No evidence supporting sex-dependent differential movements and survival in Yellow-legged Gulls

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Important biological parameters, such as movement and survival, can differ substantially between sexes, driving the demographic patterns of a population. Sex-dependent spatial segregation at the foraging grounds can evolve as a mechanism to reduce competition for resources between sexes, among other causes. Investigating such segregation, especially in scenarios of decreasing food availability, can contribute to understanding how birds adapt to a fastchanging world. The aim of the present study was to determine whether yearround movements and survival varied between sexes within a resident Yellowlegged gull Larus michahellis population. To this end we used live encounter data on colour-ringed Yellow-legged Gulls in northern Spain in the period 2009–2017. We used Generalized Linear Models to analyse distance to the colony of origin and multi-state models to estimate both survival and year-round movements, which did not provide evidence supporting an effect of sex on movement and survival. In contrast, distances travelled from the natal colony varied between seasons and all gulls were more likely to move greater than 100 km from natal sites. Juveniles showed lower survival rates (0.55) than older birds (0.90). Future research with GPS data might help to reveal, if existing, the occurrence of local spatial segregation between sexes that otherwise remains undetected.

Key words: Biscay, carrying capacity, Larus michahellis, sexual segregation

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Biological parameters, such as movement and survival, can differ substantially between sexes, so that sex can be one of the main factors driving the demographic patterns of a population (Newton 2013). When breeding, individual birds in a colony generally share the same foraging areas, although minor differences in foraging strategies are seen in some gull (Laridae) populations (Camphuysen et al. 2015). Once breeding ends, spatial segregation between sexes can increase (Cristol et al. 1999, Nebel 2005, Bosman et al. 2011, Lundblad & Conway 2020). There are several ultimate factors explaining this sexual segregation and these can vary between species. Size-dimorphic competition at an intra-specific level might force one sex (usually the smaller) to look for food elsewhere (e.g. Cristol et al. 1999, Catry et al. 2005a, but see Bosman et al. 2011). Sex-dependent geographic segregation can evolve therefore as a mechanism to reduce competition for resources (mostly food; Wearmouth & Sims 2008). When both sexes feed on similar resources, spatial overlap between the sexes may be reduced when food is a limiting factor (Cristol et al. 1999, Catry et al. 2005a). When sexes share a space, it indicates either the absence of competition behaviour or of food limitations. Competition can be reduced by exploiting different trophic resources or different foraging habitats, even at a very small spatial scale (Catry et al. 2005b, Forero et al. 2005, Alves et al. 2013, Kazama et al. 2018). Spatial segregation between sexes, however, can be explained by alternative hypotheses (Nebel & Ydenberg 2005a, b, Lundblad & Conway 2020), including (1) arrival time, when males stay closer to the colony during the non-breeding season to enable them to occupy a good site within the colony as soon as the

breeding season approaches, (2) thermal tolerance, where the larger sex is able to winter in colder places, (3) fasting endurance, where the larger sex has greater capacity to tolerate episodes of food shortage (4) resource partitioning, where sexual spatial segregation exists when sexes vary in their morphology, which is optimized to exploit a feeding resource that is spatially partitioned, or (5) predator escape performance, where the sexes can reduced their risk of predation in different areas due to spatially segregated predators.

Sexual segregation in seabirds (suborder Lari), is receiving increasing attention among scientists owing to the effects that different behaviours could have at a population level (Camphuysen *et al.* 2015, Kazama *et al.* 2018). For instance, studies with Lesser Blackbacked Gulls *Larus fuscus* have revealed that during the breeding season females forage closer to the colony and perform shorter foraging trips than males (Camphuysen *et al.* 2015), highlighting some degree of spatial segregation between sexes during the breeding season.

