Shifting individual habitat specialization of a successful predator living in anthropogenic landscapes

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ABSTRACT: Population expansions of successful species have gained importance as a major conservation and management concern. The success of these 'winners' is widely attributed to their high adaptability and behavioural plasticity, which allow them to efficiently use opportunities provided by human-modified habitats. However, most of these studies consider conspecifics as ecological equivalents, without considering the individual components within populations. This is critical for a better understanding of the main ecological mechanisms related to the success of winning species. Here, we investigated the spatial ecology of the opportunistic yellow-legged gull *Larus michahellis*, a clear example of a winning species in southern Europe, to examine its degree of individual specialization in habitat use. To test for such individual strategies, we applied specialization metrics to spatial data obtained from 18 yellow-legged gulls that were GPS-tracked simultaneously during the breeding season. The results revealed that population-level generalism in habitat use in the yellow-legged gull arises through varying levels of individual specialization, and individual spatial segregation within each habitat. Importantly, we found that the combination of individual specialization and individual spatial segregation may reduce intra-specific competition, with these 2 important mechanisms driving the success of this winning species.

KEY WORDS: Foraging strategies · Gulls · GPS · Habitat use · Individual specialization · Movement ecology · Opportunistic seabirds · Seabird · Spatial ecology · Winning species

INTRODUCTION

Human activities are globally impacting ecosystems, with important effects on biodiversity, including extinction processes (McKinney 2006, Worm et al. 2006). Species vary in their responses to human perturbations; while most seem unable to cope with drastic changes, others may persist, or even flourish within human-transformed ecosystems (McKinney & Lockwood 1999). The general pattern of expansion of some widespread non-native and native species, so-called 'winners', and the contraction of rare and often endemic native species, so-called 'losers', leads to a biotic homogenization process. This has led to biological impoverishment worldwide (Olden et al. 2004).

Population expansions of winning species have gained importance as a major conservation and management concern (Cardador et al. 2011, Sih et al. 2011, Newsome et al. 2015). The success of these winners is widely attributed to their high adaptability and behavioural plasticity, which allow them to efficiently exploit opportunities provided by novel,

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human-modified environments (Shultz et al. 2005, Clavel et al. 2011). Among marine predators, it is well-known that some gull species are particularly successful. They efficiently adapt to exploiting a wide suite of novel resources that provide direct biotic and abiotic benefits, including food, shelter and refuge from predation (Ramírez et al. 2012, Alonso et al. 2015, Osterback et al. 2015). These winning seabirds are often perceived as pests because of their impacts on urban areas, water reservoirs and threatened species (Vidal et al. 1998, Skórka et al. 2014, Rock et al. 2016). As a consequence, abundant research has been conducted on these opportunistic predators, mainly focused on their population dynamics, feeding ecology, pollution levels and pathogen load (e.g. Ramos et al. 2011, Payo-Payo et al. 2015). However, most of these studies consider conspecifics as ecological equivalents. Although this simplification can be useful to provide an overview of population-level feeding preferences or population dynamics (Ramos et al. 2011, Payo-Payo et al. 2015), taking into account the individual component within populations is essential for a better understanding of the main ecological mechanisms related to the success of winning species (Grémillet et al. 1999, Cardador et al. 2012, Chapple et al. 2012, Liebl & Martin 2014, Ceia & Ramos 2015, Potier et al. 2015)

Individual specialization occurs when some individuals within a population utilize only a subset of the resources that the population uses as a whole. This may be expressed via an animal's diet, patterns of movement or other specific behaviour (Bolnick et al. 2003, Matich et al. 2011, Ceia & Ramos 2015). Individual specialization may vary between populations and across species, which may further enhance ecological consequences at the individual level (Bolnick et al. 2003, Araújo et al. 2011). Variation in individual specialization directly affects the population dynamics of winning species, by facilitating their adaptability to a large suite of environmental conditions, while reducing competition among conspecifics (Bolnick et al. 2003, Tinker et al. 2007, Dall et al. 2012, Liebl & Martin 2014). Thus, taking into account the individual component should allow for a better understanding of ecological processes. In addition, knowing the degree of individual specialization in winning species that negatively affect human or wildlife health may help to implement more effective management actions (Sanz-Aguilar et al. 2009, Bowen & Lidgard 2013, Ceia et al. 2014).

