

Multi-event capture–recapture analysis reveals individual foraging specialization in a generalist species

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Abstract. Populations of species typically considered trophic generalists may include specialized individuals consistently feeding on certain resources. Optimal foraging theory states that individuals should feed on those resources most valuable to them. This, however, may vary according to individual differences in detecting or processing resources, different optimization criteria, and competitive abilities. White Storks (*Ciconia ciconia*) are trophic generalists at the population level. Their European population recovery has been attributed to increased wintering in southern Europe (rather than Africa) where they feed upon new anthropogenic food subsidies: predictable dumps and less predictable and more difficult to detect, but abundant, invasive *Procambarus clarkii* crayfishes in ricefields. We studied the foraging strategies of resident and wintering storks in southwestern Spain in ricefields and dumps, predicting that more experience in the study area (residents vs. immigrants, old vs. young) would increase ricefield specialization. We developed the first multi-event capture–recapture model to evaluate behavioral consistency, analyzing 3042 observations of 1684 banded storks. There were more specialists among residents (72%) than immigrants (40%). All resident specialists foraged in ricefields, and ricefield use increased with individual age. In contrast, some immigrants specialized on either dumps (24%) or ricefields (16%), but the majority were generalists (60%). Our results provide empirical evidence of high individual foraging consistency within a generalist species and a differential resource selection by individuals of different ages and origins, probably related to their previous experience in the foraging area. Thus, future changes in food resource availability at either of the two anthropogenic subsidies (ricefields or dumps) may differentially impact individuals of different ages and origins making up the wintering population. The use of multi-event capture–recapture modeling has proven useful for studying interindividual variability in behavior.

Key words: anthropogenic food subsidies; capture–recapture modeling; *Ciconia ciconia*; Doñana, southwestern Spain; ecological processes; foraging behavior; multi-event analysis; niche specialization; refuse dumps; ricefields; White Stork.

INTRODUCTION

A large number of animal species benefit from anthropogenic food subsidies (e.g., refuse dumps, fishery discards, or feeding stations) where high amounts of food are highly predictable in space and time (Oro et al. 2013). Anthropogenic food subsidies have promoted life history changes in many species, causing increases in their populations and even cascading effects in food webs and ecosystems (Robb et al. 2008, Carey et al. 2012, Cortés-Avizanda et al. 2012). However, little is known about individual consistency in the use (or lack of use) of food subsidies, or about the causes behind this

individual specialization (Oro et al. 2013). This is relevant because food subsidies affect the body condition, reproduction, home range, spatial distribution, and survival of individuals (Oro et al. 2013). For instance, Annett and Pierotti (1999) reported that Western Gulls (*Larus occidentalis*) strongly relying on human refuse had lower lifetime reproductive success than individuals feeding on natural resources (i.e., fish), and suggested that individual differences in resource use may be heritable. Moreover, individuals using food subsidies may be a nonrandom subset of the population (e.g., weaker individuals; Votier et al. 2010). Thus, not only the proportion of the population using food subsidies, but also the individual traits associated with their use, would predict the impact of food subsidies upon population dynamics. In particular, the consequences of a drastic reduction of food subsidies would greatly

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differ if the reduction affected the most successful breeders vs. the weakest individuals of the population.

This problem is thus framed within the wider topic of individual specialization, which is gaining momentum after the first review on the subject by Bolnick et al. (2003:1), who noted that “most empirical and theoretical studies of resource use and population dynamics treat conspecific individuals as ecologically equivalent. This simplification is only justified if interindividual niche variation is rare, weak, or has a trivial effect on ecological processes.” Their review challenged this “rare interindividual niche variation” by reporting a strong and widespread occurrence of individual resource specialization in different taxa, and their individual and population consequences. A recent review (Araújo et al. 2011), motivated by a sudden increase in studies on individual specialization, confirmed these conclusions. Although it was recognized that the current early development of the topic does not allow for strong hypotheses on the factors governing resource specialization in a given population, foraging theory was highlighted as a candidate framework (Araújo et al. 2011).

Optimal foraging theory states that individuals feed on those resources most valuable to them, according to the diversity and abundance of resources and on individual traits (Araújo et al. 2011). Three nonexclusive mechanisms have been proposed to explain the relationship between optimal foraging and individual traits (Araújo et al. 2011). First, phenotypic variation among individuals may change optimal diets according to individual ability to detect or process different resources, resulting in divergent rank preferences. Second, individuals may present different optimal diets due to different physiological requirements (e.g., specific nutrients for reproduction) or may differ in their optimization criteria (e.g., some prioritize safety regarding predation risk while others prioritize energy intake). Third, individuals may have the same optimal diets but different competitive abilities (e.g., dominant individuals may displace subordinate individuals from the optimal resources).

