



The trade-offs of foraging at landfills: Landfill use enhances hatching success but decrease the juvenile survival of their offspring on white storks (*Ciconia ciconia*)



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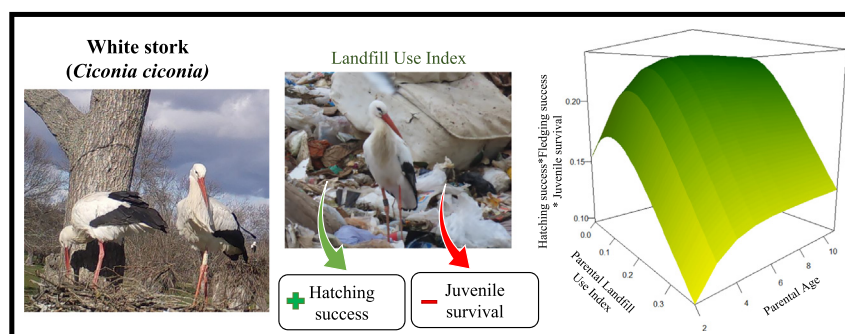
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HIGHLIGHTS

- Landfill use by parentals improves hatching success.
- Landfill use by parentals has negative effects on juvenile survival.
- Landfill use implies benefits for current reproduction but costs for future offspring survival.

GRAPHICAL ABSTRACT



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ABSTRACT

During the last decades, landfills have become a valuable food source for wildlife, being in some cases determinants of large avian population increases. Superabundant food resources at landfills can increase reproductive and/or survival parameters; however, negative effects such as intoxication, plastic ingestion, skeletal deformities, unbalanced oxidative stress, and other health problems have also been reported. White stork (*Ciconia ciconia*) commonly benefits from landfill resources. Here, we evaluate potential landfill effects on demographic parameters (reproduction and offspring survival) at the individual level in a single population.

Our results show that a more intense use of landfills by breeders has a positive effect on hatching success but a negative effect on juvenile survival probability after emancipation, at least during the first year of life. High amount of food and proximity to landfill may explain their beneficial effect on reproductive parameters. On the other hand, poor quality food, pollutants, and pathogens acquired during early development from a diet based on refuse may be responsible for reduced future survival probability. Consequently, both positive and negative effects were detected, being foraging at landfills at low to medium levels the better strategy. Although our study shows that intense foraging on rubbish can imply both costs and benefits at an individual level, the benefits of superabundant food provisioning observed at population level by other studies cannot be ignored. Management actions should be designed to improve natural food resources, reduce non-natural mortality and/or human disturbances to guarantee the species viability under current European Union regulations designed to ban open-air landfills in a near future.

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1. Introduction

Around one third of total worldwide food production is wasted or lost in supply chains (FAO, 2011). In the European Union, this translates to 88 million tonnes of food are wasted yearly and mainly end up in landfills (Stenmarck et al., 2016), transforming these facilities in a worldwide, predictable, abundant, and anthropogenic food resource for wildlife. Since feeding on landfill facilitates food accessibility, reduces energetic costs typically associated with food foraging on wilderness, and diminishes competition for feeding resources, it implies several benefits to landfill scavengers at both population and individual levels (Oro et al., 2013; Plaza and Lambertucci, 2017). As a consequence, a large diversity of animal species have changed their behaviour to take advantage of anthropogenic food refuse (Oro et al., 2013; Plaza and Lambertucci, 2017). The superabundant food provided by landfills can improve the body condition as well as the reproductive parameters of species exploiting these resources (Auman et al., 2008; Djerdali et al., 2016a; Eley et al., 1989; Steigerwald et al., 2015; Tortosa et al., 2003). Furthermore, easy food access and predictability associated with landfills imply an increase on individual survival (Eley et al., 1989; Rotics et al., 2017). Thus, for some species, landfill use promotes population growth and plays a key role for the recovery of vulnerable or endangered species (Tauler-Ametller et al., 2017).

Anthropogenic leftovers are, however, usually poor-quality food (Grémillet et al., 2008; Murray et al., 2018) and, in landfills, organic waste is mixed with other non-beneficial items (e.g., metals, plastics, glasses, wires, and different toxic products or pollutants) that may cause amputation, suffocation, and/or intoxication (Matejczyk et al., 2011). Nutrition is a key component of animal health, particularly on early development, with important consequences on future phenotypic traits (Lindström, 1999). Lack of essential micronutrients linked to low quality food available at dumps could modify morphological or behavioural traits and jeopardize future individual survival (Catoni et al., 2008; Noguera et al., 2015; Richardson et al., 2019). In the same vein, dense aggregations of individuals in predictable rubbish subsidies may also involve a wide range of health issues on immune system including higher probabilities of pathogen transmission which potentially effects reproduction and/or survival (Becker et al., 2015; Plaza and Lambertucci, 2018). Finally, landfills favour aggregation of breeding individuals in their periphery (Bialas et al., 2020), reducing the time that breeders spend away from their breeding sites (Moritzi et al., 2001). These animals are attracted by food abundance, which would lead to an increase of competence (i.e. nesting places) (Djerdali et al., 2016a; Gilchrist and Otali, 2002). In summary, both positive and negative effects on life history traits that play a key role on population dynamics can occur as a consequence of landfill use by wildlife (Oro et al., 2013).