The Yellow-legged Gull Larus michahellis is one of the most common large gulls in the southwestern Palaearctic. In Spain, the latest census assessed a population of c. 125,000 pairs (Molina 2009). Recent landfill closures led to food shortages for some mainland colonies, not only causing a population decline but also changes in movement patterns of local gulls (Arizaga et al. 2014, Egunez et al. 2017). The population breeding along the coast of northern Iberia is mostly resident, with c. 70% of the individuals remaining within 50 km from their natal colonies year-round (Egunez et al. 2017). However, long-distance movements, up to more than 1000 km, also happen, especially in first-year birds (Arizaga et al. 2010, 2015a). If there is spatial segregation between the sexes, we could test evidence supporting different hypotheses. If segregation is detected, one sex is likely to move further. Under the competition and arrival hypotheses, females should winter in more distant regions, because they are smaller and do not need to arrive at the colonies as soon as winter ends. Other hypotheses, however, would not fit with such findings when following the scenarios of a favourable food distribution and availability close to the colony where females, which wintering close by, have a higher breeding success (Lundblad & Conway 2020). Additionally, survival analyses could allow us to find evidence in favour of some previously mentioned hypotheses. The aim of the present study was to determine whether movement and survival varied between sexes within a resident Yellow-legged Gull population.

METHODS

Sampling area and data collection

The data used in this study were obtained from birds marked in three Yellow-legged Gull colonies situated along the coast of Gipuzkoa, northern Spain, in the south-eastern part of the Bay of Biscay (Figure 1); from east to west: Ulia (43°33'N, 01°95'W; with 660 breeding pairs in 2017), Santa Clara (43°32'N, 1°99'W; 100 pairs) and Getaria (43°31'N, 2°20'W; 165 pairs). Adult Yellow-legged Gulls start to occupy their breeding sites in the colony around February and the laying period is in April. With an incubation period of c. 26 days, the first hatchlings appear from mid-May onwards. The parents feed their offspring within the colony until the first half of July. During the breeding season of 2009, 2010, 2011 and 2013, 155 chicks were marked when they were close to fledging, with both a metal ring (Aranzadi ringing scheme) and a PVC ring with an alphanumeric code, allowing the identification of each individual bird from a distance (Fernández et al. 2017). Dorsal feathers were taken from each bird in order to determine its sex using molecular techniques. Feathers were kept in paper envelopes until they were sent to the laboratory (Department of Zoology and Ecology, University of Navarra).



Figure 1. Locations of the three study colonies in the Gipuzkoa province, Spain.

Gulls were sexed using DNA-analyses (Griffiths *et al.* 1998). For each bird, a sample from the base of the rachis from one to two feathers was taken and stored in a 1.5 ml vial, filled with 99% ethanol. The DNA fragment related to the CHD-protein, present in both Z and W chromosomes, was amplified by means of a Polymerase Chain Reaction (PCR) technique. PCR fragments were separated by electrophoresis on a 2.5%



Left: Adult Yellow-legged gull with colour ring at Ulia Colony, San Sebastian in May 2014. Right: A colour-ringed juvenile Yellow-legged Gull at the coast of Gipuzkoa in October 2014 (photos J. Arizaga).

agarose gel: a single band of DNA on the gel showed that a bird was male (corresponding to CHD-Z gene), while two bands were present in females (corresponding to both CHD-Z and CHD-W). From the 155 gulls sampled, 80 were males and 75 females.

Once these birds left their natal colonies, they were observed by birdwatchers and our own research team, this data was used to estimate survival as well as distance from the natal colony for the two sexes. Records of re-sighted birds were taken up to 31 December 2017. Overall, from 155 ringed chicks, 84 (54.2%) were seen at least once after they left their colonies. In total, these 84 gulls provided 671 sighting occasions.

Data analysis

Our main goal was to determine whether distances travelled from the colonies and survival varied between the two sexes. With that aim, we divided the year into four seasons (Egunez *et al.* 2017): Jan–Mar (pre-breed-

ing), Apr–Jun (breeding), Jul–Sep (post-breeding), Oct–Dec (wintering). The age of each gull was classified as juvenile (here, from the hatching year to June of the next year), immature (from June of their second year of life to June of their fourth year of life) or adult (older birds, when gulls reach sexual maturity).

