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Author-formatted, not peer-reviewed document posted on 05/03/2025

DOI: <https://doi.org/10.3897/arphapreprints.e152093>

# **Movement ecology of the Sacred ibis (*Threskiornis aethiopicus*) outside of its natural range**

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## 15 **ABSTRACT**

16 Understanding the movements of alien species in newly colonized territories is crucial for

17 addressing the challenges posed by global transformations and threats to biodiversity

18 conservation. In this study, we used mark-resight data to investigate the dispersal movements

19 of the sacred ibis in Italy, which were virtually unknown until now. We analyzed data from

20 357 colour-ringed ibises, the majority of which were marked as nestlings, including six

21 hybrids with the African spoonbill. Resightings revealed a tendency towards philopatry, with

22 most observations occurring within 10 km of the original colony. However, some individuals

23 traveled much farther, with maximum recorded distances exceeding 300 km from the ringing

24 site. The average long-distance travel speed was 15.4 km per day. Movement directions

25 showed clustering along both the North-South and East-West axes, influenced by colony

26 location. Landfills emerged as significant feeding sites, particularly in winter. Age class had a

27 significant negative effect on dispersal distance, whereas timing of hatching showed a

28 positive effect. Despite the apparent pronounced tendency towards philopatry, the high

29 dispersal potential of the sacred ibis suggests the possibility of rapid territory expansion and

30 colonization of areas far from natal colonies. These findings provide the first evidence of the

31 dispersal capability of the sacred ibis outside its natural range and should be used to inform  
32 management actions aimed at mitigating the potential effects of this invasive species.

### 33 INTRODUCTION

34 The increasing spread of invasive alien species (IAS) is considered one of the major drivers  
35 of biodiversity loss in the Anthropocene (Park 2004). This spread can vary considerably  
36 depending on species ecology and environmental conditions, ranging from a slow and  
37 localized process to the rapid colonization of extensive areas (Liu et al. 2014; Cameron and  
38 Bayne 2015). The rate, mode, and circumstances of this process depend on several factors,  
39 including species-specific dispersal strategies. In IAS, these strategies may differ from those  
40 observed in their native range and may also shift during the invasion process. Furthermore,  
41 when tracking invasion patterns, it is crucial to consider the potential increase in activity  
42 levels or exploratory behavior of the alien species (Burstal et al. 2020).

43 The sacred ibis (*Threskiornis aethiopicus*; class: Aves), native to sub-Saharan Africa and  
44 Iraq, has been present in Europe as an alien species since the 1970s, following repeated  
45 escapes from aviaries and wildlife parks (Yésou and Clergeau 2005). The presence of these  
46 escaped individuals complicates efforts to determine whether other birds could have arrived  
47 spontaneously from their native range (Cocchi et al. 2023). While the likelihood of isolated  
48 immigrants appears low, it is not implausible, as observed in other highly dispersive avian  
49 species and hypothesized by Marion (2013). In Europe, breeding in the wild has been  
50 confirmed in France, Germany, Italy, Portugal, Spain, Switzerland, and the Netherlands  
51 (Robert et al. 2013; Yésou et al. 2017). In Italy, the species has been recorded since the 19th  
52 century (Arrigoni degli Oddi 1929), but until the early 2000s, it was not yet considered  
53 naturalized (Brichetti and Fracasso 2003). The exact origin of the Italian population remains  
54 uncertain. However, since the 1990s, the population has been reinforced by numerous  
55 accidental releases and escapes from zoos in Italy and neighboring countries (Cocchi et al.  
56 2023) and possibly by individuals dispersing from the expanding French population (Cucco  
57 et al. 2021).

58 This exotic and relatively easy-to-maintain bird is commonly kept in zoological gardens,  
59 wildlife centres, and private parks. The risk of escapes and subsequent population growth  
60 remains a concern, particularly in non-EU countries where the keeping of alien species is not  
61 regulated. In recent years, over 10,000 individuals have been counted in captivity across

62 Europe. Currently, 142 facilities in EU countries and 34 in non-EU European countries house  
63 sacred ibises (Zootierliste, n.d.).

64 Until the early 2000s, the few recorded sacred ibises were concentrated in northwestern Italy.  
65 However, since 2006, their expansion has been continuous and exponential, initially across a  
66 large area of the Po Valley and later, with increasing frequency, into at least 14 regions of  
67 central and southern Italy, including the major islands of Sicily and Sardinia (Cucco et al.  
68 2021; Ercole et al. 2021). Beyond the core population in northwestern Italy, in the past five  
69 years, the species has established thriving colonies in central and northern regions (Scarton  
70 and Valle 2020; Cucco et al. 2021). This geographical expansion has been accompanied by  
71 an exponential increase in numbers, from around 70 individuals with sporadic nesting until  
72 2010, to 1,249 breeding pairs and over 11,000 wintering individuals in northwestern Italy by  
73 2019 (Cocchi et al. 2023).

