Flying the extra mile pays-off: foraging on anthropogenic waste as a time and energy-saving strategy in a generalist bird

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Abstract

Food waste disposal represents a major global source of predictable anthropogenic food subsidies and is exploited by many organisms. However, the energetic cost-benefits of foraging on these food subsidies have remained largely unexplored. Here we investigate the year-round foraging decisions of resident white storks, *Ciconia ciconia*, in Iberia and assess the energetic and time cost-benefits of foraging on both landfill waste and natural food sources. To do so, we use GPS and acceleration data from 55 individuals tagged in southern Portugal between 2016 and 2019. We find that the probability of attending landfill sites was 60% during the non-breeding season and 44% during the breeding season. Moreover, foraging on landfill waste is a time- and energy-saving strategy; although birds had to travel 20% further to exploit this resource during the breeding period, they spent overall 10% less energy than when foraging on natural prey. We show that this relationship could be mediated by a reduction in foraging time and an increase in foraging efficiency while exploiting landfill waste. Surprisingly, we did not find any evidence that landfill specialists experienced any competitive advantage during landfill exploitation over birds that visit landfills occasionally. These insights are key to predict how species that rely on landfills can be affected by waste reduction initiatives planned by the European Union, and implement the necessary management strategies.

Keywords: landfill closure; landfill waste; foraging ecology; predictable anthropogenic food subsidies; white storks.

1. Introduction

Humans produce enormous quantities of food waste; estimates suggest that 30-40% of all food produced is wasted (Parfitt et al., 2010) and deposited in locations where it can be accessible to wildlife. These predictable anthropogenic food subsidies (PAFS), in the form of organic waste on landfills, fisheries discards or crop residuals, generate impacts on animal populations at multiple scales, from the individual to the ecosystem (Oro et al., 2013). Individuals from numerous animal species have modified their movements, activity, geographical range, and home range size in response to PAFS (Gilbert et al., 2016; López-López et al., 2014; Newsome et al., 2015; Patrick et al., 2015; van Donk et al., 2019); which can affect survival and reproduction rates, and subsequently the demography of these populations (Plaza and Lambertucci, 2017).

Landfill sites, in particular, can potentially sustain high densities of scavenging individuals (Oro et al., 2013). The spatial and temporal predictability, accessibility, and nutritional value of anthropogenic food waste can provide abundant food resources for wildlife, and has been shown to be responsible for the demographic explosion of generalist animals (such as foxes, rats and gulls), but also for the sustenance of some endangered species (Plaza and Lambertucci, 2017). Landfill use has been associated with increased body mass in black vultures (*Coragyps atratus*) (Plaza and Lambertucci, 2018), kelp gull (*Larus dominicanus*) nestlings (Lenzi et al., 2019), and grizzly bears (*Ursus arctos horribilis*) (Blanchard, 1987). Landfill use has also been linked to higher reproduction performance; for example, white storks (*Ciconia ciconia*) had larger clutch sizes (Djerdali et al., 2008), glaucous gulls (*Larus hyperboreus*) experienced higher fledging rate (Weiser and Powell, 2010), and laughing gull (*Leucophaeus atricilla*) chick growth and survival was enhanced (Dosch, 1997), compared to conspecifics foraging in more natural landscapes.

According to the optimal foraging theory animals choose to forage in sites that maximize energy intake while minimizing energy and time expenditure (Stephens and Krebs, 1986; Ydenberg et al., 1994). Landfill waste offers large quantities of high-energy food (Patenaude-Monette et al., 2014; van Donk et al., 2019) but is localised in space; hence trade-offs exist between time spent in landfills sites and energetic costs of travelling, especially for central-place foragers during the breeding season (Gilbert et al., 2016). Foraging in landfill sites is likely to exacerbate inter and intraspecific competition (through agonistic interactions and food-robbing), which increases energetic costs, since they attract large numbers of individuals and at high densities (Oro et al., 2013). On the other hand, on natural heterogeneous landscapes, prey is often patchily distributed and intraspecific competition is likely to be low since individuals tend to forage in smaller groups (Catry et al., 2017). These dynamics could lead to the emergence of individual foraging strategies and specialisation, with less competitive individuals avoiding landfill sites. Despite many studies focusing on the fitness benefits for individuals exploiting landfill waste, the energetic cost-benefits of landfill use have not yet been fully quantified.

Use of landfill resources, together with the global increase of temperature due to climate change, may have facilitated the establishment of non-migratory white stork populations in Iberia (Catry et al., 2017). Resident individuals heavily rely on food waste disposal sites for foraging and no longer complete their annual migrations to and from their sub-Saharan wintering grounds. In two decades the number of resident white storks in Portugal has increased from 1,187 individuals (18% of the breeding population) in 1995 to 14,434 (62% of the breeding population) in 2015 (Catry et al., 2017). White storks' use of landfill resources in Iberia has been investigated, and evidence shows that storks nesting close to landfill sites heavily relied on them (Gilbert et al., 2016). Moreover, breeding success for these individuals was higher than for individuals nesting further away (Gilbert, 2015).

Whilst this increasing number of white storks in Iberia is widely attributed to their high adaptability and behavioral plasticity, new EU directives (1999/31/UE and, more recently, 2018/850/UE), regulating waste disposal, can greatly revert this trend. These directives have established new circular economy targets aiming to reduce municipal waste landfilled to 10% in the next decade. Recent evidence shows that landfill closure can cause declines on survival, body mass, egg volume and/or clutch size in several gull species (Payo-Payo et al., 2015; Pons and Migot, 1995; Steigerwald et al., 2015) (but see (Katzenberger et al., 2019)). Therefore, it is crucial to understand foraging decisions, and how animals search for and exploit landfill waste, as opposed to natural prey, to predict how animal populations might respond when food waste is removed, and to develop appropriate conservation and management strategies.

Here we investigate (i) the foraging decisions of resident white storks feeding on PAFS and natural food sources in Iberia; (ii) the energetic and time cost-benefits of these foraging decisions during the breeding and non-breeding seasons; and (iii) whether birds highly specialised on landfills gain a competitive advantage while exploiting PAFS, by increasing their foraging efficiency and decreasing the foraging time necessary to meet their energetic requirements, over birds that only visit landfills occasionally. These insights will be key to understand the drivers of landfill use and to predict how storks — and to some extent other birds found regularly in large numbers at landfills (e.g. egrets, herons, gulls and some raptors) — may be affected by reductions in PAFS. This understanding is key for a species that has substantially increased in numbers in the last decades due to the exploitation of landfills (Catry et al., 2017), and for which density dependent effects of food depletion are associated with high nestling mortality (Denac, 2006; Zurell et al., 2015).

