Breeding large gulls in Poland: distribution, numbers, trends and hybridisation

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The current situation of three species of large gulls (*L. argentatus*, *L. cachinnans* and *L. michahellis*) in Poland is presented based on results of own studies and published data. Herring Gulls started to breed in the country in the late 1960s and rapidly increased in numbers until the early 1990s. This exponentially increasing population trend, coupled with southward expansion and colonisation of inland areas of N Poland has been recently reverted, with the population estimated at 1,200–1,500 pairs in the early 2000s, down from some 1,900–2,100 a decade ago. The increase of Caspian Gull in southern Poland is exponential and very fast with an annual growth rate of 33% between 1997 and 2004; the population reached 480 pairs in 2004. The Yellow-legged Gull remains a rare breeder and its population probably does not exceed 5–10 pairs. Hybridisation occurs mainly between the commonest species, Herring Gull and Caspian Gull, and is caused primarily by an apparently random pairing in mixed colonies in central Poland. The high frequency of mixed pairs (c. 60% and c. 40% respectively) and a high share of hybrids were recorded at two sites in the Vistula river valley: the middle Vistula and the Włocławek Reservoir. The situation of particular breeding colonies in southern and central Poland seems to be unstable, which favours the exchange of individuals between these breeding places. Frequent dispersal along a north-south axis also favours hybridisation.

Key words: Herring Gull *Larus argentatus*, Caspian Gull *Larus cachinnans*, range expansion, colonisation, hybridisation.

1. Introduction

Expansion of large gulls from the *Larus argentatus-cachinnans-michahellis* complex in Europe is observed from the beginning of the 20th century and lasts with some fluctuations until now (HAFFER 1982; DEVILLERS 1983; SNOW & PERRINS 1998; BIRDLIFE INTERNATIONAL 2000). The first coastal breeding site of northern Herring Gull *L. a. argentatus* in Poland was recorded in the late 1960s (BEDNORZ 1971). Scarce inland breeding sites on the lakes were established in the late 1970s; since the early 1980s, the main axis of expansion from the north was the Vistula River (TOMIAŁOJĆ 1990), where most of the inland population breeds until now. Caspian Gulls *L. cachinnans* or Yellow-legged Gulls *L. michahellis* or both, colonised the middle section of Vistula first, coming from the south and south-east probably in the early 1980s (WESOŁOWSKI *et al*. 1984; BUKACIŃSKI *et al*. 1989). During the 1990s, Caspian Gull has spread to most of southern Poland with several known colonies (FABER *et al*. 2001; TOMIAŁOJĆ & STAWARCZYK 2003). Yellow-legged Gull distribution is poorly known and this taxon is the rarest among the three, with just a few breeding localities mainly in southern Poland (POLA *et al*. 1998; FABER *et al*. 2001). Rapid expansion of – especially – Herring and Caspian Gulls caused that a secondary contact zone formed on the Polish lowland, between earlier separated northern (*argentatus*) and southern (*cachinnans* and *michahellis*) taxa of large gulls. The contact zone has remained unexplored for years. However, the last seasons brought much new evidence and information about the large gull complex allowing a more detailed analysis of the Polish contact zone. The main aim of this paper is to present the most updated information on distribution, numbers and trends of all three taxa and to provide basic data on the frequency of their hybridisation in Poland.

2. Methods

Data on distribution and numbers presented in this paper include: 1. complete evidence on breeding records of large gulls in Poland since they started to breed, and 2. recent

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(2002–2004) data on numbers from surveying their breeding colonies. Studies on hybridisation and population structure were conducted in 2002–04 at Włocławek Reservoir (52° 39' N, 19° 08' E, Fig. 1: locality 1), in 1995–2004 at the middle Vistula between Dęblin and Kozienice power station (393–423 km of the river stream, central point approx.: 51° 35' N, 21° 40' E, Fig. 1: area 2), in 1999–2004 in Tarnów (50° 01' N, 20° 59' E) and Jankowice (50° 01' N, 19° 26' E, Fig. 1: localities 3 and 4, respectively). Fewer breeding gulls were trapped in Goczałkowice Reservoir and Czorsztyn Reservoir (in 1999–2004, Fig. 1: localities 5 and 6, respectively). Adult gulls were trapped on the nests, measured, ringed and released. Complete morphological documentation, including the basic measurements, wing-tip pattern characteristics and the colouration of bare parts, was taken from most of the birds. Altogether, 177 birds were trapped in Włocławek, 85 at the middle Vistula and 204 in the region of 'southern Poland' (i.e. 60 in Tarnów, 139 in Jankowice, two on Goczałkowice Reservoir and three on Czorsztyn Reservoir). In addition, visual observations in each mentioned locality were used to assign pairs to species.

Identification of each bird was based on a number of important characters, including the colouration of bare parts, wing-tip pattern and – to a lesser degree – basic measurements. As a main reference we used morphological data collected in the same way within the breeding ranges of 'pure' (allopatric) species: Molochnyy Lyman, Azov Sea, S Ukraine, 46° 38' N, 35° 21' E (for *cachinnans*), Saline di Comacchio, NE Italy, 44° 40' N, 12° 12' E (for *michahellis*) and Gdynia, N Poland, 54° 31' N, 18° 33' E (for *argentatus*) (ZAGALSKA-NEUBAUER & NEUBAUER, unpublished). Data from the literature were also included (i. e. BARTH 1968; ISENMANN 1973; HAFFER 1982; DEVILLLERS 1983; MIERAUSKAS *et al*. 1991; LIEBERS & DIERSCHKE 1997; MALLING OLSEN & LARSSON 2003).

