Partial migration in a subtropical wading bird in the southeastern United States

Simona Picardi [ID],[1],† Peter C. Frederick [ID],[2] Rena R. Borkhataria,[3] and Mathieu Basille [ID][1]

[1]Department of Wildlife Ecology and Conservation, Fort Lauderdale Research and Education Center, University of Florida, Davie, Florida, USA
[2]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida, USA
[3]Department of Wildlife Ecology and Conservation, Everglades Research and Education Center, Belle Glade, Florida, USA

Abstract.   The function of migration is to allow exploitation of resources whose availability is heterogeneous in space and time. Much effort has been historically directed to studying migration as a response to seasonal, predictable fluctuations in resource availability in temperate species. A deeper understanding of how different migration patterns emerge in response to different patterns of resource variation requires describing migration patterns of species inhabiting less predictable environments, especially in tropical and subtropical areas. We provide the first individual-based, quantitative description of migratory patterns in a subtropical wading bird in the southeastern United States, the wood stork (*Mycteria americana*). Using GPS tracking data for 64 individuals tracked between 2004 and 2017, we classified migratory behavior at the individual-year level using information theory-based model selection on nonlinear models of net squared displacement. We found that the wood stork population is partially migratory, with 59% of individuals seasonally commuting between winter ranges in Florida and summer ranges elsewhere in the population range (migrants), and 28% remaining in a single area in Florida year-round (residents). Additionally, 13% of storks act as facultative migrants, migrating in some years but not in others. Comparing the distribution of residents and migrants suggests that different migratory strategies might be associated with the use of different or differently distributed resources, possibly including food supplementation from human activities. The existence of facultative migrants shows the potential for plastic change in migratory patterns. Partial migration in wood storks may be an adaptation to high heterogeneity and unpredictability of food resources. We suggest that future research should focus on wading birds as model species for the study of partial migration as an adaptation to heterogeneous and unpredictable environments.

Key words: GPS tracking; movement ecology; *Mycteria americana*; net squared displacement; partial migration; wading birds; wood stork.

† **E-mail:** simona.picardi@ufl.edu

Introduction

Migration is a widespread phenomenon across taxa, including birds, and it has the function of allowing individuals to track resources whose distribution is heterogeneous in space and time (Dingle and Drake 2007). Different forms of migration arise in response to different patterns of resource variation (Dingle 1996, Van Moorter et al. 2013). In temperate areas, where seasonality is generally repeatable, migrations take the familiar form of back-and-forth movements between ranges that are resource-rich at different times of the year (Cox 1985). However, even seemingly nomadic or irregular movements can be considered migrations if their function is to

allow the exploitation of resources that do not follow seasonal fluctuations (Dingle 1996, Roshier et al. 2008, Van Moorter et al. 2013). For example, ephemeral resource outbreaks with no periodicity often lead to erratic migration (Kingsford et al. 2010, Pedler et al. 2014). Some bird populations exhibit facultative migration when a key environmental factor that drives the availability of resources exceeds a critical threshold (Streich et al. 2006). Partial migration, when a population includes both migratory and resident individuals, often emerges when variability in the distribution of resources is paired with ecological trade-offs—such as density dependence, the energetic cost of migration, or predator avoidance (Chapman et al. 2011). Partial and facultative migration can also be combined, when a population includes both individuals that consistently migrate and individuals that only migrate in some years (Berthold 2001, Newton 2012). Individual variability in migratory behavior is associated with demographic consequences which allow different forms of partial migration to be maintained over evolutionary time scales in spatially structured and seasonally variable environments (Reid et al. 2018). Altogether, migration is a complex phenomenon encompassing a wide spectrum of behaviors which manifest as adaptations to different patterns of resource heterogeneity in space and time (Dingle and Drake 2007).

Generally, less conventional forms of migration are thought to be associated with unpredictable environments, of which wetlands are a prime example (Fletcher and Koford 2004, Niemuth et al. 2006, Sergio et al. 2011). Variation in resource distribution can happen quickly and over broad scales in wetland ecosystems (Kushlan 1986, Weller 1999). Besides within-year variability, many wetland systems are characterized by unpredictability of local conditions between years (Niemuth and Solberg 2003, Sergio et al. 2011). Accordingly, wetland-dwelling birds evolved high mobility as an adaptation to resources that pulsate unpredictably across the landscape (Haig et al. 1998, Bennetts and Kitchens 2000, Poiani 2006). Many wading bird species (where by "wading birds" we collectively refer to Pelecaniformes, Ciconiiformes, Gruiformes, and Phoenicopteriformes; Hegemann et al. 2019) undertake large-scale movements to exploit temporary resource breakouts across the landscape (Kushlan 1981), and such movements can take many different forms and often present intraspecific differences as well (Frederick and Ogden 1997, Melvin et al. 1999, Beerens 2008).

Because they inhabit environments where resource unpredictability is brought to an extreme, wading birds seem to be a natural choice as model species to learn about the adaptive relations between migratory patterns and resource distribution. This is especially true for species inhabiting tropical and subtropical wetlands, where seasonality is fundamentally driven by rainfall rather than by temperature (Junk 1993). Recent literature has advocated for an increased focus on non-temperate species to deepen our understanding of migration as an adaptation to resource fluctuations in different contexts (Sekercioglu 2010). Nonetheless, few studies have explicitly quantified migration patterns of wading bird species (but see Mckilligan et al. 1993, e.g., on cattle egrets, *Bubulcus ibis)* and, to our knowledge, none in non-temperate areas. Studies on how unpredictable resource dynamics drive migratory movements of non-temperate wetland dwellers other than wading birds are also few, but see, for example, Bennetts and Kitchens (2000) and Pedler et al. (2014). In this paper, we provide a quantitative description of migratory patterns of a subtropical wading bird in the southeastern United States, the wood stork (*Mycteria americana*).

Wood storks are distributed in the southeastern United States (hereafter, the Southeast), east of Mississippi and as far north as North Carolina (Coulter et al. 1999). Wood storks can travel remarkably long distances over short time frames and with low energy expenditure by soaring (Kahl 1964, Ogden et al. 1978). This is an adaptation to high heterogeneity and unpredictability of food resources, which are an important driver of wood stork population responses (Frederick and Ogden 2001, Gawlik 2002, Herring 2008). Wood storks are tactile foragers that feed almost exclusively on fish (Kahl 1964, Ogden et al. 1976, Kushlan 1986). For them to forage efficiently, prey need to be highly concentrated (Kahl 1964, Kushlan 1986, Gawlik 2002). As a result of local differences in hydrological dynamics, high fish concentrations occur at different times and in different locations within

wetland systems in the wood stork range, and they are generally ephemeral (Loftus and Eklund 1994, Frederick et al. 2009, Botson et al. 2016). For example, in the Florida Everglades, where historically most wood stork nesting activities occurred in the United States (Frederick and Ogden 1997), high water levels promote the growth of fish populations during the rainy season (DeAngelis et al. 2010, Botson et al. 2016). Then, as the water recedes in the dry season, retention of pockets of water in shallow depressions across the landscape concentrates fish, making them available for birds (Kahl 1964, Kushlan 1986, Frederick et al. 2009). The result is a spatiotemporally heterogeneous mosaic of foraging habitat, where food availability changes rapidly through time and space due to the interaction of hydrology and topography (Chick et al. 2004, Ruetz et al. 2005, DeAngelis et al. 2005). Other wetland systems in the Southeast may present different phenologies and mechanisms of food concentration, but their hydrological dynamics are also largely influenced by rainfall patterns, affecting the distribution of resources (Snodgrass et al. 1996, Baber et al. 2002).

Wood stork movements reflect patterns of resource availability at fine spatiotemporal scales. For example, during the breeding season, wood storks move long distances from breeding colonies to foraging grounds to accommodate shifting resource availability patterns (Kahl 1964, Ogden 1985, Bryan and Coulter 1987). At a broad spatiotemporal scale, the annual range of wood storks includes wetlands located in different states that are subject to different, sometimes asynchronous, and usually unpredictable rainfall patterns (Frederick et al. 2009). For example, southern Florida is a winter dry, summer wet monsoonal system, while much of the rest of the southeast gets most of its rainfall in winter and dries during summer months. Because their range includes wetland systems subject to different climatic regimes, local conditions within seasonal ranges used by wood storks are characterized by high year-to-year unpredictability as well (Gawlik 2002, Frederick et al. 2009). Landscape-scale movements of wood storks might respond to heterogeneity in food resources at this scale similarly to how fine-scale movements reflect heterogeneity in food availability patterns within seasonal ranges.

