Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird

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Abstract The availability of food resources has been suggested as a major factor in the substantial increase in reproductive output, survival, recruitment and, ultimately, population growth rates in most organisms. In fact, the artificial increase in food availability resulting from human activities has been suggested as a factor in the substantial increase in population size of several seabirds in recent decades. In the present study, our primary aim was to estimate the importance of the main natural prey and two alternative feeding resources, fishery discards and the invasive American crayfish *Procambarus clarkii*, for an opportunistic seabird, the Audouin's gull *Larus audouinii*. We also assessed the influence

of age and sex in the use of those three types of food. For this purpose, we compared the analyses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in blood of male and female adults of known age and chicks with those in their potential prey. Our results reveal sex-related and age-related differences in the consumption of fish discards, small pelagic fish and American crayfish. Differences in the diet of males and females and also between adults and chicks could be related to different nutritional requirements. Age differences were probably related to their different foraging proficiency and the tendency of young breeders to opportunistically exploit anthropogenically derived food. This study illustrates the importance of considering the age and sex of individuals to obtain feasible dietary information and to understand how the exploitation of food of human origin could affect population growth.

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Introduction

The availability of food resources has been described as a major factor influencing reproductive output, survival, recruitment and, ultimately, population growth rates in most species (e.g. Sinclair and Krebs 2003; Oro et al. 2004, 2008; Rutz and Bijlsma 2006). This is especially apparent in opportunist predators situated at the top of trophic networks, such as most seabird species (e.g. Cairns 1992; Furness 2003; Votier et al. 2008). Indeed, the artificial increase in the availability of trophic resources resulting from human activities, such as fisheries discards, refuse dumps or introduced prey species, has been suggested as a factor in the substantial increase in population sizes of several seabirds in recent decades (e.g. Garthe et al. 1996; Oro et al. 2004; Tablado et al. 2010).

A clear example is the case of the Audouin's gull *Larus audouinii*. During the 1970s, it was one of the

most endangered seabirds in the world (Burger and Gochfeld 1996). Since then, its world population has experienced a dramatic growth as a result of the increase in breeding site protection and the exploitation of feeding resources of human origin (Oro and Ruxton 2001). Although Audouin's gull is considered an evolutionarily adapted specialist in the capture of clupeiforms (e.g. they show nocturnal vision, see Oro 1998 and references therein), it can also efficiently exploit fishery discards and terrestrial prey (e.g. Oro and Ruiz 1997; Oro et al. 1996a, 1997). It is also known that the differential exploitation of those preys could influence its breeding and feeding performance (Oro et al. 1996b, 1999, 2004). However, the available information of the actual value of these artificial resources in relation to age or sex of breeding adults is scarce and inaccurate. For instance, chicks of Audouin's gulls are fed with different prey compared with that consumed by parents (Pedrocchi et al. 1996). Age and experience of breeding adults could also be important factors affecting food exploitation (Ezard et al. 2007; Limmer and Becker 2009). Similarly, males and females differ in their nutritional requirements depending on the breeding period: during egg formation, fisheries discards do not necessarily meet the required energetic demand of females (Williams 2005; Navarro et al. 2009).

Today, the combination of data from long-term monitoring programs with new methodologies for the study of trophic habits is an effective tool for estimating the true importance of those aforementioned anthropogenic resources for different individuals in the population (i.e. Navarro et al. 2009). The stable isotope approach can complement and improve common means of dietary analysis since it reflects time-integrated dietary records and, thus, eliminates some of the shortcomings of traditional dietary studies, particularly when used in combination with the stable isotope values of potential prey (Forero and Hobson 2003). For marine ecosystems, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can discriminate the type of food consumed in relation to their benthic and pelagic origin (Forero and Hobson 2003; Navarro et al. 2009) or the use of marine or terrestrial food (Ramos et al. 2009). Moreover, by combining stable isotopic values of the consumers and their potential prey, isotopic mixing models can be applied to obtain estimates of the relative contribution of each potential prey to the diets of the consumer (Jackson et al. 2009).

