) proportion of snails dropped, search time, handling time, consumption rate and proportion of time in flight for adult and juvenile snail kites feeding on exotic (*P. insularum*) versus native (*P. paludosa*) apple snails in Florida.

| Behavior | Foraging for exotic snails | | | | Foraging for native snails | | | |
|---|---|---|---|---|---|---|---|---|
| | Adults | | Juveniles | | Adults | | Juveniles | |
| | Mean (95% CI) | N | Mean (95% CI) | N | Mean (95% CI) | N | Mean (95% CI) | N |
| Proportion of snails dropped (%) | 21.5 (17.3, 25.6) | 131 | 39.3 (33.2, 45.3) | 69 | 2.4 (1.8, 3.0) | 342 | 5.5 (4.0, 7.1) | 38 |
| Search time (s) | 98 (70, 126) | 86 | 78 (50, 106) | 34 | 88 (77, 99) | 232 | 70 (52, 88) | 41 |
| Handling time (s) | 349 (292, 406) | 83 | 506 (418, 594) | 44 | 80 (76, 84) | 330 | 127 (84, 170) | 21 |
| Consumption rate (snails/h) | 1.1 (0.9, 1.3) | 144 | 0.8 (0.7, 0.9) | 101 | 3.9 (3.6, 4.2) | 238 | 4.0 (3.2, 4.8) | 43 |
| Time in flight (%) | 9.5 (7.7, 11.3) | 185 | 9.2 (7.6, 10.8) | 110 | 16.7 (15.1, 18.3) | 405 | 17.1 (13.6, 20.6) | 42 |

Consumption rate was significantly affected by snail species ($\chi^2 = 195.4$, $df = 1$, $P < 0.001$), age ($\chi^2 = 5.5$, $df = 1$, $P = 0.02$) and the age by snail species interaction ($\chi^2 = 12.3$, $df = 1$, $P < 0.001$). Within age classes, consumption rates were significantly lower for exotic snails than for natives (Table 2), which supports *Prediction* 3. Consumption rates did not differ significantly between juveniles and adults when feeding on native snails (Table 2), but when feeding on exotic snails, the consumption rate of juveniles was significantly lower than that of adults (Table 2), which supports *Prediction* 7.

### 3.3. Effects of the exotic snail on activity pattern and energetics

Kites foraging for exotic snails spent a significantly smaller proportion of the day in flight relative to kites foraging for natives. Within snail species, there was no significant difference in the proportion of time in flight between adults and juveniles (Table 2). The estimated daily energetic expenditures for adult kites were 98 ± 3 kcal/day and 119 ± 3 kcal/day when feeding on exotic snails and when feeding on natives, respectively. The estimated daily energetic expenditures for juveniles were 92 ± 2 kcal/day and 111 ± 3 kcal/day when feeding exotics and natives, respectively.

The estimated gross daily energetic gain (assuming an assimilation coefficient of 0.9) for adult kites was 140 ± 4 kcal/day when feeding on exotic snails and 167 ± 5 kcal/day when feeding on natives. We estimated that juveniles assimilate an average of 97 ± 7 kcal/day when feeding on exotic snails and 175 ± 7 kcal/day when feeding on natives. Juveniles achieved a significantly lower net daily energy balance when feeding on exotic snails versus natives (Fig. 1), which supports *Prediction* 4. Furthermore, when feeding on exotic snails, the daily energy balance of juveniles was significantly lower than that of adults (Fig. 1), which supports *Prediction* 8.

## 4. Discussion

### 4.1. Effects of the exotic snail on foraging behavior, activity pattern and energetics

We have shown that the invasive exotic apple snail, *P. insularum*, significantly affects the foraging behavior and activity pattern of a native specialist, the snail kite, in Florida. The proportion of snails dropped were 8–10 times higher, handling times were 4 times longer, and consumption rates were 3–4 times lower when foraging for exotic snails relative to natives. These consequences undoubtedly arise, in part, from the significantly larger size of the exotic snail and the resultant decrease in predator to prey weight ratios. On average, exotic snails weigh 14.0% and 15.4% as much as adult and juvenile kites, respectively, while native snails only weigh 3.5% and 3.9% as much as adults and juveniles, respectively.