Landscape-scale movements of wood storks remain poorly understood. Previous literature reported large-scale movements of wood storks between different parts of their U.S. range in different seasons but defined the species as "not a true migrant" (Coulter et al. 1999). Indication that movements between different areas within the range are repeated year after year, thus presenting typical migration features, was provided by a study on juveniles (Hylton 2004). Other tracking studies have described fine-scale movements (Borkhataria et al. 2013) or dispersal (Bryan et al. 2008, Picardi et al. 2018), but not migration. Overall, we lack a formal understanding of the migratory status of the wood stork population.

The objective of this study was to address the outlined knowledge gaps by providing an individual-based, quantitative description of wood stork migratory patterns in the Southeast. By leveraging a large, long-term GPS tracking database, we quantified migratory behavior of a large number of individuals over 14 yr and evaluated behavioral consistency across years at the individual level. We assessed potential relationships between migratory behavior and life-history traits including age and sex. We mapped seasonal distribution patterns of wood storks as a result of migration patterns and quantified individual site fidelity. Our results provide the first individual-based documentation of migration patterns in a subtropical wading bird.

Methods

Study area and species

The wood stork population range in the Southeast encompasses both temperate and subtropical latitudes, with marked differences in climate between the northern and southern portions. In the southernmost part of the range (southern Florida), seasonality of rainfall is the most distinctive climatic feature; annual precipitation is concentrated between the months of May and October, and seasonal fluctuations in temperature are not pronounced (Kahl 1964). At higher latitudes, the climate is more typically temperate, with cool winters, hot summers, and less marked seasonality of precipitation. Within this geographical area, wood storks are found in a diversity of wetland habitats, ranging from freshwater

marshes and swamps (Kahl 1964), to coastal and estuarine creeks (Gaines et al. 1998), to natural and artificial ponds (Coulter and Bryan 1993). Wood stork are the only stork species breeding in North America (Coulter et al. 1999). They are large, long-legged wading birds between 85 and 115 cm tall (Coulter et al. 1999). Sexual dimorphism is not pronounced (Coulter et al. 1999). Neck and head are covered in feathers in subadults and are gradually lost with age; sexual maturity is reached at 3 yr of age (Coulter et al. 1999). Historically, wood storks used to mostly breed in the Everglades, but since the mid-1970s they naturally expanded their breeding range north into central and north Florida, Georgia, and South Carolina (Coulter et al. 1999, Brooks and Dean 2008). The timing of breeding varies with latitude, with the earliest attempts starting in December–January in southern Florida and later in the spring at higher latitudes (Coulter et al. 1999). Wood storks may attempt to breed a second time if their first breeding attempt fails (Coulter et al. 1999).

Wood stork captures and data collection

We used GPS telemetry to track wood stork individual movements throughout the population range (centroid 28.8967° N, 81.3310° E) between 2004 and 2017. Wood storks were captured at 11 sites throughout the population range (Fig. 1; Table 1) either by hand (in the case of juveniles) or using rocket nets. Juveniles were hand-captured at the nest before fledging, whereas adults were captured either in the advanced stages of breeding or while nonbreeding. Whenever reasonable, we extracted <0.5 mL of blood from the brachial vein for sexing. Captured storks were hooded to reduce stress during handling and equipped with solar-powered ARGOS-PTT GPS transmitters (Microwave Telemetry, Columbia, Maryland, USA), which are not limited by battery life. The transmitters were programmed to record a location every hour. Each individual was tracked until death or failure of the GPS transmitter, between 1 and 10 consecutive years.

Operational definitions

We operationally defined migration as a round trip between ranges that were spatially separated and used at different times during the year—thus
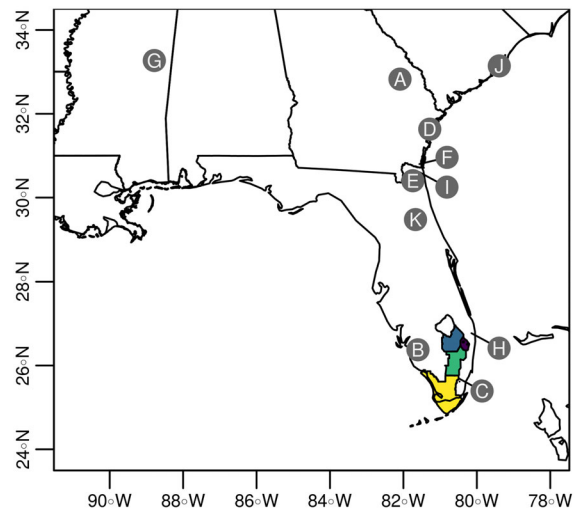

Fig. 1. Map of the study area, located within the breeding range of the southeastern U.S. wood stork population. The letters indicate capture sites: A, Chew Mill Pond; B, Corkscrew Swamp Sanctuary; C, Everglades National Park; D, Harris Neck National Wildlife Refuge; E, Jacksonville Zoo; F, Kings Bay Naval Base; G, Noxubee National Wildlife Refuge; H, Palm Beach Solid Waste Authority; I, St. Mary's; J, Washo Preserve; and K, Welaka Fish Hatchery. The colored polygons depict the boundaries of relevant management units within the Everglades watershed. Blue polygon = Everglades Agricultural Area, purple polygon = Loxahatchee National Wildlife Refuge, green polygon = Water Conservation Areas 2 and 3, and yellow polygon = Everglades National Park.

implying return to the initial range. We defined migratory choice as a binary variable at the year level, namely whether an individual migrated or not in a given year. We then combined migratory choices for an individual in different years to assess multiyear migratory strategies. Thus, we defined migratory strategy as the history of yearly migratory choices of an individual. For example, an individual whose migratory choice is migration every year adopts a pure migrant strategy, or an individual whose migratory choice is different in different years shows a facultative migrant strategy.

Classification of migratory behavior

We used GPS tracking data to investigate individual migratory choices based on net squared displacement (NSD), that is, the squared linear

Table 1. Number of individuals tagged at each capture site.

Capture site	N. captures	N. adults	N. subadults	N. juveniles
Chew Mill	2	–	1	1
Corkscrew Swamp Sanctuary	4	4	–	–
Everglades National Park	9	9	–	–
Harris Neck NWR	10	8	1	1
Jacksonville Zoo	9	9	–	–
Kings Bay Naval Base	1	–	–	1
Noxubee NWR	2	2	–	–
Palm Beach SWA	14	6	4	4
St Mary's	1	1	–	–
Washo Preserve	9	9	–	–
Welaka Fish Hatchery	3	3	–	–

Note: Adults = age > 3 yr; subadults = age between 1 and 3 yr; juveniles = age < 1 yr.

distance between any point along a movement trajectory and an arbitrarily chosen starting point (Kareiva and Shigesada 1983, Calenge et al. 2009). This metric provides an intuitive measure of how far an individual is from a reference point in space at any time (Kareiva and Shigesada 1983, Calenge et al. 2009). To classify wood stork migratory behavior at the yearly scale, we used a modeling approach adapted from a method first introduced by Bunnefeld et al. (2011) and later improved by Spitz et al. (2017). The approach consists of fitting a set of nonlinear models to yearly individual NSD time series and selecting the one that best fits the data using Akaike's information criterion (AIC). For the purpose of our study, following our binary definition of migratory choice, we took two possible models into consideration: a migrant model and a resident model (Fig. 2; see Spitz et al. 2017 for details on model specification). In the migrant model, the yearly time series of NSD follows a double sigmoid curve, indicating initial residency in one range (initial low NSD phase), displacement to a second (high NSD phase), and subsequent return to the initial range (final low NSD phase; Fig. 2). The departure range is whichever range an individual was located in at the arbitrarily chosen reference time that marks the start of the trajectory. The resident model is
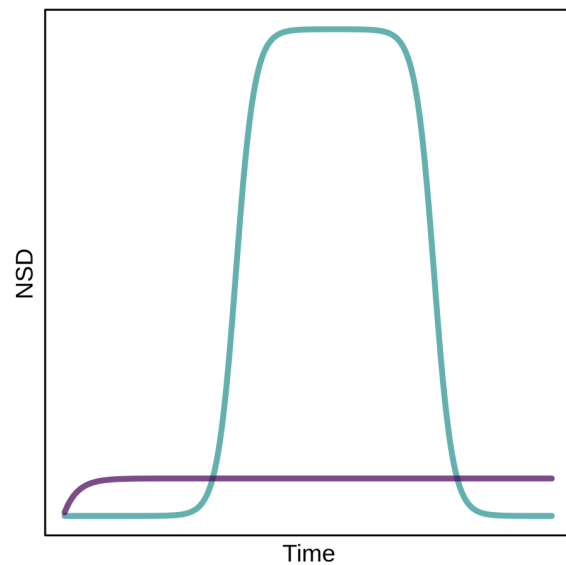

Fig. 2. Conceptual illustration of nonlinear models of net squared displacement used to classify wood stork migratory behavior at the year scale. Resident model in purple, and migrant model in blue. Figure adapted from Bunnefeld et al. (2011) and Spitz et al. (2017).

represented by a horizontal asymptotic curve, indicating permanence in a single range after an initial phase of increase in NSD until settlement around a constant value (Fig. 2). We applied model selection based on AIC differences on these two competing models to classify wood stork annual trajectories and determine migratory choice. The analysis was performed in R (R Core Team 2018) using functions implemented in the migrateR package (Spitz et al. 2017).