The White Stork (*Ciconia ciconia*; see Plate 1) is a good candidate species as a model for assessing individual foraging strategies on anthropogenic food subsidies. This large-sized migratory wading bird preys on a wide range of animals, including insects, fish, amphibians, reptiles, small mammals, and birds, but also makes use of waste resources. European populations of the species suffered a drastic decline after 1945 related to long drought periods in African wintering grounds, habitat deterioration, and casualties from power lines along their migration routes (Kanyamibwa et al. 1990, Barbraud et al. 1999, Schaub et al. 2005). Spanish stork populations have become sedentary since the 1980s, and northern European populations shortened their migration distances to overwinter in Spain. Currently, ~4000 White Storks are wintering in southwest Spain (Doñana marshlands), including indi-

viduals of different origins: local residents and immigrant individuals from Germany, France, The Netherlands, and Switzerland (Aguirre 2013). This migratory behavioral change was related to the increase in food availability (mainly in refuse dumps) in Spain in recent decades (Tortosa et al. 2002, Rendón et al. 2008, Ramo et al. 2013). Moreover, access to predictable and abundant food at dumps contributed to the concentration of breeding distribution, an increase in breeding success and juvenile survival, and to the advancement of the recruitment age of White Storks (Tortosa et al. 2002). Contemporaneous with the increase in food availability at dumps, the introduction and rapid spread of the exotic invasive red swamp crayfish (*Procambarus clarkii*) in the Doñana marshlands contributed to the substantial increase of the White Stork local breeding and wintering population (Rendón et al. 2008, Tablado et al. 2010).

The red swamp crayfish is a species native to the southeastern United States and northern Mexico that colonized the study area in 1973 and has increased in numbers since then, becoming an important food subsidy for the community of predators in the area (Tablado et al. 2010). Storks breeding in the area intensely feed on crayfish during the breeding season (Tablado et al. 2010), feeding their nestlings with this abundant food resource (Negro et al. 2000). However, during winter, feeding in dumps may be easier than feeding on crayfish in ricefields (Correia and Ferreira 1995). Dumps are easy to locate at a distance and provide a large food supply predictable in space and time (Oro et al. 2013). Crayfish in ricefields, however, require more advanced skills to locate and prey upon than organic rubbish at dumps. During the wintering season, crayfish are only easily available after the plowing of ricefields by farmers. Consequently, storks must either relate the activity of farmers to the ephemeral availability of easier-to-capture crayfish or rely on public social information to locate this prey.

Currently, refuse at dumps and crayfishes from ricefields are the main food resources for wintering (either resident or immigrant) White Storks in southern Spain (Tortosa et al. 1995, Tablado et al. 2010). Habitat changes or the occurrence of new food sources may provide new opportunities for ecological/evolutionary changes in the species, but anthropogenic food subsidies may also lead to ecological traps affecting the populations permanently (Oro et al. 2013). Moreover, if resident and immigrant individuals differ in their level of specialization on the two main food resources, any changes in the resource availability at a local level may have different consequences for birds of different origins. Thus, describing potential individual specialization and understanding their causes within this species is important from both a theoretical and an applied perspective.

This scenario represents a valuable opportunity to study the occurrence of interindividual differences in the

use of food subsidies (i.e., specialization on crayfishes or rubbish) in relation to individual traits. We hypothesized that foraging patterns differ between resident and immigrant individuals and with age. White Storks exhibit very high annual nest site fidelity (87%; Barbraud et al. 1999) and breeding dispersal distances are generally short (18 ± 41 km, mean \pm SD; Itonaga et al. 2010); thus, old residents should have better knowledge of the area than immigrants and young birds. Moreover, resident storks are known to consume high amounts of crayfish during the breeding season in the study area (Tablado et al. 2010), suggesting a high nutritional value of this prey (Negro et al. 2000). However, crayfishes are not usually found in the stork diet outside the study area (Negro et al. 2000), and thus immigrants may be unfamiliar with this food resource and more familiar with rubbish consumption, given that dumps are present throughout the species' breeding range. Consequently, in agreement with the hypothesis of interindividual phenotypic/genetic differences related to individual ability to detect particular food resources (hypothesis 1 in Araújo et al. 2011), residents may present greater abilities to detect and consume crayfishes. On the other hand, while food availability in refuse dumps is highly predictable in space and time, red swamp crayfishes remain buried under mud during the autumn–winter (Correia and Ferreira 1995), becoming available when ricefields are plowed (also during autumn–winter), thus being less predictable. Again, due to their greater experience in the area, residents and older individuals may consume crayfishes in higher proportions (hypothesis 1 in Araújo et al. 2011). In contrast, during the wintering (i.e., nonbreeding) season, no differences in physiological requirements between individuals are expected (hypothesis 2 in Araújo et al. 2011). Similarly, competitive exclusion (hypothesis 3 in Araújo et al. 2011) is not expected because both crayfishes and rubbish are widely available at the Doñana wintering area and defense of food for a single stork is difficult; in fact, storks typically forage in loose groups where aggressive interactions are rare (R. Jovani and J. L. Tella, unpublished data).

We tested the existence of divergent individual foraging preferences (hypothesis 1 in Araújo et al. 2011) in relation to residence status and age by studying individual foraging strategies (either generalization or specialization) of banded resident and immigrant White Storks in their main European wintering area (Doñana marshes, southwestern Spain; Aguirre 2013). We used state-of-the-art capture–recapture modeling, developing specific multi-event finite-mixture models originally used to account for capture heterogeneity (Pledger 2000, Pradel 2005). Models evaluated the extent of individual foraging specialization on the available anthropogenic food subsidies (rubbish at dumps and crayfishes in ricefields) and quantified resource utilization as a function of residency status (taking into account

residency uncertainty for some individuals) and individual age.

