



# Age-related spatial ecology of Audouin's gull during the non-breeding season

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**ABSTRACT:** For vulnerable and endangered migratory species, an important and often overlooked aspect of conservation is their non-breeding distributions. For long-lived species, an additional constraint is the lack of data on juvenile movements. Individual relationships between age, movement ecology, and habitat preference for long-lived migratory birds remain understudied. According to the exploration-refinement hypothesis, adults should select better and more productive areas for foraging than inexperienced juveniles. Here, we explored the differences in migratory patterns, habitat selection, and foraging behaviour between juvenile and adult Audouin's gulls *Ichthyaetus audouinii*, a species listed as Vulnerable by the IUCN. We captured 4 juveniles and 6 adults in the San Pedro colony (SE Spain) and equipped them with high-resolution 5 min programmed GPS loggers to track their postnuptial or first migration and subsequent non-breeding destinations. Our findings show that juveniles tended to migrate longer distances than adults, that the time spent foraging between age groups did not differ, and that adults used a greater variety of habitats than juveniles and positively selected some foraging habitats, such as waterbodies. Age-related differences in migratory patterns and habitat exploitation during the non-breeding period can be explained by the avoidance of competition between juveniles and adults and the adults' greater experience in foraging performance. Our results bring important insights into the age-related differences in habitat exploitation of a Vulnerable seabird, which could help improve conservation strategies across its non-breeding range.

**KEYWORDS:** Canary Current · First-year movements · Foraging behaviour · Habitat use · *Ichthyaetus audouinii* · Juvenile migration · Migratory gull · North-west African seabirds · Wintering season

## 1. INTRODUCTION

Conservation of migratory species is extremely difficult, given the huge variety of threats to which they may be exposed along their entire distribution, such as habitat degradation or climate change (Lucas & MacGregor 2006, Grémillet & Boulinier 2009). Further-

more, when distributions and migratory behaviours vary with age in long-lived species such as seabirds (Pettex et al. 2019, Souc et al. 2023), assessing valid conservation measures becomes even more challenging. The study of spatial ecology in long-lived species is therefore essential to identify and manage the threats to which these species are exposed.

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Although abundant research has focused on the influence of diverse external factors on individual movements, such as environmental variables or human-induced effects (Navarro et al. 2010, Payo-Payo et al. 2023), the focus on intrinsic individual factors such as size, age, or breeding status as potential drivers of movement patterns and habitat use is becoming a subject of interest (Marques et al. 2010, Kralj et al. 2014, Pérez et al. 2014, Fayet et al. 2016, Pettex et al. 2019, Delgado et al. 2020, Zango et al. 2020, Souc et al. 2023). In particular, the age of individuals is often overlooked in the literature when describing the spatial ecology of mobile species. This is possibly due to the challenges involved with biologging juvenile individuals; i.e. their avoidant behaviour at breeding sites or the higher mortality rate most inexperienced juveniles often face (Grémillet & Boulinier 2009, Carneiro et al. 2020). In long-lived seabird species, differences between juveniles and adults in terms of movement patterns, foraging skills, and habitat use have been well-studied during the breeding season but are less known during the non-breeding period (Zimmer et al. 2011, Carravieri et al. 2017, Campioni et al. 2020, Frankish et al. 2020, Powers et al. 2022). Understanding these differences in behaviour, space, and habitat use in the non-breeding period is key to developing conservation measures that will protect wildlife at any life stage.

In terms of spatial ecology, the experience gained by individuals through the learning process often translates into adults selecting better foraging sites and more advantageous migratory strategies (Jorge et al. 2011, Thiers et al. 2014, de Grissac et al. 2016, Votier et al. 2017). Therefore, we expect juveniles to perform large-scale exploratory movements and increase foraging effort to compensate for low efficiency during their first migratory trips until they refine the migratory route and progressively specialize their foraging sites through an 'exploration-refinement' mechanism (Weimerskirch et al. 2005, Guilford et al. 2011). At the same time, it is expected that the high intra- and inter-individual variability exhibited by juveniles in movement and habitat use will decrease as they become older and more experienced (Thiers et al. 2014, de Grissac et al. 2016, Votier et al. 2017). This ontogenetic learning process from immature stages to adulthood usually entails an increase in specialization of habitat use or migratory routes (Péron & Grémillet 2013, Phillips et al. 2017). Additional age-related differences in spatial ecology may arise from competition avoidance, as younger individuals often migrate longer distances than adults (Daunt et al. 2007, Phillips et al. 2017). Age-related spatial segregation can be observed during both the breeding season, when juveniles are not

hampered by breeding duties and can forage far from the breeding colony, and the non-breeding season, when juveniles and adults may partially or entirely shift their distribution, which may serve to minimize intraspecific competition (Weimerskirch et al. 1985, Péron & Grémillet 2013, Bécarea et al. 2016, de Grissac et al. 2016, Phillips et al. 2017, Ramos et al. 2019).