First, we conducted Generalized Linear Mixed Models (GLMM) to test whether distances travelled varied between the sexes. We log_{10} -transformed distance to the colony of origin to improve normality. The following explanatory variables were included as factors: season (using the four seasons considered above), age class and sex, and the 2- and 3-way interaction between these three factors; bird identity was included as a random factor. Age was included in the model since the movement patterns in this population vary between age classes (Egunez *et al.* 2017). For each individual bird, we only considered the maximum distance achieved per season and age category in order to remove pseudo-replicates. We used an identity link

Table 1. Mean (\pm quartile ranges; sample size) distance to the natal colony of colour-ringed Yellow-legged Gulls seen alive in the Bay of Biscay, in relation to their age class and season.

	Juvenile		Adult	
Male				
Jan–Mar	26.5 (31.6–18.3; 12)	34.9 (35.1–30.5; 19)	75.1 (30.5–15.7; 11)	
Apr–Jun	32.2 (30.5–30.5; 14)	12.3 (26.52-3.32; 10)	5.8 (3.3–1.7; 7)	
Jul–Sep	60.6 (53.0–30.5; 19)	69.1 (30.5–30.5; 19)	81.6 (65.0–3.3; 10)	
Oct–Dec	41.0 (38.6–1.7; 22)	32.9 (30.5–14.7; 20)	78.6 (50.1–13.8; 12)	
Female				
Jan–Mar	75.7 (56.6–16.9; 14)	32.5 (30.5–30.5; 17)	17.7 (30.5–3.4; 11)	
Apr–Jun	59.5 (30.5–16.8; 14)	72.5 (8.5–2.4; 7)	14.6 (27.6–1.7; 4)	
Jul–Sep	130.8 (114.3–30.5; 19)	42.2 (64.3–30.5; 13)	71.7 (47.7–30.5; 11)	
Oct–Dec	101.0 (69.4–26.4; 21)	113.5 (112.4–30.5; 17)	74.5 (39.1–13.4; 13)	

function with a Gaussian error structure. The analysis included 336 sightings of 84 individuals (for details see Table 1) and was performed in R v. 3.6.3 (R Core Team 2020) using the packages 'lme4' (Bates *et al.* 2015) and 'lmerTest' (Kuznetsova *et al.* 2017). We started with a global model with 3-way interactions, and performed a model selection procedure using the 'dredge' function of the package 'MuMIn' (Barton 2014). Models with AICs differing less than 2 were considered to fit the data equally well (Burnham & Anderson 1998).

Second, we used capture-mark-recapture (CMR) models in MARK (White & Burnham 1999) in order to estimate whether survival and presence in the breeding area (<100 km) varied in relation to sex and time of the year. We used multi-state models with live encounters, which allow the estimation of survival (φ : probability that a bird survives from *t* to *t* + 1), recapture probability (*p*: probability that a bird that survives from *t* to *t* + 1 is seen in *t* + 1) and movement probability



Figure 2. Distribution of distances to the natal colony between sex classes in relation to age categories: juveniles (from hatching year to June of the next year), immatures (from June of their second year of life to June of their fourth year of life) or adults (older birds).

(ψ : probability that a bird in site 1 moves to site 2). Since such models need relatively long time intervals between capture sessions, we only considered two seasons per year in this case: the breeding and the winter period, i.e. data collected from April to June and from October to December Overall, the design matrix had 18 columns (two seasons per year during a period of nine years, 2009 to 2017), 155 rows (individuals) with two distance categories (sightings more or less than 100 km from the natal colonies) and the two sexes. Before testing the fit of the data to candidate models, we tested if the data met the CMR assumptions. For this we used the global goodness-of-fit test performed in U-CARE (Choquet et al. 2009) and found no significant effects for either sex (females: $\chi^2 =$ 27.61, df = 22, P = 0.189; males: $\chi^2 = 14.91$, df = 21, P = 0.828) was found, indicating that our data fitted the CMR assumptions regarding trap-dependence (encounter probability biased) and occurrence of transients (emigrant individuals marked).

