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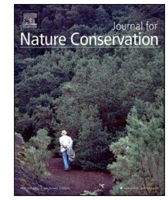

Drinking water availability patterns amplify domestication of Florida Key deer

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ABSTRACT

Natural habitat of the endangered Florida Key deer (*Odocoileus virginianus clavium*) is limited to a portion of the lower Florida Keys, large parts of which have been altered by human development. A major reason the deer have survived there is its unique geology that provides surface access to underground freshwater lenses. Such water features provide the deer access to drinking water, however, historically many of the sites have been destroyed through human activity. We examined seasonal drinking water availability to the deer on multiple islands for 3.5 years from April 2019 through September 2022. We also examined the availability of anthropogenic drinking water sources linked to human habitation. Our results show that natural drinking water sources become extremely limited or non-existent during the region's dry season in large parts of the Key deer range. Anthropogenic freshwater sources in the form of air conditioning drips, garden ponds, water buckets and bird baths are much more numerous, and the deer utilize them regularly. We posit that the existing unavailability of natural drinking water sites is a prime factor driving the domestication of Key deer. This trend of Key deer dependence on humans will only increase as projected increased hurricane activity and sea level rise will negatively affect the freshwater lenses, and hence the number of permanent freshwater sites available to Florida Keys wildlife. The dependence trend could be slowed by management's readopting natural water source enhancement efforts and installation of water guzzlers as was done in the mid-2000 s but has not been continued since.

1. Introduction

The Florida Key deer (*Odocoileus virginianus clavium*) is North America's smallest deer, naturally existing only in the Lower Florida Keys. A subspecies of the whitetail deer, it is believed to have become isolated on the islands as sea level rose some 10,000 years ago at the end of the last glaciation period, subsequently shrank in size due to insular dwarfism (Foster, 1964, Lomolino, 1985), and became genetically unique (Ellsworth et al., 1994). Initially inhabiting most of the Middle and Lower Keys, the deer were hunted and later poached to near extinction (around 1950 only 25–50 were estimated to be alive) (Dickson, 1955). As the result of the formation of the Key Deer Wildlife Refuge in 1954 and increased antipoaching enforcement, the remaining deer population began a slow increase. However, the deer were confronted with major habitat losses during the 1960 s, 70 s and 80 s due to human expansion and urban development. The Florida Key deer was officially put on the federal Endangered Species List in 1967, and remains there today.

For the past century or so, the Key deer's habitat consists of approximately 20 islands between Little Pine Key to the east and Sugarloaf Key to the west, with most of the existing herd inhabiting Big Pine and No Name Keys, with lesser permanent populations on Sugarloaf, Cudjoe, Ramrod, and Torch Keys (see Fig. 1). Semi-regular deer population surveys were begun on Big Pine and No Name Keys in the 1970 s (Silvy, 1975) and continued into recent years. Long-term trend analysis suggests annual population growth of 3.1–3.5 % between 1975 and 2015 (Lopez et al., 2016). Two events with highly negative consequences occurred in the past decade: a screwworm (*Cochliomyia hominivorax*) epidemic in 2016–17 which resulted in 135 known Key deer fatalities and an overall mortality estimate of 15 % (Lopez et al. 2016, Parker et al., 2020), and the direct passage of Hurricane Irma over the Key deer habitat as a Category 4 storm in September 2017, which resulted in a 38—–68 % mortality estimate (Parker et al. 2017). The latest comprehensive deer population survey was conducted in March

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2020, resulting in a population estimate of 748 (95 % CI 625 – 931) deer on the two main islands (Silvy et al. 2022).

While Key deer are occasionally sighted on some of the smaller islands in the habitat range, such visits tend to be transitory. The major reason for this is the seasonal lack of drinking water. The Florida Keys have a subtropical-maritime climate, with a distinct dry season lasting from approximately November through April. As our own data show, areas in the Key deer habitat receive very little or no precipitation for a month or more during the dry season. This results in most rain catchment depressions significantly increasing their water's salinity or drying out completely through evaporation, eliminating them from providing drinkable water for the deer and other wildlife. The Lower Keys' bedrock geology allows the formation of underground freshwater lenses on some of the islands. The lenses on Big Pine Key have been studied in detail (Hanson, 1980, Halley et al., 1997). Lenses on Sugarloaf and Little Torch Keys have also been mapped to some extent (Meadows et al., 2004). The islands contain solution cavities or "solution holes" as referred to by residents, that connect the lenses with the surface (Hanson, 1980), some of which are large enough to provide the deer direct access to fresh water with very low salinity year-round. Islands with such fresh water features thus represent the prime permanent habitat for the Key deer.

An important factor in assessing the effects of drinking water availability on the distribution and survival of the Florida Key deer is the question of their salinity tolerance. Since the 1970 s an unsubstantiated claim has circulated in some literature, that Key deer can survive long-term on water with salinities as high as 15 ppt (i.e. almost half seawater). This belief originated with a non-peer-reviewed report to the US Fish and Wildlife Service (USFWS) in which Klimstra et al. (1974) posited that, based on an observation of a deer drinking from a 12 ppt source and deer tracks around a 14 ppt source, Key deer have evolved long-term tolerance for drinking water with salt concentrations $\leq$ 15 ppt. This claim was accepted by Folk (1991), and Folk's work was, in turn, referenced by Lopez (2001), Lopez et al. (2003) and others. During post-Hurricane Irma in 2017, the USFWS Key Deer Refuge management used the hypothetical 15 ppt salinity value as a guide when to discontinue providing wildlife with supplemental fresh water and to discourage Keys residents from doing so.

To our knowledge, no detailed field study has ever been conducted to determine the Key deer's salinity tolerance. There are, however, published studies of drinking water salt tolerance by deer in Australia. Ru et al. (2005) found that feed intake and body weight of Fallow deer was significantly reduced at salt concentrations greater than 12 ppt. Red deer reduced their feed intake by 11–13 % compared to the control group when drinking water in the 4–8 ppt range, and had a markedly reduced growth rate at 8 ppt and higher. Results of experiments with adult Rusa deer indicate they may be able to tolerate drinking water salinities of 6 ppt for at least 9 days without harmful effects, but are unable to tolerate water with 8.5 ppt or higher (Kii and Dryden, G.M., 2005).