All the birds showing any of the features (a) falling outside the range of variation known from the literature and/or from our reference samples, (b) with intermediate characters, or (c) with part of characters associated with one species and the remaining associated with another was defined as 'hybrid'. All three species show large variability and we can expect that some individuals classified as pure species can represent in fact backcross hybrids, inseparable from parental species by morphology alone (RANDLER 2002, 2004). Therefore, the actual proportion of hybrids and degree of hybridisation in Polish populations of large gulls can be underestimated. More detailed results on morphological variability of the mid-Polish population will be presented elsewhere (CHYLARECKI *et al*., in prep.).

A hybrid (or mixed) pair is defined as a pair, which includes at least one hybrid individual or two birds of pure, but different taxa (i. e. Herring x Caspian Gull). A hybrid zone is defined as the area with colonies, where mixing between large gulls occurs regularly to a significant degree.

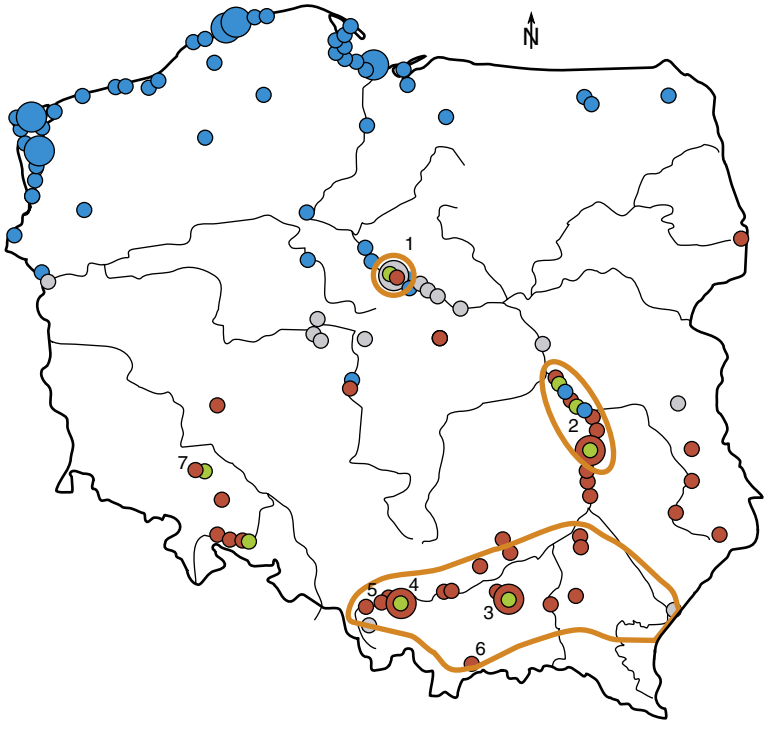

Fig. 1: Distribution of breeding Herring Gulls (blue dots), Caspian Gulls (red dots) and Yellow-legged Gulls (green dots) in Poland, 1995–2004. Grey: breeding site of unknown species or mixed colony. Large symbols: colonies > 100 bp; small symbols: < 100 bp. Orange lines show Włocławek Reservoir colony (1) and areas defined in the text as 'middle Vistula' (area 2) and 'southern Poland' (3–6). Remaining marked colonies mentioned in the text are: 3 – Tarnów, 4 – Jankowice, 5 – Goczałkowice Reservoir, 6 – Czorsztyn Reservoir and 7 – Mietków Reservoir. – *Verbreitung brütender Silbermöwen (blau), Steppenmöwen (rot) und Mittelmeermöwen (grün) in Polen, 1995–2004. Grau: Brutplatz mit unbekannter Artenzusammensetzung oder gemischte Kolonie. Große Punkte: > 100 Bp.; kleine Punkte: < 100 Bp. Orangefarbene Linien markieren den Włocławek-Stausee (1) und die im Text als „mittlere Weichsel" (2) und „Südpolen" (3–6) zusammengefassten Gebiete. Weitere im Text genannte Kolonien: 3 – Tarnów, 4 – Jankowice, 5 – Goczałkowice-Stausee, 6 – Czorsztyn-Stausee und 7 – Mietków-Stausee.*

3. Results

3.1. Distribution and numbers

Large gulls in Poland show a clear distribution pattern (Fig. 1). Herring Gull breeds mainly at the coast, with fewer inland localities confined to lower reaches of Vistula river and lakes in the northern part of the country. Caspian Gull is confined to southern and eastern part of the country, where it breeds on various artificial reservoirs (gravel pits, sedimentation basins, fish ponds and dam reservoirs) and along the middle and upper Vistula. Both species meet in central Poland, where

they breed in mixed colonies and form mixed pairs. Yellow-legged Gull has only a marginal influence on Polish population of large gulls, as it remains very rare and local.