We constructed a number of candidate models that were then subjected to a selection procedure modified for small-sample sizes (AICc), taking into account both the number of parameters of the model and its deviance (Burnham & Anderson 1998). We started by building models assuming either constant or timedependence effects on φ , ψ and p. After that we also ran all the possible combinations that included an effect of sex, period and age on φ and ψ for the two distance categories, while for p, we only considered models that also included sex and distance category. Overall, we built 101 candidate models. Models that differed less than 2 AICc units compared to the model with the lowest AICc were averaged.

RESULTS

Overall, the mean maximum distance achieved by each individual bird was 60 ± 6 km ($\pm 95\%$ CI). Mean distance travelled from the natal colony was less than 50 km in all age classes (Figure 2). According to our global GLMM, the distance was affected by age and season, but not by sex (sex: $F_{1,82} = 0.78$, P = 0.38, age: $F_{1,82} = 13.13$, P < 0.001, season: $F_{1,230} = 21.06$, P < 0.001; interactions: all P > 0.05, except age× season: $F_{1,230} = 4.80$, P < 0.001). Model selection procedure provided two models that fitted to the data equally well: a first model, considering an effect of age, season, and the age-season interaction on distance, and a second model, which also included an effect of sex. These models were averaged, and the result only

non-statistically significant effect of sex on this variable (Table 2). On average, distances travelled tended to decrease during the breeding period (Apr–Jun)), with a significant interaction between age class and season,

Table 2. Parameter estimates (β) obtained from model-averaged Generalized Linear Mixed Models testing for the effect of sex, age and season on distance to the natal colony of Yellow-legged Gulls in the Bay of Biscay.

	β	SE	Р
Parameters			
Sex: male	-0.07	0.17	0.655
Age: juvenile	+0.25	0.25	0.312
Age: immature	+0.35	0.25	0.164
Season: Jan–Mar	-0.45	0.28	0.106
Season: Apr–Jun	-2.13	0.36	< 0.001
Season: Jul–Sep	-0.16	0.29	0.571
Age-season interaction			
Juvenile×Jan–Mar	+0.19	0.37	0.614
Immature×Jan–Mar	+0.11	0.35	0.758
Juvenile×Apr–Jun	+1.95	0.43	< 0.001
Immature×Apr–Jun	+0.44	0.45	0.334
Juvenile×Jul–Sep	+0.33	0.36	0.359
Immature×Jul–Sep	+0.09	0.37	0.800

Reference values: Sex: female = 0; Age: adult = 0; Season: Oct–Dec = 0

due to juveniles being observed at larger distances from the colony in the breeding season than the other age categories (Table 2).

CMR analyses provided four best-ranking models that fitted the data equally well (Table 3). These models were very similar, and included age-dependence on survival (with one value for the juvenile birds and one for immature plus older birds), an effect of distance and season on ψ , and an effect of distance and age on *p*. The averaged model provided the following parameter estimates. For φ (±SE), adult birds had a similar apparent survival (0.90 ± 0.04) to immatures (0.87 ± 0.03) , while that of juveniles was significantly lower (0.55 \pm 0.05). However, the overlap between the two oldest categories was high and, therefore, only the juvenile fraction had a significantly lower survival value. In the case of ψ , the four best models included an effect of season (pre-breeding and breeding period vs. post-breeding and winter period), distance (less or more that 100 km from the breeding colony) and sex. Looking at Table 4, however, the effect of sex was not significant, with much overlap in parameter estimates between sexes). Finally, for p, we obtained higher values when gulls were within a radius of less than 100 km from their natal sites. Within that radius, the juvenile birds had a probability of detection that was lower (0.76 ± 0.16) than the older birds (0.99 ± 0.01) . At distances >100 km from their natal sites, the probability of detection for juveniles increased (0.26 ± 0.08) when compared to older birds (0.09 \pm 0.02).

Table 3. Ranking of the best ten models used for testing the effect of age, season and distance travelled on survival (φ), displacement (ψ) and re-sighting (p) probabilities. The reference model, with constant φ , ψ and p, is shown at the bottom. Δ AICc indicates the difference with the model with the lowest AICc. '2ages' indicates a difference between juveniles and older birds, while '3ages' indicates variation among the three age classes (juvenile, immature and adult birds). 'season' stands for a difference between the winter and summer period. 'dist' means that a parameter varies between gulls close (<100 km) or far away (>100 km) from the colony. 'Sex' indicates a difference between males and females.