METHODS

Fieldwork

From 1 October to 19 December 2003, two observers traveled through the White Stork's main wintering area in southwestern Spain, which covers $\sim 10\,000$ km² (Fig. 1), looking for foraging individuals. The study area includes seven dumps surrounding a vast surface area (43 905 ha) of marshlands transformed for rice crops since 1931 in the area of Doñana National Park (Ramo et al. 2013). Traveling via unpaved roads crossing the marshlands allowed the monitoring of a number of unplowed ricefields as well as 17 ricefield localities (Fig. 1) asynchronously plowed during the study period, where red swamp crayfishes were made available for storks during several days after plowing (Appendix A). Therefore, crayfishes were available at some ricefields throughout the study period, varying temporarily in their spatial location. Due to permit constraints, visits to dumps were periodic, about once a week. In total, we recorded foraging storks during 106 visits to ploughed ricefields and 48 visits to the dumps (see Appendix A for more fieldwork details).

Individual data

During the study period (lasting 80 days), dumps and ricefields were sampled on 35 and 42 different days, respectively (Appendix A). In total, 3042 bands were identified and georeferenced, belonging to 1684 different individuals. Thanks to a long-lasting banding program and several concurrent studies (Jovani and Tella 2004, 2007, Blas et al. 2007, Baos et al. 2012), many White Storks were known to have bred (or lived) in the study area during the previous two breeding seasons. In particular, 876 nests in 2002 and 1056 nests in 2003 were monitored, identifying a total of 535 resident individuals either breeding or living in the area during the breeding season (March–August). Of these previously identified “resident” individuals, 191 were observed during the 2003 wintering season and 161 of them (i.e., marked as chicks) were aged based on their year of banding. We classified individuals from foreign countries as “wintering immigrants” ($n = 711$): Belgium (12), Denmark (112), France (235), Germany (179), Portugal (106), Switzerland (53), and 14 individuals with unknown (but foreign) band types. Storks with Spanish bands (782) but not encountered during the breeding season were classified as “uncertain,” because an unknown number of resident individuals could have been overlooked during monitoring. Observations of marked storks during the study period at ricefields (coded 1) and dumps (coded 2) or not detected (coded 0) were encoded in individual encounter histories including 80 occasions (days) by group (i.e., 1, certain residents; 2, certain immigrants; 3, uncertain); see Appendix B, Supplement. Age during winter 2003 of known-age

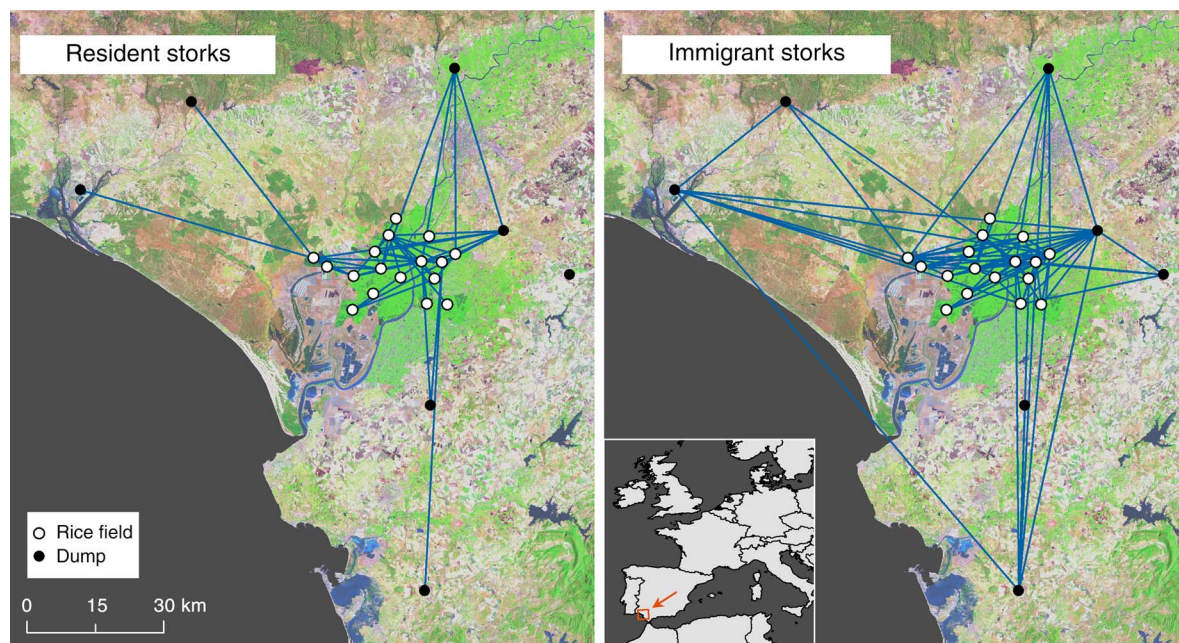


FIG. 1. Study area in southwestern Spain (inset map, orange square and arrow) showing all localities where White Storks (*Ciconia ciconia*) were observed foraging in dumps and ricefields (white and black dots, respectively). Lines link pairs of localities sharing at least one individual stork.

residents was incorporated in capture histories as an individual covariate (Appendix B, Supplement).

Biological hypotheses

We considered the following biologically plausible hypotheses 1–7 (regarding the existence or lack thereof of foraging strategies/preferences and the potential differences between individuals with different traits).

For generalist individuals only:

- 1) No difference between residents and immigrants and strictly generalist individuals. The wintering population of storks is composed of generalist individuals that forage at ricefields and dumps in the same proportions (50%).
- 2) No difference between residents and immigrants. The wintering population of storks is composed only of generalist individuals that forage at ricefields and dumps differentially.
- 3) Foraging habitat use differs between residents and immigrants. The wintering population of storks is composed only of generalist individuals of which residents and immigrants forage at ricefields and dumps differentially.

