



Research

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Fitness consequences of anthropogenic subsidies for a partially migratory wading bird

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Human activities are forcing wildlife to confront selective pressures different from those under which they evolved. In seasonal environments, migration evolved as an adaptation to fluctuating resource availability. Anthropogenic subsidies modify resource dynamics by providing a steady food source that is not subject to seasonality. Globally, many migratory populations are becoming increasingly resident in response to food supplementation. While these population-level shifts are assumed to arise from changing fitness consequences of individual behaviour in response to resource dynamics, these mechanisms are often difficult to quantify and disentangle. Here, we quantified fitness consequences of responses to anthropogenic subsidies in partially migratory wood storks (*Mycteria americana*) in the heavily urbanized southeastern United States. First, we tested whether individual migratory behaviour is linked to different responses to anthropogenic subsidies. Second, we quantified fitness consequences of these behavioural responses. We found that, in our system, migration and residency are alternative behavioural tactics associated with different responses to food supplementation. In turn, the use of anthropogenic resources alters a fitness component by enhancing nest survival. These results provide a mechanistic examination of how animals may respond to human-modified resource dynamics and how fitness consequences of individual tactics may translate into behavioural shifts at the population level.

1. Background

Anthropogenic activities are forcing wildlife to confront selective pressures different from those under which they evolved [1,2]. These novel selective pressures can cause behavioural shifts [3,4]. While behavioural change in wildlife populations in response to human-induced selective pressures has been repeatedly observed [5–7], the mechanisms by which these shifts occur are rarely quantified [8]. In this study, we evaluated individual behavioural responses to human-modified resource dynamics, linked them to migratory behaviour and quantified their fitness consequences in a partially migratory bird population inhabiting the heavily developed landscape of the southeastern United States.

Generally, animals evolve behaviours that maximize benefits and minimize costs [9]. In stochastic environments, the balance of costs and benefits may be context-dependent, resulting in the evolution of alternative behavioural tactics [10,11]. Behavioural heterogeneity can buffer populations against demographic crashes induced by rapid fluctuations of environmental conditions [12]. Alternative behavioural tactics can coexist if their fitness consequences

equalize in the long run [13,14]. For instance, northern elephant seals that exhibit weak site fidelity perform better or worse than their site-faithful conspecifics in any given year depending on annual climate conditions, but the long-term performance of the two strategies is equal [15].

Partial migration is one type of behavioural heterogeneity that arises in response to resource tradeoffs [16,17]. These tradeoffs arise because, typically, resources are only available seasonally in a certain geographic area, requiring animals to either undertake a risky and energy-demanding journey [18–20] to access resources elsewhere or to cope with local resource scarcity for part of the year to avoid the cost of that journey [16,21] (figure 1a). In unpredictable environments, the performance of each individual tactic in the face of these tradeoffs is dependent on annual conditions, such that their net benefit is equal in the long term [22]. For instance, migrant and resident tactics are maintained in a population of European shags (*Phalacrocorax aristotelis*) through strongly fluctuating natural selection due to climate variation [23].

Anthropogenic alterations to the environment are shifting the balance of costs and benefits of behaviour, often resulting in behavioural shifts [24]. For example, across taxa, many partially migratory populations are becoming increasingly resident in response to anthropogenic food supplementation [25,26]. Anthropogenic subsidies alter natural resource tradeoffs by providing a reliable and predictable food source whose availability does not vary seasonally [27] (figure 1b). Individuals who choose to take advantage of that food source may be released from the need to migrate [27,28] and experience an increased benefit without an increased cost (figure 1b). If the abundance of anthropogenic food sources is not limiting and the net benefit of exploiting them outweighs the net benefit of migrating to seasonally profitable habitat, then individuals that choose residency should become dominant in the population. However, the association between residency and the propensity to use anthropogenic food sources has been rarely demonstrated at the individual level, and the consequences of this combined behavioural tactic in terms of fitness have not been quantified.

Here, we aimed to test whether individual migratory behaviour is linked to the response to human-modified tradeoffs arising from food supplementation in a partially migratory wading bird, and to quantify fitness consequences of these different behavioural tactics. We asked whether placement along two behavioural axes—migratory behaviour and propensity to urban foraging—is correlated and how it affects individual breeding performance (figure 1c). We focused on the southeastern US population of the American wood stork (*M. americana*), a large wetland-dwelling bird distributed east of Mississippi and south of North Carolina [29]. The population's migratory patterns were recently described for the first time, revealing a partial migration strategy [30]. Migrant individuals spend the winter in south Florida and relocate north to other southeastern states during the summer, while residents stay in Florida year-round [30].

Florida is a densely populated state whose landscapes have been heavily modified by human activities [31–33]. Historically, the Everglades constituted the breeding grounds for the bulk of the wood stork population [34]. The Everglades are highly oligotrophic and have relatively low standing stocks of aquatic fauna [35], making concentration of prey in the water column necessary to make food available to birds [36–38]. Wood storks are tactile foragers and almost exclusively piscivorous, and they rely on the hydrological dynamics of the Everglades for the production of prey during the wet season and for the concentration of those prey in the water column through gradual water recession during the dry season [39–41]. Their reproduction is adaptively synchronized with the pulse of fish availability in the dry season [39–41]. Starting in the 1940s, the construction of a widespread network of canals began across south Florida, and the Everglades were partly drained to make room for cities and farmland [42]. The landscape was transformed into a mosaic of urban development and artificially controlled water bodies, with the Everglades relegated to only half of their original extent [42]. The consequent alteration of hydrological cycles resulted in massive colony failures, a drastic drop in wood stork population size and a northward shift of nesting [34,43]. After the crash, the wood stork population has been recovering since the 1980s thanks to both ecosystem restoration efforts and the expansion of the breeding range beyond south Florida [44,45].