In the present study, we investigated the spatial ecology of the opportunistic yellow-legged gull *Larus michahellis* in a breeding population of southeastern Spain, to examine its degree of individual specialization in habitat use. This species is a clear example of a winning predator in southern Europe, as a result of its ability to efficiently exploit a diverse suite of novel resources (e.g. Alonso et al. 2015, Payo-Payo et al. 2015, Martínez-Abraín & Jiménez 2016). This gull is also considered a pest within urban, agricultural and coastal areas (Vidal et al. 1998). Based on previous information (Ceia et al. 2014, Tyson et al. 2015, Ceia & Ramos 2015), we hypothesized that yellow-legged gulls present a significant level of individual differences in habitat use. Specifically, we predicted that individuals within the population would show niche segregation with respect to habitat use. To test for such individual strategies, we applied metrics previously used to identify diet specialization (Bolnick et al. 2002, Fodrie et al. 2015). These metrics were applied to spatial data obtained from 18 yellow-legged gulls that were GPS-tracked simultaneously during 4 wk of the breeding season (Bouten et al. 2013). This is one of the first studies to investigate the spatial movements of this gull species continuously across several weeks (see Ceia et al. 2014).

MATERIALS AND METHODS

Fieldwork procedures

Fieldwork was carried out at the natural protected Biosphere Reserve of Marismas del Odiel (37° 13′ N, 6° 59′ W, Gulf of Cadiz, SW Iberian Peninsula; Fig. 1) in a colony of 250 to 300 breeding pairs. To investigate spatial movements during the breeding period (May 2015), we deployed high-resolution GPS-trackers recording the positions of individuals at 5 min intervals (www.UvA-BiTS.nl; Bouten et al. 2013) on 18 breeding adult gulls >4 yr old. Age was determined from plumage characteristics. Incubating birds were caught at the nest using a walk-in wire mesh trap and devices were attached using a wing harness fixed with a reef knot in the tracheal pit, an attachment method recommended for large gulls (see Thaxter et al. 2014, 2016). The GPS logger and harness weighed less than 1.8% of the body mass of the birds (19 g for the GPS versus 1062 ± 120 g [mean ± SD] for the tracked gulls), less than the 3 to 5% threshold suggested for seabirds (Phillips et al. 2003, Passos et al. 2010). GPS data were downloaded remotely through a local base station and automatically uploaded to the central database (Bouten et al. 2013). To avoid potential biases associated with differences between individuals in the number of days with GPS
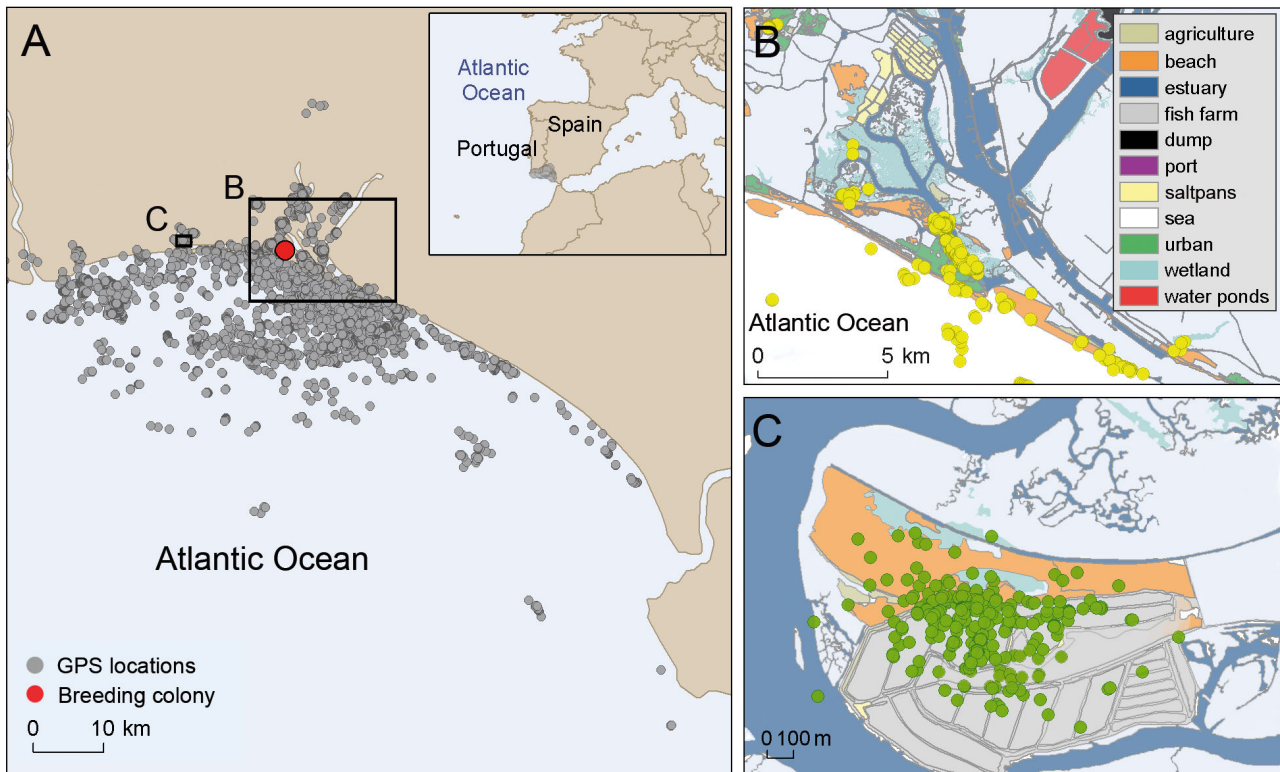
Fig. 1. (A) Study area showing the filtered GPS locations of the 18 tracked yellow-legged gulls *Larus michahellis* during the 2015 breeding season; (B) example of the habitats exploited by a generalist individual; and (C) example of an individual that specializes in the use of fish farm habitats