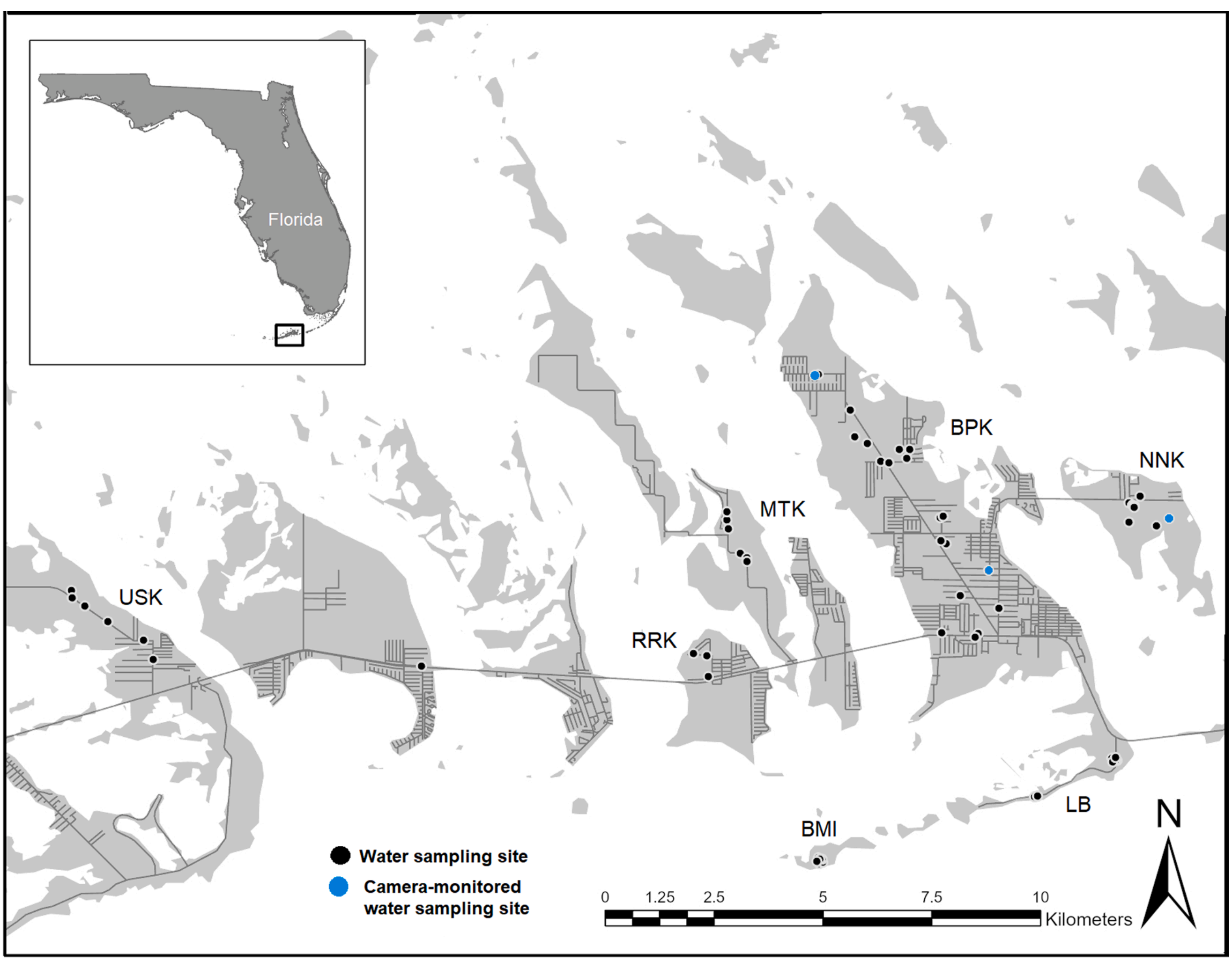

Fig. 1. Key deer natural habitat extent in the Lower Florida Keys showing locations of wildlife drinking water sites used in the study. NNK = No Name Key, BPK = Big Pine Key, LB = Long Beach Peninsula, MTK = Middle Torch Key, RRK = Ramrod Key, USK = Upper Sugarloaf Key, BMI = Big Munson Island. Sites marked in blue were used for the trail camera surveys.

In view of the Australian studies and the lack of validated extended salt tolerance data for Key deer, it thus appears likely that the availability of drinking water sources with salinities in the single digits is of great importance to their survival. As discussed above, the prime year-round natural sources of such water are solution cavities and ponds connected to and dependent upon the underlying freshwater lenses. Historically, the number and quality of such drinking water sources has been greatly compromised by human development. This included fill-ins to provide dry ground for construction, connecting inland fresh water sources to saltwater inputs via "mosquito ditches" as part of mosquito control, and dredging extensive networks of salt water boat canals that caused the underground lenses to shrink (Langevin et al., 2005). Although such environmental disruptions have ceased, sea level rise and more frequent hurricanes are expected to now be the main causes of reductions in the availability of natural drinking water sources for wildlife in the Florida Keys and similar environments worldwide. Sea level rise acts to shrink the spatial extent of the underground freshwater lenses, thus further shrinking freshwater availability to both flora and fauna (Ross et al, 2009, Miller and Harwell, 2022). Hurricanes typically cause saltwater storm surge that inundates inland water holes, rendering many of them unusable for the deer for months, despite the heavy rainfall that usually accompanies the storms (Lopez et al., 2003). Sea level rise additionally acts to enhance the storm surge effects. The effects are already being noticed: significant long-term increases in the salinities of underground freshwater lenses after Hurricane Irma in 2017 have been documented in the Keys (Kiflai et al., 2020).

The present distribution of viable drinking water sources available to the Key deer, and their seasonal variability is unknown. This study aimed to provide some of the needed answers. Specifically, our objectives were to characterize the types and relative distribution and abundance of natural drinking water sources within the Key deer habitat, and to elucidate how annual rainfall variability affects drinking water availability for the deer. To do this we monitored water salinity at selected sites on multiple islands for 3.5 years, along with rainfall data at those locations. Additionally, we examined the contribution and importance of anthropogenic drinking water sources linked to human habitation through public outreach. The results should provide a sound, contemporary basis for future management of the endangered Key deer herd with regard to its drinking water requirements, and can provide guidance on how to assess similar situations worldwide.

2. Methods

2.1. Study area

The Florida Keys are a chain of small islands approximately 200 km long extending southwest from Florida, USA. Their geologic composition is primarily oolithic limestone. The study area was comprised of 5 of the major islands spanning the Key deer habitat which is situated in the "Lower Keys" island chain section. Selected natural fresh water sites were regularly monitored for salinity on No Name, Big Pine, Middle Torch, Ramrod, and Upper Sugarloaf Keys, and the Long Beach peninsula (Fig. 1). All of these Keys have permanent Key deer populations. Several sites were also intermittently sampled on Big Munson Island.

The Florida Keys have a semitropical-maritime climate, with distinct dry and wet seasons. The dry season – December through April – receives just shy of 25 percent of the annual rainfall, while the wet season – June through October – receives approximately 65 percent of the yearly total in showers and thunderstorms. May and November are typically seen as transition months between seasons (National Weather Service, 2024). Average annual precipitation in the Lower Keys is, as per the NWS, 101.6 cm (based on measurements at two airports). However our own 3.5 year-long, more spatially detailed rain log compiled for this study indicated that there are significant precipitation volume differences within the Key deer habitat that may have affected drinking water availability for the deer.

2.2. Water sampling and rain gauge site selection

The most comprehensive survey of inland water resources within the Key deer habitat was conducted by Folk in 1988 – 90. She utilized large-format aerial photography to locate visible water sites, and conducted field transects to locate additional sites not visible from the air (Folk, 1991). In the summer of 2001 an intern working for the USFWS Key Deer Refuge revisited 276 of Folk's original sites and used a GPS receiver to compile their locations into a digital file. This data base was subsequently utilized by more recent researchers, and formed the basis for our own initial study site selection. It is important to note that the data base does not (and was never meant to) represent locations of fresh water sources for wildlife, as most of the sites represent permanent inland salt water depressions, dry out, or contain high salinity water for much of the year. Unfortunately, some researchers and wildlife managers have erroneously assumed the digital file consists entirely of "freshwater holes" and utilized it as such in, for example, species status assessments (USFWS, 2021).