The white stork (*Ciconia ciconia*) is a good model species to study landfill use effects on wildlife. The white stork is a species for which numerous positive effects of increased food availability at landfills have been described (Cheng et al., 2019; Djerdali et al., 2016b; Rotics et al., 2017; Tortosa et al., 2002). European populations experienced dramatic declines and became endangered after the 50s, but most of them have evidenced dramatic population recoveries over the last 30 years associated to an increasing use of landfills, among other factors (Barlein, 1991; Blanco, 1996; Masseurin-Challet et al., 2006; Schulz, 1999; Tortosa et al., 2002). Specifically, storks nesting near landfills show bigger clutch sizes, increased egg viability, nestling survival, and number of fledglings (Djerdali et al., 2008, 2016a, b; Tortosa et al., 2002). Moreover, the appearance and increased availability of predictable feeding resources during the last decades across Europe resulted in shortened migration distances, new wintering areas closer to breeding areas, shifts on passage at Strait of Gibraltar, or complete migration suppression resulting in enhanced survival probabilities of juveniles and adults at a population level (Cheng et al., 2019; Ciach and Kruszyk, 2010; Rotics et al., 2016, 2017; Sanz-Aguilar et al., 2015; Zurell et al., 2018). On the other hand, negative effects of anthropogenic food resources have also been

shown for white storks such as plastic or rubber band ingestion, leg deformation by strings or wires (Kwieciński et al., 2006; Peris, 2003), accumulation of metals, metaloids, PCBs, brominated flame retardants, and a variety of pathologies linked to this pollutants (De la Casa-Resino et al., 2015a; Martín-Maldonado et al., 2020; Muñoz-Arnanz et al., 2011; Pérez-López et al., 2016; Saez et al., 2009; Smits et al., 2005, 2007).

Overall, despite the inconveniences of foraging at landfills, positive effects of landfill use on demographic parameters (i.e., reproduction and survival) at the population level are well known and have been documented for several stork populations. However, populations are typically composed of individuals with different behaviours (Araújo et al., 2011; Bolnick et al., 2003). Variability in individual experience, competitive abilities, optimization criteria, or physiological requirements could tip the scale to exploiting landfills instead of agricultural or other "natural" feeding areas (Sanz-Aguilar et al., 2015). Consequently, individuals within a single population could experience differential reproductive or survival prospects associated to their use of foraging resources available at landfills.

In this study, we evaluate the demographic effects of individual foraging on landfills on reproductive parameters and offspring survival. We expected that higher use of predictable and abundant food resources at landfills may positively associate to demographic parameters as a consequence of extra-food supply (Oro et al., 2013). However, foraging on junk food could also generate impacts on future survival of nestlings. The effects may be positive if the potential quantity of food is more important than the quality of food, or negative otherwise.

2. Materials and methods

2.1. Study area

We monitored the biggest white stork breeding colony in the Madrid region (Prado Herrero, 40.44 N, 3.49 W; Spain) from 1999 to 2019 (Aguirre and Atienza, 2002). The colony is located within a private cattle farm inside a protected area (Cuenca Alta del Manzanares Regional Park) and has experienced substantial growth during the last 20 years (55 breeding pairs in 1999; 163 in 2002; 179 in 2019). It is located 12 km from the second largest landfill in the Madrid region (Colmenar Viejo, 40.39N 3.44W).

From 1999 to 2002, the colony was surveyed at least twice a month in February and March to identify breeders previously marked with PVC rings using telescopes (20 × 30–60). We considered as breeders the individuals that were observed constructing, defending, or perching on nests. Moreover, from the end March to July the colony was visited to collect data on clutch size, number of hatched nestlings and fledglings, and to mark nestlings (see Aguirre and Vergara, 2009 for further details). For each nest, we calculated hatching success (the ratio between number of nestlings and number of eggs laid) and fledgling success (the ratio between the number of fledglings and nestlings). Chicks with less and more than 40 days from hatching were considered nestlings and fledglings, respectively (Jovani and Tella, 2004). During the study period, one or the two breeders from 36 breeding pairs were individually identified at the breeding colony based on alphanumeric PVC rings. Age of marked breeders, ranging from 2 (3rd calendar year) to 11 years old (12th calendar year), was determined by their year of ringing because all individuals were marked as nestlings (more detailed information in Appendix A, Table A.1). For 30 pairs only one member was ringed but for 6 pairs both members were ringed: in 5 pairs both members had the same age and in one case they differ by one year-old.

2.2. Landfill use and individual data

Colmenar Viejo Landfill was visited regularly (at least once a week) between 1999 and 2002, always from noon to sunset (during 2 to 3 h of

observation), when storks were concentrated foraging in largest numbers and to avoid peaks of activity by rubbish trucks (Blanco, 1996).

Using observations of marked storks at the landfill during the breeding season (March to June), we created an individual *Landfill Use Index* as a proxy of the use of landfill and the importance of rubbish in the diet of marked breeders and nestlings. The index was calculated as the number of observations of one particular bird within the total number of visits to landfill per year.