In this study we examine 4 years of GPS and tri-axial acceleration data from resident white storks in Iberia and determine their behaviour, energy expenditure, foraging decisions, and landfill use. We use structural equation models (SEM) (Lefcheck et al., 2016; Lefcheck, 2016) to understand the relationships among foraging movements, energy expenditure and behaviour. We hypothesize that the choice of food resources (anthropogenic waste or natural prey) will lead to different foraging strategies, for example at landfills sites birds will reduce the time devoted to foraging and increase energy efficiency given the spatiotemporal predictability of organic waste deposition. Moreover, we predict that foraging strategies might differ between the breeding and non-breeding season, as breeding birds will have to return to the nest frequently, so their foraging range will be reduced, and landfill sites might then be outside the range. In this context, fundamental trade-offs between energetic and nutritional requirements in parental provisioning strategies are expected (Wright et al., 1998). Finally, we predict that landfill specialists will have competitive advantage over birds that only use landfills occasionally.

2. Material and methods

2.1 Bird capture and GPS tracking

Our dataset included GPS data with tri-axial acceleration from 55 resident adult white storks, tagged between 2016 and 2019 in southern Portugal. Resident individuals overwintered in the Iberian Peninsula and did not cross the Strait of Gibraltar. Storks were tagged with ‘Flyway 50’ GPS/GSM loggers from Movetech Telemetry (4 different models varying slightly in weight) and ‘Ornitrack-50’ GPS/GSM loggers from Ornitela. Adult birds were caught at multiple landfill sites using nylon leg nooses, and at several breeding colonies using a remotely activated clap net at the nests. Birds were measured and ringed, and the devices were mounted on the back of the birds as backpacks with a Teflon harness. The tag and harness together weighted 60-90 g, which represented 1.5-3.7% of a given bird's body mass at the time of tagging. Most birds were resighted in the days following tag deployment and no abnormal behaviour or adverse effects due to tagging were observed. The procedure was approved by the Instituto da Conservação da Natureza e Floresta (Portugal). The tags were programmed to record 9 consecutive GPS positions at 1 Hz every 20 minutes, and concurrently a 9 s tri-axial acceleration burst at 1 Hz. We kept the first GPS position recorded, thus location and acceleration matched. GPS data was visually examined to detect potential outliers, which were subsequently removed, together with the associated acceleration burst. We identified 75 nest locations for the tagged birds across the years after visually inspecting the GPS tracks and visiting the sites. The nests were situated between 1.5 and 40.2 km away from the closest landfill site (mean = 17. 3 km).

2.2 Data selection and processing

From each acceleration burst we derived two metrics, ODBA (overall dynamic body acceleration, 1 G = 9.8 m/s^2), a proxy of energy expenditure invested in locomotion, and behaviour (Gleiss et al., 2011; Shepard et al., 2008b). ODBA was obtained from tri-axial acceleration bursts by subtracting the smoothing of total acceleration, using a running-mean of 4 s, from the total acceleration, as recommended in (Gleiss et al., 2011; Shepard et al., 2008a, 2008b). To determine the bird behaviour at each burst, we used the tri-axial acceleration data to train random forest machine-learning algorithms (R package ‘randomForest’ ver. 4.6 (Liaw and Wiener, 2002)). Movetech Telemetry tags and Ornitela tags differ in their sensor characteristics (e.g. position of the sensor and axes orientation) hence we created device specific algorithms. We characterised four behaviours: foraging, resting (including preening), flapping, and soaring flight (including gliding and orographic and thermal soaring). To train the algorithm we manually labelled 250 tri-axial acceleration bursts for each behaviour and tag type; 70% of the data was used for training the algorithm and 30% for testing it. To label the training data we compiled information from several sources: (i) 9 tags that were programmed to continuously record GPS and acceleration data which allowed a detailed understanding of the birds’ movements and behaviour, (ii) video recordings of captive white storks that were fitted with the tracking devices, and (iii) from the 9 consecutive GPS locations that allowed to infer birds’ speed and movement during the acceleration burst. The random forest model had 96% accuracy for Movetech Telemetry tags data and 97% accuracy for Ornitela tags data. For this study, flapping and soaring flight were aggregated and considered as flying, as both behaviours occurred infrequently, representing only 5.7 % of locations.

Landfill sites were determined through visual inspection of satellite images, and in all cases, they were confirmed by visits or contact with local authorities. Each GPS location was classified as either inside or outside a landfill. Subsequently, using the behavioural and GPS data, we created daily foraging strategy metrics for each individual stork. We only included in the analyses days with more than 10 daylight GPS positions and acceleration bursts (median GPS positions per day was 29) and with more than 4 positions classified as 'foraging' to guarantee representative metrics.

We built two different datasets for the subsequent analyses. First, to assess individual and seasonal differences in attendance to landfill sites, we created a 'daily attendance dataset'. In this dataset each day was classified as a 'landfill attendance day' when at least one foraging location occurred on a landfill in the corresponding 24-h period, or as a 'non-landfill attendance day' when no foraging locations occurred on landfills. Second, to understand the foraging movements, behaviour and energy expenditure of feeding on anthropogenic waste or natural prey we built a 'daily foraging strategy dataset' that only included days where birds displayed either one or the other strategy, thus removing days where birds foraged on both waste and natural prey. To do so, we created a variable, 'foraging site' with two levels: 'landfill foraging day', when 70% of the daily foraging positions occurred in landfill sites, and 'non-landfill foraging day', when 70% of the foraging positions for a given day occurred outside landfill sites. We chose this threshold as it ensured birds spent most of the day in one of the two areas, while it minimised the number of days that had to be removed from the dataset to less than 20%.

The activity and energetic trade-offs between foraging on landfills vs natural prey were explored using several metrics: (i) daily distance travelled (km), calculated as the summed distance between consecutive locations for each day; (ii) daily relative flight time, calculated by dividing the number of burst classified as flying by the total of bursts obtained in a day; (iii) mean ODBA (G) as a proxy of daily energy expenditure (Gleiss et al., 2011), calculated as the mean ODBA of the accelerometer bursts obtained in a day; (iv) daily relative foraging time, calculated by dividing the number of burst classified as foraging by the total of burst in a day; and (v) mean foraging ODBA (G), as a proxy for foraging efficiency (lower mean foraging ODBA values indicate higher foraging efficiency), calculated as the daily mean ODBA for the foraging bursts. Daily distance travelled and relative flight time were highly correlated (Pearson correlation = 0.75), which indicates that the metrics were largely insensitive to the number of fixes; we only retained daily distance travelled in further analyses.

