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ASSORTATIVE MATING WITHOUT COMPLETE REPRODUCTIVE ISOLATION IN A ZONE OF RECENT SECONDARY CONTACT BETWEEN HERRING GULLS (*LARUS ARGENTATUS*) AND CASPIAN GULLS (*L. CACHINNANS*)

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Abstract.—The zone of secondary contact between Herring Gulls (*Larus argentatus*) and Caspian Gulls (*L. cachinnans*) in central Poland is characterized by high levels of introgression for molecular markers and several phenotypic characters, with the exception of bare-parts coloration. These patterns suggest a role for coloration as a premating isolating barrier between these species. We investigated the degree of reproductive isolation in this zone of secondary contact by testing three hypotheses: (1) postmating isolation is weak or absent, (2) a partial premating isolation is present, and (3) orbital-ring color or another closely correlated trait is involved in premating isolation, which explains the signal of disruptive selection previously observed (a lower degree of introgression). We also investigated whether differences in breeding phenology could contribute to premating isolation. We found no evidence of postmating isolation, but premating isolation occurred: heterospecific pairs were significantly scarcer than expected under random mating. This assortative mating is best explained by a combination of divergent breeding phenology and mate choice influenced by orbital-ring color. However, because the differentiation in orbital-ring color between *L. argentatus* and *L. cachinnans* is incomplete and their breeding periods overlap, premating isolation is only partial. That a previous study found a high level of genetic introgression between these species suggests that reinforcement can occur only in association with sufficiently strong postmating isolation. *Received 21 August 2008, accepted 3 January 2009.*

Key words: assortative mating, Caspian Gull, Herring Gull, hybridization, *Larus argentatus*, *L. cachinnans*, orbital-ring color, reproductive isolation.

Homogamie sans isolement reproductif complet dans une zone de contact secondaire récent entre *Larus argentatus et Larus cachinnans.*

Résumé.—La zone de contact secondaire entre *Larus argentatus* et *L. cachinnans* dans le centre de la Pologne se caractérise par des niveaux d'introgression élevés pour plusieurs marqueurs moléculaires et traits phénotypiques, à l'exception de la coloration des parties nues. Ce patron suggère que la coloration des parties nues puisse agir comme barrière à l'accouplement. Nous avons étudié le degré d'isolement reproductif dans cette zone de contact en testant trois hypothèses : (1) l'isolement postzygotique est faible ou absent, (2) il existe un isolement précopulatoire partiel et (3) la couleur du cercle orbital ou un autre trait fortement lié participe à l'isolement précopulatoire, ce qui explique le signal de sélection disruptive observé dans une étude précédente sous forme de niveau d'introgression plus faible. Nous avons aussi étudié si des différences de phénologie de reproduction contribuaient à l'isolement précopulatoire. Nous n'avons pas détecté d'isolement postzygotique, mais nous avons mis en évidence de l'isolement précopulatoire : les couples hétérospécifiques étaient significativement plus rares qu'attendu sous l'hypothèse d'appariement au hasard. Cette homogamie

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semble s'expliquer en partie par des différences dans la phénologie de la reproduction, en partie par un choix de partenaire influencé par la couleur du cercle orbital. Cependant, dans la mesure où la couleur du cercle orbital et la phénologie de reproduction des deux espèces se recouvrent en partie, l'isolement précopulatoire est incomplet. Le fort niveau d'introgression génétique observée dans une étude précédente suggère que le renforcement ne pourrait se produire que si l'isolement postcopulatoire était fort.

Speciation can be defined as the acquisition of reproductive isolation (Noor 2002) via premating or postmating barriers (extrinsic or intrinsic; see Coyne and Orr 2004, Birkhead and Brillard 2007). In contrast to other organisms, birds are often capable of producing viable and fertile hybrids at high levels of genetic divergence (Panov 1989). It may take >10 million years before two diverging populations have reached the degree of genetic separation that makes hybrids infertile, and 17 million years before hybrids are inviable (Price and Bouvier 2002). This is 5–10 times longer than in mammals (Prager and Wilson 1975, Fitzpatrick 2004) and may be one of the reasons why hybridization is so frequent among birds; >9% of bird species are known to hybridize at least occasionally in nature (Grant and Grant 1992, McCarthy 2006). Given this slow evolution of intrinsic postmating barriers in birds and the low genetic divergence among congeneric avian species (Johns and Avise 1998), premating isolation could be one of the main factors that reduce the levels of interspecific introgression among closely related bird species (Kirkpatrick and Ravigné 2002, Randler 2002). In particular, behavioral barriers, such as mate choice, are expected to be crucial (Grant and Grant 1997, Gill 1998, Randler 2008). Nongenetic mechanisms that shape assortative mate choice could also be involved, such as imprinting on the parental phenotype (Krüger et al. 2001, Brodin and Haas 2006).

If reproductive isolation relies mainly on premating mechanisms, hybridization could be favored by changes both in the environment and in population dynamics. In particular, in areas where the density of conspecifics is low, such as at the edge of a breeding range, females of a rare species may accept matings by heterospecific males of a common species more frequently (McPeek and Gavrilets 2006, Randler 2006, Reyer 2008). Time constraints on breeding may also favor heterospecific pairing, as long as the cost of hybridization can be mitigated by other mechanisms, such as extrapair copulation or sex-ratio bias (Veen et al. 2001). In the extreme, when there is no postmating isolation, it could be beneficial for a female to choose a heterospecific mate over a conspecific mate if heterospecific males are better adapted to the local environment than conspecific males (Pierotti and Annett 1993, Pfennig 2007) or if hybrids are superior (Moore 1977, Good et al. 2000). Therefore, female mate choice is influenced by the strength of postmating isolation, the relative availability of conspecific versus heterospecific partners, the males' quality, and their relative local adaptation and is, thus, expected to vary with ecological conditions (Reyer 2008).

