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ORIGINAL ARTICLE

Extensive post-breeding movements of Adriatic Yellow-legged Gulls *Larus michahellis*

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Abstract The Yellow-legged Gull *Larus michahellis* is generally considered to be sedentary and dispersive, with long-distance dispersal of young birds developing after the 1970s. In this paper, we present the analysis of the movement of the Yellow-legged Gulls from the eastern Adriatic coast based on observations of colour-ringed birds marked between 1999 and 2011. A total of 4,114 sightings of 1,559 Yellow-legged Gulls marked as chicks were analysed. Our results showed a clear preference in the direction of the movement of Yellow-legged Gulls and significant differences in the directions of movements and the longitude of the observation sites of birds from different colonies. During summer and autumn, the majority of gulls moved towards the north, to the Baltic and North Sea coasts. Maximum distances covered (1,958 km for juveniles and 1,380 km for adults) were much greater than for the other studied populations of the Yellow-legged Gull. We found no difference between the directions of the movement among age classes, while distances decreased with age. Three important features: long-distance movements, migratoriness of adults and differences in movements between colonies, do not support the theory that post-breeding movements of the Yellow-legged Gull have been recently developed as the result of population increase. We presume that the recent pattern of movements reflects the evolutionary history of the Yellow-legged Gulls and might be inherited or result from experience and have been transferred by learning between generations among birds from the same colony.

Zusammenfassung

Ausgedehnte Wanderungen von adriatischen Mittelmeermöwen *Larus michahellis* nach der Brut

Die Mittelmeermöwe *Larus michahellis* wird allgemein als umherstreifender Standvogel betrachtet, bei dem Jungvögel nach den 1970er Jahren die Ausbreitung über lange Strecken entwickelten. In diesem Artikel präsentieren wir eine Analyse der Bewegungen von Mittelmeermöwen von der östlichen Adriaküste, basierend auf der Beobachtung von Vögeln, die zwischen 1999 und 2011 farbberingt wurden. Insgesamt wurden 4114 Sichtungen von 1559 Mittelmeermöwen, die als Küken markiert worden waren, ausgewertet. Unsere Ergebnisse zeigten eine klare Präferenz in den Bewegungsrichtungen der Möwen sowie signifikante Unterschiede in den Bewegungsrichtungen und der geographischen Länge der Beobachtungsorte von Vögeln aus verschiedenen Kolonien. Im Sommer und Herbst wanderten die meisten Möwen gen Norden an die Ost- und Nordseeküste. Die maximal zurückgelegten Entfernungen (1958 km für Jungvögel und 1380 km für Altvögel) waren deutlich größer als für die anderen bislang untersuchten Populationen der Mittelmöwe. Die Bewegungsrichtung unterschied sich nicht zwischen verschiedenen Altersgruppen, während die Entfernung mit zunehmendem Alter abnahm. Drei wichtige Merkmale – Langstreckenbewegungen, „Zugwilligkeit“von Altvögeln und Unterschiede in den Bewegungen zwischen Kolonien – stützen nicht die Theorie, dass sich die Bewegungen der

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Mittelmeermöwe nach der Brut erst vor kurzem als Folge des Populationsanstiegs entwickelt haben. Wir nehmen an, dass das rezente Bewegungsmuster die Evolutionsgeschichte der Mittelmeermöwen widerspiegelt und entweder ererbt sein könnte oder aus Erfahrung resultiert und durch Lernen von Generation zu Generation innerhalb einer Kolonie weitergegeben wird.

Keywords Yellow-legged Gull · *Larus michahellis* · Long-distance movements · Adriatic Sea

Introduction

Gulls are in general migratory or dispersive and vagrancy is very common. Large gulls (with the exception of the Lesser Black-backed Gull *Larus fuscus*) that breed in temperate regions usually migrate only a few hundred kilometres or disperse to nearby feeding grounds (del Hoyo et al. 1996). The Yellow-legged Gull (*Larus michahellis*) is considered to be an originally sedentary species, with post-breeding dispersal towards the southern North Sea and Baltic Sea developing only after the 1970s, following expansion to the north and west (Cramp and Simmons 1982; del Hoyo et al. 1996). According to Hagemeijer and Blair (1997), adults breeding in the Mediterranean basin are sedentary, while immatures move towards central Europe, but the patterns of their dispersal still need to be clarified.

After several changes of the taxonomic status of the Yellow-legged Gull (Collinson et al. 2008), studies of mitochondrial DNA variations among the Herring Gull (*Larus argentatus*) complex have shown that, contrary to Mayr (1942), the Yellow-legged Gull did not derive from ancestors of the Aralo-Caspian refugium, but descended from North Atlantic ancestral populations (Liebers et al. 2004). Taxon *michahellis* therefore belongs to the Atlantic/Mediterranean clade of gulls. North Atlantic pre-*argentatus* gulls gave rise to yellow-legged pre-*atlantis*, while *michahellis* resulted from colonisation of the Mediterranean by birds from the current range of *atlantis* (Liebers et al. 2004). The current bird migration system in Europe emerged after the end of the last ice age. Recent migration routes of many species follow their historic immigration routes, showing the spreading of the species after the glaciation (Berthold 2001). Among these species are gulls which belong to the Herring Gull complex, whose evolutionary history has probably been driven by the ebb and flow of glaciations (Collinson et al. 2008). The speciation in that species group is the result of the complex past demographic events (Sternkopf et al. 2010).

Early studies of Yellow-legged Gull movements were conducted by Isenmann (1973) and were based on metal-ring recoveries. Recently, several studies have described the movements of Atlantic and western Mediterranean populations (Martinez-Abrain et al. 2002; Rodríguez and Muntaner 2004; Arizaga et al. 2010; Baaloudj et al. 2012), but not much is known about movements of the eastern Mediterranean populations. The Yellow-legged Gull is a common and widespread breeding species along the eastern Adriatic coast. It breeds in colonies from a few dozen to almost 1,000 pairs on small uninhabited rocky islands (Benussi and Brichetti 1994), and recently also on roofs in towns of the northern Adriatic. Yellow-legged Gulls have been ringed in Croatia since 1931. Low numbers of metal-ring recoveries have been obtained, which indicated the difference in the ratio of recoveries and directions of movements of birds from the north and south Adriatic (Kralj and Radović 1999). A colour-ringing project was initiated in 1999 in collaboration with the Voorne Bird Observatory, the Netherlands, with the aim of elucidating the pattern of movement of the east Adriatic population. The use of plastic (darvic) rings for large gulls are known to improve the efficacy of ringing projects (Rock 1999). Colour-ringing programmes have an advantage over traditional ringing in that they result in a higher number of observations and multiple sightings of individual birds. The main disadvantage of this method is that all ringing data (including colour-ringing data) are greatly influenced by spatial and temporal patterns in observer effort, especially if sightings are collected over a wide area and for long periods (Korner-Nievergelt et al. 2010).

