Reproductive Responses of the Endangered Snail Kite to Variations in Prey Density

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ABSTRACT Understanding how predators respond to fluctuations in prey density has important conservation and management implications, particularly for threatened and endangered specialists. However, directly linking prey densities to predator behavior and demography over broad spatial and temporal scales is rare, in part, because it can be prohibitively expensive and time-consuming to quantify prey density over large areas. We link nesting data collected by a long-term monitoring program for the endangered snail kite (Rostrhamus sociabilis plumbeus) with 44 density estimates of its primary prey, the Florida apple snail (Pomacea paludosa), collected by multiple, smaller-scale studies from 2002 to 2010. We found evidence that key components of kite breeding biology—nest density and the number of young fledged per successful nest—were positively related to snail density. Although previous studies have shown that densities greater than approximately 0.1–0.2 snails/m² may be necessary to sustain profitable foraging and that capture times for individual foraging kites begin to level off as snail densities exceed approximately 0.4 snails/m², we found continued numerical responses in snail kite reproductive parameters at greater snail densities. At occupied sites (i.e., snail-sampling sites in which ≥1 snail kite nest was present within a 2-km radius during the primary sampling period: Mar–May), the average snail density was 0.45 snails/m² (SE = 0.12, n = 17), whereas that of unoccupied sites was 0.12 snails/m² (SE = 0.02, n = 27). Along the snail density gradient from 0.2 to 0.4 to 1.2 snails/m², model predictions indicated that 1) the probability of site occupancy (by nesting kites) increased from 0.48 to 0.69 to 0.90, 2) local nest abundance of occupied sites increased from 4 to 7 to 16 nests, and 3) the probability of a successful nesting attempt fledging more than 1 young increased from 0.02 to 0.07 to 0.43. We found no evidence of a snail density effect on nest survival. Understanding the differential effects of snail density on various components of snail kite breeding biology is essential to the development and implementation of management tools used for snail kite conservation and Everglades restoration. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS apple snail, Everglades, Florida, numerical response, Pomacea paludosa, prey density, Rostrhamus sociabilis, snail kite, specialist predator.

Demographic parameters of many predator populations are closely linked to variations in prey density (Newton 1998, Sibly and Hone 2002), with dietary specialists often showing stronger numerical responses than generalists (Andersson and Erlinge 1977, Newton 1979). Indeed, dietary specialization has been implicated in the extinction risk of numerous taxa (McKinney 1997, Owens and Bennett 2000, Boyles and Storm 2007). Understanding the response of predators to fluctuations in prey density has important conservation and management implications, particularly for imperiled species that specialize on prey.

Estimating prey densities over broad spatial and temporal scales, however, can be prohibitively expensive and time-consuming. Although most recovery programs of threatened and endangered species contain a monitoring component for the focal population itself, many lack monitoring data for associated prey species (Campbell et al. 2002). Such information gaps can hinder our abilities to make informed management decisions and to quantitatively assess threats to populations (Lawler et al. 2002). However, monitoring programs of many threatened and endangered predators have amassed long-term datasets with extensive geographical coverage (Dennis et al. 1991, Campbell et al. 2002), and relevant data for associated prey species may have been collected (at some overlapping scale) by previous (possibly unrelated) studies. Integrating pre-existing datasets is a potentially valuable yet underutilized approach, especially when insufficient resources preclude the implementation of...
complementary predator–prey monitoring programs. Although such datasets may not be as tightly coupled as data collected in a coordinated protocol, the integration of pre-existing datasets can be an important first step for filling information gaps where time-sensitive management decisions (particularly for critically endangered species) cannot be delayed.

We analyzed nesting data collected by a long-term monitoring program of an endangered raptor, the snail kite (Rostrhamus sociabilis plumbaeus), and density data collected by multiple, relatively smaller-scale studies of its primary prey, the Florida apple snail (Pomacea paludosa), to assess the effects of prey density on kite breeding biology. The range of the snail kite in the United States is confined to the freshwater wetlands of central and southern peninsular Florida (Bennetts and Kitchens 1997, Martin et al. 2006). Kites feed almost exclusively on a single genus of aquatic snail (Pomacea), and historically on a single species (P. paludosa; Sykes 1987, see Cattau et al. 2010 regarding kites foraging on the newly introduced P. maculata, which was recently synonymized with P. insularum; Hayes et al. 2012). The viability of the endangered snail kite population is likely dependent on the hydrologic conditions (both short-term and long-term) that 1) maintain sufficient densities of apple snails, 2) support snail availability to kites (e.g., kites cannot capture snails in dry down conditions or in high stem density marsh; see Sykes et al. 1995), and 3) provide suitable conditions for snail kite foraging and nesting, which include a mosaic of different plant communities (Bennetts and Kitchens 1997, U.S. Fish and Wildlife Service [USFWS] 1999). Habitat fragmentation and hydroscape alteration over the past century have resulted in a highly compartmentalized and intensively managed network of wetland units, rendering many wetlands unsuitable for kite use (Bennetts et al. 1994, USFWS 1999). A primary objective of the snail kite recovery plan, as well as the Comprehensive Everglades Restoration Plan, is to develop water management regimes that better approximate the historical conditions that once supported the kite population (USFWS 1999, 2010; RECOVER 2005). Previous research has elucidated the effects of hydrology on plant community dynamics (e.g., Zweig and Kitchens 2008) and on the movement, survival, and reproduction of both snail kites (e.g., Bennetts and Kitchens 1997; Martin et al. 2006, 2008) and apple snails (e.g., Darby et al. 2002, 2005, 2008). Surprisingly, no data directly link variation in apple snail density (or availability) with the demography of snail kites (but for faring-related studies see Bennetts et al. 2006; Darby et al. 2006, 2012). Nonetheless, as drying events can render apple snails unavailable to foraging kites (Sykes et al. 1995), insufficient prey availability has frequently been implicated (circumstantially) in decreased survival and reproduction of kites in wetlands experiencing low water levels (e.g., Beissinger 1995; Mooij et al. 2002; Martin et al. 2006, 2008).