For both generalists and specialists:

- 4) No difference between residents and immigrants. The wintering population of storks is composed of a mixture of ricefield specialists, dump specialists, and generalist individuals in the same proportions of residents and immigrants.
- 5) Foraging habitat use differs between residents and immigrants. The wintering population of storks is

composed of a mixture of ricefield specialists, dump specialists, and generalist individuals in different proportions of residents and immigrants. Among generalists, residents and immigrants forage at ricefields and dumps differentially.

For the role of age:

- 6) No age effect. Probabilities of foraging at ricefields by resident storks are similar among age classes.
- 7) Age effect. Probabilities of foraging at ricefields by resident storks increase with age.

Multi-event capture–recapture models

Multi-event modeling of foraging strategy and residency status.—We applied a multi-event modeling approach (Pradel 2005) able to evaluate the degree of individual consistency in foraging specialization in relation to residency status (biological hypotheses 1–5). We will present a general multi-event model for hypothesis 5. The alternative hypotheses (1–4) were tested by alternative models fixing or constraining parameters from the general model (Table 1). Models were built and fitted to the data using E-SURGE 1.7.1 software (Choquet et al. 2009b). Model selection was based on Akaike’s information criterion (AIC). Additionally, for each model j , we calculated the Akaike weight, w_j , as an index of its relative plausibility (Burnham and Anderson 2002).

The multi-event framework distinguishes what can be observed in the field (the events coded in the encounter histories) from the underlying biological states of the individuals, which must be inferred (Pradel 2005). Here,

TABLE 1. Multi-event model constraints for White Storks (*Ciconia ciconia*) in southwestern Spain, with parameters fixed and/or constrained to be equal (=) or different (\neq).

Hypothesis	Initial state step 1	Initial state step 2	Event, step 1
1	$\pi = 0$	$(\beta_1 = \beta_2 = \beta_3 = \beta_4) = 0$	$(\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = \alpha_5 = \alpha_6) = 0.5$
2	$\pi = 0$	$(\beta_1 = \beta_2 = \beta_3 = \beta_4) = 0$	$\alpha_1 = \alpha_2 = \alpha_3 = \alpha_4 = \alpha_5 = \alpha_6$
3	π (group 1) = 1 π (group 2) = 0	$(\beta_1 = \beta_2 = \beta_3 = \beta_4) = 0$	$(\alpha_1 = \alpha_2 = \alpha_3) \neq (\alpha_4 = \alpha_5 = \alpha_6)$
4	$\pi = 0$	$\beta_1 = \beta_3 \neq \beta_2 = \beta_4$	$(\alpha_1 = \alpha_4) = 1$ $(\alpha_2 = \alpha_5) = 0$ $(\alpha_3 \neq \alpha_6)$
5	π (group 1) = 1 π (group 2) = 0	$\beta_1 \neq \beta_2 \neq \beta_3 \neq \beta_4$	$(\alpha_1 = \alpha_4) = 1$ $(\alpha_2 = \alpha_5) = 0$ $(\alpha_3 \neq \alpha_6)$

Notes: Here, π is the probability that a newly encountered individual is a resident; β is the probability of adopting a foraging strategy by resident storks type 1 and 2 (β_1, β_2) and immigrant storks type 1 and 2 (β_3, β_4); α is the probability of foraging in ricefields of resident storks type 1, 2, and 3 ($\alpha_1, \alpha_2, \alpha_3$) and immigrant storks type 1, 2, and 3 ($\alpha_4, \alpha_5, \alpha_6$); group 1 and 2 correspond to storks recognized as residents and European immigrants, respectively.

the events were “0” (stork not observed on a particular occasion), “1” (stork observed foraging in a ricefield), and “2” (stork observed foraging at a dump). The general model included seven underlying biological states: six states for live resident (R) and immigrant (I) storks belonging to three different foraging strategies, coded R1, R2, R3, I1, I2, and I3; and one state for dead individuals, coded D. States R1 and I1 represent individuals specialized in ricefields, R2 and I2 represent individuals specialized in dumps, and R3 and I3 represent generalist individuals. Exploratory analyses showed that apparent survival rate during the study period was close to 1 ($\phi = 0.99999$). This is in agreement with the short duration of the study period (80 days) and its timing (winter). Mortality and departure from the study area could therefore be neglected. Thus, we analyzed the population as a closed population, allowing an increase in the precision of parameter estimates.

Multi-event models use three kinds of parameters: the initial state probabilities, which correspond in our model to the proportions of newly encountered resident and immigrant individuals belonging to the different foraging strategy states (R1, R2, R3, I1, I2, and I3); the probabilities of transition between the states (i.e., survival probability, which in this case was fixed at 1); and the probabilities of the events, which here involve the probabilities of presence at the two trophic subsidies (ricefields vs. dumps) and resighting probabilities. These parameters were estimated simultaneously from whole-encounter histories by maximum likelihood (Choquet et al. 2009b).