There is increasing evidence that wood storks in South Florida have started to use anthropogenic food sources including trash and direct hand-feeding in cities and urban parks [46,47]. In parallel, humans have also created new foraging habitat in the form of artificial bodies of water that are both more productive—because of nutrient discharge from cities and croplands—and predictable—because of artificial flooding schedules—than natural wetlands in South Florida [46,48,49]. Wood storks intensively use these urban ponds, canals and ditches for foraging [47,49,50]. The diet of wood stork nestlings in South Florida frequently includes human food scraps, such as chicken nuggets and hot dogs [46]; non-native fish also constitute a prominent part of the gut contents, abundant in both artificial and natural bodies of water after being released from ornamental fish tanks [48]. The use of anthropogenic food sources seems to be generally on the rise among wading birds in the southeastern United States, including the sympatric white ibis (*Eudocimus albus*) [51].

Building on the existing pieces of evidence, our objectives were to determine whether the use of urban foraging sites by wood storks differed between individuals with different migratory behaviour, and if it was associated with differences in reproductive performance. First, we hypothesized that the use of anthropogenic food sources whose availability does not fluctuate seasonally would allow individuals to forgo migration. Accordingly, we predicted that residency would be associated with selection of urban foraging sites, while migration would be associated with selection of non-urban foraging sites (figure 1c). Second, we hypothesized that the benefit of anthropogenic resource use would manifest as a release from calorie limitation, and thus be reflected in an enhancement of vital rates that are energy-limited. Accordingly, we predicted that the use of urban foraging sites would result in increased nest survival (figure 1c).

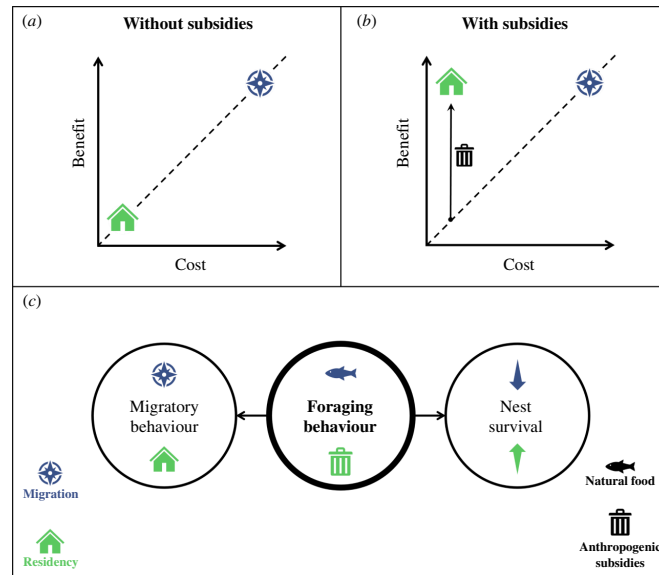


Figure 1. Conceptual diagram illustrating the framework of this study. (a) In seasonal environments, individuals face a tradeoff between maximizing resource acquisition and minimizing energy expenditure or risk exposure. In partially migratory populations, migration and residency develop as alternative behavioural tactics in response to this tradeoff. Migrants maximize the benefit of increased access to resources while paying a higher cost in terms of energy expenditure or risk exposure (a high-risk/high-reward tactic), whereas residents minimize the cost of energy expenditure and risk exposure while experiencing a reduced benefit in terms of access to resources (a low-risk/low-reward tactic). For partial migration to be maintained over evolutionary time scales, the net benefit of each behavioural tactic must be equal in the long run. (b) Anthropogenic subsidies shift the balance of costs and benefits of residency and migration by providing resources that are available year-round. We hypothesized that individuals that exploit anthropogenic subsidies would be released from the need to migrate, and that they would experience an increased benefit in terms of resource acquisition without a change in cost, thus resulting in a net increase in fitness. (c) Under these hypotheses, we predicted that, in a partially migratory population of wood storks (*M. americana*) in the southeastern United States from 2006 to 2017, the consumption of natural food sources would be associated with migration and the consumption of anthropogenic food sources would be associated with residency; further, we predicted that the consumption of anthropogenic food sources would be associated with higher nest survival.

2. Methods

(a) Data collection

Wood storks were captured between 2004 and 2012 at 11 sites spread across their United States range and equipped with solar-powered GPS tags programmed to collect one location per hour [30]. The full dataset consists of 133 wood storks monitored from 2004 to 2019 (mean \pm s.d. 2.18 \pm 2.51 years per individual), for a total of 2 197 975 GPS fixes (mean \pm s.d. 16 526 \pm 19 504 GPS fixes per individual) [52]. Details on capture colonies and age and sex composition of the dataset are reported in Picardi *et al.* [30]. For the current analysis, we focused on the subset of individuals that had at least one identified breeding attempt and for which migratory behaviour in the previous year could be categorized ($n = 43$). This subset excluded juveniles ($n = 7$), non-breeding adults ($n = 14$) and individual-years with incomplete data ($n = 69$). We provided an updated table of capture colonies and sex composition of this sample in the electronic supplementary material.