Seabirds have been the subject of extensive research with regard to their long lifespan and age-related variation in foraging and movement ecology (Daunt et al. 2007, Limmer & Becker 2009, Fayet et al. 2015). Audouin's gull *Ichthyæetus audouinii* is a generalist and long-lived species endemic to the Mediterranean Sea and is classified as Vulnerable on the IUCN Red List (BirdLife International 2021). As a long-lived migratory gull, this species provides the opportunity to study spatial segregation between age groups with respect to their migratory movements and non-breeding grounds, which is still little studied. Audouin's gulls are known to breed along the Mediterranean basin and the Atlantic coast of southern Portugal (Fernández-Chacón et al. 2013, Payo-Payo et al. 2017, Calado et al. 2018), and their non-breeding areas extend from the Western Mediterranean along the West African Coast up to Senegal and Gambia (Bécarea et al. 2016). Although Audouin's gulls were traditionally considered nocturnal, behaviours such as specialised individual feeding on small pelagic fish and foraging strategies linked to rice fields have been also reported (Burger & Gochfeld 1996, Navarro et al. 2010, García-Tarrasón et al. 2015, Calado et al. 2021). Most studies on the spatial ecology of Audouin's gull have focused exclusively on the breeding period (Oro et al. 1997, 2014, Navarro et al. 2010, Christel et al. 2012, Morera-Pujol et al. 2018), and knowledge on its habitat use during the non-breeding period, which is also crucial to ensure the conservation of the species, is limited. Although some studies have compared the non-breeding foraging strategies of juveniles and adults in other seabirds (Weimerskirch et al. 2005, Riotte-Lambert & Weimerskirch 2013, Borrmann et al. 2021), to our knowledge, no study has addressed this topic in the Audouin's gull.

In this study, we aimed to unravel the age-related spatial ecology of Audouin's gull during the non-breeding season to better identify key factors for the species' conservation. Specifically, we were interested in determining the drivers shaping migratory distances, movement characteristics, and habitat selection of juvenile and adult Audouin's gulls during the non-breeding season. We also aimed to explore potential differences in the diel activity of juveniles and adults, something that remains largely unexplored



Fig. 1. Adult Audouin's gull *Ichthyaeetus audouinii* with a tracking device secured to its back with a Teflon harness. Photo credit: Antonio Torres

in most migratory species. Based on the 'age-related segregation hypothesis' (Phillips et al. 2017), we expected (1) juveniles to display a more explorative behaviour with longer migratory distances, spending more time on their foraging activities given the variability in the quality of the habitat they explore. Furthermore, based on the 'exploration-refinement hypothesis' (Guilford et al. 2011), we expected that (2) juveniles would use a larger variety of habitats (i.e. larger intra-individual variability in habitat use) and would be less selective in the explored habitats than adults. Finally, we also expected (3) more inter-individual variability both in movement characteristics and habitat use in juveniles than in adults (Phillips et al. 2017). Thus, we expect the explorative behaviour of juveniles to be showcased in further differences in the type of habitat exploitation among and within juvenile individuals.

## 2. MATERIALS AND METHODS

### 2.1. Study site and captures

Fieldwork was conducted in the Regional Park of Las Salinas y Arenales de San Pedro de Pinatar (hereafter San Pedro: 37.835° N, 0.791° W) in Murcia,

Spain, from April to June 2020, during the incubation and chick-rearing season of Audouin's gulls. We captured 9 adults using spring traps placed on the nests and caught 8 juveniles by hand just before fledging. Birds were captured, handled, and ringed with both metal and Darvic plastic rings under licence (Dirección General de Medio Natural, Región de Murcia). GPS loggers (Fig. 1) (OrniTrack 20 3G solar GPS-GSM/GPRS/3G) weighing 17–20 g were attached to the birds' backs using wing-loop harnesses made of Teflon ribbon (Thaxter et al. 2014).

### 2.2. GPS tracking data and flight characteristics

From the 17 specimens tagged, we discarded data from 7 (4 juveniles and 3 adults), for which the GPS information was collected over <1 mo due to the failure of the device or death of the animal. We retained GPS information from 10 individuals (4 juveniles and 6 adults). Audouin's gulls start migrating from the Iberian coast towards the West African Coast (as far south as Senegal) at the end of the breeding season in June and July until the end of August (Bécares et al. 2016). We first evaluated the differences in migratory behaviour between adults and juveniles by comparing the distance from the colony to the non-breeding

area. We used the distance between the colony and the farthest point as a proxy for migratory distance. We selected the months of September and October (59 d) to compare habitat use during the non-breeding season, avoiding the migratory period.

The tracks were recorded at 1 min (70%) and 5 min resolution (30%)  $24 \text{ h d}^{-1}$  and were all homogenised to the lowest resolution (i.e. 5 min) using the 'adehabitatLT' package in R (Calenge 2019) after filtering out all points with invalid positions (<0.1%).

We calculated the home range as the 95% contour of the kernel density function using the 'kernelUD()' and 'getvertices()' functions in the 'adehabitatHR' package (Calenge 2023). We estimated the smooth parameter ( $h$ ) using the ad hoc method (href) for each individual and used the mean  $h$  parameter of all individuals to illustrate the individual kernels and age-grouped kernels.

We classified the tracking points per individual into 3 main behaviours: resting, foraging, and travelling, using the expectation-maximization binary clustering algorithm for behavioural annotation described by Garriga et al. (2016b) and implemented in the 'EMbC' package (Garriga et al. 2016a). This method differentiates 4 behaviours defined by the velocity and turning angle between consecutive positions: (1) low velocities and low turns, interpreted as resting; (2) low velocities and high turns, interpreted as intensive search; (3) high velocities and low turns, interpreted as travelling; and (4) high velocities and high turns, interpreted as extensive search. In this study, we considered both (2) and (4) to be foraging behaviours and treated them as a unique category. For each position, the EMbC algorithm provides the probabilities of belonging to each of the 4 behaviours and assigns the behaviour with the highest probability. However, we used a more conservative approach and filtered our data by retaining only the points with a minimum of 80% probability of belonging to a certain behaviour (~85–90% of the points). With this method, we obtained a percentage for each behaviour per day and per individual ( $n = 590$ ).

Based on the tracking positions obtained, we calculated the following travel characteristics for each individual: total distance (km), distance per day (km), and maximum distance to colony (km). We calculated the total distance for each individual as the sum of the distances among all tracking points (every 5 min) between September and October ( $n = 10$ ), the distance per day as the sum of the distances among points during each day of tracking ( $n = 580$ ), and the distance to colony as the linear distance from San Pedro to the furthest point for each individual ( $n = 10$ ).