Herring Gull *Larus argentatus*

Since the first breeding record in late 1960s, numbers of *argentatus* have increased continuously, reaching a maximum of some 1,900–2,100 pairs breeding at over 50 localities in 1987–1992. The population as a whole increased exponentially by about 13% per year in the 1970s and by 20% per year in the 1980s, with largest colonies showing annual growth rates between 20% and 60%. Since the early 1990s, the population decreased to more than 1,600 breeding pairs around 1996 (the total of 2,100–2,200 breeding pairs in 1994–96 given in TOMIAŁOJĆ & STAWARCZYK 2003 can be an overestimate, produced by summing up maximal numbers from a period of several years), and some 1,200–1,500 pairs in 2003–2004 (surveys by J. ANTCZAK, S. BZOMA & G. KILJAN). The largest colony situated at the Bielawki Islands, Szczecin Lagoon accounted to 900–1,000 pairs in 1991, *c.* 980 pairs in 1996, but only *c.* 70 pairs bred there in 2000 with single pairs left in 2002–03. At the same time, smaller colonies have been established on the roof-tops nearby, but they consisted of much less pairs (G. KILIAN, pers. comm.). Two more large *argentatus* colonies peaked in the 1980s and 1990s and are left nowadays: Vistula mouth near Gdańsk (up to 210 pairs 1994–95) and Gardno lake in Słowiński National Park, middle coast (up to 320 pairs in 1985, BEDNORZ 1983; GÓRSKI *et al*. 1990). At present, most of the Herring Gull population breeds on roof-tops in towns along the Baltic coast, where birds have moved from natural habitats. The largest roof-top colonies are situated close to the earlier mentioned natural breeding sites: in Ustka (450 pairs in 1996, ZIÓŁKOWSKI 1994; TOMIAŁOJĆ & STAWARCZYK 2003, but only *c.* 150 in 2004, J. ANTCZAK, pers. comm.) and Gdańsk-Gdynia-Sopot agglomeration area (estimated at *c.* 300 pairs in 2003–04, BZOMA 2001 and S. BZOMA, pers. comm.). Inland breeding sites (comprising up to 15 breeding pairs in most cases) are scattered in the northern part of the country (Fig. 1), at lakes and on river islands or in artificial reservoirs. The largest inland colony (which includes up to 30% of Caspian Gulls and hybrids) is located at Włocławek Reservoir, lower Vistula (see below, Photo 1) and comprised 135–143 breeding pairs in 2002–04. Single individuals and pairs were detected during 1995–2004 at the middle Vistula between Dęblin and Kozienice power station with Zastów Karczmiski being the southernmost locality currently known.

Caspian Gull *Larus cachinnans*

The first few breeding pairs were recorded in 1981–82 at the middle Vistula. Originally, they were reported as Herring Gulls *sensu lato* (WESOŁOWSKI *et al*. 1984), but subsequently were identified as *cachinnans* (BUKACIŃSKI *et al*. 1989; DUBOIS *et al*. 1990), although identity of these birds remained controversial (EIGENHUIS 1990; CHYLARECKI & SIKORA 1991; DUBOIS & STAWARCZYK 1991; EIGENHUIS 1991). Middle Vistula was the only place, where the putative Caspian Gull bred regularly until 1992, when the colony of unequivocal *cachinnans* in Tarnów was established (MARTYKA & SKÓRKA 1999; MARTYKA *et al*. 2002). A real information boom started in the late 1990s and coincided with a rapid increase in numbers. Breeding sites are now grouped mainly in the southern and eastern part of Poland and especially along middle and upper Vistula; these accounted together for *c.* 90% of the breeding population in 2004. The largest colonies in 2004 were the island near Zastów Karczmiski on the middle Vistula with *c.* 240 pairs (estimated to hold at least 90% of Caspian Gull, P. SZEWCZYK *et al*., pers. comm.; POTAKIEWICZ *et al*. in prep.; own data), Jankowice with *c.* 120 pairs and Mietków Reservoir with *c.* 40 pairs. The northernmost breeding site was Włocławek Reservoir, Lower Vistula (Photo 2). Between 1990 and 2004, Caspian Gulls bred in at least 31 sites (Fig. 1 and 2), rapidly increasing in numbers to reach a total of 480 breeding pairs in 2004. Between 1997 and 2004, the Polish population of Caspian Gulls

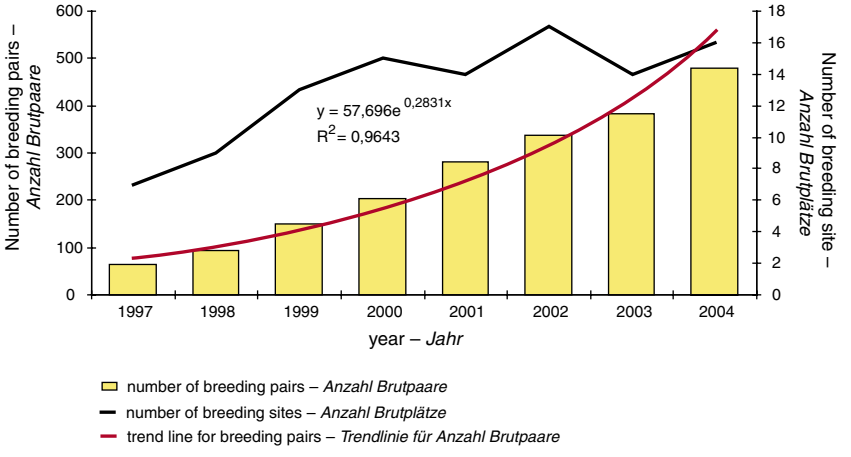

Fig. 2: Caspian Gull increase in Poland, 1997–2004. – *Zunahme der Steppenmöwe in Polen von 1997–2004.*