Matrix representations with departure states in rows and arrival states in columns are commonly used in multi-event models (see a detailed description in Appendix B and pattern matrix in the Supplement). We broke down the initial state probabilities into two steps: the first step (matrix 1, residency status assignment; Eq. 1) corresponded to the probability that a newly encountered individual was a resident “R” (π) or an immigrant “I” ($1 - \pi$), depending on the group (g) in which the individual was previously classified. For the

groups with known residency status, π values were fixed at 1 for group 1 (“certain residents”) and at 0 for group 2 (“certain immigrants”). For group 3 (“uncertain”), the proportion of residents was estimated by the model. Matrix 1 is:

$$\text{Residency status} = \begin{pmatrix} \text{R} & \text{I} \\ \pi g & 1 - \pi g \end{pmatrix}. \tag{1}$$

The second step corresponded to the individual foraging strategy adopted (matrix 2; Eq. 2). The corresponding probabilities denoted by β are conditional on the residency status (R, residents; I, immigrants), thus allowing a differential mixture of foraging strategies at dumps and ricefields between residents (R1, R2, and R3) and immigrants (I1, I2, and I3).

Foraging strategy =

$$\begin{matrix} & \text{R1} & \text{R2} & \text{R3} & \text{I1} & \text{I2} & \text{I3} \\ \text{R} & \beta_1 & \beta_2 & 1 - \beta_1 - \beta_2 & 0 & 0 & 0 \\ \text{I} & 0 & 0 & 0 & \beta_3 & \beta_4 & 1 - \beta_3 - \beta_4 \end{matrix}. \tag{2}$$

The event probabilities were broken down into two steps: the first step corresponded to the daily probabilities of foraging in ricefields (α) and dumps ($1 - \alpha$) (matrix 3). They were allowed to vary with residency status and foraging strategy. In the general model, α was fixed at 1 for the ricefield specialists (R1, I1), at 0 for dump specialists (R2, I2), and was estimated for generalists (R3, I3), representing the daily percentage of generalists foraging in ricefields (Table 1). Matrix 3 is:

$$\text{Foraging} = \begin{matrix} & \text{Ricefields} & \text{Dumps} \\ \text{R1} & \alpha_1 & 1 - \alpha_1 \\ \text{R2} & \alpha_2 & 1 - \alpha_2 \\ \text{R3} & \alpha_3 & 1 - \alpha_3 \\ \text{I1} & \alpha_4 & 1 - \alpha_4 \\ \text{I2} & \alpha_5 & 1 - \alpha_5 \\ \text{I3} & \alpha_6 & 1 - \alpha_6 \\ \text{D} & 1 & 0 \end{matrix}. \tag{3}$$

TABLE 2. Multi-event capture–recapture modeling of White Stork probabilities of foraging in ricefields vs. dumps, testing the effects of residency status and foraging strategy (hypotheses 1–5) and individual age (hypotheses 6 and 7).

Hypothesis	np	Deviance	QAIC _c	ΔQAIC _c	w _i
1	74	14 440.52	8596.51	258.13	0
2	75	14 402.66	8576.47	238.10	0
3	78	14 262.36	8500.74	162.36	0
4	78	14 051.93	8377.68	39.31	0
5	82	13 970.27	8338.37	0	1
6	65	1 127.96	1278.12	5.87	0.05
7	66	1 119.42	1272.25	0	0.95

Note: Terms are np, number of estimable 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; w_i, Akaike’s weight.

The second step involved foraging-habitat-specific probabilities of resighting (*p*) (matrix 4; Eq. 4). Resighting probabilities in all models were left to vary between ricefields and dumps and over days (*t*) correcting for unbalanced field effort in both habitats (Appendix A). Additionally, we fixed resighting probabilities at 0 in those habitats and days without fieldwork (Appendix A). To avoid overparameterized models, we only considered time effects on resighting probabilities. Matrix 4, where column heads represent events (0, stork not observed; 1, stork observed foraging in ricefield; 2, stork observed foraging at dump) is:

$$\text{Resighting} = \begin{matrix} & \begin{matrix} 0 & 1 & 2 \end{matrix} \\ \begin{matrix} \text{Ricefields} \\ \text{Dumps} \end{matrix} & \begin{pmatrix} 1 - p_{1t} & p_{1t} & 0 \\ 1 - p_{2t} & 0 & p_{2t} \end{pmatrix} \end{matrix} \quad (4)$$

Goodness-of-fit tests for multi-event models have yet to be developed. The diagnostic goodness of fit for the most general model currently available is that of the general Arnason-Schwarz multisite model (Pradel et al. 2005), but this was not appropriate here, as this model, unlike ours, assumes Markovian transitions between sites. Instead, we ran the goodness-of-fit test from the Cormack Jolly Seber model (CJS) assuming full time variation of survival and resighting parameters common to the two types of feeding habitats. We ran this test with U-CARE 2.2.2 software (Choquet et al. 2009a). This test was statistically significant ($\chi^2 = 627.57$, *df* = 366, *P* < 0.001), indicating that individuals tended to be detected on successive occasions (tests 2.CT and 2.CL: trap-dependence-like effects; Pradel et al. 2005). This was expected because of the combination of unequal detectability in the two habitats and the correlation between observations in the ricefields on successive days. Although unequal detectability was treated in our model, the autocorrelation of observations in the ricefields remained untreated. Consequently, we decided to conservatively apply an overdispersion inflation factor (\hat{c}) of 1.71 calculated as $627.57/366$ (χ^2/df), which is a reasonable value for a large data set (Burnham and Anderson 2002).