Here, our aim was to estimate the importance of three feeding resources for Audouin's gulls breeding at their largest colony. Those three resources include the primary natural prey for Audouin's gull (i.e. small pelagic fish) and two alternative prey: demersal fish (a proxy of trawling fishery discards) and a terrestrial prey (the American crayfish *Procambarus clarkii*). Prey from rice fields (such as crayfish) act as a buffer against bad environmental conditions at sea and constitute an alternative foraging resource

allowing birds from that population to increase their breeding performance (Oro et al. 1996a). We estimated the contribution of those prey types to the diet of male and female adults, adults of different ages and small and large chicks using recent Bayesian isotope models (SIAR model, Jackson et al. 2009). For that purpose, we compared the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in blood of male and female adults of known ages and chicks with those of their potential food. Even though previous information about the influence of sex and age on diet of seabirds is scarce, here we can test the following hypotheses: foraging segregation between males and females should be low since sexual dimorphism in Audouin's gull is very low (but see Gray and Hamer 2001); it is also expected that chicks will be fed with prey of a higher energetic content (in our case, small pelagic fish) than those consumed by adults (Pedrocchi et al. 1996; Forero et al. 2002; Navarro et al. 2009). In relation to age of adults, we predict that younger breeders, with lower foraging experience, will more frequently exploit opportunistic foods, such as trawling discards and/or American crayfish, than small pelagic fish, their natural prey (MacLean 1986; Ratcliffe et al. 1998).

Materials and methods

Study area and sampling procedure

The study was conducted during 2003 at the reserve of Punta de la Banya, in the Ebro Delta Natural Park, north-western Mediterranean (40°33'N, 0°39'E). The Punta de la Banya is a flat, sandy salt marsh of 2514 ha, partially occupied by saltworks, next to extensive rice field areas (20000 ha). This location holds around 12,000–13,000 breeding pairs of Audouin's gull, approximately 60% of the world population. The marine ecosystem of the Ebro Delta is one of the most important fishing grounds in the Mediterranean Sea, resulting in one of the largest fishing fleets in this region, generating a high availability of fishery discards, mainly from trawlers (Coll et al. 2008). Moreover, during the early 1980s, the invasive American crayfish, a crustacean native to south-eastern United States and north-eastern Mexico, was introduced in the rice field areas of the Ebro Delta (Gutierrez-Yurrita et al. 1999).

During the incubation period of 2003, we sampled 50 breeding adults (30 males and 20 females). Later, during the post-hatching period (between 15 and 30 days after the incubation period), 29 small chicks (less than 15 days old) and 28 large chicks (more than 40 days old) were sampled. Both incubating adults and chicks were captured at their nests by nest traps and by hand, respectively. We determined the age of 35 of the 50 sampled adults because they were previously ringed as chicks, such ages ranging from

4 to 17 years old. From each individual, we took 0.1 ml of blood from the brachial vein. The blood was stored in 70% ethanol at room temperature until stable isotope analyses. A subsample of blood was also used for determining the sex of adults by molecular procedures (Ellegren 1996).

Stable isotopes analyses

Ethanol was removed from blood samples prior to analysis by decanting and freeze-drying. All samples (about 0.5–1 mg) were combusted at 1020°C using a continuous-flow isotope-ratio mass spectrometry (CFIRMS) system by means of a Carlo Erba 1500NC elemental analyser interfaced with a Delta Plus XL mass spectrometer. All isotope abundances are expressed in δ -notation as parts per thousand (‰) deviation from the IAEA standards AIR ($\delta^{15}\text{N}$) and VPDB ($\delta^{13}\text{C}$). Based on within-run replicate measurements of laboratory standards (urea, shark cartilage), we estimated measurement error to be $\pm 0.2\text{‰}$ and $\pm 0.1\text{‰}$ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively.

