

Florida Field Naturalist

PUBLISHED BY THE FLORIDA ORNITHOLOGICAL SOCIETY

VOL. 34, No. 2

MAY 2006

PAGES 37-68

Florida Field Naturalist 34(2):37-47, 2006.

APPLE SNAIL DENSITIES IN HABITATS USED BY FORAGING SNAIL KITES

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Abstract.—Despite their dietary specialization and endangered status, the use of wetland habitats by Snail Kites (*Rostrhamus sociabilis*) has not been associated with a range of densities of its exclusive prey, the Florida apple snail (*Pomacea paludosa*). We present data that suggest to us that the conservation and management of the network of wetlands that supports kites requires an assessment of snail density as well as relying on Snail Kite behavior and hydrology as has been done in the past. We report snail densities in wet-prairie habitats estimated from field surveys in 1995-2004 in association with presence/absence data on foraging kites. In 2002-2003 we also measured snail densities and associated numbers of foraging kites in a systematic survey in two wetland units of the Everglades. There was a positive association between snail density and the number of foraging kites (Spearman $r = 0.67$, $n = 12$, $P = 0.016$). Our data also suggest that kites, at least at some scales, choose areas in which to forage partly based on snail density. Both the presence/absence data and systematic kite survey data suggest that snail densities < 0.14 snails/m² do not support foraging kites. Here we report a range of snail densities typical of wet-prairie habitats within which kites were observed foraging successfully. We conclude with recommendations that habitat quality assessments for Snail Kites and other snail predators should include density estimates for apple snails, because observations of low (or no) predator use do not necessarily reflect a low density of prey.

Snail Kites (*Rostrhamus sociabilis*) are raptors that hunt for prey in wetland habitats in South and Central America, Cuba, and Florida (Sykes et al. 1995). All three recognized subspecies, *R. s. plumbeus*,

R. s. sociabilis, and *R. s. major*, rely on several species of *Pomacea* snails for food, although alternative prey such as freshwater crabs may be a significant portion of their diet, e.g., as much as 25% for kites foraging in South America (Beissinger 1990). In Florida only one subspecies of Snail Kite (*R. s. plumbeus*) exists as a single closed population (Bennetts and Kitchens 1997) and it appears to rely much less on alternative prey compared to the species' populations farther south (Sykes and Kale 1974, Beissinger 1990, Sykes et al. 1995). Since only one native species of apple snail occurs in Florida (*Pomacea paludosa*), much of what we can learn about Florida Snail Kites and their conservation could be obtained through understanding the distribution and abundance of this one prey species while avoiding subjective interpretations regarding prey choice and availability common to most predators (see Johnson 1980). It seems surprising that no data have been reported that relate snail density to the distribution and abundance of kites in Florida, especially given that *R. s. plumbeus* has been listed as endangered for over 35 years (Sykes et al. 1995).

Lack of data on Florida apple snails in habitats used by kites likely stems from the difficulty (in time and labor) of estimating snail density in wetlands (Darby et al. 1999). As an alternative to direct measures of snail abundance, apparent spatial and temporal variation in snail abundance have been made indirectly through hydrology and observations of kites, especially their response to drying events (Steiglitz and Thompson 1967, Sykes 1979, Beissinger 1988, 1995). This link, however, appears to have had limited value as we have accumulated evidence on snail demographics. First, calls to avoid drying events in support of kites were premised on unsubstantiated evidence that dry downs directly kill apple snails (see Darby et al. 2003). We now know that adult-sized snails survive at a rate of 100% to 75% after 1 month to 3 months in dry marsh conditions (Darby and Percival 2000), which is consistent with dry down tolerance in other *Pomacea* snails (Cowie 2002). Therefore, not all drying events have substantial impacts on snails. Second, although snails in dry marsh become temporarily unavailable to foraging kites (Sykes 1979), the reported departure of kites from dry wetland habitats (Takekawa and Beissinger 1989) may reflect limitations of their foraging behavior, not necessarily a decrease in snail density. Third, the highly nomadic Snail Kite (see Bennetts and Kitchens 1997) has been shown to leave one wetland to explore the potential forage base of another, even though foraging success decreased after the move (Bennetts and Kitchens 2000). This suggests that kite departures and arrivals to and from different wetlands, even in the absence of drying events, tells us little about relative snail abundance. Even if some aspects of kite foraging (e.g., capture rates) could be linked to snail density, natural resource managers should not have to depend on kite use

in any particular time frame as an indicator of habitat quality (i.e., an absence of kites does not mean an absence of snails). Clearly, effective conservation of this endangered raptor requires that we have data on the density and distribution of their nearly exclusive prey.