To account for the potential effect of season on the foraging site choice (landfill sites or non-landfill sites), we located the nesting site of each individual, and using the GPS data, we defined the beginning of the breeding season as the first three consecutive days that an individual occupied the nest; and the end of the breeding period as last three consecutive days the nest was occupied.

To explore if birds that visited landfill sites more often had a competitive advantage when exploiting this resource, we used the ‘daily attendance dataset’ to create a landfill specialisation index, from 0 (natural prey specialist; never visits landfill sites) to 1 (waste specialist; only forages on landfill sites), for each individual. We divided the number of days that the bird attended a landfill by the total numbers of days that the bird was tagged.

2.3 Statistical analysis

To understand seasonal variability in foraging site attendance we fitted a generalised linear mixed-effects model (GLMM) with foraging site attendance (landfill or non-landfill) as the response variable and season (breeding or non-breeding) as the explanatory variable, using the *glmmPQL* function with a binomial structure (R package 'MASS' ver. 7.3 (Ripley et al., 2013)); the model included bird ID nested in tag type (5 levels: 4 types of Movetech tags and 1 type of Ornitela tag) as random effects and an autocorrelation structure of order 1 to account for the potential temporal correlation between consecutive days. Subsequently, to understand the potential constraints of reproduction in the choice of foraging site, we used the data from the breeding season to fit a GLMM with a binomial structure, using the *glmer* function (R package 'lme4' ver. 1.1-21 (Bates et al., 2015)). We considered foraging site attendance as the response variable, and included as explanatory variables, distance from the nest site to the closest landfill site, and its quadratic term, to account for potential non-linearity in the relationship; we also included bird ID nested in tag type as random effects. We used the R package 'MASS' when the inclusion of an autocorrelation structure was necessary as 'lme4' does not allow the implementation of GLMMs with that structure.

Using the 'daily foraging strategy dataset', we explored the effect of landfill use on time and energy budgets, by implementing 3 linear mixed-effects models (LMM) with daily distance travelled (km), mean ODBA (G), and mean foraging ODBA (G) as response variables and foraging site (landfill or non-landfill), season (breeding or non-breeding), and its interaction, as explanatory variables, using the *lme* function (R package 'nlme' ver. 3.1 (Pinheiro et al., 2017)). The model with daily distance travelled as response variable, included an additional covariate, the number of GPS positions, to account for its the potential effect on the response. We implemented a GLMM with the *glmmPQL* function for relative foraging time with a binomial structure that included foraging site, season, and its interaction as fixed effects as well. All four models included bird ID nested in tag type as random effects and an autocorrelation structure of order 1. Subsequently, we calculated for each model the coefficient of determination R^2 (Nakagawa et al., 2017).

We explored the relative contribution of individuals' foraging decisions into the overall energy expenditure when using different foraging sites and during different seasons. To do so, we implemented multigroup analysis for piecewise SEM with foraging site and season as grouping variables, using the functions *psem* and *multigroup* (R package 'piecewiseSEM' ver. 2.1 (Lefcheck et al., 2016; Lefcheck, 2016)). The SEM included two sub-models: 1. an LMM with mean ODBA as the response variable, and daily distance travelled, relative foraging time and mean foraging ODBA as explanatory variables; and 2. a GLMM with relative foraging time as the response variable, and mean foraging ODBA as explanatory variables. Both models included random effects and autocorrelation structure as described above. The global structure of the SEM model was well supported according to the global goodness-of-fit: Fisher's C = 0.098 with $p = 0.952$.

To test the role of landfill specialisation on landfill exploitation we selected only days classified as landfill foraging days. We modelled a LMM with mean foraging ODBA and a GLMM with relative foraging time as the response variables, and season and specialisation index as explanatory variables. We used random effects and an autocorrelation structure as previously specified. Normality of the residuals was checked for all LMMs performed.

3. Results

We obtained two datasets of movement and acceleration data; the 'daily attendance dataset' contained data of 12,616 stork-days (median ± SE; 162 ± 28 days per individual); and the 'daily foraging strategy dataset' of 10,183 stork-days (136 ± 22 days per individual, see detailed information in Table S1and S2). During both the breeding and non-breeding season foraging occurred in southern Portugal, but during the non-breeding season white storks increased their foraging range towards southern Spain (Fig 1). All individuals but one foraged both on landfill sites and outside of landfill sites. The probability of attending landfill sites varied with season (Estimate = 0.63; SE = 0.07; $p < 0.001$); it was 60% during the non-breeding season and 44% during the breeding season. Moreover, during the breeding season, the probability of attending a landfill was constrained by the distance from the nest to the closest landfill site (Estimate = -0.16; SE = 0.03; $p < 0.001$) in a linear way (quadratic term was non-significant; $\chi 2 = 2.882$; $p = 0.09$), with individuals nesting closer to a landfill site foraging there more often (Fig 2).

White storks travelled further during the breeding season to visit landfill sites (Estimate ± SE; 27.02 ± 0.98 km) than when foraging outside landfill areas (22.01 ± 0.79 km); while during the non-breeding season, storks travelled less overall, and birds that used landfills travelled shorter distances (13.11 ± 0.82 km) than those feeding outside of landfills (15.76 ± 0.80, Table 1, Fig 3). The results for mean ODBA, relative foraging time and mean foraging ODBA were similar. The three parameters were higher during the breeding season in the days birds foraged outside landfill sites (mean ODBA 0.10 ± 0.01 G; relative foraging time 0.37 ± 0.05; mean foraging ODBA 0.19 ± 0.01 G, Table 1, Fig 3), and decreased during the non-breeding season and in days that birds foraged in landfill sites, reaching the lowest values when both conditions occurred (mean ODBA 0.07 ± 0.01 G; relative foraging time 0.26 ± 0.05; mean foraging ODBA 0.15 ± 0.01 G, Table 1, Fig 3). Thus, mean ODBA, relative foraging time, and mean foraging ODBA decreased 34.6 %, 30.1 %, and 12.4 %, respectively, from the days that birds foraged outside landfills during the breeding season to days that birds foraged in landfills during the non-breeding season.

