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1 Multievent capture-recapture analysis reveals individual foraging specialisation in a generalist
2 species

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22 *Running Head:* Foraging specialisation in generalist storks

23 ABSTRACT. Populations of species typically considered trophic generalists may include
 24 specialised individuals consistently feeding on certain resources. Optimal foraging theory states
 25 that individuals should feed on those resources most valuable to them. This, however, may vary
 26 according to individual differences in detecting or processing resources, different optimization
 27 criteria, and competitive abilities. White storks (*Ciconia ciconia*) are trophic generalists at the
 28 population level. Their European population recovery has been attributed to increased wintering in
 29 Southern Europe (rather than Africa) where they feed upon new anthropogenic food subsidies:
 30 predictable dumps and less predictable and more difficult to detect but abundant invasive
 31 *Procambarus clarkii* crayfishes in ricefields. We studied the foraging strategies of resident and
 32 wintering storks in SW Spain in ricefields and dumps, predicting that more experience in the study
 33 area (residents vs. immigrants, old vs. young) would increase ricefield specialisation. We
 34 developed the first multievent capture-recapture model to evaluate behavioural consistency,
 35 analysing 3,042 observations of 1,684 banded storks. There were more specialists among residents
 36 (72%) than immigrants (40%). All resident specialists foraged in ricefields, and ricefield use
 37 increased with individual age. On the other hand, immigrants specialised on either dumps (24%) or
 38 ricefields (16%) but the majority were generalists (60%). Our results provide empirical evidence
 39 of high individual foraging consistency within a generalist species and a differential resource
 40 selection by individuals of different ages and origins probably related to their previous experience
 41 in the foraging area. Thus, future changes in food resource availability at either of the two
 42 anthropogenic subsidies (ricefields or dumps) may differentially impact individuals of different
 43 ages and origins making up the wintering population. The use of multievent capture-recapture
 44 modelling has proven useful for studying inter-individual variability in behaviour.

45 *Keywords*: ecological processes, anthropogenic food subsidies, niche specialisation, foraging
 46 behaviour, White stork, *Ciconia ciconia*, multievent.

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INTRODUCTION

49 A large number of animal species benefit from anthropogenic food subsidies (e.g. refuse dumps,
 50 fishery discards or feeding stations) where high amounts of food are highly predictable in space
 51 and time (Oro et al. 2013). Anthropogenic food subsidies have promoted life history changes in
 52 many species, causing increases in their populations and even cascading effects in food webs and
 53 ecosystems (Robb et al. 2008, Carey et al. 2012, Cortés-Avizanda et al. 2012). However, little is
 54 known about individual consistency in the use (or lack of use) of food subsidies, or about the
 55 causes behind this individual specialisation (Oro et al. 2013). This is relevant because food
 56 subsidies affect the body condition, reproduction, home range, spatial distribution, and survival of
 57 individuals (Oro et al. 2013). For instance, Annett and Pierotti (1999) reported that Western gulls
 58 (*Larus occidentalis*) strongly relying on human refuse had lower life-time reproductive success
 59 than individuals feeding on natural resources (i.e., fish), and suggested that individual differences
 60 in resource use may be heritable. Moreover, individuals using food subsidies may be a non-
 61 random subset of the population (e.g., weaker individuals, Votier et al. 2010). Thus, not only the
 62 proportion of the population using food subsidies, but also the individual traits associated with
 63 their use would predict the impact of food subsidies upon population dynamics. Particularly, the
 64 consequences of a drastic reduction of food subsidies would greatly differ if it affects the most
 65 successful breeders vs. the weakest individuals of the population.

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

78 Optimal foraging theory states that individuals feed on those resources most valuable to
 79 them, according to the diversity and abundance of resources and on individual traits (Araújo et al.
 80 2011). Three non-exclusive mechanisms have been proposed to explain the relationship between
 81 optimal foraging and individual traits (Araújo et al. 2011). First, phenotypic variation among
 82 individuals may change optimal diets according to individual ability to detect or process different
 83 resources resulting in divergent rank preferences. Second, individuals may present different
 84 optimal diets due to different physiological requirements (e.g., specific nutrients for reproduction)
 85 or may differ in their optimization criteria (e.g., some prioritizing safety regarding predation risk
 86 while others prioritizing energy intake). Third, individuals may have the same optimal diets but
 87 different competitive abilities (e.g. dominant individuals may displace subordinate individuals

88 from the optimal resources).