Since our interest was not to conduct a habitat-wide watering hole survey but rather to monitor seasonal and annual variability of drinking water sites that were relatively persistent, we utilized notes by Folk and the intern to chose 89 initial sites on No Name, Big Pine, Middle Torch, Ramrod, and Upper Sugarloaf Keys, Long Beach Peninsula, and Big Munson Island. Within the study's first year, it became clear that some of the initially prescreened sites hold water with single digit salinity concentrations (deemed useful to the deer) only infrequently, and are thus of minimal if any importance to the deer as a drinking water source. These were dropped from the study to ease the workload on participating volunteers. The final sampling site distribution for the 3.5 year monitoring was No Name Key (7), Big Pine Key (16), Middle Torch Key (6), Upper Sugarloaf Key (6), Long Beach Peninsula (6) and Big Munson Island (4) (Fig. 1).

The Florida Keys Mosquito Control District (FKMCD) is a county-funded organization maintaining an aerial and ground mosquito control program (https://www.keysmosquito.org). As part of this program, it maintains rain gauges on populated islands throughout the Keys that are checked daily by their staff. The FKMCD made their rain data available for this project. On islands with multiple gauges available, we chose to use data from gauges closest to the general area of our water sampling sites. For the relatively large Big Pine Key, we used a gauge situated midway on the island.

2.3. Water salinity measurements

Water salinity measurements were done by volunteers belonging to the non-profit Save Our Key Deer, Inc. (SOKD) advocacy group. SOKD provided multiple Control Company Traceable® (Cat. No. 4367) salinity meters to participating volunteers after training. Each volunteer took responsibility for obtaining regular measurements at sampling stations close to their area of residence. The original sampling interval was set at approximately 2 weeks. Although SOKD requested a regular sampling schedule, the ultimate sampling frequency was dictated by the volunteers themselves, with some being more punctual than others. The 2-week schedule was most closely followed by a SOKD volunteer who sampled Middle Torch Key. Gaps on other islands were mostly due to switching of volunteers. Some hard-to-get-to areas like Upper Sugarloaf Key and Big Munson Island were sampled sparingly by the authors.

The sampling procedure involved using a plastic collection cup attached to the end of an extendable boom to collect a water sample from the surface layer. Upon retrieving the cup, the salinity probe was dipped into the water sample and, while agitating, the salinity reading was read on the meter. Both the collection cup and the meter probe were rinsed in distilled water after each sampling use. The meters were recalibrated by SOKD every 6 months.

2.4. Trail camera deployment

The deployment of trail cameras to document deer behavior at particular drinking hole locations stemmed from our gaining understanding during the study's first two years of the water hole types and their salinity cycles. Certain locations showed a gradual increase in salinity during the dry season from single digits to beyond 15 ppt. We thus deemed them an opportunity to photographically document at what salinities the deer no longer utilize a particular water hole. Based on their previous years' salinity profile, two locations on Big Pine Key and one location on No Name Key were chosen. (They are shown in Fig. 1.) The locations represented the lowest salinity drinking water sources within several hundred meters, ostensibly making them the most attractive (or "last resort") regional water source for the deer to visit. Three Browning Dark OPS ProXD (Model BTC-6PXD) cameras were available for the project. They were set to record 90 s videos during day and night upon detection of movement. They were deployed at the end of February in 2021 and 2022 when the locations' salinities reached 6–7 ppt and were increasing. The cameras were retrieved after 3 days (to check/replace batteries) and were redeployed each time when subsequent salinity measurements showed an approximate 2 ppt increase. The monitoring was stopped when salinities exceeded 17–18 ppt – mid to late April in all cases. Since the gradual salinity increase took several months through each annual dry season, only one sampling run was possible for each camera each year. Six time series were thus acquired over the two years.

2.5. Resident surveys

In addition to its website (https://www.saveourkeydeer.org), SOKD maintains an active presence on social media such as Facebook, and publishes a regular Key deer-related column in a local newspaper "News Barometer". In October 2021 SOKD used the press and social media to reach out to residents about a survey addressing deer-human interactions, including the drinking water availability issue in preparation for one of its newspaper articles. Residents were informed the survey would be anonymous in that no person-identifiable data would be retained. Those willing to participate relayed their address to SOKD, and were sent a questionnaire with a prepaid return envelope. Responses from 70 households were received. Some of the data were subsequently deemed significant for this research project, and in 2024 SOKD converted the returned surveys' property locations to approximate latitude/longitude coordinates (± 60 m) using Google Earth Pro. The coordinates were logged in an Excel spreadsheet. Three questions from the newspaper survey were deemed useful for this project: 1) "Do you provide or have a source of fresh water available to wildlife; if so what kind?"; 2) "How many deer visit your property?"; 3) "How frequently do the deer visit?" All other information was discarded.

3. Results

3.1. Water hole characterizations

With a few exceptions such as the "Blue Hole" quarry on Big Pine Key, inland water depressions on the sampled islands are quite shallow (≤ 1 m) even during the rain season. As the multi-year water salinity monitoring data series grew during the project, it became clear that each sampled water hole reveals one of three distinct annual salinity patterns that re-occurred on the different islands. We thus created 3 classification categories to group each sample site into one of them, based on its long-term salinity pattern:

1) "LP" (**L**ens-connected, **P**ermanent) – A hole or depression usually 0.5 to 10 m in diameter that maintains a relatively narrow range of salinity (± 2 – 4 ppt) in the single digits and maintains a relatively stable water level (± 5–10 cm) year-round. We interpret the steady salinity profile as an indicator that the hole has a permanent connection to an underground freshwater lens since the shallow depths and relatively low overall volume precludes it from maintaining steady water levels and low salinities during the multi-month dry season.
2) "LD" (**L**ens-connected, **D**ries out) – Same general characteristics as LP, but dries out occasionally for periods of a week to more than a month. Because the salinity remains low, such a depression provides drinking water for the deer as long as there is some water present. In the majority of cases the dry-out intervals occur during the mid to later part of the dry season. We interpret this salinity pattern as the result of the depression's temporarily losing its freshwater lens connection. Hourly photos from trail cameras at several of the LD-type depressions on Big Pine and No Name Keys showed that the dry condition is not related to tidal cycles.
3) "RD" (**R**ain **D**epression) – A depression or pond up to 50 + m in diameter. Its salinity profile is characterized by large swings related to precipitation and evaporation. Some ponds hold water year-round (although with a much lowered water level) and may become hypersaline during the dry season. Others progressively increase in salinity until they dry out completely. The steady increase in salinity during rain-free intervals markedly differs them from the LD type. We interpret this difference as that the depression is not connected to an underground lens and is solely dependent on rainwater and surrounding runoff for input.

Fig. 2 shows salt profile examples of the three water hole types, and Fig. 3 shows photos of typical LP and RD ponds. The LP and LD types include mostly natural water bodies but also a few man-made ponds dug out on private property, and a shallow quarry (in recent decades named the "Blue Hole"). The RD type includes natural depressions but also man-made features. Most prominent of those are unfilled sections of the "mosquito ditches" mentioned earlier that are no longer connected to the sea. Table 1 lists the make-up of water hole subsets that were used for further analysis.

3.2. Precipitation trends

Fig. 4 shows the monthly rain totals for the study period from 1 April 2019 through September 2022 for the 5 main study locations (Big Munson Island does not have a regularly checked rain gauge). As expected, a clear seasonal trend is evident, with all locations receiving most of their annual precipitation between approximately July and November, and minimal precipitation between December and April. Year 2020 was by far the wettest year during the study period. No hurricanes affected the study area during the monitoring years.

