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Colonization and population growth of Yellow-legged Gull *Larus cachinnans* in southeastern Poland: causes and influence on native species

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The Yellow-legged Gull *Larus cachinnans* was first recorded in Poland in the 1980s. We analysed the probable factors responsible for its successful colonization of new areas. We also expected that such a large species should affect populations of other colonial waterbirds. We studied the breeding and feeding ecology in the largest inland colony of the Yellow-legged Gull in Poland, located in a sedimentation basin near Tarnów (southeastern Poland). The first breeding pair was recorded in 1992 and the population reached 177 pairs in 2001. The population growth rate in this colony, of about 58% per year, fits an exponential model. Nine localities with breeding pairs have been found recently in southern Poland and we now estimate the total population size to be 200–250 pairs. The large clutch size, and high hatching and breeding success in the Tarnów colony suggest that food was plentiful. Food items were frequently found at the nests. Fish, mainly Carp *Cyprinus carpio*, were the predominant food items delivered to chicks; however, there was more refuse brought to nests during the incubation stage. Immigration probably caused the growth of the colony studied, although our calculations have shown that natal productivity alone is sufficient to maintain this population. The study showed that the growing population of Yellow-legged Gull might cause considerable reduction in the population sizes of some of the native waterbird species.

Many hypotheses attempt to explain the range size and distribution of species (Lawton 1993, Brown *et al.* 1996, Gaston 1996, Kirkpatrick & Barton 1997, Sagarin & Gaines 2002). It is believed that populations in the centre of the range occupy habitat of better quality and have a higher intrinsic rate of growth than those at the range margin (Lawton 1993). However, as populations of some species have increased rapidly, others have become vulnerable to extinction, and this is often associated with boundary range changes. Finding the factors that affect these changes is important in understanding the processes occurring in populations at a species' geographical boundary; this may be crucial for predicting the effects of population growth in invasive species, and may be helpful for conservation of endangered species. Yet few studies have addressed these issues.

There are essentially two possible explanations for range-size changes. First, range size may increase when high productivity occurs in central source populations, which causes intensive immigration into sink habitats located mainly at the range edge (Pulliam 1988). In this situation, range size relates to the source populations' productivity at the range centre, and range size should extend during periods of higher productivity. However, when the productivity of source populations drops, this should cause a reduction in range size because sink populations at the range boundary are unable to sustain themselves alone. Alternatively, sink habitats at the range edge may become source habitats. This is possible when individuals living in the sink habitats adapt to local conditions, or the habitat quality changes. In such cases, range size should grow rapidly over large areas and this change should last for long periods of time.

Colonial birds are excellent for the study of population processes (Boulinier & Lemel 1996, Barbraud *et al.* 2003), and they meet criteria proposed by Wells and Richmond (1995) for population studies to be comparable. In recent decades, populations of several gull species have grown rapidly and range

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expansion has followed (Hagemeijer & Blair 1997, Snow & Perrins 1998). It is believed that the availability of trawler discards, human refuse and the development of settlement along the shores of water bodies are the main factors. It has been demonstrated that the availability of anthropogenic food resources may be an important factor influencing the probability of winter survival and higher breeding success of some gulls (Kihlman & Larsson 1974, Bergman 1982, Wells 1994, Pons & Migot 1995, Gonzales-Solis *et al.* 1997, Oro *et al.* 1999, Bertellotti & Yorio 2000).

The Yellow-legged Gull *Larus cachinnans* belongs to a group of large white-headed gulls inhabiting the Holarctic region. Originally, this species occurred in the Mediterranean and Black Sea basins. The population size of this species has risen recently, and northward range expansion has followed (Fasola *et al.* 1993, Filchagov 1996, Scarton & Valle 1996, Hagemeijer & Blair 1997, Jonsson 1998, Snow & Perrins 1998). The first breeding pairs in Poland were recorded in the Middle Vistula valley in the late 1980s (Bukaciński *et al.* 1989, Dubois *et al.* 1990), and inland reservoirs in southern Poland have been colonized simultaneously (Faber *et al.* 2001). However, Yellow-legged Gull breeding biology in inland populations is poorly documented. The Yellow-legged Gull populations of southern Poland are at the northern edge of the species' range and are ideal for studying the functioning of marginal populations of an expansive species. Moreover, this gull is large and its presence as a breeder may have an important impact on native species.

We present new data on the breeding and feeding biology of this expanding Polish Yellow-legged Gull population, studied in the largest inland colony of this species. Our objectives were to verify whether populations at the range limit always exist in poorer habitats, as Lawton (1993) argues, and to determine which factors underlay the successful expansion of this species into inland areas. We also present evidence that the Yellow-legged Gull may have a negative impact on native waterbirds.