The snail kite population in Florida has declined by more than 50% (to fewer than 1,500 individuals) since 1999 (Martin et al. 2007a), largely because of decreased reproduction and recruitment (Martin et al. 2008). In relation to maintaining the long-term stability of the snail kite population, Water Conservation Area 3A (WCA3A) has often been considered one of the most critical wetlands within the kite’s range, acting as a stronghold for kite reproduction since the early 1970s (Bennetts et al. 1994; USFWS 1999, 2010; Martin et al. 2007a, 2008); however, nest numbers and fledgling production in WCA3A decreased sharply after 1998 (Martin et al. 2008). Multiple factors have likely contributed to these observed declines, including short-term natural disturbances (e.g., dry downs) and long-term habitat degradations (e.g., the conversion of wet prairies to sloughs; Martin et al. 2008, Zweig and Kitchens 2008), as well as declines in apple snail densities (Darby et al. 2005). Given that reproduction may be largely limiting snail kite population growth and recovery (Martin et al. 2008), understanding how apple snail density (in conjunction with other factors) affects kite reproduction is critical to conservation planning.

Using pre-existing datasets from multiple studies conducted in WCA3A over a 9-year period (2002–2010), we linked snail density estimates to reproductive parameters of the snail kite. Our objectives were to determine the effects of snail density on the presence and abundance of nests, nest survival, and the number of young fledged per successful nest, as these reproductive metrics provide essential information for modeling population demography (Beissinger 1995, Martin et al. 2008) and are often used as performance measures by natural resource managers (USFWS 1999, 2010). Snail kites are nomadic (Bennetts and Kitchens 2000) and typically non-territorial, nesting solitarily or in loose colonies (Sykes 1987b, Bennetts et al. 1988). Given that nomadic specialist predators often track prey resources without a lag time (Andersson and Erlinge 1977, Terraube et al. 2012), we predicted that snail density (a key component of prey availability) would influence the occurrence and abundance of snail kite nests. Breeding performance of raptors can also be limited by food resources (Newton 1979, 1998), and previous authors have suggested that snail kites may abandon nests or provision fewer young in times of food stress (Beissinger and Snyder 1987, Sykes 1987b). Consequently, we predicted that nest survival and the number of young fledged per successful nest would increase with increasing snail density.

STUDY AREA

Located near the center of the remnant Everglades ecosystem, WCA3A is an impounded wetland bordered by Big Cypress National Preserve to the west and Everglades National Park to the South. All data used in our study were collected in the approximately 130,000-ha section of WCA3A lying south of Alligator Alley (see Bennetts et al. 1988, Darby et al. 2006).

METHODS

Data Collection

Apple snail (P. paludosa) densities were estimated at numerous sites in WCA3A from 2002 to 2010 (see Table 1...
and below), and were initially collected to address the effects of hydrology and vegetation on snail density and reproduction (Darby et al. 2005, Karunaratne et al. 2006). A portion of these data were also used to assess the role of snail density in foraging patch selection (Bennetts et al. 2006, Darby et al. 2006) and foraging success (Darby et al. 2012) of snail kites. In all studies, site-specific snail densities (corrected for capture probability) were estimated using the throw trap method, with an average of 75 (SD = 27) 1-m² aluminum-walled traps (deep enough to contain the entire water column) deployed across approximately 1 ha of each site sampled during a given year (detailed in Darby et al. 1999). We used data from 16 sites, many of which were sampled multiple times over the 9-year period, resulting in 44 separate snail density estimates from unique site-years (hereafter sites; Table 1). As kites rarely consume snails smaller than 20 mm (Sykes 1987a, Cattau et al. 2010), we considered only densities of so-called adult-sized snails (>20 mm; sensu Darby et al. 2012) in our analyses.

Snail kite nests in WCA3A were located during systematic surveys conducted at regular intervals throughout the breeding season as part of a long-term population monitoring program. Surveys were conducted by experienced observers, and to the extent possible, survey effort was uniform across WCA3A and constant among years. Nest searching and monitoring protocols are detailed elsewhere (Bennetts et al. 1988; Bennetts and Kitchens 1997; Martin et al. 2007a, 2008). We used only nests containing at least 1 egg or young during the primary sampling period (Mar–May) in our analyses, and we considered nests successful when at least 1 nestling reached 24 days old (i.e., 80% of average fledging age; Steenhof 1987, Bennetts and Kitchens 1997).