The multigroup analysis for piecewise SEM indicated that mean ODBA increased when white storks had to travel further, when they spent a higher proportion of time foraging, and for storks that presented higher mean foraging ODBA (Table 2). The effect was stronger when foraging occurred outside of landfills during the breeding season (Fig 4). The relationship between relative foraging time and mean foraging ODBA differed depending on the foraging site (Table 2). When foraging on outside of landfills, an increase on mean foraging ODBA led to a significant increase in relative foraging time; while on landfill sites, an increase on mean foraging ODBA led to slight decrease in foraging time (Fig 5).

Finally, we did not find any relationship between relative foraging time and landfill specialisation, and between mean foraging ODBA and landfill specialisation when birds foraged on landfill waste (Table 3).

4. Discussion

This study unravels some of the mechanisms that determine landfill use in a generalist and opportunistic species. In Iberia, expansion and population growth of white storks is widely attributed to their high adaptability and behavioural plasticity, which allow them to efficiently use opportunities provided by anthropized environments such as landfills (Catry et al., 2017; Elliott et al., 2020). Here, we show that foraging on landfill waste is a time- and energy-efficient strategy for white storks compared to foraging on natural habitats. Remarkably, although storks had to travel further to exploit this resource during the breeding period, they spent overall less energy, in terms of locomotion, than when foraging on natural prey (Fig 3). Our results indicate that this could be mediated by a reduction in foraging time and an increase in foraging efficiency (i.e. a decrease in mean foraging ODBA) while exploiting landfill waste (Fig 3). These findings contrasts with previous evidence from herring gulls (*Larus argentatus*), which increase energy expenditure 34 % when foraging on PAFS compared to natural prey (van Donk et al., 2019). These differences between species are likely to be ascribed to their flight mode; while herring gulls tend to use flapping flight, which is energetically costly, white storks soar, which allow them to fly longer distances to reach landfill sites at a cheaper energetic cost, especially at certain times of day when flight conditions (e.g. uplift) are favorable (Duriez et al., 2014).

Nevertheless, we find that white storks experience constraints during the breeding season and reduce landfill attendance to 44% of days compared to 60% in the non-breeding period. This reduction is mostly a function of distance to nest location: white storks nesting further to landfill sites visit them less often than birds nesting closer (Fig 2). These differences in foraging site preference indicate that the energetic compensation of longer flights, with increased foraging efficiency and decreased foraging time at landfill sites, compensate for longer flights only up to a certain limit, after which it is no longer beneficial to travel further to forage at landfills.

The hindrance imposed by reproduction is reflected on all the parameters that we studied; storks increased distance travelled, energy expenditure, foraging time, and mean foraging ODBA during the breeding season (Fig 3). These parameters are likely to increase in response to the spatial restrictions that impose returning to the nest frequently and the higher energetic demands derived from raising chicks (Johst et al., 2001). On the contrary, during the non-breeding period, storks are not constrained by nest location and often roost closer to landfill sites, thus reducing daily distances travelled. Moreover, foraging just to meet their own energy demands could be leading to a reduction in foraging time and daily energy expenditure.

Our results show that daily energy expenditure is highly influenced by distance travelled, foraging time and foraging efficiency, with higher energy expenditure with increasing distance travelled and foraging time and decreasing foraging efficiency (Fig 4). The slopes of these relationships were maintained when foraging at landfill sites and non-landfill sites, both during the breeding and non-breeding season. However, in all cases the intercept was lower when foraging at landfill sites, indicating that there could be other unaccounted factors decreasing the daily energy expenditure on days that birds forage at landfill sites, such as a reduction on flight energetics, a change of flight mode (soaring vs flapping), or a decrease on time spent preening.

Interestingly, we found that the relationship between relative foraging time and energy efficiency differed depending on the foraging site. At natural sites, birds with high levels of energy expenditure (low energy efficiency) during foraging, increased the time spent foraging. On the contrary, at landfill sites, birds that were less energy-efficient during foraging spent less time foraging, this effect was stronger during the non-breeding season (Fig 5). This divergence is likely to steam from the different characteristics of foraging on landfill waste versus natural prey. Individuals foraging at landfill sites, where large numbers of white storks congregate, are likely to experience easy access to food but also density dependence effects, such as direct competition from conspecifics (Oro et al., 2013). This could lead to an increase of energy expenditure during foraging due to antagonistic interactions with other individuals, but also to a reduction in foraging time, since birds could be displaced from optimal foraging sites (Burger, 1981). On natural areas, however, white storks hunt large invertebrates and small vertebrates and do not aggregate in such large numbers (Elliott et al., 2020). Thus, an increase of mean foraging ODBA is likely to be linked to active hunting, which could then favour an increase in relative foraging time.

Surprisingly, we did not find any evidence that landfill specialists experienced any competitive advantage during landfill exploitation in terms of foraging time and energy efficiency. Thus, our results suggest that landfill use is mainly driven by distance from the nest to the nearest landfill site, rather than by the ability of individuals to exploit this resource. Therefore, it is likely that white storks compete for nests located in close proximity to landfill sites (Itonaga et al., 2011; Janiszewski et al., 2015).

In this study we have quantified one of the aspects required to define optimal foraging strategies: time allocation and energy expenditure related to locomotion. However, we could not quantify energy intake, a key aspect for energetic balances. Natural prey is patchily distributed, and energetic values can be variable. For example, the energetic value of red-swamp crayfish (*Procambarus clarkii*), an invasive alien species that occurs in rice fields and is widely consumed by white storks (Ferreira et al., 2019; Negro et al., 2000; Tablado et al., 2010), is ~ 3 kJ/g (Elvira et al., 1996). On the other hand, landfill waste is abundant, easily accessible and predictable in space and time, and highly energetic (up to 10–25 kJ/g (van Donk et al., 2019, 2017)). Recent evidence shows that white stork nestlings in Iberia whose parents exploit landfill sites present better body condition and nutritional status than nestlings whose parents feed on natural resources, which complements our findings (Pineda-Pampliega et al., 2021).

However, landfill waste exploitation can also have associated costs, such as higher exposure to heavy metals, poisons, pathogens, and plastics (Ahlstrom et al., 2018; de la Casa-Resino et al., 2014; Plaza and Lambertucci, 2017; Tongue et al., 2019). For example, a recent study of white storks in Iberia found that nestlings from birds foraging on landfill waste had a higher presence of antibiotic-resistant *Escherichia coli* than nestlings from birds feeding on natural resources (Pineda-Pampliega et al., 2021); while another found that nestlings from white storks near landfill sites presented higher blood levels of lead, mercury, selenium, iron, zinc, and arsenic, which can be toxic at high concentrations (de la Casa-Resino et al., 2014). Moreover, the occurrence of plastics in landfills can lead to their ingestion, which can hurt the digestive organs of the birds (Peris, 2003).