MATERIALS AND METHODS

Study area

The study was carried out in Poland's largest Yellow-legged Gull breeding colony, situated in the 'Czajki' sedimentation basins of the Nitrogen Works in Tarnów (a city of 130 000 inhabitants in southeastern Poland) (Fig. 1). These sedimentation basins cover 56 ha and the breeding colony was located in the former carbide residue sedimentation basin (20.7 ha). There were 85 small islets (1–50 m^2) and a larger island (1 ha). The islets offer breeding sites for gulls and many other species (Martyka & Skórka 2002). The study area is situated in the Biała and Dunajec river valleys. There are a few gravel pit complexes within the river valleys (about 500 ha in area), 2–4 km from the colony. There are also some fishponds (totalling about 150 ha), and a refuse dump in Tarnów 5 km to the east (Fig. 1).

Apart from Yellow-legged Gulls, Black-headed Gulls *Larus ridibundus* (over 2500 pairs in some years), Common Gulls *Larus canus* (11–18 pairs) and Mediterranean Gulls *Larus melanocephalus* (2–3 pairs) also bred in the study colony (Martyka & Skórka 2002).

Breeding biology

The Yellow-legged Gull population size was monitored from the first pair nesting in 1992 until 2001 (except in 1994, when gulls were not counted). To estimate population size all nests were counted between 25 April and 5 May by which time almost all clutches have been completed (Borowiec *et al.* 1981). In 1999, the colony was surveyed once a week while we made preliminary observations on Yellow-legged Gull breeding biology. Detailed breeding biology was studied in 2000 and the colony was surveyed from 20 March to 15 July at 1-day intervals during the egg-laying period and 2-day intervals during chick rearing. In addition, to determine the annual population dynamics in the colony and adjacent areas, all water reservoirs within a 5-km radius from the colony were visited from November 1999 to December 2000. This area covered most of the gull foraging grounds and all gulls that were seen within it were counted 1–3 times per month.

In 2000, during breeding-biology studies, each nest was counted and mapped on a plan of the sedimentation basin, and marked with a numbered wooden stake. Each egg was marked with a permanent marker and measured with a slide calliper to the nearest 0.1 mm. Egg volumes (V) were estimated from the formula: $V = L * B^2 * 0.476$, where L is length and B is breadth (Harris 1964). The first egg in each brood was labelled A, the second B and the third C. For several nests it was difficult to establish the succession of eggs directly and these nests were excluded from analyses.

Hatching success was established as the ratio of hatched chick number to (1) the number of eggs laid and (2) the number of eggs that survived up to