74 Regulation 1143/2014 of the European Parliament requires Member States to implement  
75 measures for managing IAS, including provisions to prevent their introduction and control  
76 their spread (European Parliament and Council 2014). Since 2016, the sacred ibis has been  
77 listed as an IAS of Union Concern, meaning it is subject to management measures and  
78 restrictions on keeping, importing, selling, breeding, and releasing into the environment. This  
79 classification is primarily due to its predation on amphibians and the eggs of native bird  
80 species, as well as its potential competition for breeding sites with native species such as the  
81 Eurasian spoonbill (*Platalea leucorodia*), colonial herons, and egrets. In response, Italy  
82 approved a national management plan for the species in 2023 (Cocchi et al. 2023), aiming to  
83 eradicate, reduce, and control the population in the Po Plain while preventing its expansion  
84 into currently unoccupied areas.

85 However, the effectiveness of a species management plan—both in terms of economic cost  
86 and technical feasibility—relies on a comprehensive understanding of the target species’  
87 ecology, population dynamics, and distribution. One critical factor in this context is dispersal,  
88 which significantly influences the extent and pace of invasion. Without robust quantitative  
89 ecological data clarifying the mechanisms driving species demography, developing a targeted  
90 control strategy and evaluating its effectiveness may be challenging, if not impossible.

91 In this study, we analyse a 19-year capture-mark-resight dataset to assess the dispersal  
92 capacity of the sacred ibis outside its native range. We also evaluate the role of dispersal in  
93 the context of the management strategies applied to this invasive species of Union Concern.

94 **METHODS**

95 *a. Mark-resight data.*

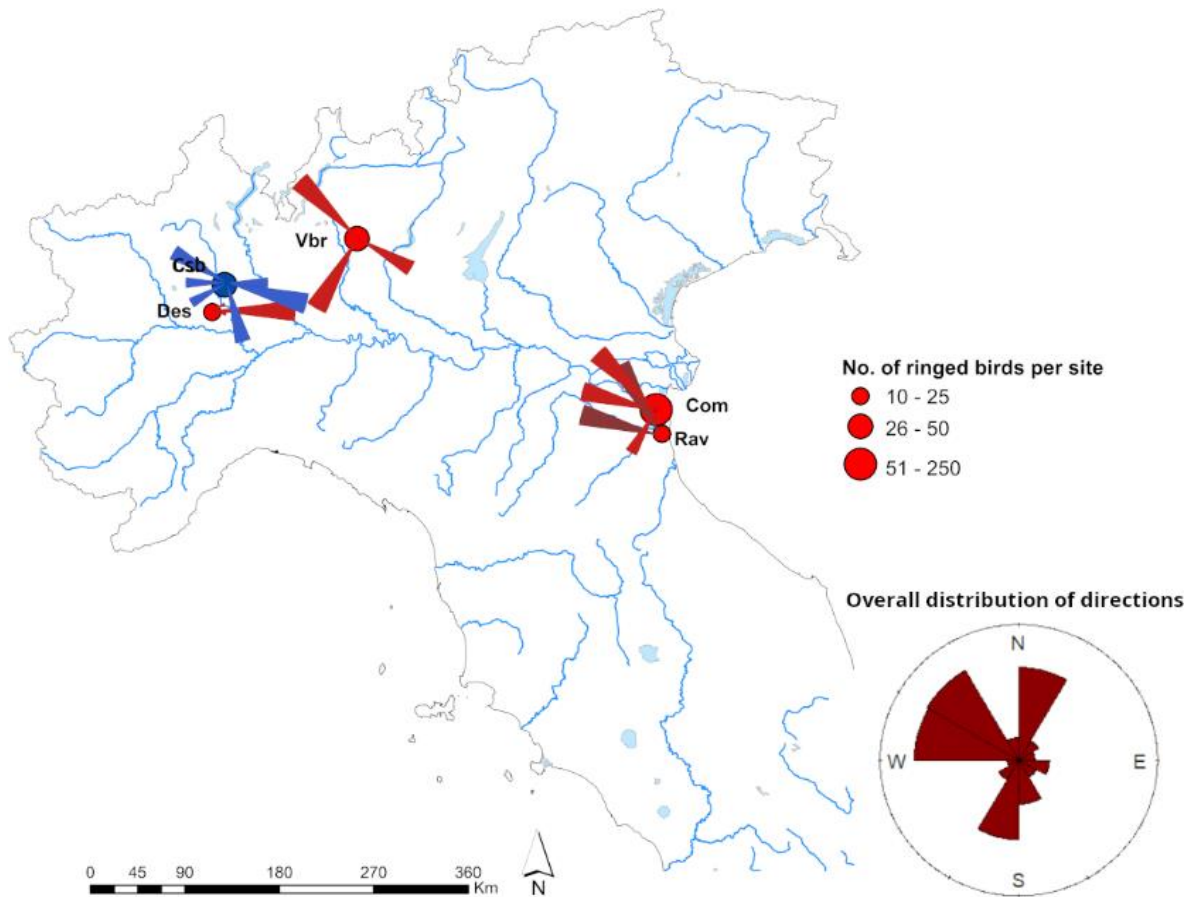
96 From 2004 to 2023, a total of 357 nestlings and fledged ibises were marked with metal rings  
 97 provided by the Italian Ringing Scheme and a yellow plastic ring with a unique 2- or 3-digit  
 98 alphanumeric code. These colour-rings can be read from a distance of up to 100 metres using  
 99 a telescope or digital images taken with a telephoto lens. Nestlings (n = 321) were marked in  
 100 five colonies located either in inland locations (Desana and Valbrembo) or coastal wetlands  
 101 (Comacchio and Ravenna) (Table S1 in Supplementary material, Figure 1). Most of the fledged  
 102 birds were accidentally caught in cages originally intended for anatids and herons at the  
 103 Casalbeltrame ringing station (province of Novara), and occasionally in colonies during nest  
 104 monitoring.