2.3. Reproductive parameters modelling

To evaluate the effect of Landfill Use Index by breeders on breeding success, we performed General Linear Mixed Models (GLMM) with *clutch size*, *number of nestlings*, *number of fledglings* (with a Poisson error distribution and a logit link function), and *hatching success and fledging success* (with binomial distribution and logit function) as response variables. The factors analysed were Landfill Use Index, parental age and year, and their interactions. For those pairs in which both members were marked ($N = 36$), we used the average age and Landfill Use Index of both parents to avoid pseudo-replication in the data. Parental age was included in all analyses to control for a potential effect of individual breeding experience, as age in the white stork has been previously related with breeding performance (Nevoux et al., 2008; Schaub et al., 2005; Vergara et al., 2007; Vergara and Aguirre, 2006). Year of breeding was also included as a factor. Individual identity was considered as a random factor to avoid pseudo-replication (Hurlbert, 1984). Models were performed with package “lme4” in R 3.2.3 (<https://www.r-project.org/>). Sample sizes varied among models (see the Results section) because we were unable to collect clutch size or number of fledglings in all nests.

Model selection was based on the Akaike's Information Criterion corrected by sample size (AICc) (Burnham and Anderson, 2002). Models were ranked based on the differences between the AICc of a given model and the AICc of the model with the lowest AICc ($\Delta AICc$) and models with a $\Delta AICc < 2$ points were considered equivalent (Burnham and Anderson, 2002). To minimise the potential for overfitting and significance-by-chance effects, models included those single variables and interactions that ranked lowest AICc.

2.4. Survival modelling

We studied future survival of nestlings marked between 1999 and 2002 in our study area by means of capture-recapture models (Lebreton et al., 1992). As we were interested in evaluating the potential effects of parental food provisioning on future individual survival, we only considered for our analyses those individuals marked at nests in which at least one parent was identified by PVC rings, resulting in 130 birds that were descendants from 26 breeders (i.e. 26 families of storks). To build life histories, we considered seeing “1” or not seeing “0” each year, independently of the number of individual resighting per year. We also calculated a field effort covariate based on the standardised number of visits to Colmenar Viejo per year as a potential predictor of resighting probabilities.

We used the software U-CARE 2.2.2 (Choquet et al., 2009a) to assess goodness-of-fit of the Cormack Jolly Seber model (CJS) with two age classes ($\phi_{2a,t}$, p_t) to our data (Pradel et al., 2005). As individuals were marked as nestlings, all the models considered at least two age classes in survival (Pradel et al., 2005). Goodness of fit tests indicated a good fit of the data ($\chi^2 = 25.857$, $df = 24$, $p = 0.360$) and an overdispersion inflation factor ($c\text{-hat} = 1.077$) was applied to all models (Burnham and Anderson, 2002).

We started from a general model including age dependent variation in survival (3 biologically meaningful age classes, see below) and resighting probabilities (2 biologically meaningful age classes, see below), and temporal variation for resighting parameters. Since juveniles (in their first year of life) return late to breeding areas or

even remain their first year in Africa while adults could even not migrate, we considered that first year resighting probability may differ from that of older individuals (Cuadrado et al., 2016; Doligez et al., 2004; Martín et al., 2016; Nevoux et al., 2008; Shephard et al., 2015). Regarding survival, previous studies have demonstrated that: Survival differs between first year and older individuals (Barbraud et al., 1999; Nevoux et al., 2008; Schaub et al., 2005); survival differs among first year (juveniles), second year (subadults or young breeders), and individuals from 3 years old onwards (breeding individuals) (Kanyamibwa et al., 1993); and survival differs among first year (juveniles), individuals from 2 to 5 year-old (young-breeders starting reproduction, here after young breeders) and individuals from 6 years old onward (experienced breeding adults) (Doligez et al., 2004; Nevoux et al., 2008). In our case, and given that storks start breeding at age 2 in our study area (Vergara and Aguirre, 2006), we used this last structure to start model selection.

We started model selection by testing the effect of time, the potential effect of effort devoted to identify marked birds, and the effect of age on resighting probabilities. Once we identified the best structure for resighting parameters, we tested alternative age structures for survival. Using the retained basic structure of resighting and survival parameters, we tested our hypothesis of interest on survival probabilities. For that purpose, we included three variables that could affect offspring survival: a) Landfill Use Index: “poor” quality food provided by parents during early development could affect survival on different life-stages, b) Parental age: older parents have more experience and may have a better performance in parental care improving offspring survival (Vergara et al., 2007; Vergara and Aguirre, 2006), and c) Family effect: since individuals from the same pair share similar genes, parental care, and parental diet, their survival probability could be more similar (Choquet et al., 2013). The effects of parental age and Landfill Use Index were modelled as individual covariates affecting future survival. The potential effect of familiarity (parents-offspring quality on the survival probabilities of siblings) was assessed and included the family identity as a random cluster effect (Choquet et al., 2013). The factors potentially affecting survival were first tested on juvenile survival. As the immediate effects in early life are the more plausible and if significant, we tested for long-lasting effects when young breeders and adults. Models were built and fitted to the data using E-SURGE 2.1.4 software (Choquet et al., 2009b). Model selection was based on Akaike's information criterion by overdispersion and sample size (QAICc) (Burnham and Anderson, 2002). The effect of covariates was statistically significant when beta estimate corresponding to the linear slope did not include zero. To determine significance of cluster effect we performed an LRT test for the random effect(s) on the best fixed-effect model at the 5% significance level (Choquet et al., 2013).