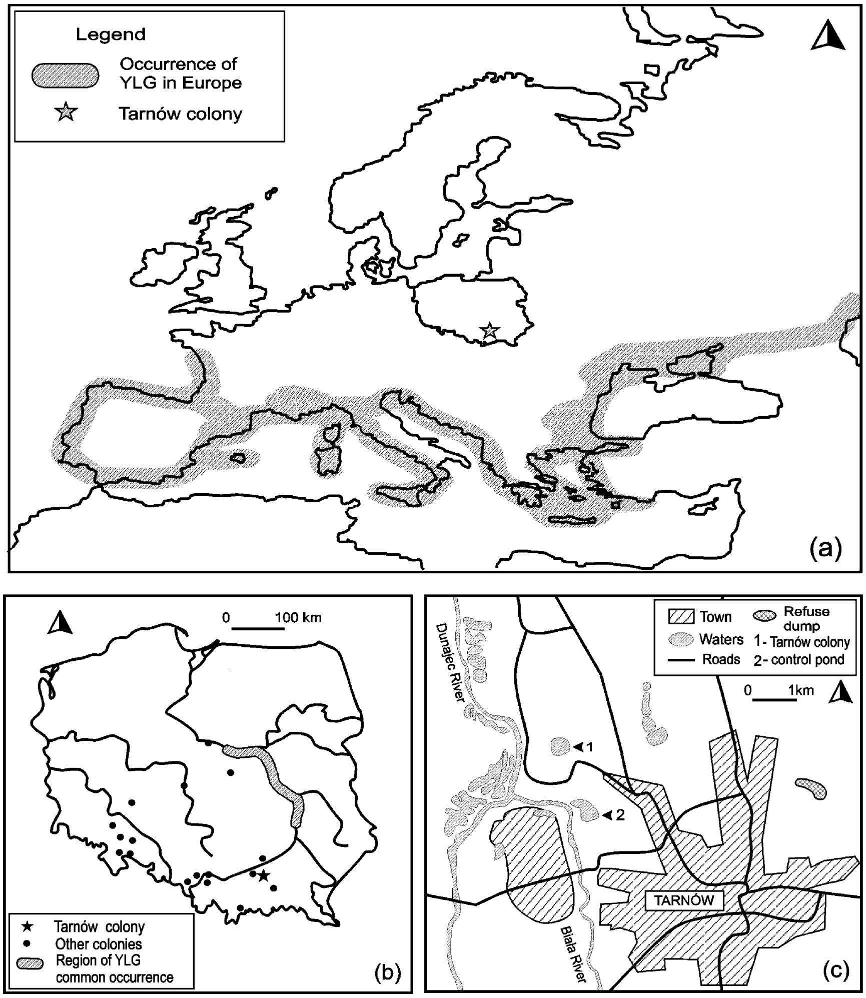

Figure 1. Location of the Tarnów colony in relation to (a) common occurrence of Yellow-legged Gulls in Europe (based on Hagemeijer & Blair 1997), (b) the most recent occurrence of Yellow-legged Gulls in Poland, based on Tomiałojć & Stawarczyk (2003) and our own data, and (c) the study area.

hatching. The breeding success was determined by counting all chicks with an average age of 40–50 days in mid-June; we also counted any chicks hidden in grass near nests or escaping onto water. The escaping chicks usually flocked close to the natal islets; moreover, counts were made such as to minimize the probability of pseudoreplication. Three counts were made within 10 days and we used the arithmetic mean to calculate breeding success (ratio of fledgling number to the number of pairs). The bias of this estimation is probably negligible because of a low gull chick mortality rate after the age of 2 weeks (Davis 1975, Hunt & Hunt 1976, Kilpi 1990, Brouwer *et al.* 1995). In 2001, breeding success was estimated roughly by counting juvenile birds present in the colony at the beginning of July. Because some young birds are able to fly at this time the count underestimated the breeding success. However, on the basis of exact counts in 1999 and 2000 as well as counts of juveniles made in July during these years, correction of breeding success estimation from 2001 was possible. At the beginning of July about 15% of juveniles leave the colony.

Diet

As food availability is a crucial measurement of habitat quality, all food items found at nests in 2000 were identified and measured. The food items were classified into two categories: eaten or uneaten. ‘Eaten’ food items were those entirely or partially eaten. The classification procedure was as follows:

when food items (e.g. fish) were first found during a visit as fresh and entire (probably just brought to nest) they were measured and marked and left at the nest as not classified. At the next visit these items might still be uneaten, in which case they were then classified as uneaten, or were partially eaten or there were remains of them. In both these latter cases they were classified as eaten. Food items that were no longer present at the next visit, without remains, were assumed to have been eaten. Sometimes during a visit, only the remains of food (not marked heads or fins, bones, etc.) were found and they could be classified directly as 'eaten'. Nevertheless, these remains were adequate to identify the species.

To mark fresh fish, after measuring their body length, dorsal and tail fins were cut and the skull was punctured. Food items other than fish were marked with a waterproof marker and by cuts on each side: in the case of dead birds and mammals, by cutting the left leg. This enabled us to recognize them from the new food items at the next survey. All food items, once classified, were removed from the colony. In our opinion, removing once-classified food from the breeding colony did not influence the frequency of food delivery to nests by adult birds, because food older than 2 days was not used by gulls and accumulated at the nest. Weather conditions, gull excrement and insects caused food items to decay very quickly. Fresh and partly eaten fish were identified according to Bryliñska (1992), and measured to the nearest 1 cm. Some fish had damaged heads, probably as a result of killing by adult gulls or of initial food preparation for chicks. It was therefore impossible to measure their body length. We also noted at which nest a given food item was found.

Regurgitations were excluded from the food analysis because sample sizes were too small (at 19 nests, in total 27 regurgitations were found, of which 26 contained fish debris and one contained a mole). A lack of regurgitations probably resulted from the fact that 90% of nests were situated adjacent to water, and they could be regurgitated by the gulls directly into the basin.

Population growth

To calculate the observed rate of population growth, the standard equation defining exponential growth was used: $N_{t+1} = N_t e^{rt}$, where N_{t+1} is the population size at time $t + 1$, N_t is the population size at time t, r is the rate of population growth, t is the time interval and e is the natural logarithm base. This equation may be rewritten as $r = (\ln N_{t+1} - \ln N_t)/t$.

