

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/235915089>

# Reproductive Performance and Changes in Relative Species Abundance in a Mixed Colony of Herring and Caspian Gulls, *Larus argentatus* and *Larus cachinnans*

Article in *Acta Ornithologica* · December 2012

DOI: 10.3161/000164512X662296

CITATIONS

8

READS

232

2 authors:



Magdalena Zagalska-Neubauer

University of Wrocław

28 PUBLICATIONS 596 CITATIONS

[SEE PROFILE](#)



Grzegorz Neubauer

University of Wrocław

110 PUBLICATIONS 544 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Monitoring Ptaków Polski [View project](#)



Long-term studies of nest box breeding birds on Gotland [View project](#)

## Reproductive performance and changes in relative species abundance in a mixed colony of Herring and Caspian Gulls, *Larus argentatus* and *Larus cachinnans*

Magdalena ZAGALSKA-NEUBAUER & Grzegorz NEUBAUER

Museum and Institute of Zoology, Ornithological Station, Polish Academy of Sciences, Nadwiślańska 108, 80–680 Gdańsk, POLAND, e-mail: magzag@miiz.waw.pl

Zagalska-Neubauer M., Neubauer G. 2012. Reproductive performance and changes in relative species abundance in a mixed colony of Herring and Caspian Gulls, *Larus argentatus* and *Larus cachinnans*. *Acta Ornithol.* 47: 185–194. DOI 3161/000164512X662296

**Abstract.** Following range expansion and colonization, hybridization between Herring and Caspian Gulls, *Larus argentatus* and *L. cachinnans*, takes place in central and eastern Europe. To examine how hybrid zone is affected by the abundance dynamics of these species and their reproductive performance, we studied a mixed colony at Włocławek Reservoir, central Poland, for over 7 years, from 2002 to 2009, and included data from the species monitoring from 1990 to 2001. To evaluate the species abundance dynamics and possible mechanisms of reproductive isolation, breeders ( $n = 226$  individual birds) were trapped on nests and colour-ringed; breeding performance was studied in detail for 202 breeding pairs with both mates known. Between 2002 and 2009 the proportion of Caspian Gulls among breeders had strongly increased (from 14% to 42%), whereas the proportion of Herring Gulls had declined (from 70% to 35%). The frequency of hybrids varied a little with no clear trend (mean 20%, range 15–28%). The colony size during that time was approximately stable, with 125–135 breeding pairs. 32 individuals originating from outside the zone, ringed as nestlings in the core range of either species, were recorded as breeders at the study site, documenting dispersal of parental species into the zone. The immigration of the two parental species showed contrasting temporal patterns in the two compared decades, 1990–1999 vs. 2000–2009. The immigration of Herring Gulls as measured by the reencounter probability declined nearly three times, while approximately twofold increase was seen in Caspian Gulls. Birds tended to choose phenotypically similar mates, so that there were fewer heterospecific pairs than expected under random mating. Numbers of homospecific, heterospecific and mixed pairs were similar during 7 years. On average, males of Caspian Gulls were significantly heavier than males of Herring Gulls. Caspian Gull pairs bred on average 7 days earlier than pairs of Herring Gulls. No differences in clutch size, clutch volume or hatching success among pairs of different composition were found, indicating weak postzygotic isolation. Current abundance of species in the hybrid zone is changing dynamically and is primarily driven by the strength of immigration from outside the zone.

**Key words:** gulls, hybridization, hybrid zone, immigration, reproductive performance, native invader

Received — Sept. 2012, accepted — Dec. 2012

### INTRODUCTION

Hybrid zones exist between the populations of two related species, whose geographical ranges overlap, and contain hybrids resulting from mating between two different species. In birds, hybridization is relatively widespread in nature (Grant & Grant 1992, Arnold 1997, Jiggins & Mallet 2000, Barton 2001, Avise 2004, Price 2008). Hybrid zones are maintained by a balance between dispersal and selection against hybrids, as states the “tension zones” model, and can move from one place to another since their maintenance is not a response to local environment (Barton &

Hewitt 1985). The other model, the “bounded-hybrid superiority”, is dispersal-independent, and refers to a situation where gradual habitat change occurs with respective changes in fitness of individuals (Moore 1977, Good et al. 2000). Here, hybrid individuals in the centre of the zone are better adapted to the local environment than parental forms. Studies on hybrid zones provide insights into the mechanisms of reproductive isolation between two species. However, most studies on hybrids zones rely on ‘snap-shot’ sampling — static pictures taken of processes that are in fact continuous, take place every season and are potentially rapid. For instance, many of hybrid

zone examples enlisted by Price (2008) have not been studied for multiple years and that precludes any inference on zone movement, to say the least. Few studies have lasted long enough to properly examine the persistence of hybrid zones and the processes key to hybridization as dispersal of the parental species or movement of the hybrid zone (Price 2008). The other frequently faced problem is that sampling of individuals in local populations is insufficient to study temporal (or annual) changes in abundance. In the case of species whose range is quickly expanding and whose numbers increase, strength of dispersal can represent the basic factor responsible for changes in abundance of hybridizing species and thus can affect the frequency of hybridization and in effect, the persistence of the zone.

Gulls Laridae hybridize relatively frequently, and over a half of species from this group is known to hybridize (Pierotti 1987, Panov 1989, Pierotti & Annett 1993, McCarthy 2006, Price 2008). Existing hybrid zones of gulls have frequently been formed due to range expansions and colonizations of new areas (Bell 1996, 1997, Good et al. 2000, Gay et al. 2007, Vigfúsdóttir et al. 2008, Pálsson et al. 2009). Our model species are Herring *Larus argentatus* and Caspian *L. cachinnans* Gulls, which both have invaded central-European lowlands expanding from opposite directions, the former from the north and the latter from the south-east (Neubauer et al. 2006). Both taxa are colonial, long-living and socially monogamous (Devillers 1983, Snow & Perrins 1998). They are closely related phylogenetically, similar in appearance and breeding ecology (Malling Olsen & Larsson 2004, Pons et al. 2005). They usually breed at watersides, in open habitats with low vegetation. Herring Gull originally inhabited coasts of northern and western Europe and Scandinavia, and represents the so-called native invader (Devillers 1983, Carey et al. 2012). During the 20th century, Herring Gull had started to expand breeding range southwards and to colonize inland waterbodies in central Europe (Neubauer et al. 2006). Caspian Gull originates from south-eastern Europe (Malling Olsen & Larsson 2004), and also has been expanding its range, but west- and northwards in recent decades, and is regarded as a non-native species in central Europe (Skórka et al. 2005, Neubauer et al. 2006, Lenda et al. 2010, Carey et al. 2012). These two species have expanded their ranges in opposite directions, which resulted in forming a secondary contact zone in lowlands of central and eastern Europe,

including Germany, Poland, Belarus and Russia. Herring Gulls and Caspian Gulls breed in mixed colonies where heterospecific pairs and hybrids raising young are regularly observed (Neubauer et al. 2006, 2009, Yakovets 2006, Gay et al. 2007, own data).