data and the potential differential spatial behaviour during the breeding period, we focused our analyses on the time period from 14 May to 15 June 2015 (incubation period). We considered only locations recorded outside the colony (using a radius of 500 m around each nest) and we removed all travelling locations (speed > 4 km h^{-1}; Navarro et al. 2016). The total number of GPS locations ranged from a mean of 8200 to 9129, with a mean of 8644 ± 495 locations ind.$^{-1}$.

Individual specialization and individual spatial segregation

Individual specialization in habitat use by each tracked yellow-legged gull was quantified following Bolnick et al. (2002) and Fodrie et al. (2015). Specifically, we calculated the proportional habitat use by each yellow-legged gull as the number of habitat-specific positions divided by the total number of GPS positions recorded during the entire tracking period for a particular individual. Habitat was determined by merging all filtered foraging GPS locations with high-resolution land cover information (SIOSE, Soil Information System of Spain, Junta de Andalucía;

scale was 1:2500; last update 2011). Using this information, we calculated the proportional similarity index (PSi) following Schoener (1968). PSi is a measure of individual specialization based on habitat-by-habitat deviations in an individual's habitat use relative to population level, average habitat use (0 = more specialized; 1 = more generalist). PSi is based on the average pairwise overlap of the niche distribution of individuals and the population (Bolnick et al. 2002). Mean PSi among individuals was used to determine the average amount or prevalence of individual specialization in habitat use in the population (IS). We ran Monte Carlo permutations to test whether observed PSi values differed significantly from a random distribution of values subsampled from the population. We randomly reassigned habitat use for each yellow-legged gull in equal proportion to our observed data, and then calculated individual and population-level metrics for the random population. We generated random habitat use data for 10 000 populations, thereby creating a null distribution of PSi values. We concluded that individuals were not sampling from a shared distribution of habitat use if our observed PSi values were < 95% of all randomly generated values (Araújo et al. 2007).