Large white-headed gulls are an excellent model for studying the importance of premating mechanisms in reproductive isolation. First, reproductive isolation quite often seems to be incomplete in this group because of its recent origin (Liebers et al. 2004). Interspecific hybrids between large gull species have frequently been recorded (Pierotti 1987, Good et al. 2000, Crochet et al. 2003, Malling Olsen and Larsson 2004). Moreover, the genetic differentiation at nuclear loci is particularly low between taxa (Crochet et al. 2003, Gay et al. 2007), even considering that the initial vicariance may have occurred as recently as 300,000 years ago (Liebers et al. 2004). This low differentiation in nuclear loci often contrasts with a higher differentiation in mitochondrial DNA (mtDNA), a discrepancy that has been explained by a combination of recent species origin and interspecific gene flow after speciation (Crochet et al. 2003). Second, behavioral mechanisms are important for reproductive isolation in this group. Cross-fostering experiments between Herring Gull (*Larus argentatus*) and Lesser Black-backed Gull (*L. fuscus*) showed that mate choice was partly driven by imprinted preferences (Harris et al. 1978). In addition, divergence in habitat selection and nesting phenology may also limit hybridization between taxa of large gulls (Harris 1970, Yésou 1991, Klein and Buchheim 1997). Finally, the bare parts of most gull species are intensely colored in adults, with carotenoid-based pigments during the breeding season (Blount 2004), including yellow-to-red orbital rings, gape flanges, legs, and bill, as well as red bill spots. Nearly four decades ago, Smith (1966) suggested that orbital-ring color plays a role in species recognition in gulls; these results, however, are now considered inconclusive (Sutton 1968, Snell 1989, Smith 1991). Pierotti (1987) suggested that leg and bill colors are involved in reproductive isolation in seabirds. Interestingly, Kristiansen et al. (2006) recently showed that the coloration of bare parts could also play a role in intraspecific mate choice in the Great Black-backed Gull (*L. marinus*) as an honest signal of quality. Thus, it is interesting to further investigate the role of bare-parts coloration in mate choice, especially in the context of premating isolation, because this trait appears to be a good candidate for a study linking mate-quality signals and species-recognition signals.

Here, we focus on a zone of recent secondary contact between two European gull species, the Herring Gull and the Caspian Gull (*L. cachinnans*), and investigate both premating and postmating barriers to gene flow. Herring and Caspian gulls differ in size, in wing-tip pattern, and in bare-parts coloration: the latter species is larger and has blacker wing-tips and more intensely colored orbital rings, gape flanges, and legs than the former (Malling Olsen and Larsson 2004). Herring Gulls breed in western and northern Europe, from Iceland to the Kola peninsula (Malling Olsen and Larsson 2004). Populations of this species increased markedly during the 20th century, which resulted in a considerable southward range expansion (Devillers 1983, Pons and Migot 1995). The first breeding attempt by this species in Poland was in the late 1960s (Neubauer et al. 2006). The Caspian Gull was long considered conspecific with the Yellow-legged Gull (*L. michahellis*) and was only recently officially designated as a full species by the British Ornithologists' Union (Sangster et al. 2007). Its distribution extends from the Black Sea to eastern Kazakhstan (Malling Olsen and Larsson 2004). Caspian Gulls have been expanding westward and northward (e.g., reaching Poland); in these areas of expansion, the population has been increasing exponentially ever since the first breeding events were recorded in the late 1980s (Skórka et al. 2005).

At present, the ranges of the two species overlap in central and eastern Europe (Panov and Monzikov 1999), where