Using sampling (and monitoring) dates and global positioning system coordinates of snail-sampling sites and observed kite nests, we integrated overlapping data based on temporal and spatial selection criteria (see below), pairing each nest with a site-specific snail density estimate. Although we were primarily concerned with determining how kite reproduction was affected by variation in snail densities, some analyses also warrant consideration of hydrologic effects (see below) because hydrology may have a proximate bearing on certain aspects of snail kite behavior and demography (Beissinger 1995, Bennetts and Kitchens 1997). We obtained daily water level data for WCA3A from the 3-gauge average (station CA3AVG) maintained by the South Florida Water Management District (SFWMD; see USFWS 2010). We also obtained daily water depths specific to kite-nest and snail-sampling site locations from the Everglades Depth Estimation Network (EDEN), which interpolates continuous water surface data at 400-m × 400-m resolution across WCA3A (Palaseanu and Pearlstine 2008, Liu et al. 2009).

### Linking Datasets

To integrate datasets, we took care to ensure that data were as biologically relevant and comparable as possible. Given the nature of the data, we had to make 2 critical assumptions: 1) that the snail density measured at a site with which a nest was paired was representative of the snail density encountered by the respective kite(s) when deciding to nest (which may affect nest presence and abundance) and when foraging after a nest was established (which may affect nest survival and the number of young fledged), and 2) that the relationship between snail density and snail availability (the former being used as a proxy for the latter) was constant among sites. No foraging observations or home range estimates were available for the breeding kites whose nests we used in the analyses; therefore, we attempted to minimize potential bias that may arise from a violation of the first assumption by using snail density and kite nesting data that were temporally and spatially proximal. We used snail density estimates from sites that were sampled during the primary snail kite breeding season, which typically spans from January to June (Bennetts and Kitchens 1997). Given that sampling at these sites occurred almost entirely in March, April, and May (Table 1), we restricted our analyses to nests that contained eggs or young during at least part of this time period. Snail kites generally forage within 2 km of their nests, but they have been observed occasionally traveling >6 km (Beissinger and Snyder 1987, Sykes et al. 1995). Field work conducted in WCA3A in 2011 found that 99% of the foraging bouts made by nesting kites fell within 2 km of the nest, with a maximum distance traveled of 2.7 km (W. M. Kitchens, U.S. Geological Survey, and R. J. Fletcher Jr., University of Florida, unpublished data). Thus, we further restricted our analyses to nests that were ≤2 km from the centroid of a snail-sampling site (mean ± SD: 1.2 ± 0.5 km). Given the distances between snail-sampling sites, we paired each nest with a single site-

### Table 1. Midpoint sampling date (month/day) for 44 snail density estimates from 16 sites in Water Conservation Area 3A (WCA3A), Florida, USA, 2002–2010 (excluding 2008, in which no snail sampling occurred). Site numbers from previous studies (Darby et al. 2009, 2012) were retained for comparison. Note that site-years are simply referred to as sites in the text.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Site 4</th>
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<th>Site 6</th>
<th>Site 7</th>
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specific snail density estimate. Note that we evaluated the data using a more conservative ≤1-km cutoff and obtained similar results; however, parameter estimation in some analyses was problematic because of sample size limitations.

As for the second assumption, several factors other than (or in combination with) snail density can influence the availability of snails to foraging kites, but potential bias introduced by these factors was likely minimal. Although temperatures less than approximately 13°C have a strong negative influence on apple snail activity (Stevens et al. 2002) and kite foraging success (Cary 1985), the average daily air temperature in WCA3A during the primary sampling period (Mar–May) ranged from 21.6°C in 2005 to 24.8°C in 2003 (SFWMD, station 3AS3WX; note that no data were available for 2006). Consequently, temperature likely had a minimal effect on variation in snail availability. Second, drying events can reduce apple snail availability because snails frequently burrow in the substrate when water falls to or below ground level (i.e., ≤0 cm; Darby et al. 2008). Water depths at snail-sampling sites temporarily fell to ≤0 cm (during the period Mar–May) on only 2 occasions, but snail density (and likewise, snail availability) at each site was so low (0.00 and 0.03 snails/m²) that any additional negative effect of dry conditions on snail availability can be safely ignored. Finally, snail availability can vary among habitat types, as vegetation can be an impediment (visually and/or physically) to snail kite foraging (Sykes 1987a, Bennetts et al. 2006). Most snail sampling in WCA3A occurred in similar habitat (i.e., low to moderate stem density emergent marsh dominated by *Eleocharis* spp. and *Panicum* spp.), and minor variation in vegetation structure among sites was unlikely to have significant effects on snail availability (Darby et al. 2009, 2012). Although site selection does limit our inferences to certain habitat types, low to moderate stem density emergent marsh is the most commonly used foraging habitat of snail kites (Sykes 1987a, Bennetts et al. 2006).

Darby et al. (2012) suggested that densities greater than approximately 0.1–0.2 snails/m² may be necessary to sustain profitable foraging (for non-breeding snail kites) and that foraging efficiency may level off as densities exceed approximately 0.4 snails/m². Snail density estimates used in our study ranged from 0.00 to 1.78 (mean ± SD: 0.23 ± 0.35) snails/m². Within-year minimum and maximum snail density estimates differed by a factor of approximately 3–40 (except in 2010 when min. and max. density only differed by a factor of 1.1), providing a suitable range and sufficient variability to test our hypotheses.