Data preparation

After visual exploration of the trajectories, we divided the tracking data into yearly individual trajectories starting on 15 January, to minimize the probability of the starting point falling within a migration (following recommendations in Spitz et al. 2017). We used the R packages adehabitatLT (Calenge 2006) and rpostgisLT (Dukai et al. 2016) for data processing and exploration, respectively. We screened the resulting yearly individual trajectories to assess whether they included sufficient data for model fitting. In order to ensure detection of migrations, we set the minimum data requirements for an

individual-year to at least 15 locations every 4 months (January–April, May–August, September–December). The resulting dataset consisted of 212 individual-years from 66 storks, of which 20 had a single individual-year and 46 had multiple individual-years (range = 2–10, mean = 3.96 ± 1.73 SD).

A-priori model constraints

Following recommendations in Spitz et al. (2017), we enforced a-priori constraints in the model parameters to satisfy the following quantitative characterization of migration: For an individual to be considered a migrant on a given year, it has to spend at least 60 d in a range at least 260 km away from the departure range. The chosen spatial threshold corresponds to double the maximum distance documented for wood stork trips from the colony to foraging grounds (130 km; Kahl 1964, Ogden et al. 1978), which is presumably a distance that storks are able to cover within their everyday movements. Thus, this value seems appropriate to discriminate between the scales of within-ranges vs. between-ranges movements. Temporal fluctuations of resource availability usually occur with seasonal (i.e., multiple months) periodicity at a broad spatial scale in the wood stork population range, which is expected to reflect in the emergence of migration as a seasonal phenomenon. The function of repeatedly tracking resource availability over broad spatial and temporal scales is what distinguishes migration from other types of movements which were not the focus of this study. Thus, the chosen temporal threshold of ~2 months has the purpose of preventing brief but spatially broad excursion movements, which are functionally different from migration, from being misclassified as migrations. We performed a sensitivity analysis on the use of different constraint values (see Appendix S1) and found both the chosen spatial and temporal thresholds to be conservative, since classification results were robust to the use of a broad range of values around the chosen one, within a range of biologically meaningful values.

Stepwise specification of starting parameter values

In addition to specifying constraints for two of the model parameters as described above, we ensured model convergence on all trajectories by progressively specifying different starting values for model parameters, following recommendations in Spitz et al. (2017). These include, for the migrant model, the midpoint of the departing migratory movement, the duration of the migratory movement, the permanence time in the arrival range, and the distance between seasonal ranges (Spitz et al. 2017). For the resident model, parameters include the average NSD of the resident range and the rate of the initial NSD increase (Spitz et al. 2017). Stepwise manual specification of starting parameter values facilitates parameter optimization, helping to overcome commonly encountered convergence issues due to the use of a single set of starting values for all trajectories in a sample (Spitz et al. 2017). All models converged after 21 iterations with a different set of starting parameters (see Appendix S2).

Post hoc model evaluation

Following recommendations in Spitz et al. (2017), we visually inspected results of model fitting as a post hoc evaluation. While the minimum data requirements we chose were adequate in most cases (200 individual-years), for 12 individual-years the placement of the 15+ locations within the first or third quadrimester did not allow for an unequivocal classification (see Appendix S3). The most common issue was failure to classify seemingly migratory individual-years as migrants because of insufficient temporal cover of the data ($n = 8$): While the first range shift was identified, the return movement from the second range and the subsequent residency back in the first range were not captured in the data, resulting in a poor fit of both the migrant and the resident models. Conversely, 4 individual-years that did not seem to exhibit migratory behavior, and were thus classified as residents, had similar limitations in terms of temporal cover of data that did not allow for reliable classification: We cannot exclude that migrations were not observed because they simply happened outside of the tracking period. Therefore, we discarded these 12 individual-years from further analyses. Out of the remaining 200 individual-years, two consecutive years for one migrant individual were erroneously classified as residents because the individual migrated over the start of the new tracking year, resulting in the

migratory movement being split into two. For this individual only, we repeated model fitting and selection after splitting the yearly trajectories on 1 December instead of 15 January. Finally, by visual comparison between model output and mapped trajectories, we identified two individual-years that were classified as migrations as controversial cases. These individuals continuously performed movements at a broader spatial scale than other resident individuals in the sample, but without a clear pattern of seasonal periodicity or spatial separation. Because these movements did not fit the chosen definition of migration, we manually assigned these individual-years to the resident category.

Seasonal distributions, range fidelity, and migratory consistency

The output of the NSD models provided estimates for key migratory parameters, including the time of migration start and end where applicable. Based on these, we subsetted individual tracking datasets into residency and migration phases. For migrant individuals, we computed seasonal home ranges (winter and summer) using locations during residency phases only (i.e., excluding locations during migration trips). For resident individuals, we computed both year-round home ranges, and seasonal home ranges using locations included between the mean spring and fall migration dates observed in the population. All home ranges were computed using the kernel density estimation method, extracting the 90% density isopleth of the utilization distribution, as recommended by Börger et al. (2006), using the R package adehabitatHR (Calenge 2006). We used linear mixed models to assess differences in home range size between migrants and residents in each season while taking individual variation into account. We log-transformed home range size before fitting the model. We fit an interaction between season and migratory behavior and added the individual identity as a random effect using the R package lme4 (Bates et al. 2015). We evaluated model predictions at the fixed effects level to assess differences between migrants and residents in different seasons and used bootstrapping to estimate 95% confidence intervals using functions in the lme4 package (Bates et al. 2015). We evaluated model fit using the pseudo-R^2 method of Nakagawa and Schielzeth (2013). For individuals that were tracked for multiple years ($n = 46$), we investigated seasonal range fidelity using home range overlap. For summer and winter separately, we computed the percent area of overlap between all pairwise combinations of ranges of each individual and averaged them in a synthetic index of individual site fidelity. A value of 1 represents perfect overlap, while 0 represents disjunct ranges. Finally, we quantified migration strategies at the individual level by modeling migratory choices of an individual in different years as a binomial process, where the number of trials is the number of years an individual was tracked and the number of successes is the number of migrations observed for that individual. Using the binomial likelihood in closed form, we obtained maximum-likelihood estimates of individual migration probability along with 95% confidence intervals computed using profile likelihood. Values reported in the *Results* are mean ± SD.