Photo 1. Yellow-legged Herring Gull *L. argentatus* '*omissus*' male near nest, Włocławek Reservoir, April 2004. – *Gelbfüßige Silbermöwe* L. argentatus "omissus", *Männchen nahe Nest, Włocławek-Stausee, April 2004.* Photo: G. NEUBAUER

Photo 2. Caspian Gull at nest, Włocławek Reservoir, April 2004. – *Steppenmöwe am Nest, Włocławek-Stausee, April 2004.* Photo: G. NEUBAUER

Photo 3-4: Presumed hybrid male Herring x Caspian Gull, ringed as a chick in 1994 at Włocławek Reservoir. May 2002. – *Vermutlicher Hybrid (Männchen) Silber- x Steppenmöwe, 1994 als Küken am Włocławek-Stausee beringt, Mai 2002.* Photos: M. ZAGALSKA-NEUBAUER

Photo 5-6: Presumed hybrid male Caspian x Yellow-legged Gull, ringed as chick in 1997 at Włocławek Reservoir. May 2004. – *Vermutlicher Hybrid (Männchen) Steppen- x Mittelmeermöwe, 1997 als Küken am Włocławek-Stausee beringt, Mai 2004.* Photos: M. ZAGALSKA-NEUBAUER

showed an exponential growth, with an annual rate of increase of 33% (Fig. 2).

Yellow-legged Gull *Larus michahellis*

Until now, breeding of this species has been proven at six sites (Fig. 1): Mietków Reservoir, Lower Silesia – single pairs in 1998 (POLA *et al*. 1998) and 2001; Nysa Reservoir, Lower Silesia – mixed pair with Caspian Gull in 2000–2001 (TOMIAŁOJĆ & STAWARCZYK 2003); Tarnów – three females trapped on two different nests in 2000 (including female-female pair, BETLEJA *et al*. in prep.); Jankowice, where two males were trapped in 1999 and 2001 (FABER *et al*. 2001), a female paired with a male Caspian Gull was found in 2003 (raised three young) and a female ringed as a chick in Italy – Basson, Porto Tolle, Rovigo (25th May 1997; 44° 58' N, 12° 32' E) was caught on the nest in 2004 (again a female-female pair, with Caspian Gull); Włocławek Reservoir with single female trapped at the nest in 2003 and seen again breeding next year. The only small 'population' breeding regularly was present in 1995–1999 at the middle Vistula islands between Dęblin and Kozienice power station: 1–3 breeding pairs were observed every year and 10 birds were trapped in total on the nests (Fig. 1, Fig. 3). After 1999, these birds probably moved to the newly established colony near Zastów Karczmiski (*c.* 70 km south of previous breeding sites), where in 2004 an alarming pair, probably with chicks nearby, one single bird paired with a Caspian Gull with chicks and one subadult were seen. Currently, it seems that no more than 5–10 pairs of Yellow-legged Gulls breed in Poland, some in mixed pairs with Caspian and Herring Gulls.

3.2. Hybrid zone

Until now, the most precise data about hybridisation come from three areas: Włocławek Reservoir ('northern zone'), middle Vistula river ('central zone') and