After eight years of method development and testing hypotheses regarding the effects of hydrology and habitat structure on snail demography, we can now report several snail density estimates from areas in which Snail Kites were observed foraging. As an indication of what constitutes an insufficient forage base, we also have snail density estimates from nearby sites within the same wetland units where we did not see kites. In 2004, we also conducted a small scale quantitative assessment of the relationship between snail density and the number of foraging kites in two wetland units designated as critical habitat by the US Fish and Wildlife Service in 1977 (Federal Register 42: 40685-40688). These data provide, for the first time, a range of snail densities in which foraging Snail Kites can be found, and some indication as to a minimum snail density sufficient to support foraging Snail Kites.

STUDY SITES AND METHODS

Study sites.—We sampled snail density and observed foraging Snail Kites from 1995 to 2004 in 30 sites in five wetlands throughout the range of the Florida Snail Kite population as reported by Bennetts and Kitchens (1997) (Fig. 1). All sampling sites were wet-prairie habitats characterized as shallow marsh dominated by emergent macrophytes such as grasses, sedges, rushes, and other wetland plants with stems and leaves above water level (Loveless 1959). Emergent vegetation of the littoral zone of Lake Kissimmee consisted primarily of *Panicum hemitomon*, *Panicum repens*, and *Pontederia cordata*. The remaining wetlands sampled were shallow marshes dominated by *Eleocharis* spp. and *Panicum hemitomon*. The Blue Cypress Water Management Area (BCWMA) is part of the Upper St. Johns River basin. Water Conservation Area 3A (WCA3A) and WCA1 are impounded units within the Everglades ecosystem. WCA1 resides within the boundaries of the A.R.M. Loxahatchee National Wildlife Refuge (LNWR). We also sampled in LNWR impoundments (IM) C6, C7 and C8 that are managed to attract wetland avifauna for viewing by the general public.

Estimates of snail density.—Apple snail densities were estimated using a 1-m² × 60-cm high throw trap sampled with dip nets as per Darby et al. (1999). Once the throw trap was placed over the vegetation, it was quickly pushed down into the substrate to prevent snails from escaping. All plants were removed from the trap and the uprooted material was searched thoroughly for snails. Traps were then swept 20 times with dip nets. If an apple snail was collected, the sweeps count would start over until 20 clean sweeps were completed. After sweeping with dip nets, the trap was searched by hand for 30 seconds to find any snails that might have fallen into depressions left by uprooting vegetation or that were pushed up against the trap walls. We estimated the capture probability of snails by randomly placing from 0-3 marked snails in each trap prior to disturbance of the vegetation. Whether or not marked snails had been placed in the trap and/or the number of marked snails were unknown to everyone but the person who had placed them in order to minimize observer expectancy bias (Balph and Balph 1983, Darby et al. 1999). The reported snail density estimates were adjusted for capture probability by dividing the mean raw density estimate by the mean capture probability for a