In addition to the annual precipitation cycle, the data show significant regional precipitation differences within the Key deer habitat that have not been noted in published research before. No Name Key, the easternmost island on which rain measurements were available, received 488.4 cm (192.3 in.) of rain during the study period (4/1/2019 – 9/30/2022). The mid-island rain gauge on Big Pine Key, located approximately 5 km northwest of the No Name Key gauge, received 456 cm (179.6 in.). In contrast, the gauge on Long Beach Peninsula located approximately 7 km southwest recorded only 72 % of the No Name Key total. The more westward islands of Middle Torch and Upper Sugarloaf Keys recorded 74 % and 85 % respectively. This hierarchy, with No Name and Big Pine Keys receiving the greatest precipitation volumes and Long Beach receiving the least was repeated annually. In this context it should be noted that Long Beach has no known freshwater lens-connected water sources, and Middle Torch Key has only one known (and likely the only) permanent lens-connected water source. The regional precipitation variability pattern within the Key deer-inhabited islands may be a contributor to the differences in natural drinking water availability between the different islands.

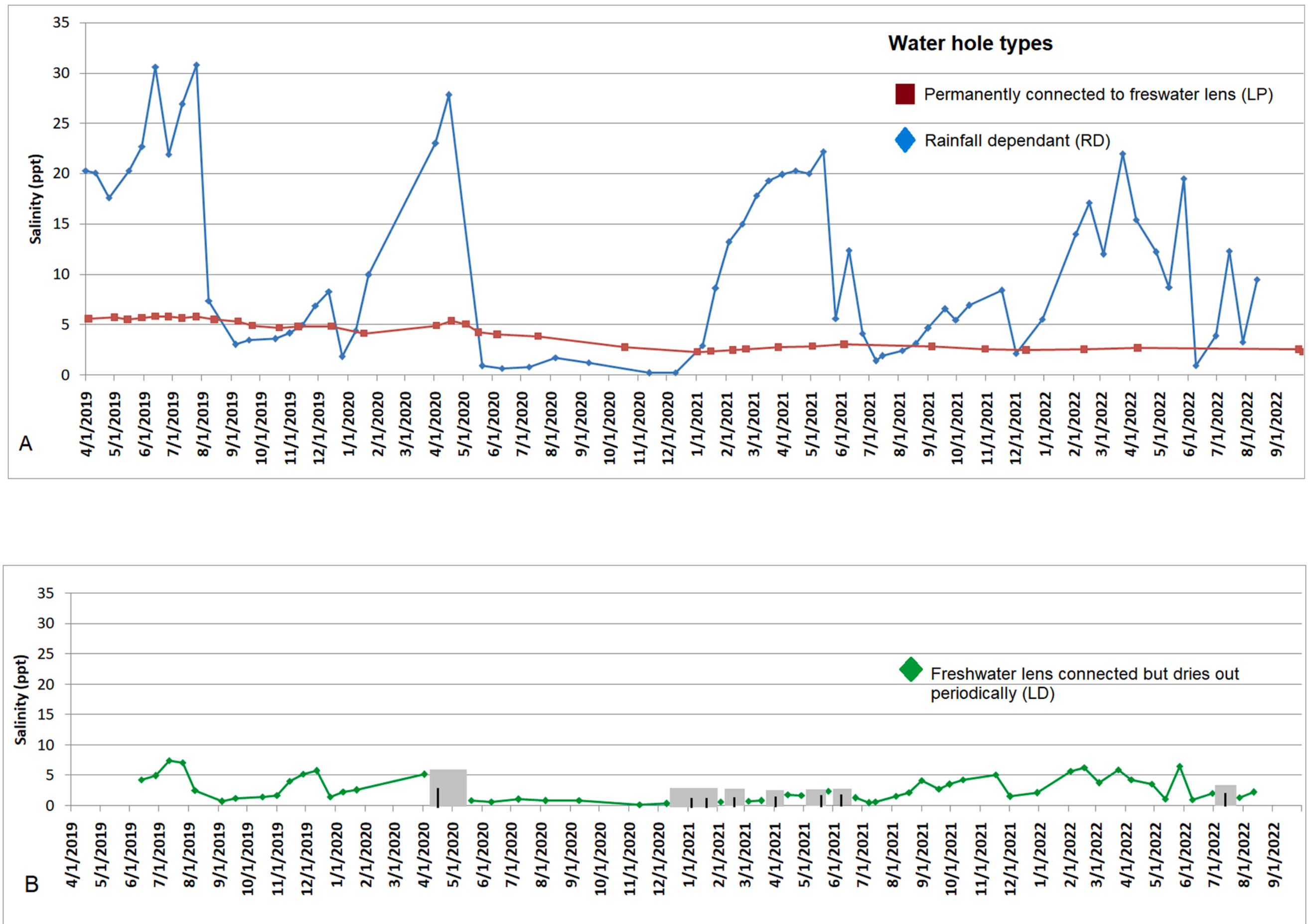

Fig. 2. Examples of wildlife drinking water hole types based on their long-term salinity profiles. (A) "LP" (red) permanently connected to underground freshwater lens. The example shown is from the "Blue Hole" quarry on Big Pine Key; "RD" (blue) rain-dependent depression on Middle Torch Key. (B) "LD" (green) on Middle Torch Key is connected to underground freshwater lens but dries out periodically (shown by grey intervals). The dates of the dry observations are indicated by black lines.

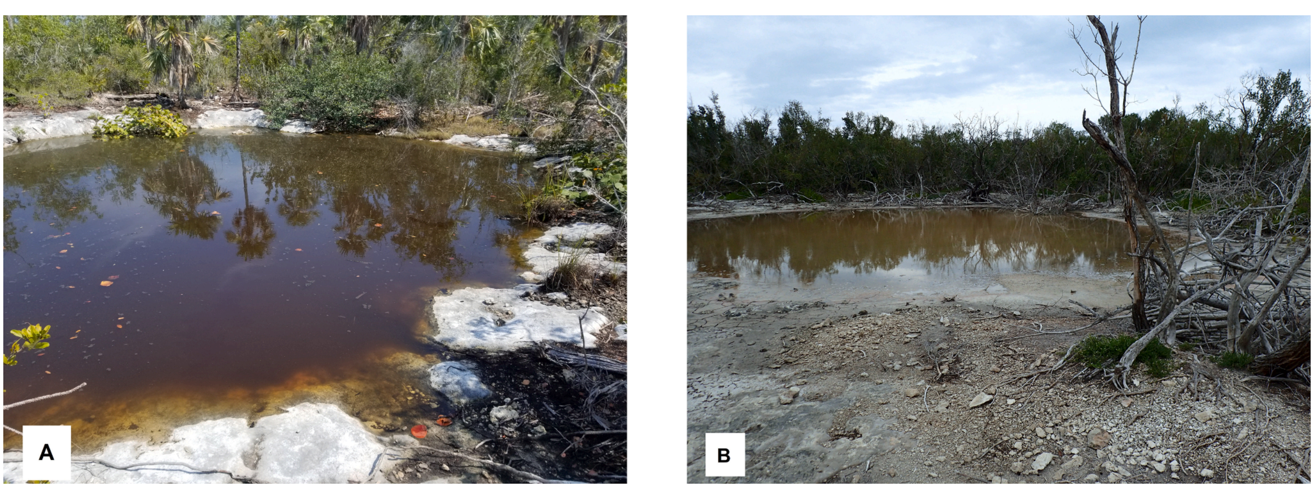

Fig. 3. Examples of drinking water sites: (A) Permanently freshwater lens-connected "LP" type; (B): Rainwater-dependant "RD" type.