RESULTS

Migratory choices and strategies

The final classification of wood stork migratory choices consisted of 200 individual-years from 64 individuals (15 captured as juveniles of unknown sex, 25 adult females, and 24 adult males), of which 121 were migrations (~60%) and 79 (~40%) residencies. The binomial maximum-likelihood estimates of migration probability, which describe individual migratory strategies, were 1 for 36 individuals (of which 27 tracked for multiple years), 0 for 22 (of which 13 tracked for multiple years), and between 0 and 1 for 6 (all tracked for multiple years; Fig. 3). Confidence intervals around the estimates of migration probability were large due to the limited number of tracking years (range: 1–10). Among the individuals tracked for multiple years, 40 showed consistent migratory choices across years, thus adopting a pure migrant (~59%) or pure resident strategy (~28%), while 6 (~13%) showed variable migratory choices across years. Among pure migrants, 15 were male and 16 female (5 were of unknown sex); among pure residents, 6 were male and 7 female (8 were of unknown sex); among individuals with variable migratory
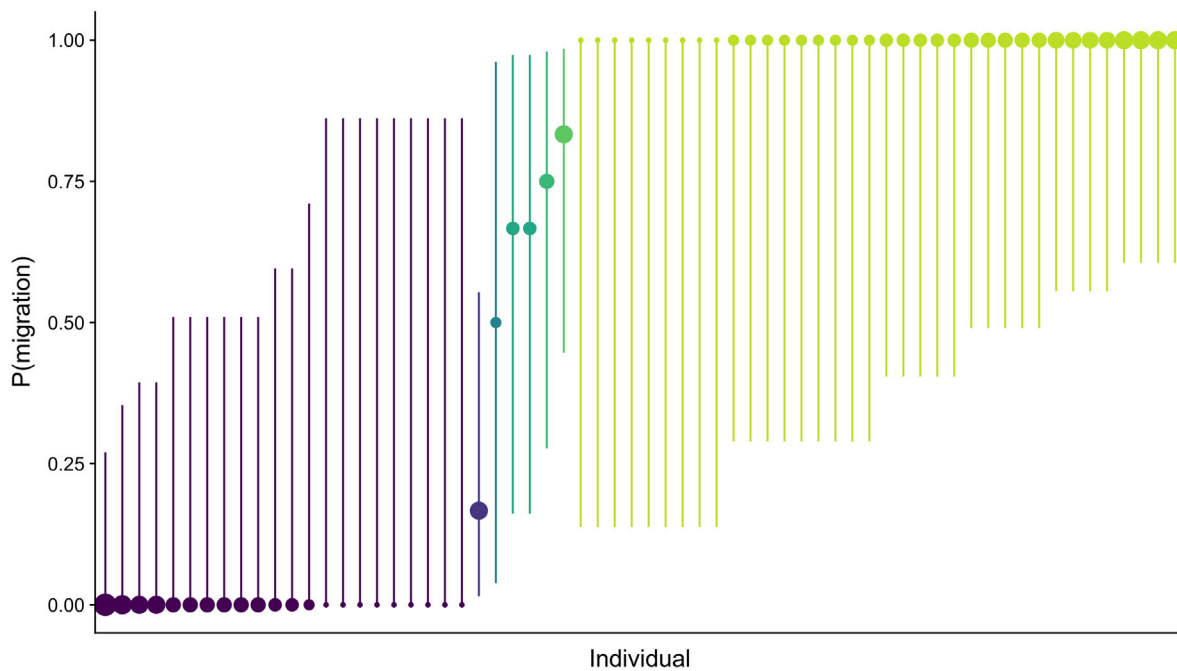
Fig. 3. Maximum-likelihood estimates of individual migration probabilities with 95% confidence intervals. Colors vary on a gradient according to the values of migration probability. The size of the points is proportional to the number of tracking years for each individual.

choices, 3 were male and 2 female (2 were of unknown sex). Among the 15 storks that were captured as juveniles, 8 were tracked into subsequent years as subadults ($n = 8$) or adults ($n = 2$). Of these, 6 exhibited consistent behavior across years (3 pure migrants and 3 pure residents), while 2 showed variable migratory choices in different years. Overall, we found no correlation between individual migratory choices and age or sex.

Migration routes and timing

The mean departure dates were 7 May and 2 October for spring ($n = 121$) and fall migrations ($n = 121$), respectively. The distribution of migration departure dates was bimodal in spring, with a peak in late March and one in June (Fig. 4A), while departure dates in fall showed an early surge followed by a single peak in mid-October (Fig. 4A). Storks followed two general migration routes along the east and west coastline of Florida, with the east one used more in spring and the west in fall (Fig. 4B).

Seasonal ranges and population distribution

The overall population distribution was highly dispersed throughout the Southeast in summer, while highly concentrated in south Florida in winter (Fig. 5). However, the year-round ranges of resident individuals were concentrated in a few hotspots in southeast Florida and in the Jacksonville area (Fig. 6). Therefore, migrant individuals are responsible for most of the spread across the Southeast pictured in the left panel of Fig. 5. The interaction between season and migratory behavior significantly affected home range size ($p < 0.05$). The marginal R^2 was 0.07 and the conditional R^2 was 0.44, suggesting that individual variability explained most of the variance rather than the fixed effects. Migrants, but not residents, showed larger seasonal ranges in winter than in summer (Fig. 7). Migrant winter ranges were larger than both summer and winter ranges of residents (Fig. 7). Wood storks exhibited moderate range fidelity (migrants = 0.51 ± 0.37 and residents = 0.62 ± 0.38 in winter, migrants = 0.51 ± 0.43 and residents = 0.61 ± 0.41 in summer).
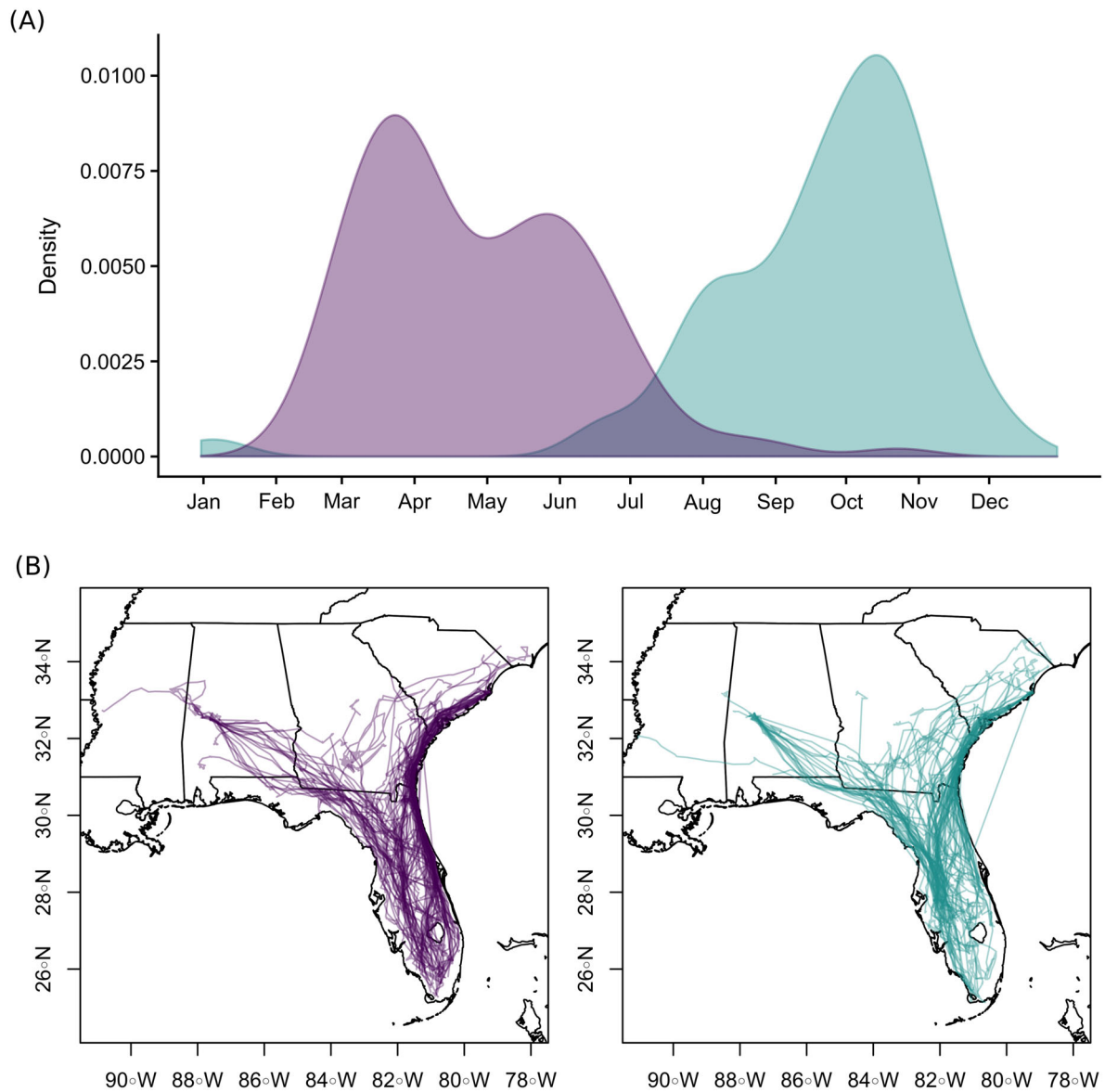
(A)

(B)

Fig. 4. Wood stork migration routes and timing. (A) Frequency distribution of departure times for spring (purple) and fall (blue) migration. (B) Routes of migration for spring (purple, left panel) and fall (blue, right panel).