89 The white stork (*Ciconia ciconia*) is a good candidate species as a model for assessing
 90 individual foraging strategies on anthropogenic food subsidies. This large-sized migratory wading
 91 bird preys on a wide range of animals, including insects, fish, amphibians, reptiles, small
 92 mammals and birds, but also makes use of waste resources. European populations of the species
 93 suffered a drastic decline after 1945 related to long drought periods in African wintering grounds,
 94 habitat deterioration, and casualties from power lines along their migration routes (Kanyamibwa et
 95 al. 1990, Barbraud et al. 1999, Schaub et al. 2005). Spanish stork populations have become
 96 sedentary since the 1980s, and northern European populations shortened their migration distances
 97 to overwinter in Spain. Currently, ca. 4,000 storks are wintering in southwest Spain (Doñana
 98 marshlands), including individuals of different origins: local residents and immigrant individuals
 99 from Germany, France, Netherlands and Switzerland (Aguirre 2013). This migratory behavioural
 100 change was related to the increase in food availability (mainly in refuse dumps) in Spain in recent
 101 decades (Tortosa et al. 2002, Rendón et al. 2008, Ramo et al 2013). Moreover, access to
 102 predictable and abundant food at dumps contributed to the concentration of breeding distribution,
 103 an increase in breeding success and juvenile survival, and to the advancement of the recruitment
 104 age of white storks (Tortosa et al. 2002). Contemporaneous with the increase in food availability at
 105 dumps, the introduction and rapid spread of the exotic invasive red swamp crayfish (*Procambarus*
 106 *clarkii*) in the Doñana marshlands contributed to the substantial increase of the white stork local
 107 breeding and wintering population (Rendón et al. 2008, Tablado et al. 2010).

108 The red swamp crayfish is a species native to the southeastern United States and northern
 109 Mexico that colonized the study area in 1973 and has increased in numbers since then, becoming

110 an important food subsidy for the community of predators in the area (Tablado et al. 2010). Storks
 111 breeding in the area intensely feed on crayfish during the breeding season (Tablado et al. 2010),
 112 feeding their nestlings with this abundant food resource (Negro et al. 2000). However, during
 113 winter, feeding in dumps may be easier than feeding on crayfish in ricefields (Correia and Ferreira
 114 1995). Dumps are easy to locate at a distance and provide a large food supply predictable in space
 115 and time (Oro et al. 2013). Crayfish in ricefields, however, require more advanced skills to locate
 116 and prey upon than organic rubbish at dumps. During the wintering season, crayfish are only
 117 easily available after the ploughing of ricefields by farmers. Consequently, storks have to either
 118 relate the activity of farmers to the ephemeral availability of easier-to-capture crayfish or rely on
 119 public social information to locate this prey.

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

130 This scenario represents a valuable opportunity to study the occurrence of inter-individual
 131 differences in the use of food subsidies (i.e., specialisation on crayfishes or rubbish) in relation to

132 individual traits. We hypothesized that foraging patterns differ between resident and immigrant
 133 individuals and with age. White storks exhibit very high annual nest-site fidelity (87%, Barbraud
 134 et al. 1999) and breeding dispersal distances are generally short (18 ± 41 Km) (Itonaga et al. 2010);
 135 thus, old residents should have better knowledge of the area than immigrants and young birds.
 136 Moreover, resident storks are known to consume high amounts of crayfish during the breeding
 137 season in the study area (Tablado et al. 2010), suggesting a high nutritional value of this prey
 138 (Negro et al. 2000). However, crayfishes are not usually found in the stork diet outside the study
 139 area (Negro et al. 2000), and thus immigrants may be unfamiliar with this food resource and more
 140 familiar with rubbish consumption given that dumps are present throughout the species breeding
 141 range. Consequently, in agreement with the hypothesis of inter-individual phenotypic/genetic
 142 differences related to individual ability to detect particular food resources (hypothesis 1 in Araújo
 143 et al. 2011), residents may present greater abilities to detect and consume crayfishes. On the other
 144 hand, while food availability in refuse dumps is highly predictable in space and time, red swamp
 145 crayfishes remain buried under mud during the autumn-winter (Correia and Ferreira 1995),
 146 becoming available when ricefields are ploughed (also during autumn-winter), thus being less
 147 predictable. Again, due to their greater experience in the area, residents and older individuals may
 148 consume crayfishes in higher proportions (hypothesis 1 in Araújo et al. 2011). On the contrary,
 149 during the wintering (i.e., non-breeding) season no differences in physiological requirements
 150 between individuals are expected (hypothesis 2 in Araújo et al. 2011). Similarly, competitive
 151 exclusion (hypothesis 3 in Araújo et al. 2011) is not expected as both crayfishes and rubbish are
 152 widely available at the Doñana wintering area and defense of food for a single stork is difficult; in
 153 fact, storks typically forage in loose groups where aggressive interactions are rare (authors' own

154 data).

155 We tested the existence of divergent individual foraging preferences (hypothesis 1 in
 156 Araújo et al. 2011) in relation to residence status and age by studying individual foraging
 157 strategies (either generalism or specialisation) of banded resident and immigrant white storks in
 158 their main European wintering area (Doñana marshes, SW Spain, Aguirre 2013). We used state-of-
 159 the-art capture-recapture modelling, developing specific multievent finite-mixture models
 160 originally used to account for capture heterogeneity (Pledger 2000, Pradel 2005). Models
 161 evaluated the extent of individual foraging specialisation on the available anthropogenic food
 162 subsidies (rubbish at dumps and crayfishes in ricefields) and quantified resource utilisation as a
 163 function of residency status (taking into account residency uncertainty for some individuals) and
 164 individual age.