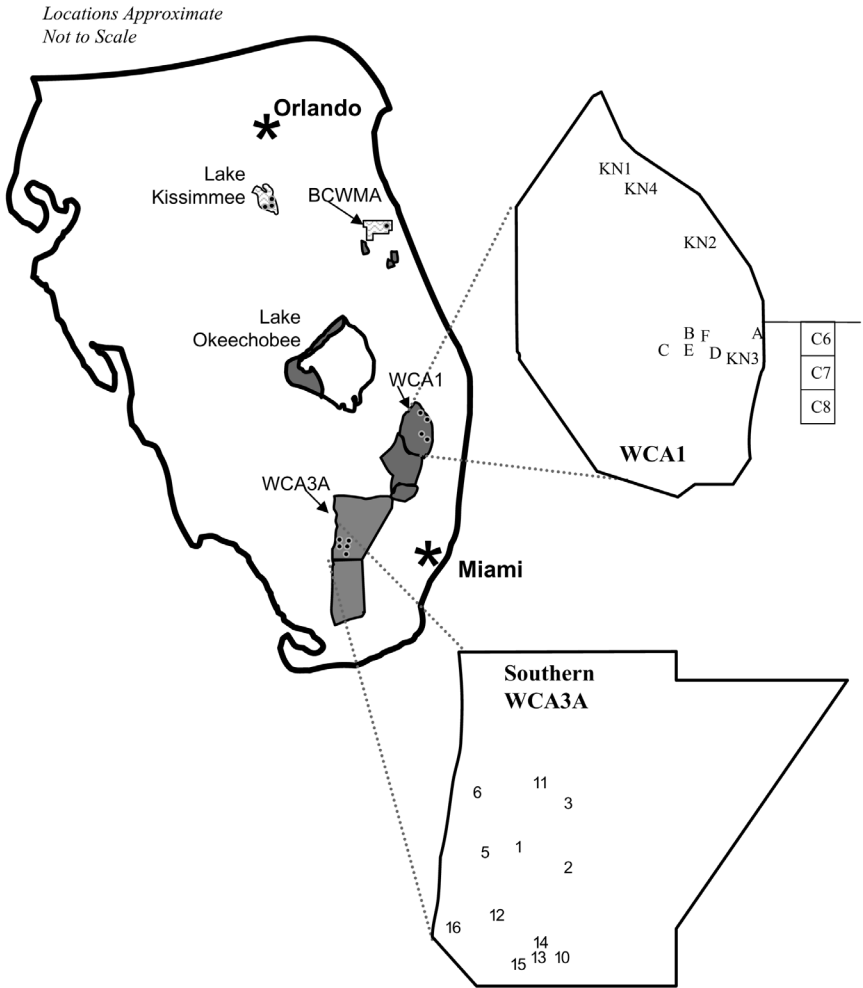


Figure 1. Location of wetland units and sites sampled for snail density estimates reported. Dark gray areas represent critical habitat as designated by USFWS (see text). Sampling sites are represented as black dots (in some cases representing two nearby sites) with more detailed representation of sites in WCA3A (letter designations), WCA1 (letter designations) and LNWR impoundments (C6-C8).

given site. Standard errors for adjusted snail density estimates were calculated based on Loery et al. (1997) as presented in Bennetts et al. (2006).

Counts of foraging Snail Kites.—For 12 out of the 30 sites, we only had a record of the presence or absence of foraging Snail Kites documented by crews sampling for snails, and therefore no indication as to the number of unique individuals (i.e., no systematic count was done). These include three sites in Lake Kissimmee, two sites in

BCWMA, and seven sites in LNWR (including four in WCA1). These data are reported separately and were not included in the test for an association between numbers of foraging kites and snail density. For the remaining 18 sites in WCA3A and WCA1 sampled in 2002-2003, we have a record of the number of individual kites foraging at one time. We estimated the number of Snail Kites within a 1- km² area centered on each of our snail sampling sites during the same period in which we collected snail abundance data. Snail kites are conspicuous and relatively habituated to airboats. Thus, given the open habitat and relatively small size of our sampling units, we were able to conduct what we believe was a reasonable "census" (i.e., complete count) at each site, using systematic transects conducted by airboat.

Using a global positioning system (GPS) for guidance, transects were spaced approximately 200 m apart. Conducting an entire survey required approximately 30 minutes to complete. Under these conditions, kites could be observed with little difficulty. The short time interval and small spatial scale made it unlikely that we double counted. Given these conditions, we do not believe that estimation of detection probabilities (e.g., using distance sampling) was warranted. In most cases, the number counted also corresponded well to the number of nests we documented to be in the area. The exceptions to this were a few sites that had no known nests, but a small (1 or 2) number of foraging kites.

Only the data from the 2002-2003 seasons in WCA3A and WCA1 were included in a quantitative analysis of kite counts and snail density since all the other data were only records of Snail Kite presence or absence. We used Spearman rank correlation to test for a positive association between the number of foraging Snail Kites and snail density.

RESULTS

Snail density estimates (adjusted for capture probability) ranged from 0 to 1.8 snails per m² (Tables 1 and 2). We did not observe foraging kites at any location with snail densities at or below 0.14 snails per m². We observed only one Snail Kite foraging in WCA1 in the two years we sampled (2002-2004), and this site had the highest snail density estimated for WCA1 (Table 1). Conversely, the two sites in WCA3A with the lowest densities of snails are the only two sites sampled in which we did not observe foraging kites in WCA3A. During our systematic 1-km² surveys, densities of foraging kites >5 per km² were only observed where snail densities exceeded 0.25 snails/m².