**Data Analysis**

To assess the effects of snail density and other biologically relevant variables (below) on kite reproduction, we created an a priori model set for each of the 4 response variables of interest (nest presence and abundance, nest survival, and the number of young fledged per successful nest; defined below). We used generalized linear models (GLMs) with the appropriate error distributions and link functions to generate maximum likelihood estimates of parameter values (McCullagh and Nelder 1989). We ranked models and evaluated their relative performance using Akaike’s Information Criterion corrected for small sample size (AICc) and AIC, weights (wAIC; Burnham and Anderson 2002). We considered effects of a covariate significant when the 95% confidence interval for its parameter estimate did not overlap 0. When we found model selection uncertainty, we used high-ranking models (i.e., ΔAICc < 4) to calculate model-averaged parameter estimates and unconditional 95% confidence intervals (Burnham and Anderson 2002). We log-transformed snail density (+0.01) prior to all analyses (Darby et al. 2012). We conducted statistical analyses in program R, version 2.15.0 (R Development Core Team 2012).

**Nest presence and abundance.—** We defined local nest abundance (i.e., site-specific nest abundance) as the maximum number of simultaneously occurring nests recorded within a 2-km radius (of the centroid) of each snail-sampling site during the primary sampling period (Mar–May) in a given year. As parental duties in snail kites are shared (Sykes et al. 1995), our definition of nest abundance equates to the number of breeding pairs. We used the maximum number of co-occurring nests rather than the total cumulative number of nesting attempts to define local nest abundance (and to compare relative abundances among sites) because of the potential for the latter to be biased by among-site differences in nest survival and re-nesting rates. We defined occupied sites as those snail-sampling sites in which local nest abundance was ≥1 nest. We modeled nest presence (i.e., occupied vs. unoccupied sites; n = 44 sites) using binomial GLMs (logit link). We modeled nest abundance of occupied sites (n = 17 sites) using negative binomial GLMs (log link). Both analyses included the same set of independent variables. In addition to snail density, we included average daily water depth (Mar–May) in the snail-sampling site as a covariate (derived from EDEN data), as kites may use water depth as a direct cue in nest site selection (Sykes 1987b, Bennetts et al. 1988). We included year as a nuisance categorical variable to account for annual variation that may derive from factors beyond the scope of our study (e.g., habitat conditions in other wetlands, fluctuating size of the overall kite population). We started with a global model that included all 3 covariates (additive effects only) and considered all possible reduced models.

**Nest survival.—** Low water levels can expose kite nests to terrestrial predators leading to predation and can weaken supporting vegetation leading to collapse (Sykes 1987b, Snyder et al. 1989). Our primary goal was to test for the effect of snail density on nest survival while also accounting for proximate hydrologic effects. Time-specific targets for the annual hydrologic cycle in WCA3A are based on daily mean water level data from the CA3AVG station (USFWS 2010). Two hydrologic metrics derived from these data have been shown to influence annual apparent snail kite nest success. The annual minimum water level is positively correlated with nest success, whereas the recession rate from 1st January to the date on which the minimum level was reached is negatively correlated with nest success (Cattau et al. 2008, USFWS 2010). We implemented package RMark (White and Burnham 1999, Laake and Rexstad 2009) to assess the
factors influencing daily survival rate of nests (detailed in Dinsmore et al. 2002). Seventy-six nests that had multiple visits (constituting 2,302 exposure days) met our selection criteria, and the number of exposure days observed annually ranged from 42 in 2007 to 925 in 2002 (note that no known-fate nests met the criteria in 2005 or 2009). This framework allows for the inclusion of time-dependent variables and greatly improves the ability to simultaneously assess multiple covariates (Rotella et al. 2004). Therefore, in addition to year-specific variables, we considered 2 other hydrologic variables: 1) the daily mean water level across WCA3A as a time-specific covariate (data from station CA3AVG), and 2) water depth on the day each nest was last checked as a nest-specific covariate (data from EDEN). Because the 4 hydrologic variables were highly correlated, we did not consider models containing more than 1 hydrologic term.

Young fledged.—We modeled the number of fledglings per successful nest as a function of snail density using GLMs with Gaussian error and the identity link. When analyzing bounded count data with means less than 2, linear regression often outperforms both Poisson and multinomial regressions (McDonald and White 2010). We included only nests in which the number of fledglings could be confirmed (n = 29 nests) in the analysis. To account for the possibility that food resources may decline throughout the breeding season (and that this may be a function of predator density), we also tested for effects of time (i.e., Julian date on which the nest was considered successful), local nest abundance (site-specific), and their interaction.

RESULTS

Nest Presence and Abundance

Local nest abundance (within a 2-km radius of a snail-sampling site) ranged from 0 to 28 nests. The proportion of occupied sites (i.e., sites with ≥1 nest present) and the average number of nests per site (and per occupied site) increased incrementally as snail densities went from <0.2 to 0.2–0.4 to >0.4 snails/m² (Table 2). The average snail density of sites occupied by nesting kites was 0.45 snails/m² (SE = 0.12, n = 17), whereas that of unoccupied sites was 0.12 snails/m² (SE = 0.02, n = 27). The average snail density of occupied sites with high nest abundance (i.e., ≥5 nests) was 0.80 snails/m² (SE = 0.19, n = 8), whereas that of occupied sites with low nest abundance (i.e., 1–4 nests) was 0.14 snails/m² (SE = 0.03, n = 9).