165 **METHODS**

166 **Field work** —From October 1st to December 19th 2003, two observers travelled through
 167 the white stork's main wintering area in SW Spain, which covers ca. 10,000 Km² (Fig. 1), looking
 168 for foraging individuals. The study area includes seven dumps surrounding a vast surface area
 169 (43,905 ha) of marshlands transformed for rice crops since 1931 in the area of Doñana National
 170 Park (Ramo et al. 2013). Travelling via unpaved roads crossing the marshlands allowed the
 171 monitoring of a number of unploughed ricefields as well as to locate a total of 17 ricefield
 172 localities (Fig. 1) asynchronously ploughed during the study period where red swamp crayfishes
 173 were made available for storks during several days after ploughing (Appendix A). Therefore,
 174 crayfishes were available at some ricefields throughout the study period, varying temporarily in
 175 their spatial location. Due to permit constraints, visits to dumps were periodic, ca. once a week. In

176 total, we recorded foraging storks during 106 visits to ploughed ricefields and 48 visits to the
 177 dumps (see Appendix A for more field work details).

178 **Individual data**—During the study period (lasting 80 days) dumps and ricefields were
 179 sampled on 35 and 42 different days, respectively (Appendix A). A total of 3,042 bands were
 180 identified and georeferenced, belonging to 1,684 different individuals. Thanks to a long-lasting
 181 banding program and several concurrent studies (Jovani and Tella 2004, 2007, Blas et al. 2007,
 182 Baos et al. 2012), many white storks were known to breed (or live) in the study area during the
 183 previous two breeding seasons. In particular, 876 nests in 2002 and 1,056 nests in 2003 were
 184 monitored, identifying a total of 535 resident individuals either breeding or living in the area
 185 during the breeding season (March-August). 191 of these previously identified “resident”
 186 individuals were observed during the 2003 wintering season and 161 of them (i.e., marked as
 187 chicks) were aged based on their year of ringing. We classified individuals from foreign countries
 188 as “wintering immigrants” (N=711): Belgium (12), Denmark (112), France (235), Germany (179),
 189 Portugal (106), Switzerland (53), and 14 individuals with unknown (but foreign) band types.
 190 Storks with Spanish bands (782) but not encountered during the breeding season were classified as
 191 “uncertain”, since an unknown number of resident individuals could have been overlooked during
 192 monitoring. Observations of marked storks during the study period at ricefields (coded 1) and
 193 dumps (coded 2) or not detected (coded 0) were encoded in individual encounter histories
 194 including 80 occasions (days) by group (i.e., 1=certain residents, 2=certain immigrants and
 195 3=uncertain) (Appendix B, Supplement SD1). Age during winter 2003 of known-age residents
 196 was incorporated in capture histories as an individual covariate (Appendix B, Supplement SD2).

197 **Biological hypotheses**—We considered the following biologically plausible hypotheses

198 (regarding the existence or lack thereof of foraging strategies/preferences and the potential
 199 differences between individuals with different traits):

200 **A. Only generalist individuals:** **1.** *No difference between residents/immigrants and strictly*
 201 *generalist individuals.* The wintering population of storks is composed of generalist individuals
 202 that forage at ricefields and dumps in the same proportions (50%). **2.** *No difference between*
 203 *residents/immigrants.* The wintering population of storks is composed only of generalist
 204 individuals that forage at ricefields and dumps differentially. **3.** *Foraging habitat use differs*
 205 *between residents/immigrants.* The wintering population of storks is composed only of generalist
 206 individuals of which residents and immigrants forage at ricefields and dumps differentially.

207 **B. Generalists and specialists:** **4.** *No difference between residents/immigrants.* The
 208 wintering population of storks is composed of a mixture of ricefield specialists, dump specialists
 209 and generalist individuals in the same proportions of residents and immigrants. **5.** *Foraging*
 210 *habitat use differs between residents/immigrants.* The wintering population of storks is composed
 211 of a mixture of ricefield specialists, dump specialists and generalist individuals in different
 212 proportions of residents and immigrants. Among generalists, residents and immigrants forage at
 213 ricefields and dumps differentially.

214 **C. The role of age:** **6.** *No age effect.* Probabilities of foraging at ricefields by resident storks
 215 are similar among age classes. **7.** *Age effect.* Probabilities of foraging at ricefields by resident
 216 storks increase with age.

217 **Multievent capture-recapture models** —*Multievent modelling of foraging strategy and*
 218 *residency status.* We applied a multievent modelling approach (Pradel 2005) able to evaluate the
 219 degree of individual consistency in foraging specialisation in relation to residency status

220 (biological hypotheses 1-5). We present a general multievent model for hypothesis 5 (see below).
 221 The alternative hypotheses (1-4) were tested by alternative models fixing or constraining
 222 parameters from the general model (Table 1). Models were built and fitted to the data using E-
 223 SURGE 1.7.1 software (Choquet et al. 2009b). Model selection was based on the Akaike's
 224 Information Criterion (AIC). Additionally, for each model j , we calculated the Akaike weight, w_i ,
 225 as an index of its relative plausibility (Burnham and Anderson 2002).