Our analysis from the systematic surveys in WCA3A indicated a positive association between the number of foraging Snail Kites and apple snail densities (Spearman $r = 0.67$, $n = 12$, $P = 0.016$) (Fig. 2). If WCA1 were included in this analysis, the association is stronger (Spearman $r = 0.85$, $n = 18$, $P < 0.001$). However, 5 of 6 sites sampled in WCA1 had no foraging kites and very few snails; therefore, the stronger association may be strongly influenced by the overall low densities of snails we have observed in WCA1. The presence-absence Snail Kite records from seven other sites in LNWR support the assertion that LNWR (including WCA1) has a relatively low forage base (Table 2). Sites from other wetlands in which we sampled snails and that supported foraging kites (Lake Kissimmee, BCWMA) consistently had densities >0.14 snails/m² (Table 2).

Table 1. The number of foraging Snail Kites per km² and associated apple snail densities per m² in WCA1 (letter designated sites) and WCA3A (number designated sites).

Wetland	Site	Year	Foraging Kites	Snail Density Mean \pm SE
WCA1	A	2002	0	0.00 \pm 0.00
WCA1	F	2003	0	0.01 \pm 0.01
WCA1	D	2003	0	0.01 \pm 0.01
WCA1	E	2003	0	0.03 \pm 0.01
WCA3A	11	2003	0	0.10 \pm 0.01
WCA3A	3	2002	0	0.13 \pm 0.02
WCA1	B	2002	0	0.14 \pm 0.01
WCA3A	6	2002	4	0.18 \pm 0.02
WCA3A	2	2002	2	0.20 \pm 0.04
WCA1	C	2002	2	0.22 \pm 0.01
WCA3A	1	2002	2	0.25 \pm 0.04
WCA3A	14	2003	14	0.32 \pm 0.01
WCA3A	5	2002	4	0.38 \pm 0.06
WCA3A	15	2003	7	0.61 \pm 0.03
WCA3A	13	2003	8	0.89 \pm 0.03
WCA3A	12	2003	1	1.04 \pm 0.03
WCA3A	16	2003	15	1.18 \pm 0.04
WCA3A	10	2002	12	1.77 \pm 0.25

DISCUSSION

The positive association between the number of foraging Snail Kites and snail density was not surprising given the nearly exclusive reliance of this raptor on a single prey. At the extreme, we would not expect kites to commonly attempt to forage in habitats devoid of snails. Although our quantitative assessment of kite foraging was limited to two wetland units (WCA3A and WCA1), our data do support the idea

Table 2. 1995-2004 records of foraging Snail Kite presence/absence in sites for which we have snail density estimates.

Wetland	Site	Year	Foraging Kites	Snail Density Mean \pm SE
LNWR	IMC6	2004	0	0.00 \pm 0.00
LNWR	IMC7	2004	0	0.00 \pm 0.00
WCA1	KN3	2004	0	0.03 \pm 0.01
WCA1	KN4	2004	0	0.08 \pm 0.01
LNWR	IMC8	2004	0	0.09 \pm 0.01
WCA1	KN1	2004	0	0.12 \pm 0.01
WCA1	KN2	2004	0	0.12 \pm 0.01
LKISS	7	2002	≥ 1	0.16 \pm 0.04
BCWMA	1	1996	≥ 1	0.22 \pm 0.03
LKISS	2	2002	≥ 1	0.29 \pm 0.01
BCWMA	2	1996	≥ 1	0.60 \pm 0.08
LKISS	5	1995	≥ 1	0.92 \pm 0.18