All highly ranked models (i.e., ΔAICc < 4) explaining the probability of nest presence included a snail-density effect (Table 3). The univariate snail-density model was the top-ranked model (with 52% of the AIC, weight; Table 3) and indicated that the probability of nest presence increased with snail density (β = 1.24, 95% CI = 0.46–2.29; Fig. 1A). The model-averaged estimate showed a similar snail-density effect (β = 1.25, 95% CI = 0.07–2.42). Although average water depth (Mar–May) at the snail-sampling site was included in the second-ranked model (Table 3), its relatively minor positive effect on the probability of nest presence was not significant (β = 0.05, 95% CI = –0.03–0.16). The model-predicted probability of a site being occupied by ≥1 snail kite nest increased from 0.48 to 0.69 to 0.90 as snail densities increased from 0.2 to 0.4 to 1.2 snails/m² (Fig. 1A).

The top-ranked model explaining local nest abundance (of occupied sites) held 60% of the AIC, weight (Table 3) and indicated that nest abundance increased with snail density (β = 0.63, 95% CI = 0.33–0.94) and, to a lesser extent, average water depth (Mar–May) at the snail-sampling site (β = 0.04, 95% CI = 0.002–0.08). The univariate snail-density model was the second-ranked model (holding 40% of the AIC, weight and differing from the top model by only 0.81 AIC, units; Table 3) and indicated a slightly stronger (though statistically equivalent) snail-density effect (β = 0.73, 95% CI = 0.41–1.08; Fig. 1B). All highly ranked models included snail density (Table 3), and the model-averaged estimate revealed a similar effect (β = 0.68, 95% CI = 0.33–1.03). Predicted mean nest abundance increased from 4 to 7 to 16 nests as snail densities increased from 0.2 to 0.4 to 1.2 snails/m² (Fig. 1B).

Nest Survival

The top-ranked model explaining the daily survival rate of nests was the univariate model that included the annual minimum water level in WCA3A (Table 4), which indicated a positive effect (β = 1.00, 95% CI = 0.11–1.90). None of the other univariate models ranked above the intercept-only model (Table 4) nor did they show evidence of significant covariate effects (snail density: β = 0.13, 95% CI = –0.11–0.37; annual recession rate: β = –1.98, 95% CI = –17.10–13.13; daily water levels in WCA3A: β = 0.33, 95% CI = –0.61–1.26; water depth at the nest: β = –0.01, 95% CI = –0.03–0.01). Univariate hydrologic models were not significantly improved by the addition of a snail-density effect, and only 1 such model (annual minimum water level + snail density) ranked above the intercept-only model (Table 4). Parameter estimates from this model (annual minimum water level: β = 0.97, 95% CI = 0.09–1.85; snail density: β = 0.11, 95% CI = –0.12–0.34) were similar to estimates from the respective univariate models.

Table 2. The proportion of sites occupied by ≥1 snail kite nest within a 2-km radius and the average number of nests per site for 3 ranges of snail densities measured in snail-sampling sites in Water Conservation Area 3A (WCA3A), Florida, USA, 2002–2010 (excluding 2008, in which no snail sampling occurred).

<table>
<thead>
<tr>
<th>Snail density (snails/m²)</th>
<th>Number of sites</th>
<th>Proportion of sites occupied</th>
<th>Nests per site, mean (SE)</th>
<th>Nests per occupied site, mean (SE)</th>
</tr>
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<tbody>
<tr>
<td>&lt;0.2</td>
<td>32</td>
<td>0.25</td>
<td>0.6 (0.3)</td>
<td>2.5 (0.8)</td>
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<tr>
<td>0.2–0.4</td>
<td>6</td>
<td>0.50</td>
<td>2.8 (2.4)</td>
<td>5.7 (3.5)</td>
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<tr>
<td>&gt;0.4</td>
<td>6</td>
<td>1.00</td>
<td>13.8 (3.8)</td>
<td>13.8 (3.8)</td>
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</table>
with GLMs with negative binomial error and the log link using data from sites in which
we modeled nest abundance (of occupied sites)
date (average water depth (Mar–May) at the snail-sampling site, and a categorical year effect.

Young fledged
Successful nests fledged an average of 1.38 (SD = 0.56) young. The top-ranked model explaining the number of young fledged per successful nest was the univariate snail-density model, which held 46% of the AIC, weight (Table 5). This univariate model indicated that the number of young fledged per successful nest increases with snail density (β = 0.25, 95% CI = 0.09–0.42; Fig. 2A). Model-averaged parameter estimates indicated a similar snail-density effect (β = 0.25, 95% CI = 0.06–0.45), whereas effects of Julian date (β = −0.004, 95% CI = −0.015–0.007) and nest density (β = 0.01, 95% CI = −0.03–0.05) were not signifi-

Because only 1 nest fledged 3 young and it was associated with the greatest measured snail density (i.e., 1.78 snails/m²; Fig. 2A), we reran the GLMs excluding this data point to ensure it was not driving the significant relationship. Given the binary outcome of this censored dataset, we used binomial GLMs with the logit link to model the probability of fledging 2 (rather than 1) young. Again, the top-ranked model was the univariate snail-density model (Table 5), which indicated a positive snail-density effect (β = 2.05, 95% CI = 0.58–4.32). The model-predicted probability of a successful nest fledging 2 (rather than 1) young increased from 0.02 to 0.07 to 0.43 as snail densities increased from 0.2 to 0.4 to 1.2 snails/m² (Fig. 2B).

DISCUSSION
By combining pre-existing, spatiotemporally overlapping datasets from 1) a long-term monitoring program of the endangered snail kite and 2) multiple, smaller-scale studies of the Florida apple snail conducted in WCA3A from 2002 to 2010, we found strong correlations in some aspects of snail kite reproduction and snail density. Our results indicate that observed differences in nest presence and abundance at a
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local scale (i.e., within a 2-km radius of a snail-sampling site) are largely attributable to variations in snail density, and to a lesser extent, to average water depths during the primary breeding season. We also found a positive association between snail density and the number of young fledged per successful nest. Yet we found no support for an effect of snail density on nest survival.