DISCUSSION

We provided an individual-based quantitative description of migratory patterns in a subtropical wading bird, the wood stork, in the southeastern United States. Our findings revealed that the population is partially migratory, with a group of individuals that seasonally commute between spatially distinct ranges and others that remain resident in the same area year-round. Migration

and residency appeared to be alternative choices adopted by different individuals, but less frequently by the same individuals in different years. Thus, the population exhibits a combination of partial and facultative migration. Between-year consistency of migratory choices was high for most storks, but flexible behavior of a few individuals provided an indication of the potential for plastic responses. The coexistence of different migratory strategies in wood storks
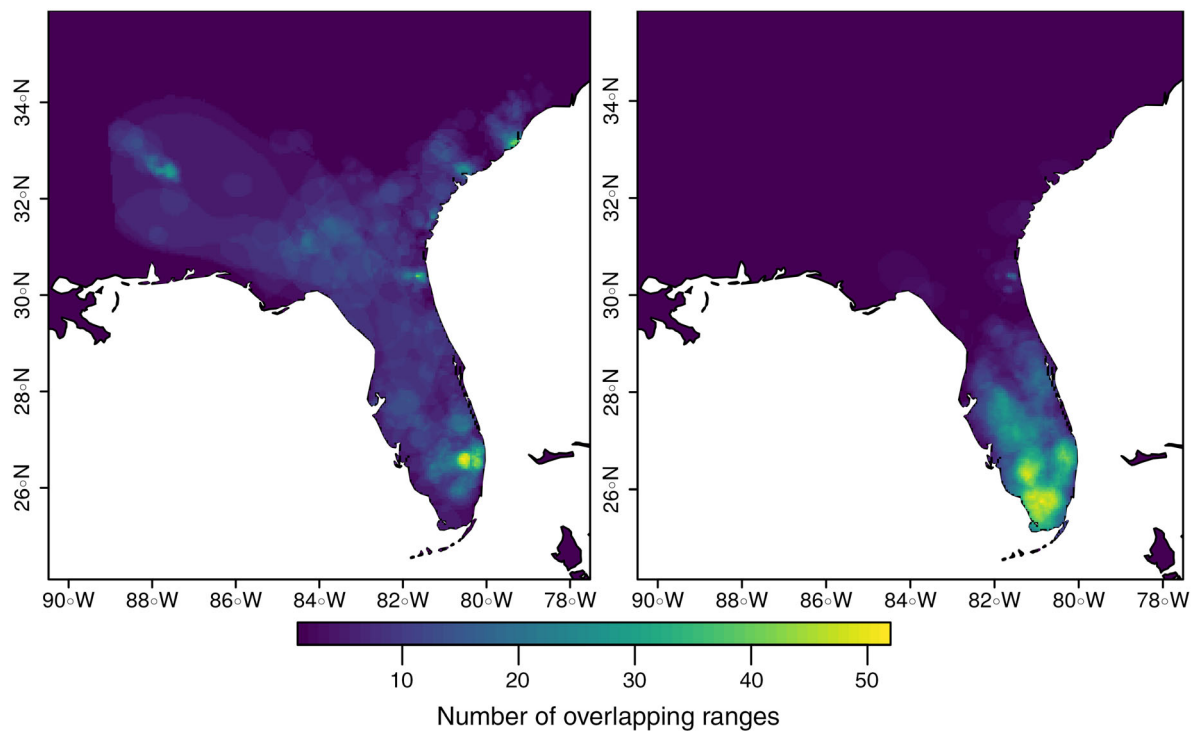
Fig. 5. Heat map of wood stork population distribution in summer (left panel) and winter (right panel). Seasonal ranges of both migrant and resident individuals are included. Home ranges used in different years are overlaid. Most of the seasonal difference in distribution is due to migrant individuals because residents spend the whole year in a single range (Fig. 6).

may be an adaptation to high spatiotemporal heterogeneity and unpredictability of resource availability within their range. Partial migration has been increasingly recognized as a widespread form of migration across taxa, if not the most common (Chapman et al. 2011). Our findings provide the first individual-based description of migration patterns in a subtropical wading bird.

Our analysis of migratory strategies at the individual level revealed three strategies in the wood stork population: consistent migration, consistent residency, and an intermediate, flexible behavior of facultative migration (Fig. 3). Individuals adopting different migratory strategies also differed in their collective seasonal distribution. The distribution of migrants was widely dispersed across the Southeast in the summer and densely concentrated in south Florida in the winter (see overall distribution in Fig. 5). This is consistent with previous literature

on wood stork seasonal movements (Kahl 1964, Coulter et al. 1999). Migrants likely relocate to south Florida to exploit the winter pulse of food availability in the Everglades as rains cease, pools are isolated and reduced in extent and depth, and fishes are more concentrated and available, and then move north when the rains start, dispersing prey (Kahl 1964, Kushlan 1986). Migration to southern Florida in the winter may also be driven by reduced prey availability in the northern part of the range because of cold temperatures (Frederick and Loftus 1993).

It is unclear whether all migrant storks that spend the winter in south Florida also attempt to nest there. The bimodal distribution we observed for departure dates in the spring (Fig. 4A) might result from the fact that some of the migrants leave the winter grounds in south Florida early to go breed elsewhere. An alternative explanation is that among migrant wood storks that attempt to nest in south Florida, those that fail go
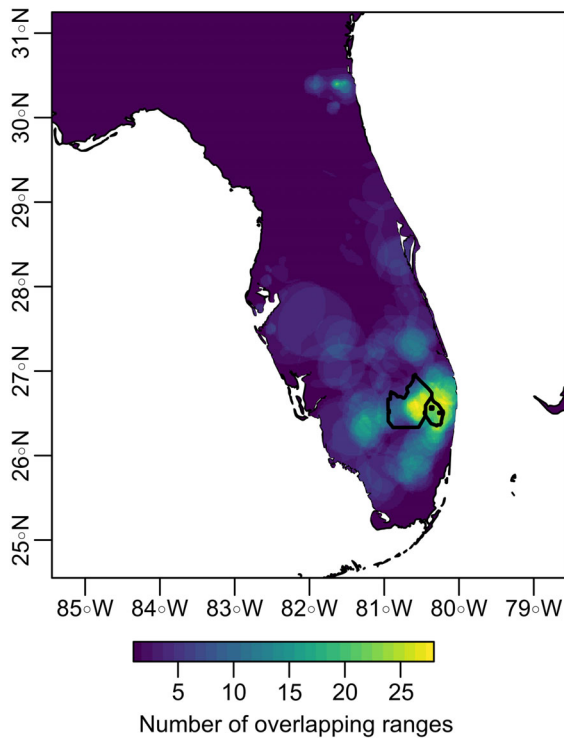
Fig. 6. Heat map of year-round distribution of resident wood storks. Yearly ranges used by resident individuals in different years are overlaid. The black outlines depict the boundaries of Everglades Agricultural Area (left polygon) and Loxahatchee National Wildlife Refuge (right polygon).

Fig. 7. Model predictions for seasonal range size of migrants (left) and residents (right) in summer (purple) and winter (blue).

back to their summer range before those that are successful and stay longer to care for their offspring. The existence of different migratory strategies within the population, and particularly of facultative migrants, also suggests that wood storks may behave as comparison shoppers when selecting general areas for nesting on any given year. Variable migratory patterns may be associated with variable choices of nesting locations as well, based on a relative comparison of conditions in different parts of the population range. The routes followed by migrant storks varied between seasons, possibly as a response to seasonal variation of thermal air currents which may determine least-cost migratory paths for soaring birds (Kahl 1964, Bohrer et al. 2012, Vansteelant et al. 2017; Fig. 4B).

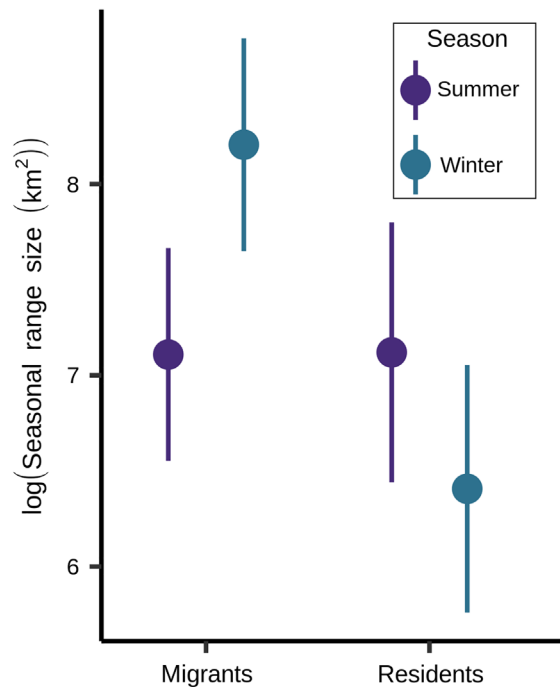The degree of seasonal range fidelity we observed for migrants suggested that storks tended to repeatedly use the same areas across years, both in winter and in summer. For comparison, values of home range overlap corresponding to highest year-to-year breeding site fidelity for wild turkeys (*Meleagris gallopavo*; Badyaev and Faust 1996), on one hand, and capercaillie (*Tetrao urogallus*; Storch 1997) and Egyptian vultures (*Neophron percnopterus*; López-López et al. 2014), on the other, are smaller or comparable, respectively, to those we found for wood stork ranges in both seasons. We found that home range size can vary widely for the same individual in different years, possibly according to the degree of dispersion of food resources (Ford 1983, Zabel et al. 1995, Schradin et al. 2010). Consequently, overlap between ranges in different years was rarely exact, but storks tended to return to the same general area equally in summer and winter. Range fidelity may be a critical adaptation to achieve reliable access to resources (Switzer 1993, Vergara et al. 2006), but it might entail susceptibility to changes in habitat quality, which may lead birds into an ecological trap if they remain faithful to

areas that were formerly suitable but deteriorated (Schlaepfer et al. 2002, Weldon and Haddad 2005, Lok et al. 2011).