Data analysis was performed to determine whether the Tarnów population could have sink or source characteristics (Pulliam 1988). First we investigated whether the study population could be maintained by 'native' birds alone in the absence of immigration. To determine this, we assessed what part of the observed population growth was caused by the production of young in the colony, using the equation $\lambda = \Phi_A + B\Phi_Y$, where Φ_A is the annual survival rate of adult birds, Φ_Y is the probability that young birds survive to reproduction age, and B is the mean number of female fledglings per pair. As $\lambda = e^r$, it is possible to calculate r after rewriting $r = \ln \lambda$. Thus, by comparison with what might be expected if this were a closed population, in which all birds were descended from the founder pair from 1992, r calculated in this way could also tell us whether the population is a source ($r > 0$) or a sink ($r < 0$). Because Φ_A and Φ_Y are unknown parameters in our population, the following published data for other similar and related gull species were used: 40% survival probability between fledging and breeding, 90% annual survival probability for adults, 5 years as the mean age at first breeding and a balanced sex ratio (Chabrzyk & Coulson 1976, Anderson *et al.* 1985, Migot 1992, Spear & Nur 1994, Pyle *et al.* 1997, Annett & Pierotti 1999). The nominal range sensitivity method (Saltelli *et al.* 2000) was used to assess the robustness of our conclusions within the range of possible input variables (survival rates). Thus, the rate of population growth, r, and predicted population size were also calculated assuming 70% and 95% adult survival rate, as well as 30% and 50% survival between fledging and breeding.

Impact on native species

Black-headed and Yellow-legged Gulls are protected by law in Poland. The Black-headed Gull, which is the most common gull species in Poland, occupies similar habitats to those of the Yellow-legged Gull. Thus, it is possible that the former is vulnerable to a Yellow-legged Gull increase in population. The number of breeding pairs of Black-headed Gulls has been monitored since 1996 in the Tarnów colony as well as in a control pond located about 1 km south, where the Yellow-legged Gull was absent. All Black-headed Gull nests were counted following the standardized method of Borowiec *et al.* (1981). Counts were made between 15 and 25 May, and in areas of high density of breeding pairs each nest was marked with white paint, to avoid double counting.

We also mapped the islets where these gulls nested, and noted whether the two species occurred on any one islet at the same time. Any aggressive behaviour between those gulls was also noted (P. Skórka *et al.* unpubl. data). In 2000, the time of clutch initiation of Black-headed Gulls was monitored on a sample plot of 213 nests in a way similar to that for Yellow-legged Gulls.

Statistics

ANOVA was used to test differences between egg size and number of food items found at nests of early, peak and late breeders during the incubation and chick-rearing stages. Our expectations were that differences in size between consecutive eggs as well as differences in the number of food items found at nests should be small if feeding conditions were good. A *t*-test was performed to test whether differences in size between eaten and uneaten fish were significant, to verify whether uneaten fish might simply be too large for gulls to swallow. We used goodness-of-fit χ^2 tests to test whether the number of nests at which food items were found differed from what was expected during the incubation and chick-rearing stages. Similarly, as with the ANOVA, we expected small differences between early, peak and late breeders under good feeding conditions, because the late breeders are usually young birds and are less experienced. We used linear regression to test whether the population growth fitted an exponential model. We used Spearman's rank correlation to verify whether changes in the number of pairs of Yellow-legged and Black-headed Gulls were related. The level of significance (alpha) was set at a probability of 0.05.

RESULTS

Phenology and breeding biology

Yellow-legged Gulls arrived in the breeding area at the beginning of December. At this time, they were recorded mainly in the Tarnów refuse deposit but during warm periods they often flew over the breeding site. We observed courtship behaviour and sporadic copulation at this time. The number of birds rose during winter and at the beginning of February birds started to hold territories in the colony. The first eggs were laid at the end of March; in 2000, the first egg was found on 24 March. Egg laying peaked between 5 and 12 April. The breeding colony was vacated in July, and the last birds were observed in mid-August. Until the end of November Yellow-legged Gulls were noted only sporadically in the study area. This is interesting because Yellow-legged Gulls are commonly observed throughout the autumn in the vicinity of Kraków and in the Upper Vistula valley (100–200 km west of the studied colony).

In 1999, we found 117 nests, among which three were recognized as female–female nests and two as repeated broods. In 2000, we found 130 nests, among which three probably belonged to female–female pairs and two were repeated broods. In 2000, the average egg volume was 87.4 ± 7.0 cm^3 for the A-egg ($n = 94$), 88.3 ± 9.2 cm^3 for the B-egg ($n = 94$) and 83.1 ± 7.3 cm^3 for the C-egg ($n = 94$). The C-egg was significantly smaller than eggs A and B (4.9% and 5.9% on average, respectively; ANOVA with Tukey's test, $F_{2,279} = 11.6$, $P < 0.001$, $n = 282$ eggs from three-egg clutches).