Predators can exhibit 2 types of responses to fluctuations in prey densities: functional (e.g., variation in prey consumption rate or diet composition) and numerical (e.g., variation in relative or absolute abundance through either aggregational or demographic mechanisms; Solomon 1949). The response of generalist predators is often functional, whereas that of specialists is typically numerical (Andersson and Erlinge 1977, Newton 1979). Demographic parameters of many specialist predators are closely linked to variations in prey density, and numerical responses can be direct or delayed (Newton 1998, Sibly and Hone 2002). The local abundance of breeding pairs of nomadic specialists often tracks prey densities without a substantial lag time, and the direct numerical response typically represents a relative change in distribution due to immigration and emigration (Andersson and Erlinge 1977, Korpimaki and Norrdahl 1991, Newton 1998). If prey density is limiting, individuals attempting to exploit areas of low prey density may experience reduced rates of survival and reproduction, and a delayed numerical response may be manifest in declined abundance at a local (or population) scale in the future. Our results indicate that snail kites likely adjust local nest numbers (via habitat selection) in accordance with fluctuations in snail density, thus exhibiting a direct numerical response in relative breeding density. We also found that snail density may be limiting brood size at fledging, which could potentially affect kite abundance at the population level.
The snail kite is an extreme dietary specialist (Sykes 1987a), and although rare instances of alternative prey items being taken by kites in Florida have been documented (Sykes et al. 1995), snail kites in the United States principally exhibit numerical responses to fluctuations in apple snail density (Takekawa and Beissinger 1989). Darby et al. (2006) found that the density of foraging kites (individuals/km²) was positively related to snail density and noted that no kites were observed foraging proximal to sites with snail densities below 0.14 snails/m². Darby et al. (2012) propose that densities greater than approximately 0.1–0.2 snails/m² may be necessary to support profitable foraging. Our results show a similar direct numerical response; few sites with densities below 0.2 snails/m² were occupied by kite nests, and local nest abundance increased with snail density (Table 2, Fig. 1). Given the additional energetic demands of reproduction (and the longer residence times spent by breeders in a local foraging area relative to non-breeding transients), one could expect that greater snail densities may be required to support kite nesting (particularly at greater nest densities), and our results support this notion. Although capture times (for individual foraging kites) begin to level off as snail densities exceed approximately 0.4 snails/m², which suggests that the extent to which increasing snail density improves individual foraging profitability may be limited (Darby et al. 2012), we found that kites continue to respond numerically at greater snail densities (consistent with Darby et al. 2006). Our models indicate that as snail densities increase from 0.2 to 0.4 to 1.2 snails/m² the probability of nest presence increases by a factor of 1.4 and again by a factor of 1.3 (Fig. 1A). Along the same snail density gradient, local nest abundance of occupied sites increases by a factor of 1.8 and again by a factor of 2.3 (Fig. 1B). Our observations also support the prediction of Bennetts et al. (1988) that high local nest densities would be associated with high snail densities.

Nest density ultimately reflects the nest-site selection decisions made by individuals in the population, a process that is likely driven by not only current (and expected) prey availability, but also perceived predation risk, as well as past success and experience (Chalfoun and Schmidt 2012). Our results suggest that snail kites use snail density as a cue in nest-site selection and that relative nest abundances were associated with variations in snail density. Similar trends in the local presence and abundance of breeding pairs (or nests) have been observed for other nomadic dietary specialist raptors, such as the short-eared owl (Asio flammeus), long-eared owl (A. otus), common kestrel (Falco tinnunculus; Korpimaki and Norrdahl 1991), Montagu’s harrier (Circus...
pygargus; Salamolard et al. 2000), and pallid harrier (C. macrourus; Terrabue et al. 2012). Although snail density had the highest relative importance among variables explaining the presence and abundance of nests (Table 3), other local conditions may also be important. The availability of nesting substrate limits the breeding density of many raptors (Newton 1979, 1998), including (in some wetland systems) the snail kite (Bennetts et al. 1994); however, nesting substrate was likely not a limiting factor in our study. Snail kites use a wide variety of nesting substrates, including both woody (e.g., Annona glabra, Salix caroliniana, Taxodium spp.) and herbaceous (e.g., Typha latifolia, Cladium jamaicense, Scirpus californicus) plant species (Bennetts et al. 1988, Snyder et al. 1989), and suitable substrates were widely available in close proximity to all snail-sampling sites. Local hydrologic conditions may also affect nesting decisions, as snail kites almost always select nest sites over water (Sykes 1987b), typically 20–80 cm deep (Bennetts et al. 1988), which is thought to deter terrestrial predators (Sykes et al. 1995). Average water depths (Mar–May) at all but 2 snail-sampling sites fell within this typical range, which likely explains why water depth showed only a weak positive association with nest presence and abundance in our study. Variation in local nest presence and abundance not explained by site-specific factors may derive from larger-scale, population- or landscape-level dynamics. For example, we found some evidence that the probability of nest presence varied among years (Table 3), and this could be linked to changes in the size or age structure of the snail kite population (Martin et al. 2008, Reichert et al. 2012), or to changes in the relative distribution of natal locations among individuals in the population (Martin et al. 2007b). Among-year variation could also have stemmed from habitat conditions (including prey densities) in other wetlands because kites may sample numerous wetlands throughout their range before selecting a breeding location (Bennetts and Kitchens 2000).