We observed the highest density of year-round residents in southeast Florida—near the northern Everglades and urban coastal areas—and in Jacksonville (Fig. 6). Neither of these areas appeared to be intensively used by migrants. The hotspot of resident distribution we observed in the northern Everglades overlaps with the Everglades Agricultural Area (EAA) and Loxahatchee National Wildlife Refuge (i.e., Water Conservation Area [WCA] 1; Fig. 6). Water levels are artificially managed throughout the EAA and WCAs through a system of levees and canals according to agricultural schedules and water supply or flood protection needs (Bancroft et al. 2002, Pearlstine et al. 2005). The EAA covers former marsh habitat which was converted to agricultural use starting in the mid-1900s (Pearlstine et al. 2005). In the EAA, whole fields are periodically flooded as part of their crop rotation strategy, often in coincidence with the beginning of the rainy season and rapidly rising water levels in the Everglades (Schueneman et al. 2001, Sizemore 2009, Sizemore and Main 2012). Canals and ditches are periodically drawn down in response to crop needs, and this may provide patches of concentrated fish for foraging wading birds (Pearlstine et al. 2005). The WCAs were impounded in the 1960s with the double purpose of providing water for agricultural and municipal use and flood protection (Light et al. 1989, Light and Dineen 1994). Loxahatchee National Wildlife Refuge is composed of different vegetation communities and characterized by greater micro-topographic relief than other parts of the Everglades, which may provide suitable foraging habitat for storks over a wider temporal range than in situations of uniform topography (Hoffman et al. 1994, Bancroft et al. 2002). The high density of year-round residents we observed in Loxahatchee and the EAA may be ascribed to these features of topography and artificial flooding-and-drying schedules which may result in foraging chances even out of season and out of sync with natural water-level regimes.

We hypothesize that the high concentration of residents near urban areas might be partly linked to the exploitation of supplemental food sources provided deliberately or unintendedly by humans. Resident wood storks in the Jacksonville area were captured at the Jacksonville Zoo. These storks are wild and free-roaming, but regularly receive food supplementation (D. Bear, *personal communication*). The high density of storks we observed in Jacksonville might be an artifact of the unequal number of tracked storks at different capture sites, but remarkably most storks captured at the Jacksonville Zoo were consistently resident (7 out of 9). We do not have any direct evidence of food supplementation for storks in southeast Florida, but this is one of the most densely populated urban areas in the Southeast and likely presents several supplementation opportunities. Landfills are a possible source of supplemental food, and there is growing evidence that their use by bird populations, including bald eagles (*Haliaeetus leucocephalus*, Turrin et al. 2015), yellow-legged gulls (*Larus michahellis*, Egunez et al. 2017), and white storks (*Ciconia ciconia*, Gilbert et al. 2016), is increasing in different parts of the world. White ibises (*Eudocimus albus*) have been increasingly observed in the same urban areas of south Florida where we observed the highest concentration of resident storks (Hernandez 2016), and a recent study showed that they heavily rely on artificial food provisioning in urban parks and landfills (Murray et al. 2018). We have anecdotal evidence of wood storks regularly being hand-fed and eating trash in urban environments (Picardi S., personal observation), and ongoing studies on the diet of chicks in urban colonies in southeast Florida have revealed consumption of a diversity of human-derived food that may come from landfills and other sources of trash (B. Evans, *personal communication*). Together, these clues lead us to hypothesize that the availability of supplemental food sources of an artificial nature might be playing a role in determining the distribution of resident storks.

The wood stork population is facing environmental change pressures in many regards, from alterations of the natural hydrological dynamics in the Everglades (Kushlan 1987, Sklar et al. 2001, Sklar 2005) to increasing urbanization (Hefner and Brown 1984, Reynolds 2001, Terando et al. 2014), to which the population might respond in the long run by altering migratory patterns. This is an increasingly documented phenomenon in bird populations in response to

various drivers, including climate change, changes in resource phenology, and supplemental feeding (Cotton 2003, Visser et al. 2009, Satterfield et al. 2018). Changes in migratory patterns might be expected both through adaptation and behavioral plasticity (Pulido 2007, Ghalambor et al. 2007, Charmantier and Gienapp 2013). Our analysis on consistency of individual migration choices across years highlighted that most of the population (87% of individuals among those monitored over several years) showed highly consistent yearly migratory choices (Fig. 3). Notably, the inference we can draw from our data in this sense is limited by the fact that individuals were tracked for only a few years each, if more than one. However, a small proportion of individuals (13% of those monitored over several years) showed some degree of plasticity, making different migratory choices in different years and behaving as facultative migrants (Fig. 3). Thus, storks seem to be able to adjust their migratory strategies within the course of a lifetime, implying some potential for plastic changes in migratory behavior at the population level.

Understanding the adaptive significance of partial migration requires a comprehensive assessment of how species inhabiting different ecosystems differ in their migration patterns. By looking at which populations exhibit partial migration or not, researchers can comparatively assess which characteristics of environmental variability lead to its emergence. Studies on multiple species across avian orders have highlighted that partial migration is associated with environments where resource distribution is unstable and highly variable between years (Chan 2001, Jahn et al. 2012). For this reason, most comparative studies of ecological drivers of avian partial migration have focused on the Australian continent, whose trademark is high climatic variability and unpredictability (Chan 2001). Wetlands worldwide are another prime example of heterogeneous and unpredictable environments. Thus, wading birds are good model species to evaluate predictions on partial migration in relation to unpredictable resources, and yet their migration patterns are understudied. To our knowledge, among wading bird species and before the present study, partial migration patterns have only been described at

the individual level in a population of cattle egrets in the temperate zone of eastern Australia (Mckilligan et al. 1993). While we did not directly analyze resources in this paper, seasonality of resource availability within the wood stork range has been described in detail by previous studies, which have established broadscale annual patterns of resource dynamics in the Southeast (Kahl 1964, Kushlan 1986, Frederick and Ogden 1997). In agreement with previous literature, our findings exemplify that in a highly heterogeneous and unpredictable environment, where the availability of key resources varies substantially between years according to variations in rainfall patterns, a combination of partial and facultative migration may be advantageous. Partial migration may buffer between-year stochasticity in survival or reproduction, if the conditions that promote fitness of migrants are different than those of residents. Concurrently, the behavioral flexibility of facultative migrants may work as a reservoir of plasticity, improving population responses to year-to-year variation and allowing rapid change in migratory patterns in response to environmental change. Future research should focus on explicitly testing this hypothesis.

Acknowledgments

Literature Cited

Baber, M. J., D. L. Childers, K. J. Babbitt, and D. H. Anderson. 2002. Controls on fish distribution and abundance in temporary wetlands. Canadian Journal of Fisheries and Aquatic Sciences 59:1441–1450.

Badyaev, A. V., and J. D. Faust. 1996. Nest site fidelity in female wild Turkey: potential causes and reproductive consequences. Condor 98:589–594.

Bancroft, G. T., D. E. Gawlik, and K. Rutchey. 2002. Distribution of wading birds relative to vegetation and water depths in the northern everglades of Florida, USA. Waterbirds 25:265–277.

Bates, D., M. Maechler, B. M. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beerens, J. M. 2008. Hierarchical resource selection and movements of two wading bird species with divergent foraging strategies in the Everglades. Florida Atlantic University, Boca Raton, Florida, USA. https://search.proquest.com/docview/304568853/abstract/E7EAD8D8C1094AA7PQ/1

Bennetts, R. E., and W. M. Kitchens. 2000. Factors influencing movement probabilities of a nomadic food specialist: Proximate foraging benefits or ultimate gains from exploration? Oikos 91:459–467.