(b) Regional groups

We split the resulting sample into three regions based on nest locations: South Florida, Jacksonville and the rest of the Southeast. The South Florida group included nests located in the historical breeding range of the wood stork population (i.e. the Greater Everglades Ecosystem [53]). Because the Everglades are naturally oligotrophic and their seasonal hydrological dynamics have been severely impacted by human development in South Florida [54–57], and because all evidence of urban foraging in wood storks comes from that region [46–49], we expected urban foraging to bring a benefit to wood storks that forage within that system during the breeding season. It is not clear whether the same expectation should apply to wood storks breeding elsewhere in the Southeast, because wetland systems on the coastal plain are different from the Everglades in terms of hydrology, seasonality, nutrient loads and hydroperiod, resulting in different resource dynamics [58–61]. Thus, we analyzed breeding attempts occurring elsewhere in the Southeast separately. Finally, our dataset includes a group of wood storks that, albeit free-ranging, reside at the Jacksonville Zoo and are heavily subsidized with anthropogenic food (D. Bear, 2017, personal communication). This group represents a special case of urban foraging behaviour which warranted treating it separately. Breeding attempts were assigned to the South Florida group if the nest location was within 130 km of the boundary of the Greater Everglades Ecosystem; 130 km is the maximum documented foraging trip distance for wood storks [40,62], and thus these individuals may have been foraging in the Everglades watershed during their breeding attempts regardless of whether they nested directly within it (although most did; refer electronic supplementary material). Breeding attempts were assigned to the Jacksonville group if the nest location was located at the Jacksonville Zoo. All other breeding attempts were assigned to the Southeast group.

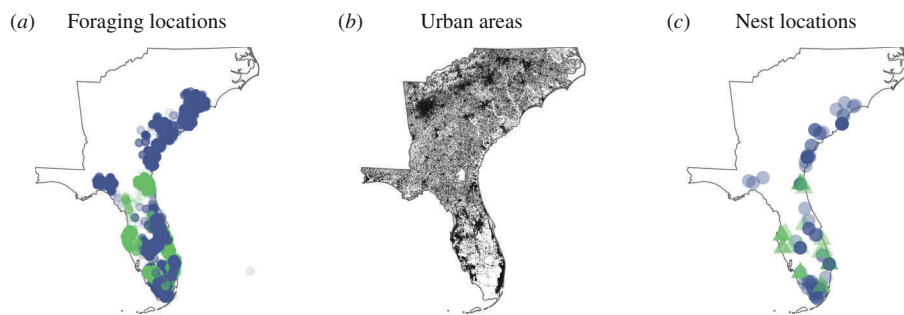


Figure 2. Maps of data components. (a) Map of foraging locations used by migrant (in blue) and resident (in green) wood storks (*M. americana*) during breeding attempts in the southeastern United States from 2006 to 2017. (b) Map of urban development in the southeastern United States. (c) Map of nest locations for migrant ($n = 97$, blue circles) and resident ($n = 48$, green triangles) wood storks from 2006 to 2017.

(c) Breeding attempts

We focused on breeding because of its critical importance for wood stork population dynamics [63]. Nest survival is energy-limited, and each wood stork nestling needs to consume an estimated 16.5 kg of fish to survive until fledging [40]. Thus, we expected that the release from calorie limitation provided by abundant, energy-dense and consistently available anthropogenic subsidies would result in increased nest survival (figure 1c). We identified nesting attempts within yearly individual tracks of adult wood storks based on the analysis of recursive movement patterns, following a procedure described in a previous publication [64] and using the R package ‘nestR’ v. 1.1.1 [65]. We expected to be equally likely to detect breeding attempts of males and females because wood storks perform parental care equally [66,67]. Based on previous analyses, we did not expect to detect breeding attempts that failed before the 14 days mark [64]. Nests were identified among repeatedly visited locations based on distinctive temporal patterns of re-visitation, using known nesting attempts as a reference [64]. The algorithm returned information on the location of the nest, the start and end dates of the breeding attempt, and a history of nest re-visitation whereby locations within an individual track are classified as either on the nest or away from it. Locations were classified as on the nest if they fell within the 40 m buffer used to spatially define re-visitation [64]. We considered any location away from the nest during a breeding attempt as a foraging location (figure 2a).

(d) Migratory behaviour

We classified individual migratory behaviour in each year as either migration or residency using nonlinear models of net squared displacement [30], using the R package ‘migrateR’ v. 1.0.9 [68]. Successfully classifying migratory behaviour using this method required having GPS-tracking data available throughout the annual cycle [30]. We retained for further analyses any individual breeding attempt for which migratory behaviour in the season prior to breeding was determined. From here on, we refer to individuals that performed migration in the year prior to a breeding attempt as migrants and to the remaining as residents. Because we used annual breeding attempts as the analytical units, facultative migrants—who may switch migratory behaviour year-to-year—were labelled as migrants in years when they performed migration and as residents in years when they did not.