Overall, our study shows that white storks nesting in the proximity of landfill sites and foraging there frequently save energy and time, thus exploiting landfill waste can be an advantageous strategy. Increased breeding success and population growth driven by waste exploitation has been described for other bird species (Bialas et al., 2020; Djerdali et al., 2008; Gilbert, 2015; Tauler-Ametller et al., 2017), thus a potential reduction of landfill waste could have dramatic impacts on the population, since alternative food resources might not be available to meet the energetic requirements of such large number of individuals (but see (Katzenberger et al., 2019)). In light of the European Union directives that will lead to a substantial reduction of landfill waste in the next few years, our results indicate that species that heavily rely on landfill waste will be severely affected and will have to radically change their behaviour, for example by increasing foraging time and energy expenditure while foraging, affecting energetic and time balances. However, it is currently unknown whether alternative foraging resources will be able to sustain these populations in the future.

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Authors' contributions

ASR conceived the study, carried out the statistical analyses, and drafted the manuscript; AMAF and FM coordinated the study, and critically revised the manuscript; MA processed data, collected field and behavioural data, and critically revised the manuscript; BHM collected field and behavioural data, and critically revised the manuscript; IC conceived the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

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(a) Distance travelled	Estimate	SE	*t*	*p*
Fixed effects				
Intercept	20.32	1.50	13.58	<0.001
Season	-13.90	0.81	-17.15	<0.001
Foraging site	-5.001	0.71	-7.07	<0.001
Season:Site	7.65	0.87	8.83	<0.001
GPS positions	0.23	0.04	6.05	<0.001
Random effects				
Bird ID | Tag type	4.98			
Tag type	0.01			
AR(1)	0.50			
Residual variance	15.50			
Marginal R^2	0.08			
Conditional R^2	0.17			
(b) Mean ODBA				
Fixed effects				
Intercept	0.09	0.01	10.36	<0.001
Season	-0.02	0.00	-16.24	<0.001
Foraging site	0.01	0.00	12.57	<0.001
Season:Site	0.00	0.00	-1.78	0.0755
Random effects				
Bird ID | Tag type	0.01			
Tag type	0.02			
AR(1)	0.54			
Residual variance	0.03			
Marginal R^2	0.17			
Conditional R^2	0.46			
(c) Relative foraging time				
Fixed effects				
Intercept	-0.83	0.06	14.08	<0.001
Season	-0.20	0.03	-5.82	<0.001
Foraging site	0.33	0.03	11.91	<0.001
Season:Site	-0.03	0.03	-0.90	0.3694
Random effects				
Bird ID | Tag type	0.25			
Tag type	0.05			
AR(1)	0.59			
Residual variance	1.58			
Marginal R^2	0.01			
Conditional R^2	0.03			
(d) Foraging ODBA				
Fixed effects				
Intercept	0.17	0.01	15.46	<0.001
Season	-0.02	0.002	-9.59	<0.001
Foraging site	0.02	0.002	15.42	<0.001
Season:Site	-0.02	0.002	-8.71	<0.001
Random effects				

Bird ID | Tag type	0.01			
Tag type	0.02			
AR(1)	0.32			
Residual variance	0.03			
Marginal R^2	0.15			
Conditional R^2	0.44			

Table 1: Estimates from LMMs and GLMM explaining (a) total distance travelled, (b) mean overall dynamic body acceleration (mean ODBA), (c) relative foraging time, and (d) mean foraging ODBA. Reference level for season is ‘breeding’, and for foraging site is ‘landfill’.

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(a) Model-wide Interactions	Predictor	Estimate	SE	*p*
Response				
Mean ODBA	Distance travelled			<0.001
Mean ODBA	Relative foraging time			<0.001
Mean ODBA	Foraging ODBA			<0.001
Relative foraging time	Foraging ODBA			<0.001
(b) Breeding, non-landfill				
Response				
Mean ODBA	Distance travelled	0.0005	0.0000	<0.001
Mean ODBA	Relative foraging time	0.1049	0.0020	<0.001
Mean ODBA	Foraging ODBA	0.3150	0.0091	<0.001
Relative foraging time	Foraging ODBA	0.8266	0.2827	0.0035
(c) Non-Breeding, non-landfill				
Response				
Mean ODBA	Distance travelled	0.0005	0.0000	<0.001
Mean ODBA	Relative foraging time	0.1016	0.0020	<0.001
Mean ODBA	Foraging ODBA	0.2536	0.0091	<0.001
Relative foraging time	Foraging ODBA	1.6589	0.3157	<0.001
(d) Breeding, landfill				
Response				
Mean ODBA	Distance travelled	0.0006	0.0000	<0.001
Mean ODBA	Relative foraging time	0.0985	0.0068	<0.001
Mean ODBA	Foraging ODBA	0.2218	0.0184	<0.001
Relative foraging time	Foraging ODBA	-0.0627	0.5119	0.9026
(e) Non-Breeding, landfill				
Response				
Mean ODBA	Distance travelled	0.0004	0.0000	<0.001
Mean ODBA	Relative foraging time	0.0691	0.0033	<0.001
Mean ODBA	Foraging ODBA	0.1696	0.0085	<0.001
Relative foraging time	Foraging ODBA	-0.7308	0.2773	0.0085

Table 2: Estimates from structural equation models (SEM) explaining the relationship among total distance travelled, mean overall dynamic body acceleration (ODBA), relative foraging time, and mean foraging ODBA. Estimates for (a) the whole model, (b) breeding period outside landfills, (c) non-breeding period outside landfills, (d) breeding period in landfills, and (e) non-breeding period in landfills.