We analysed the sightings of colour-ringed birds collected between 1999 and 2011 in search of patterns of their post-breeding movements to find out: (1) the difference if any between young and adult birds with respect to the direction and distance of post-breeding movements; (2) what differences there were in dispersal patterns between birds from different colonies; (3) whether movements of Yellow-legged Gulls from the eastern Adriatic coast represent a true dispersal or a migration; and (4), in the light of the recent understanding of the Herring Gull's complex evolution, whether the existing pattern of post-breeding movements is recently developed as the result of the population increase or, as we suggest, is inherited or transferred by learning between generations.

Methods

Between 1999 and 2011, some 12,800 Yellow-legged Gull chicks were marked in Croatia with individually recognisable darvic rings. Ringing took place on 47 small islands along the eastern Adriatic coast, from Istria to the Dubrovnik area. The eastern Adriatic coast extends from northwest towards southeast, so studied colonies were situated between 45°13′N, 13°35′E and 42°34′N, 18°12′E

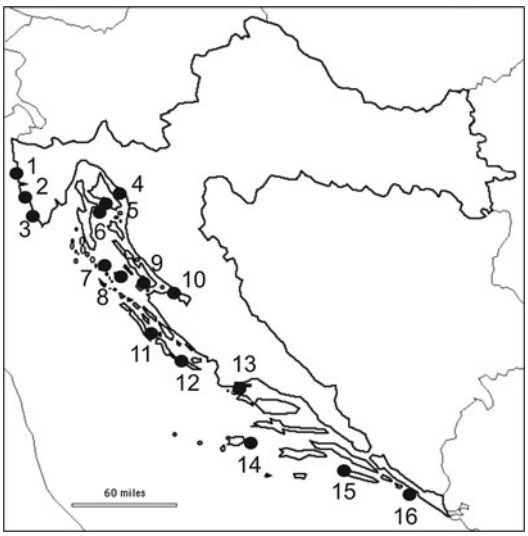

Fig. 1 Geographic position of Yellow-legged Gull *Larus michahellis* colonies along the eastern Adriatic coast. Colonies are numbered: *1* Poreč, *2* Rovinj, *3* Brijuni, *4* Zečevo, *5* Galun, *6* Plavnik, *7* Silba, *8* Olib, *9* Pag, *10* Ražanac, *11* Dugi otok, *12* Kornati, *13* Drvenik, *14* Vis, *15* Mljet, *16* Cavtat

(Fig. 1). After excluding recoveries of birds found dead, a total of 4,114 sightings of 1,559 birds were analysed. As all birds were ringed as pulli, the age of the bird for each sighting could be calculated. Birds observed during the first year of their life, i.e. until May of the next calendar year, were categorised as juveniles. Birds observed until May of their fifth year were labelled as immatures, while those older than 5 years were considered to be adults. To avoid pseudoreplication, repeated sightings of the same bird at the same site in 1 month were excluded from the analysis.

Stages of the Yellow-legged Gull's annual cycle were assessed as: the breeding period lasting from April to June, post-breeding period from July to November and wintering from December to March. For the analyses of colony-specific movements, we used only sightings of birds from nine colonies at which the most intensive ringing has been carried out. They were grouped according to their geographical position: Istria (islets around Poreč), Kvarner archipelago (Zečevo, Galun and Plavnik), mid-Adriatic (Ražanac, Dugi otok and Kornati archipelago) and southern Adriatic (islands around Mljet and Cavtat). For the purpose of the spatial analysis, the area in which colour-ringed Yellow-legged Gulls were observed was divided into: Adriatic region (coastal Croatia, Slovenia, Bosnia and Herzegovina, Montenegro and Italy), central Europe (localities between 45° and 50°N, excluding data from the Adriatic coast) and northern Europe (north of 50°N).

For each observation, we analysed the direction and the longitude (transformed to decimal value) of the finding place. Rayleigh statistic was used to test the null hypothesis that the directions of movements of gulls from each colony are randomly distributed (i.e. there is no preferred direction). The mean directions are presented as mean vectors (r) whose lengths vary between zero (uniform distribution of directions) and one (all points in the same direction). We calculated the mean values and standard error of vectors and longitudes for all sightings from the respective colony, and separately for sightings from central and northern Europe. Data for juvenile, immature and adult birds were analysed separately. The difference in directions between birds from different colonies was analysed with Watson–Williams F test, while for linear data (longitudes) ANOVA was used.

The observation effort and likelihood that the colour-rings would be reported varies across Europe. We could not quantify it, so the bias cannot be measured. To test the hypothesis about different dispersion of birds from distinct colonies, we therefore analysed the ratio of birds from different colonies observed at one locality (as suggested by Camphuysen et al. 2011). As the number of birds ringed per colony varied, a correction factor for each colony (average number of birds ringed per colony/number of birds ringed on the specific colony) was applied.

To determine if movements of eastern Adriatic gulls represent dispersion or migration, we used the methodology developed by Coulson and Brazendale (1968). All observations were grouped into 200-km distance zones from the natal colonies. The number of observations in each zone and further afield was calculated. Logarithms of those numbers were plotted against the distances. If linear relationships resulted, it would indicate dispersion, while a step-shaped curve would indicate migratory movements. The dispersal rate (r) representing the mean ratio (±SE) of birds moving between distance belts was calculated to compare the dispersion rate among colonies and age classes outside the breeding period. Oriana 3 software (Kovach Computing Services 2010) was used for analysing circular data, while Statistica v.7.0 (Stat.Soft 2004) was used for linear data.

Results

Sightings

Overall, 4,114 sightings of 1,559 individuals were analysed. The ratios of both number of observations and number of individuals observed significantly varied between colonies (Table 1; observations: $\chi^2 = 1{,}799.4$, $df = 15$, $P < 0.001$, observed birds: $\chi^2 = 384.3$, $df = 15$, $P < 0.001$). The highest rates were obtained for gulls from Istria (Poreč) and the lowest for two southern Adriatic colonies (Mljet and Cavtat).