We calculated the night flight index (NFI) per day and per individual, considering only the location points classified as 'active' behaviours (i.e. travelling and foraging) and excluding resting behaviours ( $n = 590$ ). The NFI estimates the nocturnal and diurnal activity as the difference between the percentage of time spent in flight during the darkness and during the daylight divided by the highest value of both percentages (Dias et al. 2012). The index ranges from  $-1$  (only diurnal activity) to  $1$  (only nocturnal activity). We classified day and night by using the function 'classify\_DayTime()' in the 'RchivalTag' package in R (Bauer 2020), which estimates the time period based on the timing of sunrise and sunset in each geographical area.

We compared the behavioural, flight, and NFI characteristics between juveniles and adults. We used Mann-Whitney-Wilcoxon analyses for the total distance and the maximum distance from the colony. To compare the distance per day, the NFI, and the percentages of each behaviour, we performed separate linear mixed models (LMMs) using age as an explanatory variable and individual as a random effect in the 'lme4' package with the function 'mer()' in R (Bates et al. 2015), as we had several values for each individual.

### 2.3. Habitat use

We obtained the habitat-use type information by overlapping the tracking locations with the global land cover layer (years 2015–2019) from Copernicus Global Land Service at 100 m resolution (Buchhorn et al. 2020), using the function 'extract()' in the 'raster' package in R (Hijmans & van Etten 2014). This layer provides 23 classes of land cover, which we grouped into 7 categories: forests, herbaceous shrubland, herbaceous wetlands, permanent waterbodies, urban areas, agricultural areas, and ocean. We joined all forest types into one layer and the herbaceous shrublands in another unique layer, as our study species rarely occur in forests or brushy environments. We recorded the habitat use for all individuals while resting, foraging, and travelling independently. Using separate analyses for each age group (juveniles and adults), we compared the percentage of habitat used ( $n = 7$  habitats) by all individuals while performing each of the 3 behaviours (resting, foraging, and travelling). Finally, we compared the total habitat use (combining all behaviours) between juveniles and adults. For these calculations, we used the chi-squared test in the R package 'MASS' (Ripley et al. 2013).



## 2.4. Habitat selection

For each individual and behaviour, we calculated habitat selection by computing the Manly selectivity index (Wi; Manly et al. 2002), which compares the habitat used versus habitat available. Given that each individual exploits different areas, we used an approach where both 'use' and 'availability' are measured for each individual (III data type approach; Calenge 2007) for both juveniles and adults. First, we calculated the individual home range as the minimum convex polygon using the function 'mcp()' in the package 'adehabitatHR' (Calenge 2023). Then, we used the 'crop()' and 'mask()' functions in 'raster' (Hijmans & van Etten 2014) to obtain the land cover values within each individual's range extent. We then randomly created 10 000 points within each individual's home range using the 'sampleRandom()' function in the 'raster' package (Hijmans & van Etten 2014) to represent habitat availability within the home range. From the random points obtained from the home range, we calculated the proportions of the habitats each individual had access to (i.e. habitat availability). We also transformed the number of locations per habitat and individual (as described above) into proportions, to compare them with the habitat availability. Habitat selection was defined by the MSI (selection index = used / available), where values from 0 to 1 indicate avoidance of the habitat, values >1 indicate preference or selection of the habitat, and values equal to 1 indicate non-selection (i.e. neither preference for nor avoidance of the habitat). We considered that habitat selection had occurred when the minimum value of the 95% confidence interval (CI) was >1 and habitat avoidance had occurred when the maximum value of the 95% CI was <1.

## 2.5. Repeatability of habitat use

We calculated Krippendorff's alpha to estimate how repeatable individuals are with respect to each behaviour and the use of habitat during the non-breeding period, following Zango et al. (2019). We first calculated the repeatability of habitat use between individuals in each age group (juveniles and adults) during each behaviour ( $n_{\text{juveniles}} = 4$ ,  $n_{\text{adults}} = 6$ ). This index ranges from 0, meaning individuals of the same age do not select similar habitats, to 1, meaning that individuals of the same age select the same habitat. Second, we calculated the repeatability within each individual during each behaviour, comparing the use of habitat per day ( $n = 59$  per behav-

iour and per individual). In this case, values near 0 indicate that individuals do not select the same habitats every day and values equal to 1 indicate that each individual selects the same habitats during the non-breeding season. We calculated the index using the 'kripp.alpha()' function of the 'irr' package (Gamer et al. 2022) in R.

## 2.6. Diversity of habitat use

Finally, to test habitat use specialisation for each behaviour (foraging, resting, or travelling) at an individual and age group level, we calculated the diversity habitat use index (DHU) based on the Shannon index (Jakubas et al. 2020):  $DHU = -\frac{\sum p_i \ln(p_i)}{\ln(j)}$ , where  $p_i$  is the proportion of positions in each habitat and  $j$  is the number of total habitats considered. This index ranges from 0 (birds use only one habitat), to 1 (birds equally use all available habitats).

## 3. RESULTS

Of the 6 tagged adults, 4 migrated to the Senegal coast, and 2 remained in the Alboran Sea in the Western Mediterranean (~250 km from the colony), performing short movements within the basin (Fig. 2, Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/n055p155\\_supp.pdf](http://www.int-res.com/articles/suppl/n055p155_supp.pdf)). All juveniles migrated and remained along the African coast from the Western Sahara to Senegal. We found that juveniles travelled significantly longer distances overall than adults during the non-breeding period (mean [ $\pm$ SD] total distance, juveniles:  $5922.3 \pm 1452.7$  km; adults:  $4101.5 \pm 699.2$  km; Wilcoxon  $t$ -test,  $n = 10$ ,  $W = 2.0$ ,  $p = 0.038$ ). Juveniles travelled farther south than adults (based on maximum distance from colony; juveniles:  $2909.7 \pm 188.5$  km; adults:  $1565.1 \pm 1031.4$  km; Wilcoxon  $t$ -test,  $n = 10$ ,  $W = 0.0$ ,  $p = 0.010$ ) and travelled longer distances per day (juveniles:  $98.3 \pm 69.1$  km; adults:  $69.4 \pm 46.8$  km; LMM-age:  $n = 580$ ,  $t = 2.5$ ,  $df = 8$ ,  $p = 0.037$ ).