The hybrid zone of Herring and Caspian Gulls is unique as both species breed under novel conditions. So far, few studies have addressed hybridization and reproductive isolation in this zone of contact (Gay et al. 2007, Neubauer et al. 2009), but information on the dynamics of species abundance is virtually lacking. With its explosive range expansion and rapid colonization of central European inland (Lenda et al. 2010), the Caspian Gull may heavily affect the number of Herring Gulls in the zone, despite the fact that the two species do hybridize. In this paper we investigate changes in the abundance of Herring and Caspian Gulls in a single mixed colony, located in the centre of a narrow hybrid zone. We also report aspects of reproductive biology to characterize fitness components of parental species and hybrids. We paid special attention to immigration as a measure of invasion, and potential component of species or hybrid success. To evaluate the possible reproductive isolation mechanisms we use body masses and breeding performance of parental species and their hybrids.

## METHODS

### Study area

The studied colony is located at the dam of Włocławek Reservoir, at the Vistula River, central Poland (52°39'12"N, 19°08'18"E). It was established in the late 1980's and has remained one of the biggest inland colonies of large gulls in Poland (Neubauer et al. 2006). During the time of the study, 2002–2009, the colony was stable in numbers and included 125–135 breeding pairs. Data on numbers in 1990–2001 were taken from the avifaunistic database of the Ornithological Station (Museum and Institute of Zoology PAS). In the colony most pairs bred on artificial dike (10 × 410 m), approximately 3 m above the water surface. Just single pairs bred on other constructions around the main colony and these were unavailable for the study. The area is protected by law, so there is almost no human disturbance, and boats or yachts are only rarely moored. No presence of terrestrial predators was noted until 2008 and 2009, when both the Red Fox *Vulpes vulpes* and

American Mink *Neovison vison* reduced breeding success (own data).

### Phenotypic assignment of birds and pair composition

Adult gulls were nest-trapped each year between mid April and late May. In total, 226 gulls, 121 females and 105 males, were caught during the incubation period. Each individual was assigned to one of three categories based on its phenotype: Caspian Gull, Herring Gull or intermediate. This phenotypic assignment was based on morphological characteristics of pure populations collected in their core ranges during other studies. Additionally, intensive observations of adult breeders in the Włocławek colony were conducted to classify as many individuals into species categories as possible. Principal Component Analysis was used to produce principal components from six morphological traits that differed most between species, i.e.: bill length, bill depth at gonys, number of primaries with black, length of black on seventh primary, iris pigmentation and orbital ring colour (for details see Gay et al. 2007 and Neubauer et al. 2009). Individuals whose score of the principal component fell within 95% confidence intervals for means of either species (Herring or Caspian Gull) were classified as belonging to this species, others were classified as intermediates (morphological hybrids). Values of PC1 were positive for Herring Gull, negative for Caspian Gull and scattered around zero for intermediate individuals. Phenotypic assignment was done once for each individual, at first trapping, although all birds were measured each time they were trapped. Birds were ringed with a standard ornithological ring and with a coded colour rings. Individual colour ringing allowed us to identify birds in their breeding territories. All trapped birds were sexed on the basis of the head length and minimal bill depth according to discriminant function equation (Neubauer & Zagalska-Neubauer 2006).

Pair composition was based on phenotypic assignment. Pairs included in the analysis involved pairs with: (i) both mates trapped, (ii) one mate trapped and the other one identified visually and (iii) both mates identified visually. In total 202 pairs were analyzed, including 76 with both mates trapped. The following abbreviations were used: HG — Herring Gull, CG — Caspian Gull and h — hybrid. Pair classification included three main categories: homospecific pairs — when both mates represented the same species

(HG × HG and CG × CG), heterospecific pairs — when mates were of different species (in two combinations, females always at the first position: CG × HG and HG × CG), mixed pairs — when at least one of the mates was assigned as morphological putative hybrid (HG × h, h × HG, CG × h, h × CG, h × h). In mixed pairs, depending on analysis, five (mentioned above) or three pair categories (HG × h, CG × h, regardless which sex was a hybrid, and h × h) were distinguished. We used chi-square test to compare expected and observed numbers of pairs (Zar 1999). All calculations were performed in Statistica 6.0 (StatSoft 2003).

To estimate the annual rate of change in the abundance of the two species and hybrids, we combined data from trapping, resighting and visual identification of breeding gulls for each season. Owing to variable numbers of breeding pairs, difficulties in identification of individual birds in a dense colony and varying observational effort, the absolute numbers of breeders of either species and hybrids remained unknown. We therefore expressed the abundance of Caspian Gulls, Herring Gulls and hybrids as percentages: in a given year, number of birds in given category was divided by the total number of identified (classified into one of three categories) birds.