Table 1 Number of ringed Yellow-legged Gulls *Larus michahellis* and sightings per colony

Colony	Number ringed	Number of sightings						Total sightings		Birds observed	
		Juvenile		Immature		Adult					
		No.	Ratio	No.	Ratio	No.	Ratio	No.	Ratio	No.	Percentage
Poreč	694	400	57.6	498	71.7	157	22.6	1,055	152.0	253	36.5
Rovinj	140	24	17.1	14	10.0			38	27.1	19	13.6
Brijuni	253	15	5.9	8	3.2			23	9.1	20	7.9
Zečevo	2,506	405	16.2	384	15.3	83	3.3	872	34.8	306	12.2
Galun	1,321	117	8.9	255	19.3	45	3.4	417	31.6	183	13.9
Plavnik	871	74	8.5	126	14.5	71	8.2	271	31.1	101	11.6
Silba	13			3	23.1	1	7.7	4	30.8	4	30.8
Olib	5					1	20.0	1	20.0	1	20.0
Pag	91	8	8.8	13	14.3			21	23.1	11	12.1
Ražanac	2,364	185	7.8	399	16.9	137	5.8	721	30.5	328	13.9
Dugi otok	1,084	109	10.1	163	15.0	91	8.4	363	33.5	141	13.0
Kornati	667	25	3.7	34	5.1	18	2.7	77	11.5	42	6.3
Drvenik	18	2	11.1	3	16.7	1	5.6	6	33.3	4	22.2
Vis	194	15	7.7	20	10.3	1	0.5	36	18.6	14	7.2
Mljet	1,144	54	4.8	53	4.6	8	0.7	115	10.1	60	5.2
Cavtat	1,435	57	4.0	34	2.4	3	0.2	94	6.6	72	5.0
Total	12,800	1,490	11.6	2,007	15.7	617	4.8	4,114	32.1	1,559	12.2

Ratio is the number of sightings weighted against the number of birds ringed

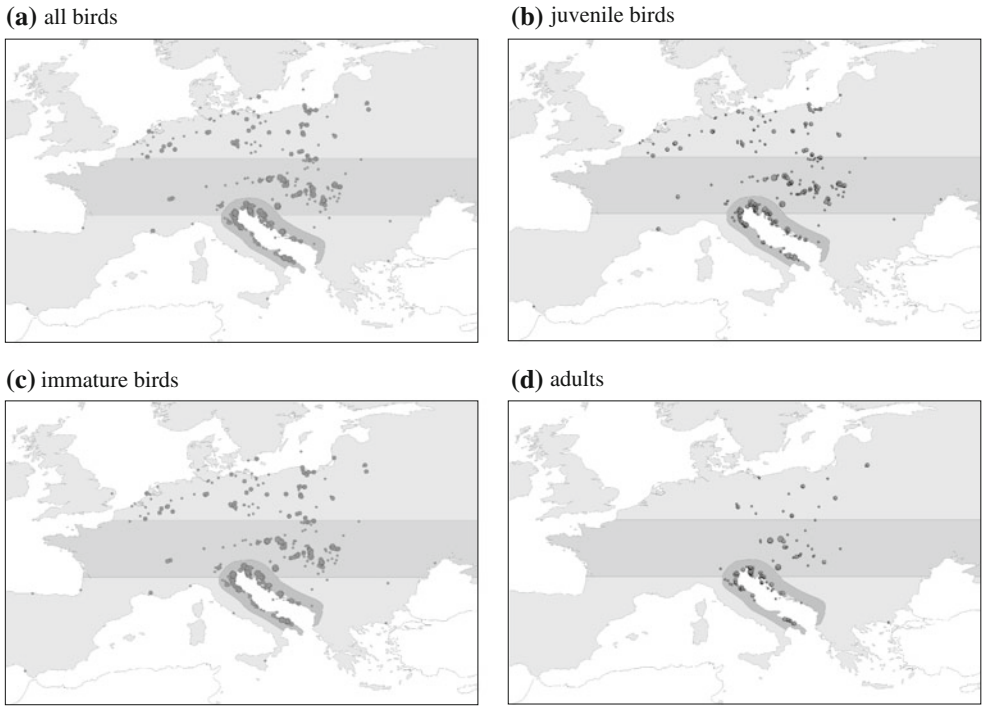

Fig. 2 Localities of observations of Yellow-legged Gulls colour-ringed as chick at eastern Adriatic colonies. Regions: northern Europe (north of 50°N), central Europe (45°–50°N) and the Adriatic region are given in different shades of *grey*

Gulls ringed at eastern Adriatic colonies were observed in 23 countries (Fig. 2a). The highest number of reported sightings originated from Italy (1,532), Croatia (1,058) and Austria (704). Between 200 and 300 sightings originated from Hungary, Germany and Poland each, while 1–59 observations were reported from a further 17 countries.

Age-specific movements

Young birds mostly leave their natal colonies in July. During the post-breeding period, almost half of the reported sightings came from the Adriatic region, while others were seen in central and northern Europe (Table 2). During winter, the majority of observations originated from the Adriatic region, but some birds stayed in central and northern Europe during their first winter and the following spring. Immature and adult birds also moved towards the north. The ratio of reported observations in northern Europe during the post-breeding period decreased with age, while the ratio of birds observed in central Europe increased. The majority of winter sightings of both immature and adult Yellow-legged Gulls originated from the Adriatic and inland Croatia, with distances of up to 200 km from the natal colonies. During the breeding season, sightings of immature and adult birds in northern Europe were sporadic. The frequencies of age-classes observed per region differed significantly for both the post-breeding period (total $\chi^2 = 42.39$, $df = 4$, $P < 0.001$) and the winter (total $\chi^2 = 96.83$, $df = 4$, $P < 0.001$). However, the number of sightings obtained for adult birds was much smaller when compared to the first-year and immature birds (Fig. 2b–d).