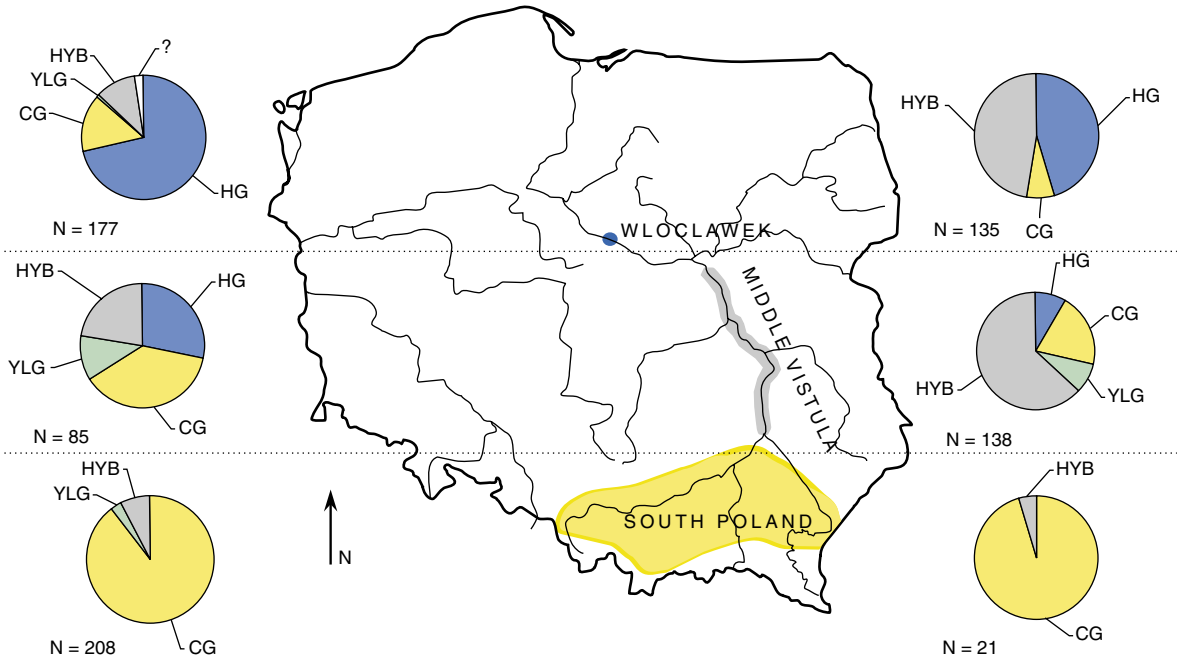

Fig. 3: Species structure in local large gulls populations, based on trapped birds (left side) and pair composition (right side) within the north-south gradient in Poland. HG Herring Gull (individuals left, pairs right), CG Caspian Gull, YLG Yellow-legged Gull, HYB hybrids or mixed pairs, '?' not identified individuals. – *Artenzusammenstzung lokaler Großmöwenbestände nach Fänglingen (links) und Paarzusammensetzung (rechts) innerhalb eines Nord-Süd-Gradienten in Polen. HG Silbermöwe (links Individuen, rechts Paare), CG Steppenmöwe, YLG Mittelmeermöwe, HYB Hbriden bzw. Mischpaare, "?" unbestimmte Individuen.*

southern-Polish area ('southern zone'). Hybridisation between the three forms is proven here by the presence of hybrids among trapped birds and mixed pairs (of which many are trapped as well; see methods). In general, mixed pairs are most common at the middle Vistula, where species composition is most balanced, with none of the species strongly predominating (Fig. 3); they are twice less common at Włocławek Reservoir where Herring Gull makes up *c.* 70% of the population. Again in southern Poland, where Caspian Gull dominates (90%), mixed pairs remain rare. This pattern suggests that mating is apparently random with respect to species identity (see below), with the frequency of interspecific pairs being roughly proportional to the frequency of various taxa in the local mate pool. The hybrid zone was inhabited by approximately 350–400 breeding pairs in 2003–04.

3.2.1. Population size in the hybrid zone

The first two nests at Włocławek Reservoir were found in 1985, followed by a continuous increase in colony size, reaching 32 pairs in 1990, *c.* 60 pairs in 1993, 116 pairs in 1998 and fluctuating between 133 and 143 pairs in the subsequent years. Caspian Gull numbers are still increasing at Włocławek Reservoir, with more birds and pairs observed each year, which is consistent with its range expansion.

The middle Vistula population initially increased strongly, from one pair in 1981–82 to 29 pairs in 1993 (BUKACIŃSKI & BUKACIŃSKA 1994) and 55–60 in 1998, but almost disappeared in 2002–04, when only 3–5 pairs remained. At the same time, a new colony was established in middle Vistula, *c.* 70 km south of the area occupied previously, where numbers rapidly grew from 5 pairs in 1999 to 240 pairs in 2004 (P. SZEWCZYK, pers. comm.). Among settlers in the new Zastów colony, there were birds coming from both the north and the south (Fig. 4; see also below).

In southern Poland, the colony in Tarnów was established in 1992 (1 pair) and increased continuously, reaching a maximum of 177 pairs in 2001. Increase in water level caused dramatic decline since 2002, coupled with simultaneous emigration of birds to Jankowice and Zastów (west and north, Fig. 4). This example also clearly shows the potential for a very rapid colonisation and range extension in Caspian Gulls. Another large colony, in Jankowice, has been established in 1998 (10 pairs) and after a rapid increase appeared to stabilise at *c.* 120 pairs in 2004.

To summarise, the number of breeding pairs in the hybrid zone still increases, which is mainly the result of range expansion and increasing numbers of Caspian Gulls. The fate of particular colonies remains unstable. Rapidly increasing new colonies, such as the one near

Zastów, are inhabited predominantly by Caspian Gulls which immigrated from the south. The local population is mostly homogenous, thus hybridisation frequency should remain at a low level.

3.2.2. Population structure and mixed pairing within the north-south gradient

At Włocławek Reservoir ('northern zone'), the population structure (based on 177 trapped birds in 2002–04) shows strong dominance of Herring Gull (126 individuals, 71%), followed by Caspian Gull (27 individuals, 15%) and hybrids (19 individuals, 11%), a single Yellow-legged Gull female and four unidentified birds (Fig. 3). Most of 19 birds classified as hybrids (16 individuals) showed characters intermediate between Herring Gull and Caspian Gull (Photo 3–4), and we suppose they were F1 hybrids. Six of them were ringed as chicks in Włocławek colony during 1992–99 (1992 – 1, 1993 – 1, 1994 – 2, 1999 – 2), except for one bird that originated from the middle Vistula (ringed 1995 as a chick near Tyrzyn Dworski, 51° 39' N, 21° 38' E). Another two putative hybrids showed a mixture of characters of all three species (newly ringed 2003–04 as adults in Włocławek) and one was clearly intermediate between Caspian Gull and Yellow-legged Gull (ringed as a chick in Włocławek in 1995, Photo 5–6). Assuming that these birds are F1 hybrids (which seems probable as intermediacy is most likely to be detected in the F1 generation), this would indicate that hybridisation occurred in the colony at least since 1992. At Włocławek Reservoir mixed pairs comprised about the half of the breeding pairs sampled (samples averaged *c.* 33% of all pairs) during 2002–04. Moreover, about a half of all mixed pairs in each season were comprised of two pure species – Herring Gull x Caspian Gull. Other mixed pairs included hybrids paired with pure birds or two paired hybrids. With four species categories distinguished (*argentatus*, *cachinnans*, *michahellis* and hybrids), mating in Włocławek was not significantly different from that expected if taxa do pair at random (G-test: $G^2 = 7.11$, df = 6, exact $P = 0.43$). Interestingly, however, in the 15 pairs of pure Herring Gull mated with other species or hybrids, 11 cases involved a male Caspian Gull or hybrid paired with a Herring Gull female while in only four cases a Herring Gull male was paired with a female of either Caspian Gull, Yellow-legged Gull or hybrid.