Model	AICc	AAICo	AIC c weight	Number of	Deviance
	Alce	Ande	Alce weight	parameters	Deviance
$arphi_{ ext{2ages}}, \psi_{ ext{season+dist}}, p_{ ext{dist+2ages}}$	1164.31	0.00	0.33	9	589.87
$arphi_{ ext{3ages}},\psi_{ ext{season+dist}},p_{ ext{dist+2ages}}$	1165.01	0.70	0.23	10	588.45
$arphi_{ ext{2ages}}, \psi_{ ext{season+dist+sex}}, p_{ ext{dist+2ages}}$	1165.98	1.67	0.14	13	582.96
$arphi_{ ext{3ages}}, \psi_{ ext{season+dist+sex}}, p_{ ext{dist+2ages}}$	1166.19	1.88	0.13	14	581.00
$arphi_{ ext{3ages}},\psi_{ ext{season+dist}},p_{ ext{dist}}$	1168.11	3.80	0.05	8	595.78
$arphi_{ ext{2ages}}, \psi_{ ext{season+dist}}, p_{ ext{dist}}$	1168.17	3.86	0.05	7	597.94
$arphi_{ ext{3ages}}, \psi_{ ext{season+dist+sex}}, p_{ ext{dist}}$	1169.12	4.81	0.03	12	588.27
$arphi_{ ext{2ages}}, \psi_{ ext{season+dist+sex}}, p_{ ext{dist}}$	1169.65	5.34	0.02	11	590.95
$arphi_{2ages+season+dist},\psi$, p_{dist}	1176.18	11.87	0.00	6	608.04
$arphi_{ ext{3ages}}, \psi_{ ext{3ages}}, p_{ ext{dist}}$	1176.21	11.89	0.00	8	603.87
φ, ψ, p	1228.14	63.82	0.00	3	666.17

Table 4. Movement probabilities (mean \pm SE) obtained after model-averaging (best four models from Table 3) of a Yellow-legged Gull population, in relation to season, distance and sex. As example, a value of 0.5 means that there is a probability of 50% to move from site A to site B.

	Male	Female
Breeding to winter season		
Move close (<100 km)	0.56 ± 0.070	0.57 ± 0.075
Move away (>100 km)	0.32 ± 0.047	0.25 ± 0.053
Winter to breeding season		
Move close (<100 km)	0.67 ± 0.059	0.64 ± 0.059
Move away (>100 km)	0.12 ± 0.036	0.15 ± 0.042

DISCUSSION

Using data from a Yellow-legged Gull population breeding in the North of Spain, we did not find evidence supporting sex-dependent variation in either distance travelled from the natal colony or survival. Our results suggest that there is limited or no competition for feeding resources, perhaps because there is enough food available (Zorrozua et al. 2020b) or because females feed on different food items than males (Camphuysen et al. 2015). Even though a number of landfills within the region have been closed, food ecology studies suggest that there is still enough food available, in part because some landfill sites remained open during the study period, and also because the gulls are able to shift to other resources (Zorrozua et al. 2020a). Furthermore, the lack of spatial segregation between the sexes during the non-breeding season suggests that the Yellow-legged Gull population in the Bay of Biscay may not be influenced by natural and sexual selection processes that promote sexual segregation in winter (Cristol et al. 1999, Catry et al. 2005b, Nebel & Ydenberg 2005b, Lundblad & Conway 2020).

Our findings are also compatible with some other explanations. For example, females might tend to disperse more (longest distance records were detected in females; Figure 2), but the fraction of birds doing so is small. Furthermore, the relatively small sample size (155 birds in total), makes it difficult to detect small differences due to limited statistical power. However, such small differences may have marginal biological meaning. Additionally, it can be also mentioned that the sighting effort at distances >100 km was notably smaller than at distances <100 km, and this may cause a bias in the number of long-distance dispersers (reducing sample size), although there was no difference in the proportion of male-females found outside this radius of 100 km. Thus, the uneven observation effort across the distribution range of these birds should not have a significant impact on the fact that we did not find differences in distances travelled between the sexes.