All of these analyses were performed using the RInSp package (Zaccarelli et al. 2013) in the software package R (R Core Team 2015). Pearson correlation tests indicated that no significant relationship exists between the number of GPS positions and the PSi values at the individual level (p = 0.71). We did not consider a sex effect because no significant differences in PSi values were found between sexes (ANOVA tests: $F_{1,17}$ = 1.92, p = 0.19).

In addition to the PSi values, we quantified the degree of individual spatial segregation within each habitat using Schoener's overlap index *D*-metric (Schoener 1968), indicating the relative use of particular microhabitats (Friedlaender et al. 2011). For this, we overlaid all filtered locations onto a grid of 100 m^2 (corresponding to the minimum area used by the tracking gulls in the present study) to estimate the proportion of locations in any grid cell. The cell size was based on the minimum area encompassing a single habitat. *D*-metric values of 1 indicate a complete spatial overlap between 2 yellow-legged gulls in a pair, whereas values of 0 indicate complete spatial segregation. ANOVA and post hoc tests were applied to test differences in the *D*-metric index between individuals.

Table 1. Habitat type and the main potential behaviours of the yellow-legged gull *Larus michahellis*

Habitat type	Main potential behaviours
Sea	Foraging (marine resources and fishery discards)
Estuary	Foraging (estuarine fish and crustaceans) Resting and socializing
Wetland	Foraging (fish and other resources such as bird chicks or eggs) Resting (safe places)
Beach	Scavenging (dead cetaceans/fish and human food)
Fishing port	Scavenging (fishery discards)
Fish farm	Foraging (farm fish)
Saltpans	Foraging (fish and crustaceans) Resting (safe places)
Water pond	Foraging (fish) Cleaning (freshwater) Resting (safe place)
Agriculture area	Foraging (olives, insects and other terrestrial prey)
Urban	Scavenging (human food) Foraging (urban birds and other prey) Cleaning (freshwater ponds in urban parks)
Garbage dump	Scavenging (human food) Preying (small mammals and insects)

RESULTS

Based on the 28 917 filtered locations recorded during 1 mo of the 2015 breeding season from the 18 tracked yellow-legged gulls, we detected the use of 11 different habitats (Table 1, Figs. 1 & 2). At the population level, the relative use of each habitat (percentage of total locations) ranged from 28.4% for fishing ports and estuaries (22.3%) to ~1.0% for garbage dumps, agricultural lands and fish farms (Fig. 2).

Individual specialization in habitat use

At the individual level, we found PSi values ranging from 0.37 to 0.78, with specialized individuals (low PSi values) mainly exploiting habitats such as fish farms, sea or estuarine areas, and less specialized individuals (high PSi values) using a higher diversity of habitats (Fig. 2). Monte Carlo analyses of individual-versus-population niche variation indicated that specialized individuals were significantly prevalent within the population (IS = 0.52, p < 0.001; Fig. 2).

Individual spatial segregation within each habitat

Based on *D*-metric values (spatial segregation between individuals within the same habitats), we found marked differences between habitats ($F_{10,1710}$ = 136.69, p < 0.001; Fig. 3). Post hoc tests indicated that spatial overlap between individuals was significantly higher in garbage dumps (*D*-metric = 0.78 ± 0.06), followed by water ponds, fish farms and fishing ports (*D*-metric ranging from 0.36 to 0.41), and estuaries (*D*-metric = 0.24 ± 0.15). The lowest spatial overlap values were found for urban, wetland, saltpans, beach, sea and agricultural areas (*D*-metric ranging from 0 to 0.16) (Fig. 3).