In 2000, the mean clutch size was 2.85 eggs (range 1–4, $n = 123$). Among 351 eggs, 11 (3.1%) did not survive to hatching. One nest was destroyed by a fox as it was situated on the shore of the sedimentation basin. In the other nests, the reason for disappearance of the eggs is unknown. Hatching success expressed as a ratio of hatched eggs to eggs laid was 96.9% ($n = 351$), and hatching success as a ratio of hatched eggs to eggs that survived to hatching was 98.8% ($n = 340$). Breeding success was 1.7 and 1.5 fledglings per pair in 1999 and 2000, respectively. In 2001 it was estimated at 1.7 fledglings per pair.

Food found at nests

We were surprised by the large number of food items found at nests. Many more food items were found during the chick-rearing period than during the incubation period (Appendix). In both periods fish were numerically dominant, but during incubation there was significantly more human refuse at nests, and less of other bird species from the breeding colony (Fig. 2).

Among fish, Carp *Cyprinus carpio* was the dominant species (Appendix). Of 255 fish noted at nests during chick rearing, 168 (66%) were at least partially eaten (among them 66 were originally recorded as uneaten, but by the next visit they were eaten or had disappeared). With regard to fish stored at nests, we found no significant differences in body length between fish classified as eaten (mean ± sd 14.5 ± 3.7 cm, $n = 43$) or uneaten (16.1 ± 5.6 cm, $n = 52$; $t_{93} = 1.631$, $P = 0.11$). Almost all fish noted at nests during incubation were entirely or partially eaten. Food items were noted at 23 nests during the incubation period

Table 1. Number of food items found at nests of Yellow-legged Gulls during the incubation stage and chick-rearing stage in relation to the date of clutch initiation.

		Time of clutch initiation			
		Early (before 5 April)	Peak (5–12 April)	Late (after 12 April)	Test of significance
Total number of nests		32	58	33	
Incubation stage					
Number of nests at which food items were found	Observed	3	15	5	$\chi^2_2 = 3.366$, ns
	Expected	6	10.8	6.2	
Mean number of food items per nest (± SD)		2.3 ± 1.5	2.6 ± 1.8	2.2 ± 0.8	ANOVA, $F_{2,17} = 0.122$, ns
Chick-rearing stage					
Number of nests at which food items were found	Observed	20	39	13	$\chi^2_2 = 2.882$, ns
	Expected	18.7	34	19.3	
Mean number of food items per nest (± SD)		4.9 ± 2.3	4.7 ± 2.3	3.1 ± 1.4	ANOVA, $F_{2,69} = 3.262$, $P < 0.05$

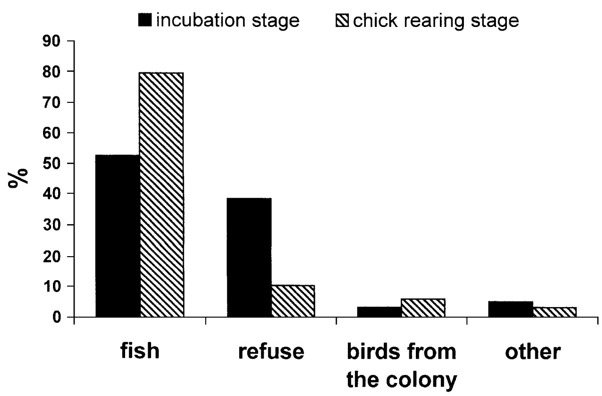

Figure 2. Comparison of the percentage share of different groups of foods found at nests of Yellow-legged Gulls during the incubation and chick-rearing stages. Differences between incubation and chick-rearing stages were significant ($\chi^2_3 = 85.4$, $P < 0.0001$).

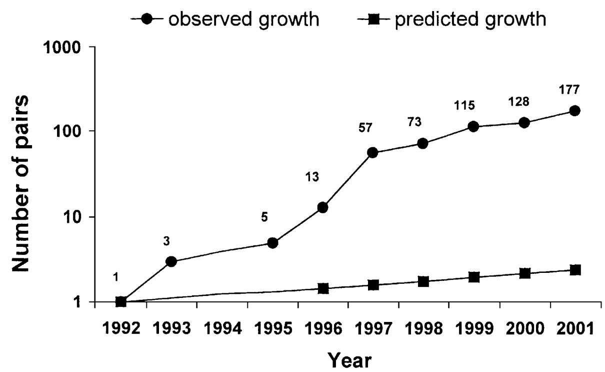

Figure 3. The observed population growth in the Tarnów colony (number of breeding pairs is shown) and predicted growth assuming that the population is closed. Note the logarithmic *y*-axis.

and at 72 nests during chick rearing (Table 1). The frequency of nests at which food was found did not differ significantly from that expected for early, peak and late breeders in either period. However, the late breeders probably delivered less food during the chick-rearing period (Table 1). The mean number of food items per nest was almost twice as high during chick rearing as during the incubation stage.