2.5. Combined effects of landfill use on reproductive parameters and future offspring survival

In order to better assess the effects of foraging at landfills on parental fitness we estimated the probabilities of having that a laid egg becomes a one-year-old stork by multiplying the estimated values of hatching success, fledging success and juvenile survival from best models in model selection (Tables 1 and 2 in the Results section).

3. Results

During the course of the study (1999–2002), Landfill Use Index ranged between 0 and 0.36, with no differences with breeders age ($\beta = -0.019 \pm 0.112$, $Z = -0.16$, $p = 0.873$) or between years ($\chi^2 = 1.339$, $df = 3$, $p = 0.720$).

Table 1

Reproductive parameters in relation to Landfill Use Index by breeders, age of breeder, and year of breeding. We include additive (+) and interaction (*) effects. Estimates and 95% confidence intervals (CI) were calculated by model averaging of models with a $\Delta AIC < 2$. In bold best models and variables receiving strong support (i.e., the 95% confidence interval did not overlap with zero).

Model selection						Model averaging			
M	Effects	K	AICc	$\Delta AICc$	w	Variable	Est	2.5%CI	97.5%CI
Clutch size									
M_c1	Null	2	169.27	0.00	0.34	Age	0.04	-0.02	0.09
M_c2	Age	3	169.93	0.66	0.25	Landfill	-0.78	-2.54	0.97
M_c3	Landfill	3	170.76	1.49	0.16				
M _c 4	Landfill + Age	4	171.61	2.34	0.11				
M _c 5	Year	4	172.99	3.72	0.05				
M _c 6	Landfill * Age	5	173.73	4.46	0.04				
M _c 7	Age + Year	5	173.84	4.57	0.04				
M _c 8	Landfill + Year	5	175.02	5.75	0.02				
M _c 9	Landfill * Age + Year	7	178.53	9.26	0.00				
Number of nestlings									
M_n1	Null	2	195.88	0.00	0.24	Age	0.04	-0.02	0.10
M_n2	Age	3	196	0.12	0.22	Year2000	0.29	-0.49	1.07
M_n3	Year	5	197	1.12	0.14	Year2001	0.16	-0.53	0.86
M_n4	Landfill + Age	4	197.16	1.28	0.12	Year2002	-0.22	-0.91	0.47
M_n5	Landfill	3	197.19	1.31	0.12	Landfill	0.83	-0.78	2.44
M _n 6	Age + Year	6	198.58	2.70	0.06				
M _n 7	Landfill + Year	6	198.76	2.88	0.06				
M _n 8	Landfill * Age	5	199.56	3.68	0.04				
M _n 9	Landfill * Age + Year	8	203	7.12	0.01				
Number of fledglings									
M_f1	Age	3	165.55	0.00	0.49	Age	0.08	0.01	0.15
M_f2	Landfill + Age	4	167.15	1.60	0.22	Landfill	0.93	-1.19	3.04
M _f 3	Landfill * Age	5	168.36	2.80	0.12				
M _f 4	Null	2	168.86	3.30	0.09				
M _f 5	Landfill	3	170.71	5.16	0.04				
M _f 6	Age + Year	6	171.4	5.85	0.03				
M _f 7	Year	5	173.23	7.68	0.01				
M _f 8	Landfill + Year	6	175.58	10.03	0.00				
M _f 9	Landfill * Age + Year	8	175.6	10.04	0.00				
Hatching success									
M_{hs}1	Landfill + Age	4	52.36	0.00	0.32	Landfill	9.45	0.50	18.39
M_{hs}2	Landfill	3	53.26	0.91	0.20	Age	0.25	-0.05	0.55
M _{hs} 3	Landfill + Year	5	54.76	2.40	0.10				
M _{hs} 4	Landfill * Age	5	54.88	2.52	0.09				
M _{hs} 5	Age + Year	5	55.28	2.92	0.08				
M _{hs} 6	Year	4	55.32	2.96	0.07				
M _{hs} 7	Age	3	55.65	3.29	0.06				
M _{hs} 8	Null	2	56.28	3.92	0.05				
M _{hs} 9	Landfill * Age + Year	7	56.95	4.59	0.03				
Fledging success									
M_{fs}1	Age	3	27.45	0.00	0.61	Age	0.91	0.13	2.63
M _{fs} 2	Landfill + Age	4	29.71	2.26	0.20				
M _{fs} 3	Null	2	31.28	3.83	0.09				
M _{fs} 4	Landfill * Age	5	31.91	4.46	0.07				
M _{fs} 5	Landfill	3	33.43	5.98	0.03				
M _{fs} 6	Year	5	36.98	9.53	0.01				
M _{fs} 7	Landfill + Year	6	39.62	12.17	0.00				
M _{fs} 8	Age + Year	5	55.28	27.82	0.00				
M _{fs} 9	Landfill * Age + Year	7	56.95	29.50	0.00				

Note: terms are **M**, model abbreviation; **np**, number of parameters; **AICc**, Akaike information criterion corrected for small sample size; $\Delta AICc$, the AICc difference between the current model and the one with the lowest AICc value; **w**, Akaike weights; **Est**, estimate; **Landfill**, Landfill Use Index; **Age**, breeder's age.