In addition to the direct numerical response in local nest presence and abundance, we found that variations in apple snail density also affect 1 of the 2 breeding performance measures of snail kites that we considered: the number of young fledged per successful nest was strongly influenced by snail density (Fig. 2). Provisioning rates by nesting snail kites increase with brood size (Beissinger and Snyder 1987), and based on a brood manipulation experiment of snail kites in Venezuela, Beissinger (1990) suggested that most nestling mortality resulted from starvation. Although we did observe 6 successful nests near sites with densities <0.2 snails/m², only 1 young was fledged from each. All nests that fledged 2 or more young were near sites with densities between 0.59 and 1.78 snails/m², and our models indicate that the probability of a successful nest fledging 2 (rather than 1) young increases by about 20-fold as snail densities increase from 0.2 to 1.2 snails/m² (a 1-unit increase; Fig. 2B). This implies that snail density may limit kite brood size at many of the densities observed in our study. Beissinger (1990) reported a maximum of 2 young fledging from natural broods in Venezuela and postulated that food supply limits snail kite brood size. He implicated lower nest provisioning rates and the frequent use of less-profitable prey items (i.e., crabs in addition to snails) by kites in Venezuela. Historically, 3 young were regularly observed fledging from snail kite nests in Florida (Bennetts et al. 1988, Snyder et al. 1989). However, apple snail abundances in many wetlands in the

### Table 5. Model selection results explaining the number of snail kite young fledged per successful nest within 2 km of snail-sampling sites in Water Conservation Area 3A (WCA3A), Florida, USA. Successful nests (that had a confirmed number of young fledge) were observed in 2002–2004 and 2006. We compared models using Akaike's Information Criterion corrected for small sample size (AICc) and AICc weights (wi). We report model differences (ΔAICc) as a measure of comparison. We modeled the number of fledglings with 1) generalized linear models (GLMs) with Gaussian error and the identity link using all observations (n = 29 nests), and 2) GLMs with binomial error and the logit link using nests that fledged either 1 or 2 young (n = 28 nests). Covariates included snail density, Julian date on which the nest was considered successful, and number of simultaneously occurring nests present within 2 km of the snail-sampling site (i.e., local nest density).

<table>
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<tr>
<th>Response</th>
<th>Model</th>
<th>K*</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
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<td>2.48</td>
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<tr>
<td></td>
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<td>2.97</td>
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<td>4.55</td>
<td>0.05</td>
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<td>7.54</td>
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* Number of parameters.
The snail kite’s range (and in WCA3A in particular) may have declined in the last 10–15 years (Darby et al. 2009, 2012; USFWS 2010), and young production from successful nests in WCA3A may also be declining. Snyder et al. (1989) found an average of 1.88 young fledged per successful nest in WCA3A from 1978 to 1983, with 52% and 18% of successful nests fledging 2 and 3 young, respectively. Bennetts et al. (1988) found an average of 1.59 young fledged per successful nest in WCA3A from 1986 to 1987, with 44% and 7% of successful nests fledging 2 and 3 young, respectively. We found an average of 1.38 young fledged per successful nest, with only 31% and 3% of successful nests fledging 2 and 3 young, respectively (note that this estimate only includes nests that met our selection criteria, which represents a subset of all nests observed during this time period). The only nest that we observed fledging 3 young was near the greatest measured snail density (1.78 snails/m²). The average snail densities for sites paired with nests fledging 2 and 1 young were 1.48 (SE = 0.15, n = 19) and 0.72 (SE = 0.15, n = 9) snails/m², respectively. Although compelling, cautious interpretation is warranted because our nesting data were insufficient to estimate initial clutch size or hatching success for many nests. Snail kites typically lay a 3-egg clutch (sometimes laying 2, and rarely 1, 4, or 5 eggs; Sykes et al. 1995); however, we could not differentiate between hatch failure and brood reduction. With snail kite egg viability estimated to be around 80% (Bennetts et al. 1988, Snyder et al. 1989), we suspect that hatch failure may be responsible for much of the unexplained variation that we observed in the number of young fledged per successful nest (Fig. 2). Future studies should consider clutch size, hatching success, and other potential sources of brood reduction (e.g., partial predation).

We analyzed nest survival and brood size at fledging (i.e., the constituents of nest productivity) separately because these 2 processes are likely influenced differentially by different mechanisms. For example, snail kite nest survival is strongly influenced by depredation, which typically results in complete nest failure (Bennetts et al. 1988). Food deprivation, on the other hand, may more commonly lead to brood reduction than to complete nest abandonment (Bennetts et al. 1988). Although kites may forgo nesting or provision fewer young during times of food stress (Beissinger and Snyder 1987, Sykes 1987b), low prey availability may only lead to complete nest failure under extreme conditions. Accordingly, snail density did not perform well as a predictor of nest survival in our analysis (but we did expect to detect at least a slight effect). Although the cause of nest failure for most nests could not be determined unambiguously—a common issue with snail kite nesting studies (Bennetts et al. 1988, Snyder et al. 1989) we did not confirm any cases of nest abandonment. In line with previous studies (e.g., Beissinger and Snyder 2002, Cattau et al. 2008), the minimum annual water level performed well in predicting nest survival. As is the case for many wetland birds (Pimman et al. 1993, Fletcher and Koford 2004, Hoover 2006), low water levels can expose nests to terrestrial predators leading to depredation and can weaken supporting vegetation leading to collapse. Previous studies provide strong evidence that these are the 2 most common causes of nest failure for the snail kite (e.g., Sykes 1987b, Bennetts et al. 1988, Snyder et al. 1989).