Population growth

The increase in number of Yellow-legged Gulls fits an exponential model of population growth (Fig. 3). The regression of pair number recorded by year from 1992 to 2001 was statistically significant ($F_{1,7} = 47.41$, $r^2 = 0.871$, $P < 0.001$). The average annual rate of population growth r was 0.58. This means that the population doubled in 1.2 years. Our calculation (assuming that all birds were descendants of the founder pair from 1992) showed that the production of young in this population is high enough to maintain it without immigration ($r = 0.21$); however, this explains only about 5% of the observed growth. A sensitivity analysis confirmed our results and showed that 70 and 95% adult survival rates would give 0.02 and 0.24 of the rate r of population growth, respectively, which would explain 1 and 6%, respectively, of the observed population growth. Similarly, juvenile survival rates of 30 and 50% calculations give 0.13 and 0.22 of the value of r, respectively, which means that only 2 and 8%, respectively, of the population growth could be explained by natal

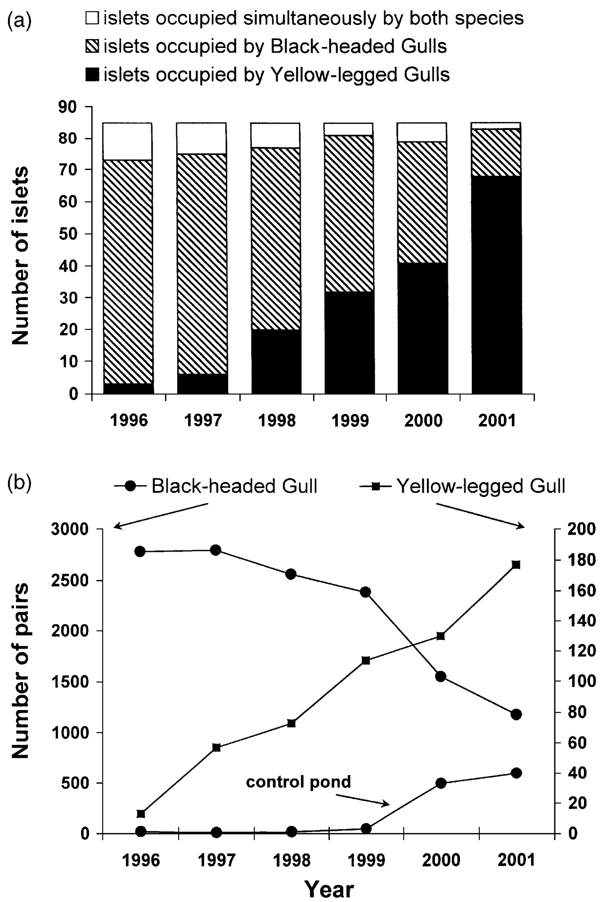

Figure 4. Effects of Yellow-legged Gull population growth on Black-headed Gulls. (a) Changes in number of islets occupied by both species, and (b) changes in number of pairs of both species ($r_s = -0.94$, $n = 6$, $P < 0.005$); the population trend of Black-headed Gulls at a control pond is also shown.

productivity. Thus, it is clear that the population was not maintained by descendants alone, but largely by immigration.

Impact on native species

Yellow-legged Gulls replaced Black-headed Gulls on breeding islets (Fig. 4a). These species cannot nest together on the same islet because the larger Yellow-legged Gulls are aggressive towards Black-headed Gulls, which are unable to compete successfully. Hence the number of Black-headed Gull pairs breeding in the colony was correlated negatively with the number of breeding Yellow-legged Gulls, whilst at the control pond the Black-headed Gull population increased simultaneously (Fig. 4b). Moreover, the Yellow-legged Gulls occupied territories from

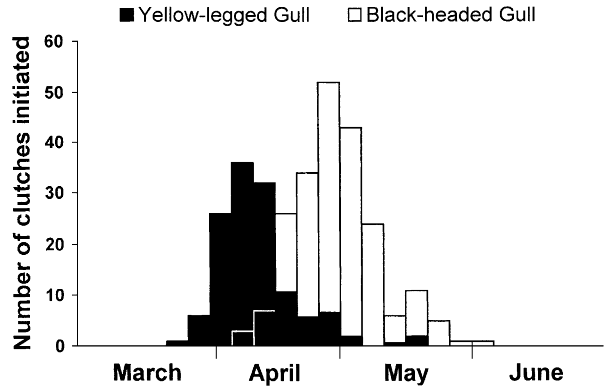

Fig. 5. Comparison of clutch initiation date distribution between Yellow-legged Gulls ($n = 123$ nests) and Black-headed Gulls ($n = 213$ nests) in the Tarnów colony.