DISCUSSION

We examined the spatial ecology of yellow-legged gulls to test the degree of individual specialization in their habitat use, by tracking 18 individuals simultaneously over 1 mo during the breeding period. Our results support the hypothesis about winning spe-
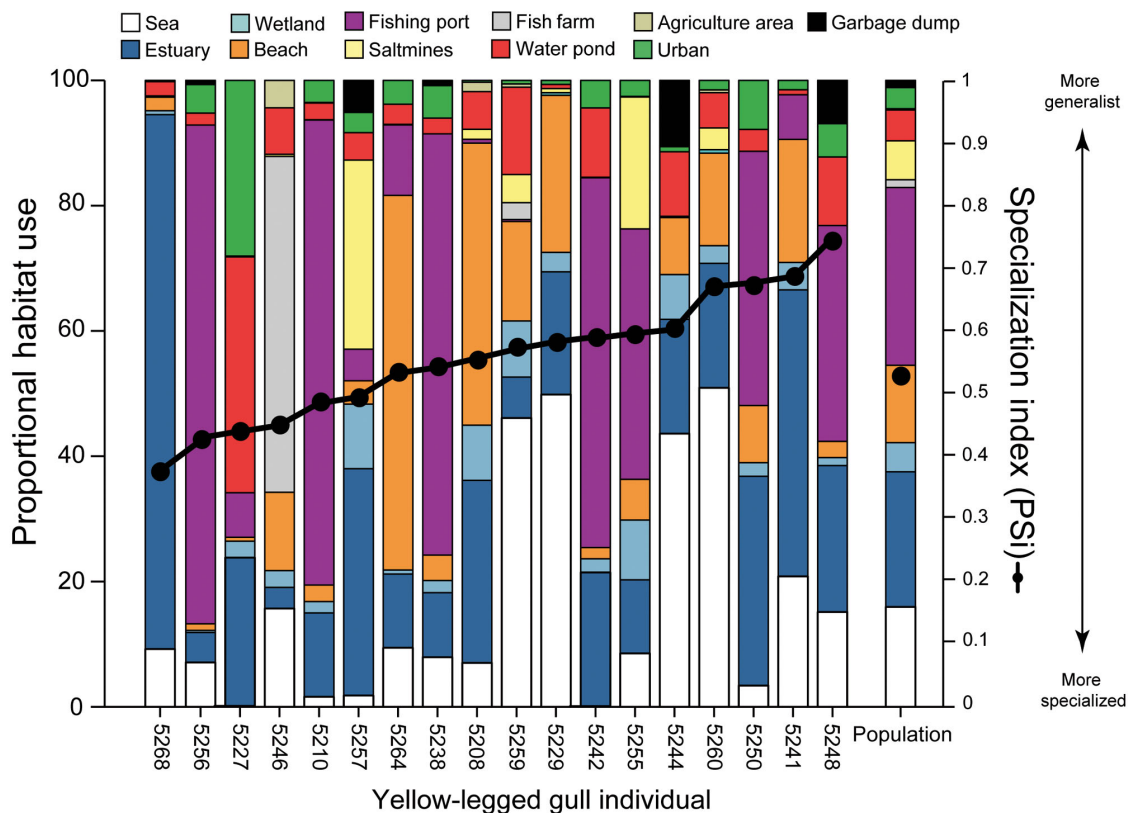
Fig. 2. Individual variation in habitat use between the 18 GPS-tracked yellow-legged gull *Larus michahellis* individuals during one month of the 2015 breeding season. Each individual (*x*-axis) is represented by a vertical bar, subdivided by the proportion of locations in each habitat in relation to the total GPS locations and the specialization index PSi (black dots; 0 = more specialized; 1 = more generalist). Mean habitat use and the prevalence of individual specialization in habitat use in the population (IS; black dot in the population bar) are also represented (right bar)

cies, as they revealed a high diversity of habitats used by the yellow-legged gulls. Moreover, in accordance with ecological theory related to generalist species (Bolnick et al. 2003, Araújo et al. 2011), we also showed that variation within the population predominately derives from individual specialization in habitat use. Importantly, we found that the degree of spatial segregation between individuals differed markedly between habitats.