Isotopic mixing model

Dietary composition of breeding adults (males, females and adults of different age) and chicks (small and large chicks) was estimated based on their isotopic values and those of their potential prey. To estimate the contribution of different prey, we adopted a Bayesian multi-source stable isotope mixing model, SIAR (see Jackson et al. 2009 for more details). We used published reference values for demersal and small pelagic fish from the Ebro Delta area during year 2003 (Fig. 1, demersal fish: $\delta^{15}\text{N} = 9.54 \pm 1.39\text{‰}$, $\delta^{13}\text{C} = -18.19 \pm 0.76\text{‰}$, $n = 51$; small pelagic fish: $\delta^{15}\text{N} = 7.95 \pm 1.08\text{‰}$, $\delta^{13}\text{C} = -18.99 \pm 0.71\text{‰}$, $n = 39$; Navarro et al. 2009) and unpublished values for American crayfish from the Ebro Delta rice fields sampled during the year 2003 (Fig. 1, $\delta^{15}\text{N} = 8.27 \pm 2.21\text{‰}$, $\delta^{13}\text{C} = -27.73 \pm 1.56\text{‰}$, $n = 20$; authors' unpublished data). To build the SIAR mixing model, we used diet-blood isotopic fractionation values between prey and blood of 2.91‰ for $\delta^{15}\text{N}$ and 1.15‰ for $\delta^{13}\text{C}$ (see Caut et al. 2009).

Statistical analyses

We used ANOVA tests to examine the differences in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values among small chicks, large chicks, adult males and adult females. Post hoc comparisons were tested with a Tukey's test. We performed general linear models (GLM) using GENMOD procedure (SAS 1997) to analyze variations in stable isotopes with age of adults. Age and sex of adults and their interaction were fitted to the stable isotope values applying a normal error and identity link function. The Bayesian mixing

model was fitted using R software (R Development Core Team 2005).

Results

Isotopic analysis for different age and sex classes

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values differed among small chicks, large chicks, adult males and adult females (Fig. 1, $\delta^{15}\text{N}$: $F_{3, 106} = 31.31$, $P < 0.0001$; $\delta^{13}\text{C}$: $F_{3, 106} = 8.64$, $P < 0.0001$). In particular, large chicks showed lower $\delta^{15}\text{N}$ values than small chicks, adult males and adult females (Fig. 1, Tukey test, all $P < 0.05$). Small chicks showed lower $\delta^{15}\text{N}$ values than adult males (Fig. 1, Tukey test, $P < 0.05$) and similar $\delta^{15}\text{N}$ values to adult females (Fig. 1, Tukey test, $P = 0.18$). Regarding $\delta^{13}\text{C}$ values, small chicks showed lower values than large chicks and adult males (Fig. 1, all Tukey tests $P < 0.05$) and similar values to adult females (Fig. 1, Tukey test, $P = 0.99$). Adult females showed lower $\delta^{13}\text{C}$ values than adult males and large chicks (Fig. 1, all Tukey tests $P < 0.05$). Adult males and females differed in both their $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, with males showing higher values of both isotopes (Fig. 1, $\delta^{15}\text{N}$: $F_{1, 50} = 1.85$, $P = 0.01$; $\delta^{13}\text{C}$: $F_{1, 50} = 6.57$, $P = 0.01$).

When analyzing the effect of age on stable isotope values of adults and subsequently including the significant effect of sex, we obtained two models that included the significant effect of age on the $\delta^{13}\text{C}$ values (sex: $\chi^2 = 4.04$, $df = 1, 33$, $P = 0.04$; age: $\chi^2 = 6.37$, $df = 1, 33$, $P = 0.01$) and the $\delta^{15}\text{N}$ values (sex: $\chi^2 = 5.95$, $df = 1, 33$, $P = 0.01$; age: $\chi^2 = 4.03$,

Fig. 1 Blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean $\pm$ SE) of 29 small chicks, 28 large chicks and 50 breeding adults (20 males and 30 females) of Audouin's gull sampled at the Ebro Delta area. White points correspond to potential prey groups sampled in the Ebro Delta area (demersal fish and small pelagic fish from Navarro et al. 2009; American crayfish from the present study)

$df = 1,33$, $P = 0.04$). These models explained 24 and 25% of the original deviance on stable isotopes of nitrogen and carbon, respectively. Older male and female adults showed lower and higher levels of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively.