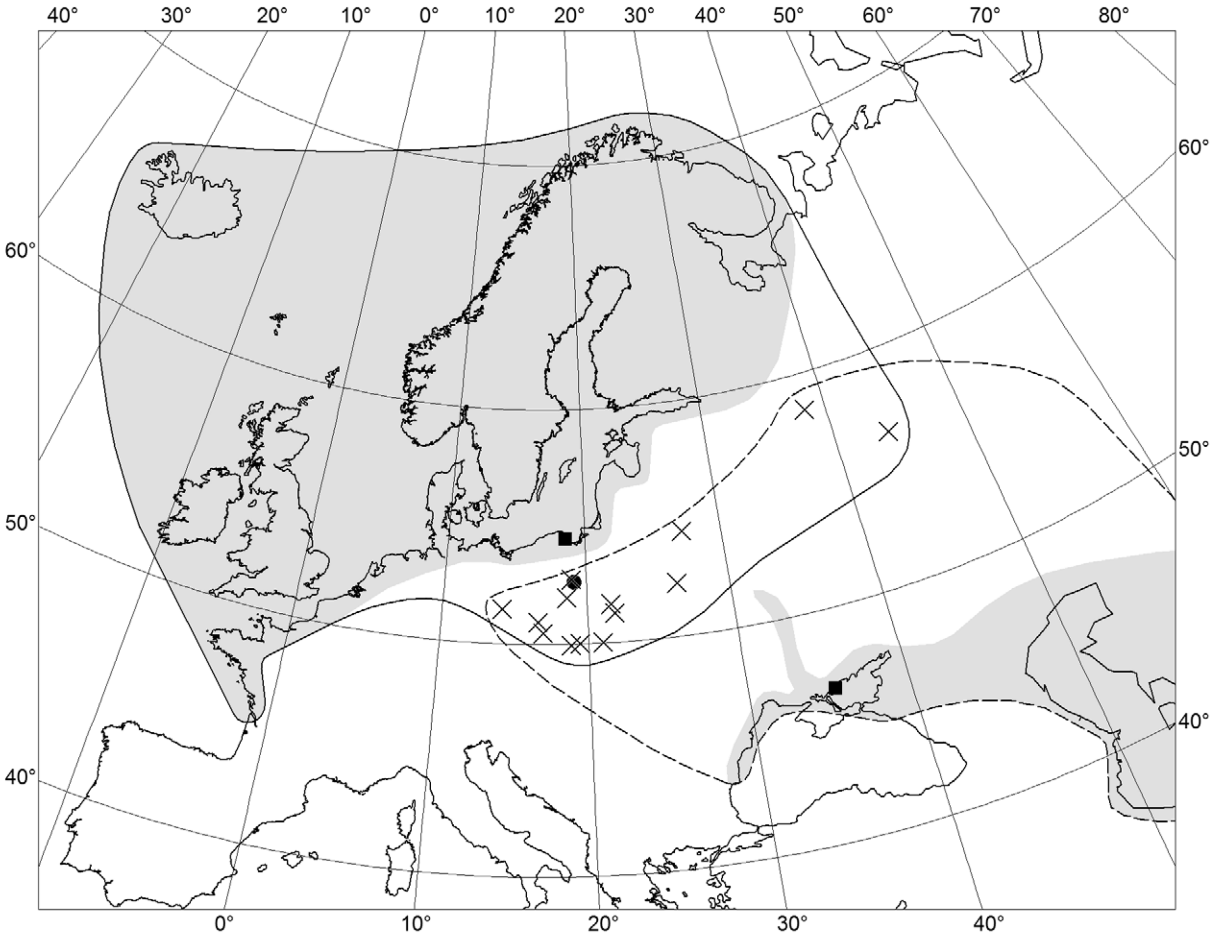

FIG. 1. Breeding distributions of Herring and Caspian gulls (Hagemeijer and Blair 1997). Solid and dashed lines show the approximate boundaries of areas recently colonized by Herring Gulls and Caspian Gulls, respectively; crosses indicate sites where hybridization between the two species has been documented (see text). The black dot shows the location of the mixed colony in central Poland (Włocławek Reservoir) that we studied. Black squares indicate the allopatric populations sampled as references.

hybridization has been recorded at several sites: in central and southern Poland (Faber et al. 2001, Neubauer et al. 2006), European Russia (Panov and Monzikov 1999), Belarus (Yakovets 2006), and eastern Germany (Klein 2001) (Fig. 1). A previous study of a zone of contact between these two species in central Poland demonstrated surprisingly high levels of introgression for molecular markers and several phenotypic characters for such a recent contact (30 years—i.e., two to three generations; Migot 1992). This suggests that interspecific barriers to gene flow are weak for most loci (Gay et al. 2007). Nevertheless, several phenotypic characters showed reduced introgression in comparison with neutral markers: individuals with intermediate coloration of bare parts were scarcer in sympatry than expected if the genomes recombined freely. Gay et al. (2007) suggested that, in this zone of secondary contact, the coloration of bare parts (e.g., orbital-ring color) may be subject to divergent selection, possibly because it is involved in premating isolation via assortative mate choice. In the present study, we investigated the degree of reproductive isolation between Herring and Caspian gulls in the same colony.

We tested the hypothesis that postmating isolation is weak or absent by comparing the breeding success of homospecific, heterospecific, and hybrid pairs. We then assessed the strength of premating isolation by comparing the number of heterospecific pairs observed with the expectation that pair formation was random. Next, we tested whether assortative mating for orbital-ring color could be one of the mechanisms contributing to this partial premating barrier to gene flow. Assortative mate choice for orbital-ring color or another closely linked trait could create the selective pressure that maintains a low level of introgression for this trait. Finally, we investigated the differences in breeding phenology between the two taxa and their potential role in premating isolation.

METHODS

Study areas.—The study colony is located in the zone of secondary contact between Herring and Caspian gulls at the Włocławek Reservoir on the Vistula River in central Poland (Fig. 1). Field

Table 1. Total number of individuals sampled from three populations and assigned to *Larus argentatus*, intermediate, or *L. cachinnans* using phenotypic data from northern Poland (allopatric *L. argentatus*) and Ukraine (allopatric *L. cachinnans*). "n_{morpho}" refers to sample size for morphological measurements, and "n_{micro}" to sample size of individuals genotyped at nine microsatellite loci (see Gay et al. 2007).

	Locality	Phenotypic assignment	n_{morpho}	n_{micro}
Allopatric *argentatus*	Gdynia, northern Poland (54°31′N, 18°33′E)	*L. argentatus*	20	20
		Intermediate	4	4
Sympatry	Włocławek Reservoir, central Poland (52°39′N, 19°08′E)	*L. argentatus*	97	21
		Intermediate	81	17
		L. cachinnans	82	24
Allopatric *cachinnans*	Molochnyy Lyman, Ukraine (46°38′N, 35°21′E)	Intermediate	9	9
		L. cachinnans	46	46

surveys were conducted each year, 2002–2008, during the breeding season. During this period, the size of the colony varied between 125 and 135 breeding pairs. In total, 260 adults (144 females and 116 males, among which 80 complete pairs were present) were trapped on the nests (Table 1). Breeding adults were also trapped in two allopatric populations in spring in 2000 and 2001 to obtain phenotypic data on non-introgressed birds: Herring Gulls ($n = 24$) in Gdynia, northern Poland, and Caspian Gulls ($n = 55$) on the islands of Molochnyy Lyman, Ukraine (Table 1). No voucher specimens were taken; all individuals were released after being ringed and measured. Blood samples were collected in allopatry and sympatry (Table 1). Total genomic DNA was extracted, and nine microsatellite loci were amplified following the protocol described by Gay et al. (2007).