3.3. Patterns in natural drinking water availability.

As was discussed in the introductory section, the adage that Key deer have somehow adapted to water intake with salinities up to 15 ppt is unfounded. As was also discussed, the results of Australian experiments with other deer species raised in arid environments concluded that drinking water with salinities greater than 6–8 ppt had deleterious consequences. Our field camera deployments during 2021 and 2022 yielded 6 series at three locations where salinity was increasing through time. In all cases the captured videos showed deer visiting the sites and actively drinking until water measured around 10 ppt. At 11 ppt and above, the few deer that were logged on the videos walked through the

Table 1
Sample sites at each location shown in Fig. 1 classified by water hole type.

Location	LP	LD	RD	Total Sites
No Name	2	2	3	7
Big Pine	5	6	5	16
Middle Torch	1	2	3	6
Sugarloaf	2	3	1	6
Long Beach	0	0	6	6
Big Munson	0	1	3	4

mud, "tasted" the water but did not drink any appreciable quantity before leaving. It must be emphasized that our video observations were very limited (n=6), and thus cannot provide conclusive salinity tolerance guidance. It also cannot be fully assumed that the Australian deer test results apply to Key deer. The actual Key deer salinity tolerance is thus unknown and needs further investigation. The Australian results and our own observations do, however, support the general notion that double digit salinities are likely unfavorable for the deer. We thus classified the salinity field measurements into three categories: "Good"= 0–8.99 ppt, "Marginal"= 9–11 ppt, and "Unavailable"= >11 ppt or dried-out. This is the first time natural drinking water hole sites have been regularly monitored for a multi-year period in the Florida Keys.

Fig. 5 shows the categories as percentages of total sites on each survey day on the four main islands, along with the monthly rain totals for each island. As was previously noted, the sites monitored through the entire study period consist only of sites that held "Good" water for extended periods of time during the project's first year and were thus deemed useful as wildlife drinking water sources. We do not assume that they include all viable drinking water sources on each island, but they are likely representative of the seasonal availability of their type (LP, LD or RD). Especially on No Name, Middle Torch and Upper Sugarloaf Keys, however, we do not expect the actual number of viable water holes to be greatly higher, because the areas not subject to king tide flooding and thus available to hold fresh water sources long-term are relatively small and well surveyed.

The data clearly reflect the annual wet/dry season cycle on all islands, with the greatest percentage of sites providing "Good" drinking water conditions from approximately June through January, and the lowest percentages in approximately February through May. Our initial hypothesis was that a lagged correlation exists between the amount of rainfall and the number of subsequent "Good" watering holes, potentially allowing the construction of a rough precipitation-based prediction model for drinking water availability on each island. Correlation results show, however, mostly weak correlations. The highest are at a one month lag (previous 30 days' total rainfall vs. percentage of "Good" holes sampled), with Middle Torch ($r = 0.63$), Big Pine Key ($r = 0.58$), No Name ($r = 0.38$) and Upper Sugarloaf showing no correlation. Several factors may explain the lack of a stronger relationship: First, the response time to a rain event is immediate for the RD sites, but is unclear for the LP and LD sites, and likely differs with underground lens size and site location relative to the lens. On Middle Torch Key (with the highest correlation), half of our sample sites were of the RD type, while on Upper Sugarloaf Key (with no correlation) only one site out of six was of the RD type. Second, analysis of the "Marginal" water salinity class contribution to the results (which is solely associated with the RD water source type) indicates that in some cases lens-connected LD sample sites dried out, regardless of recent rains, earlier than neighboring rain-dependant sites became "Unavailable". Third, variations in each water hole size, salt load and sampling frequency introduced additional variability into the relationship.

On a longer time scale, our data suggest that the availability of fresh water at the lens-connected sites is influenced by interannual effects. As Fig. 4 shows, the 2020 rain season was exceptionally wet and long on all islands, beginning in May and lasting through November. Through much of that time most or all of the test sites on the 4 islands maintained water with < 9 ppt salinity. Advancing into the dry season of early 2021, significantly fewer sites became "Unavailable" than in the spring months of 2019, 2020, and 2022, particularly of the LD type. This indicates the previous heavy wet season recharged the underground freshwater lenses to an extent that they were able to sustain many watering sites through the ensuing dry season into the following year.

Not shown in Fig. 5 are the monitoring results from the Long Beach Peninsula and Big Munson Island. Both contain multiple relatively large ponds of the RD type. The ponds were subject to storm surge flooding during Hurricane Irma in 2017, and likely during previous hurricanes. As was noted above, the Long Beach Peninsula was found to consistently receive significantly less annual rainfall than the other monitored islands. Big Munson Island is an extension of the peninsula and likely experiences similar conditions. Our monitoring showed that the ponds hold very high salt concentrations and provide a source of single digit salinity water only for a total of a few weeks during each rain season.

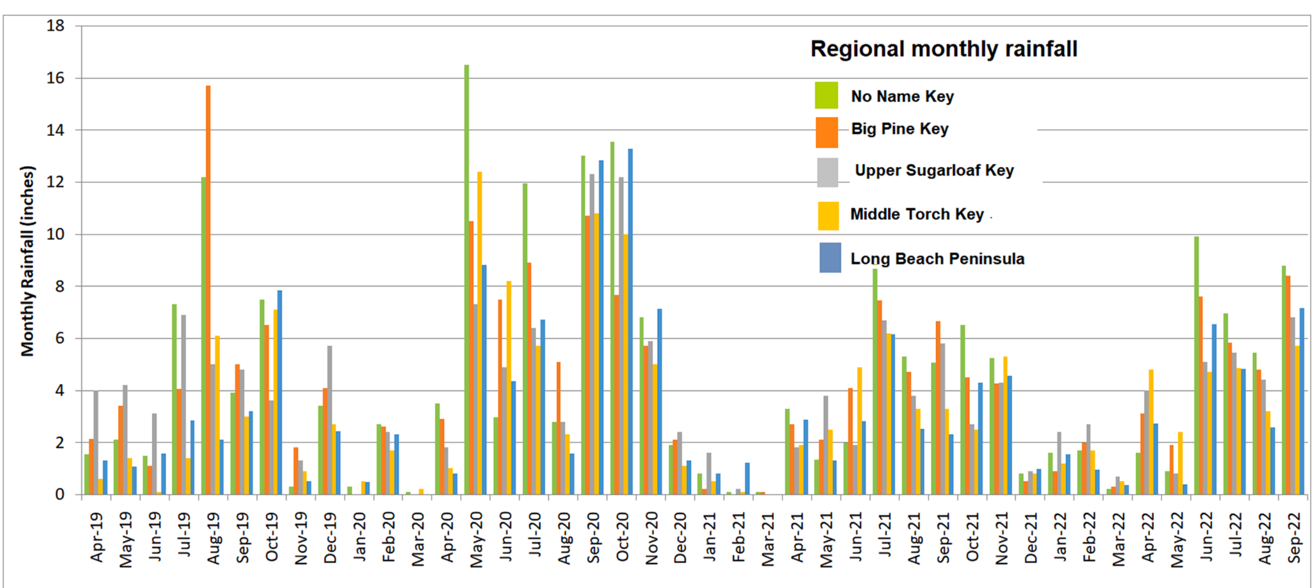

Fig. 4. Monthly rain totals for five regions within the Key deer habitat study area.