Both juveniles and adults showed comparable NFI values (LMM-age:  $n = 590$ ,  $t = -0.8$ ,  $df = 8$ ,  $p = 0.467$ ; Table S1, Fig. S2), indicating a slightly more diurnal behaviour for individuals in both age groups (NFI: juveniles:  $-0.12 \pm 0.03$ ; adults:  $-0.07 \pm 0.12$ ). Nevertheless, juveniles and adults diverged in their activity peaks. Juveniles tended to be more active at dawn, while adults tended to be more active from noon until dusk.

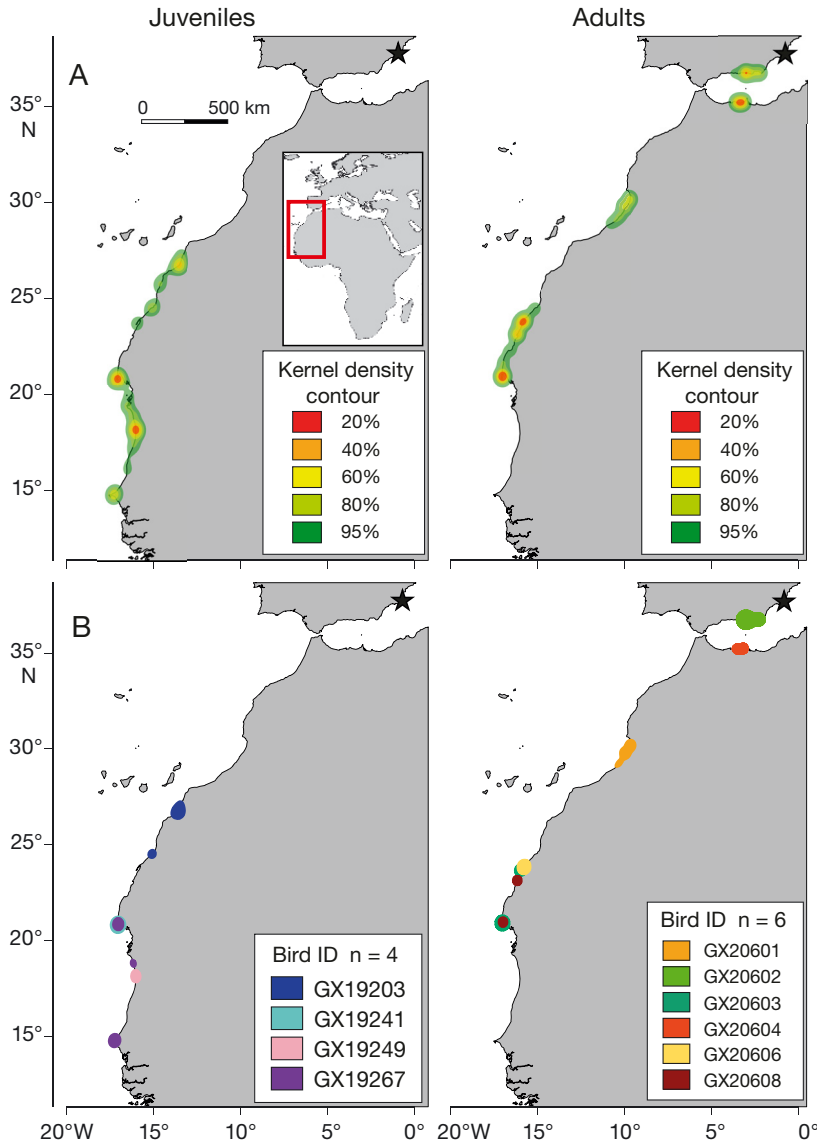


Fig. 2. (A) Kernel density distribution of juvenile and adult Audouin's gulls from September to October; (B) 50% kernel density contours designating core areas for each juvenile and adult individual. Black star: the San Pedro colony (Spain)

Between age groups, there was no evidence of a difference in the percentage of time spent per day in each behaviour (LMM-age; foraging:  $n = 590$ ,  $t = -1.0$ ,  $df = 8$ ,  $p = 0.335$ ; resting:  $n = 590$ ,  $t = 0.5$ ,  $df = 8$ ,  $p = 0.629$ ; travelling:  $n = 590$ ,  $t = 1.9$ ,  $df = 8$ ,  $p = 0.093$ ). Both juveniles and adults spent approximately 50% of their time in foraging activities (Table , Table S1).

### 3.1. Habitat use

Both juveniles and adults used different habitats while travelling than while resting or foraging ( $\chi^2_{\text{juveniles}} = 48.6$ ,  $df = 12$ ,  $p < 0.001$ ;  $\chi^2_{\text{adults}} = 57.0$ ,  $df =$

12;  $p < 0.001$ ; Figs. S3 & S4). Individuals of both age groups consistently increased the use of oceanic habitats while travelling, whereas habitats such as grasslands and waterbodies were more often used during foraging or resting periods (Fig. 3). Habitat use also differed among individuals of the same group for both juveniles and adults (Fig. 3). Most of the differences found among individuals of the same group occurred during foraging and resting behaviours, whereas habitat use during travelling was more consistent among individuals. However, if we consider all locations and behaviours together, there was no significant difference in habitat use between juveniles and adults ( $\chi^2_{\text{juveniles-adults}} = 0.1$ ,  $df = 6$ ,  $p = 1.0$ ).