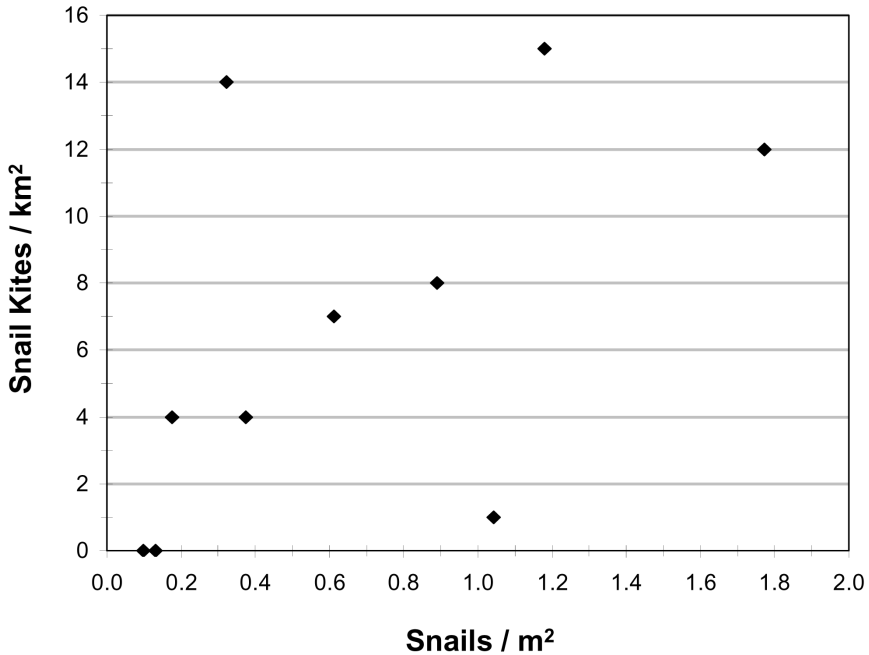


Figure 2. Number of Snail Kites counted within 1 km² in Water Conservation Area 3A in relation to the mean number of apple snails per m² of prairie habitat.

that at a regional scale Snail Kites concentrate in wetland areas with higher snail density (WCA3A). Although food abundance has been linked to habitat use at a broad scale, once in an area there may be habitat attributes that affect availability that dictate forage patch selection at a more refined scale (Orians and Wittenberger 1991). Bennetts et al. (2006) showed that Snail Kites captured fewer snails from habitat patches with relatively dense vegetative structure and high snail densities compared to more open habitat with similar or lower snail densities. Avoidance of more dense structure reflected lower visibility of the water surface associated with higher stem densities and/or structural attributes of different macrophytes (see Bennetts et al. 2006). In this study, we purposefully limited our analyses to habitats with similar structure (moderate stem density wet prairie) to control for characteristics of habitat that might affect vulnerability of snails to predation by kites. Therefore, the numbers of foraging kites were most likely related to snail densities and not to accessibility to the snails.

The snail densities estimated during this study fall within the range reported in previous studies (Darby et al. 1999, 2004). Among all our data reported here and elsewhere, we have rarely encountered

snail densities $>1.5/m^2$. The exceptions include three sites on Lake Kissimmee in 1995 (Darby et al. 2004) and some spring fed rivers north of the kite's current range (Carrao et al. 2006). [Historically Snail Kites had been documented near springs of the Florida panhandle (Sykes 1984).] In addition, in all sampling efforts from 1996-2003, we consistently found one or more sites in WCA3A with >1.0 snail per m^2 (Darby et al. 1997, 1999, this study). Snail Kites have consistently foraged and established nests in WCA3A during the period to which our density data apply (J. Martin, V. Dreitz and W. Kitchens, U.S. Geological Survey, Gainesville, FL, unpublished data). In contrast, it appears overall that WCA1 supports relatively lower snail densities and, based on our own observations, little to no kite use. This is consistent with the overall less frequent use of WCA1 by Snail Kites for either foraging or nesting indicated by USFWS reports (USFWS A.R.M. Loahatchee Annual Narrative Reports 1996-2004) as compared to kite surveys in WCA3A in the same period (J. Martin, V. Dreitz and W. M. Kitchens, unpublished data). Based on Sykes (1984) and Bennetts (unpublished data), the relatively greater concentration of kites nesting and foraging in WCA3A compared to WCA1 has been consistent since the 1970s.