Morphological data.—Seven quantitative or ranked qualitative variables describing body size and shape, wing-tip pattern (plumage melanism), and bare-parts coloration were measured on adults in the three populations. Bill length (1), bill depth at gonys (2), and length of the black spot on the seventh primary (3) were measured with Vernier calipers to the nearest millimeter. The number of primaries with black pigment (4) was counted. The colors of the orbital ring (5) and tarsus (6) and the amount of dark flecking on the iris (7) of each trapped individual were estimated visually using the following scales: orbital ring, pale yellow–pale orange–deep orange–red; tarsus, pale pink–intense pink–pale yellow–medium yellow–intense yellow; iris spots, 0%–1 to 10–11 to 50–51 to ≥90% of spots covering the iris. Photographs were taken of most individuals (available from the authors on request). All measurements were recorded by the same observer. The repeatability of the measurements was estimated on a subsample of 22 birds from the sympatric colony in central Poland measured twice during the same breeding season (Lessells and Boag 1987). The repeatability was very high and significant for all measurements (all $r > 0.77$ and all $P < 0.01$) except tarsus color ($r = 0.456$, $P = 0.13$), the high variability of which, we suppose, may have resulted from variation in the birds' physiological state. Therefore, tarsus color was omitted from further analyses.

Individuals for which a blood sample had been collected were sexed using universal primers for birds (Griffiths et al. 1998). All individuals also were sexed using a discriminant analysis combining total head length (also measured) with minimal bill depth. Because morphological determination of sex matched the genetic sex in all cases ($n = 138$; tested with individuals from both allopatric and mixed colonies), we sexed the remaining individuals using the discriminant analysis on morphological traits alone.

Species assignment and pair formation in sympatry.—Differences in orbital-ring color between allopatric Herring and Caspian gulls were tested in a Kruskal-Wallis analysis of variance (ANOVA) in STATXACT, version 4.0.1. We performed a principal component analysis (PCA) on six morphological traits measured in three populations (Gdynia, $n = 24$; Ukraine, $n = 55$; central Poland, $n = 260$). We analyzed samples for each sex separately. Individuals from the mixed colony, whose first-principal-component (PC1) scores fell outside the boundaries defined by one standard deviation around means of PC1 distributions for allopatric Herring Gull and allopatric Caspian Gull populations, were classified as morphological intermediates. This method tends to overestimate the number of intermediates but avoids assigning introgressed individuals to parental species, which is conservative in a study of assortative mating. Sixty-two individuals sampled from the same colony were genotyped at nine microsatellite loci (Gay et al. 2007). We tested the efficacy of our morphological assignment by comparing it with assignment results from the Bayesian assignment method implemented in STRUCTURE (Pritchard et al. 2000) using microsatellite data. Both assignment scores were highly correlated (Spearman $r = 0.76$, $P < 0.0001$, $n = 62$), which reinforces our confidence in the morphological assignment.

The 80 pairs were grouped into three categories (female × male): homospecific (*L. argentatus* × *L. argentatus*, hereafter $A_{♀}A_{♂}$; and *L. cachinnans* × *L. cachinnans*, hereafter $C_{♀}C_{♂}$), heterospecific (*L. argentatus* × *L. cachinnans*, hereafter $A_{♀}C_{♂}$; and *L. cachinnans* × *L. argentatus*, hereafter $C_{♀}A_{♂}$), and mixed (including at least one intermediate bird). To avoid pseudoreplication, we included each pair only once, even if it was recorded during successive years.

Breeding performance.—Reproductive performance was recorded in the mixed colony from 2003 to 2008. Laying dates were estimated by visiting nests every day during the laying peak (10–25 April). Clutch size (number of eggs laid) and egg length (L) and breadth (B) (to the nearest 0.1 mm) were measured in each nest. Repeatability for egg length and breadth was very high ($r > 0.99$, $n = 29$ eggs measured twice in 2004). Egg volume (V, in cm^3) was estimated as $V = L \times B^2 \times 0.000476$ (Harris 1964). Total clutch volume was then calculated as the sum of egg volumes in a complete clutch (2–3 eggs). Hatching success was estimated as the ratio of chicks hatched to eggs laid. There was no significant year effect in either clutch volume or hatching success (ANOVA, clutch volume: $F = 0.77$, df = 4 and 63, $P = 0.57$; ANOVA, hatching success: $F = 1.16$, df = 4 and 62, $P = 0.34$); hence, data were pooled across years. The breeding performances of homospecific, heterospecific, and mixed pairs where both members were trapped ($n = 80$) were compared using ANOVAs in STATISTICA, version 6.0.

Female preference and assortative mating.—In the mixed colony, we investigated whether assortative mating with respect to species could form a premating barrier to gene flow, using the chi-square test and a log-linear association model (Agresti 1984). This model assumes a constant log odds ratio (denoted as B) for adjacent rows and adjacent columns in the contingency table. The null hypothesis tested is H_0: $B = 0$ against $B \neq 0$. The rejection of H_0 indicates dependence between the row and column entries. The strength of association increases with the row or column number or both.

We tested for assortative mating for orbital-ring color using the Jonckheere-Terpstra test for ordered treatments in STATXACT. Orbital-ring color was chosen because previous studies had reported that this trait could play a role in mate choice in the large gulls (Smith 1966, Pierotti 1987, Gay et al. 2007). Additionally, orbital-ring color diverges most between these species, which indicates its potential importance in mate choice; however, this is not the case with bill color.