### 3.2. Habitat selection

The Manly selectivity index ( $W_i$ ) showed strong evidence of habitat selection (positive or negative selection) for all groups (juveniles and adults) and behaviours (foraging, resting, and travelling) (Table 2). During foraging activities, juveniles showed no positive selection for any habitat but negative selection for agricultural areas, forests, and ocean. However, adult gulls showed a preference for waterbodies, even though this habitat was among the least abundant habitats within the regions used by all adult individuals (Table 2; Table S2). Other

habitats, such as wetlands, grasslands, or urban areas, were preferred during foraging; urban areas were also preferred during resting. Furthermore, adults avoided the ocean, agricultural areas, and forests when they foraged. (Table 2). Waterbodies emerged as the most favoured habitat for both adults and juveniles. However, juveniles primarily selected waterbodies for resting, which was the sole positively favoured habitat across all behaviours, whereas adults consistently selected waterbodies during all their behaviours. Both juveniles and adults avoided agricultural areas and forests in almost every behaviour. The exception was for juveniles while travelling, as they did not exhibit a negative selection for agricul-

Table 1. Movement characteristics of juvenile and adult Audouin's gulls. Flight stats show main trip characteristics including total distance travelled during September and October, distance travelled per day, and distance to the colony. NFI: proportion of time spent flying in darkness ( $-1.0$  indicates only diurnal activity;  $1.0$  indicates only nocturnal activity). Behavioural mode: behaviour during movement. Values correspond to the mean  $\pm$  SD; p-values are from the linear mixed models and Mann-Whitney-Wilcoxon analyses (see Table S1). Significant p-values ( $p < 0.05$ ) are in **bold**

	Juveniles	Adults	p
Individuals	4	6	
Flight stats			
Total distance (km)	5922.3 $\pm$ 1,452.6	4101.5 $\pm$ 699.2	<b>0.038</b>
Distance $d^{-1}$ (km)	98.3 $\pm$ 69.1	69.4 $\pm$ 46.8	<b>0.037</b>
Distance to colony (km)	2909.7 $\pm$ 188.5	1565.1 $\pm$ 1031.4	<b>0.010</b>
NFI	$-0.12 \pm 0.06$	$-0.07 \pm 0.12$	0.467
Behavioural mode (%)			
Foraging	49.3 $\pm$ 10.0	55.8 $\pm$ 9.5	0.335
Resting	35.8 $\pm$ 13.0	32.5 $\pm$ 7.7	0.629
Travelling	14.8 $\pm$ 3.0	11.8 $\pm$ 2.2	0.093

tural areas. While travelling, however, gulls from both age groups tended to fly over the sea, avoiding terrestrial habitats and favouring the selection of water-body habitats (Table 2).

### 3.3. Repeatability of habitat use

Krippendorff's alpha values showed that repeated use of a given habitat was moderate to low among individuals (i.e. within each age group) in any behaviour. The more repeatable use of a habitat was during the resting behaviour for both juveniles and adults ( $\alpha_{\text{juveniles}} = 0.23$ ;  $\alpha_{\text{adults}} = 0.14$ ), whereas foraging ( $\alpha_{\text{juveniles}} = 0.07$ ;  $\alpha_{\text{adults}} = 0.11$ ) and travelling ( $\alpha_{\text{juveniles}} = 0.07$ ;  $\alpha_{\text{adults}} = 0.02$ ) showed low repeatability. However, overall individual repeatability values were higher when compared to those measured across individuals within age groups. During the resting period, both juveniles and adults showed repeatable use of habitat ( $\alpha_{\text{juveniles}} = 0.40 \pm 0.02$ ;  $\alpha_{\text{adults}} = 0.38 \pm 0.06$ ). The individual Krippendorff's alpha coefficient was also high during foraging ( $\alpha_{\text{juveniles}} = 0.36 \pm 0.03$ ;  $\alpha_{\text{adults}} = 0.34 \pm 0.06$ ) and travelling ( $\alpha_{\text{juveniles}} = 0.30 \pm 0.03$ ;  $\alpha_{\text{adults}} = 0.31 \pm 0.05$ ).

### 3.4. Diversity of habitat use

Audouin's gulls exhibited high individual diversity (Table 3). Habitat use in juveniles tended to be less diverse during foraging and resting and more diverse during travelling than in adults, but differences were

not significant (Wilcoxon  $t$ -test, foraging:  $n = 10$ ,  $W = 13.0$ ,  $p = 0.914$ , resting:  $n = 10$ ,  $W = 11.0$ ,  $p = 0.914$ , travelling:  $n = 10$ ,  $W = 10.0$ ,  $p = 0.762$ ). For adult gulls, the diversity of habitat use was higher during foraging, followed by resting and then travelling behaviour.

## 4. DISCUSSION

This study describes, for the first time, ontogenic differences in the habitat use and foraging behaviour of a gull species during the non-breeding season, which should be considered in any management or conservation plan. We found that juvenile Audouin's gulls travelled farther south than adults and were less selective of specific foraging habitats. Although we found high inter-individual variability of habitat use regardless of age, adults tended to exploit a greater diversity of habitats than juveniles did, given the different habitat availability that each individual exploited.