(e) Urban areas

We used proximity to urban areas as a proxy for the use of anthropogenic food sources of various types, including landfills, artificial water bodies and urban parks. The landscape of the Southeast, and of South Florida in particular, encompasses a gradient of development that ranges from metropolitan areas (such as Miami) to the vast undeveloped wetlands of the Everglades; between these extremes lies a spectrum of suburban and peri-urban development [69]. It is these suburban and peri-urban areas that we hypothesized provide foraging opportunities to wood storks—in the form of suburban parks, ponds in residential areas, golf courses, canals adjacent to roads and crops, etc. [46–49]—rather than the core of cities. Thus, a metric of proximity to urban areas modelled with a quadratic term would allow us to capture responses of wood storks to development along this gradient. We obtained information on the location of urban areas across the wood stork population range using a land cover layer from LANDFIRE v. LF 2016 (<https://www.landfire.gov/>). The LF 2016 Existing Vegetation Type classifies land cover at 30 m resolution. We defined urban land use by pooling together the categories labelled ‘developed—high intensity’, ‘developed—medium intensity’, ‘developed—low intensity’, ‘developed—roads’ and ‘developed—open space’, and aggregated the resulting raster at 1 km resolution. We then computed the distance of each foraging location from the closest urban area (figure 2b). Because this static layer did not capture changes in urban land cover throughout the time frame of the study (2006–2017), we also calculated distance to urban areas using the LANDFIRE Existing Vegetation Type from 2001 and the TIGER 2010 Urban Area Census data (<https://catalog.data.gov/dataset/tiger-line-shapefile-2019-2010-nation-u-s-2010-census-urban-area-national>) and used them as alternative predictors (electronic supplementary material). Furthermore, we assigned each foraging location to an ‘urban/non-urban’ binary variable using either the 2001, 2010 or 2016 data, and used these categories as alternative predictors (electronic supplementary material).

(f) Resource selection analysis

We evaluated the effect of proximity to urban areas on selection of foraging sites during breeding attempts using resource selection functions [70]. We evaluated resource selection by comparing used with available foraging locations for each individual breeding attempt. For each breeding attempt, we defined available locations by randomly placing points around the location of the nest. To account for constraints to availability imposed by the movement process, we simulated points with decreasing density as the distance from the nest increases [71]. We fitted an exponential function to the empirical distribution of foraging trip distances observed across all individuals to define the decay in the density of available points as a function of distance from nest (electronic supplementary material). We sampled available points by drawing random distance values from the fitted distribution and random bearings, discarding any points that fell in the ocean and only retaining those on land until we reached the desired number of available points (10 times as many available points as used). We used conditional logistic regression with use versus availability (i.e. 1/0) as a response variable, fitting a separate model for each region. We included distance to urban areas both as a linear and quadratic term as predictors, in interaction with migratory behaviour, and the breeding attempt ID as a stratifying parameter. We assigned infinite weights to the available points [72]. We quantified results in terms of log-relative selection strength (log-RSS [73]). The value of log-RSS quantifies the selection or avoidance of habitat characteristics with respect to an arbitrarily chosen reference condition; positive values indicate selection and negative values indicate avoidance with respect to reference conditions [73]. We used 0 km as the reference value of distance from urban areas, so that log-RSS values would quantify selection or avoidance with respect to being in a city. We used the standard error method to compute 95% confidence intervals around mean RSS estimates. We fit alternative versions of this model using distance values from 2001 and 2010 and using the binary ‘urban/non-urban’ categorical predictor from 2001, 2010 and 2016 (electronic supplementary material).

(g) Nest survival analysis

We evaluated the effect of proximity to urban areas on reproductive performance of wood storks using a daily nest survival model based on the history of nest re-visitation obtained from the GPS-tracking data, specified in a Bayesian hierarchical modelling framework. We used daily nest survival probability as a measure of reproductive performance. Nests were considered active so long as they were visited, and dead once visits were interrupted, while accounting for imperfect detection of nest visits and missing GPS fixes. To be considered successful, a nest must have survived (i.e. remained active for) 110 days [66]. We built upon the model specification described in Picardi *et al.* [64], where survival is modelled as a latent, unobserved process which is inferred through the observed history of nest re-visitation. For each attempt, i , we modelled daily nest survival status, z , as a Bernoulli random variable that was a function of survival probability, Φ , and status on the previous day:

$$z_{i,t} \sim \text{Bern}(z_{i,t-1} \times \phi_{i,t-1}).$$

With t ranging from 1 to 110. We expanded the binomial generalized linear model formula described in Picardi *et al.* [64] to include the mean distance of foraging sites to urban areas, d , in interaction with dummy variables encoding the three regions (with South Florida as the reference category), as predictors of probability of survival:

$$\text{logit}(\phi_{i,t}) = \beta_{\phi_0} + \beta_{\phi_1} \times d_i + \beta_{\phi_2} \times \text{Southeast}_i + \beta_{\phi_3} \times \text{Jacksonville}_i + \beta_{\phi_4} \times d_i \times \text{Southeast}_i + \beta_{\phi_5} \times d_i \times \text{Jacksonville}_i.$$

We did not directly model the effect of migratory behaviour on nest survival because our hypothesis was that foraging behaviour, rather than migratory behaviour, would affect nest survival (figure 1c). However, if migratory behaviour correlates with differences in foraging behaviour as hypothesized, we expected a correlation between nest survival and migratory tactic to also emerge from this model.

We modelled observed nest visits on each day, Y , as a binomial random variable, with probability of success as a function of current nest survival status, probability of visit detection, p , and number of GPS fixes available, N :

$$Y_{i,t} \sim \text{Bin}(N_{i,t}, z_{i,t} \times p_t).$$

Where the probability of detection is conditional on N_t and the nest being active on that day:

$$p_t = \text{Pr}(\text{visit detected} \mid z_t = 1, N_t).$$

Note that, while the probability of survival is estimated at the individual-attempt level, the probability of visit detection is estimated at the population level. We allowed the detection probability to vary through time by modelling it as a function of the day of the attempt using a binomial generalized linear model:

$$\text{logit}(p_t) = \beta_{p_0} + \beta_{p_1} \times t.$$

We used uninformative priors on the beta parameters, specified as normal distributions with a mean of 0 and precision of 1e-2.