3.1. Reproductive parameters

Reproductive parameters in the studied colony were: clutch size (mean = 3.44 ± 0.40 eggs, range 0–5, n = 45 nests), number of hatchlings (mean = 2.48 ± 0.34 , range 0–5, n = 56 nests), and number of fledglings (mean = 2.14 ± 0.37 , range 0–4, n = 49 nests).

In absolute numbers, landfill use did not influence clutch size, number of nestlings, or number of fledglings (Table 1). In fact, for clutch size and number of nestlings, the null model was the best one (Table 1), while for number of fledglings the best model included age and landfill effects (Table 1). However, the 95% CI of the model averaged estimates indicate that only the age effect was significant.

On the contrary, when the relative success of the nest was modelled, model selection indicated that individuals using landfill with more intensity had a higher hatching success of their clutches (Model M_{hs}1 and M_{hs}2, Table 1) (Fig. 1). Regarding fledgling success, we detected a significant increase with breeder's age (Model M_{fs}1, Table 1) but not an effect of landfill use (Table 1).

3.2. Offspring survival

We started model selection by testing different hypotheses on resighting probabilities (Table A.2, Appendix A). Our results indicated that resighting probabilities varied with the effort invested in field

Table 2

Modelling of white stork survival probabilities depending on age structure (up to 3 age classes with biological meaning, see **Materials and methods** section), age of parents, Landfill Use Index by parents, and family resemblance (cluster effect). Recapture probabilities were modelled as a function of 2 age classes (first year vs. older birds) and temporal variations in field effort equally affecting both age classes (see Table A.2 Appendix A).

Model	Survival hypothesis	np	Deviance	QAIC _c	ΔQAIC _c
1s	($\phi_j, \phi_{yb}, \phi_{ad}$) + landfill	7	510.53	488.45	0.00
2s	$\phi(j, \text{landfill}), \phi_{yb}, \phi_{ad}$	7	510.59	488.51	0.06
3s	(ϕ_j, ϕ_{yb}) + landfill, ϕ_{ad}	7	488.32	488.74	0.29
4s	$\phi(j, \text{landfill}), \phi_{yb}, \text{landfill}, \phi_{ad}$	8	510.07	490.15	1.70
5s	$\phi_j, \phi_{yb}, \phi_{ad}$	6	516.25	491.66	3.20
6s	$\phi(j, \text{parental age}), \phi_{yb}, \text{landfill}, \phi_{ad}, \text{landfill}$	9	509.46	491.73	3.27
7s	$\phi_j, \phi_{yb}, \text{landfill}, \phi_{ad}$	7	515.10	492.70	4.25
8s	$\phi_j, \phi_{yb}, \phi_{ad}, \text{landfill}$	7	515.29	492.88	4.42
9s	$\phi(j, \text{family}), \phi_{yb}, \phi_{ad}$	7	516.04	493.57	5.12
10s	$\phi(j, \text{parental age}), \phi_{yb}, \phi_{ad}$	7	516.13	493.66	5.20
11s	$\phi_{j=yb}, \phi_{ad}$	5	523.11	495.94	7.49
12s	$\phi_j, \phi_{yb2}, \phi_{yb3-5=ad}$	6	523.09	498.01	9.56

Note: terms are **np**, number of parameters; **QAIC_c**, Akaike information criterion corrected for overdispersion and small sample size; **ΔQAIC_c**, the QAIC_c difference between the current model and the one with the lowest QAIC_c value; **j**, juvenile (first year individuals); **yb**, young breeder including 2 to 5 years individuals; **yb2**, second year individuals; **yb3–5**, young breeder from 3 to 5 years old; **ad**, adult birds with 6 or more years old; **landfill**, parental Landfill Use Index effect; **parental age**, parental age effect on offspring survival; **family**, cluster effect regarding to sibling resemblance.

monitoring over the study period and were lower for first year individuals (Model 1p, Table A.2, Fig. A.1 in Appendix A).

For survival, different age structures (i.e., no differences in survival between young breeders (ages 2 to 5) and adults (age > 5) or differences in survival among youngest breeders (age 2) and older adults (age > 2)) did not reduce the QAIC_c of the general model (Table 2). Consequently, we used the general and biologically meaningful age structure (Model 5s, Table 2) for testing the hypotheses of interest. Mean survival probabilities for juveniles, young breeders (ages 2 to 5), and older adults (age > 5) were 0.34 (95%CI = 0.25–0.44), 0.75 (95%CI = 0.64–0.83), and 0.92 (95%CI = 0.83–0.96), respectively (Model 5s, Table 2).