105 The first nestlings were ringed in the southern Po Delta, where the sacred ibis settled in a large  
 106 mixed heronry, breeding in close association with Eurasian spoonbills and other colonial  
 107 waterbirds (Volponi, 2020). In fact, the very first ringed nestlings were hybrids from a mixed  
 108 pair formed by a male sacred ibis and a female African spoonbill (*Platalea alba*) nesting in a  
 109 flooded *Salix* bush (Volponi et al. 2008). In 2016-2018, nestlings were ringed at the colony  
 110 situated within the Valbrembo zoological park (province of Bergamo), where free sacred ibises  
 111 bred on tall coniferous trees (Castiglioni, 2017). There, ringing was only possible by  
 112 approaching the nests from a mobile aerial platform during tree maintenance work. More  
 113 regular and intensive ringing started in 2017 in the colony inside the large coastal lagoon of  
 114 Comacchio (province of Ferrara) where ibis nests were built on the ground, again close to the  
 115 spoonbills nests. In addition, a small number of nestlings were ringed from ground nests in the  
 116 Desana colony, located near the city of Vercelli in an area of intensive rice cultivation.

117 Most of the resighting data came from the observation of colour-ringed birds and to a lesser  
 118 extent (less than 2% of the total number of records) from the recovery of dead birds.  
 119 Birdwatchers, wildlife photographers and amateur ornithologists provided most of the  
 120 observations outside the ringing sites. Such observations were often reported via social media  
 121 or, secondarily, directly to the Italian ringing scheme or to the ringers themselves. Searches for  
 122 ringed birds were regularly carried out during visits to known ibis colonies, heronries and their  
 123 surroundings. Other resightings were obtained from images taken by camera traps used to  
 124 monitor nests in the Comacchio colony.

125 Resightings of individuals marked as nestlings and seen in or near the ringing site were only  
 126 included in the analysis if they occurred after 40 days of marking, in order to exclude records  
 127 before fledgling. Data collection for resightings ended on 30 September 2024.

128



129 **Figure 1.** Map of ringing sites in Northern Italy and the corresponding movement directions  
 130 observed. The size of each dot is directly proportional to the number of individuals ringed. Red  
 131 dots represent breeding colonies, while the blue dot marks the location of the Casalbeltrame  
 132 ringing station. Abbreviations: Com: Comacchio; Vbr: Valbrembo; Csb: Casalbeltrame; Des:  
 133 Desana; Rav: Ravenna. The circular plot in the bottom-right corner illustrates the overall  
 134 distribution of movement directions for resighted birds.

135 *b. Movement Analysis.*

136 Data from resightings were analysed to derive quantitative metrics of ibis movement and  
 137 dispersal. To perform the analysis, when more than one resighting of the same individual  
 138 occurred within the same month, only the one furthest from the ringing site was retained.  
 139 Specifically, we (i) calculated both the orthodromic distance and direction between an  
 140 individual marking site and each resighting location; (ii) calculated the average travel speed

141 using the method of Smith and Munro (2011), which involves dividing the distance travelled  
142 by individuals covering significant distances (>150 km in our case) in a short period of time  
143 (<4 months) by the number of days elapsed; (iii) calculated the percentage of resightings per  
144 habitat to highlight any differences in occurrence among habitat types; (iv) checked whether,  
145 if an individual was resighted in a breeding colony, the latter was its hatching colony or not, to  
146 explore the possible tendency for philopatry or reproductive exchange among different  
147 colonies; (v) estimated how age class and hatching time of resighted individuals affected their  
148 travel distance, using Generalized Linear Mixed Model (GLMM) fitted using restricted  
149 maximum likelihood (REML). We used age groups and hatching time (or “brood class”) as  
150 predictive variables and ring code (i.e. individual) as random factor to avoid pseudoreplication.  
151 This analysis was performed using the R (R Core Team, 2022) package lme4 (Bates et al.  
152 2015). All classes were determined only for birds marked as nestlings. Age classes 1-, 2-, 3-,  
153 and 4-year old or older were categorised as follows: 1) birds resighted the same year they  
154 hatched, 2) birds resighted the year following their hatching, 3) birds resighted two years after  
155 hatching, and 4) birds resighted three or more years after hatching. We considered three brood  
156 classes: early broods (nestlings marked before 15 May), intermediate broods (nestlings marked  
157 between 16 May and 30 June), and late broods (nestlings marked from 1 July).