We fit the described model using JAGS v. 4.3.0 [74] through the R package ‘rjags’ v. 4-13 [75]. We evaluated model predictions for daily nest survival probability as a function of proximity to urban areas and regions using 95% Bayesian credible intervals. We constructed cumulative survival curves for migrants and residents in each region from the model output.

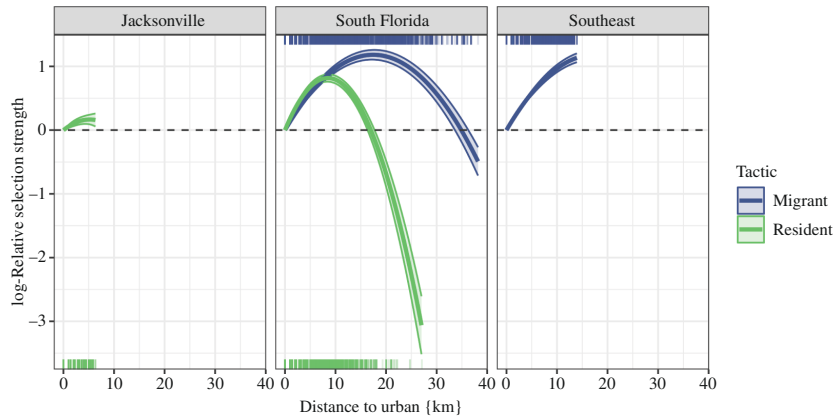


Figure 3. Results of resource selection functions that evaluate foraging-site selection of migrant (in blue) and resident (in green) wood storks (*M. americana*) as a function of distance to urban areas from 2006 to 2017 in the southeastern United States. Each panel shows results for one of three regions: Jacksonville, South Florida and the Southeast (see §2). Lines indicate the mean prediction of log-RSS and shaded envelopes indicate 95% confidence intervals. Positive values of log-RSS, above the dashed line, indicate selection with respect to a reference distance (0 km) from urban areas, while negative values, below the dashed line, indicate avoidance. Rug plots at top and bottom display the distribution of data points along the range of possible distances to urban areas.

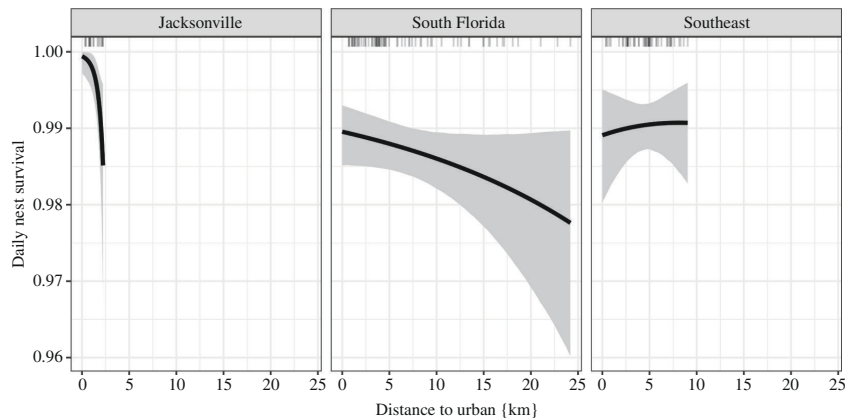


Figure 4. Results of nest survival model as a function of foraging-site distance from urban areas for wood storks (*M. americana*) from 2006 to 2017 in the southeastern United States. Each panel shows results for one of three regions: Jacksonville, South Florida and the Southeast (refer §2). The black line indicates the mean prediction and the shaded envelope indicates 95% credible intervals. Note that the y-axis ranges from 0.96 to 1.00. Rug plot at the top displays the distribution of data points along the range of possible distances to urban areas.

(h) Reproducibility

The full wood stork GPS-tracking dataset is published and freely accessible [52]. The subset of data used in this article is available on Dryad [76]. The code to reproduce the analysis is published on Zenodo [77] and on GitHub [78].

3. Results

The final dataset consisted of 145 breeding attempts, of which 97 were associated with migration and 48 with residency, from 43 different individuals between 2006 and 2017 (figure 2c). The South Florida group included breeding attempts made by both migrants ($n = 45$) and residents ($n = 30$), while the Southeast group included only migrants ($n = 52$) and the Jacksonville group only residents ($n = 18$). The dataset included only two facultative migrants, both of which adopted a resident tactic in most years but migrated once during their monitoring period (electronic supplementary material). Among the 52 breeding attempts we detected in the Southeast, 14 were from individuals that had already attempted to breed in South Florida earlier in the same year; the remaining 38 were from individuals that had migrated to South Florida but for which we did not detect a breeding attempt.