### Immigration

We compared immigration from core ranges of Herring and Caspian Gulls to the hybrid zone, using data on reencountered birds which were ringed as nestlings. To investigate temporal changes in the number of immigrants, we summed up the number of known immigrant Herring and Caspian Gulls that were breeding in the colony each year within 20 years period, from 1990 to 2009. If a given bird was not found in a given year, but was a breeder during both previous and subsequent years, we assumed it was present and breeding, but overlooked. Non-detection is very likely in the denser parts of the colony, while breeding dispersal (i.e., desertion from the breeding place used hitherto) is relatively rare in large gulls (Greenwood & Harvey 1982). The number of immigrants known to be breeding in the colony was presented for each year, separately for Herring and Caspian Gulls. We also assessed the temporal patterns of immigration for both species, using the reencounter probability as an index of immigration strength (Kania 2006, 2009). Assuming similar survival probability and because the reencounter probability is the same for both species, the numbers of immigrants

reencountered at the study place depend only on the numbers ringed and the probability that an individual has moved. The numbers of birds ringed as nestlings and then recovered as breeders were known (ringed/recovered; 1990–99: Herring Gull 4626/20, Caspian Gull: 191/1, 2000–09: Herring Gull 614/1, Caspian Gull: 759/8). In such situation, reencounter probability depends only on the probability of moving and can be viewed as an index of immigration strength. While it cannot be estimated how many individuals immigrated, it is possible to gain some information in terms of rate of change if the indices between discrete periods of time are compared. Here we compared two decades: 1990–1999 and 2000–2009. For both periods, numbers of ringed birds were obtained by summing the numbers of all nestlings ringed in the ranges of Herring (Baltic coast) and Caspian (southern Poland) Gulls. Given that gull species start to breed at the age of four or five, in both these areas we considered all years of ringing up to four years before our study ended, given — at minimum — four years of pre-breeding immaturity (resightings of younger birds in the studied colony were not included, as they refer to prospectors). We combined information on recaptures (all adults trapped at nests while breeding at Włocławek Reservoir) and resightings (conditioned on that breeding status for these individuals could be ascertained). In this analysis we omitted two individuals originating from abroad and found breeding within 1990–2009 at Włocławek Reservoir colony: a Herring Gull from Finland (ringed as nestling in 1991), and a Caspian Gull from Ukraine (ringed as nestling in 2000). The data on ringed nestlings and birds controlled as breeders at Włocławek Reservoir before 2000 were obtained from the database of the Polish Ringing Centre.

#### Breeding ecology and reproductive success

The data were collected for 226 reproductive episodes for pairs with both mates identified ( $n = 202$ ) from 2003 to 2009. We observed that most of ringed birds formed pairs that lasted for the whole 7 year study (own data). There were data available for more than one breeding season for 24 pairs, and for these pairs we used averaged values to avoid pseudoreplication. Field work was conducted from late March to early July and the colony was visited with 1–4 days intervals. During laying peak, incubation period and chick ringing, visits were performed daily. To determine breeding phenology nests were marked and mapped.

Laying phenology was standardized using the date on which the first egg in the colony was laid each year. Gulls usually lay 3 eggs, but the clutch size varies from 1 to 4. Within a single clutch all eggs were marked individually to determine the laying order. Breeding performance was assessed using clutch size (number of eggs in a clutch), clutch volume (the sum of individual eggs volume) and hatching success (number of chicks raised per nest). Length and breadth of each egg was measured to the nearest 0.1 mm with a caliper (repeatability = 0.99, see also Neubauer et al. 2009) and the volume was calculated from the equation:  $\text{Volume} = \text{length} \times \text{breadth}^2 \times 0.000476$  (Harris 1964). Laying date, clutch size and volume were tested for the species and sex effect with general linear models (GLMs).

Trapped birds were weighed to the nearest 10 g with Pesola spring balance. We compared body masses of breeding females and males with the general linear model (GLM) with species category as a factor in Statistica 6.0 (StatSoft 2003).

## RESULTS

### Changes in species composition

After the increase over the first decade of its existence (Fig. 1), the colony size during the study was approximately stable, with 125–135 breeding pairs. During 2002–2009 opposite trends in proportions of breeding Herring and Caspian Gulls were recorded, while the proportion of morphological hybrids was rather stable at approximately 20% level (range 15–28%). In contrast, the proportion of Herring and Caspian Gull considerably changed, with the former species significantly declining and the latter increasing (Fig. 2). Both these trends were significant ( $n = 8$  years, Spearman correlation, Herring Gull:  $r_s = -0.86$ ,  $t = -4.08$ ,  $p = 0.007$ , Caspian Gull:  $r_s = 0.81$ ,  $t = 3.38$ ,  $p = 0.015$ ).

### Immigration pattern

Changes observed in phenotype proportions were confirmed by results obtained from the ring recovery analysis. 32 birds ringed as nestlings outside the colony were recorded among gulls trapped as breeders in the Włocławek colony from 1990 to 2009. Among them, 20 originated from the Polish Baltic coast (Herring Gull breeding range) and 10 from southern Poland (Caspian Gull core range) plus single individuals hatched in Finland (Herring Gull) and Ukraine (Caspian Gull, see

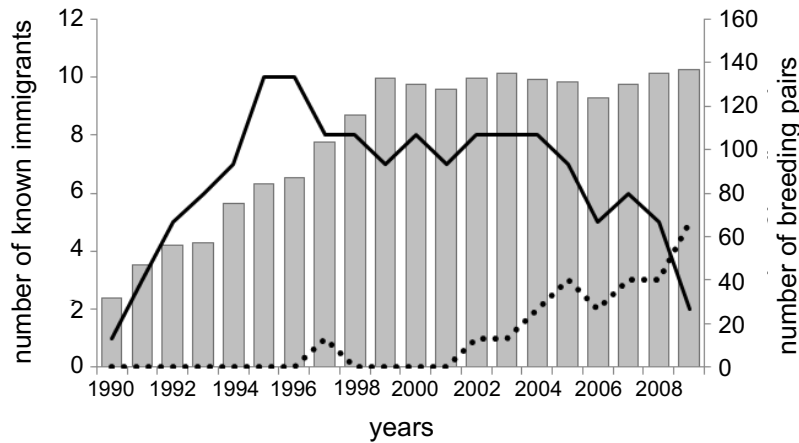


Fig. 1. Lines and left axis: numbers of immigrant Herring Gulls (solid line) and Caspian Gulls (dotted line) known to be breeding in the colony at Włocławek Reservoir, central Poland, 1990–2009. Bars and right axis: annual numbers of breeding pairs (regardless of composition) in the studied colony.