In the near future other landfills will be closed (e.g. Arizaga *et al.* 2014, Steigerwald *et al.* 2015) and, at the same time, fish discards will be reduced in northern Spain. Therefore, the availability of food is expected to decrease substantially within the region and it will be interesting to test whether competition between sexes will change, and if this may lead to spatial segregation between the sexes.

We detected a significant effect of age on distance to the natal colony. As expected (Munilla 1997), adults and immatures remained closer to the colony than juveniles during the breeding season. Greater distances to the colony were detected for juveniles (from the hatching year to June of the next year) compared to older individuals in the breeding season. This is a very common phenomenon in seabirds, and it can be due to either the saturation of the area around the colonies by breeding adult birds (Gaston 2004) or simply because adults are restricted in their range as they must return to the colony for reproduction. Immatures could benefit from staying close to the colonies, since this would allow them to learn where to find food and gain social experience when prospecting areas for breeding (Dittmann et al. 2005). Our findings indicate that this population was very faithful to its natal area. This finding is in contrast with the Mediterranean Yellowlegged Gull population, that is partially migrant (Galarza et al. 2012), but not with the Macaronesian population, that is also sedentary (Romero et al. 2019).

The multi-state CMR models did not reveal different movements patterns between the sexes. Overall, our gulls had a higher probability of moving further than 100 km away than to return to areas near their natal colonies, with such a pattern being more marked in winter. This pattern, however, does not mean that our population acts as a source from a demographic view (i.e. emigration exceeding return rate considering birds born within the region), because immigration was not measured. Finally, survival was found to be lower among first-year birds (c. 0.55) than in older birds (around 0.90). These apparent survival estimates are similar to those estimated in previous studies, indicating that survival has remained rather constant in the last decade (Arizaga *et al.* 2015b, Juez *et al.* 2015). Future research with GPS-tracking will be key to learning when and where juvenile mortality rates is at its highest, leading to a better understanding of their risks and vulnerable periods. Such new technologies may also reveal otherwise undetectable small-scale niche partitioning between the sexes (e.g. Camphuysen *et al.* 2015).

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SAMENVATTING

Binnen een populatie bestaan soms aanzienlijke verschillen tussen mannetjes en vrouwtjes in de jaarlijkse afgelegde afstand en de overleving. Het geslacht kan daardoor een van de factoren zijn die de demografische patronen van een populatie aansturen. Onderzoek naar verschillen in voedselecologie tussen mannetjes en vrouwtjes binnen een soort kan, vooral bij een afnemende voedselbeschikbaarheid, inzicht geven in de mate waarin een soort zich kan aanpassen aan een snel veranderende wereld. Wij onderzochten in de periode 2009-2017 in Noord-Spanje de jaarlijkse bewegingen en overleving van mannetjes en vrouwtjes binnen een broedpopulatie van Geelpootmeeuwen Larus michahellis (ter plekke standvogel) met kleurringen. We gebruikten bij de analyse van de verkregen terugmeldingsgegevens gegeneraliseerde lineaire modellen om de afstand van vogels tot de geboortekolonie te schatten en 'multi-state' modellen om zowel de overleving als de jaarlijks afgelegde afstand te schatten. Wij vonden geen aanwijzing dat er een verschil tussen beide geslachten bestond wat betreft de jaarlijks aflegde afstand en de overleving. Wel waren er seizoenafhankelijke verschillen in de afstand van de vogels tot de geboortekolonie. Er was een grotere kans om naar plaatsen op meer dan 100 km van de geboortekolonie te verhuizen dan naar plaatsen dichter bij oorspronkelijk kolonie. Juveniele vogels hadden een lagere overlevingskans (0,55) dan oudere vogels (0,90). Onderzoek met GPS zou kunnen helpen om het bestaan van een kleinschalige ruimtelijke segregatie tussen beide geslachten (indien aanwezig) te onthullen die anders onopgemerkt blijft.

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