The average distances recorded were longest between July and November for all age groups and shortest for adults during the breeding season (March–June). During the post-breeding period (July–November), the differences between the mean monthly distances covered by age groups were either insignificant or their significance was the result of low values for immature birds (Table 3). The maximum distances were lowest for adults in almost all months, with the smallest difference outside the breeding season (Fig. 3). During the breeding season, both adult and immature gulls tended to stay closer to colonies than juveniles. For all three periods (breeding, post-breeding and wintering), the maximum reported distances showed a much steeper decline against age (breeding $y = -130.87x + 1{,}396.1$, $r^2_{12} = 0.82$; post-breeding $y = -118.41x + 1{,}861$, $r^2_{13} = 0.72$; wintering $y = -120.45x + 1{,}351$, $r^2_{12} = 0.76$) than log-transformed mean distances (breeding $y = -10.38x + 162.36$, $r^2_{12} = 0.20$; post-breeding $y = -8.86x + 274.18$, $r^2_{13} = 0.13$; wintering $y = -8.41x + 184.26$, $r^2_{12} = 0.53$). In general, the direction of movements did not change with increasing age; significant differences were obtained only for gulls from Dugi otok (Table 4).

Colony-specific movements

Yellow-legged Gulls from different colonies showed differences in both direction of movements and longitude of the observation sites. Rayleigh's Uniformity Test confirmed that movements from all colonies showed evidence of a preferred direction and were not uniformly distributed

Table 2 Percentage of sightings of Yellow-legged Gulls of different age classes per regions

Period	Number of sightings	Adriatic region	Central Europe	Northern Europe	Other
Juvenile/post-breeding	469	47.1	30.7	22.0	0.2
Juvenile/winter	453	62.7	31.1	6.0	0.2
Immature/breeding period	262	37.4	54.6	8.0	
Immature/post-breeding	687	49.6	35.7	14.6	0.1
Immature/winter	575	38.8	60.2	1.0	
Adult/breeding period	56	59.0	35.7	3.6	1.7
Adult/post-breeding	277	36.5	51.6	11.9	
Adult/winter	110	56.4	41.8	1.8	

For description of age classes, periods of annual cycle and regions, see "Methods"

Table 3 Mean and maximum distances (in km) from the natal colony during post-breeding period (July–November) for different age classes

	Juvenile		Immature		Adult		ANOVA
	Mean	Maximum	Mean	Maximum	Mean	Maximum	
July	486	1,156	**324**	1,344	348	1,114	6.04*
August	413	1,202	380	1,344	392	1,073	0.30
September	408	1,295	**307**	1,289	392	1,380	3.45*
October	386	1,470	386	1,674	386	1,380	0.0002
November	351	1,958	**254**	1,224	338	958	4.95*

ANOVA was used to test the differences between mean distances, * $P < 0.05$. Values that differed significantly are highlighted in bold (Tukey HSD for unequal sample size, $P < 0.05$)

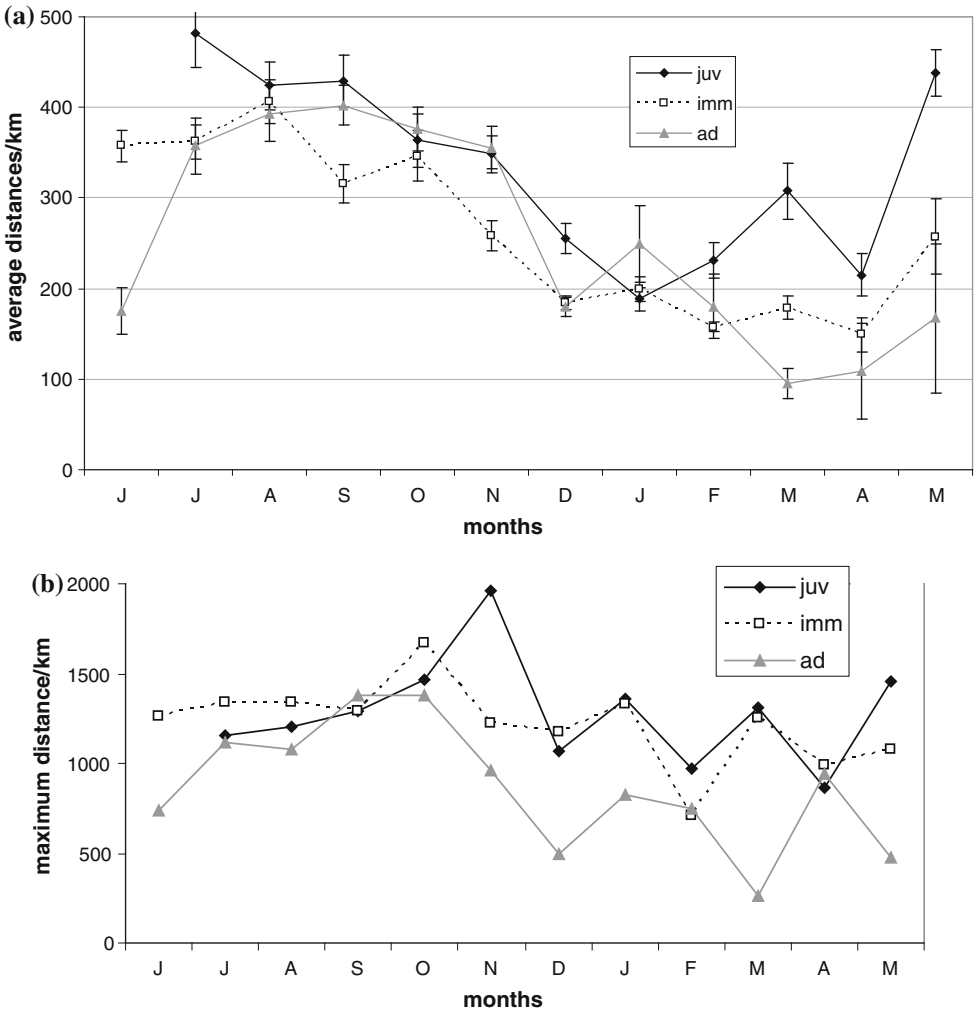

Fig. 3 Monthly average distance (km ± SE) (**a**) and maximum distance (**b**) from natal colonies recorded for Yellow-legged Gulls. Months of the year beginning with June

Table 4 Direction of movements of the Yellow-legged Gulls of different age classes from different colonies during post-breeding dispersal