At middle Vistula ('central zone') 85 large gulls were trapped during 1995–1998 (Fig. 3). Among them, Caspian Gulls (32 individuals, 38%), Herring Gulls (24 individuals, 28%) and putative hybrids (19 individuals, 22%) were most numerous, with Yellow-legged Gulls being the rarest (10 individuals, 12%). Similarly to the 'northern zone', most hybrids showed characters

Photo 7: Part of the largest colony of large gulls in Poland, near Zastów Karczmiski, middle Vistula. May 2004.– *Ausschnitt aus der größten polnischen Großmöwenkolonie nahe Zastów Karczmiski, mittlere Weichsel, Mai 2004.*
Photo: G. NEUBAUER

intermediate between the two most numerous species, i.e. between Herring Gull and Caspian Gull. Despite high fluctuations in the number of breeding pairs, the percentage of pairs with both partners identified was rather high, on average 69%. The proportion of pure pairs was always lower or equal to the proportion of mixed pairs, and among the former the most frequent were pure Caspian Gull pairs, followed by Herring Gull pairs (Fig. 3). Again, among mixed pairs Herring x Caspian Gull pairs occurred most frequently.

Species structure in the 'southern zone' is the most homogenous, with very strong predominance of Caspian Gull, followed by hybrids (Fig. 3). Pure Herring Gulls were not recorded, but 11 of 16 hybrids showed characters intermediate between Herring and Caspian Gull (see FABER *et al*. 2001). Individuals intermediate between Caspian and Yellow-legged Gulls were less numerous. Data on pair composition in south Poland are scarce, due to difficulties with observations on the nests (dense herbage growth on islands): only in 21 pairs both birds were successfully assigned to species category. In 20 cases they were pure Caspian Gull pairs and one pair was comprised of Caspian and Yellow-legged Gull (2003, in Jankowice colony).

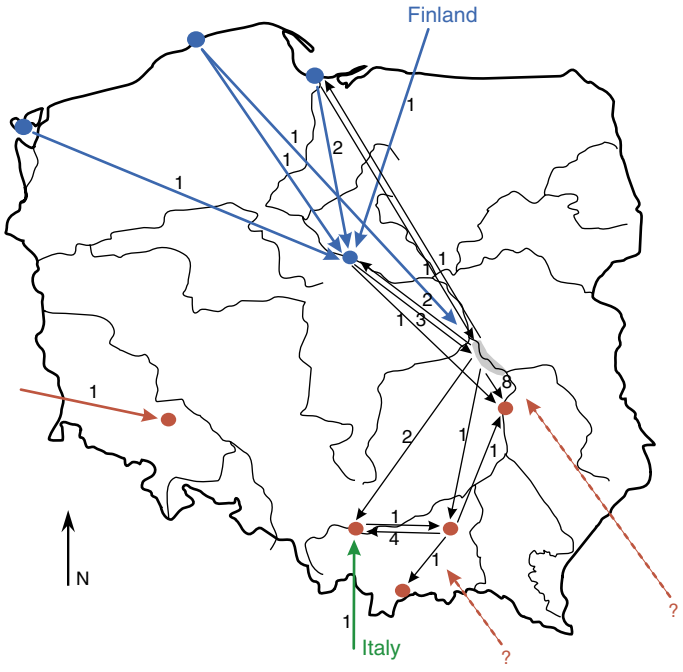

Fig. 4: Origin of foreign settlers in Polish colonies of large gulls and exchange of individuals between colonies within Poland. Numbers given at each arrow represent the number of individuals that moved between colonies and from abroad. – *Herkunft von Fremdansiedlern in und Austausch von Individuen zwischen polnischen Großmöwenkolonien. Zahlen geben die Anzahl der jeweiligen Fälle wieder.*

3.2.3. Other hybridisation cases

The only known case of hybridisation outside regularly studied colonies comes from Lower Silesia, SW Poland. A single mixed pair Caspian x Yellow-legged Gull was recorded at the Nysa Reservoir in 2000–01 (STAWARCZYK & TOMIAŁOJĆ 2003).