Results of the resource selection function indicated a significant difference in foraging-site selection of migrant and resident wood storks according to distance from urban areas (figure 3, table 1). Resident wood storks in South Florida selected foraging sites located between 0.39 and 17 km from urban areas, and they strongly avoided foraging sites located farther away than 17 km compared to the reference distance of 0 km. Their selection peaked at 8.49 km from urban areas. Migrant wood storks in South Florida selected foraging sites located between 0.39 and 34.7 km from urban areas. Their selection peaked at 17.36 km from urban areas. Resident wood storks in Jacksonville selected foraging sites located between 0.06 and 6.33 km from urban areas. Their selection peaked at 5.18 km from urban areas. Migrant wood storks in the Southeast selected foraging sites located between 0.14 and 13.93 km from urban areas. Their selection peaked at 13.93 km from urban areas—the greatest distance they

Table 1. Results of resource selection functions for foraging sites selected during breeding as a function of distance to urban areas and migratory behaviour in wood storks (*M. americana*) from 2006 to 2017 in the southeastern United States. We fit separate models for breeding attempts occurring in South Florida, Jacksonville and the rest of the Southeast (refer S2). The focal regions are listed in the 'model' column, predictors are listed in the 'variable' column, mean coefficient estimates are listed in ' β ', standard errors are listed in 's.e.' and p -values are listed in ' p -value'.

model	variable	β	s.e.	p -value
Jacksonville	distance to urban	0.07	0.05	0.18
	distance to urban ²	-0.13	0.05	0.01
South Florida	distance to urban	0.48	0.01	<0.001
	distance to urban ²	-0.08	0.00	<0.001
	distance to urban \times resident	-0.02	0.02	0.49
	distance to urban ² \times resident	-0.16	0.01	<0.001
Southeast	distance to urban	0.96	0.01	<0.001
	distance to urban ²	-0.24	0.01	<0.001

were observed using. Qualitatively, these patterns were robust to the type of variable used (distance to urban versus binary 'urban/non-urban'), data source (LANDFIRE versus TIGER) and year (2001, 2010 or 2016; electronic supplementary material).

We found a negative association between daily nest survival rate and distance to urban areas in South Florida and Jacksonville, but no relationship in the Southeast. In South Florida, daily nest survival was highest ($\varphi = 0.99$, 95% CI = 0.99–0.99) for birds foraging in close proximity to urban areas and quadratically decreased as the distance increased ($\beta_{\varphi 0} = 4.57$, 95% CI = 4.19–4.96; $\beta_{\varphi 1} = -3.02e-5$, 95% CI = $-6.86e-5$ – $-1.04e-5$; table 2; figure 4). In Jacksonville, daily nest survival was highest ($\varphi = 1$, 95% CI = 1–1) for birds foraging in close proximity to urban areas and steeply decreased as the distance increased ($\beta_{\varphi 3} = 3.752$, 95% CI = 1.27–6.96; $\beta_{\varphi 5} = -1.76e-3$, 95% CI = $-3.51e-3$ – $-0.41e-3$; table 2; figure 4). In the Southeast, daily nest survival was unaffected by distance to urban areas ($\varphi = 0.99$, 95% CI = 0.98–1; $\beta_{\varphi 2} = 1.76e-3$, 95% CI = -0.77 – -0.82 ; $\beta_{\varphi 4} = -4.84e-5$, 95% CI = $-9.78e-5$ – $-1.93e-4$; table 2; figure 4). Across regions, residents had higher cumulative nest survival than migrants ($z_{110} = 0.00$ for migrants and 0.33 for residents in South Florida; $z_{110} = 0.27$ for migrants in the Southeast; and $z_{110} = 0.59$ for residents in Jacksonville; figure 5), although values of z_{110} were estimated with high uncertainty (range 0–1 for all combinations of region and migratory tactic).

4. Discussion

Anthropogenic activities alter the balance of costs and benefits of animal behaviour, modifying tradeoffs that occur in natural ecosystems [3,4]. We demonstrated that, in our system, migration and residency are alternative behavioural tactics associated with different responses to anthropogenic food supplementation. In turn, we showed that the use of anthropogenic resources alters a fitness component by enhancing breeding performance. These results provide a mechanistic examination of how animals may respond to altered resource tradeoffs and how fitness consequences of individual tactics may translate into human-induced behavioural shifts at the population level.

Migration evolved in response to fluctuating resource availability in seasonal environments [79,80]. Anthropogenic food subsidies modify natural tradeoffs by introducing resources whose availability is not subject to seasonality [25,27]. We hypothesized that the exploitation of this steady source of food would release individuals from the need to migrate. Our results supported this hypothesis in wood storks, showing an association between residency and selection of anthropogenic foraging sites at the individual level. Conversely, migration was associated with selection of natural foraging sites, where resource availability varies seasonally. These patterns were consistent across regions. These results do not necessarily indicate that resident wood storks exclusively specialize in anthropogenic subsidies while migrants never exploit those; it is possible that both migrants and residents use anthropogenic subsidies to different degrees [47]. However, the strong avoidance of foraging sites located farther than intermediate distances from urban areas by residents in South Florida indicates that these individuals rarely forage in the Everglades—which is where those distance values occur. Residents of the Jacksonville Zoo exhibit more extreme behaviour, not only selecting urban foraging sites, but rarely even using any foraging sites farther than a few kilometres from the city. This pattern reflects the fact that these individuals are systematically subsidized at the Zoo (D. Bear 2017, personal communication). All individuals in the Southeast group were migrants, probably because the temperatures get too cold for wood storks to spend the winter at those latitudes [81]. In the Southeast, migrants selected foraging sites as far away as possible from urban areas, whereas in South Florida, they exhibited stronger selection for sites at intermediate distances. This is consistent with the species' ecology, as the largest distance values in South Florida occur in portions of the Everglades where the water is often too deep for efficient tactile foraging [82,83]. Thus, migrants in South Florida select for sites farthest away from cities among the ones with suitable hydrology. Overall, these results highlight the mechanistic link between spatio-temporal patterns of resource availability and migratory behaviour, which is well established theoretically [79,84–86] and empirically supported with population-level studies [87–89], but rarely demonstrated at the individual level in partially migratory populations.