Neubauer et al. 2007). The number of recorded immigrant Herring Gulls increased over the first few years of colony existence and reached maximally 10 individuals recorded in a single year. This was followed by a marked decline during the last few years (Fig. 1). Most of the Caspian Gull immigrants were recorded after 2002, and in 2009 they outnumbered Herring Gulls (Fig. 1). Based on birds number ringed in the respective breeding ranges and reencountered in studied colony, immigration of Herring Gulls appeared approximately three times smaller during 2000–2009 than during 1990–1999 (respective reencounter probabilities were 0.0016 vs 0.0045). In contrast, an

approximately twofold increase has been noted in Caspian Gull immigration (0.0051 vs 0.0119). These results document the increase of Caspian Gull and suggest that immigration from outside the zone is important.

**Pair composition and phenotypic similarity between mates**

In 2002–2009, the observed proportion of heterospecific and mixed pairs was 58% versus 69% expected (Table 1;  $\chi^2 = 27.599$ ,  $df = 8$ ,  $p < 0.001$ ; with categories pooled into three classes  $\chi^2 = 17.402$ ,  $df = 2$ ,  $p < 0.001$ ). At the same time, homospecific pairs were more frequent than expected under random mating (42% observed vs 31%

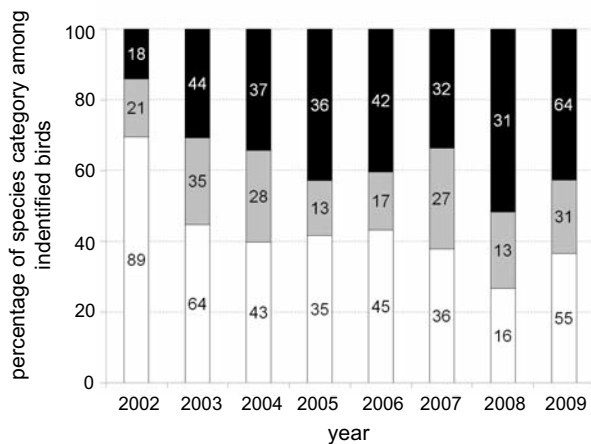


Fig. 2. Annual numbers of breeding gulls classified into three categories: Herring Gulls (white bar), morphological hybrids (grey bar) and Caspian Gulls (black bar) in the colony at Włocławek Reservoir, central Poland, 2002–2009. Sexes pooled within categories; numbers of birds identified in each category given inside the bars.

Table 1. Numbers of expected and observed homospecific, heterospecific and mixed breeding pairs in the colony at Włocławek Reservoir, central Poland, 2002–2009. Female always listed first; HG — Herring Gull, CG — Caspian Gull, h — hybrid. <sup>1</sup> — mixed pairs are all pairs which include at least one hybrid.

	n	%	n	%
	expected	expected	observed	observed
Homospecific	69.4	31.1	94	42.2
HG × HG	37.8	16.9	43	19.3
CC × CC	31.6	14.2	51	22.9
Heterospecific	69.5	31.2	45	20.2
HG × CG	38.7	17.3	22	9.9
CG × HG	30.9	13.8	23	10.3
Mixed <sup>1</sup>	84.1	37.7	84	37.7
HG × h	21.5	9.7	22	9.9
h × HG	17.4	7.8	13	5.8
CG × h	17.6	7.9	14	6.3
h × CG	17.8	8.0	26	11.7
h × h	9.9	4.4	9	4.0
Total	223	100	223	100

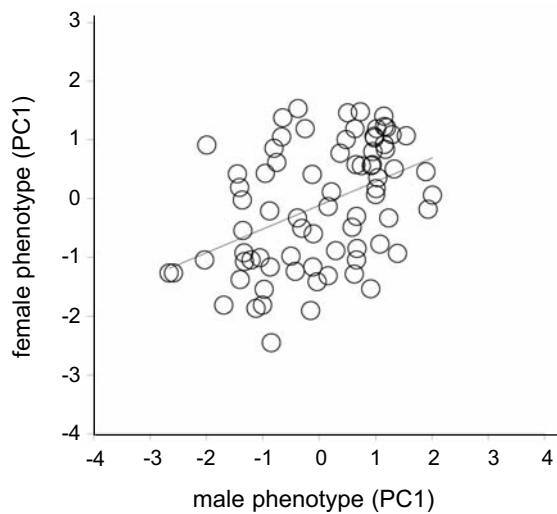


Fig. 3. Relationship between phenotypes of mates forming social pairs in gulls. Each point represents a single breeding pair.

expected). Numbers of pairs falling into particular categories varied in subsequent years without any directional trend: for homospecific pairs mean was 40% (range 21–48%), for heterospecific pairs 18% (range 15–24%) and for mixed pairs 42% (range 27–58%).

Due to the observed assortative mating we expected linear correlation between phenotype of mates forming social pairs. There was moderate but significant correlation between phenotypes of mates ( $r = 0.43$ ,  $t = 4.07$ ,  $p = 0.0001$ ,  $n = 76$  pairs, Fig. 3).

### Breeding performance

Body masses of females of both species and hybrids were not significantly different (GLM:  $F_{2,113} = 2.45$ ,  $p = 0.09$ ), however Herring Gulls were the heaviest (mean  $\pm$  SD:  $1009 \pm 58$  g),

Caspian Gulls intermediate ( $998 \pm 65$  g) and hybrids the lightest ( $976 \pm 59$  g). In contrast, significant differences in body masses of breeders were found in males ( $F_{2,66} = 3.47$ ,  $p = 0.04$ ). Caspian Gulls were significantly ( $p = 0.04$ , Tukey's test) heavier ( $1268 \pm 62$  g) than Herring Gulls ( $1219 \pm 86$  g) and hybrids ( $1222 \pm 68$  g).