158 We used the Rao’s spacing test (R package circular; Agostinelli and Lund, 2024) to test whether  
159 the calculated directions were randomly distributed or clustered. This analysis was performed  
160 by first considering the total movements and then separately examining the movements of birds  
161 ringed in coastal (provinces of Ravenna and Ferrara) and inland sites (provinces of Bergamo,  
162 Novara and Vercelli).

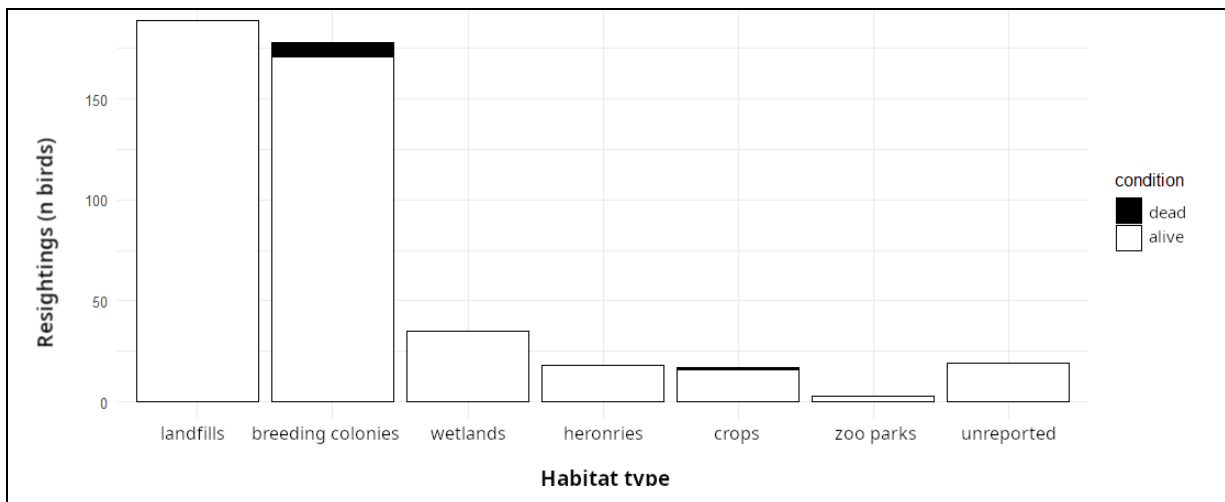
## 163 **RESULTS**

### 164 *Mark-resight.*

165 In total, 491 resightings were achieved during the study period, representing 138 different  
166 individuals (38.7% of the total number of individuals ringed). The year with the highest number  
167 of resightings (234) was 2024, with 64 different individuals. There were no resightings before  
168 2006 and none in 2015. The vast majority of resightings involved live birds, but six concerned  
169 birds were found dead. Of these, three died of natural causes, two were shot, and one died as a  
170 result of a severe weather event. One of the shot birds was killed by a poacher in 2009, and the  
171 other by a wildlife ranger during a culling in Friuli-Venezia Giulia in 2023. Apart from the  
172 authors and ringers, 71 observers reported 215 resightings from 68 localities, spread across



173 eight administrative regions and 19 provinces. Ringed birds were resighted at ibis and heron  
 174 colonies, daytime aggregations, night roosts, and feeding sites in various habitats, including  
 175 natural wetlands, ditches and canals, agricultural fields, and artificial environments (e.g.  
 176 landfills, dung heaps). Most resightings were made at landfill sites (41.2%) and breeding  
 177 colonies (38.8%) (Figure 2). In 97.8% of cases, where resighting occurred at a breeding colony,  
 178 it was the same colony where the individual was ringed as a nestling.