February, and started nesting at the end of March: about 2 weeks earlier than Black-headed Gulls, which arrive in March and lay their first eggs in early April (Fig. 5). Similar results were found for Common Terns *Sterna hirundo*, which were entirely excluded from the breeding colony in 1999, despite there having been 49–60 pairs breeding in 1995 and 1996. This exclusion was caused by both Yellow-legged and Black-headed Gulls, which started to breed on islets that were formerly occupied only by Common Terns. It is worth noting that the Common Tern starts breeding in mid-May in the colony. There were too few pairs of ducks and grebes breeding in the colony to assess the effect of the increasing Yellow-legged Gull population on these species (see Martyka & Skórka 2002).

DISCUSSION

Population size and habitat selection

The first breeding attempt of Yellow-legged Gulls in southeastern Poland was recorded at the Starzawa Fishponds in 1989 (Walasz & Mielczarek 1992). Our studies of local literature and surveys of larger water habitats indicate that this species has recently been found in nine locations in southern Poland. We estimate the total population in southeastern Poland (over 60 000 km^2) at 200–250 pairs (Table 2). All recently discovered breeding sites were located in man-made habitats (artificial reservoirs, gravel pits and sedimentation basins), despite the fact that the predominant water habitats in southern Poland are fishponds (almost 70% of the area of all water habitats). The study colony was the largest of this

Table 2. Breeding colonies of Yellow-legged Gulls in southeastern Poland.

Location	Habitat	No. of pairs and population trend	Year of colonization
Tarnów (50°03′N, 20°56′E)	Sedimentation basin (20.7 ha)	177 (↑)	1992
Tarnów (50°01′N, 20°55′E)	Sedimentation basin (10 ha)	1 (↑)	2000
Radłów (50°05′N, 20°51′E)	Gravel pit (100 ha)	3–4 (↑)	1997
Bielowy (49°97′N, 21°05′E)	Gravel pit (110 ha)	2–3 (↑)	2001
Jankowice (50°30′N, 19°26′E)	Gravel pit (60 ha)	80 (↑)*	1998
Dwory (50°02′N, 19°15′E)	Gravel pit (30 ha)	1 (↓)‡	2000
Palczowice (49°99′N, 19°25′E)	Gravel pit (10 ha)	2 (?)‡	2001
Goczałkowice (49°55′N, 18°49′E)	Dam reservoir (3700 ha)	8 (?)*	2000
Czorsztyn (49°25′N, 20°18′E)	Dam reservoir (1200 ha)	7 (?)†	2000

Data from *Faber *et al.* (2001), †Walasz (2000) ‡Wiehle *et al.* (2002). Explanations: (↑)/(↓) increase/decrease of population size, (?) lack of data.

species in Poland and probably in central Europe (see Hagemeijer & Blair 1997, Snow & Perrins 1998).

Habitat quality within the studied colony

The large number of food items found in nests in the Tarnów colony indicates the high quality of feeding conditions in the area. Breeding success is also an accurate indicator of food supply (Pierotti & Annett 1990, Ricklefs 1990, Bukaciński *et al.* 1998, Oro *et al.* 1999, Gill *et al.* 2002). The small differences in size between eggs in the Tarnów colony (C-egg differed by only 4.9 and 5.9%, respectively, from A- and B-eggs) further support the view that feeding conditions were good. Many studies suggest an association between reduced variation in size between eggs within a clutch and high breeding success (Davis 1975, Pierotti & Bellrose 1986, Kilpi 1995, Kilpi *et al.* 1996). Kilpi *et al.* (1996) showed that a difference between the third egg (C) and the first two (A and B) of less than 10% was indicative of very good feeding conditions. Birds from Tarnów made extensive use of the refuse dump to forage during the prebreeding and laying periods (our pers. obs.). During warmer periods some birds were seen fishing in the Dunajec and Biała rivers and in gravel pits. During the breeding season fishponds provided the main source of food, and carp dominated in the food items brought to the nests. Carp farming is an ancient tradition in Poland: Carp is the dominant species in fishponds (Brylińska 1992, Dobrowolski 1995). In our opinion the management of fish in southern Poland may be a key factor contributing to the high breeding success of Yellow-legged Gulls and its successful colonization (see also Hüppop & Hüppop 1999).