Berthold, P. 2001. Bird migration: a general survey. Oxford University Press, Oxford, UK.

Bohrer, G., D. Brandes, J. T. Mandel, K. L. Bildstein, T. A. Miller, M. Lanzone, T. Katzner, C. Maisonneuve, and J. A. Tremblay. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. Ecology Letters 15:96–103.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393–1405.

Borkhataria, R. R., A. Lawrence Bryan, and P. C. Frederick. 2013. Movements and habitat use by fledgling wood storks (*Mycteria Americana*) prior to dispersal from the natal colony. Waterbirds 36:409–417.

Botson, B. A., D. E. Gawlik, and J. C. Trexler. 2016. Mechanisms that generate resource pulses in a fluctuating wetland. PLoS ONE 11:e0158864.

Brooks, W. B., and T. Dean. 2008. Measuring the biological status of the U.S. breeding population of wood storks. Waterbirds 31:50–62.

Bryan, A. L., W. B. Brooks, J. D. Taylor, D. M. Richardson, C. W. Jeske, and I. L. Brisbin. 2008. Satellite tracking large-scale movements of wood storks captured in the gulf coast region. Waterbirds 31:35–41.

Bryan, A. L., and M. C. Coulter. 1987. Foraging flight characteristics of wood storks in east-central Georgia, USA. Colonial Waterbirds 10:157–161.

Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Calenge, C., S. Dray, and M. Royer-Carenzi. 2009. The concept of animals' trajectories from a data analysis perspective. Ecological Informatics 4:34–41.

Chan, K. 2001. Partial migration in Australian landbirds: a review. Emu - Austral Ornithology 101:281–292.

Chapman, B. B., C. Brönmark, J.-Å. Nilsson, and L.-A. Hansson. 2011. The ecology and evolution of partial migration. Oikos 120:1764–1775.

Charmantier, A., and P. Gienapp. 2013. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. Evolutionary Applications 7:15–28.

Chick, J. H., C. R. Ruetz, and J. C. Trexler. 2004. Spatial scale and abundance patterns of large fish communities in freshwater marshes of the Florida Everglades. Wetlands 24:652–664.

Core Team, R. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Cotton, P. A. 2003. Avian migration phenology and global climate change. Proceedings of the National Academy of Sciences 100:12219–12222.

Coulter, M. C., and A. L. Bryan. 1993. Foraging ecology of wood storks (*Mycteria americana*) in east-central Georgia I. Characteristics of foraging sites. Colonial Waterbirds 16:59–70.

Coulter, M. C., J. A. Rodgers, J. C. Ogden, and F. C. Depkin. 1999. Wood Stork (*Mycteria americana*). Birds of North America: 24.

Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. American Naturalist 126:451–474.

DeAngelis, D. L., J. C. Trexler, C. Cosner, A. Obaza, and F. Jopp. 2010. Fish population dynamics in a seasonally varying wetland. Ecological Modelling 221:1131–1137.

DeAngelis, D. L., J. C. Trexler, and W. F. Loftus. 2005. Life history trade-offs and community dynamics of small fishes in a seasonally pulsed wetland. Canadian Journal of Fisheries and Aquatic Sciences 62:781–790.

Dingle, H. 1996. Migration: the biology of animals on the move. Oxford University Press, Oxford, UK.

Dingle, H., and V. A. Drake. 2007. What is migration? BioScience 57:113–121.

Dukai, B., M. Basille, and D. Bucklin. 2016. rpostgisLT: managing animal movement data with 'PostGIS' and R. https://CRAN.R-project.org/package=rpostgisLT

Egunez, A., N. Zorrozua, A. Aldalur, A. Herrero, and J. Arizaga. 2017. Local use of landfills by a yellow-legged gull population suggests distance-

dependent resource exploitation. Journal of Avian Biology 49:jav-01455. https://doi.org/10.1111/jav. 01455

Fletcher Jr., R. J., and R. R. Koford. 2004. Consequences of rainfall variation for breeding wetland black-birds. Canadian Journal of Zoology 82:1316–1325.

Ford, R. G. 1983. Home range in a patchy environment: optimal foraging predictions. Integrative and Comparative Biology 23:315–326.

Frederick, P., D. E. Gawlik, J. C. Ogden, M. I. Cook, and M. Lusk. 2009. The White Ibis and Wood Stork as indicators for restoration of the everglades ecosystem. Ecological Indicators 9:S83–S95.

Frederick, P. C., and W. F. Loftus. 1993. Responses of marsh fishes and breeding wading birds to low temperatures: a possible behavioral link between predator and prey. Estuaries 16:216.

Frederick, P. C., and J. C. Ogden. 1997. Philopatry and Nomadism: contrasting long-term movement behavior and population dynamics of white ibises and wood storks. Colonial Waterbirds 20:316.

Frederick, P. C., and J. C. Ogden. 2001. Pulsed breeding of long-legged wading birds and the importance of infrequent severe drought conditions in the Florida Everglades. Wetlands 21:484–491.

Gaines, K. F., A. L. Bryan, P. M. Dixon, and M. J. Harris. 1998. Foraging habitat use by wood storks nesting in the coastal zone of Georgia, USA. Colonial Waterbirds 21:43–52.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329–346.

Ghalambor, C. K., J. K. McKAY, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21:394–407.

Gilbert, N. I., R. A. Correia, J. P. Silva, C. Pacheco, I. Catry, P. W. Atkinson, J. A. Gill, and A. M. A. Franco. 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. Movement Ecology 4:7.

Haig, S. M., D. W. Mehlman, and L. W. Oring. 1998. Avian movements and wetland connectivity in landscape conservation. Conservation Biology 12:749–758.

Hefner, J. M., and J. D. Brown. 1984. Wetland trends in the Southeastern United States. Wetlands 4:1–11.

Hegemann, A., A. M. Fudickar, and J.-Å. Nilsson. 2019. A physiological perspective on the ecology and evolution of partial migration. Journal of Ornithology 1–13.

Hernandez, S. M., et al. 2016. Urbanized White Ibises (*Eudocimus albus*) as carriers of *Salmonella enterica* of significance to public health and wildlife. PLOS ONE 11:e0164402.

Herring, G. 2008. Constraints of landscape level prey availability on physiological condition and productivity of Great Egrets and White Ibises in the Florida Everglades. Florida Atlantic University, Boca Raton, Florida, USA.

Hoffman, W., G. T. Bancroft, and R. J. Sawicki. 1994. Foraging habitat of wading birds in the Water Conservation Areas of the Everglades. Pages 585–614 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida, USA.

Hylton, R. A. 2004. Survival, movement patterns, and habitat use of juvenile Wood Storks, Mycteria americana. University of Florida, Gainesville, Florida, USA. http://purl.fcla.edu/fcla/etd/UFE0007007

Jahn, A. E., S. P. Bravo, V. R. Cueto, D. J. Levey, and M. V. Morales. 2012. Patterns of partial avian migration in northern and southern temperate latitudes of the New World. Emu - Austral Ornithology 112:17–22.

Junk, W. J. 1993. Wetlands of tropical South America. Pages 679–739 in D. F. Whigham, D. Dykyjová and S. Hejný, editors. Wetlands of the world: inventory, ecology and management Volume I: Africa, Australia, Canada and Greenland, Mediterranean, Mexico, Papua New Guinea, South Asia, Tropical South America, United States. Springer Netherlands, Dordrecht, The Netherlands.

Kahl, M. P. 1964. Food ecology of the wood stork (*Mycteria americana*) in Florida. Ecological Monographs 34:97–117.

Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56:234–238.

Kingsford, R. T., D. A. Roshier, and J. L. Porter. 2010. Australian waterbirds – time and space travellers in dynamic desert landscapes. Marine and Freshwater Research 61:875.

Kushlan, J. A. 1981. Resource use strategies of wading birds. Wilson Bulletin 93:145–163.

Kushlan, J. A. 1986. Responses of wading birds to seasonally fluctuating water levels: strategies and their limits. Colonial Waterbirds 9:155–162.

Kushlan, J. A. 1987. External threats and internal management: the hydrologic regulation of the Everglades, Florida, USA. Environmental Management 11:109–119.

Light, S. S., and J. W. Dineen. 1994. Water control in the Everglades: a historical perspective. Pages 47–84 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida, USA.

Light, S. S., J. R. Wodraska, and S. Joe. 1989. The Southern Everglades. National Forum 69:11–14.

Loftus, W. F., and A.-M. Eklund. 1994. Long-term dynamics of an everglades small-fish assemblage. Pages 461–483 in S. M. Davis and J. C. Ogden, editors. Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida, USA.