226 The multievent framework distinguishes what can be observed in the field (the events
 227 coded in the encounter histories) from the underlying biological states of the individuals, which
 228 must be inferred (Pradel 2005). Here, the events were '0' (stork not observed on a particular
 229 occasion), '1' (stork observed foraging in a ricefield) and '2' (stork observed foraging at a dump).
 230 The general model included 7 underlying biological states: 6 states for live resident (R) and
 231 immigrant (I) storks belonging to 3 different foraging strategies (see below), coded R1, R2, R3, I1,
 232 I2 and I3; and one state for dead individuals, coded D. R1 and I1 represent individuals specialised
 233 in ricefields, R2 and I2 represent individuals specialised in dumps, and R3 and I3 represent
 234 generalist individuals. Exploratory analyses showed that apparent survival rate during the study
 235 period was close to 1 ($\phi = 0.99999$). This is in agreement with the short duration of the study
 236 period (80 days) and its timing (winter). Mortality and departure from the study area could
 237 therefore be neglected. Thus, we analysed the population as a closed population, allowing an
 238 increase in the precision of parameter estimates.

239 Multievent models use three kinds of parameters: the initial state probabilities, which
 240 correspond in our model to the proportions of newly encountered resident/immigrant individuals
 241 belonging to the different foraging strategy states (R1, R2, R3, I1, I2 and I3); the probabilities of

242 transition between the states (i.e., survival probability, which in this case was fixed at 1); and the
 243 probabilities of the events, which here involve the probabilities of presence at the two trophic
 244 subsidies (ricefields vs. dumps) and resighting probabilities. These parameters were estimated
 245 simultaneously from whole encounter histories by maximum likelihood (Choquet et al. 2009b).

246 Matrix representations with departure states in rows and arrival states in columns are
 247 commonly used in multievent models (see a detailed description in Appendix B and pattern matrix
 248 in Supplement SP1 and SP2). We broke down the initial state probabilities into two steps: the first
 249 step (residency status assignment, matrix 1) corresponded to the probability that a newly
 250 encountered individual was a resident “R” (π) or an immigrant “I” ($1 - \pi$) depending on the group
 251 (g) in which the individual was previously classified. For the groups with known residency status,
 252 π values were fixed at 1 for group 1 (“certain residents”) and at 0 for group 2 (“certain
 253 immigrants”). For group 3 (“uncertain”), the proportion of residents was estimated by the model.

254 Residency Status = $\begin{matrix} \text{R} & \text{I} \\ \pi_g & 1 - \pi_g \end{matrix}$ matrix 1.

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

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

260 The event probabilities were broken down into two steps: the first step corresponded to the
 261 daily probabilities of foraging in ricefields (α) and dumps ($1 - \alpha$) (matrix 3). They were allowed to

262 vary with residency status and foraging strategy. In the general model, α was fixed at 1 for the
 263 ricefield specialists (R1, I1), at 0 for dump specialists (R2, I2) and α was estimated for generalists
 264 (R3, I3), representing the daily percentage of generalists foraging in ricefields (Table 1).

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

266 The second step involved foraging-habitat-specific probabilities of resighting (p) (matrix
 267 4). Resighting probabilities in all models were left to vary between ricefields and dumps and over
 268 days (t) correcting for unbalanced field effort in both habitats (Appendix A). Additionally, we
 269 fixed resighting probabilities at 0 in those habitats and days without fieldwork (Appendix A). To
 270 avoid overparameterized models we only considered time effects on resighting probabilities.

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

272 Goodness-of-fit tests for multievent models have yet to be developed. The diagnostic
 273 goodness-of-fit for the most general model currently available is that of the general Arnason-
 274 Schwarz multisite model (Pradel et al. 2005), but this was not appropriate here, as this model,
 275 unlike ours, assumes Markovian transitions between sites. Instead, we ran the goodness-of-fit test
 276 from the Cormack Jolly Seber model (CJS) assuming full time variation of survival and resighting
 277 parameters common to the two types of feeding habitats. We ran this test with U-CARE 2.2.2
 278 software (Choquet et al. 2009a). This test was statistically significant ($\chi^2 = 627.57$, d.f.=366,

279 P<0.001) indicating that individuals tended to be detected on successive occasions (tests 2.CT and
 280 2.CL: trap dependence-like effects, Pradel et al. (2005)). This was expected because of the
 281 combination of unequal detectability in the two habitats and the correlation between observations
 282 in the ricefields on successive days. Although unequal detectability was treated in our model, the
 283 autocorrelation of observations in the ricefields remained untreated. Consequently, we decided to
 284 conservatively apply an overdispersion inflation factor (c-hat) of 1.71 calculated as $627.57/366$
 285 (χ^2/df) , which is a reasonable value for a large dataset (Burnham and Anderson 2002).

286 *Multievent modelling of resident age.* The encounter histories of 161 known-age residents
 287 were coded as in the previous analyses and an individual covariate indicating their age at the time
 288 of this study (ranging from 3 to 18 years) was included. We developed a simpler multievent model
 289 (Appendix B) in which the daily probability of presence at ricefields (α , matrix 5) was modelled as
 290 a linear function of age (hypothesis 7) or as a constant (i.e., no age effects, hypothesis 6).