Partial migration is thought to have evolved in response to a tradeoff between the benefit of increased access to resources and the benefit of minimizing risk and energetic expenditure associated with the migratory journey [16,21]. By increasing local

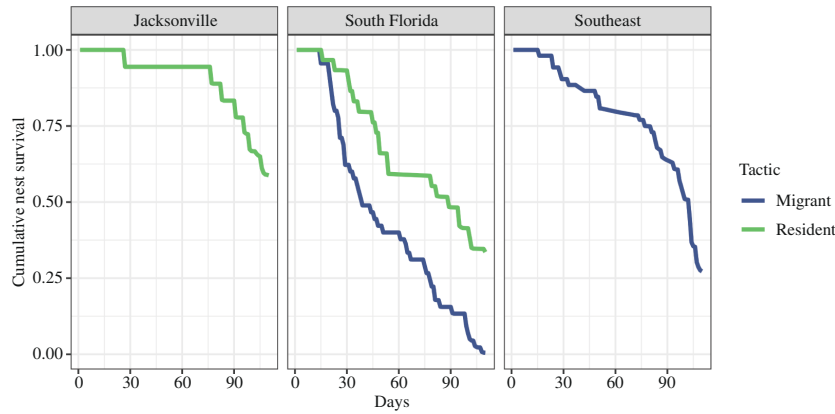


Figure 5. Cumulative nest survival curves for migrant (in blue) and resident (in green) wood storks (*M. americana*) from 2006 to 2017 in the southeastern United States. Each panel shows results for one of three regions: Jacksonville, South Florida and the Southeast (see §2).

Table 2. Results of nest survival model as a function of distance to urban areas in wood storks (*M. americana*) from 2006 to 2017 in the southeastern United States. Model parameters are listed in the 'parameter' column, mean parameter estimates are listed in 'mean' and lower and upper 95% Bayesian credible intervals are listed in 'lower 95% CI' and 'upper 95% CI'.

parameter	mean	lower 95% CI	upper 95% CI
β_{p0}	1.02	1.00	1.04
β_{p1}	-0.03	-0.03	-0.03
$\beta_{\varphi0}$	4.57	4.19	4.96
$\beta_{\varphi1}$	-3.02e-5	-6.86e-5	-1.04e-5
$\beta_{\varphi2}$	1.76e-3	-0.77	0.82
$\beta_{\varphi3}$	3.72	1.27	6.96
$\beta_{\varphi4}$	-4.84e-5	-9.78e-5	1.93e-4
$\beta_{\varphi5}$	-1.76e-3	-3.51e-3	0.41e-3

resource availability, food subsidies may increase the net benefit of residency compared to migration [25,27]. We hypothesized that the use of food subsidies would enhance fitness components that depend on resource intake—in the case of wood storks, nest survival. Particularly, we expected that anthropogenic subsidies would provide a fitness benefit to wood storks breeding in South Florida, where urban development has severely degraded the quality of natural foraging sites [56,63]. Our results supported this hypothesis, showing a positive relationship between the use of urban foraging sites and nest survival in South Florida. The same pattern emerged for wood storks breeding at the Jacksonville Zoo, which exhibited the highest values of nest survival across regions—again, consistent with the heavy food supplementation they receive (D. Bear 2017, personal communication). However, we found no relationship between urban foraging and nest survival in the rest of the Southeast. We attribute this result to regional differences in wetland dynamics and prey availability. On one hand, the Everglades are a naturally oligotrophic system, where prey production is limited by nutrient loads and prey concentration in the water column depends on steady and gradual water recession across a vast expanse [36,39,90]. Because the Everglades cover a very large area, the amount of prey biomass produced can be massive when conditions are right [91], but when they are not, there are hardly any other foraging opportunities available in the region because the Everglades make up most of the watershed. Furthermore, the seasonal dynamics of flooding and drying in the Everglades have been severely compromised by the urbanization of South Florida [55,92], which means optimal conditions are rarer than they were historically [63]. On the other hand, the rest of the Southeast encompasses wetlands of a variety of types, including small, isolated and often ephemeral water bodies such as Carolina Bays [58], river floodplains [59] and tidal creeks and estuaries [60]. While none of these wetland types in isolation may be as productive as the Everglades can be in a good year, they are generally much less oligotrophic and provide wood storks with several options which are hydrologically less synchronized and may be profitable at different times [93–95]. Thus, urban foraging appears to benefit wood storks in South Florida, where prey availability in natural wetlands is unpredictable and natural foraging grounds are degraded, but not elsewhere in the Southeast, where redundancy in foraging habitat may make prey availability more reliable.

Animals may respond to changes in tradeoffs by developing new behavioural strategies or by repurposing ones that are already part of their behavioural repertoire [96,97]. For instance, it is unclear whether wood storks have always been partially migratory or whether partial migration emerged as a result of anthropogenic change and the increasing availability of food subsidies. In one scenario, we could envision partial migration developing in response to naturally occurring tradeoffs created by density dependence in combination with high interannual unpredictability of wetland foraging conditions. In this scenario, partial migration originally served as a bet hedging strategy, whereby having individuals that adopt different tactics protected the population from demographic fluctuations due to environmental stochasticity [98]. Later, with the widespread development

of South Florida, individuals that were already resident might have started to specialize in exploiting anthropogenic food subsidies. In another scenario, wood storks might have originally been fully migratory, and they might have become partially migratory in response to the emergence of anthropogenic subsidies. This latter scenario was verified for white storks (*Ciconia ciconia*) in Europe, which transitioned from full to partial migration in response to the availability of food in landfills [99]. Long-term studies will be essential in providing empirical evidence of behavioural repurposing versus the development of new behaviours in response to anthropogenic tradeoffs.