Breeding phenology.—We investigated the breeding phenology of both species by comparing the relative species abundances across the breeding season. We divided the breeding season into two-day intervals starting from the earliest brood each year (except for the first and last intervals, which were three and five days long, respectively, because of sparse data). We then estimated the relative abundance of Herring Gulls, Caspian Gulls, and intermediates among all individuals that started to breed during each interval, separately for males and females. Under the assumption of random mating, we estimated the probability of forming an *L. argentatus* (or *L. cachinnans*) homospecific pair at a given time as the relative abundance of *L. argentatus* (or *L. cachinnans*) females multiplied by the relative abundance of *L. argentatus* (or *L. cachinnans*) males during this interval. Using Wilcoxon tests, we then reanalyzed assortative mating, taking into account mate availability, by comparing observed and expected numbers of homospecific pairs across the breeding season (estimated as the probability of homospecific pairing for each two-day interval). Similarly, we reanalyzed assortative mating for orbital-ring color after splitting the breeding season into three periods differing in mate availability for Herring Gulls and Caspian Gulls. In the middle period of the breeding season, the availability of a conspecific mate was similar for both species (see below). If there is significant assortative mating for orbital-ring color during this period, it implies that orbital-ring color or another closely correlated trait contributes to assortative mating, independently from differences in breeding phenology. To determine this, we used the Jonckheere-Terpstra test for ordered treatments in STATXACT.

RESULTS

Divergence in allopatry and species composition in sympatry.—Orbital-ring color differed significantly between allopatric Herring Gulls and Caspian Gulls (Kruskal-Wallis test, males: $\chi^2 = 4.93$, $P = 0.028$; females: $\chi^2 = 26.38$, $P < 0.001$), but the variation was large in both species, which led to an overlap in the distributions of orbital-ring color in the two species, even in allopatry (i.e., independently of introgression; Fig. 2).

In the mixed colony in central Poland, Herring Gulls were slightly more abundant than Caspian Gulls (females: 36.8% vs. 28.5%, $n = 144$; males: 37.9% vs. 35.3%, $n = 116$; Table 1). Intermediate individuals accounted for 34.7% of females and 26.7% of males (Table 1).

No postmating barriers to gene flow.—We did not detect any effect of pair composition on clutch size, clutch volume, or hatching success (Table 2). Hence, there were no signs of decreased fitness in heterospecific pairs, or in pairs including at least one intermediate, which would have suggested postmating reproductive barriers to gene flow.

Mate choice.—In the mixed colony, female Caspian Gulls paired with conspecific males more often than female Herring Gulls did (58.6% and 53.6%, respectively; Table 3). Overall, the observed number of homospecific pairs (both $A_{♀}A_{♂}$ and $C_{♀}C_{♂}$)

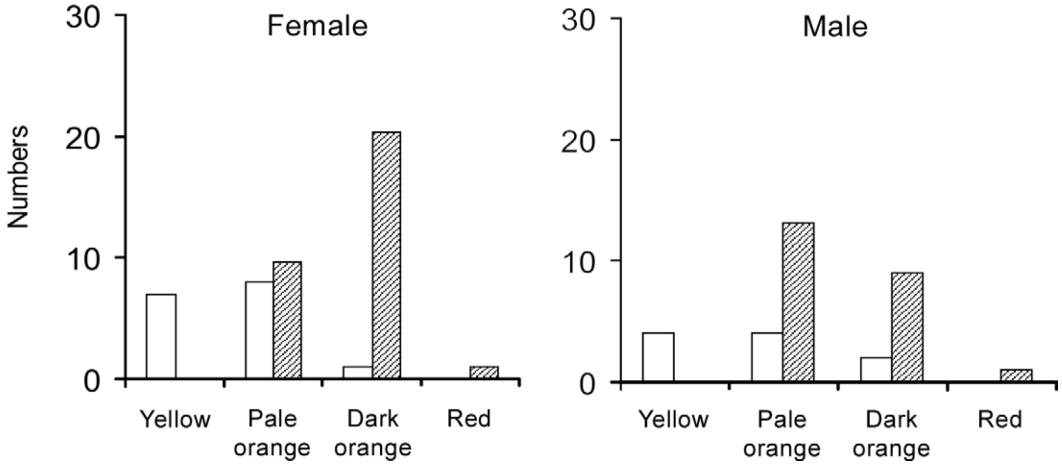

FIG. 2. Distribution of orbital-ring color in male and female Herring Gulls (white) and Caspian Gulls (hatched) in allopatric populations.

TABLE 2. Breeding performance of Herring and Caspian gull pairs of various composition (see text for pair abbreviations) in the colony in central Poland. Laying date is numbered in days from the first day of breeding in each year; hatching success is expressed as the proportion of eggs hatched. All values are given as means ± SD.