We found that 2 out of 6 adults remained in the Mediterranean during our defined non-breeding period, and all juveniles migrated to the West African Coast in their first migratory journey, crossing several political borders and entering offshore areas where there is a lack of an effective global management policy (Beal et al. 2021). As previously reported, we found juveniles to generally perform migrations that were longer and farther south than the adults. Jacob (1979) and Oro & Martinez (1994) already reported that most of Audouin's gulls that remained in the Mediterranean basin during the non-breeding period were adult individuals. Contrary to our expectations (i.e. age-related segregation hypothesis; Weimerskirch et al. 2005), we found no difference between juveniles and adults in the time spent foraging, resting, or travelling. While juvenile seabirds generally tend to forage less efficiently than adults (Fayet et al. 2015), they may compensate by travelling longer distances to reach higher productive upwelling areas at the southern West African Coast. In contrast, adults remain in the Mediterranean, where waters are less productive and are characterised by low circulation and high stratification (Pinardi & Masetti 2000).

Audouin's gull was formerly described as a nocturnal pelagic forager (Burger & Gochfeld 1996). On average, we did not find any time preference (diurnal vs. nocturnal) for foraging between age classes during

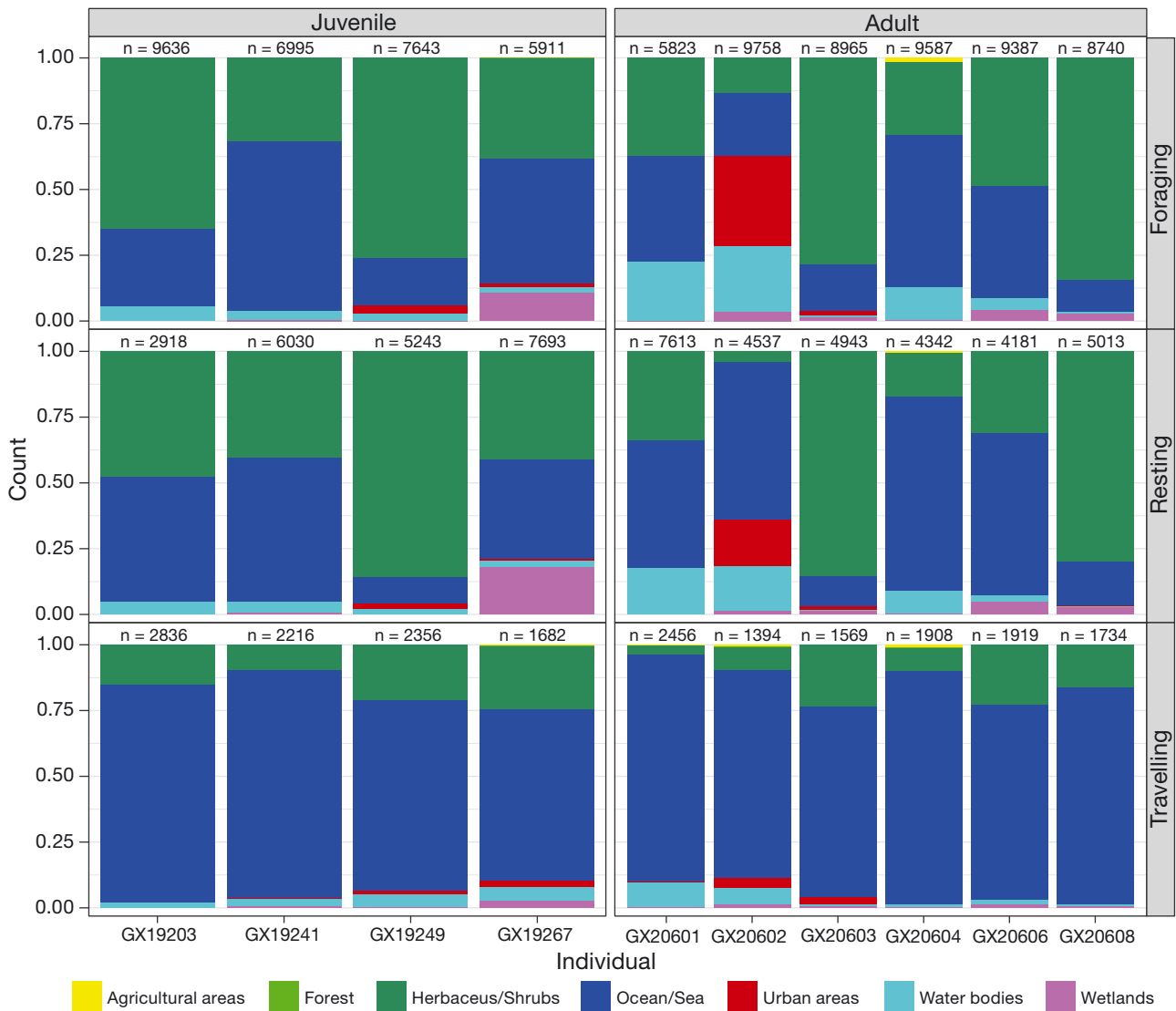


Fig. 3. Proportional habitat use by each individual and type of behaviour (foraging, resting, and travelling) for juvenile and adult Audouin's gulls; n: number of positions from each individual and type of behaviour

the non-breeding season. However, we did find relevant differences in their flying activity in the dusk and dawn periods. Juveniles tended to be more active at dawn whereas adults showed greater activity from noon to dusk. This different pattern seems to be in accordance with the 'age-related segregation hypothesis' (Weimerskirch et al. 2005), and although we cannot make strong conclusions based on the sample size, our results indicate that the species' foraging activities are not limited to night-time and, thus, Audouin's gulls can take advantage of fishery discards or other anthropogenic activities operating during the daytime. Indeed, several studies have shown that the daily foraging activity of Audouin's gulls during the

breeding period is strongly linked to fishery activities and terrestrial crops (Bécares et al. 2015, Calado et al. 2018, Vilaplana et al. 2024), which has likely had a positive effect and contributed to the global increase in Audouin's gull populations (Oro et al. 2004).