Anthropogenic food supplementation has modified the behaviour of migratory animals worldwide [25,26]. The question of whether a shift towards complete residency will occur in wood storks remains open. First, for a food supplementation-induced shift in population migratory patterns to occur, there needs to be a correlation between the use of anthropogenic food sources and migratory behaviour. Our results showed that this correlation exists. Second, the use of anthropogenic food sources needs to provide a fitness advantage to the individuals that forgo migration. Our results partially support this; we found that urban foraging enhances nest survival. However, we cannot assume that this gain would not be balanced out by losses in other fitness components, such as brood size, post-fledging survival or adult survival. Third, there needs to be a mechanism for behavioural change, whether through adaptation or plasticity. We cannot speak to adaptation, because we do not know if migratory behaviour in wood storks is heritable; but we can speak to plasticity, because wood stork individuals are capable of switching tactic year-to-year, indicating that the potential for plastic responses exists [30]. The expansion of the breeding range that occurred in the 1970s provides further evidence of the ability of wood storks to expand their behavioural repertoire in response to anthropogenic change [44]. Individual plasticity was identified as the mechanism underlying a population-level shift of migratory patterns in another long-lived bird, the whooping crane (*Grus americana*) [100].

Behavioural heterogeneity can have important implications for demography through portfolio effects, which occur when variation in behaviour within a population increases its stability and resilience [12]. In our system, the fitness benefit gained by resident wood storks through urban foraging could provide a critical demographic buffer against population crashes in years when food availability in natural wetlands is low and migrant breeding performance is poor as a consequence. Thus, residents may be key in ensuring population resilience under continued global change. While unpredictable year-to-year, the availability of food sources in the Everglades on a good year can support huge reproductive events for wood storks [91]. It is possible that the benefit of foraging in natural wetlands in a good year outweighs the cost of gambling in the long run, so that the lifetime fitness consequences of migration and residency and their demographic contributions end up equalizing. Furthermore, our results showed that some migrant individuals attempt to nest in both their winter (South Florida) and summer (Southeast) range. The opportunity to breed again in the same year may compensate for the lower nest survival experienced by migrants in South Florida and equalize the net benefit of residency and migration. Another critical element on which we lack information is how food quality affects vital rates other than nest survival, such as brood size or post-fledging survival. Generally, anthropogenic food sources tend to have lower nutritional content than their natural counterparts [51,101,102]. For instance, the tradeoff between quantity and quality of anthropogenic food has been shown to increase adult mass gain but reduce post-fledging survival in red-winged starlings (*Onychognathus morio*) [101]. Consumption of urban foods can also affect gastrointestinal health; for instance, white ibis that forage in urbanized areas have altered gut microbial composition, which could impact their health and survival [103].

While responding to human-induced changes in tradeoffs can help species acclimate or adapt to novel conditions, it can also have detrimental long-term consequences if it leads animals into evolutionary traps [104]. One possible pathway for this is the alteration of disease transmission patterns [28,105,106]. A recent meta-analysis showed that, depending on the types of food subsidies and pathogens, food provisioning can result in increased host contact rates and higher pathogen exposure through crowding effects [107]. These consequences may be more or less severe depending on the degree of resource specialization exhibited by individuals [108]. Although food-supplemented wildlife sometimes better tolerate infection, higher tolerance might in turn facilitate the emergence of more virulent pathogen strains in the long run [107,109]. The increased transmission also poses a public health risk by increasing the risk of pathogen spillover from wildlife to humans [109,110]. Thus, while the use of food subsidies may provide a short-term demographic benefit through individual fitness effects, it can ultimately result in severe long-term costs for both wildlife and society.

Responses to human-modified tradeoffs are reshaping ecological communities as a result of global change. While population-level responses are often assumed to arise from unequal fitness advantages gained by individuals depending on the behaviours they adopt, these mechanisms are often difficult to quantify and disentangle. Addressing this gap requires developing theoretical expectations of the cost/benefit balances of individual behaviour in the face of human-modified tradeoffs, as well as simultaneously measuring behaviour and fitness at the individual level to empirically test those expectations. Additionally, quantifying multiple vital rates (e.g. adult survival as well as reproductive success) is necessary to predict demographic consequences of individual behaviour at the population level. An intentional shift of research focus from pattern description to mechanistic examination of how individual decisions scale up to determine population-level outcomes is necessary to improve our ability to predict the demographic and evolutionary trajectories of populations in response to global change.

Ethics. Handling of wood storks was conducted under US Fish and Wildlife Service Threatened and Endangered Species Permits TE051552, TE801914, and TE37498B-0; Florida Fish and Wildlife Conservation Commission Special Purpose Permit WX07646; Georgia Department of Natural Resources Scientific Collecting Permit 29-WJH-05-79; U.S. Geological Survey Bird Banding Permit 22598-E; and University of Florida IACUC Protocol #E013 and ARC Protocol 002-11BGL.

Data accessibility. The full wood stork GPS-tracking dataset is published and freely accessible on Movebank [52]. The subset of data used in this manuscript is available on Dryad [76]. The code to reproduce the analysis is available on Zenodo [77] and on GitHub [78].

Supplementary material is available online [111].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.P.: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing—original draft, writing—review and editing; P.F.: funding acquisition, project administration, supervision, writing—review and editing; M.B.: funding acquisition, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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