At the population level, yellow-legged gulls were able to use up to 11 main habitats present both in marine and terrestrial domains, including natural and human-made habitats. This high plasticity reflects the pronounced ability and behavioural flexibility of the yellow-legged gull to exploit a diverse suite of trophic resources, some of which are novel resources provided by humans, or use them for other activities such as resting, bathing or socializing. For example, it has been reported that in the marine environment or in fishing ports the yellow-legged gull exploits marine resources by foraging on natural prey in the open sea, or opportunistically forages on

fishery discards (Duhem et al. 2003, Ramos et al. 2009). In the saltpans, estuaries and wetlands, birds exploit different resources such as fish, crustaceans and bivalves, predate on eggs and chicks of other birds, or use undisturbed areas to rest or socialize with conspecifics (Bosch 1996, Munilla 1997, Vidal et al. 1998, Buechley & Şekercioğlu 2016). In beaches or urban areas, individuals scavenge on organic matter present in human waste or dead marine organisms, predate on urban vertebrates such as pigeons, or use the ponds present in the urban parks to bath or drink freshwater (Britton & Morton 1994, Buechley & Şekercioğlu 2016, Huig et al. 2016). In some specific habitats such as water ponds, in addition to preying on amphibians or freshwater fish, the gulls wash their feathers or rest (Sebastián-González et al. 2012). Most published studies indicate the high importance of trophic resources present in garbage dumps for the yellow-legged gull (Duhem et al. 2003, Ramos et al. 2009). Surprisingly, in our study, the importance of this habitat was very low. This result may be related to the low availability of urban dumps in the area
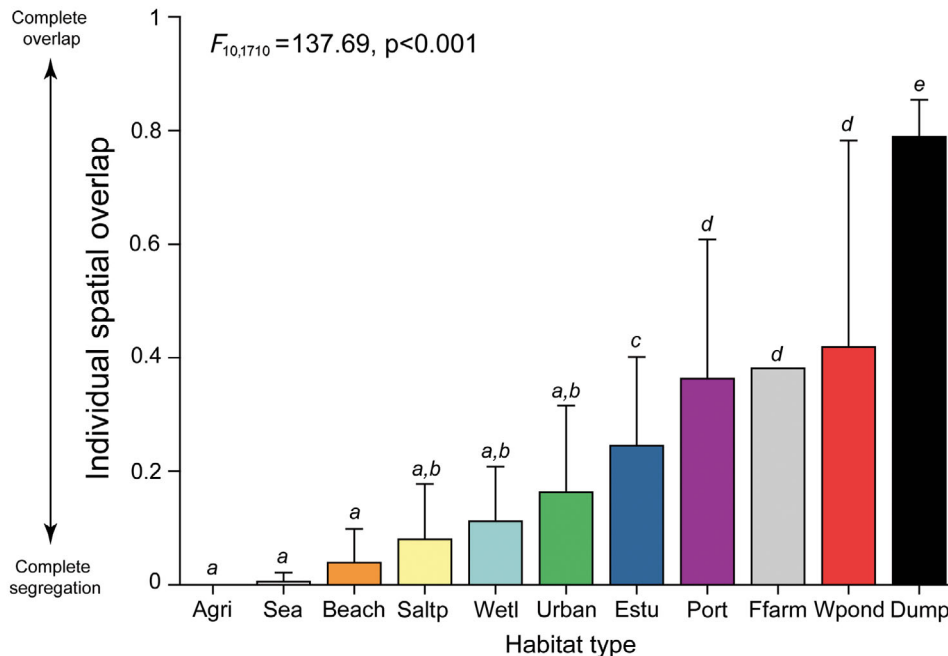
Fig. 3. Spatial overlap (mean and SD) between yellow-legged gull *Larus michahellis* individuals within each habitat (Agri = agriculture area, Saltp = saltpans, Wetl = wetlands, Estu = estuaries, Port = fishing ports, Ffarm = fish farms, Wpond = water ponds, Dump = garbage dumps) based on Schoener's spatial overlap metric (0 = more segregation; 1 = more overlap). The results of post-hoc Tukey HSD tests are shown by the lowercase letters above each bar: for individual spatial overlap, the means of habitats with the same letter were not significantly different

covered by GPS-tracked individuals (Navarro et al. 2016).