Contrary to the 'exploration-refinement hypothesis' (Phillips et al. 2017), we found that adults exploited a higher diversity of habitats while foraging than did juveniles and, therefore, adults are not more specialised than juveniles. Indeed, gulls showed individual preferences for some habitats regardless of their age, exhibiting a certain degree of individual specialization within this generalist species (Bolnick et al. 2003). Diversity indices of habitat use only dif-



Table 2. Habitat selection by juvenile and adult Audouin's gulls after the migratory period, as indicated by the Manly selectivity index. Habitat selection is presented separately for each behavioural mode (foraging, resting, and travelling); **bold** indicates habitats with positive selection and *italics* indicates habitats with negative selection. Availability: proportion of habitats within the minimum convex polygon of juveniles or adults; used: habitat used by juveniles and adults; Wi: habitat selection ratio; SE: standard error of Wi; 95% CI: confidence intervals for Wi

Habitats	Juveniles					Adults				
	Availability	Used	Wi	SE	95% CI	Availability	Used	Wi	SE	95% CI
<b>Foraging</b>										
Herbaceous/shrubs	24.03	54.86	1.88	1.21	[-1.07, 4.84]	<b>29.94</b>	<b>48.12</b>	<b>1.60</b>	<b>0.23</b>	[1.03, 2.18]
Agricultural areas	<i>0.12</i>	<i>0.02</i>	<i>0.17</i>	<i>0.11</i>	[-0.10, 0.43]	3.72	<i>0.28</i>	<i>0.10</i>	<i>0.15</i>	[-0.25, 0.46]
Urban areas	0.12	1.13	11.09	9.60	[-12.44, 34.62]	<b>0.48</b>	<b>6.69</b>	<b>13.13</b>	<b>2.90</b>	[6.03, 20.23]
Water bodies	0.25	3.55	14.50	8.06	[-5.25, 34.25]	<b>0.26</b>	<b>10.57</b>	<b>47.41</b>	<b>17.04</b>	[5.65, 89.17]
Wetlands	0.18	2.20	13.02	14.44	[-22.35, 48.39]	<b>0.04</b>	<b>2.06</b>	<b>50.48</b>	<b>19.89</b>	[1.75, 99.21]
Forest	<i>0.03</i>	<i>0.00</i>	<i>0.13</i>	<i>0.02</i>	[0.08, 0.18]	0.98	<i>0.02</i>	<i>0.02</i>	<i>0.03</i>	[-0.05, 0.09]
Ocean/sea	75.28	38.24	0.54	0.16	[0.15, 0.94]	64.58	32.25	0.49	0.09	[0.28, 0.70]
<b>Resting</b>										
Herbaceous/shrubs	24.03	17.03	3.42	2.52	[-2.74, 9.58]	29.94	42.56	1.45	0.22	[0.90, 2.00]
Agricultural areas	<i>0.12</i>	<i>0.10</i>	<i>0.00</i>	<i>0.00</i>	[0.00, 0.00]	3.72	<i>0.11</i>	<i>0.02</i>	<i>0.03</i>	[-0.06, 0.10]
Urban areas	0.12	1.00	5.76	4.71	[-5.79, 17.31]	<b>0.48</b>	<b>2.86</b>	<b>6.16</b>	<b>1.96</b>	[1.36, 10.97]
Water bodies	0.25	3.41	12.97	6.46	[-2.87, 28.80]	<b>0.26</b>	<b>8.63</b>	<b>27.18</b>	<b>7.54</b>	[8.72, 45.64]
Wetlands	0.18	0.69	33.45	34.14	[-50.20, 117.10]	0.04	1.41	39.40	22.51	[-15.76, 94.56]
Forest	<i>0.03</i>	<i>0.01</i>	<i>0.00</i>	<i>0.00</i>	[0.00, 0.00]	0.98	<i>0.01</i>	<i>0.01</i>	<i>0.01</i>	[-0.01, 0.02]
Ocean/Sea	75.28	77.76	0.44	0.13	[0.12, 0.76]	64.58	44.43	0.70	0.10	[0.45, 0.95]
<b>Travelling</b>										
Herbaceous/shrubs	24.03	52.62	0.59	0.45	[-0.51, 1.70]	29.94	13.25	0.45	0.09	[0.23, 0.67]
Agricultural areas	0.12	0.00	1.02	0.69	[-0.68, 2.71]	3.72	0.35	0.07	0.07	[-0.11, 0.25]
Urban areas	0.12	0.89	10.19	4.14	[0.04, 20.34]	0.48	0.93	2.27	1.00	[-0.18, 4.72]
Water bodies	<b>0.25</b>	<b>3.15</b>	<b>13.77</b>	<b>4.01</b>	[3.94, 23.60]	<b>0.26</b>	<b>3.82</b>	<b>13.09</b>	<b>1.74</b>	[8.82, 17.36]
Wetlands	0.18	6.36	4.03	3.17	[-3.73, 11.79]	0.04	0.53	15.86	6.07	[0.99, 30.73]
Forest	<i>0.03</i>	<i>0.00</i>	<i>0.44</i>	<i>0.08</i>	[0.26, 0.63]	0.98	<i>0.15</i>	<i>0.13</i>	<i>0.11</i>	[-0.14, 0.40]
Ocean/sea	75.28	36.99	1.10	0.34	[0.26, 1.94]	64.58	80.99	1.26	0.15	[0.89, 1.64]

Table 3. Individual and age-related Shannon diversity index of the habitat used by Audouin's gulls during foraging, resting and travelling behaviours