Lok, T., O. Overdijk, J. M. Tinbergen, and T. Piersma. 2011. The paradox of spoonbill migration: Most birds travel to where survival rates are lowest. Animal Behaviour 82:837–844.

López-López, P., C. García-Ripollés, and V. Urios. 2014. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. Ecological Applications 24:938–949.

Mckilligan, N. G., D. S. Reimer, D. H. C. Seton, D. H. C. Davidson, and J. T. Willows. 1993. Survival and seasonal movements of the Cattle egret in Eastern Australia. Emu 93:79–87.

Melvin, S. L., D. E. Gawlik, and T. Scharff. 1999. Long-term movement patterns for seven species of wading birds. Waterbirds: the International Journal of Waterbird Biology 22:411–416.

Murray, M. H., A. D. Kidd, S. E. Curry, J. Hepinstall-Cymerman, M. J. Yabsley, H. C. Adams, T. Ellison, C. N. Welch, and S. M. Hernandez. 2018. From wetland specialist to hand-fed generalist: shifts in diet and condition with provisioning for a recently urbanized wading bird. Philosophical Transactions of the Royal Society B 373:20170100.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Newton, I. 2012. Obligate and facultative migration in birds: ecological aspects. Journal of Ornithology 153:171–180.

Niemuth, N. D., M. E. Estey, R. E. Reynolds, C. R. Loesch, and W. A. Meeks. 2006. Use of wetlands by spring-migrant shorebirds in agricultural landscapes of North Dakota's Drift Prairie. Wetlands 26:30–39.

Niemuth, N. D., and J. W. Solberg. 2003. Response of waterbirds to number of wetlands in the Prairie Pothole Region of North Dakota, USA. Waterbirds 26:233–238.

Ogden, J. C. 1985. The Wood Stork. In Di Silvestro, R. L., editor. Audubon Wildlife Report 1985. The National Audubon Society, New York, New York, USA.

Ogden, J. C., J. A. Kushlan, and J. T. Tilmant. 1976. Prey selectivity by the wood stork. Condor 78:324–330.

Ogden, J. C., J. A. Kushlan, and J. T. Tilmant. 1978. The food habits and nesting success of Wood Storks in Everglades National Park 1974. Department of the Interior, National Park Service, Washington, D.C., USA.

Pearlstine, E. V., M. L. Casler, and F. J. Mazzotti. 2005. A checklist of birds of the Everglades Agricultural Area. Florida Scientist 68:84–96.

Pedler, R. D., R. F. H. Ribot, and A. T. D. Bennett. 2014. Extreme nomadism in desert waterbirds: flights of the banded stilt. Biology Letters 10:20140547.

Picardi, S., R. R. Borkhataria, A. L. Bryan Jr., P. C. Frederick, and M. Basille. 2018. GPS telemetry reveals occasional dispersal of wood storks from the Southeastern US to Mexico. Caribbean Naturalist 2:23–29.

Poiani, A. 2006. Effects of floods on distribution and reproduction of aquatic birds. Advances in Ecological Research 39:63–83.

Pulido, F. 2007. Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effects of weather and condition. Climate Research 35:5–23.

Reid, J. M., J. M. J. Travis, F. Daunt, S. J. Burthe, S. Wanless, and C. Dytham. 2018. Population and evolutionary dynamics in spatially structured seasonally varying environments. Biological Reviews 93:1578–1603.

Reynolds, J. E. 2001. Urbanization and land use change in Florida and the South. Current Issues Associated with Land Values and Land Use Planning Proceedings of a Regional Workshop.

Roshier, D. A., V. A. J. Doerr, and E. D. Doerr. 2008. Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. Oecologia 156:465–477.

Ruetz, C. R., J. C. Trexler, F. Jordan, W. F. Loftus, and S. A. Perry. 2005. Population dynamics of wetland fishes: Spatio-temporal patterns synchronized by hydrological disturbance? Journal of Animal Ecology 74:322–332.

Satterfield, D. A., P. P. Marra, T. S. Sillett, and S. Altizer. 2018. Responses of migratory species and their pathogens to supplemental feeding. Philosophical Transactions of the Royal Society B 373:20170094.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17:474–480.

Schradin, C., G. Schmohl, H. G. Rödel, I. Schoepf, S. M. Treffler, J. Brenner, M. Bleeker, M. Schubert, B. König, and N. Pillay. 2010. Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. Animal Behaviour 79:195–203.

Schueneman, T. J., C. Rainbolt, and R. Gilbert. 2001. Rice in the crop rotation. Extension Service Institute of Food and Agricultural Sciences (EDIS), University of Florida, Gainesville, Florida, USA.

Sekercioglu, C. H. 2010. Partial migration in tropical birds: the frontier of movement ecology. Journal of Animal Ecology 79:933–936.

Sergio, F., J. Blas, L. López, A. Tanferna, R. Díaz-Delgado, J. A. Donázar, and F. Hiraldo. 2011. Coping with uncertainty: breeding adjustments to an unpredictable environment in an opportunistic raptor. Oecologia 166:79–90.

Sizemore, G. 2009. Foraging quality of flooded agricultural fields within the Everglades Agricultural Area for wading birds (Ciconiiformes). University of Florida, Gainesville, Florida, USA.

Sizemore, G. C., and M. B. Main. 2012. Quality of flooded rice and fallow fields as foraging habitat for little blue herons and great egrets in the everglades agricultural area, USA. Waterbirds 35:381–393.

Sklar, F. H., et al. 2005. The ecological–societal underpinnings of Everglades restoration. Frontiers in Ecology and the Environment 3:161–169.

Sklar, F., C. McVoy, R. VanZee, D. Gawlik, K. Tarboton, D. Rudnick, S. Miao, and T. Armentano. 2001. The effects of altered hydrology on the ecology of the everglades. Pages 39–82 in J. E. Porter and K. G. Porter, editors. The Everglades, Florida Bay, and Coral Reefs of the Florida Keys. CRC Press, Boca Raton, Florida, USA.

Snodgrass, J. W., A. L. Bryan, R. F. Lide, and G. M. Smith. 1996. Factors affecting the occurrence and structure of fish assemblages in isolated wetlands of the upper coastal plain, USA. Canadian Journal of Fisheries and Aquatic Sciences 53:443–454.

Spitz, D. B., M. Hebblewhite, and T. R. Stephenson. 2017. 'MigrateR': extending model-driven methods for classifying and quantifying animal movement behavior. Ecography 40:788–799.

Storch, I. 1997. Male territoriality, female range use, and spatial organisation of capercaillie Tetrao urogallus leks. Wildlife Biology 3:149–161.

Streich, W. J., H. Litzbarski, B. Ludwig, and S. Ludwig. 2006. What triggers facultative winter migration of Great Bustard (Otis tarda) in Central Europe? European Journal of Wildlife Research 52:48–53.

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533–555.

Terando, A. J., J. Costanza, C. Belyea, R. R. Dunn, A. McKerrow, and J. A. Collazo. 2014. The Southern Megalopolis: using the past to predict the future of Urban Sprawl in the Southeast U.S. PLOS ONE 9: e102261.

Turrin, C., B. D. Watts, and E. K. Mojica. 2015. Landfill use by Bald Eagles in the Chesapeake Bay Region. Journal of Raptor Research 49:239–249.

Van Moorter, B., N. Bunnefeld, M. Panzacchi, C. M. Rolandsen, E. J. Solberg, and B.-E. Sæther. 2013. Understanding scales of movement: animals ride waves and ripples of environmental change. Journal of Animal Ecology 82:770–780.

Vansteelant, W. M. G., J. Shamoun-Baranes, W. van Manen, J. van Diermen, and W. Bouten. 2017. Seasonal detours by soaring migrants shaped by wind regimes along the East Atlantic Flyway. Journal of Animal Ecology 86:179–191.

Vergara, P., J. I. Aguirre, J. A. Fargallo, and J. A. Dávila. 2006. Nest-site fidelity and breeding success in White Stork Ciconia ciconia. Ibis 148:672–677.

Visser, M. E., A. C. Perdeck, J. H. V. Balen, and C. Both. 2009. Climate change leads to decreasing bird migration distances. Global Change Biology 15:1859–1865.

Weldon, A. J., and N. M. Haddad. 2005. The effects of patch shape on indigo buntings: evidence for an ecological trap. Ecology 86:1422–1431.

Weller, M. W. 1999. Wetland birds: habitat resources and conservation implications. Cambridge University Press, Cambridge, UK.

Zabel, C. J., K. McKelvey, and J. P. Ward Jr.. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (Strix occidentalis caurina). Canadian Journal of Zoology 73:433–439.

Supporting Information