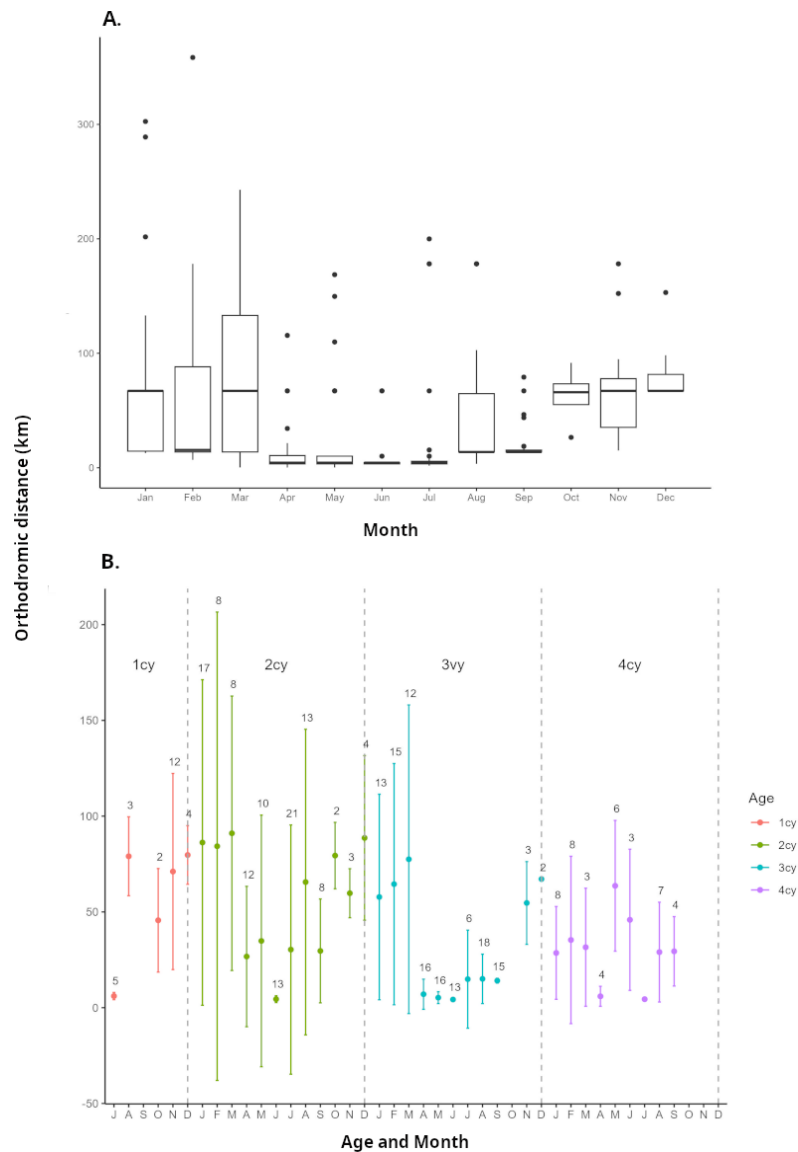
179 **Figure 2.** Number of resightings per habitat type. Recovery of dead individuals are shown in  
 180 black.

181 *Movement Analysis.*

182 a. Dispersal distances.

183 Local movement after fledging, calculated as the mean orthodromic distance, was 40.97 km  
 184 (SD = 58.33 km). However, the longest orthodromic distance travelled by an individual was  
 185 358.48 km, and five birds travelled distances of over 250 km. The movements of hybrid  
 186 individuals were much more restricted, with an average dispersal of 3.5 km and a maximum  
 187 orthodromic distance covered of approximately 13 km. Around 42.7% of resightings  
 188 (excluding hybrids) occurred within 10 km of the ringing location (Figure 3). The average  
 189 travel speed calculated for birds covering long distances (i.e. >150 km) in a short (<4 months)  
 190 time was found to be 15.4 km per day, with the highest speed achieved by an individual  
 191 covering 316.7 km in just over 3.5 months (26.6 km per day).





192 **Figure 3.** A. Mean orthodromic distance travelled by resighted birds, divided by month of  
 193 resighting, without distinction by age class. B. Mean orthodromic distance (± standard  
 194 deviation; in kilometers). Resightings are grouped by month and age class (calculated in  
 195 calendar years, see methods). The numbers on each bar indicate sample size.

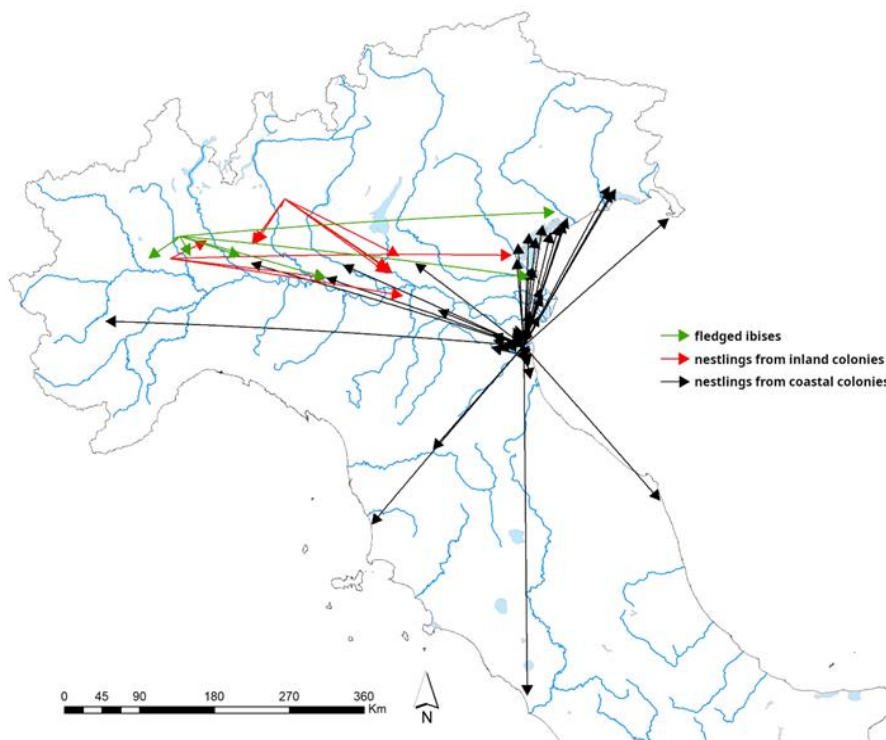
196

197 Results from the GLMM, revealed significant associations between distance travelled and both  
 198 age and brood class factors (Figure 3, Table S). In particular, age group had a significant  
 199 negative effect on distance travelled (mean effect and 95% CI = -29.28, [-50.99, -7.57], t value  
 200 = -2.645 for age class 3 and -33.17, [-59.16, -7.18], t value = -2.502 for age class 4), suggesting  
 201 that older individuals tended to travel shorter distances. Conversely, brood class 3 had a  
 202 significant positive effect on distance travelled (mean effect and 95% CI = 51.49, [17.53,

203 85.45],  $t$  value = 2.968 for brood class 3), while brood class 2 effect was positive but not  
 204 significant - indicating that only birds from the latest broods tended to travel longer distances.