Females paired to Caspian Gull males laid eggs 4.3 days earlier than females paired with Herring Gull males (GLM with male and female species as factors:  $F_{2,214} = 6.06$ ,  $p < 0.003$ , Table 2). The same was true of males: those paired to female Herring Gulls started broods on average 4.4 days later than those paired to female Caspian Gulls ( $F_{2,214} = 6.56$ ,  $p < 0.002$ ). The interaction of male and female species was however insignificant ( $F_{4,214} = 0.43$ ,  $p = 0.79$ ), suggesting that these differences are mutually independent. When two types of homospecific pairs were compared, the difference between mean reproduction date was 7 days (Table 2). There was no difference in clutch size between pair categories: all pairs showed a very high proportion of three-egg clutches (homospecific:  $0.98 \pm 0.02$  SE,  $n = 94$  broods, heterospecific:  $0.96 \pm 0.03$  SE,  $n = 45$  broods, mixed:  $0.96 \pm 0.02$  SE,  $n = 89$  broods). Clutch volume was significantly affected only by female body mass (GLM:  $F_{4,206} = 1.14$ ,  $p = 0.34$ , Table 3) and tended to differ among pairs of different composition (interaction in Table 2 marginally significant). Hatching success, expressed as the proportion of eggs that hatched to all eggs laid was moderate to high (range 0.63–0.92), and depended on pair composition (GLM:  $F_{4,210} = 2.69$ ,  $p = 0.03$ , Table 3). Pairs composed of two hybrids had the highest hatching success among all pair categories ( $0.92 \pm 0.14$  SD), while the homospecific Herring Gull pairs had the lowest hatching success ( $0.63 \pm 0.41$  SD), but none of these differences have been found significant.

Table 2. Laying date, number of eggs laid, clutch volume and hatching index in pairs of different composition. Laying date standardized within seasons and expressed in days numbered from the earliest brood in a given year. All values given as means  $\pm$  SD and 95% confidence intervals in parentheses (except number of eggs). <sup>1</sup> — mixed pairs are all pairs which include at least one hybrid.

	n	laying date	number of eggs laid	clutch volume (cm <sup>3</sup> )	hatching index
HG $\times$ HG	42	$14.6 \pm 6.7$ (12.5–16.7)	$3.0 \pm 0.00$	$249.4 \pm 14.5$ (244.9–253.9)	$0.63 \pm 0.41$ (0.50–0.76)
CG $\times$ CG	50	$7.7 \pm 5.0$ (6.3–9.1)	$3.0 \pm 0.14$	$258.9 \pm 25.3$ (251.7–266.1)	$0.71 \pm 0.36$ (0.60–0.81)
HG $\times$ CG, CG $\times$ HG (heterospecific)	42	$10.4 \pm 4.2$ (9.1–11.7)	$3.0 \pm 0.00$	$250.4 \pm 255.8$ (244.9–255.8)	$0.83 \pm 0.26$ (0.75–0.92)
Mixed <sup>1</sup>	80	$10.9 \pm 6.1$ (9.6–12.3)	$3.0 \pm 0.03$	$251.9 \pm 18.7$ (247.7–256.0)	$0.70 \pm 0.38$ (0.62–0.79)

Table 3. Factors affecting clutch volume and hatching success in the gulls mixed colony at Włocławek Reservoir — results of the general linear model. For clutch volume analysis only 3-egg clutches for pairs with both mates trapped were included (n = 67).

Effect	SS	df	F	p
Clutch volume				
female body mass	1971.4	1	5.34	0.02
male body mass	557.4	1	1.51	0.22
female species	326.3	2	0.44	0.65
male species	103.6	2	0.14	0.87
male × female species	3428.0	4	2.32	0.07
error	20681.2	56		
Hatching success				
female species	0.20	2	0.77	0.46
male species	0.29	2	1.10	0.34
male × female species	1.42	4	2.69	0.03
error	27.68	210		

## DISCUSSION

We found opposite trends in the abundance of breeding species: numbers of Herring Gulls have declined while numbers of Caspian Gulls have increased. Such changes observed at a single location are consistent with trends evident on a wider geographical scale — Caspian Gull is expanding its range west- and northwards in central Europe (Skórka et al. 2005, Neubauer et al. 2006, 2009, 2010, Lenda et al. 2010), while Herring Gull is no longer an expanding species in the Baltic and elsewhere in western Europe (Neubauer et al. 2006, van Dijk et al. 2008, Hario & Rintala 2008, Eaton et al. 2009). These patterns were assessed on the basis of phenotypes and were additionally documented by records of individuals which were reared outside the hybrid zone, and dispersed into it. Changes in numbers of known immigrants from both core ranges were consistent with frequency changes observed in phenotypes alone. During 1990–1999, the number of immigrant Herring Gulls was the highest and was followed by its decline after 2000. Caspian Gull immigrants were scarce during the 1990's and became more numerous after 2002. This trend is also obvious in indices of immigration strength: when the two decades are compared (1990–1999 and 2000–2009) it can be seen that the immigration of Herring Gull declined approximately three times, while that of Caspian Gull increased about two times. More generally, these results confirm that immigrants support local populations in the hybrid zone and that they do reproduce there. This also implies that the colony was established mainly by

Herring Gulls, and after a decade, Caspian Gull became the dominant species; both these changes can be deduced from the observed changes in numbers of breeders and immigrant individuals. Such a clear picture is rarely documented by ring-ing recoveries in nature, although at least stable hybrid zones must be maintained due to the immigration of individuals from outside the zone (Price 2008). Skórka et al. (2005) have also indicated immigration as a primary source of population growth in the Caspian Gull colony in southern Poland. At Włocławek Reservoir, immigration was found to be related to the changes in species abundance, while the colony size showed only small fluctuations. The increase in numbers of Caspian Gull is still evident in the core range in Ukraine (Grishchenko et al. 2006, A. Poluda, pers. comm.) and newly established mixed colonies have been recently discovered in Lithuania (V. Pareigis, pers. comm.). Successful invasion of Caspian Gull is likely to result from high productivity of populations outside the hybrid zone, in the core range, which support most immigrants. The higher reproductive success, the more recruits disperse and settle outside the natal colonies, including the hybrid zone. It is however possible, that apart from breeding conditions in the core range, Caspian Gull can be more successful in hybrid zone due to its earlier breeding (Neubauer et al. 2009 and this study), bigger body mass (this study) and size (Malling Olsen & Larsson 2004, own data). Our observations also suggest, that Caspian Gulls are more aggressive which can result in higher breeding success due to better protection of their nestlings from predators. Caspian Gulls successfully utilize a variety of food resources available, feeding mainly on rubbish dumps outside the breeding season, and on fish ponds during chick rearing (Skórka & Wójcik 2008). Within the hybrid zone, the diet of both species seems to be similar and consists mainly of fish and food remnants taken from rubbish dumps (Gwiazda et al. 2011).