Parental age did not affect survival probabilities of offspring (Model 10s, Table 2), as the model did not reduce the QAIC_c value of model 5s and the 95%CI intervals of the beta estimate accounting for parental

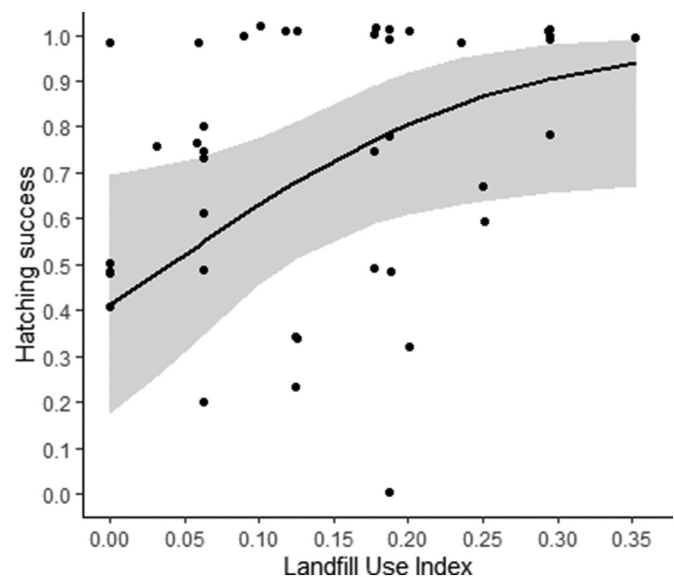


Fig. 1. Hatching success in relation to Landfill Use Index (and 95% CI given by shaded area) (Model M_{h52}, Table 1).

age largely overlapped zero (95%CI β: −1.29, +1.78). Similarly, family identity did not have a significant effect on offspring survival ($\chi^2 = 0.19, p = 0.33$; Models 9s, Table 2). On the contrary, models including an effect of the Landfill Use Index by parents on survival probabilities of offspring greatly reduced the QAIC (Table 2). Four models were equivalent in terms of QAIC_c, having less than 2 points of QAIC_c difference among them (Models 1s–4s, Table 2). All of them included an effect on juveniles, but some of them also included an effect on young breeders (Model 3s, 4s) or older adults (Model 1s). The effect on juveniles was clear (Model 2s; 95%CI β: −9.64 to −0.58) but the effect on adults was only significant (i.e., the 95%CI of beta estimate did not include zero) when considered as additive (Models 1s, 3s) but not when a single slope (i.e., interaction) was applied to young and old adult survival (e.g., Model 3s; Young breeders: 95%CI β = −1.15, 95%CI: −6.88 to +4.58.; Older adults: 95%CI β = −4.66, 95%CI: −15.93 to +6.61). The effect of parental landfill use on offspring survival was negative: individuals whose parents showed a lower use of the landfill had higher survival probabilities (Fig. 2).

3.3. Combined effects of landfill use on reproductive parameters and future offspring survival

Probability that a laid egg becomes a one-year-old stork was higher for older breeders with a low to moderate landfill use (Fig. 3). An intensive landfill use index, although beneficial for hatching success implied high juvenile mortality, resulting in costs for parental fitness (Fig. 3).

4. Discussion

Despite the typical benefits of foraging at abundant and highly predictable food supplies provided by landfills described in the literature (see references in Oro et al., 2013; Plaza and Lambertucci, 2017), our study highlights the existence of higher costs at individual level. In agreement with previous studies, our study reveals that a more intense landfill use by breeders can increase hatching success (Djerdali et al., 2008, 2016a; Tortosa et al., 2003) but not fledging success, clutch size of the total number of fledglings produced. However, breeders foraging intensively at landfills pay fitness costs in terms of future offspring survival. Our study highlights the existence of trade-offs at individual level: the absence of landfill foraging or an intense landfill use implied lower probabilities of having a one year-old descendent. On the contrary, storks with low to medium Landfill use index were the more successful.

Several studies provide evidence that white storks breeding near landfills have higher reproductive parameters and survival prospects than individuals from populations located at more “natural” areas (Djerdali et al., 2008, 2016a; Massemin-Challet et al., 2006; Rotics et al., 2017; Tortosa et al., 2002, 2003). Here, at Prado Herrero colony, productivity parameters (see the Results section) were relatively lower than in other European populations breeding near landfills (clutch size = 4.1 to 4.6, nestlings = 3.6, fledglings = 2.4 to 3.2) (Barbraud et al., 1999; Massemin-Challet et al., 2006). The number of fledglings was quite similar to those documented for eastern European populations not foraging intensively at landfills (fledglings = 2.1 to 2.3) (Fasolă-Mătăsarú et al., 2018; Tobolka et al., 2013, 2015). Similarly, hatching success (0.73 ± 0.09) and fledging success (0.88 ± 0.08) were similar to other of European “natural” populations not foraging at landfills (hs = 0.79, fs = 0.67 to 0.95) (Barbraud et al., 1999; Massemin-Challet et al., 2006). Mean survival of juveniles (0.34, 95%CI = 0.25–0.44) and young breeders (0.75, 95%CI = 0.64–0.83) was similar, while adult survival (0.91, 95%CI = 0.83–0.96) was slightly higher to that estimated for other European populations (j = 0.33 to 0.60; ad = 0.78 to 0.86 (Barbraud et al., 1999; Nevoux et al., 2008; Schaub et al., 2005)). Therefore, mean demographic parameters of the Prado Herrero colony were more similar at the population level to those exhibited by European storks foraging at natural areas, even with being located near a landfill. These results seem to indicate that