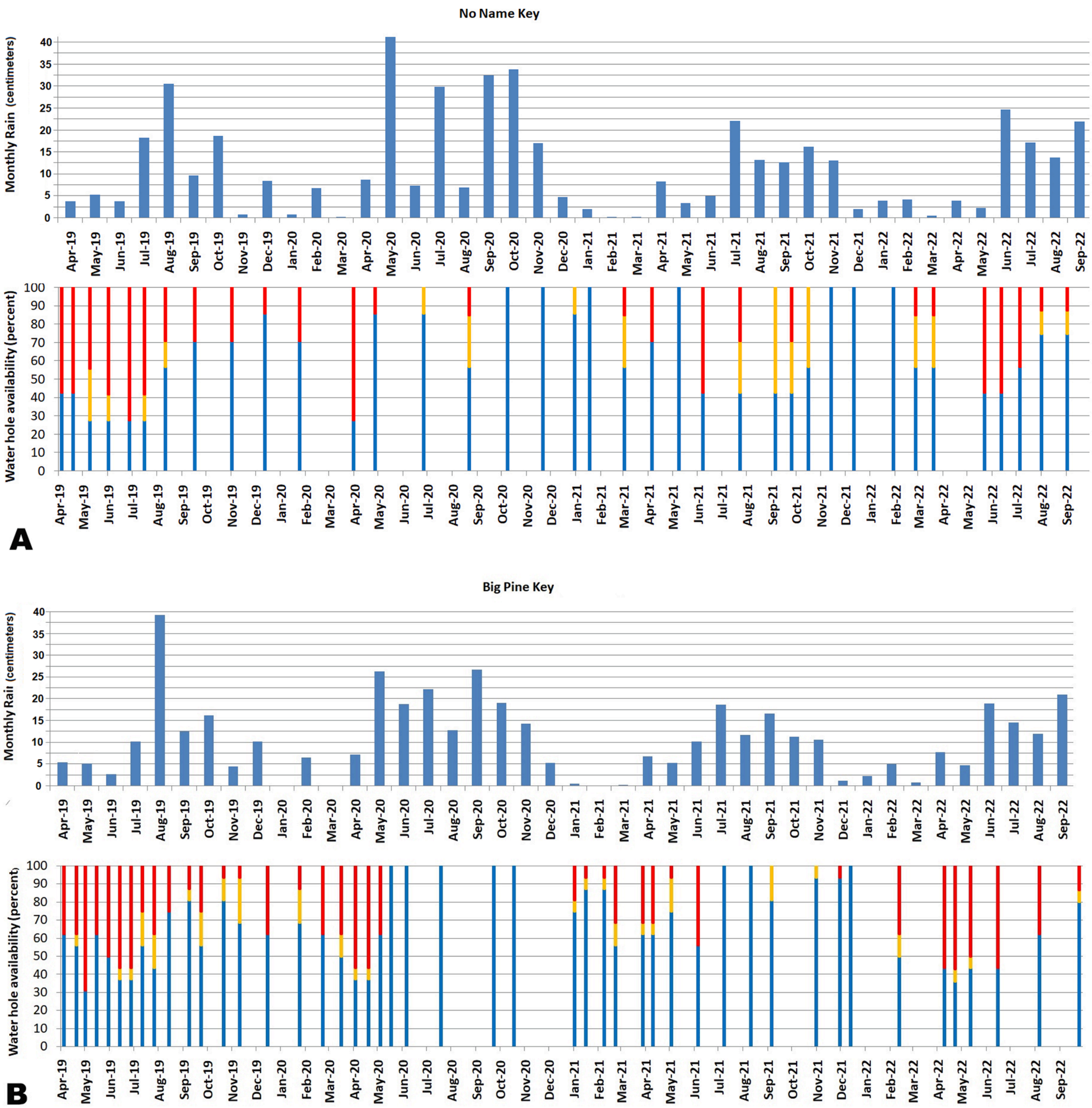

Fig. 5. Monthly rain totals (upper graph) and percentage composition (lower graph) of "Good" (blue), "Marginal" (orange) and "Unavailable" (red) water sites on each sampling day.

They rapidly become hypersaline during intervals between rain events, and thus cannot be considered a reliable water source for the Key deer. One exception is a small (60 cm in diameter) solution hole on Big Munson Island which, based on our long-term salinity monitoring measurements (consistently 3 – 6.5 ppt when water present), is of the LD type, indicating a freshwater lens exists under the island. This water source was also noticed by Folk (1991). Our (rather infrequent) monitoring revealed deer prints, live deer and one direct observation of deer drinking from this water source. The water hole is part of a recognized archeological site #8Mo1981 (Harke, 2021), suggesting this isolated drinking water source was known to ancient human inhabitants of the Florida Keys.

3.4. Resident survey results

70 surveys were returned from: No Name Key (5, 11.6 % of households), Big Pine Key (33, 1.7 %), Long Beach Peninsula (5, 13.2 %), Upper Sugarloaf Key (6), other islands (21). Of the 70 responses, 49 (70 %) indicated they have some sort of fresh water source on their property that Key deer utilize. Sources cited were: Air conditioning drips (32 %), buckets/bowls (30 %), ponds (13 %), bird baths/fountains (11 %), and unspecified (23 %). (Total exceeds 100 % because some households listed multiple sources.) It must be noted that since the returned surveys were the result of social media queries by SOKD, it can be assumed that the responding residents represent a subgroup that follows SOKD's posts and has a direct interest in the Key deer, rather than a random sample of