	Mean direction						
	Juvenile	$r \pm$ SE	Immature	$r \pm$ SE	Adult	$r \pm$ SE	F
Poreč	279.1	0.60 ± 0.20	275.7	0.65 ± 0.18	275.2	0.25 ± 0.25	0.173
Zečevo	3.7	0.40 ± 0.12	9.1	0.39 ± 0.12	16.1	0.44 ± 0.22	1.503
Galun	360.0	0.62 ± 0.16	12.9	0.43 ± 0.17	21.6	0.32 ± 0.19	1.777
Ražanac	339.1	0.41 ± 0.12	351.0	0.54 ± 0.17	353.2	0.43 ± 0.14	1.097
Dugi otok	330.0	0.47 ± 0.12	5.8	0.47 ± 0.12	2.7	0.54 ± 0.15	8.203*

Watson–Williams F test (* $P = 0.01$). For dispersal rate (r) see "Methods". Only colonies with more than 100 observations during post-breeding dispersal were analysed

(Table 5). Gulls mostly moved towards the north, to the Baltic and North Sea coasts. Those from Istria and southern Adriatic also showed pronounced movements towards the west and were observed on the Italian Adriatic coast. For observation sites in northern Europe, the main direction was towards the north, with only birds from Poreč heading towards the NNW. Watson–Wiliams F test revealed a significant difference among the directions of movements of birds reported in northern Europe ($F = 11.97$, $df = 8$, $P < 0.001$) with the greatest difference in directions of gulls ringed in Poreč compared to other colonies. The longitudes of observation sites in northern Europe also differed between colonies (ANOVA $F = 7.00$, $df = 8$, $P < 0.001$). Tukey HSD for unequal

sample sizes indicated that significant differences exist among Poreč and other colonies ($P < 0.05$) due to the more western position of observation sites for gulls ringed at the Poreč colony. The analysis of variance for colonies grouped according to their geographical position (ANOVA $F = 14.17$, $df = 3$, $P < 0.05$) revealed that both Istrian and Kvarner birds differ from other breeding colonies (Tukey HSD for unequal sample sizes, $P < 0.05$). The longitude for observation sites in central Europe differed among three groups of colonies: birds from Poreč were observed between 14° and 15°E, those from southern Adriatic east of 18°E, and others (Kvarner and mid-Adriatic) between 16° and 17°E (all colonies: ANOVA $F = 19.81$, $df = 8$, $P < 0.001$, group of colonies ANOVA $F = 49.64$, $df = 3$, $P < 0.001$).

Table 5 Mean direction of movements of the Yellow-legged Gulls from different colonies

Colony	All sightings			Sightings north of 50°N		Dispersal rate ($r \pm$ SE)
	Z	Mean vector	Mean angle (°)	Mean vector	Mean angle (°)	
Poreč	577.4**	0.73	278	0.94	336	0.53 ± 0.17
Zečevo	414.8**	0.68	4	0.90	353	0.39 ± 0.10
Galun	206.1**	0.69	23	0.90	350	0.46 ± 0.12
Plavnik	126.1**	0.68	20	0.97	353	0.35 ± 0.09
Ražanac	322.8**	0.65	5	0.97	8	0.39 ± 0.10
Dugi otok	196.2**	0.71	1	0.96	0	0.39 ± 0.08
Kornati	28.0**	0.58	355	0.98	350	0.39 ± 0.10
Mljet	3.6*	0.12	234	0.99	3	0.57 ± 0.13
Cavtat	22.4**	0.45	275	0.96	335	0.56 ± 0.14

Rayleigh test (* $P < 0.05$; ** $P < 0.01$). For dispersal rate (r) see "Methods"

Connectivity between natal colonies and observation sites

From the perspective of sites at which a higher number of observations was reported, it is apparent that some areas were preferred by birds from certain Adriatic colonies (Table 6). Birds from Poreč were either presented in low numbers or completely absent from important feeding sites in central Europe (Austria, inland Croatia and Hungary). They were commonly observed in northern Italy (Venice lagoons and Gulf of Trieste), while gulls observed in southern Italy (Bari) originated from Mljet and Cavtat. The dispersal of birds from Zečevo differed from other two Kvarner colonies (Galun and Plavnik): they were over-represented in Austria and underrepresented in Zagreb ($\chi^2 = 139.0$, $df = 1$, $P < 0.001$), and ten times more frequent in Trieste comparing to Venice ($\chi^2 = 124.75$, $df = 1$, $P < 0.001$). Gulls from the other two Kvarner colonies did not show such pronounced difference in the observation rate at the two Italian sites (Galun: $\chi^2 = 0.23$, $df = 1$, $P = 0.63$; Plavnik: $\chi^2 = 0.06$, $df = 1$, $P = 0.80$) or between Croatia and Austria (Galun: $\chi^2 = 2.79$, $df = 1$, $P = 0.09$; Plavnik: $\chi^2 = 5.29$, $df = 1$, $P < 0.05$).

Dispersal rates

Dispersal rates during the post-breeding period showed somewhat lower values for adult birds (juveniles 0.43 ± 0.09, immatures 0.43 ± 0.09, adults 0.37 ± 0.07), but analysis of particular colonies showed different trends (Table 4). In general, the highest values were obtained for birds from Poreč and the southern Adriatic (Table 5). When data from all colonies and age categories were pooled, the curve of distribution of birds in successive distance zones during the post-breeding period (following Coulson and Brazendale 1968) showed real dispersal movements of Yellow-legged Gulls. Only juvenile and

Table 6 The origin (percentage of observations) of Yellow-legged Gulls reported at sites with higher number of recorded observations

	Melk, Austria	Zagreb, Croatia	Venice, Italy	Trieste, Italy	Bari, Italy	Budapest, Hungary	Csongrad, Hungary	Leipzig, Germany	Gdansk, Poland
Poreč	0.8	4.1	89.4	69.3	0	0	0	7.3	27.4
Zečevo	38.8	5.0	0.2	16.8	6.5	19.7	13.7	12.1	19.0
Galun	15.8	18.4	1.6	3.6	3.4	7.5	2.6	15.4	16.8
Plavnik	16.2	23.1	2.8	2.7	1.0	26.4	0	20.4	3.6
Ražanac	9.3	24.9	1.8	5.5	7.2	15.3	18.9	8.6	5.4
Dugi otok	18.2	16.0	2.5	2.2	8.3	21.2	9.5	21.1	14.6
Kornati	0.8	7.5	1.8	0	12.1	9.9	15.5	15.2	4.8
Mljet	0	0.4	0	0	34.6	0	30.1	0	8.3
Cavtat	0	0.8	0	0	26.9	0	9.6	0	0
Number	310	658	499	96	149	45	44	50	42