Multi-event modeling of resident age.—The encounter histories of 161 known-age residents were coded as in the

previous analyses and an individual covariate indicating their age at the time of this study (ranging from 3 to 18 years) was included. We developed a simpler multi-event model (Appendix B) in which the daily probability of presence at ricefields (α , matrix 5) was modeled as a linear function of age (hypothesis 7) or as a constant (i.e., no age effects, hypothesis 6). Matrix 5 is:

$$\text{Foraging} = \begin{matrix} & \begin{matrix} \text{Ricefields} & \text{Dumps} \end{matrix} \\ \begin{matrix} \text{R} \\ \text{D} \end{matrix} & \begin{pmatrix} \alpha & 1 - \alpha \\ 1 & 0 \end{pmatrix} \end{matrix} \quad (5)$$

In this analysis, we did not consider uncertainty in residency status (all individuals were known residents) or different individual foraging strategies. Consequently, individuals belonged to a unique departure state (R, resident) and survival as in the previous model was fixed at 1 (Appendix B). Resighting probabilities were modeled as in the previous modeling approach (Eq. 4). The goodness of fit of the CJS model was not statistically significant ($\chi^2 = 55.89$, *df* = 70, *P* = 0.89), indicating a good fit to the data.

RESULTS

Individual patterns of foraging according to residency status

Overall, 813 storks (1332 band readings) were found only at ricefields, 621 individuals (896 readings) only at dumps, and 250 individuals (800 band readings) were observed foraging in both habitats. Although this cannot be converted to absolute abundances of birds foraging on each type of food subsidy, it firmly illustrates that the species behaved as a generalist forager. The best-supported model in terms of QAIC_c was the general model (hypothesis 5; Table 2). Models considering alternative hypotheses showed much larger QAIC_c values (hypotheses 1–4; Table 2). The selected model (hypothesis 5; Table 2) estimated that 19% (8–40%) of the 782 individuals of uncertain origin would actually be classified as “residents” (*n* = 149), with the remaining uncertain individuals classified as “immigrants” (*n* = 633). This leads to mean estimates of 340 (i.e., 191 + 149) resident and 1344 (i.e., 711 + 633) immigrant marked storks wintering in the study area.

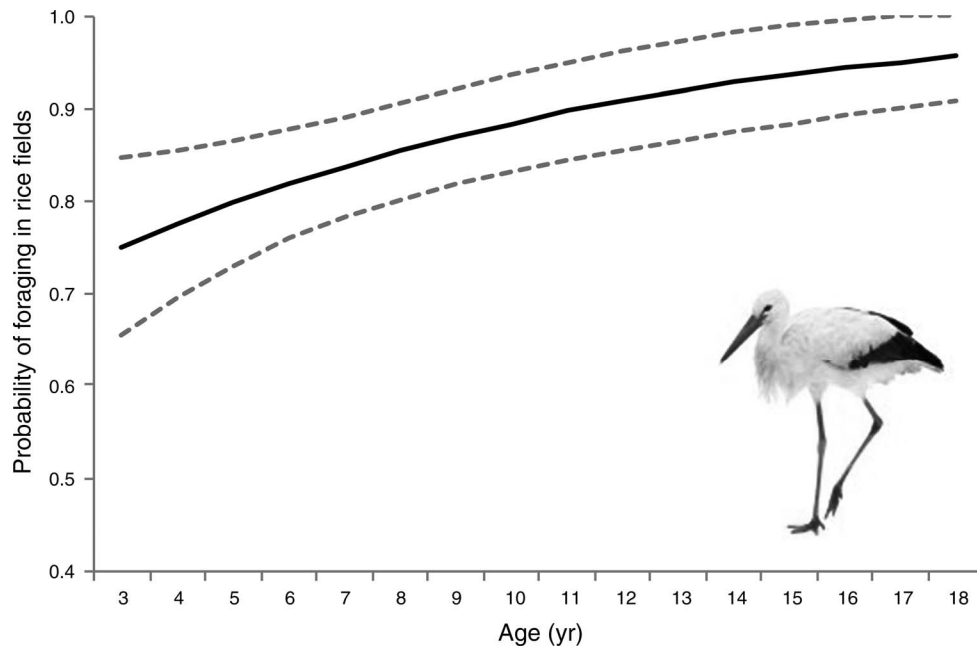


FIG. 2. Probability (and 95% CI given by dashed lines) of resident White Storks foraging in ricefields rather than in dumps during the 2003 wintering season in southern Spain in relation to individual age.

Resident individuals showed a high consistency in their choice of food subsidies: 72% (95% CI: 60–81%) of residents daily foraged exclusively in ricefields (i.e., were ricefield specialists, $n = 245$ individuals), whereas the remaining individuals (28%; 95% CI: 19–40%, $n = 95$ individuals) behaved as generalists. Among resident generalists using both foraging habitats during the study period, 31% (95% CI: 18–49%) and 69% (95% CI: 51–82%) of individuals daily foraged in ricefields and dumps, respectively. Dump specialization did not occur among residents, as the proportion of dump specialists (R2 foraging strategy) was 0. In contrast, immigrants exhibited the three different foraging strategies: 16% (95% CI: 9–18%) were ricefield specialists ($n = 215$ individuals), 24% (95% CI: 19–31%) were dump specialists ($n = 323$ individuals), and 60% (95% CI: 50–68%) were generalists ($n = 805$ individuals). Of the immigrant generalists, 60% (95% CI: 52–67%) and 40% (95% CI: 33–48%) daily foraged in ricefields and dumps, respectively. Consequently, on a daily basis, 81% of resident and 52% of immigrant storks foraged in ricefields. These percentages yielded estimates of 710 marked storks daily foraging in dumps (65 residents and 645 immigrants) and 974 marked storks daily foraging in ricefields (275 residents and 699 immigrants).