Although all GPS-tracked yellow-legged gulls could potentially exploit all available habitats, based on PSi values—a metric to test individual specialization (Bolnick et al. 2002, Fodrie et al. 2015)—we found clear differences in habitat use among individuals within the population. These results are coherent with the prediction that some generalist or opportunistic species are composed of ecologically heterogeneous individuals that repeatedly differ in behaviour and use of different subsets of available resources (Bolnick et al. 2002, Bearhop et al. 2004, Bell et al. 2009). Individual specialization is known to be widespread across a diverse set of taxa (Bolnick et al. 2003, Bell et al. 2009, Ceia & Ramos 2015), including different seabird species and other marine predators (e.g. Vander Zanden et al. 2010, Votier et al. 2010, Masello et al. 2013, Ceia & Ramos 2015, Tyson et al. 2015, Towner et al. 2016, Yurkowski et al. 2016). In general, individual specialization may have a strong impact on ecological processes and population dynamics, and there is evidence that this mechanism may reduce intra-specific competition among individuals, increase individual foraging efficiency and improve breeding success (Pierotti & Annett 1991, Bolnick et al. 2003, Woo et al. 2008, Araújo et

al. 2011). For this reason, the existence of individual specialization within populations of winning species could partially explain their success (Grémillet et al. 1999, Cardador et al. 2012, Chapple et al. 2012, Liebl & Martin 2014, Ceia & Ramos 2015, Potier et al. 2015). Specifically, individual specialization could help opportunistic species to exploit the wide range of ecological opportunities provided by human activities (food or shelter, among others) in heterogeneous landscapes, thereby becoming more competitive than losing species (Carrete et al. 2010, Cardador et al. 2011, Layman et al. 2015, Newsome et al. 2015, Robertson et al. 2015).

The high degree of specialization across yellow-legged gulls of southern Spain has management and conservation implications related to the implementation of effective actions to reduce specific impacts on human or conservation interests (Sanz-Aguilar et al. 2009, Bowen & Lidgard 2013). For example, if the owners of fish farms wish to reduce the potential impact of yellow-legged gulls on their installations, one tractable management option is to remove gulls that specialize in this resource. One piece of clear evidence of the efficacy of such targeted measures is the reduction of the predation of the European storm petrel *Hydrobates pelagicus* by yellow-legged gulls, through the removal of specific petrel predators

within the gull population (Sanz-Aguilar et al. 2009). However, it is important to point out that although these management measures could be efficient in the short term, other individuals can occupy the empty niche over longer periods.

Interestingly, we also found that the degree of spatial segregation between yellow-legged gulls differed between habitats. Based on the principle of competitive exclusion, competing individuals exploiting similar habitats are expected to segregate, especially when particular resources are limited (Gause 1973, Pianka 2000). Although we did not measure the availability of trophic resources or other types of resource related to other particular behaviours in each habitat, some of these observed differences may be explained by inter-habitat differences. For example, in garbage dumps or fish farms, high availability of resources and limited profitable surface area could allow some degree of spatial overlap between individuals exploiting similar trophic resources (Cortés-Avizanda et al. 2012, Arizaga et al. 2014). In contrast, in other habitats with prey resources for gulls, such as fishery discards at sea, individuals probably need to segregate in space to find food, or to reduce competition between conspecifics or with other bird species (Navarro et al. 2013, Patrick et al. 2014, Tyson et al. 2015). For this reason, the different degrees of individual spatial segregation between habitats may be viewed as a consequence of the distribution or availability of the resources used by gulls, or as a potential mechanism to reduce intra-specific competition (Bolnick et al. 2007, Matich et al. 2011, Robertson et al. 2015).

CONCLUSIONS

Our findings revealed that population-level generalism in habitat use in the yellow-legged gull arises through varying levels of individual specialization in habitat use and individual spatial segregation within each habitat, rather than all individuals being broad generalists. This combination of individual specialization and individual spatial segregation may reduce intra-specific competition, serving as 2 important mechanisms related to the success of these winning species in comparison to other, less successful species. Further multispecific investigations involving long-term GPS-tracking data covering the annual cycle of different colonies located in different environmental contexts would be useful to confirm that individual specialization in habitat use is a common phenomenon in winning and successful predators.

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