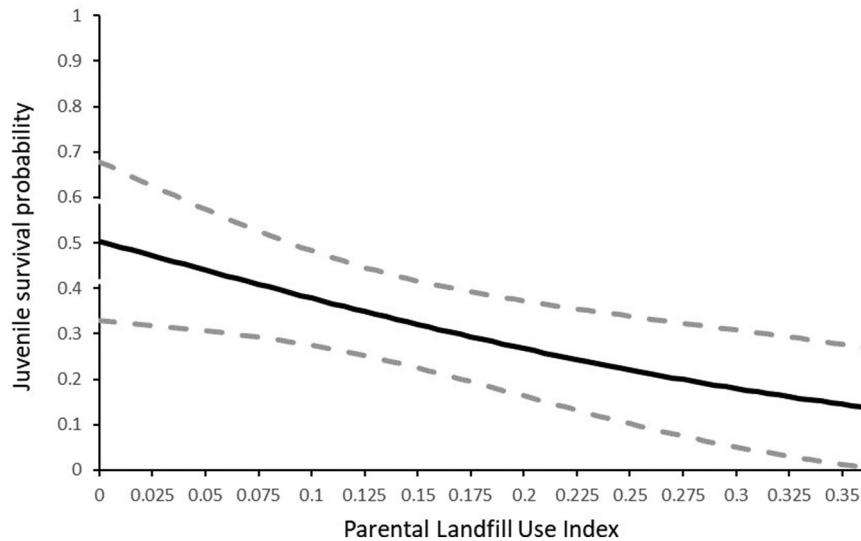


Fig. 2. Effect of Landfill Use by parents on future juvenile survival probability (and 95% CI given by dashed lines). Survival values change as a function of the Landfill Use Index described by Logit (ϕ_j) = 3.1519 + (-3.35287 * Landfill Use Index).

this population may partially feed on landfill but not depend totally on landfill refuses.

Population level variation among individuals exists: not all individuals exploit foraging resources equally (Araújo et al., 2011; Bolnick et al., 2003). The Landfill Use Index used here was calculated during the breeding season when storks barely spend time outside their nests on other activities that foraging (Gilbert et al., 2016; Moritz et al., 2001). Consequently, it may reflect quite accurately the main source of individual diet, with individuals infrequently identified in the rubbish dump probably foraging in more “natural” areas and individuals seen multiple times and considered “landfill specialists”. In this sense, previous studies on wintering areas indicate that foraging at landfills could be related to individual age, with old and experienced individuals with foraging preferences for more natural areas and potentially higher quality resources than young birds (Sanz-Aguilar et al., 2015) and lower neophobia in juvenile individuals (Cambefort, 1981). Individual variation in landfill exploitation found here differs from this previous study since age was not correlated with Landfill Use Index and other factors like morphological, physiological, or behavioural traits (i.e., personality) may influence individual diet especially during the breeding season.

The use of anthropogenic food subsidies during breeding season allows breeders to reduce the energetic costs of foraging, resulting in an

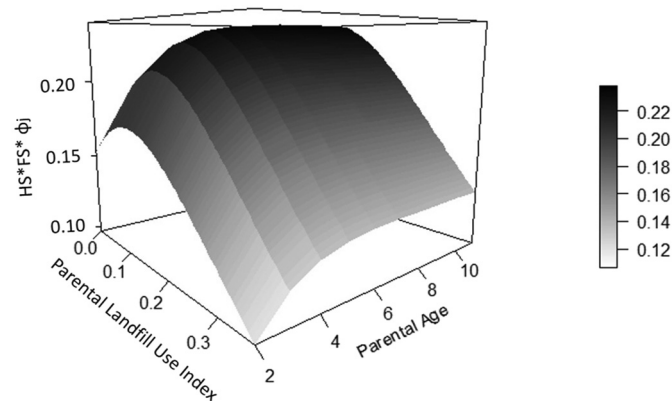


Fig. 3. Representation of the annual probability that a laid egg becomes a one-year-old stork ($HS * FS * \phi_j$) next year as a function of parental age and landfill use.

increased parental investment in nest attendance (Gilbert et al., 2016; Moritz et al., 2001). In birds, warmth and care provided by parents are crucial at incubation and during the first days of life when hatchlings are particularly sensitive to adverse weather conditions (Jovani and Tella, 2004; Tobolka et al., 2015). Therefore, higher parental care may explain incremental hatching success associated to higher landfill foraging use observed in this and previous studies (Djerdali et al., 2008). Furthermore, breeders not only would obtain food from landfills, but nest materials such as plastics, cardboard, and other items that would provide insecticide or thermoregulation benefits contribute to hatching success (Jagiello et al., 2018). As well as landfills, parental age influenced positively the productivity of the nest, particularly for fledging success, as has been previously reported for several bird species (Newton, 1989). Older individuals are more efficient obtaining food (Marchetti and Price, 1989; Rotics et al., 2016), provide a better parental care (Vergara et al., 2006, 2010; Vergara and Aguirre, 2006) return earlier from wintering areas and occupy best nests (Belabed et al., 2019; Vergara et al., 2007, 2010; Vergara and Aguirre, 2006), explaining their better performance.