205 b. Directions.

206 Rao's spacing test on the directions (in degrees) taken by resighted individuals significantly ( $t=$   
 207 292.2,  $p<0.001$ ) indicated that angular directions were not uniformly distributed in space.  
 208 When considered all together, the dispersal paths of the ibises were not randomly directed;  
 209 instead, they exhibited a clear clustering, predominantly directed towards the northwest and  
 210 roughly along the north-south axis (Figure 1). Two individuals showed interesting commuting  
 211 movements along the east-west axis between the Adriatic coast and the western Po valley.



212 **Figure 4.** Movements of the Sacred ibises ringed in Italy. The colour of the arrows corresponds  
 213 to individuals ringed as fledged birds (green) or as nestlings from inland (red) and coastal  
 214 (black) colonies. The arrowheads indicate the recapture sites.

215 For both birds ringed in coastal and inland colonies, the directionality of movement was found  
 216 to be non-random and highly clustered (assessed by Rao's spacing test,  $t = 237.6$  for inland and  
 217 301.0 for coastal, both  $p<0.001$ ). The Watson's two-sample test of homogeneity yielded a test  
 218 statistic of 1.261 and a  $p$ -value of less than 0.001, indicating a significant difference between  
 219 the directional movement angles of individuals ringed in coastal colonies compared to those  
 220 ringed in inland colonies. This suggests distinct directional patterns between the sampled

221 populations. While birds from inland colonies showed a prevalence of movement along the  
222 east-west axis, those ringed in coastal colonies showed a distinct directional trend along the  
223 north-south axis, accompanied by a secondary dispersal cluster towards the west-northwest  
224 direction. (Figure 2, 4).

225

## 226 **DISCUSSION**

227 Understanding the dispersal of alien species beyond their native range is crucial for addressing  
228 the challenges of managing them in a constantly changing environment (Webber and Scott,  
229 2011). Although ringing has inherent limitations—such as potential sampling biases (e.g.,  
230 certain age groups of birds being more likely to be resighted; Giuntini et al. 2023) and its  
231 inability to track entire migration routes, capturing only segments through resightings (Smith  
232 and Munro, 2011)—the exploration of movement ecology through ringing has consistently  
233 proven its worth (Baillie et al. 1999; Thorup et al. 2014; Dalui and Mondal, 2023). In this study,  
234 we used this technique to unravel previously unknown dispersal movements of this alien  
235 species during a period of population expansion outside its native range.

236 The analysis of resightings showed a rather pronounced tendency for adults and juveniles  
237 (probably during prospecting movements) to be philopatric towards the colony where they had  
238 been marked as nestlings. In fact, about half of the resightings occurred within 10 km of the  
239 ringing site. Specifically, whenever a bird was resighted in a breeding colony—the most  
240 common resighting habitat after landfills—was consistently the same breeding colony where  
241 the individual had been ringed. On the other hand, nest site fidelity is indeed quite characteristic  
242 of the species (Maillard et al. 2020), and has also been observed in the closely related Australian  
243 white ibis (*Threskiornis molucca*, Smith and Munro 2011). Nevertheless, we acknowledge the  
244 presence of possible bias in this result, as several resightings were obtained within the colonies  
245 of origin during nest monitoring. However, the large number of observers and their extensive  
246 geographical distribution (see Results) should help mitigate such bias.

247 In our sample, local post-fledgling dispersal consistently averaged less than 50 km. However,  
248 substantial movements of more than 350 km were documented as early as the first autumn-  
249 winter of life. The much shorter distances observed for hybrids, never exceeding 12 km and  
250 averaging less than 4 km, are not particularly surprising, as all hybrid observations were  
251 restricted to the first few months after fledging. Except for hybrids, the observed dispersal

252 distances align with findings from other invasion areas, such as France, where ibises have  
253 dispersed over hundreds of kilometres (Clergeau and Yésou, 2006), and with patterns in their  
254 native range, where adult ibises travel significant distances during post-breeding dispersal,  
255 often accompanied by juveniles (Hancock and Kushlan, 1992). In Africa, the extent and  
256 direction of movements vary with seasonal rainfall. Ringing records indicate that birds ringed  
257 in South Africa have been recovered across a wide territory, reaching as far as Zambia,  
258 Botswana, and Namibia, with the most distant recovery recorded 1,474 km from the ringing  
259 site (Clark and Clark, 1979). Similarly, the Australian white ibis (*T. molucca*)—once  
260 considered a subspecies of *T. aethiopicus* (Hancock and Kushlan, 1992; Christidis and Boles,  
261 2008) and now recognized as one of three species in the *Threskiornis aethiopicus* superspecies  
262 complex (Lowe and Richards, 1991)—frequently travels distances exceeding 300 km, with  
263 occasional movements surpassing 1,000 km (Smith and Munro, 2011).