Dietary differences among individuals of different age and sex classes

The proportion of each potential prey, estimated by SIAR models, varied in relation to the age and sex of Audouin's gull in the Ebro Delta area (Fig. 2). The diet of adult males was composed mostly of demersal Wsh (mean of the credibility interval: 48%), followed by small pelagic Wsh (30%) and then American crayWsh (20%). In contrast, the SIAR mixing model revealed that females included a similar proportion of small pelagic Wsh (29%), demersal Wsh (39%) and American crayWsh (31%) in their diets (Fig. 2).

The diet of small chicks was similar to the diet of adult females, composed of demersal Wsh (34%), small pelagic Wsh (34%) and American crayWsh (32%). For large chicks, the diet was mainly composed of small pelagic Wsh (53%), followed by demersal Wsh (28%) and American crayWsh (19%). The SIAR isotopic mixing model estimated that the diet of individuals between 4 and 10 years old was composed of a similar proportion of the three potential prey groups: demersal Wsh (28–39%), small pelagic Wsh (27–33%) and American crayWsh (26–44%) (Fig. 3). However, adults from 11 to 17 years old consumed mainly demersal (36–43%) and small pelagic Wsh (35–37%) and, to a lesser extent, American crayWsh (19–28%) (Fig. 3).

Fig. 2 Results of SIAR (95, 75 and 50% credibility intervals) showing estimated prey contributions to the diet of adults, small chicks and large chicks of Audouin's gulls sampled in the Ebro Delta area during the year 2003. Dem (Demersal Wsh); Pel (Small pelagic Wsh); Cray (American crayWsh)

Fig. 3 Mean percentage of the contribution of small pelagic Wsh, demersal Wsh and American crayWsh in the diet of adults of Audouin's gulls sampled in the Ebro Delta area during the year 2003 in relation to their age (between 4 and 17 years old) estimated from Bayesian mixing models (SIAR)

Discussion

In this work, we show the differential importance of two anthropogenic food resources, demersal Wsh (i.e. Wsheries discards) and the invasive American crayWsh, and a natural resource, the small pelagic Wsh, for the Audouin's gull. Differences in the diet of incubating adults and chicks and also between males and females could be related to different nutritional requirements. Age-related variation in the use of these trophic resources was probably associated with variations in the foraging abilities of adults of different ages (i.e. intra- and interspecific competition in the feeding areas). The difference in the diet between adults and chicks probably was related to a differential nutritional requirement of the food consumed. These results illustrate the importance of considering different ages and sexes of a breeding population to obtain feasible dietary information and to understand the relative importance of the different food resources.

It is well documented that opportunist seabirds take advantage of Wsheries even at great distances from their breeding colonies, feeding on discarded Wsh and oVal (e.g. Furness and Tasker 2000; Arcos and Oro 2002b; Votier et al. 2008). In our case and in concordance with previous studies (Oro et al. 1997; Arcos et al. 2001; Pedrocchi et al. 2002; Sanpera et al. 2007), the SIAR isotopic mixing model also estimated the presence of demersal Wsh, only available through Wsheries discards, in the diet of incubating adults and chicks at the Ebro Delta. Nonetheless, the SIAR results also revealed that the introduced American crayWsh was an important food resource for the Audouin's gull in the Ebro Delta area. This resource has been

previously reported as an important alternative prey not only for Audouin's gulls, but also for yellow-legged *Larus michahellis* and lesser black-backed gulls *L. fuscus* from the Ebro Delta, particularly when marine resources were not readily available (Bosch et al. 1994; Oro et al. 1996a, 1997; Oro 1996).