The effect of age as a driver of individual specialization

Resident storks showed higher probabilities of foraging in ricefields with age (Fig. 2). Accordingly, the model considering an individual age effect on probabilities of foraging in ricefields was better supported in terms of AIC_c than the model without age effects (hypothesis 7

vs. hypothesis 6; Table 2). The effect of age was statistically significant, as confidence intervals of the beta estimate corresponding to the linear slope did not include zero ($\beta = 1.32$; 95% CI: 0.38–2.27).

Spatial foraging patterns

For individuals seen in at least two localities, the distance between the farthest pair of localities was slightly longer for immigrants than for resident individuals (average, range): 22.8, 3.5–116.0 km, and 17.8, 3.5–72.2 km, respectively (Mann-Whitney $W = 6833$, $P = 0.09$). This was due to the fact that distances between dumps (highly used by immigrants) were greater than distances between ricefields (Fig. 1). However, both immigrants and residents moved throughout the study area (Fig. 1).

DISCUSSION

Individual traits as drivers of foraging specialization

The existence of intraspecific differentiation in niche or personality has received special attention during the last decade (Bolnick et al. 2003, Araújo et al. 2011, Dall et al. 2012). Less is known, however, about the ecological causes of individual specialization (Araújo et al. 2011) or its long-term evolutionary consequences (Dall et al. 2012). Here, we studied the role of individual traits (residence status and age) on foraging specialization under the optimal foraging theory framework (Araújo et al. 2011). We found that at the population level, wintering White Storks in southwestern Spain used two anthropogenic food subsidies in large numbers, as would be expected in an opportunistic generalist species.



PLATE 1. White Stork (*Ciconia ciconia*) flying over Doñana marshlands in southwestern Spain. Photo credit: Héctor Garrido/EBD-CSIC.

However, individual storks were either specialists or generalists on their foraging substrates (ricefields or dumps) during the study period (autumn–winter 2003). Although our study reflects a specialization on a particular foraging habitat type rather than on a specific diet (i.e., prey items), crayfishes are the prey most frequently consumed by wintering White Storks in ricefields (ranging from 86% to 98% in two different winters; Tablado et al. 2010). In contrast, storks can forage on a large variety of refuse items at dumps of likely lower nutritional quality than that of crayfish, a prey very rich in carotenoids (Negro et al. 2000).

As predicted, residents were highly specialized in feeding at ricefields, with no residents specialized in feeding at dumps. In contrast, we found a slightly higher percentage of immigrants specializing in dumps than in ricefields, but most immigrant individuals (60%) were generalists. Moreover, diet preferences changed with age. According to our prediction, older resident storks had a higher probability of foraging in ricefields than did younger individuals, suggesting that foraging skills in this particular habitat may increase with age and thus with accumulated learning and experience in the area (Marchetti and Price 1989, Giraldeau and Caraco 2000). Wintering immigrants were similarly specialized on dumps and ricefields. High annual fidelity to wintering areas observed in other long-lived birds (Sanz-Aguilar et

al. 2012) could explain the ricefield specialization of some wintering immigrant individuals (as in residents) through the acquisition of experience in the area. On the other hand, supplementary feeding programs carried out in several European countries for the conservation of the species may have habituated certain individuals to highly predictable food resources such as dumps (Doligez et al. 2004, Schaub et al. 2004, Massemin-Challet et al. 2006). A nonexclusive alternative hypothesis would be that specialization on dumps may only occur among juvenile immigrants. Note that resident juvenile storks (younger than three years old) were not present in our sample. In fact, all 42 satellite-tracked juveniles born in the study area wintered in Africa during their first years of life (J. Blas, *unpublished data*). This could also explain the lack of dump specialization among residents. Unfortunately, we have no data on the previous experience of immigrant storks wintering in the study area to test this hypothesis.

Ecological implications and consequences of foraging specialization

At the individual level, two studies on seabirds related the existence of individual foraging specialization on anthropogenic food subsidies to long-term fitness consequences: Northern Gannets, *Morus bassanus*, foraging on fisheries discards and Western Gulls

foraging on refuse showed lower body condition and lifetime reproductive success, respectively, than did individuals actively preying upon live fish (Annett and Pierotti 1999, Votier et al. 2010). In our study case, an alternative but nonexclusive hypothesis to explain the age-related increased probability of foraging in ricefields would be differential survival (Curio 1983, Marchetti and Price 1989); i.e., if individuals consistently foraging in ricefields have higher survival, they would be overrepresented among older age classes. However, because our study only covered one wintering season, further research on long-term consistency of individual foraging specialization and its potential demographic and population effects is needed.

At the population level, the high availability of food resources at rubbish dumps throughout the wintering range and along the breeding range of White Storks has promoted behavioral, demographic, and population changes in this (Tortosa et al. 1995, 2002, Doligez et al. 2004, Schaub et al. 2005, Massemin-Challet et al. 2006) and other species (Oro et al. 2013). Moreover, selection processes (e.g., wintering mortality or nest failure) have been relaxed by shortened migratory distances and greatly increased food availability (Tortosa et al. 2002, Schaub et al. 2004). Our study model demonstrates the existence of both consistent (i.e., specialist) and flexible (i.e., generalist) individual foraging strategies among the wintering population of White Storks in the Doñana marshlands. The existence of consistent individual behaviors has been recognized as a driver of adaptation to new environments (i.e., new anthropogenic niches; Carrete and Tella 2011, 2013). Moreover, individual experience (shaped by age and origin) seems to be the most plausible mechanism responsible for differential use of subsidies. This has implications for our understanding of how a population-level generalist species such as the White Stork could cope with anthropogenic habitat changes (Oro et al. 2013).