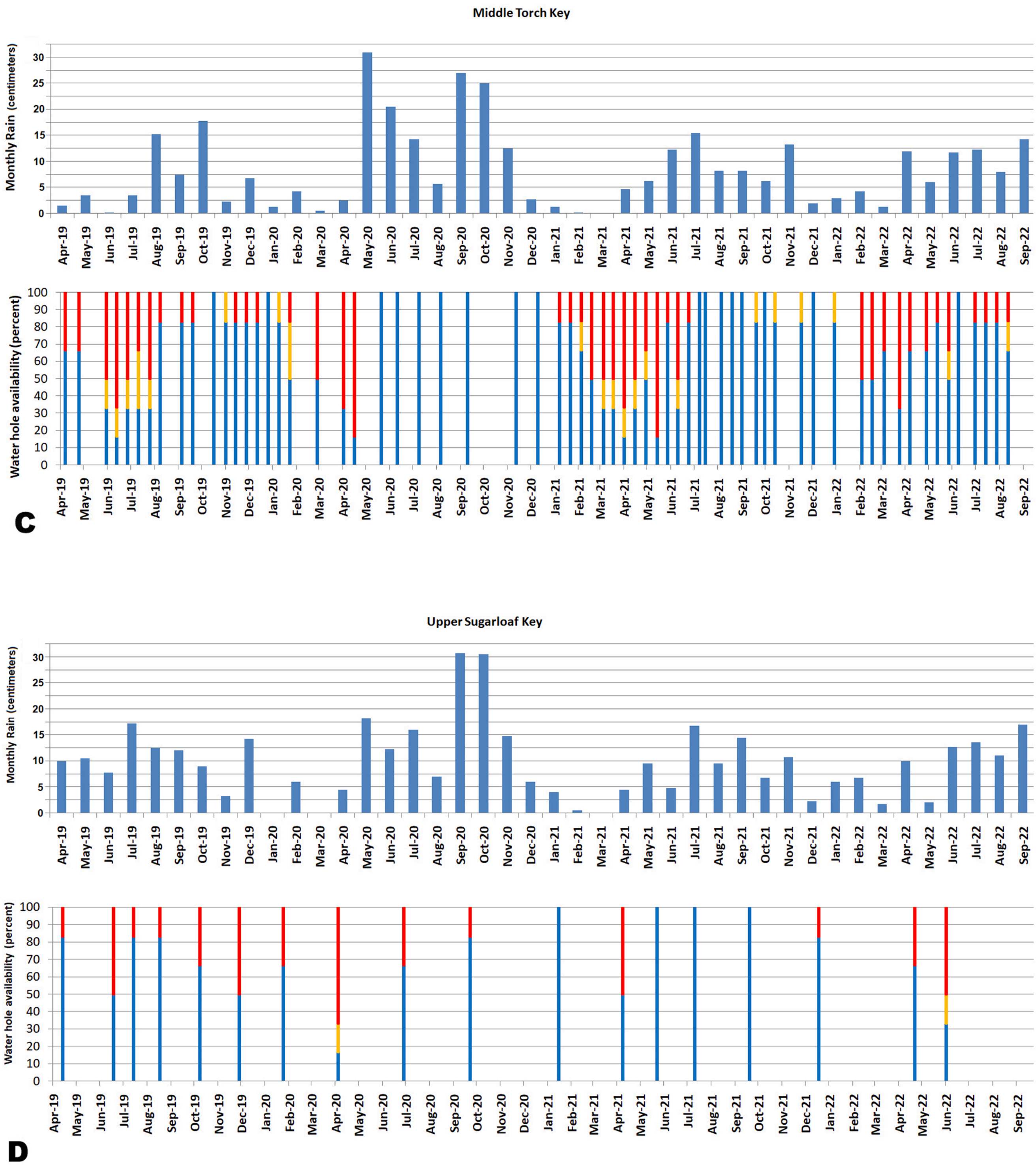

Fig. 5. (*continued*).

the resident population.

Key deer group size has been shown to vary with season (fawning, rut, postrut) (Folk and Klimstra, 1991). The SOKD news article-related survey was not planned as part of this project and happened to be conducted by coincidence during the rut season (October). It did not let the responder specify whether the listed numbers referred to the specific time of the survey or represented more general year-round numbers. However, the listed group sizes were clearly location-specific, as respondents from a same neighborhood tended to list closely matching group sizes and compositions. Of special note were large deer groups containing 4–6 males and 5–7 females, which were noted in several parts of Big Pine Key, and on the Long Beach Peninsula. Since no persistent low salinity water source was found to exist on Long Beach, the large group size there likely reflects the deer's sociological adjustment to having to concentrate near and share the few available anthropogenic drinking water sources. Visit frequency was consistently daily or near-daily on all islands, suggesting strong habituation or downright dependence on the water sources.

3.5. Impact of anthropogenic water sources

To illustrate that anthropogenic drinking water sources (and resulting urbanization) are now a necessity for Key deer survival in many parts of their habitat, we use Peterson et al.'s (2005) concept of centering 42 ha circular plots representing the annual range of female Key deer (as determined by Lopez et al. (2005)) on Big Pine and No Name Keys. While Peterson et al. (2004) centered the range plots on houses known to supply feed and water, we centered the plots on known locations of available natural drinking water sites sampled on 4/9/2022. The data represent a typical condition at the late stage of the dry season, near-identical to conditions encountered in April 2019 and 2020 (see Fig. 5A and B). The blue circles in Fig. 6 show the result. From the total Big Pine Key (including Long Beach) land area of 26.7 km2 (US Census, 2022), the 42 ha ranges centered on known natural water sources on 4/9/2022 covered 2.9 km2 (11 %) of usable range. Multiple large areas of the island that are known to traditionally harbor Key deer were far distant from a viable natural water source during that time of year, and would thus have required many females to relocate, just ahead of fawning season. As was noted earlier, we are not claiming that no other viable natural water sites existed on the islands on that date, but feel confident the data are representative of the overall natural drinking water availability condition at the time. The yellow circles in Fig. 6 show the same simulation with ranges added centered on anthropogenic water locations as per the resident survey. The combined coverage area increases to 11.8 km2 (44 %). This simple simulation underscores the concept that lack of naturally occurring, permanent drinking water sources within the Key deer habitat has created a strong pressure for the animals to domesticize and rely on anthropogenic freshwater sources in large part of their habitat. In some areas, like the northernmost part of Big Pine Key, the Long Beach peninsula, and the "Doctor's Arm" development between Big Pine and No Name Keys, the Key deer

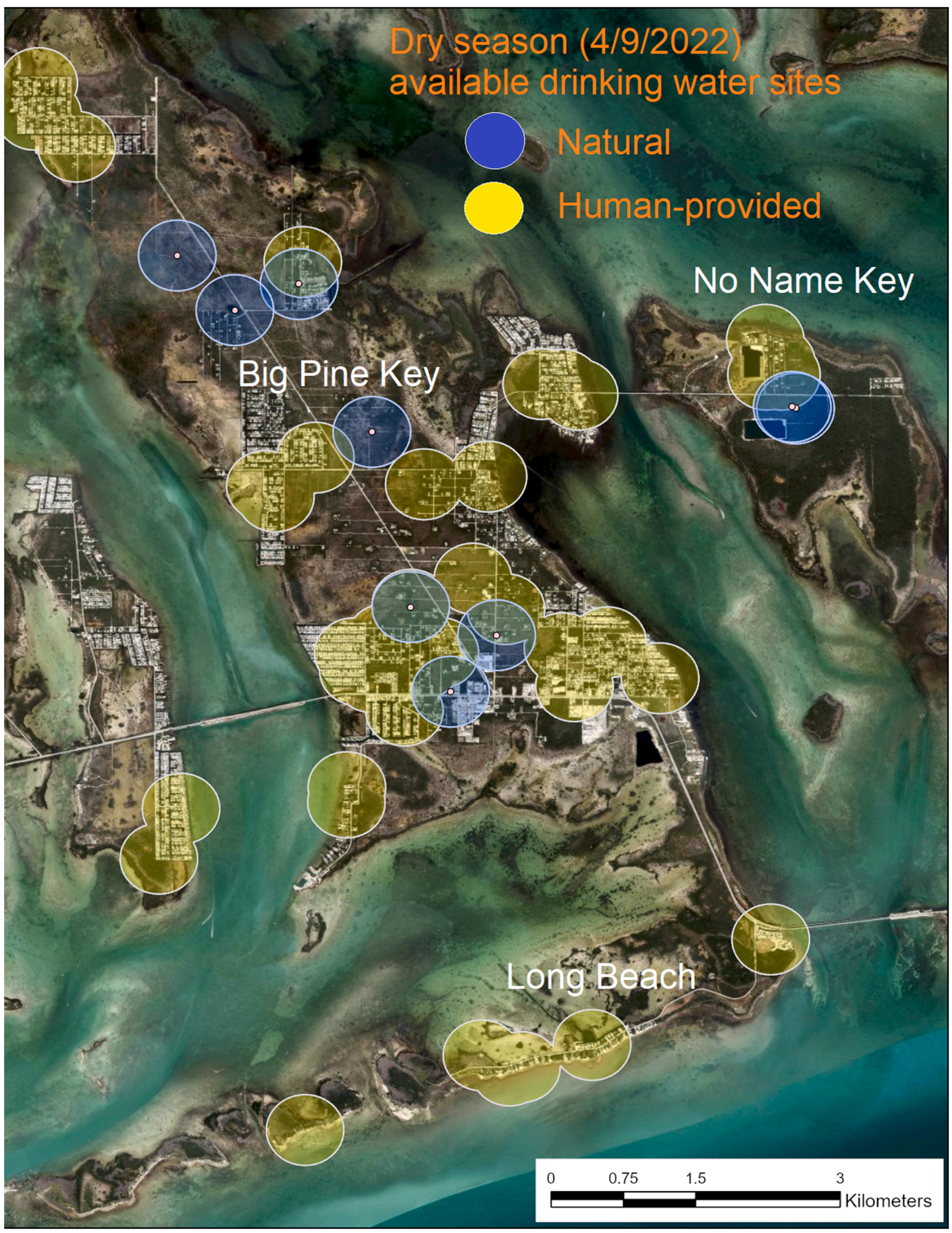

Fig. 6. 42 ha range circles centered on natural drinking water sources known available to the deer on 4/9/2022 (blue), and additional sources known provided by residents (yellow).