Pair	n	Laying date	n	Clutch size	n	Clutch volume	n	Hatching success
$A_♀A_♂$	11	15.6 ± 6.8	11	3.0	11	250.8 ± 11.5	11	0.79 ± 0.31
$A_♀C_♂$	5	12.2 ± 2.7	5	3.0	5	243.7 ± 12.7	5	0.87 ± 0.18
$C_♀C_♂$	16	7.6 ± 5.2	16	2.9 ± 0.3	16	248.1 ± 40.4	16	0.70 ± 0.35
$C_♀A_♂$	5	7.0 ± 3.7	5	3.0	5	242.2 ± 27.8	6	0.93 ± 0.15
Mixed	31	12.4 ± 6.6	32	2.9 ± 0.3	32	250.1 ± 24.5	31	0.76 ± 0.31
Test statistic	68	$F = 3.92$ df = 4 and 63 $P = 0.007$	69	$F = 0.61$ df = 4 and 61 $P = 0.661$	69	$F = 0.15$ df = 4 and 61 $P = 0.963$	68	$F = 0.72$ df = 4 and 63 $P = 0.584$

was higher than expected under random mating (40% vs. 28%); consequently, the number of heterospecific pairs (both $A_♀C_♂$ and $C_♀A_♂$) was lower (15% vs. 28% expected; Table 3). Thus, assortative mating was highly significant (test performed on pooled data: homospecific, heterospecific, and mixed pairs: $\chi^2 = 8.98$, df = 2, $P = 0.011$). A log-linear association model confirmed assortative mating: the null hypothesis of no association between all pairwise comparisons was not supported, which indicates an excess of homospecific pairs and a deficit of heterospecific pairs ($B = 0.448$, $P = 0.004$). Nevertheless, there was a substantial number of heterospecific pairs in the population (Table 3).

We found a significant correlation in orbital-ring color between males and females within pairs (Jonckheere-Terpstra test, exact $P = 0.02$, $n = 80$; Table 4). This indicates assortative mating for orbital-ring color or another species-recognition trait highly correlated with orbital-ring color.

Variation in species abundance: Breeding phenology.—Caspian Gulls were more abundant than Herring Gulls early in the season, and, regardless of the partner, both sexes bred earlier, on average (t-test: females: 5.5 days earlier, $t = -4.22$, df = 76, $P < 0.001$; males: 3.1 days earlier, $t = -2.27$, df = 73, $P = 0.026$). This divergence in breeding phenology resulted in different probabilities of homospecific pairing for each species across the breeding season: the probability of pairing with a conspecific partner decreased strongly for Caspian Gulls as the season progressed (Spearman's $r = -0.666$, $P = 0.001$, $n = 13$; Fig. 3), whereas the opposite trend was clear in Herring Gulls (Spearman's $r = 0.637$, $P = 0.019$, $n = 13$; Fig. 3). The difference increases if we include homospecific pairs only ($C_♀C_♂$ bred, on average, eight days earlier than $A_♀A_♂$; Table 2). Throughout the breeding season, the average probability of homospecific pairing was slightly higher for Caspian Gulls (0.180) than for Herring Gulls (0.154).

When we reanalyzed assortative mating, taking mate availability into account, we found that the observed number of homospecific pairs in Caspian Gulls was higher than expected across the breeding season (Wilcoxon test for matched pairs: $Z = 2.400$, $P = 0.016$, $n = 13$), which confirms positive assortative mate choice. By contrast, the observed proportion of homospecific Herring Gull pairs did not differ from expectation ($Z = 0.235$, $P = 0.814$, $n = 13$). This suggests that partial premating isolation results from positive assortative mate choice by Caspian Gulls rather than by Herring Gulls or from a general preference for male Caspian Gulls (also see Table 3).

Similarly, we found evidence of assortative mating for orbital-ring color during the middle period of the breeding season (Jonckheere-Terpstra test, exact $P = 0.047$, $n = 27$; Table 5), when mate availability was approximately equal for both species (Table 5). This indicates that orbital-ring color or some other closely correlated trait contributes to assortative mating, regardless of differences in breeding phenology.

DISCUSSION

Phenotypic divergence, but no evidence of postmating isolation.—When two geographically isolated, diverging taxa expand their geographic ranges, they can form a zone of secondary contact and produce hybrids if reproductive isolation is incomplete (Barton and Hewitt 1989). There are many examples of secondary contact zones in European birds (Saino et al. 1992; Helbig et al. 2001, 2005; Veen et al. 2001; Randler 2007) where hybridizing species exchange genes yet remain distinct, thanks to a balance between dispersal and selection against hybrids (Barton and Hewitt 1985, 1989). Partial premating barriers to gene flow, such as assortative mating, are often involved. Our analysis of allopatric populations of Herring Gulls and Caspian Gulls highlighted well-marked

TABLE 3. Numbers of pairs of different composition among *Larus argentatus* and *L. cachinnans* in central Poland. "Expected" is the number of pairs expected under random mating.

	Male *L. argentatus*		Male intermediate		Male *L. cachinnans*	
	Observed	Expected	Observed	Expected	Observed	Expected
Female *L. argentatus*	15	11.6	7	6.0	6	10.5
Female intermediate	12	9.5	4	4.9	7	8.6
Female *L. cachinnans*	6	12.0	6	6.2	17	10.9

Table 4. Observed and expected numbers of pairs of Herring and Caspian gulls with different orbital-ring colors in central Poland. "Expected" is the number of pairs expected under random mating.

	Yellow, male		Pale orange, male		Dark orange to red, male	
	Observed	Expected	Observed	Expected	Observed	Expected
Yellow, female	8	5.5	9	9.1	9	11.4
Pale orange, female	5	4.9	10	8.1	8	10.1
Dark orange to red, female	4	6.6	9	10.9	18	13.6

interspecific differences in orbital-ring color, which is redder in the latter. Other differences that have been reported between these species include differences in voice and courtship display (Panov 1989, Mierauskas et al. 1991). Despite phenotypic differences, we did not find any evidence of postmating isolation, given that neither heterospecific nor mixed pairs appeared to suffer from lower breeding success.