Our data suggest that a density of fewer than approximately 0.14 snails per m^2 may be a minimum threshold to support one or more foraging kites. Although we could have reported many other sites containing snails that did not contain kites, the data from which we estimated this threshold were from sites near those in which we found foraging kites over the observation period. In other words, kites were in the vicinity and low snail density sites were well within the range of routine kite movements. Sykes et al. (1995) estimated that most kites forage within 2 km of their nest and daily flight distances measured by Darby et al. (1996) were frequently between 2 and 5 km on Lake Kissimmee and in WCA3A. Our systematic counts included Site 3 in WCA3A, a low snail-density site with no foraging kites, which was 3.5 and 4.8 km from Sites 1 and 2, respectively, where kites were foraging. Similarly, Site C, the only WCA1 site with foraging kites, was 2.5 km from Site B, a low snail-density site with no foraging kites. Casual observation of kites over several months in WCA3A (no record for WCA1) following our systematic counts were consistent with the data; kites were still in the vicinity, but not observed in site 3. We recognize that our data do not reflect systematic tracking of kite movements coupled to snail densities from locations selected for foraging compared to those passed over; this would require an intensive effort of sampling for snails nearly impossible to achieve with our equipment and personnel. However, both the systematic counts and presence/absence records for several wetland units consistently show kites foraging in sites with snail density >0.14 snails/ m^2 , but not in sites with lower snail densities. We

see these data as a preliminary indication of what constitutes a sufficient forage base. In addition, our data suggest that a sufficient snail supply for several nesting pairs of kites, pertinent given their characterization as loosely colonial nesters (Sykes et al. 1995), would be approximately 0.25 snails per m^2 .

Caution should be exercised with respect to interpreting kite use of an area as any indication of relative snail abundance or habitat quality in general. Although there was a positive association between foraging kites and snail density, we observed several kites foraging in a relatively low snail-density site (WCA3A Site 6), and only one kite foraging in a site with snail density $>1.0/m^2$. The movement patterns of these raptors reflect nomadic tendencies that do not necessarily reflect foraging conditions. At any one time there most likely exist many high snail-density sites that for a variety of reasons simply had not yet been discovered by foraging kites. Once kites establish a nest, which some in our survey had done, movements may be constrained by the need for making frequent visits to feed brooding mates and hatchlings. As such birds may forage in areas with lower snail density than they might otherwise if not constrained by parental duties. Short-term observations of kites foraging in low-density sites may also reflect the period of time required for kites to assess low profitability before moving to a more productive foraging site (Bourne 1985). For these reasons, we in no way want to suggest that observations of Snail Kites are reliable indicators of relative snail abundance between different locations.

The temporal and spatial scales at which Snail Kite movements and demography occur far exceed the scale represented by snail density estimates reported here and elsewhere over the past 10 years. Although a more reliable assessment of habitat quality for kites, estimating snail density may simply be too labor and time intensive to be a routine (i.e., seasonal or even annual) component of a monitoring program tied to wetlands habitat management for a species as mobile as the kite. Monitoring kite use of any particular wetland unit certainly does provide some indication of habitat suitability; i.e., successful foraging and nesting tells us that a sufficient forage base exists. However, it is equally clear that kite use alone does not reflect relative habitat quality among sites or within a site over time, especially if we consider differences in habitat structure. As we continue to test hypotheses regarding hydrology and habitat structure on snails and how these ultimately affect Snail Kite foraging success, we can identify a range of hydrologic conditions and plant community types that reflect relative habitat quality for these species (e.g., Darby and Percival 2000, Karunaratne 2004, Bennetts et al. 2006). Ultimately, however, snail density estimates will be an essential component of conceptual and quantitative models to understand kite demography, movements and habitat use.

We have reported a range of snail densities typical of wet prairie habitats within which kites were observed foraging successfully. In addition, we now have some indication of a density below which kites appear to find an area unprofitable in terms of hunting for snails. We recommend that habitat quality assessments associated with management and restoration efforts in support of Snail Kites and other snail predators include sampling for apple snails, because a observations of low (or no) predator use do not necessarily reflect a low density of prey.

ACKNOWLEDGMENTS

This research was funded through grants from the U.S. Fish and Wildlife Service, U.S. Geological Survey, Florida Fish and Wildlife Conservation Commission, Florida Wildlife Foundation, St. John's River Water Management District and South Florida Water Management District. We appreciate the field assistance of Tanya Alvarez, Amy Busch, Jessica (Cerveny) Karunaratne, Sara LaPorte, Jason Liddle, Jennifer (DuPree) Liddle, Dave Mellow, Donald Napier, Alex Ren, Steven Slack, Tiffany Trent and Patricia Valentine-Darby.

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