Beyond positive effects of foraging at landfills on hatching success probabilities at an individual level, we did not find any landfill use effects on productivity parameters. The number of eggs, nestlings, or fledging success was similar among breeders differing in their landfill use. Other studies conclude that landfill use can increase productivity in white storks (Djerdali et al., 2008, 2016a; Tortosa et al., 2002, 2003). However, these studies were conducted at the population level comparing different populations. Differences in foraging habits of storks breeding in different populations are probably much higher than the among individual differences within populations. Moreover, in our study area all individuals have access to a close landfill being able to increase landfill exploitation when other food resources are scarce. It may mask landfill benefit on other no critical reproductive traits (Steigerwald et al., 2015).

While a higher use of landfills by breeders of the Prado Herrero colony resulted in short-term benefits in terms of hatching success, our results show a clearly negative impact on future offspring survival. The effect was especially noticeable during the first year of life when birds become independent of their parents. This first year of life is a critical period in which individuals need to grow and rapidly acquire the skills necessary to survive and early life conditions can make some individuals more prone to dying (Briga et al., 2017). Parents foraging at landfills can provide better parental care and almost unlimited food but

anthropogenic food remains are often poor quality food (Annett and Pierotti, 1999; Murray et al., 2018). Thus, offspring from parents using landfills with high intensity could be receiving low quality food during early life or even later in life if they inherit the parental foraging preferences (Annett and Pierotti, 1999). Nutrition during early development can have important consequences in adulthood (Krause et al., 2009; Lindström, 1999). For example, an antioxidant-rich diet contributes to reducing telomere attrition, and a lack of antioxidants on landfill diet may shorten life span (Tauler-Ametller et al., 2019). In addition, rooting food and health conditions in landfills stimulate presence of several pathogens (Matejczyk et al., 2011). Storks transport these pathogens from landfill to nest on their body, nesting material or food and modifying the microbiota of the nest. In fact, several harmful and multidrug-resistant microorganism have been detected in stork populations near landfills (Camacho et al., 2016; Höfle et al., 2003, 2020; Martín-Maldonado et al., 2020). Beyond this, toxic products as PCBs, flame retardants, metals, and metalloids are incorporated from a landfill diet (De la Casa-Resino et al., 2015a, 2015b; Pérez-López et al., 2016; Saez et al., 2009; Sáez et al., 2008). These pollutants are accumulated on different bird tissues and can cause health problems in white storks (e.g. skeletal deformation) (Smits et al., 2005, 2007). Therefore, the negative relationship between parental landfill use and juvenile survival may be a consequence of several potential risks associated to rubbish food resources (Henry et al., 2011; Peris, 2003). Probably the first year of life acts as a filter in which mortality processes operate more intensively and because of this the effect of a poor-quality diet during early life is not evident on survival probabilities of older storks (Payo-Payo et al., 2016).

Overall, our results show a compromise for parental fitness in using anthropogenic food resources: enhances hatching success but reduces juvenile survival probabilities. Although high levels of feeding on landfill lead to fitness costs, a low or moderate use of landfill improve the probabilities of having a surviving descendant by each egg laid. Thus, complementing natural diet by food resources available at landfills seems the optimal strategy based on results (Zorroza et al., 2020). Therefore, breeders may increase food provisioning from landfill during adverse environmental conditions and/or when offspring necessities are higher.

In conclusion, our study shows the existence of trade-offs associated with parental landfill use in the white stork that influence parental fitness: low to medium levels of use are beneficial but very low or medium to high levels of use counterproductive. However, we think that, at population level in some populations, the current benefits that anthropogenic food supplies at landfills provide to white storks may exceed the costs in terms of offspring survival reduction. Superabundant food provisioning at landfills contributed to the growth of the Spanish white stork population (Blanco, 1996; Tortosa et al., 2002). Although this population could be composed of suboptimal individuals (Genovart et al., 2010) reproducing thanks to the extremely high food abundance (Steigerwald et al., 2015), the population recovered and greatly reduced their extinction probabilities (Molina and Del Moral, 2005; Tortosa et al., 2002). Traditional foraging areas of storks are degraded due to agricultural intensification and urbanisation (Barlein, 1991; Vitousek et al., 2008). Under this scenario, and given that open air landfills, as an abundant and predictable food resource, are condemned to disappear soon due to European Union regulations (Landfill Waste Council European Directive 1999/31/CE and Directive 2018/850/EC) stork populations are expected to be heavily influenced. Management actions designed to compensate a potential future decline of stork populations could include the recovery and protection of natural traditional foraging areas, the reduction of non-natural mortality and temporal supplementary feedings areas to a soft transition between actual open landfills to new landfill management (Garrido and Fernández-Cruz, 2003; Martín et al., 2018; Molina and Del Moral, 2005; Tobolka, 2014). Otherwise, avian population that feed in landfills, such as white storks, may have an uncertain future.

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CRediT authorship contribution statement

Alejandro López-García: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Visualization. **Ana Sanz-Aguilar:** Methodology, Formal analysis, Writing – original draft, Supervision. **José I. Aguirre:** Conceptualization, Investigation, Writing – review & editing, Supervision, Project administration.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix A. Supplementary data

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