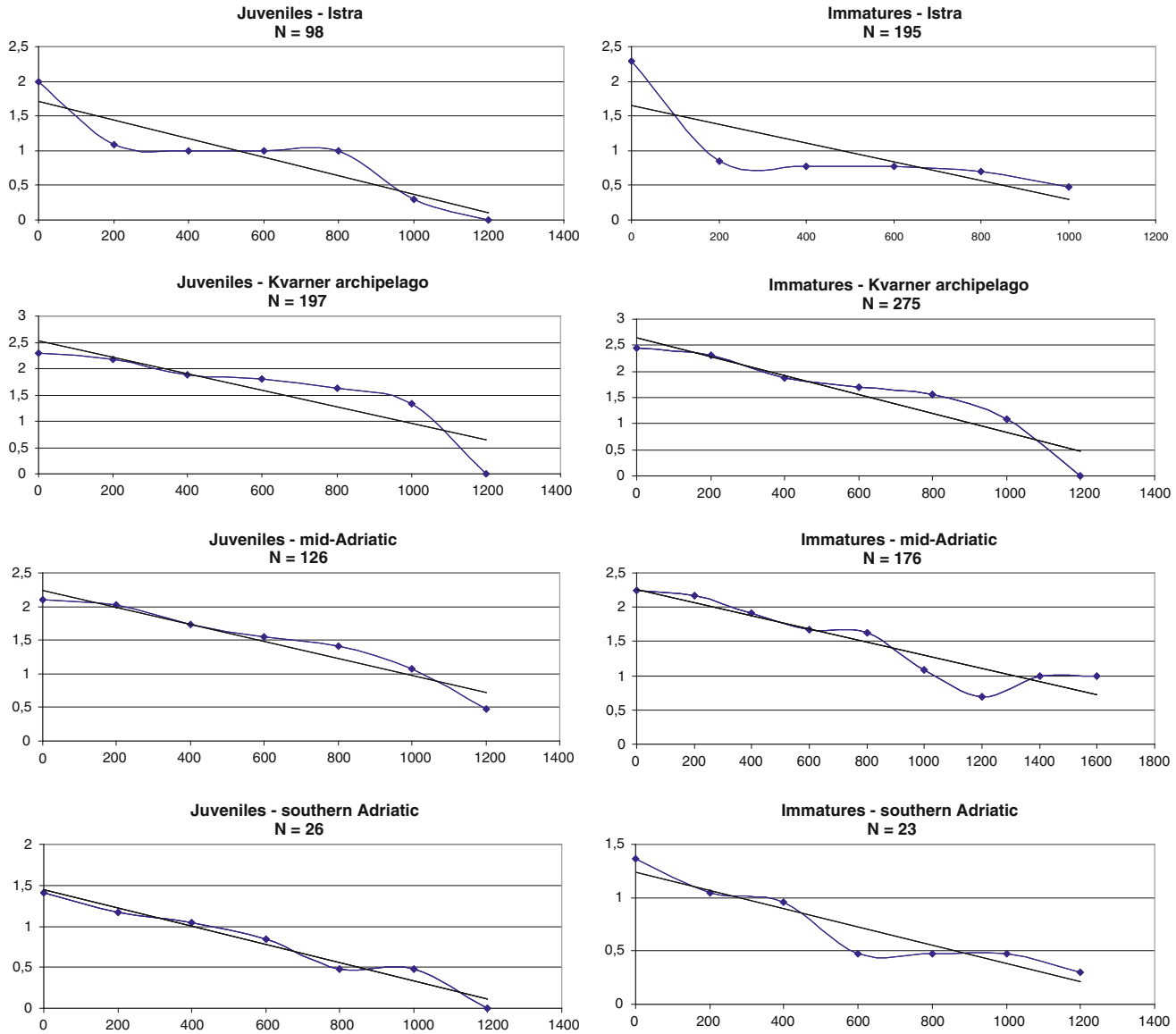

Fig. 4 Post-breeding movements (July–November) through succeeding distance zones of juvenile and immature Yellow-legged Gulls from different regions of the eastern Adriatic (according to the methodology developed by Coulson and Brazendale 1968). *X* axes: 200 km distance zone; *y* axes: log of number of birds remaining in or moving beyond the each successive zone

immature birds from Istrian and southern Adriatic colonies showed a step-shape curve characteristic for the migratory movements (Fig. 4).

Discussion

Sightings of colour-ringed Yellow-legged Gulls from the eastern Adriatic coast showed that during the post-breeding period they disperse to much greater distances than west Mediterranean and Iberian breeding populations of that species (Martinez-Abrain et al. 2002; Rodríguez and Muntaner 2004; Arizaga et al. 2010) or other European large gulls with the exception of the migratory Lesser Black-backed Gull (Kilpi and Saurola 1983; Camphuysen et al. 2011). Birds from different colonies showed significantly different directions of movements and visited different subregions of central and northern Europe. Directions of their post-breeding movements did not change with age, while distances covered decreased. The eastern Adriatic coast extends from the northwest towards the southeast, so southern colonies are situated further east than the northern ones. As a consequence, the same direction will lead birds from different colonies to different longitudes, while different directions would be needed for birds with different origins to reach the same location. But both the directions of movements and the longitudinal positions of the observation sites differed significantly

among colonies, so we can conclude that gulls from different colonies have different dispersal patterns.

Movements of Yellow-legged Gulls from the west Mediterranean and Iberian colonies are also directed towards the north. Young Iberian Yellow-legged Gulls spend both summer and winter on the French Atlantic coast (Martinez-Abrain et al. 2002; Arizaga et al. 2010), while Algerian gulls return to the breeding areas during the autumn (Baaloudj et al. 2012). Algerian juvenile Yellow-legged Gulls cover distances of up to 1,300 km and showed a difference in dispersal routes among birds from different colonies (Baaloudj et al. 2012). Contrary to Croatian Yellow-legged Gulls, adults from the Iberian peninsula are mostly sedentary or undertake only short-term dispersal movements, which has been attributed to their previous experience in locating available food sources (Martinez-Abrain et al. 2002).