	Foraging	Resting	Travelling
<b>Individuals</b>			
GX19203 (Juvenile)	0.41	0.44	0.27
GX19241 (Juvenile)	0.40	0.44	0.26
GX19249 (Juvenile)	0.37	0.27	0.40
GX19267 (Juvenile)	0.57	0.60	0.51
GX20601 (Adult)	0.55	0.53	0.26
GX20602 (Adult)	0.74	0.57	0.41
GX20603 (Adult)	0.34	0.27	0.38
GX20604 (Adult)	0.53	0.40	0.23
GX20606 (Adult)	0.50	0.46	0.36
GX20608 (Adult)	0.27	0.31	0.27
<b>Groups</b>			
Juveniles	0.49	0.53	0.36
Adults	0.63	0.57	0.25

ferred slightly between age groups and there were no differences in habitat repeatability between juveniles and adults, which suggests that juveniles and adults can exploit habitats in a similar way during their non-

breeding period. This pattern may be difficult to detect during the breeding season, when most adults rear their chicks, as they behave as central-place foragers, limiting their foraging ranges close to colony sites and thus becoming more specialised (Phillips et al. 2017). Indeed, in other gull species, such as the black-backed gull *Larus fuscus*, adults were found to preferably visit the same habitat near the colony throughout the breeding season, gradually exploiting a larger variety of habitats after the breeding season ended (Spelt et al. 2019). Similarly, high variability in habitat use can be found in populations of gulls during the non-breeding season, as observed in herring gulls *L. argentatus* (Anderson et al. 2019).

We found that both juveniles and adults used waterbodies (defined as inland fresh or permanent saltwater bodies) as a preferred habitat in at least one of the behaviours. Despite the low availability of ponds and rivers over their migratory routes and non-breeding areas, Audouin's gulls preferentially selected this habitat. We did not find a significant positive habitat selection for juveniles during foraging.

Still, the proportional use of waterbodies was higher than its availability (Table 2). Indeed, this habitat already constitutes an important food source in the breeding range of the species, possibly related to the spread of the invasive red swamp crayfish *Procambarus clarkii* in southern Europe (Suárez-Serrano et al. 2010), which has been identified as an important food source for Audouin's gulls in the Ebro Delta in the NW Mediterranean (Navarro et al. 2010). Since there are no native crayfish species in Africa and the invasive American crayfish has not yet been detected in West Africa (but it is widely spread in Europe), the relevance of this habitat during the non-breeding period could be related to other food resources available within the waterbodies. It could also be because waterbodies represent less exposed habitats than the open ocean (Bécares et al. 2015), as this habitat was also selected for resting. Although juvenile gulls did not select herbaceous or shrubland habitats, adults did. The selection of this type of habitat could be explained by the fact that such habitats are usually rich in terrestrial arthropods, which comprise an important part of the Audouin's gulls diet (Pedrocchi et al. 1996, Matos et al. 2018). Surprisingly, both juveniles and adults avoided agricultural lands. Since rice fields are one of the most exploited habitats in the Ebro Delta (García-Tarrasón et al. 2015, Morera-Pujol et al. 2018), we expected to find some crop preferences during the non-breeding season. However, the agricultural land classification we used included other crops in addition to rice fields, which may blur our ability to detect a preference for specific crop types. Indeed, the use of pesticides and heavy metal pollution associated with agriculture in the non-breeding areas, especially in West Africa (Fayiga et al. 2018), might affect the availability of prey in such habitats. Furthermore, although our results showed non-selection of the sea or ocean as foraging habitat, it still constitutes an essential food source for other populations of Audouin's gulls, especially as it is linked to fisheries discards (Cama et al. 2013, Calado et al. 2021). Differences in fishery management plans between Europe and Africa in addition to the difficulty involved with controlling and managing artisanal fisheries in West Africa (Nunoo et al. 2015) might increase the potential risks for this vulnerable seabird. Thus, the variety of habitats and areas with human activities that both juvenile and adult Audouin's gulls use make conservation plans challenging. However, the new insights obtained in this study, such as preferred habitats and areas where juveniles and adults spend the non-breeding season, may help managers understand which areas should

be prioritized when new conservation plans are developed and in place.

Finally, we acknowledge that the small sample size and reduced time period of our study are limitations that may bias our results. In addition, the low-resolution data on land use in the African continent could also have affected our findings regarding preferences in habitat use. A longer time interval for the spatial evaluation of the individuals could have informed us better about the entire non-breeding period and the temporal variability within that period. However, it is extremely challenging to gather such information, given the high mortality of juvenile gulls during the first months of life and the limitations of the devices, such as malfunctioning or loss (Bécares et al. 2016). In addition, potential population differences in habitat use and migratory patterns could arise depending on the gulls' colony of origin (e.g. Italy or Greece). Further investigation in this direction would thus provide a more comprehensive understanding of the species' spatial ecology.

## 5. CONCLUSIONS

Our study provides evidence for both the age-related segregation hypothesis and the exploration-refinement hypothesis in Audouin's gulls. For instance, with respect to the age-related segregation hypothesis, juveniles travelled longer distances in their migrations than adults but they did not spend more time foraging. In accordance with the explorative-refinement hypothesis, adults were more selective than juveniles in their non-breeding foraging habitat. Conversely, our hypotheses and expectations of higher intra- and inter-individual variability of habitat use by juveniles compared to adults were not supported. The most likely explanation regarding the latter could be related to the difference in habitat quality of the non-breeding area used by each juvenile and adult gull, which should be further explored in the future. Moreover, regardless of their age, each gull showed some habitat preferences, interpreted as a degree of individual specialization within this generalist species.

Overall, our approach provides a basis for further investigations on the ecology of migratory gulls during the non-breeding season, which is important for a more complete understanding of migratory bird dynamics. Understanding the potential differences in the ecological requirements of juvenile and adult communities will help to better define any conservation plan that ensures the survival of this species.

**Data Availability.** Raw tracking data used during the current study are available in the Seabird Tracking Database (<https://data.seabirdtracking.org/>) with the following code: 1757 GPS\_ICHAUD\_SanPedro\_RRamos\_2020-2021\_STDB.

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