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

292 In this analysis no uncertainty in residency status (all individuals were known residents) or
 293 different individual foraging strategies were considered. Consequently, individuals belonged to a
 294 unique departure state (R) and survival as in the previous model was fixed at 1 (Appendix B).
 295 Resighting probabilities were modelled as in the previous modelling approach (matrix 4). The
 296 goodness-of-fit of the CJS model was not statistically significant ($\chi^2=55.89$, d.f.=70, P=0.89)
 297 indicating a good fit to the data.

298 **RESULTS**

299 **Individual patterns of foraging according to residency status**— Overall, 813 storks

300 (1,332 band readings) were found only at ricefields, 621 individuals (896 readings) only at dumps,
 301 and 250 individuals (800 band readings) were observed foraging in both habitats. While this
 302 cannot be converted to absolute abundances of birds foraging on each type of food subsidy, it
 303 firmly illustrates that the species behaved as a generalist forager. The best-supported model in
 304 terms of QAICc was the general model (hypothesis 5, Table 2). Models considering alternative
 305 hypotheses showed much larger QAICc values (hypotheses 1-4, Table 2). The selected model
 306 (hypothesis 5, Table 2) estimated that 19% (8-40%) of the 782 individuals of uncertain origin
 307 would actually be classified as “residents” (n=149), with the remaining uncertain individuals
 308 classified as “immigrants” (n=633). This leads to mean estimates of 340 (i.e., 191+149) resident
 309 and 1,344 (i.e., 711+633) immigrant marked storks wintering in the study area.

310 Resident individuals showed a high consistency in their choice of food subsidies: 72% (CI:
 311 60-81%) of residents daily foraged exclusively in ricefields (i.e., were ricefield specialists, n=245
 312 individuals), while the remaining individuals (28%, CI: 19-40%, n=95 individuals) behaved as
 313 generalists. Among resident generalists using both foraging habitats during the study period, 31%
 314 (CI: 18-49%) and 69% (CI: 51-82 %) of individuals daily foraged in ricefields and dumps,
 315 respectively. Dump specialisation did not occur among residents as the proportion of dump
 316 specialists (R2 foraging strategy) was 0. In contrast, immigrants exhibited the three different
 317 foraging strategies: 16% (CI: 9-18%) were ricefield specialists (n=215 individuals), 24% (19-31%)
 318 were dump specialists (n=323 individuals) and 60% (CI: 50-68%) were generalists (n=805
 319 individuals). 60% (CI: 52-67%) and 40% (CI: 33-0.48%) of immigrant generalists daily foraged in
 320 ricefields and dumps, respectively. Consequently, on a daily basis, 81% of resident and 52% of
 321 immigrant storks foraged in ricefields. These proportions lead to estimates of 710 marked storks

322 daily foraging in dumps (65 residents and 645 immigrants) and 974 marked storks daily foraging
 323 in ricefields (275 residents and 699 immigrants).

324 **The effect of age as a driver of individual specialisation**— Resident storks showed
 325 higher probabilities of foraging in ricefields with age (Fig 2). Accordingly, the model considering
 326 an individual age effect on probabilities of foraging in ricefields was better supported in terms of
 327 AICc than the model without age effects (hypothesis 7 vs. hypothesis 6, Table 2). The effect of age
 328 was statistically significant, as confidence intervals of the beta estimate corresponding to the linear
 329 slope did not include zero (1.32, CI: 0.38-2.27).

330 **Spatial foraging patterns**— For individuals seen in at least two localities, the distance
 331 between the farthest pair of localities was slightly longer for immigrants than for resident
 332 individuals (average, range): 22.8, 3.5-116.0 Km, and 17.8, 3.5-72.2 Km, respectively (Mann-
 333 Whitney $W = 6833$, $p = 0.09$). This was due to the fact that distances between dumps (highly used
 334 by immigrants) were higher than distances between ricefields (Fig. 1). However, both immigrants
 335 and residents moved throughout the study area (Fig. 1).

336 DISCUSSION

337 Individual traits as drivers of foraging specialisation

338 The existence of intraspecific differentiation in niche or personality has received special attention
 339 during the last decade (Bolnick et al. 2003, Araújo et al. 2011, Dall et al. 2012). Less is known,
 340 however, about the ecological causes of individual specialisation (Araújo et al. 2011) or its long-
 341 term evolutionary consequences (Dall et al. 2012). Here, we studied the role of individual traits
 342 (residence status and age) on foraging specialisation under the optimal foraging theory framework
 343 (Araújo et al. 2011). We found that at the population level wintering white storks in SW Spain

344 used two anthropogenic food subsidies in large numbers as would be expected in an opportunistic
 345 generalist species. However, individual storks were either specialists or generalists on their
 346 foraging substrates (ricefields or dumps) during the study period (autumn-winter 2003). Although
 347 our study reflects a specialisation on a particular foraging habitat type rather than on a specific diet
 348 (i.e. prey items), crayfishes are the prey most frequently consumed by wintering white storks in
 349 ricefields (ranging from 86% to 98 % in two different winters, Tablado et al. 2010). On the
 350 contrary, storks can forage on a large variety of refuse items at dumps of likely lower nutritional
 351 quality than that of crayfish, a prey very rich in carotenoids (Negro et al. 2000).