Doñana marshlands represent the most important European wintering area for the species and numbers of immigrant storks largely exceed the number of residents. Although ricefields were preferentially selected by resident storks, many individuals foraged daily at dumps; mainly immigrants (48%) and young residents (Fig. 2). Storks at Doñana benefited from two anthropogenic subsidies, but crayfishes are not available in other wintering areas. European environmental policies are now directed at curtailing food accessibility (i.e., biodegradable waste) to animals in rubbish dumps by 2016 (Directive 2001/77/EC), and an effect on wintering White Storks is expected. Although White Stork populations have grown spectacularly during the last two decades after becoming endangered in the 1950–1960s, several populations remain small (Thomsen and Hötter 2006).

Our results predict interesting consequences of potential dump management. Future food limitations may

have important consequences at the population level (Oro et al. 2013), with wintering migrant storks from northern European populations being potentially more affected due to the large number of wintering birds and their greater use of dumps. Although dump closure could appear to be a local phenomenon, our results suggest that it would directly affect stork populations thousands of kilometers away (immigrant storks), rather than just the local population (Peters et al. 2007). However, immigrant storks were highly generalist at the individual level. Thus, an eventual dump closure would increase the number of immigrant storks feeding on ricefields, increasing competition and reducing resource availability for the resident population.

Methodological aspects and opportunities of multi-event models

Repeated observations over time in individual foraging choices are essential to correctly study and quantify the consistency of individual foraging specialization (Bolnick et al. 2003, Araújo et al. 2011, Dall et al. 2012). However, perfect detection of individuals in natural conditions is often rare or costly. Here, we developed for the first time a capture–recapture modeling approach to calculate consistency in individual behavior using capture–recapture data. This new method allowed a robust quantification (including confidence intervals) of individual strategies with the incorporation of imperfect detection of individuals. Additionally, we extended our modeling approach to allow uncertainty in individual classification (which in other cases may correspond to sex, breeding status, or other factors; Pradel 2005, Frederiksen et al. 2013; in particular, see Gourlay-Larour et al. [2014] for another study separating immigrants from residents on a wintering ground). In this way, we were able to estimate the proportion of resident individuals missed despite intense breeding monitoring, a parameter currently impossible to derive with other methods. Our model assumes that observations of the same individual on different dates are uncorrelated and that individuals move independently of each other. This is probably not true, as individuals may preferentially return to a site where they were able to forage successfully and individuals may also use the behavior of conspecifics as clues to find suitable sites. These types of dependency and any remaining heterogeneity among individuals beyond the factors incorporated in our model (foraging strategy and residency status) are why goodness-of-fit tests were significant. When such nonstructural departures are involved, the use of a variance inflation factor protects against the detection of spurious effects at the expense of power (Burnham and Anderson 2002). This is the approach we adopted. Moreover, our large numbers of individuals with certain residency status allowed us to repeat the analyses without the individuals of uncertain residency status, but obtain similar results, demonstrating the robustness of our multi-event approach, which deals

well with uncertainty (Appendix B). This approach is therefore useful when sample sizes are logistically constrained and the proportion of individuals of uncertain status/behaviors is necessarily large. A step-by-step description of the analyses is provided in the Supplemental Material with the aim of encouraging the application of our multi-event model to other studies.

This study emphasized the application of longitudinal data on replicated observations of individual resource use over time for quantitative studies on individual foraging specialization (Araújo et al. 2011). Tracking technologies are becoming very valuable tools to monitor individuals over large temporal and spatial scales (Millspaugh and Marzluff 2001), including European storks.⁶ However, sample size is usually small due to high costs. In contrast, extensive marking programs, such as those carried out with European White Storks, allowed the identification and monitoring of a large number of individuals. Capture–recapture methods were developed to estimate demographic parameters while accounting for imperfect detection of individuals. Today, the flexibility of multistate and recently of multi-event models, as presented here, has allowed the study of additional parameters of interest (Clutton-Brock and Sheldon 2010, Frederiksen et al. 2013) and the incorporation of discrete individual heterogeneity classes (i.e., finite-mixture models) in capture–recapture modeling (Pledger 2000, Pradel 2005). Our study provides a robust new modeling approach for the study of individual behavioral specialization from noninvasive and imperfect individual resightings in the wild. Further studies could also consider the potential dependence among individual decisions as White Storks usually gather at foraging sites forming large groups, both in our study area and in other populations (e.g., Carrascal et al. 1990, Giraldeau and Caraco 2000). However, models including dependence among individuals forming groups have only been developed for fixed groups (with individuals belonging to the same group during the whole study period, Choquet et al. 2013), and further research is needed to determine the consistency of membership composition of foraging groups in White Storks. Nonetheless, survival parameters have been found to be robust when dependence in recapture among individuals occurs (Choquet et al. 2013).

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⁶ <http://www.bto.org/science/migration/tracking-studies/stork-tracking>

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B and the Supplement are available online: <http://dx.doi.org/10.1890/14-0437.1.sm>