dependence on urbanization is now permanent, since those areas have no natural freshwater sources but continue to have significant year-round Key deer populations and recruitment as per the resident surveys.

We are using the term "domestication" here and throughout this paper in the general sense for "wild animals" that regularly enter urbanized areas and take advantage of their resources. It should be noted, however, that Key deer exhibit multiple levels of domestication behavior on an individual and in some cases neighborhood level. Most commonly, Key deer entering urbanized areas utilize resources available there, and tolerate human (and potentially dog) presence from some distance. This contrasts with a considerably smaller but significant number of Key deer that have become "domesticated" to the point of acting like pets: being hand-fed, tolerating being touched, and sometimes even entering residences themselves.

4. Discussion

Our results indicate that natural drinking water within the Key deer habitat is available from two main sources: 1) depressions in the bedrock that hold rainwater; 2) depressions that are connected to an underground freshwater lens. The deer's utilization of the rainwater-dependant depressions is restricted by the region's distinct wet and dry season cycle. During the dry season such water sources dry out or become too saline for long-term deer consumption. The underground lens-connected water depressions provide consistently low salinity water, but some also dry out during periods of low or no rainfall due to, we assume, seasonal shrinkage of the underlying lens. Through time, the number of lens-connected depressions that provide permanent drinking water sites for the deer has been compromised directly by having been filled-in as part of construction and urban development, and indirectly by shrinking the size and extents of the freshwater lenses through dredged saltwater canal networks on some of the islands (Langevin, 2005). Despite the Key deer's existing population being within its upper numbers since surveys began to be conducted, the animals face a historically lowest availability of natural drinking water in their habitat. This has led, we posit, to major domestication of their herd, as they become evermore dependant on anthropogenic water sources for their drinking requirements.

The aspects of Key deer's domestication have been studied in the past 30 years. Folk and Klimstra (1991) recorded group size and social behavior of Key deer in three house subdivisions on Big Pine Key during 1989–1990. Comparing their observations to similar data from 1968 to 1973 (Hardin et al., 1976), they found group sizes significantly increased from the earlier study, and the deer's home range size reduced, particularly in a subdivision where "large amounts of commercial feed were provided". In a more recent study Peterson et al. (2005) also found that deer densities and group sizes increased in the vicinity of houses that provided "feeding and watering" compared to randomly selected non-urban control sites. Both studies mention drinking water as a possible attractant, but the emphasis was on supplemental feeding (which, unlike water, is illegal). The Peterson study does not mention if the control sites contained viable drinking water sources, whose absence could have significantly skewed the results toward the residential sites. Harveson et al. (2007) found Key deer group size to have increased historically in both urban and wild areas, and attributed this unilateral increase to overall increased deer densities.

None of the former studies suggest that sparsity of wild forage could be a major factor driving the deer into urbanized areas. Additionally, in a study of Key deer behavior in urban areas Lopez et al. (2003) concluded that human-provided feeding is more of an opportunistic behavior rather than the primary reason in the deer's using urban areas. Hence, even with the increased deer densities, food is not likely the limiting factor. Instead, our results strongly suggest that very limited natural drinking water resources, not supplemental food, is a major force driving the Key deer into urbanized areas, not by choice but by necessity. The dependence on a regional water source would also contribute to increasing group size, since the animals in its vicinity have to tolerate each other or be driven out and potentially die. We do not dispute that urban areas attract Key deer with resources other than drinking water (e.g. nutritious non-native plants, garbage, and supplemental feeding). In light of the former studies and our own results at this point in time, however, drinking water availability appears to be a major if not prime resource sought out by the deer regularly visiting residents' properties.

Two main factors can be expected to accelerate the urbanization dependence pressure on the Key deer in the future: increased frequency and intensity of hurricanes, and sea level rise. Current models are in general agreement about future increases in hurricane events (NOAA, 2017). The loss of natural drinking water sources, in some cases for months, has been documented after Hurricane Georges in 1998 (Lopez et al., 2003). Using electrical resistivity tomography Kiflai et al. (2020) tracked the recovery of Big Pine Key's freshwater lenses after Hurricane Irma in 2017. They found 40 % recovery after 8 months and 60 % recovery after 15 months, indicating prolonged post-storm losses of natural drinking water sources for wildlife. Worldwide, the shrinkage and ultimate destruction of freshwater lenses due to sea level rise is already of great concern because many human populations residing on atolls around the world rely on the lenses for their own drinking water supply (Werner et al., 2017). In the Florida Keys, the existing and future predicted impact of rising sea levels on the freshwater lenses are changes in vegetation strata and loss of natural drinking water sources (Ross et al. 2009, Miller and Harwell, 2022), both of which will negatively impact the Key deer well before the land itself will become submerged. Climate change-related detrimental effects on freshwater resources are thus the prime factors shrinking the Key deer's future natural habitat.

As part of management of the Key deer herd, there has historically been considerable emphasis on keeping the herd "wild" by discouraging humans from providing any resources to the deer. Findings from this project indicate, however, that without anthropogenic drinking water sources, the deer's usable habitat extents would be severely limited. The limitations may be seasonal in some areas but are already permanent in others. Such limitations can only be expected to increase due to climate change. The importance of maintaining natural drinking water sites to limit the deer's domestication was recognized in the mid-2000 s, when National Key Deer Refuge management financed and oversaw projects that enhanced several natural freshwater lens-connected ponds on Big Pine Key by dredging out accumulated mud sediment and other debris, installing culverts to allow water flow where interrupted by roadways, and installing several water guzzlers in freshwater source-poor areas like Long Beach (USFWS, 2004, unpublished data). Although successful at the time, such activities were abandoned in the next 20 years (with the exception of one freshwater marsh project completed on Big Pine Key in early 2024). It is our opinion that if minimizing or slowing of Key deer domestication is a continuing management goal, along with maintaining sufficient usable habitat for the existing herd, natural freshwater site maintenance efforts should be again considered and implemented. Additionally, our findings that precipitation-based drinking water hole availability cannot be readily forecast points to the need for continued regular monitoring of drinking water sites within the Key deer range. Such data will be important for assessing the rate of future freshwater resource losses due to sea level rise and storm events, and formulating Key deer management strategies to counter such effects.

CRediT authorship contribution statement

Jan Svejkovsky: Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Valerie J. Preziosi:** Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **James M. White:** Visualization, Software, Formal analysis. **Corinne DeGazon:** Investigation, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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