352 As predicted, residents were highly specialised in feeding at ricefields, with no residents
 353 specialised in feeding at dumps. On the contrary, we found a slightly higher proportion of
 354 immigrants specialising in dumps than in ricefields, but most immigrant individuals (60%) were
 355 generalists. Moreover, diet preferences changed with age. According to our prediction, older
 356 resident storks had a higher probability of foraging in ricefields than younger individuals,
 357 suggesting that foraging skills in this particular habitat may increase with age and thus with
 358 accumulated learning and experience in the area (Marchetti and Price 1989, Giraldeau and Caraco
 359 2000). Wintering immigrants were similarly specialised on dumps and ricefields. High annual
 360 fidelity to wintering areas observed in other long-lived birds (Sanz-Aguilar et al. 2012) could
 361 explain the ricefield specialisation of some wintering immigrant individuals (as in residents)
 362 through the acquisition of experience in the area. On the other hand, supplementary feeding
 363 programs carried out in several European countries for the conservation of the species may have
 364 habituated certain individuals to highly predictable food resources such as dumps (Doligez et al.
 365 2004, Schaub et al. 2004, Massemin-Challet et al. 2006). A non-exclusive alternative hypothesis

366 would be that specialisation on dumps may only occur among juvenile immigrants. Note that
 367 resident juvenile storks (younger than three years old) were not present in our sample. In fact, all
 368 42 satellite-tracked juveniles born in the study area wintered in African quarters during their first
 369 years of life (J. Blas, unpubl. data). This could also explain the lack of dump specialisation among
 370 residents. Unfortunately, we have no data on the previous experience of immigrant storks
 371 wintering in the study area to test this hypothesis.

372 **Ecological implications and consequences of foraging specialisation**

373 At the individual level, two studies on seabirds related the existence of individual foraging
 374 specialisation on anthropogenic food subsidies with long-term fitness consequences: Northern
 375 gannets, *Morus bassanus*, foraging on fisheries discards and Western gulls foraging on refuse
 376 showed a lower body condition and lifetime reproductive success, respectively, than individuals
 377 actively preying upon live fish (Annett and Pierotti 1999, Votier et al. 2010). In our study case, an
 378 alternative but non-exclusive hypothesis to explain the age-related increased probability of
 379 foraging in ricefields would be differential survival (Curio 1983, Marchetti and Price 1989); i.e., if
 380 individuals consistently foraging in ricefields survive more, they would be overrepresented among
 381 older age classes. However, since our study only covered one wintering season, further research on
 382 long-term consistency of individual foraging specialisation and its potential demographic and
 383 population effects is needed.

384 At the population level, the high availability of food resources at rubbish dumps throughout
 385 the wintering and along the breeding range of white storks has promoted behavioural,
 386 demographic and population changes in this (Tortosa et al. 1995, 2002, Doligez et al. 2004,
 387 Schaub et al. 2005, Massemin-Challet et al. 2006) and other animal species (Oro et al. 2013).

388 Moreover, selection processes (e.g., wintering mortality or nest failure) have been relaxed by
 389 shortened migratory distances and greatly increased food availability (Tortosa et al. 2002, Schaub
 390 et al. 2004). Our study model demonstrates the existence of both consistent (i.e., specialist) and
 391 flexible (i.e., generalist) individual foraging strategies among the wintering population of white
 392 storks in the Doñana marshlands. The existence of consistent individual behaviours has been
 393 recognized as a driver of adaptation to new environments (i.e., new anthropogenic niches, Carrete
 394 and Tella 2011, 2013). Moreover, individual experience (shaped by age and origin) seems to be
 395 the most plausible mechanism responsible for differential use of subsidies. This has implications
 396 for our understanding of how a population-level generalist species such as the white stork could
 397 cope with anthropogenic habitat changes (Oro et al., 2013).

398 Doñana marshlands represent the most important European wintering area for the species
 399 and numbers of immigrant storks largely exceed the number of residents. Although ricefields were
 400 preferentially selected by resident storks, many individuals foraged daily at dumps; mainly
 401 immigrants (48%) and young residents (Fig. 2). Storks at Doñana benefited from two
 402 anthropogenic subsidies, but crayfishes are not available in other wintering areas. European
 403 environmental policies are now directed at curtailing food accessibility (i.e., biodegradable waste)
 404 to animals in rubbish dumps by 2016 (Directive 2001/77/EC), and an effect on wintering white
 405 storks is expected (<http://www.bto.org/science/migration/tracking-studies/stork-tracking>).

406 Although white stork populations have grown spectacularly during the last two decades after
 407 becoming endangered in the 1950-60's, several populations remain small (Thomsen and Hötker
 408 2006).