264 The average dispersal speed we calculated appears to be particularly high. When considered  
265 alongside observations from other newly invaded areas and the inherently high mobility of  
266 ibises in their native range (Clark and Clark, 1979), this underscores the species' potential to  
267 expand across a significant portion of the Italian territory within a few years. Theoretically, our  
268 results suggest that ibises could traverse the entire length of Italy in less than three months.  
269 This finding aligns with the dispersal speeds calculated by Smith and Munro (2011) for *T.*  
270 *molucca*, where the fastest ringed individual traveled at an average speed of 14.5 km per day.  
271 It is also important to note that our estimated speed is likely conservative, as it remains  
272 unknown whether the resighted bird arrived at the resighting site on the day of observation or  
273 had been there for several days. This potential for range expansion is particularly relevant given  
274 the extensive suitable habitat available throughout Italy, as outlined by Cucco et al. (2021),  
275 much of which remains uncolonized.

276 Indeed, while the species has primarily been recorded in northern Italy, recent years have seen  
277 an increasing number of regular sightings in central and southern regions (Nicoli et al. 2022;  
278 Pantalone et al. 2023; Fraticelli, 2024; Maio et al. 2024). Given the species' high mobility, it is  
279 reasonable to assume that its range expansion could impact countries near Italy that are either  
280 not yet colonized or only partially so. Colonies in northwestern Italy (e.g., Piedmont) could  
281 expand into neighboring France, where an eradication program has been in place since 2007,  
282 leading to a significant reduction in the French ibis population (Yésou et al. 2017). Moreover,  
283 ibises dispersing from colonies in other Italian regions may have already contributed to the  
284 colonization of nearby countries. For instance, the six immature birds that spent a few weeks

285 in the Magadino Plain (Canton Ticino, Switzerland) in early 2021 (Mordasini, 2021) may have  
286 originated from colonies in Piedmont or Lombardy. Similarly, some of the at least 30 ibises  
287 observed in Corsica (France) in 2021 (CorseOrnitho, 2021) could have arrived from Tuscany,  
288 possibly following migrating Eurasian spoonbills that were present in the same coastal wetland  
289 at the time. Finally, at least one of the 12 individuals recorded in Slovenia in February 2024  
290 (Maks Sešlar, pers. comm.) was confirmed to have been born and ringed in the Comacchio  
291 colony in 2023. The prevalence of movements along the east-west axis (and vice versa) in the  
292 Po Valley and northwards from the Emilia-Romagna colonies appears to be guided by the  
293 hydrographic network of the Po River and the sequence of wetlands along the northern Adriatic  
294 coast. Similar behaviour has been observed in spoonbills, herons, cormorants, and other  
295 colonial wading birds ringed in the Po Delta (Volponi S. unpublished data). Elsewhere, closely  
296 related species, such as the Glossy Ibis (*Plegadis falcinellus*), have been found to follow  
297 wetland flyways (Samroui et al. 2023). Additionally, sacred ibises within the same roost and  
298 colony seem to consistently maintain an awareness of local foraging areas from one day to the  
299 next. This is supported by the relatively stable and directional flight paths of birds departing in  
300 the morning (Evans et al. 1981) or returning at dusk (Volponi, unpublished data). This pattern  
301 may help to explain tendency of some ringed individuals to exhibit east-west commuting  
302 movements from their original coastal colony towards the core area of initial settlements (i.e.,  
303 the western Po Valley). Such behaviour could be an extended form of the commuting  
304 movements between foraging areas and roosts characteristic of the species. However, it is  
305 important to note that typical commuting movements generally cover shorter distances (less  
306 than 1 km, Evans et al. 1981; Yésou et al. 2017) and are therefore likely distinct from the  
307 longer-range movements (several tens of kilometres) observed in this study. The most plausible  
308 hypothesis remains that these movements involve individuals returning in spring to their  
309 marking colony following breeding or prospecting dispersal.

310 The location of resightings underscores the key role of landfills as feeding sites and, more  
311 specifically, as winter hotspots. Across three winters (2021–2023), a total of 35 distinct  
312 individuals, accounting for 81 observations, were resighted at five landfill sites in the provinces  
313 of Cremona, Ferrara, Ravenna, and Venice. These sites, which hosted anywhere from a few  
314 dozen to over 1,000 ibises, served as foraging grounds where the birds scavenged a mix of  
315 animal, plant, and human waste alongside other bird species. The majority of ibises observed  
316 at landfills were juveniles and immatures, with adults present in smaller numbers. This suggests

317 that landfills play a role in winter survival, particularly for younger individuals, which are  
 318 generally more vulnerable to winter mortality.