3.2.4. Origin of the central Polish population and exchange of birds between colonies within Poland

At the beginning, the population in central Poland was established by Herring Gulls from the Baltic Sea (Fig. 4), as six birds ringed as chicks at the coast were recovered as breeders at Włocławek Reservoir colony and another one at the middle Vistula. The origin of the numerous Caspian Gulls that breed in Poland is not known, probably due to scarce ringing activities coupled with huge populations in the Ukraine. The only Caspian Gull of known origin, recorded at Mietków Reservoir colony in 2001, was ringed as chick in another mixed colony near Sedlitz, E Germany in 1998 (T. STAWARCZYK, pers. comm.). The only Yellow-legged Gull of known origin was ringed in northern Italy and recovered on the nest in Jankowice in 2004.

In inland Poland, several movements of birds – ringed as either chicks or breeding adults and recovered as breeding birds – were noted, with almost equal numbers from north to south (from Włocławek to middle Vistula, from middle Vistula to southern colonies) and in the opposite direction (from southern colonies to middle Vistula, from middle Vistula to Włocławek and Vistula mouth). A significant east-west (five cases) and west-east (one case) exchange among southern colonies is documented as well (mainly between Tarnów and Jankowice, Fig. 4). Documented movements between middle Vistula and the southern zone concerned Caspian Gull, hybrids or Yellow-legged Gull (but not Herring Gull), whereas those between middle Vistula and the northern areas concerned Herring Gull, Caspian Gull or hybrids, but never Yellow-legged Gull. These data indicate that dispersal of birds occurs in almost all directions, with east-west movements dominating within the current range of Caspian Gull, and birds moving frequently in both directions along the north-south axis within the rest of inland Poland.

4. Discussion

Large gulls are new species in the breeding avifauna of Poland. All three species discussed here show a rapid range expansion and population increase, but in the case of Herring Gull this trend seems to be reversed more recently. Some old-established colonies in the

coastal zone tend to decrease or even disappear for various reasons, among which, in two known cases, the competition with Great Cormorant *Phalacrocorax carbo* (at Gardno and Łebsko lakes; GÓRSKI *et al*. 1990) and clutch predation by mammals (Wild Boar *Sus scrofa* and/or American Mink *Mustela lutreola* in Karsibórz islands, Szczecin Lagoon) are of greatest importance. Simultaneously, roof-top breeding became more common.

Caspian Gulls show a general trend of an extremely rapid increase, especially since 1990. However, the fate of particular breeding sites is highly variable (see above). The first breeding attempts are usually preceded by the presence of adult birds at the site for a few seasons. Numerous such observations made recently in southern Poland lead to the expectation of many new breeding sites appearing soon (P. SKÓRKA, pers. comm.) and suggest that the increase has not yet finished. As the Caspian Gull is the bigger, stronger, more aggressive bird and its laying peak is about one week earlier than in the Herring Gull (our unpublished data), the former is likely to win the possible competition between these two species. However, this may be considerably weakened due to partial mixing. Caspian Gull has bred as far north as in Włocławek (locality 1 on Fig. 1 – the northernmost breeding site in Poland) since 1990, when among 29 pairs of Herring Gulls the first three pairs were observed. Few birds ringed 1991–92, as either chicks or breeding adults, were still breeding there during 2002–04. This suggests that the expansion of Caspian Gulls has started well before than it was documented, but precise data are lacking. The numbers of Yellow-legged Gulls breeding in Poland could be higher than stated here, due to identification problems: misidentification with yellow-legged Herring Gulls of *omissus*-type and hybrids, low awareness of observers plus difficulties of finding – usually single – birds or pairs of this species in dense inland colonies.

The hybrid zone extends for not more than 300 km of Polish lowlands from north to south, as only Herring Gulls are breeding north of Włocławek Reservoir, whereas south of middle Vistula Caspian Gull is reported exclusively, with very few hybrids. The hybrid zone probably runs through the whole country from west to east, as mixed colonies are also reported east and west of Poland. Within the hybrid zone, as we mentioned earlier, mixed pairs constitute slightly less (Włocławek Reservoir) or a bit more (middle Vistula) than half of the local breeding population. We can therefore estimate that, in absolute numbers, about 200 pairs of large gulls took part annually in hybridisation events in Poland. It seems to be characteristic that hybrids and hybrid pairs are most often a mixture of Herring and Caspian Gull, i.e. the two commonest species at both Włocławek Reservoir and middle Vistula. Recoveries documenting movements of birds breeding in the hybrid zone support the hypothesis of probably unconstrained gene flow between northern Herring Gull and southern Caspian and Yellow-legged Gulls.

Hybridisation between closely related species is a relatively common phenomenon in birds (BARTON & HEWITT 1989), but usually occurs rarely in the areas inhabited by sympatrical, old, and stable populations of distinct taxa. On the other hand, inter-specific hybridisation may occur much more often in the areas of secondary contact established after expansion of one or two species. On newly colonised breeding sites at the edges of the breeding ranges, where one of the species is rare, and has limited chances to find the partner of its own species, inter-specific pairing may present the only mating option (MAYR 1963; HELBIG *et al*. 2002). The pattern of hybridisation among large gulls in Poland fits the classical scenario of a hybrid zone formed in the area of secondary contact of – three in this case – expanding and still closely related taxa.