In contrast to parental species, whose abundance has considerably changed, the proportion of morphological hybrids was rather stable (at approximately 20% level) for over seven years. Assuming random mating, the highest proportion of heterospecific pairs should occur when species numbers are approximately equal. With the increase of one species and decline of the another, the number of heterospecific pairs should decline. During our study, the numbers of both parental species were relatively balanced, indicating that



the observed number of heterospecific pairs was close to the highest expected number.

Dynamics of the hybrid zone may also be influenced by the isolation mechanisms which can restrict hybridization. We examined breeding performance, including mating pattern, breeding phenology, clutch size, clutch volume and hatching success. In line with the earlier results, we confirmed assortative mating, most likely based on phenotypic traits (Neubauer et al. 2009). The previous results indicated the important role of orbital-ring colouration for assortative mating (Neubauer et al. 2009), as the theory predicts (Pierotti 1987). It is however more likely that mate choice is more complex than based only on a combination of phenotypic traits. First of all, it is the availability of mates that affects the observed frequency of pairs: a female cannot mate with a male of the same species if no homospecific mates are available. One cannot exclude also that mistakes are possible, especially if parental species are similar as in the case of Herring and Caspian Gulls. Most phenotypic traits in these species are overlapping (Malling Olsen & Larsson 2004) and some hybrids are probably not recognizable from parental species based on phenotype alone (Gibbins et al. 2011). Different timing of breeding is another important prezygotic mechanism acting in Caspian and Herring Gulls, with Caspian Gull being earlier breeder than Herring Gull (Neubauer et al. 2009 and this study). Regardless of the female species, females paired to Caspian Gull males on average bred earlier than those paired to Herring Gull. Because early breeding is advantageous (Merilä & Sheldon 2000), males holding territories early in the season are likely to be more attractive. This was shown in many bird species that early breeders experience higher breeding success (e.g. Davis & O'Donald 1976, Johnson & Burnham 2013). The role of a divergent breeding phenology is known as the isolation mechanism in large gulls (Yésou 1991). In addition, Caspian Gull males are slightly, but significantly heavier, which, coupled with their size bigger by 5–10% (Malling Olsen & Larsson 2004), suggests that they may easily overcompete Herring Gull males. We previously suggested that both mate choice based on phenotypic traits and divergent breeding phenology could be responsible for assortative mating (Neubauer et al. 2009).

Postzygotic isolation and selection against hybrids between Herring and Caspian Gull are most likely weak, at least at the stage of breeding and chick rearing. Heterospecific and mixed pairs

produced viable offspring as many of these hybrid individuals have been later found successfully breeding at Włocławek Reservoir colony. We found only slight and insignificant differences among both pure species and putative hybrids in respect to clutch size and volume. Clutch volume was significantly positively affected only by female body mass and tended to differ among pairs of different composition. Moreover, hatching success was moderate to high, and did not depend on pair composition. Bell's (1997) study conducted on the Pacific coast of North America revealed that Western Gull *L. occidentalis* pairs experienced greater reproductive success than mixed pairs, while Glaucous-winged Gull *L. glaucescens* pairs experienced the lowest reproductive success. These results remain in contrast with Hoffman et al. (1978) and Good et al. (2000), whose studies suggested significantly higher reproductive success of mixed and heterospecific pairs in comparison to homospecific pairs. Good et al. (2000) argued that the primary determinant of reproductive success appeared to be the choice of breeding habitat, as in some habitats nestlings could hide from predators in vegetation, while on bare sand this was impossible.

To summarize, the recent hybrid zone between Herring and Caspian Gull in Poland changes dynamically with time, with the latter species outnumbering the former during last few years. An unbalanced dispersal from outside the zone, resulting most likely from productivity in core ranges, is the main reason for changes in the colony composition. Currently, more Caspian than Herring Gulls immigrate to reproduce in the hybrid zone, opposite to what was found there a decade ago. Assortative mating is the reproductive isolation mechanism known to limit hybridization frequency between the two species. Caspian Gull males are heavier, larger, more intensively coloured and reproduce earlier than Herring Gull males. Breeding success of all kinds of pairs is similar and selection against hybrids seems weak, but this deserves further studies.

#### ACKNOWLEDGEMENTS

We are grateful for critical comments from reviewers. For language correction we thank Klaudia Kubis. The study was supported by projects from the Ministry of Science and Higher Education: Nr N304 073 31/2805, Nr N N304 339334. We gratefully acknowledge the effort of all students and

volunteers who participated in our fieldwork. We also thank Professor Maciej Gromadzki and Polish Ringing Centre for the help.