(a) Relative foraging time	Estimate	SE	*t*	*p*
Fixed effects				
Intercept	-1.21	0.11	-11.29	<0.001
Season	-0.03	0.09	-0.28	0.7795
Specialisation index	0.31	0.19	1.65	0.1062
Season:Specialisation index	-0.11	0.14	-0.79	0.4323
Random effects				
Bird ID | Tag type	0.14			
Tag type	0			
AR(1)	0.25			
Residual variance	1.01			
(b) Foraging ODBA				
Fixed effects				
Intercept	0.16	0.01	11.22	<0.001
Season	-0.02	0.01	-2.51	0.0120
Specialisation index	0.01	0.01	0.42	0.6756
Season:Specialisation index	0.01	0.01	0.82	0.4142
Random effects				
Bird ID | Tag type	0.01			
Tag type	0.02			
AR(1)	0.10			
Residual variance	0.03			

Table 3: Estimates from GLMM and LMM explaining (a) relative foraging time, and (b) mean foraging overall dynamic body acceleration (ODBA), while foraging on landfills. Reference level for season is ‘breeding’.

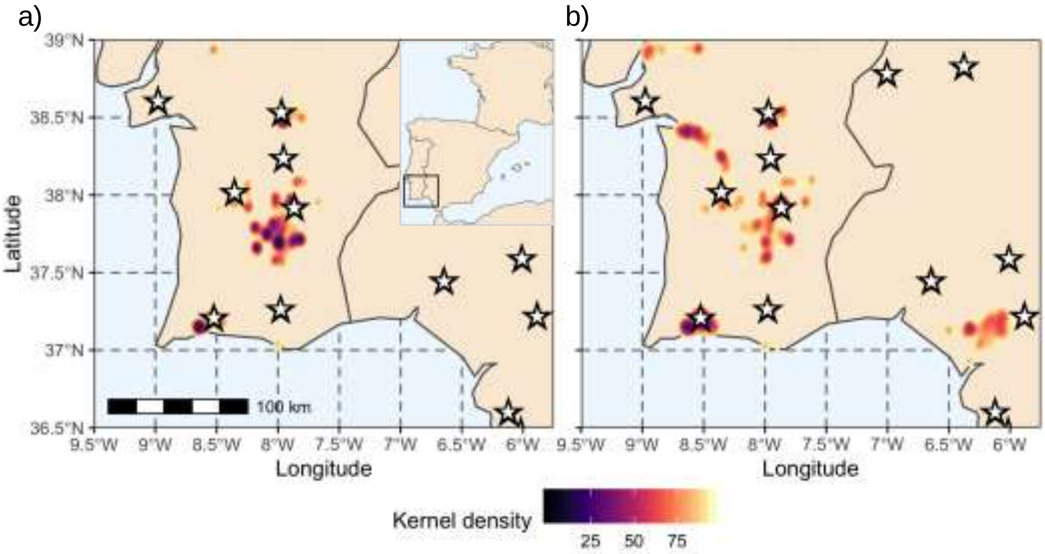

Figure 1: Foraging areas of tracked white storks in southern Iberia (Portugal and Spain) between 2016 and 2019 during a) the breeding and b) the non-breeding periods. Stars indicate landfill sites.

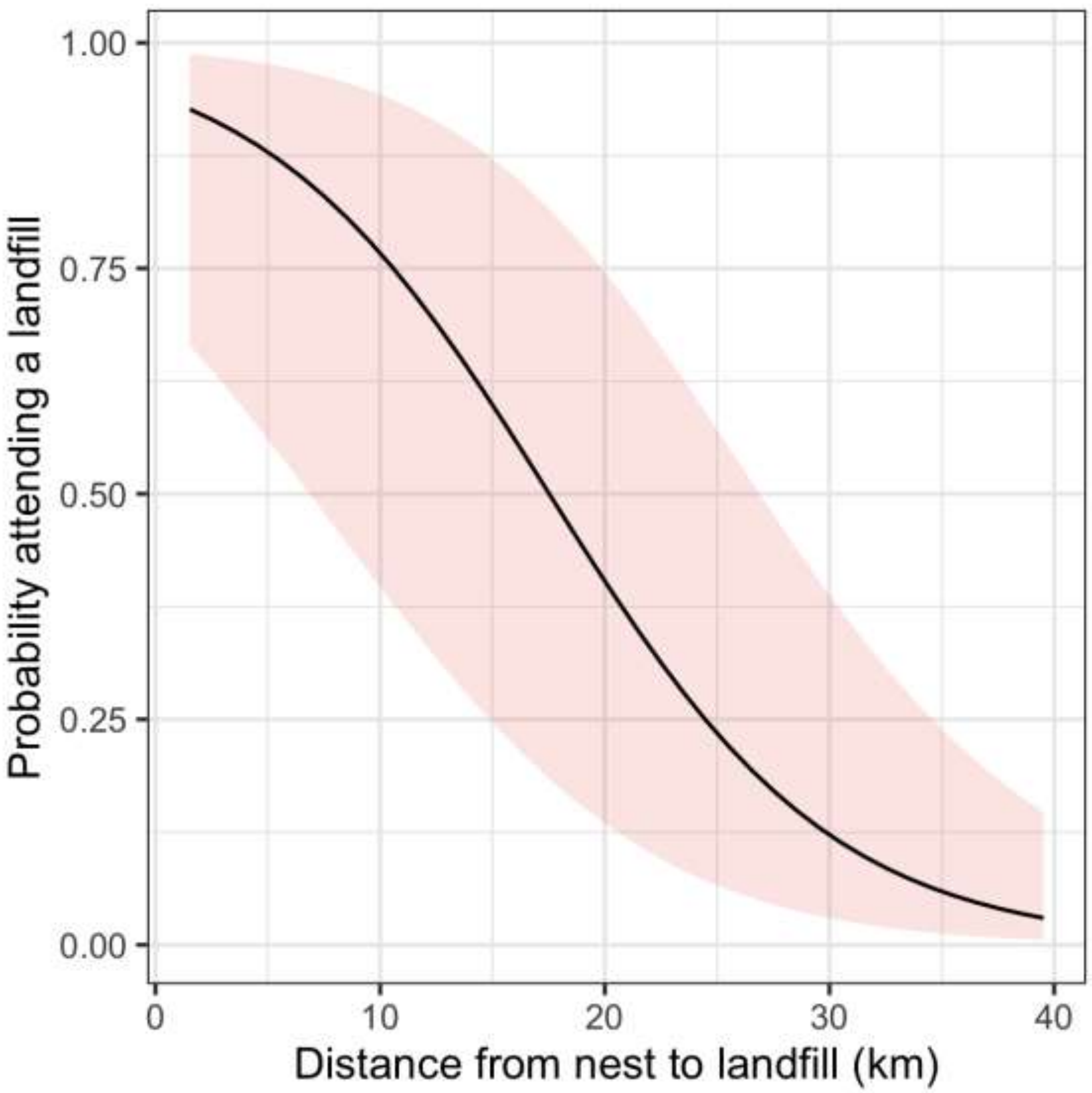

Figure 2: Estimates from GLMMs explaining the probability of white storks attending a landfill during the breeding season as a function of the distance from the nesting site to the closest landfill.