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

410 limitations may have important consequences at the population level (Oro et al. 2013), with
 411 wintering migrant storks from northern European populations being potentially more affected due
 412 to the large number of wintering birds and their greater use of dumps. While dump closure could
 413 appear to be a local phenomenon, our results suggest that it would directly affect stork populations
 414 thousands of kilometres away (immigrant storks), rather than just the local population (Peters et al.
 415 2007). However, immigrant storks were highly generalist at the individual level. Thus, an eventual
 416 dump closure would increase the number of immigrant storks feeding on ricefields, increasing
 417 competition and reducing resource availability for the resident population.

418 **Methodological aspects and opportunities of multievent models**

419 Repeated observations over time in individual foraging choices are essential to correctly study and
 420 quantify the consistency of individual foraging specialisation (Bolnick et al. 2003, Araújo et al.
 421 2011, Dall et al. 2012). However, perfect detection of individuals in natural conditions is often rare
 422 or costly. Here, we developed for the first time a capture-recapture modelling approach to
 423 calculate consistency in individual behaviour using capture-recapture data. This new method
 424 allowed a robust quantification (including confidence intervals) of individual strategies with the
 425 incorporation of imperfect detection of individuals. Additionally, we extended our modelling
 426 approach to allow uncertainty in individual classification (which in other cases may correspond to
 427 sex, breeding status or other factors, Pradel 2005, Frederiksen et al. 2013; see in particular
 428 Gourlay-Larour et al. (2014) for another study separating immigrants from residents on a
 429 wintering ground). In this way, we were able to estimate the proportion of resident individuals
 430 missed despite intense breeding monitoring, a parameter currently impossible to derive with other
 431 methods. Our model assumes that observations of the same individual on different dates are

432 uncorrelated and that individuals move independently of each other. This is probably not true as
 433 individuals may preferentially return to a site where they were able to forage successfully and
 434 individuals may also use the behaviour of conspecifics as clues to find suitable sites. These types
 435 of dependency and any remaining heterogeneity among individuals beyond the factors
 436 incorporated in our model (foraging strategy and residency status) are why goodness-of-fit tests
 437 were significant. When such non-structural departures are involved, the use of a variance inflation
 438 factor protects against the detection of spurious effects at the expense of power (Burnham and
 439 Anderson 2000). This is the approach we adopted. Moreover, our large numbers of individuals
 440 with certain residency status allowed us to repeat the analyses without the individuals of uncertain
 441 residency status with similar results, demonstrating the robustness of our multievent approach,
 442 which deals well with uncertainty (Appendix B). The use of this approach is therefore useful when
 443 sample sizes are logistically constrained and the proportion of individuals of uncertain
 444 status/behaviours is necessarily large. A step-by-step description of the analyses is provided in the
 445 supporting information with the aim of encouraging the application of our multievent model to
 446 other studies.

447 This study emphasised the application of longitudinal data on replicated observations of
 448 individual resource use over time for quantitative studies on individual foraging specialisation
 449 (Araújo et al. 2011). Tracking technologies are becoming very valuable tools to monitor
 450 individuals over large temporal and spatial scales (Millsbaugh and Marzluff 2001), including
 451 European storks (<http://projekt-storchenzug.com/>). However, sample size is usually small due to
 452 high costs. In contrast, extensive marking programs, such as those carried out with European white
 453 storks, allowed the identification and monitoring of a large number of individuals. Capture-

454 recapture methods were developed to estimate demographic parameters while accounting for
 455 imperfect detection of individuals. Today, the flexibility of multistate and recently of multievent
 456 models, as presented here, has allowed the study of additional parameters of interest (Clutton-
 457 Brock and Sheldon 2010, Frederiksen et al. 2013) and the incorporation of discrete individual
 458 heterogeneity classes (i.e., finite-mixture models) in capture-recapture modelling (Pledger 2000,
 459 Pradel 2005). Our study provides a robust new modelling approach for the study of individual
 460 behavioural specialisation from non-invasive and imperfect individual resightings in the wild.
 461 Further studies could also consider the potential dependence among individual decisions as white
 462 storks usually gather at foraging sites forming large groups, both in our study area and in other
 463 populations (e.g., Carrascal et al. 1990, Giraldeau and Caraco 2000). However, models including
 464 dependence among individuals forming groups have only been developed for fixed groups (with
 465 individuals belonging to the same group during the whole study period, Choquet et al. 2013), and
 466 further research is needed to determine the consistency of membership composition of foraging
 467 groups in white storks. Nonetheless, survival parameters have been found to be robust when
 468 dependence in recapture among individuals occurs (Choquet et al. 2013).

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- 598
- 599 Appendix A. Field work details.
- 600 Appendix B. Multievent analyses details.
- 601 Supplement SD1. Dataset: capture histories of all resident, immigrant and uncertain storks.
- 602 Supplement SD2. Dataset: capture histories of resident known-age storks.
- 603 Supplement SP1. Pattern files for the general model.
- 604 Supplement SP2. Pattern files for the simplified model for known-age residents.