It is likely that experience also plays a large role in the ability of kites to efficiently exploit apple snails. Holding snail species constant, juvenile kites dropped a significantly greater proportion of snails and had significantly longer handling times compared to adults. Furthermore, when feeding on exotic snails, the consumption rate of juveniles was significantly lower than that of adults.

The effects of the exotic apple snail on the foraging behavior of the snail kite cannot be viewed, substantively, outside the context of energetic ramifications. On average, exotic apple snails consumed by kites had roughly three times more energetic content than native snails. Yet, given the significantly lower consumption rates for exotic snails, kites achieved lower gross daily energetic gains when foraging on exotic snails. However, kites feeding on exotic snails spent over 30% less time in flight per day than did

kites foraging for native snails. Since flight is one of the most energetically expensive activities in which birds engage (Stephens and Krebs, 1986), this behavioral shift resulted in substantially lower daily energetic expenditures when foraging for exotic snails. The resulting net daily energy balances achieved when feeding on exotic versus native snails were similar for adult kites. Juvenile kites, on the other hand, experienced a significantly lower net daily energy balance when feeding on exotic snails. Our estimates show that this discrepancy may even result in a net loss of energy for juveniles attempting to feed on exotic snails (Fig. 1). The equations from Koplin et al. (1980) used to estimate energetic expenditures do not account for growth, reproduction or molt, nor do they account for potential increases in energetic expenditure that may arise due to the larger size of and/or the longer handling time required for the exotic snail; therefore, the daily energy balances presented here are likely overestimates, especially for growing juveniles. Furthermore, although adult kites maintain a similar net energy balance when feeding on exotic versus native snails, it is unclear whether the lower gross daily energetic gain achieved when feeding on exotic snails will limit their reproductive capacity.

It must be noted that factors other than foraging experience and relative prey size can affect consumption rates, particularly those factors influencing prey availability. However, during this study, average search times did not differ between snail species (Table 2), which suggests that the significantly lower consumption rates of kites foraging for exotic versus native snails did not result from differences in prey availability.

Little is known about the life history strategy of *P. insularum*, especially in the context of novel environments. At some point during growth, exotic snails must be comparable in size to the native snail; however, our data shows that kites on Toho are capturing exotics in a significantly larger size class. This suggests that either: (i) during this growth phase exotic snails typically inhabit areas unsuitable for snail kite foraging (e.g., dense vegetation) or (ii) kites are selecting the larger exotic snails despite the associated foraging difficulties. The latter is less likely because the range of *P. insularum* overlaps that of the snail kite (*R.s. sociabilis*) in South America, but kites there have not been documented feeding on *P. insularum*; however, they have been documented feeding on smaller *Pomacea* species instead (Darby et al., 2007). Therefore, it is likely that "native-sized" exotic snails were largely unavailable to foraging kites in Toho. Unfortunately, the distribution of *P. insularum* during our study (i.e., only exotic snails were available in Toho and only native snails were available in WCA3A, WCA2B and Kiss) precluded our ability to test hypotheses of optimal foraging theory. However, the native snail population on Toho may have begun to rebound in 2008 (Desa, 2008), which could provide a setting where both native and exotic snails are simultaneously available to foraging kites.

### 4.2. Potential population consequences

Energetic deficiencies could affect the snail kite population in numerous ways. As with many vertebrate species, the reproductive activity of snail kites is limited, in large part, by the availability of food resources (Stephens and Krebs, 1986), and kites may abandon initiated nests or provision fewer young in times of food stress, resulting in lower nest productivity (Beissinger and Snyder, 1987). The availability of suitable prey also directly affects survival in many species (Stephens and Krebs, 1986), and in the snail kite population, starvation has been identified as a leading cause of death for both adults and juveniles (Beissinger, 1988; Sykes et al., 1995). Except during severe drought events, adult snail kite survival remains relatively constant from year to year, while juvenile survival varies widely (Bennetts and Kitchens, 1999; Martin

et al., 2006). Experience, and in turn, foraging efficiency may play a large role in this disparity.