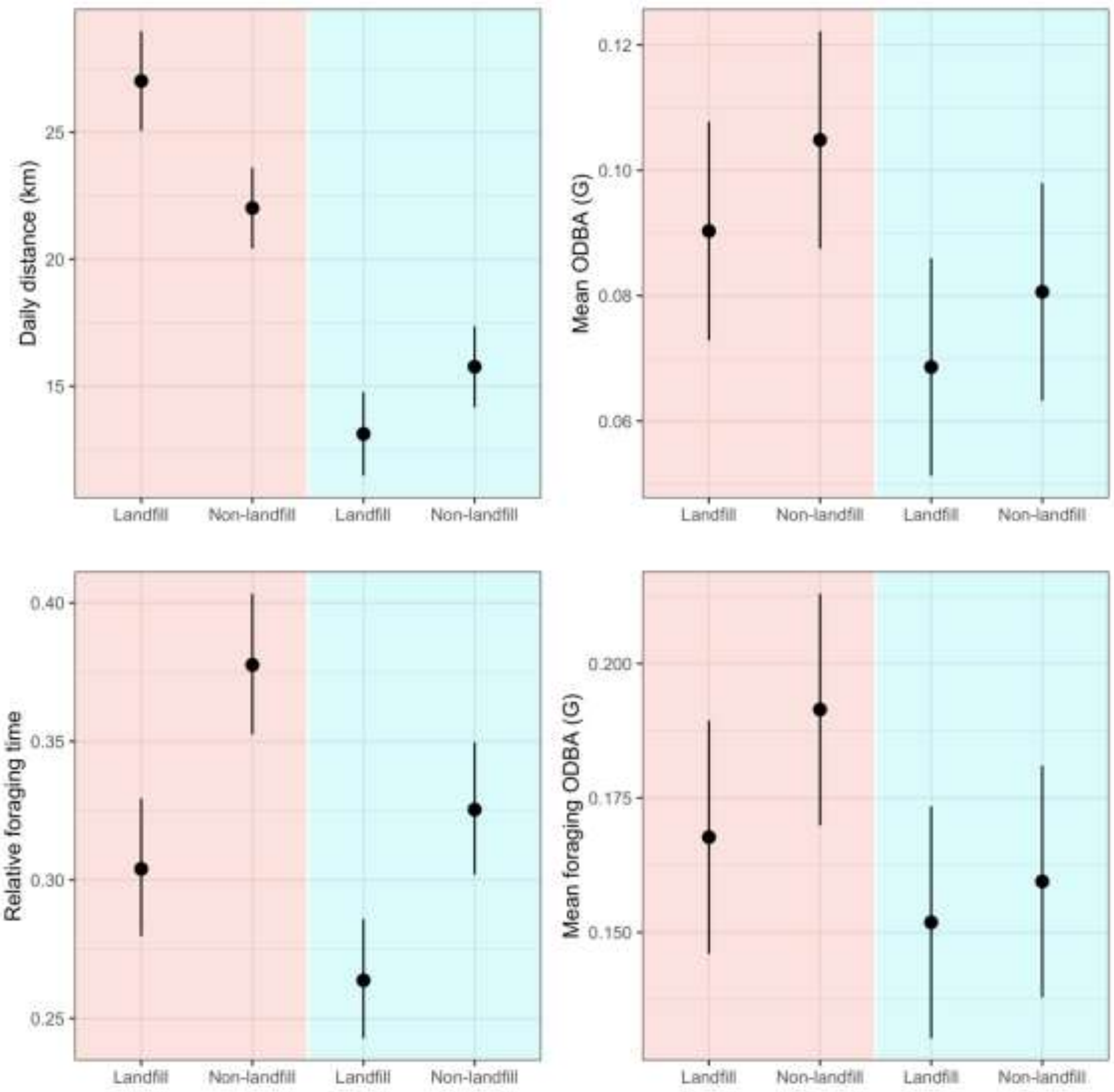

Figure 3: Predicted values and 95 % confidence intervals from GLMMs explaining (a) daily distance travelled, (b) mean overall dynamic body acceleration (ODBA), (c) relative foraging time, and (d) mean foraging ODBA of foraging white storks, as a function of season (breeding or non-breeding) and foraging site (landfill or non-landfill).