Our results show a direct numerical response in relative nest abundance at a local level and suggest the possibility of a delayed (absolute) numerical response at the population level (that may arise if low snail densities are limiting fledging...
production), both of which are consistent with our predictions and supportive of previous studies that hypothesize that snail density is a determinant of kite demography (e.g., Bennetts et al. 1988; Darby et al. 2006, 2012). Nonetheless, 2 issues need further work to generalize and validate the results presented here. First, better integration of field sampling and estimates of snail density and reproductive biology of kites is needed. Bennetts et al. (1988) observed that, later in the nesting season, some kites traveled greater distances from the nest to forage, which suggests the occurrence of localized resource depletion due to foraging pressure and/or seasonal declines in prey availability due to post-reproductive die-offs of adult apple snails (Darby et al. 2008). Although the sampling effort is distributed among snail sites throughout the season to reduce potential bias from temporal variation (Darby et al. 2005), the mid-point sampling dates can vary among sites by up to a month or more in some years, and in 2010, sampling started later in the season (Table 1). Even though we attempted to account for potential spatial and temporal issues in the pre-existing datasets, the snail density estimates with which some nests were paired still might not have been wholly representative of the local snail densities encountered by the respective nesting kites. Resolving these uncertainties will require coupling snail sampling with spatially explicit behavioral observations of nesting kites.

Second, coupling snail density effects on major reproductive components to interpret seasonal fecundity, and ultimately population growth, of kites is needed. For example, nest survival is known to be a critical component to seasonal fecundity and population growth in birds (Newton 1998, Woodworth 1999, Fletcher et al. 2006), and has been shown to effectively trump some other reproductive components that may appear important in isolation, such as brood parasitism (Fletcher et al. 2006). Because we found no relationship between snail density and nest survival, and responses on the number of young fledged per successful nest typically only differed between fledging 1 versus 2 offspring, the extent to which snail density ultimately may influence fecundity in kites remains unclear. Yet we expect that snail density may influence other reproductive components not measured here, such as re-nesting and multi-brooding, both of which can occur with snail kites (Sykes et al. 1995) and are known to be influenced by food limitation in other birds (e.g., Nagy and Holmes 2005). In addition, variation in prey density may have effects on both juvenile and adult survival, which are known to have major impacts on population growth in birds (Saether and Bakke 2000), including kites (Martin et al. 2008). By understanding if, and the extent to which, snail density influences each of these vital rates, and the influence of these vital rates on fecundity and population growth in kites, we will be better positioned to focus management on the most relevant factors for the recovery of this species.

Water Conservation Area 3A is one of the most important wetlands in the snail kite network and is a commonly studied system from which findings are often generalizable to other palustrine wetlands in central and south Florida (RECOVER 2005, USFWS 2010). However, observations made over the last several years indicate that the number of snail kite nests in the Kissimmee Chain of Lakes is increasing, and several studies emphasize the importance of the entire wetland network to the population viability of the snail kite (Bennetts and Kitchens 1997, 2000; Martin et al. 2006, 2007a). In addition, the exotic *P. maculata*, whose morphology and life history differs from that of the native apple snail (Horgan et al. 2014), was recently introduced to Florida (Rawlings et al. 2007) and are found in many wetlands throughout the range of the snail kite (C. E. Cattau, University of Florida, personal observation). Given the importance of reproduction to the recovery of the kite population (Martin et al. 2008) and the potential for snail densities to influence breeding decisions and performance, it will be important to determine how the relationships shown by this study apply to 1) lacustrine wetlands and 2) *P. maculata* densities. Coordinated studies of snail kite reproduction and (both native and exotic) apple snail densities collected in palustrine and lacustrine systems would help further elucidate these relationships.

**MANAGEMENT IMPLICATIONS**

Managers often develop hydrologic regimes that are intended to facilitate species and community conservation (USFWS 1999, 2010, RECOVER 2005); however, Everglades restoration depends on understanding not only the direct effects of hydrology on plant and animal populations but also the complex interactions among species. The differential effects of snail density on nest presence and abundance, nest survival, and fledgling production identified in our study can be used to help improve modeling tools used in Everglades restoration (e.g., EVERKITE; see Mooij et al. 2002) that currently assume all components of snail kite breeding biology are similarly affected by prey availability (via hydrologically derived proxies for habitat suitability or quality). The hydrologic management of WCA3A currently takes into account, among other things, the proximate effects of hydrology on plant communities, apple snail survival and reproduction, and snail kite nest success (USFWS 2010). In conjunction with these established relationships, the results from our study can help managers predict the potential direct and delayed numerical responses of kites to variation in snail densities, providing a quantitative metric with which to 1) weigh alternative hydrologic management scenarios and 2) improve mechanistic underpinnings of habitat suitability indices. Our study also highlights the potential utility of combining pre-existing (possibly unrelated) datasets to help fill critical information gaps, which may be particularly important for critically endangered species where time-sensitive management decisions cannot be delayed.

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LITERATURE CITED