## REFERENCES

- Arnold M. L. 1997. Natural hybridization and evolution. Oxford University Press, UK.
- Avise J. C. 2004. Molecular markers, natural history and evolution. Sinauer Associates, Inc. Publishers, Sunderland.
- Barton N. H. 2001. The role of hybridization in evolution. *Mol. Ecol.* 10: 551–568.
- Barton N. H., Hewitt G. M. 1985. Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.* 16: 113–148.
- Bell D. A. 1996. Genetic differentiation, geographic variation and hybridization in gulls of the *Larus glaucescens-occidentalis* complex. *Condor* 98: 527–546.
- Bell D. A. 1997. Hybridization and reproductive performance in gulls of the *Larus glaucescens-occidentalis* complex. *Condor* 99: 585–594.
- Carey M. P., Sanderson B. L., Barnas B. A., Olden J. D. 2012. Native invaders — challenges for science, management, policy, and society. *Front. Ecol. Environ.* 10: 373–381.
- Davis J. W. F., O'Donald P. 1976. Territory size, breeding time and mating preference in the Arctic Skua. *Nature* 260: 774–775.
- Devillers P. 1983. Plumage, bare parts and geographical variation of *Larus argentatus*. In: Cramp S., Simmons K. E. L. (eds). *The Birds of Western Palearctic*. Vol. III. Oxford University Press, Oxford, pp. 831–837.
- van Dijk A., Boele A., Hustings F., Koffijberg K., Plate C. 2008. Broedvogels in Nederland in 2006. SOVON-monitoring-rapport 2008/01. [http://www.sovon.nl/pdf/Mon\\_2008\\_01\\_Broedorap.pdf](http://www.sovon.nl/pdf/Mon_2008_01_Broedorap.pdf)
- Eaton M. A., Balmer D. E., Conway G. J., Gillings S., Grice P. V., Hall C., Hearn R. D., Musgrove A. J., Risely K., Wotton S. 2009. The state of the UK's birds 2008. RSPB, BTO, WWT, CCW, NIEA, JNCC, NE and SNH. Sandy, Bedfordshire.
- Gay L., Neubauer G., Zagalska-Neubauer M., Bebaïn C., Pons J.-M., David P., Crochet P.-A. 2007. Molecular and morphological patterns of introgression between two large white-headed gull species in a zone of recent secondary contact. *Mol. Ecol.* 16: 3215–3227.
- Gibbins C., Neubauer G., Small B. J. 2011. Identification of Caspian Gull. Part 2: phenotypic variability and the field characteristics of hybrids. *British Birds* 104: 702–742.
- Good T. P., Ellis J. C., Annett C. A., Pierotti R. 2000. Bounded hybrid superiority in an avian hybrid zone: effects of mate, diet, and habitat choice. *Evolution* 54: 1774–1783.
- Grant P. R., Grant B. R. 1992. Hybridization of bird species. *Science* 256: 193–197.
- Greenwood P. J., Harvey P. H. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Ecol. Syst.* 13: 1–21.
- Grishchenko V. N., Gavrilyuk M. N., Yablonovskaya-Gavrilyuk E. D. 2006. Number dynamics of Yellow-legged Gull in the colony near Kaniv hydroelectric power station in 1991–2006. *Avifauna of Ukraine* 3: 59–64.
- Gwiazda R., Bukaciński D., Neubauer G., Faber M., Betleja J., Zagalska-Neubauer M., Bukacińska M., Chylarecki P. 2011. Diet composition of the Caspian Gull (*Larus cachinnans*) in inland Poland: effects of breeding area, breeding stage and sympatric breeding with the Herring Gull (*Larus argentatus*). *Ornis Fennica* 88: 80–89.
- Hario M., Rintala J. 2008. [Population trends of the Common Eider and four gull species in Finnish coastal areas in 1986–2007]. *Linnut vuosikirja*: 52–59.
- Harris M. P. 1964. Aspects of the breeding biology of the gulls *Larus argentatus*, *L. fuscus* and *L. marinus*. *Ibis* 106: 432–454.
- Hoffman W., Wiens J. A., Scott J. M. 1978. Hybridization between gulls (*Larus glaucescens* and *L. occidentalis*) in Pacific Northwest. *Auk* 95: 441–458.
- Jiggins C. D., Mallet J. 2000. Bimodal hybrid zones and speciation. *Trends Ecol. Evol.* 15: 250–255.
- Johnson J. A., Burnham K. 2013. Timing of breeding and offspring number covary with plumage colour among Gyrfalcons *Falco rusticolus*. *Ibis* 155: 177–188.
- Kania W. 2006. Movements of Polish White Storks *Ciconia ciconia* — an analysis of ringing results. In: Tryjanowski P., Sparks T. H., Jerzak L. (eds). *The White Stork in Poland: studies in biology, ecology and conservation*. Bogucki Wyd. Nauk., pp. 249–294.
- Kania W. 2009. Relative re-encounter ratio — an alternative approach to infer bird distribution from the re-encounter distribution. EURING Analytical Meeting. Estimation, modelling and conservation of vertebrate populations using marked individuals, 14–20 September 2009, Abstract book, p. 89.
- Lenda M., Zagalska-Neubauer M., Neubauer G., Skórka P. 2010. Do invasive species undergo metapopulation dynamics? A case study of the invasive Caspian Gull *Larus cachinnans* in Poland. *J. Biogeogr.* 37: 1824–1834.
- Malling Olsen K., Larsson H. 2004. Gulls of Europe, Asia and North America. Christopher Helm London.
- Merilä J., Sheldon B. C. 2000. Lifetime reproductive success and heritability in nature. *Am. Nat.* 155: 301–310.
- McCarthy E. M. 2006. Handbook of avian hybrids of the world. Oxford University Press, Oxford, New York.
- Moore W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. *Q. Rev. Biol.* 52: 263–277.
- Neubauer G., Faber M., Zagalska-Neubauer M. 2010. Yellow-legged Gulls in Poland: status and separation from yellow-legged Herring Gulls and hybrids. *Dutch Birding* 32: 163–170.
- Neubauer G., Zagalska-Neubauer M. 2006. [Sexual dimorphism and sex identification of the Herring Gull *Larus argentatus* group using biometric measurements]. *Not. Orn.* 47: 185–191.
- Neubauer G., Zagalska-Neubauer M., Betleja J. 2007. Origin of Caspian Gulls *Larus cachinnans* breeding in Poland. *Brit. Birds* 100: 554–557.
- Neubauer G., Zagalska-Neubauer M., Gwiazda R., Faber M., Bukaciński D., Betleja J., Chylarecki P. 2006. Breeding large gulls in Poland: distribution, numbers, trends and hybridisation. *Vogelwelt* 127: 11–22.
- Neubauer G., Zagalska-Neubauer M., Pons J.-M., Crochet P.-A., Chylarecki P., Przystalski A., Gay L. 2009. Assortative mating without complete reproductive isolation in a zone of recent secondary contact between Herring Gulls (*Larus argentatus*) and Caspian Gulls (*L. cachinnans*). *Auk* 126: 409–419.
- Pálsson A., Vigfúsdóttir F., Ingólfsson A. 2009. Morphological and genetic patterns of hybridization of Herring Gulls (*Larus argentatus*) and Glaucous Gulls (*L. hyperboreus*) in Iceland. *Auk* 126: 376–382.
- Panov E. N. 1989. Natural hybridization and ethological isolation in birds. M. Nauka Press, Moscow, USSR.
- Pierotti R. J. 1987. Isolation mechanisms in seabirds. *Evolution* 41: 559–570.
- Pierotti R., Annett C. 1993. Hybridization and male parental investment in birds. *Condor* 95: 670–679.
- Pons J.-M., Hassanin A., Crochet P.-A. 2005. Phylogenetic relationships within the *Laridae* (Charadriiformes: Aves)