319 The use of landfills as feeding sites by ibises has been documented in other populations. Clark  
 320 and Clark (1979) noted that ibises tend to concentrate in areas where food is produced by  
 321 human activities, such as animal farms and rubbish dumps. Clergeau and Yésou (2005)  
 322 reported over 600 ibises feeding at a single landfill, while Marion (2013) identified landfills as  
 323 the primary feeding grounds for the species in Brittany. Similarly, the Australian white ibis  
 324 exhibits the same foraging behaviour in its native range. Smith and Munro (2011) found that  
 325 landfills played a dominant role in the species' feeding habits, with over 90% of resightings  
 326 occurring at these sites. Despite their ecological significance, the role of landfills as key feeding  
 327 areas has not been previously highlighted in the Italian context. This is particularly important  
 328 for population management initiatives, as the easy access and constant availability of food in  
 329 landfills—especially during winter—can promote aggregation and enhance survival rates in  
 330 large numbers of birds (Oro et al. 2013).

331 The analysis revealed a significant effect of age class on dispersal distance, which decreased  
 332 with increasing age. This may reflect natal dispersal—i.e., the movement from the birth site to  
 333 the site of first (or potential) reproduction—of immature birds (Greenwood and Harvey, 1982).

334 Although this might seem to contradict the observed philopatric tendencies, a plausible  
 335 hypothesis, at least in our case study, is that juvenile ibises engage in extensive prospecting  
 336 movements before returning to their natal colonies to breed, having gathered information on  
 337 potential breeding sites during their first two years of life (Morales et al. 2010). This would  
 338 also align with the observed non-random directionality of movements, which, as mentioned  
 339 above, appears to follow the distribution of wetlands.

340 Even immature northern gannets (*Morus bassanus*), although highly faithful to their natal  
 341 colony, tend to explore and assess the habitat quality of other colonies (Votier et al. 2011)—a  
 342 behaviour also documented in the glossy ibis (Santoro et al. 2013).

343 By contrast, the observed positive effect of hatching time on dispersal distance is less  
 344 straightforward. While no comparable analyses exist for the sacred ibis or other  
 345 Pelecaniformes, Oudman et al. (2017) found a positive relationship between chick condition  
 346 and hatching date in stable Eurasian spoonbill colonies in the Netherlands. Moreover, in several  
 347 bird species, better body condition is associated with greater dispersal distances (Barbraud et  
 348 al. 2003; Liu and Zhang 2008). However, this aspect requires further investigation.



349 Our data show that sacred ibises born in a single colony exhibit different dispersal behaviours  
350 and may be nomadic, as recorded in their native range (Clark and Clark, 1979) and in the  
351 closely related *T. molucca* (Carrick, 1962; Smith and Munro, 2011). These results have  
352 implications for the spread of this alien bird into new territories and the establishment of new  
353 settlements, highlighting the importance of understanding the movement ecology of alien  
354 species in order to prevent or mitigate potential negative impacts. At the same time, the high  
355 dispersal capacity of the sacred ibis can affect the effectiveness of management measures for  
356 this invasive species. Taking in consideration these results, a regular and effective monitoring  
357 programme should be implemented to enable adaptive resource management.

358

## 359 CONCLUSIONS

360 Our findings provide crucial insights into the dispersal patterns of the sacred ibis outside of its  
361 native range, demonstrating its high mobility and potential for rapid range expansion across  
362 Italy and beyond. This study represents the first attempt to analyse the dispersal dynamics of  
363 the species in Europe, offering novel data on its movements during a phase of population  
364 expansion. The observed dispersal distances, comparable to those documented in both the  
365 species' native and invasive ranges, underscore its ability to colonize new areas swiftly,  
366 facilitated by a network of suitable habitats and anthropogenic food sources such as landfills.  
367 Given the species' capacity for long-distance movements and its reliance on human-altered  
368 landscapes, targeted conservation actions, including habitat monitoring and population control  
369 measures, should be adapted accordingly. Ultimately, this study underscores the necessity of  
370 ongoing, large-scale monitoring to inform evidence-based management and mitigate the  
371 ecological impact of this expanding invasive species.

## 372 Acknowledgements.

373 We thank the Ente Biodiversità Parco Delta del Po Emilia-Romagna (Comacchio, FE) and Mrs.  
374 Elisabetta Accatto (Desana, VC) for granting the access to the ringing colonies; Pietro Cassone  
375 and Alessandro Re for sharing the data of ibises ringed at Casabeltrame; Roberta Castiglioni,  
376 Marco Cucco, Davide Emiliani, Mauro Fasola and Daniela Mengoni for their assistance and  
377 invaluable help during ringing operation and search for ringed birds; the numerous  
378 birdwatchers, amateur ornithologists and photographers who provided a large amount of the  
379 ibis resightings.



380 Marking of the Sacred ibises was carried out by ringers licensed by the Italian Ringing Scheme  
381 of ISPRA. Activities carried out after the year 2020 were concerted with the Italian Ministry  
382 of the Environment and the Piedmont and Emilia-Romagna Regional Administrations as a part  
383 of the management plan of this alien species.

384

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