In the newly established zone of sympatry in central Poland, and in the apparent absence of differences in habitat selection, all three gull taxa interbreed to a large extent. At the moment, pairing seems random with respect to species identity. Apparently, other prezygotic isolation mechanisms (like the display behavior or morphological differences, PIEROTTI 1987; PANOV 1989) are not strong enough to preserve species from interbreeding. This is very much in contrast to the situation reported from the Black Sea coast (KLEIN & BUCHHEIM 1997), where Caspian Gull and Yellow-legged Gull are clearly separated by habitat choice alone (although Herring Gull is absent there) or the situation described from Atlantic coast of France (YESOU 1991), where Yellow-legged Gull does not interbreed with Herring Gull. The hybrid zone in Poland is very young, lasting probably for no more than only 2–3 generations and at the moment it is impossible to predict what happens in the next years.

Further studies are needed to establish whether the hybrid zone will persist, extend or perhaps disappear after a short transition period. Persistence of hybrid zones occurs frequently and may be maintained by a balance between dispersal of parental taxa into the hybrid zone and inferiority of hybrids (a 'dynamic equilibrium' scenario; MOORE & BUCHANAN 1985) or by local, 'bounded superiority' of hybrids (as in Western/Glaucous-winged Gull complex [*Larus occidentalis/L.glaucescens*]; GOOD *et al.* 2000). Lack of selection against hybrids may result in an extension of the hybrid zone and eventually even in a merging of the parental taxa. In any case, extensive hybridisation opens gates to extensive gene flow between formerly differentiated taxa, challenging their status of separate species. Such extensive introgression may be asymmetric, favouring expansion of genes and phenotypes of only one parental species. In line with this, Włocławek

data suggests that hybridisation of Caspian and Herring Gulls is driven mostly by males of Caspian Gull (and their hybrids) mating with Herring Gull females. This fits the data of LIEBERS *et al*. (2004) showing mtDNA polyphyly of Herring Gull. On the other hand, possible inferiority of hybrids should lead to reinforcement of mechanisms isolating the three taxa. Clearly, comparative data on the fitness of hybrids versus pure taxa are badly needed here.

The phenomenon of hybridisation between large gulls, albeit relatively new, is not confined to Poland and probably includes other areas of inland, central Europe with eastern Germany, Poland, Belarus and Russia. Apart from Poland, mixed colonies of Herring and Caspian Gulls are known here from Volga River, central European Russia (MONZIKOV & PANOV 1996; PANOV & MONZIKOV 1999), probably also from eastern Germany (R. KLEIN pers. comm), and Belarus (YAKOVETS 2006). Thus, relationships between all the three taxa, particularly between *cachinnans* and *argentatus* that recently developed on lowlands of central and eastern Europe may indeed be quite different from those reported from other areas of their contact as suggested a decade ago (CHYLARECKI 1993). It remains to be seen, whether such a situation is just transitionary or represent a more stable phenomenon. At the moment, numerous hybrids produced in the contact zone described above will certainly add to the difficulties in separating large gulls in the field. In more general terms, the situation described here adds a new layer of complexity to the already notoriously difficult taxonomy of the complex. At the same time, however, it provides a quite unique area of further exciting research studies exploring mechanisms and dynamics of the hybrid zone.

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5. Zusammenfassung

Neubauer, G., M. Zagalska-Neubauer, R. Gwiazda, M. Faber, D. Bukaciński, J. Betleja & P. Chylarecki 2006: Brütende Großmöwen in Polen: Verbreitung, Bestände, Bestandstrends und Hybridisierung. Vogelwelt 127: 11 – 22.

Mit Silbermöwe *Larus argentatus*, Steppenmöwe *L. cachinnans* und Mittelmeermöwe *L. michahellis* brüten gegenwärtig drei Großmöwenarten in Polen, deren Situation hier aufgrund von eigenen Untersuchungen und publizierten Daten beschrieben wird. Silbermöwen siedelten sich in den späten 1960er Jahren an und nahmen bis zu den frühen 1990er Jahren rapide bis auf 1900–2100 Brutpaare zu. Das exponentielle Populationswachstum, das mit einer Arealerweiterung nach Süden und der Besiedlung des nordpolnischen Binnenlands einher ging, kehrte sich in den letzten Jahren wieder um, so dass zu Beginn des 21. Jahrhunderts etwa 1200–1500 Paare in Polen brüteten. Im Süden des Landes nahm der Brutbestand der Steppenmöwe von 1997–2004 jährlich um 33 % zu und erreichte im Jahr 2004 480 Paare. Die Mittelmeermöwe blieb dagegen eine seltene Brutvogelart, deren Brutbestand vermutlich nicht über 5–10 Paare hinaus geht. Hybridisierung findet vor allem zwischen den beiden häufigen Arten Silber- und Steppenmöwe statt. Verursacht wird sie vermutlich durch zufällige Paarbildungen in gemischten Kolonien im mittleren Polen. Am Mittellauf der Weichsel und im Włocławek-Stausee sind Mischpaare mit Anteilen von ca. 60 % bzw. ca. 40 % sehr häufig, in beiden Gebieten haben deshalb Hybriden einen hohen Anteil. Da die Brutkolonien in diesen Bereichen relativ instabil sind, wird der Austausch von Individuen zwischen Brutkolonien gefördert. Auch die häufig zu beobachtende Dispersion entlang einer Nord-Süd-Achse begünstigt Hybridisierungen.

6. Literature

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