The first caveat that limits our conclusions is the small number of homospecific pairs, which results from the large introgression frequency. Second, we restricted our study of reproductive success to the hatching stage. The majority of posthatching mortality in gulls takes place before fledging (Parsons 1975, Davis and Dunn 1976, Griffiths 1992), mainly before two days of age (J. Blount pers. comm.). Nevertheless, further studies are required to exclude the possibility of lower survival between hatching and fledging or lower recruitment of hybrids in the breeding population. Ecological divergence, particularly in habitat selection (Klein and Buchheim 1997) or adaptation against predation (Good et al. 2000), could also contribute to the selection against hybrids, even though the few data available (unpublished) suggest similar habitat requirements and diet for both species. A proper estimation of hybrid fertility also would require a more precise classification of intermediates—using a hybrid index, for example. Finally, a paternity analysis is necessary to exclude the possibility that females paired with heterospecifics achieve good breeding success thanks to extrapair copulations with conspecifics, as has been shown in Collared Flycatchers (*Ficedula albicollis*), Pied Flycatchers (*F. hypoleuca*), Black-capped Chickadees (*Poecile atricapillus*), and Carolina Chickadees (*P. carolinensis*) (Veen et al. 2001, Reudink et al. 2006). However, extrapair paternity seems to be rare in larids (Gilbert et al. 1998). The evidence of weak postmating isolation presented here is in agreement with the extensive introgression reported by Gay et al. (2007) across this zone of contact. A similar lack of postmating barriers was observed in the hybrid zone between Western Gulls (*L. occidentalis*) and Glaucous-winged Gulls (*L. glaucescens*) (Bell 1997, Good et al. 2000, Good 2002), a pair of species that are more distantly related than Herring and Caspian gulls (Pons et al. 2005). In the absence of postmating isolation, we anticipate the formation of a hybrid swarm, where introgression leads to merging of the two taxa (Jiggins and Mallet 2000).

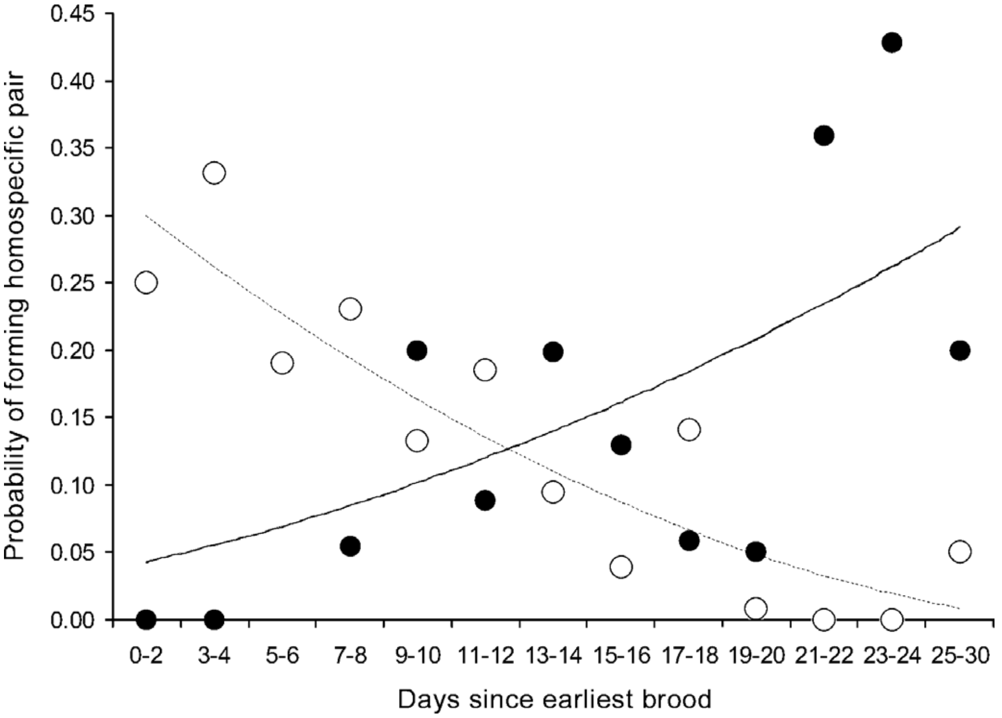

Fig. 3. Probabilities of homospecific pairing, assuming random mating, for female Caspian Gulls (empty circles, dashed line) and Herring Gulls (black circles, solid line) across the breeding season in the sympatric colony in central Poland. Square multinomial curves are fitted to visualize the trend.

Table 5. Probabilities of homospecific pairing among Herring and Caspian gulls in the early, middle, and late breeding season (see text for pair abbreviations) and the observed and expected (in parentheses) numbers of pairs with similar or different orbital-ring colors.

	Early	Middle	Late
	Days 1–10	Days 11–20	Days 21–30
Probability of homospecific pairing under random mating:			
$C_{♀}C_{♂}$	0.204	0.099	0.006
$A_{♀}A_{♂}$	0.089	0.116	0.361
Observed numbers of pairs			
With similar orbital-ring colors	12 (12.4)	12 (8.9)	5 (3.1)
With different orbital-ring colors	21 (20.6)	15 (18.1)	3 (4.9)
Total	33	27	8
Jonckheere-Terpstra test	P = 0.312	P = 0.047	P = 0.084

Alternatively, premating barriers to gene flow could limit the formation of hybrids and slow down introgression (Grant and Grant 1997, Gill 1998).