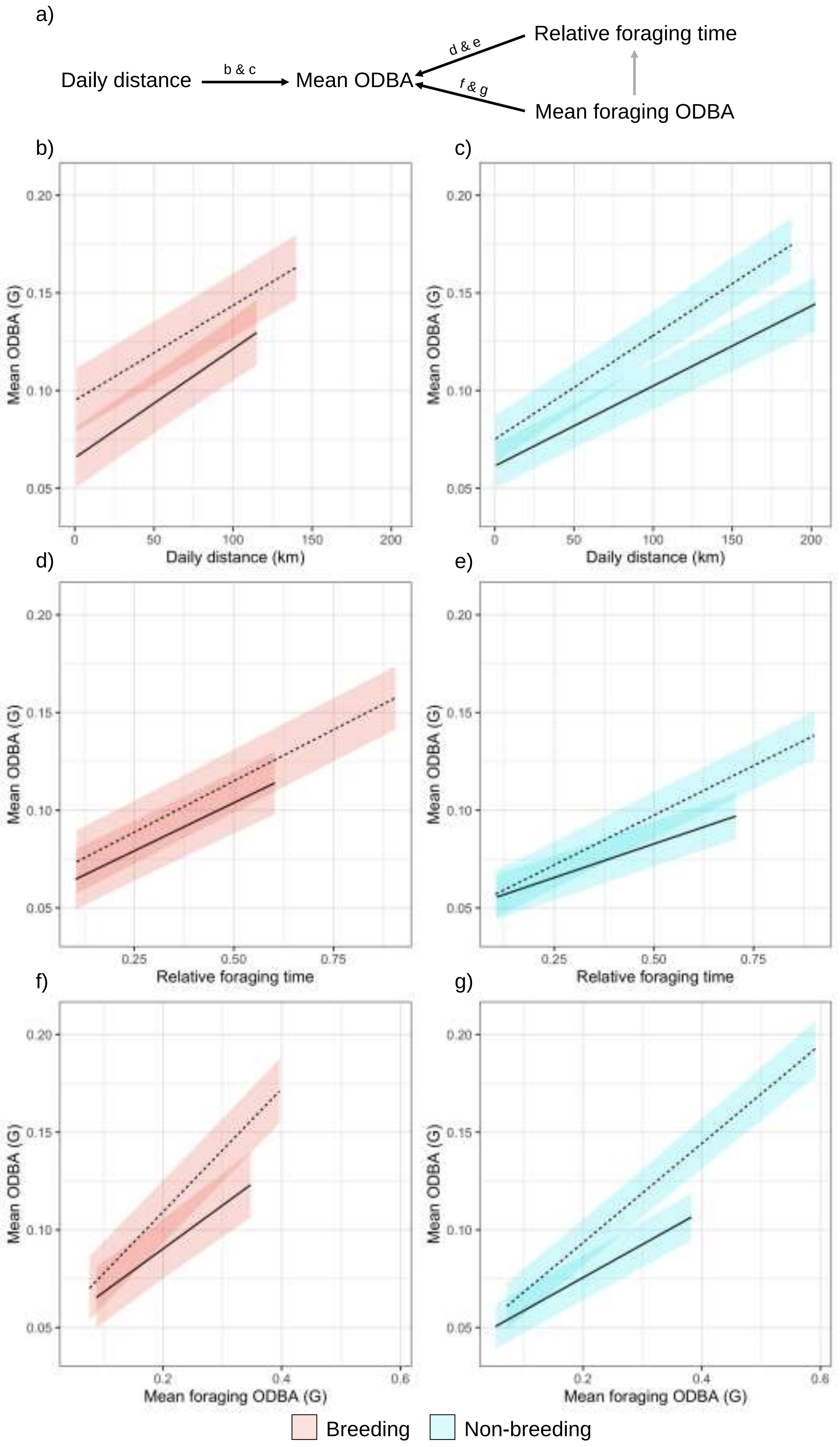
a)
Daily distance
b & c
Mean ODBA
d & e
f & g
Relative foraging time
Mean foraging ODBA
b)
c)
d)
e)
f)
g)
Mean ODBA (G)
0.05
0.10
0.15
0.20
Daily distance (km)
0
50
100
150
200
Relative foraging time
0.25
0.50
0.75
Mean foraging ODBA (G)
0.2
0.4
0.6
Breeding
Non-breeding

Figure 4: (a) Graphical explanation of the structural equation model (SEM) showing the relative contribution of white storks' foraging decisions into the mean overall dynamic body acceleration (ODBA). Black arrows indicate relationships represented in the figure and the grey arrow relationship not represented in the figure. Mean ODBA as a function of daily distance travelled for (b) the breeding season and (c) the non-breeding season; mean ODBA as a function of relative foraging time for (d) the breeding season and (e) the non-breeding season; and mean ODBA as a function of mean foraging ODBA for (f) the breeding season and (g) the non-breeding season. Solid line on landfill sites and dashed line on non-landfill sites.

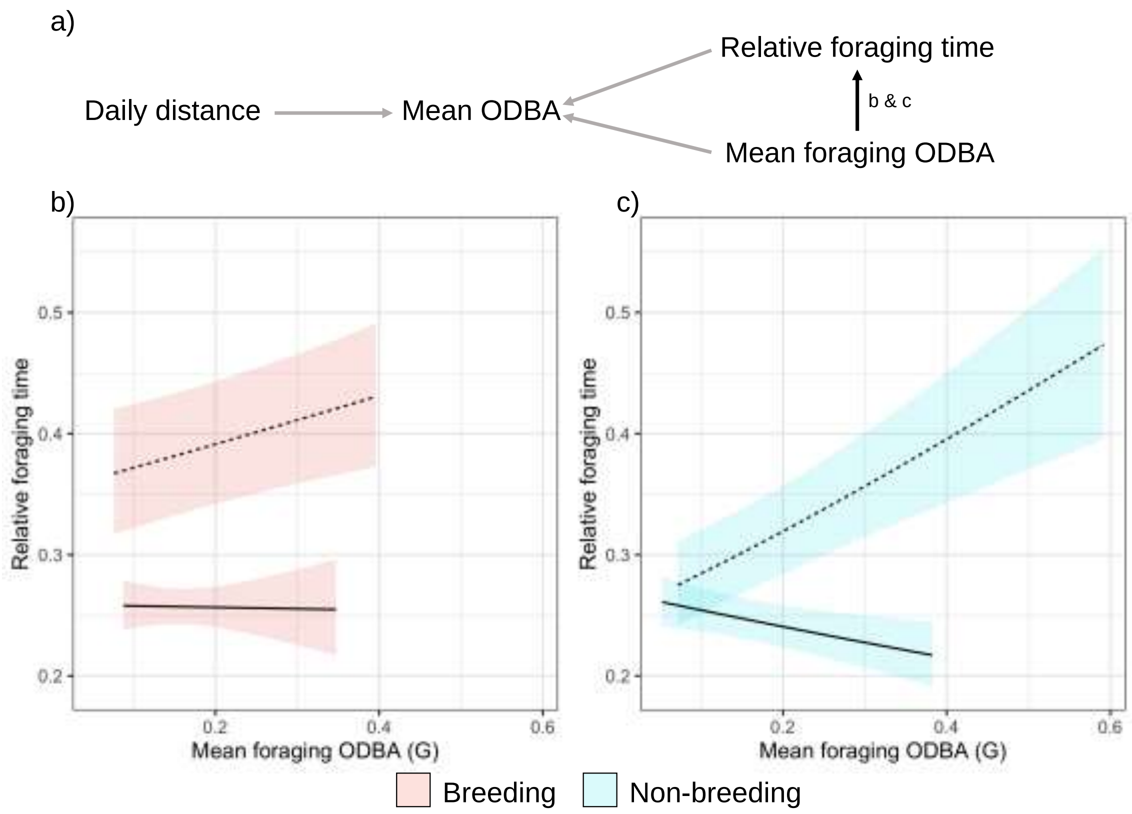

Figure 5: (a) Graphical explanation of the structural equation model (SEM) showing the relative contribution of white storks' foraging decisions into the mean overall dynamic body acceleration (ODBA). Black arrows indicate relationships represented in the figure and the grey arrow relationship not represented in the figure. Relative foraging time as a function of mean foraging ODBA for (b) the breeding season and (c) the non-breeding season. Solid line on landfill sites and dashed line on non-landfill sites.