In spite of the large number of colour-ringed gulls in the eastern Adriatic, the relatively low rate of sightings obtained compared to similar studies (Martinez-Abrain et al. 2002; Arizaga et al. 2010) was the result of low observation effort in the area surrounding colonies. The majority of observations therefore originated from inland Croatia or other countries. The ratio of sightings is exceptionally high for the Poreč colony, which is situated around 100 km from the northern Italian lagoons, from where large numbers of observations were reported. On the other hand, sightings from central Europe for those birds were among the lowest. The observation rate for the two southern Adriatic colonies is extremely low, which might be attributed to either lower dispersal of those birds or different directions of their dispersal. However, Coulson and Brazendal's dispersal rate (r) did not show lower values and several sightings suggested movements also towards the east, which had already been indicated by recoveries of metal-ringed birds (Kralj and Radović 1999). Observation effort in Eastern Europe is much lower than in Central Europe, which might be the underlying reason for the lower observation rate. One of the predispositions for the method developed by Coulson and Brazendale (1968) is equal probability of observations. The probability of observation varies across the continent, depending on the number of birdwatchers, and especially gull-watchers who regularly observe at locations where gulls gather (such as rubbish-heaps and harbours). However, we believe that the relatively wide belts used in the analysis (200 km) helped to overcome local differences in observation effort in Central and Northern Europe. The curves showing the movements of gulls between successive zones had a more or less linear shape for the majority of age- and colony-groups, while juvenile and immature gulls from Istria (Poreč) and immatures from the southern Adriatic showed a more step-shaped curve, indicating migratory movements without predicable numbers of birds moving between zones (Galbraith et al. 1986). However, gulls from both colonies were regularly observed along the western Adriatic coast, and the concentration of observations at those distances led to a step-shaped curve. Repeated sightings of the same birds (max. 76) showed that some birds (mostly from Poreč) never leave the Adriatic. Due to the relatively low observation effort along the eastern Adriatic coast, it was not possible to calculate the ratio of predominantly resident birds from each colony. Croatian Yellow-legged Gulls never completely abandon the breeding areas, confirming that they are dispersive rather than migratory. The clear preference in direction of Croatian Yellow-legged Gulls distinguishes their movements from true dispersal. This type of movement is similar to "directed intermittent" migration (Berthold 2001), but unlike herons and Starlings (*Sturnus vulgaris*) (Fliege 1984), such movements of Yellow-legged Gulls also include adult birds. Although the dispersal rate (r) during the post-breeding period showed a difference among age classes, no general rule was identified: it decreased with age for birds from Poreč and Galun and increased for Zečevo and Dugi otok.

It is generally accepted that long-distance movements of young Yellow-legged Gulls evolved in the 1970s (Cramp and Simmons 1982; del Hoyo et al. 1996). However, migratoriness may change with time, and during the last century we witnessed the change in the migratory behaviour of several bird populations. Some populations have become increasingly sedentary, while a few have developed migratory behaviour (Berthold 2001). The increase in migratoriness appeared in species that were expanding their ranges, either naturally (European Serin *Serinus serinus*; Berthold 2001) or by human intervention (House Finch *Carpodacus mexicanus*; Able and Belthoff 1998). With a population increase, the competition for resources becomes stronger and dominance interactions among adult and immature birds may elicit the movement of young birds to other feeding areas (Pulido 2007). However, it is likely that in such cases that spatial segregation between the age groups and dispersion in all directions occur, as recorded for the Herring Gull in The Netherlands and Finland (Spaans 1971; Kilpi and Saurola 1983). Such dispersive movements cover much smaller distances: only 4.5 % of first-year Herring Gulls from southern Finland moved more than 500 km between August and October (Kilpi and Saurola 1983). In contrast, of 546 sightings (July–November) of first-year Yellow-legged Gulls from Croatia, 154 (28.2 %) were longer than 500 km in spite of the fact that appropriate feeding sites exist at much shorter distances and that they are visited by these gulls on their way north. Also, in cases in which the movement is driven only by intraspecific competition, adult birds should in general be sedentary.

The prevailing opinion that Yellow-legged Gulls were originally sedentary and that their post-breeding dispersal was developed as a result of their expansion to the north and west in the 1970s (Cramp and Simmons 1982) is in line with the rapid evolution of novel migration patterns (Berthold 2001; Alerstam et al. 2003). However, it cannot explain the difference in dispersal of birds from different colonies, the migratoriness of adult birds or the long-distance movements regardless of available food resources at closer distances. Therefore, we presume that the patterns of their movements are not recently developed. They might be either inherited or result from cultural transmission (Sutherland 1998) and be transferred by learning between generations among birds from the same colony (Alerstam et al. 2003). Although non-genetic variance components may be important, within-population variation in migratory behaviour largely reflects genetic variation (Pulido 2007). High genetic variability between birds from breeding colonies in the same geographical region has already been found in the Herring gull complex (Sternkopf et al. 2010).

The marked increase in numbers of Yellow-legged Gulls along the southern North Sea and Baltic coasts in the 1970s is not necessarily the result of the recent development of the new dispersal patterns. It could be the result of a combination of several factors: (1) an increasing number of breeding birds, (2) the growth in public interest, especially observer activity and skilfulness (Garner 1997; Neubauer et al. 2009), including the development of "yellow-legged" gull taxonomy and identification, and (3) greater connectivity of gulls with human settlements (harbours, refuse dumps, etc.). Large gulls with yellow legs were certainly already known on North European coasts in the early nineteenth century, no matter that they were thought to be *L. cachinnans* from the Caspian Sea or *L. omissus* from the eastern Baltic (Voipio 1993). In the twentieth century, increases in numbers and range expansion occurred across Europe (Mierauskas and Greimas 1992; Voipio 1993; Hagemeijer and Blair 1997), accompanied by a shift in feeding (Kilpi and Saurola 1983) and, to a certain extent, breeding habitat. This behavioural change is attributable to the increased availability of food at refuse dumps (Hagemeijer and Blair 1997). The first recoveries of Yellow-legged Gulls ringed along the Adriatic Sea in the 1960s showed movements towards the Carpathian basin and the Dutch coasts. Birds ringed along the Mediterranean coast of France and Spain were recovered along the French Atlantic coast, while those from Tunisia moved towards north Mediterranean coasts. Certainly, northward movements were present in the 1960s in all Yellow-legged Gull populations from the Mediterranean (Isenmann 1973).