605 **Table 1.** Multievent model constraints. Parameters fixed and/or constrained to be equal (=) or
 606 different (\neq). Notation: π is the probability that a newly encountered individual is a resident; β is
 607 the probability of adopting a foraging strategy by resident storks type 1 and 2 (β_1, β_2) and
 608 immigrant storks type 1 and 2 (β_3, β_4); α is the probability of foraging in ricefields of resident
 609 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
 610 correspond to storks recognized as residents and European immigrants, respectively.
 611

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

612 **Table 2.** Multievent capture-recapture modelling of white stork probabilities of foraging in
 613 ricefields and dumps testing the effects of residency status and foraging strategy
 614 (Hypotheses 1-5) and individual age (Hypotheses 6-7). Notation, np: number of estimable
 615 parameters; QAICc: Akaike information criterion corrected for overdispersion and small
 616 sample size; Δ QAICc: the QAICc difference between the current model and the one with
 617 the lowest QAICc value; w_i : Akaike's weight.

618

Model	np	Deviance	QAICc	Δ QAICc	w_j
Hypothesis 1	74	14440.52	8596.51	258.13	0
Hypothesis 2	75	14402.66	8576.47	238.10	0
Hypothesis 3	78	14262.36	8500.74	162.36	0
Hypothesis 4	78	14051.93	8377.68	39.31	0
Hypothesis 5	82	13970.27	8338.37	0	1
Hypothesis 6	65	1127.96	1278.12	5.87	0.05
Hypothesis 7	66	1119.42	1272.25	0	0.95

619

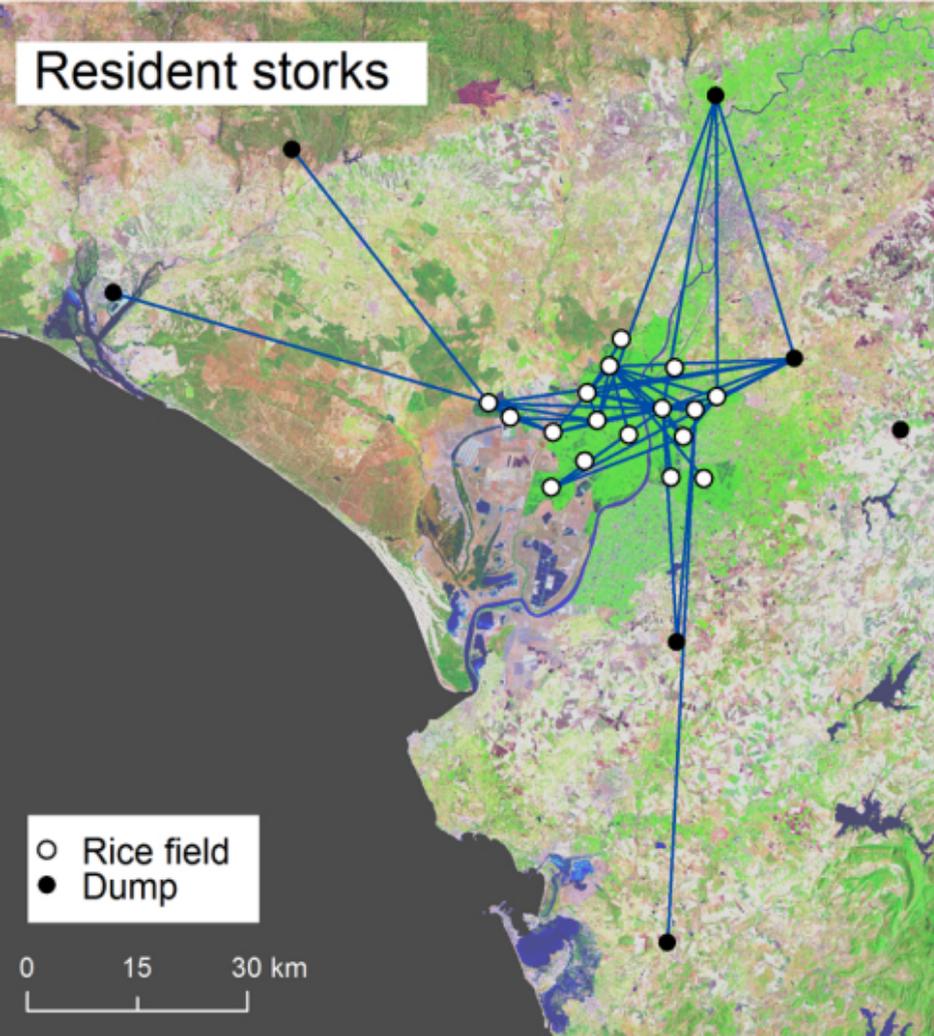
620 **Figure 1.** Study area in SW Spain (inset map, orange square and arrow) showing all
621 localities where white storks were observed foraging in dumps and ricefields (white and
622 black dots). Lines link pairs of localities sharing at least one individual stork.

623

624

625 **Figure 2.** Probability of resident storks foraging in ricefields rather than in dumps during
626 the 2003 wintering season in southern Spain (solid line) and CI (dashed line) related to
627 individual age.

Resident storks



Immigrant storks