On rare occasions, kites in Florida have been observed attempting to feed on alternative prey items (e.g., small turtles, crawfish), usually during times of food scarcity (e.g. droughts), and most of these observations are attributed to inexperienced juvenile kites (Sykes and Kale, 1974; Sykes, 1987; Beissinger, 1990). Kites in Florida are rarely successful, and certainly not efficient, at extracting edible body parts of non-snail prey (Sykes and Kale, 1974; Beissinger, 1990). During this study, partially consumed exotic snails that had the operculum still attached to the shell were commonly found under feeding perches and in snail kite nests. Adult kites deliver extracted pieces of snail meat to young nestlings, but often, as nestlings reach fledging age, only whole snails are delivered (Sykes et al., 1995). The uneaten snails found in nests can likely be attributed to inexperienced juveniles. In 2008, three juvenile snail kite carcasses were recovered from Toho and necropsies performed by the USFWS determined that all three died from emaciation (Sandra Sneckenberger, personal communication).

As of this study, Toho was the only major wetland utilized by the snail kite in Florida that was dominated by P. insularum. Since the kite population in Florida does not function as a metapopulation (Bennetts and Kitchens, 1997; Martin et al., 2006), any demographic consequences that the exotic snail has on kites in Toho may affect the kite population as a whole. If the native P. paludosa population rebounds on Toho or if juveniles can disperse to wetlands in which native apple snails are available before succumbing to starvation, demographic consequences resulting from the exotic snail may be averted. If not, however, Toho may function as an ecological trap for kites. A formal test of the ecological trap hypothesis would require demonstrating: (1) that adult kites preferentially nest on Toho even though other wetlands, devoid of the exotic snail, are available and (2) that the exotic snail does in fact lead to increased juvenile mortality such that recruitment is significantly lower on Toho relative to other wetlands. A mark-resight study similar to Martin et al. (2006, 2007) would allow one to test for these two conditions.

Recruitment is one of the predominant factors limiting the growth and viability of the snail kite population in Florida (Martin et al., 2008). Confirmed populations of the exotic snail exist in close proximity to many of the other primary wetlands used by the snail kite in Florida (Rawlings et al., 2007), making it important to further elucidate the potential population consequences that could result from the spread of this exotic species.

### 4.3. Conclusion

Species extinctions are occurring at a rate unparalleled in recent geological history (McKinney and Lockwood, 1999), yet the underlying factors responsible for many population declines remain unknown (Wilcove et al., 1998; Gurevitch and Padilla, 2004). The role that exotic species play in species extinctions has received much attention over the last decade. Native populations may respond negatively to exotic invasions through well known mechanisms such as predation, competition, and hybridization (Strauss et al., 2006; Vellend et al., 2007); however, more subtle mechanisms are less well understood, and the role that exotic species may play in the population decline of native predators has been largely overlooked. Our research demonstrates the ability of an exotic prey species to affect the foraging behavior, activity pattern and energetics of a native predator. This work also suggests that such changes may affect demographic parameters of native populations. In addition to the scenario demonstrated here (energetic deficiencies arising due to inexperienced and/or smaller-sized juveniles attempting to feed on a larger exotic species), other foreseeable scenarios of exotic prey species influencing demographic parame-

ters of native populations exist. Exotic prey species that require longer searching or handling times than their native counterparts may negatively affect native predators. For example, native predators distracted by searching and handling may lower vigilance, which in turn may increase predation risk. Furthermore, increased searching and handling times may lead to a decrease in parental care, which could translate into the provisioning of fewer offspring or an increased risk of offspring mortality in the absence of a defensive parent. Any such influences may have population consequences, especially for species dependent upon specialized niches or for species with declining populations that are limited by recruitment. A better understanding of the interactions between exotic species and native specialists would be beneficial in the design of conservation strategies for native species.

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