The long-distance movements of both juvenile and adult birds include the Adriatic breeders as among the most dispersive Yellow-legged Gull populations. The differences in directions of movements for birds from different colonies may indicate that post-breeding movements of Adriatic Yellow-legged Gulls result from its evolutionary history. The continuation of the study should include a greater observation effort in the Adriatic that will enable the assessment of the percentage of the population that is resident, as well as the use of tracking devices for the detailed study of gull movements. The genetic analysis of birds from different colonies is needed to elucidate eventual genetic variation and differentiation among Adriatic and Mediterranean Yellow-legged Gull populations and to identify eventual heritability bases in their dispersal behaviour.

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References

Able KP, Belthoff JR (1998) Rapid "evolution" of migratory behaviour in the introduced house finch of eastern North America. Proc R Soc Lond B 265:2063–2071

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103:247–260

Arizaga J, Herrero A, Galarza A, Hidalgo J, Aldalur A, Cuadrado JF, Ocio G (2010) First-Year Movements of Yellow-Legged Gull (*Larus michahellis lusitanius*) from the Southeastern Bay of Biscay. Waterbirds 33(4):444–450

Baaloudj A, Samraoui F, Laouar A, Benoughidene M, Hasni D, Bouchahdane I, Khaled H, Bensouilah S, Alfarhan AH, Samraoui B (2012) Dispersal of Yellow-legged Gulls *Larus michahellis* ringed in Algeria: a preliminary analysis. Ardeola 59(1):137–144

Benussi E, Brichetti P (1994) Distribution and population-size of colonies of Yellow-legged Gull *Larus cachinnas michahellis* breeding in North-Eastern Adriatic sea. Avocetta 18:107–113

Berthold P (2001) Bird migration. A general survey. Oxford University Press, Oxford

Camphuysen CJ, Vercruijsse HJP, Spaans AL (2011) Colony- and age-specific seasonal dispersal of Herring Gulls *Larus argentatus* breeding in The Netherlands. J Ornithol 152:849–868

Collinson JM, Parkin DT, Knox AG, Sangster G, Svensson L (2008) Species boundaries in the Herring and Lesser Black-backed Gull complex. Br Birds 101:340–363

Coulson JC, Brazendale MG (1968) Movements of Cormorants ringed in the British Isles and evidence of colony-specific dispersal. Br Birds 61:1–21

Cramp S, Simmons KEL (1982) The Birds of Western Palearctic, vol 3. Oxford University Press, Oxford

del Hoyo J, Elliott A, Sargatal J (1996) Handbook of the birds of the world, vol 3. Lynx, Barcelona

Fliege G (1984) Das Zugverhalten des Stars (*Sturnus vulgaris*) in Europa: eine Analyse der Ringfunde. J Ornithol 125(4):393–446

Galbraith H, Baillie R, Furness RW, Russell S (1986) Regional variations in the dispersal of Shags *Phalacrocorax aristotelis* in northern Europe. Ornis Scand 17:68–74

Garner M (1997) Identification of yellow-legged gulls in Britain. Br Birds 90:25–62

Hagemeijer WJM, Blair MJ (1997) The EBCC atlas of European breeding birds: their distribution and abundance. Poyser, London

Isenmann P (1973) Donnees sur les deplacements erratiques de Goelands argenets a pieds jaunes (*Larus argentatus michahellis*) nes en Mediterranee, L'Oiseaux R.F.O. 43:187–195

Kilpi M, Saurola P (1983) Pre-migration movements of coastal Finnish herring gulls (*Larus argentatus*) in autumn. Ann Zool Fenn 20:245–254

Korner-Nievergelt F, Sauter A, Atkinson PW, Guélat J, Kania W, Kéry M, Köppen U, Robinson RA, Schaub M, Thorup K, van der Jeugd H, van Noordwijk AJ (2010) Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. J Avian Biol 41:8–17

Kovach Computing Services (2010) Oriana version 3.21. Pentraeth

Kralj J, Radović D (1999) Differences in dispersive movements between Yellow-legged Gulls *Larus cachinnans michahellis* from northern and middle/southern Croatian Adriatic coast. In: EURING: bird ringing 100 years. Results and perspectives of bird ringing. Conference programme and abstracts. Wilhelmshaven & Helgoland, p 54

Liebers D, de Knijff P, Helbig AJ (2004) The herring gull complex is not a ring species. Proc R Soc Lond B 271:893–901

Martinez-Abrain A, Oro D, Carda J, del Señor X (2002) Movements of Yellow-legged Gulls *Larus* [*cachinnans*] *michahellis* from two small western Mediterranean colonies. Atl Seabirds 4(3):101–108

Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York

Mierauskas P, Greimas E (1992) Taxonomic status of yellow-legged Herring Gulls in eastern Baltic. Dutch Birding 14:91–94

Neubauer G, Faber M, Betleja J, Gębski P, Iciek T, Kajzer Z, Ławicki L, Meissner W, Orłowski G, Sidelnik M, Wiehle D, Winiecki J (2009) Wintering of the Lesser Black-backed Gull *Larus fuscus* in Poland 1996-2009. Not Ornitol 50:194–205

Pulido F (2007) The genetics and evolution of avian migration. Bioscience 57(2):165–174

Rock P (1999) The efficacy of the colour-ringing system used for Herring Gulls *Larus argentatus* and Lesser-backed Gulls *Larus fuscus* in Bristol 1980–1997. Ring Migr 19:306–310

Rodríguez A, Muntaner J (2004) First results from marking the Yellow-legged Gull *Larus michahellis* with rings readable at distance in the Balearic Islands. Annu Ornitol Balears 19:69–77

Spaans AL (1971) On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of the Netherlands. Ardea 59:73–188

StatSoft (2004) STATISTICA version 7 for Windows. StatSoft, Tulsa

Sternkopf V, Liebers-Helbig D, Ritz MS, Zhang J, Helbig AJ, de Knijff P (2010) Introgressive hybridization and the evolutionary history of the herring gull complex revealed by mitochondrial and nuclear DNA. Evol Biol 10:348

Sutherland WJ (1998) Evidence for flexibility and constraint in migration systems. J Avian Biol 29:441–446

Voipio P (1993) Differences in ecological properties in the herring gull (*Larus argentatus*) as a basis for explaining and predicting colonisation events—a case history in retrospect. Ann Zool Fenn 30:3–15