- inferred from mitochondrial markers. *Mol. Phylogenet. Evol.* 37: 686–699.
- Price T. D. 2008. *Speciation in birds*. Roberts & Company Publishers, Greenwood, Colorado.
- Skórka P., Wójcik J. D. 2008. Habitat utilisation, feeding tactics and age related feeding efficiency in the Caspian Gull *Larus cachinnans*. *J. Ornithol.* 149: 31–39.
- Skórka P., Wójcik J. D., Martyka R. 2005. Colonization and population growth of Yellow-legged Gull *Larus cachinnans* in southeastern Poland: Causes and influence on native species. *Ibis* 147: 471–482.
- Snow D. W., Perrins C. M. 1998. *The Birds of the Western Palearctic. Concise Edition*. Oxford University Press, Oxford.
- StatSoft 2003. *Statistica electronic manual, Version 6*. StatSoft, Tulsa.
- Vigfúsdóttir F., Pálsson S., Ingólfsson A. 2008. Hybridization of glaucous gull (*Larus hyperboreus*) and herring gull (*Larus argentatus*) in Iceland: mitochondrial and microsatellite data. *Phil. Trans. R. Soc. B.* 363: 2851–2860.
- Yakovets N. 2006. Hellmantelige Großmöwen *Larus spec.* in Belarus — Status und Probleme. *Vogelwelt* 127: 23–30.
- Yésou P. 1991. The sympatric breeding of *Larus fuscus*, *L. cachinnans*, and *L. argentatus* in western France. *Ibis* 133: 256–263.
- Zar J. 1999. *Biostatistical analysis*. 4<sup>th</sup> ed. Prentice Hall, New Jersey.

## STRESZCZENIE

**[Dynamika liczebności i biologia rozrodu mew: srebrzystej i białogłowej w strefie hybrydyzacji]** Hybrydyzacja, czyli kojarzenie się dwóch różnych taksonów i produkowanie mieszańcowego potomstwa, jest stosunkowo powszechna wśród ptaków. Mewa srebrzysta i białogłowa hybrydują na obszarze środkowej i wschodniej Europy, tam, gdzie spotykają się ich zasięgi. W wyniku gwałtownej ekspansji trwającej od kilku dziesięcioleci, mewa białogłowa kolonizuje nowe tereny m. in. w południowej Polsce i w strefie hybrydyzacji w środkowej Polsce. Dotychczas jednak brak było badań omawiających dynamikę liczebności tych gatunków w strefie sympatycznego występowania. W niniejszej pracy omówiono wyniki badań prowadzonych w latach 2002–2009 w kolonii mieszańcowej na Zbiorniku Włocławskim, w środkowej Polsce. Dla zobrazowania wybranych aspektów użyto również danych z lat 1990–2001, uzyskanych z bazy Krajowej Centrali Obrączkowania i kartoteki awifaunistycznej SO MiZ PAN. Zbadano dynamikę liczebności gatunków i oceniono potencjalne mechanizmy izolacji rozrodczej u mew. Ptaki lęgowe były odławiane na gniazdach i znakowane kolorowymi obrączkami z indywidualnym kodem; łącznie odłowiono 226 osobników. Schwytane ptaki mierzono wg standardowego protokołu, pobierając komplet pomiarów szczegółowo opisujących fenotyp osobnika. By przyporządkować osobnika do kategorii gatunkowej, korzystano z analogicznych danych

zebranych w allopatrycznych populacjach obu gatunków, a przypisanie oparto na pierwszej składowej głównej z analizy czynnikowej (PCA). Corocznie prowadzono także intensywne obserwacje przy użyciu lunet, mające na celu klasyfikację do kategorii gatunkowych jak największej liczby osobników; odczytywano także obrączki założone ptakom w poprzednich latach, umożliwiające identyfikację osobnika bez potrzeby chwytania go. Dla 202 par ze znaną przynależnością gatunkową obu partnerów oceniono parametry sukcesu lęgowego, w tym: termin przystąpienia do lęgu, wielkość zniesienia, objętość lęgu i wykluwalność. Kolonia, w której prowadzono badania powstała w latach 1980. Liczba lęgowych mew srebrzystych wzrastała przez pierwsze 15 lat (Fig. 1), a po roku 2000 ustabilizowała się na poziomie około 130 par.

W okresie od 2002 do 2009 liczebność mewy białogłowej wzrosła z 14% do 42%, liczebność mewy srebrzystej spadła z 70% do 35%, natomiast liczebność mieszańców utrzymywała się na zbliżonym poziomie około 20% (Fig. 2). W kolonii stwierdzono jako lęgowe aż 32 osobniki pochodzące spoza strefy hybrydyzacji, zaobrazowane jako pisklęta w zwartych zasięgach mewy srebrzystej albo białogłowej. W latach 1990–1999 imigracja mew srebrzystych z polskiego wybrzeża była około dwukrotnie wyższa niż w ciągu następnej dekady (lata 2000–2009). W przypadku mewy białogłowej zanotowano tendencję odwrotną: w latach 1990–1999 imigracja z południowej Polski była około dwukrotnie niższa niż w latach 2000–2009. Stwierdzono kojarzenie pozytywnie asortatywne — osobniki fenotypowo podobne wykazywały tendencję do kojarzenia się ze sobą (Fig. 3), co skutkowało mniejszą niż oczekiwana liczbą par heterospecyficznych (Tab. 1). Mimo obserwowanych zmian w liczebności gatunków, liczba par heterospecyficznych, homospecyficznych i mieszańcowych pozostawała zbliżona w kolejnych siedmiu latach badań. Samce mew białogłowych były znacząco cięższe niż samce mew srebrzystych; pary z samcami mew białogłowych gniazdowały średnio 4 dni wcześniej niż pary z samcami mew srebrzystych. Dla par homospecyficznych, różnica w średnim terminie przystępowania do rozrodu sięgała aż 7 dni. Nie stwierdzono różnic w wielkości zniesienia, objętości lęgu i wykluwalności między wyróżnionymi typami par. Wskazuje to na słabo wyrażone różnice międzygatunkowe, a tym samym słabą izolację postzygotyczną, przynajmniej do okresu wykluwania się piskląt (Tab. 2 i 3).