The importance of these two anthropogenic food resources varied according to the age and sex of individuals. Lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of adult females in relation to adult males and the results from the isotopic mixing model indicated a higher proportion of American crayfish in the diet of females than in males. Mañosa et al. (2004) found that females spent more time than males outside of the colony, suggesting that foraging at the rice fields might have the advantage of reducing competition (Arcos et al. 2001) but that encounter rates with the crayfish would be rather low (authors' personal observations). It is also known that during the courtship feedings, males feed females and that such feedings are composed mainly by fish (Oro 1998). This difference in the diet between males and females might be the consequence of differential nutritional requirements of both sexes relating to egg formation (Williams 2005). During the formation of the egg, besides lipids and proteins, females need a high amount of carotenoids (Blount et al. 2001, 2004), a micronutrient present in high concentration in the American crayfish (Negro et al. 2000). For this reason, although the nutritional value of crustaceans is, in general, lower than that of marine fish (Massias and Becker 1990; Arcos and Oro 2002a), the high availability of the American crayfish at the Ebro Delta (Gutiérrez-Yurrita et al. 1999) and its high content of carotenoids could confer a reproductive benefit to the females that consume such prey.

Similarly, the present study revealed that young adults (from 4 to 10 years old) included in their diet the three prey groups considered (small pelagic fish, demersal fish and American crayfish) in similar proportions, whereas older birds (from 11 to 17 years old) mainly consumed small pelagic and demersal fish. For long-lived seabirds, feeding abilities and foraging performance should increase with age (Ezard et al. 2007; Limmer and Becker 2009). Due to their reduced ability and experience, young adults are less proficient foragers and they could be limited to feeding on easy and usually less profitable food (Daunt et al. 1999; Limmer and Becker 2009). At the Ebro Delta, there is a high intra- and interspecific competition for the use of fishery discards, a profitable food, by seabirds (Arcos et al. 2001; González-Solís et al. 1997; Martínez-Abraín et al. 2003; Skórka and Wójcik 2008). Probably, the lower competitive ability of young adults precludes them from feeding often on trawling discards, and the American crayfish may represent an alternative

foraging resource that may act as a buffer for this constraint, allowing young breeders to enhance their breeding performance (Oro et al. 1996b).

In the case of small chicks, their stable isotope values and the proportion of consumed prey estimated by the isotopic mixing model were quite similar to adult females during incubation. Stable isotope values of whole blood represent the diet during the month prior to blood sampling (Bearhop et al. 2002; Pearson et al. 2003). For this reason, and as we sampled 15-day-old chicks, stable isotopes were partially reflecting the diet of females during egg formation (Hobson 1995). Alternatively, in the case of large chicks, we found that their diet was different from the diet of adults during the incubation period, who fed them mainly on small pelagic fish and a low proportion of demersal species and American crayfish. Two factors likely explain the high representation of pelagic fish in the diet of growing chicks: the nutritional value of these species and food availability. Previous studies have shown that adults of Audouin's gulls fed their large chicks mainly on anchovies and pilchards (Pedrocchi et al. 1996), pelagic fish with a higher nutritional value than demersal fish and crustaceans (Massias and Becker 1990; Arcos and Oro 2002a; Grémillet et al. 2008). In fact, in other gull species, a positive relationship has been found between the percentage of fish in the diet of chicks and breeding success (Pierotti 1982; Murphy et al. 1984; Sydeman et al. 1991). Additionally, the chick-rearing period of Audouin's gull also coincides with the increase in the natural abundance of small pelagic fish during May–June at the Ebro Delta (Lloret et al. 2004).

In conclusion, this study shows that natural prey (small pelagic fish) are the main prey in the diet of the offspring of the Audouin's gull in the Ebro Delta area. Moreover, other trophic resources of human origin, fishery discards and American crayfish, are used by adults of a particular age and sex. The supply of fishery discards has been previously described as the main reason for the spectacular increase in the breeding population of the Audouin's gull at the Ebro Delta, with an average increase of 22% per annum over the last 28 years (Oro 1998; Oro and Ruxton 2001). In addition, we suggest that the presence of American crayfish might also have contributed to this increase, by providing a trophic subsidy for the species, especially for young breeders and when marine resources were not available (Oro 1996; Oro et al. 1996a). This invasive crustacean was introduced during the early 1980s in the rice field areas of the Ebro Delta area for harvesting, in the same years that Audouin's gulls colonized the site. These results highlight the complexity of the impact of both invasive species (American crayfish) and overharvesting (trawling fishery in the Mediterranean) in ecosystems, particularly when designing conservation guidelines.

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