Premating isolation: The role of orbital-ring color and breeding phenology.—Heterospecific pairs were significantly scarcer than expected under random mating, which indicates a partial premating barrier to gene flow. The divergence in both orbital-ring color and breeding phenology probably contributes to this partial premating isolation. The correlative evidence presented here, combined with the indirect evidence of disruptive selection based on the reduced introgression rate observed for this trait (Gay et al. 2007), strongly suggests that orbital-ring color is involved in mate choice in these species, or that the genes encoding it are linked to some other traits of species recognition that we did not measure. Nevertheless, further direct experimental testing is still needed. The importance of orbital-ring color in mate choice and reproductive isolation in gulls has been suggested previously, but the experimental evidence suffered from potential flaws (Smith 1966). Other color-based traits, such as leg and bill color, have been suggested to be implicated in reproductive isolation in seabirds (Pierotti 1987). Our results also highlighted a divergence in breeding phenology between the two species, which could significantly reduce the frequency of heterospecific pairs in sympatry. In some bird species, the laying date is partly under genetic control. For example, on the Atlantic coast of France, Yellow-legged Gulls (*L. michahellis*) sympatric with Herring Gulls lay eggs two weeks later than their Mediterranean counterparts in southern France, but still two weeks earlier than the sympatric Herring Gulls (Yésou 1991). This suggests that in gulls, the laying date is partly genetically determined, as is the case in Blue Tits (*Parus caeruleus*; Blondel et al. 1990). This divergence in breeding phenology could also be attributable to differences in nesting habitat or winter migration, though the nesting habitat is remarkably homogeneous at the scale of the colony and winter migration seems very similar (the limited evidence available suggests even larger wintering distances for Caspian Gulls). Female preference could also drive the divergence in breeding phenology. In Arctic Skuas (*Stercorarius parasiticus*), for example, melanic males are preferred by females and can find new mates faster than pale males (O'Donald 1980). Consequently, they breed earlier with greater success (Davis and O'Donald 1976). In our mixed colony of Herring and Caspian gulls, both breeding phenology and orbital-ring color seem to contribute to partial premating isolation simultaneously, given that assortative mating for orbital-ring color was significant even when the availability of homospecific mates was equal for both taxa (middle period). This implies that the divergence in breeding phenology is not sufficient to explain the significant assortative mating for orbital-ring color.

Mate choice: Intra- versus interspecific signals.—Orbital-ring color thus seems to be involved in a partial premating isolation mechanism, which can be overridden under a variety of circumstances, such as when mate availability is limited or if breeding early in the season is advantageous. Owing to the apparent absence of postmating isolation, this results in substantial introgression across this zone of secondary contact (Gay et al. 2007). We suggest that this incomplete premating isolation could be a consequence of strong intraspecific mate choice that predates the secondary contact. The orbital-ring color has a carotenoid origin (Blount et al. 2002) and was shown to be an honest signal of quality in the Great Black-backed Gull (*L. marinus*), another member of the Herring Gull complex (Kristiansen et al. 2006). Carotenoid availability also limits egg-laying capacity in Lesser Black-backed Gulls (*L. fuscus*; Blount et al. 2004). More generally, carotenoid ornaments seem to be reliable indicators of condition in many bird species (McGraw and Hill 2000, Senar et al. 2003). If orbital-ring color is a signal of quality in large gull species but is not sexually dimorphic, it could have evolved through reciprocal mate choice—the highest-quality individuals have intensive coloration and pair together. Similarly, in the Crested Auklet (*Aethia cristatella*), Jones and Hunter (1993) showed that ornaments expressed in both sexes could be favored by mutual mate preferences. Such reciprocal mate choice would result in assortative mating and could constitute some partial premating isolation between species that partially diverged for orbital-ring color.

Female mate choice and asymmetric introgression.—Using molecular markers, Gay et al. (2007) suggested asymmetric introgression of the mitochondrial genome, because the *L. argentatus* haplotype (mtDNA) was associated with intermediate nuclear genotypes more often than expected. Two hypotheses were set up to explain this asymmetry: a lower success of crosses involving female Caspian Gull*s* and male Herring Gulls than the reciprocal cross or asymmetry in pair formation. The present results support the latter explanation: female Caspian Gulls form homospecific pairs more often than female Herring Gulls (Table 3). Clutch volume and hatching success are similar for both types of heterospecific pairs (Table 2), which does not support the hypothesis of lower success of pairs involving female Caspian Gulls and male Herring Gulls. This larger proportion of homospecific pairs in Caspian Gulls—the less abundant species in this sympatric colony—could result from differences in breeding phenology, given that the average probability of homospecific pairing in Caspian Gulls over the breeding season is only slightly higher than that in Herring Gulls (Fig. 3). However, our analysis of assortative mating that took mate availability into account showed that, for Caspian Gulls only, there were more homospecific pairs observed than expected by random association of available homospecific mates. This indicates that, in Caspian Gulls, assortative mating is not only a byproduct of breeding phenology. This asymmetry in pair formation could also be the result of a general preference for the bigger, more intensely colored male Caspian Gulls, which look like high-quality male Herring Gulls. An occasional preference for heterospecific or hybrid males has been found before in Mallards (*Anas platyrhynchos*) and Black Ducks (*A. rubripes*; Pierotti and Annett 1993), flycatchers (Veen et al. 2001), and large gulls (Good et al. 2000). Our results also show that male Caspian Gulls breed earlier than male Herring Gulls. In many birds in temperate regions, breeding early in the season could be advantageous for females (Daan et al. 1990, Wiggins et al. 1994, Verhulst et al. 1995, Merilä and Sheldon 2000). However, this hypothesis alone does not explain why we observed pairs of female Caspian Gulls and male Herring Gulls early in the season (Table 2). We suggest that these pairs may form as a result of limited mate availability and the constraint to breed as early as possible in the season. A better understanding of asymmetric introgression requires sequencing more individuals and studying pair formation in the field to validate the hypothesis of asymmetric pair formation more firmly.

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