The most interesting phenomenon was the number of food items brought by gulls to the nests. Fish and human refuse were common items and were observed during each year of the study. Originally, we believed that the uneaten fish were simply too large for chicks to swallow. However, the analysis showed that these fish were no larger than those eaten by the chicks. In fact, at one nest we simultaneously found uneaten small fish as well as the remains of a much larger fish. Moreover, observation showed that gulls usually tear food into pieces while eating, and only small fish are swallowed whole. Numerous uneaten fish were also discovered by Atwood and Kelly (1984) in colonies of Least Tern *Sterna antillarum browni*, where the number of stored fish was greater during years of higher tern breeding success. Similar observations were made by Pierotti and Bellrose (1986) for Western Gulls *Larus occidentalis*. Thus, it is possible that gulls from the Tarnów colony also stored food for chicks. Källander and Smith (1990) and Olech and Pruszyñski (2000) present data for such behaviour for other bird species. These authors indicated that food storing was associated with high food availability and greater than average clutch and egg sizes. We have also found numerous uneaten fish in Poland's next-largest colony of Yellow-legged Gulls, located in a gravel pit near Jankowice. We believe therefore that the numerous food items recorded at nests in the Tarnów colony reflect the rich food resources available in this habitat, and most significantly that these resources probably do not fluctuate considerably from season to season.

There are further clues that the feeding conditions for breeding birds are good at these sites. For example, we recorded no instances of behaviours associated with food shortage, such as cannibalism or a bird eating its own eggs (Chardine & Morris 1983, Spaans *et al.* 1987, Hario 1990); indeed we recorded almost no egg losses. Only sporadic cases of kleptoparasitism were recorded in either the colony or the feeding areas during the breeding season. This behaviour in gulls is recognized as a dominating strategy when food is in short supply (Oro 1996, Gonzales-Solis *et al.* 1997). The date of clutch initiation probably also has no impact on food availability. Our analysis showed that early breeders probably stored food at nests at the same frequency as middle and late breeders. However, late breeders stored fewer food items during the chick-rearing period, probably because they are mainly young, inexperienced birds (Pyle *et al.* 1991, Sydeman *et al.* 1991, Sydeman & Emslie 1992). All these elements indicate very good feeding conditions for breeding gulls in the Tarnów colony, and this is probably true of other Yellow-legged Gull colonies in southern Poland. Breeding success in the Tarnów colony was amongst the highest noted for any gulls in Europe (Kilpi 1990, Yésou 1991, Kilpi *et al.* 1996, Bosch & Sol 1998).

There are probably no environmental factors other than food resources influencing breeding success in the Tarnów colony. Yellow-legged Gulls nest on islets where they encounter few natural enemies other than the Yellow-legged Gulls themselves; foxes rarely reached the islets. Moreover, the Yellow-legged Gull is a large bird, which successfully competes for nest-sites with other species (see below), and which is effective in defending chicks. Weather conditions might influence birds in extreme cases, but no such conditions occurred during this study.

Population growth and colonization process

The population growth observed during the study was very high, and the exponential model fits the data well. Our calculations (assuming all birds are descended from the founder pair from 1992) showed that immigration was probably almost exclusively responsible for the high growth rate of the Tarnów population. Moreover, on average, large gulls start breeding at the age of 5 years. Thus, if birds were descended from the founder pair, the population's growth would first be noticed in 1996. This is also confirmed by the study of Oro and Ruxton (2001), who found a population of Audouin's Gull *Larus audouinii* that grew at 44% per year. They showed that observed growth could not be explained without large-scale immigration of individuals. However, our calculations also proved that breeding success is high enough to maintain this population through natal recruitment ($r > 0$), thus indicating that the population could itself be a source. The assumptions and parameters used in the calculations are, in our opinion, realistic and the results of simulation are close to what was observed.

Our results suggest several possible mechanisms for population development of Yellow-legged Gulls in southern Poland. One mechanism suggests that suitable habitats were present in southern Poland, but they could not be colonized until considerable immigration had occurred. The number of habitats available at the range boundary is lower than in the centre, and thus colonization of these areas could only be achieved by immigration (Lawton 1993, Holt & Keitt 2000). Colonization and population development of the Yellow-legged Gull in southern Poland could therefore result from population explosions in the Mediterranean and Black Seas basins (Fasola *et al.* 1993, Hagemeijer & Blair 1997, Jonsson 1998, Snow & Perrins 1998, Vidal *et al.* 1998).

Alternatively, because Yellow-legged Gulls have been observed in southern Poland during breeding periods since the 1980s but the first cases of breeding were only noted in the 1990s (Walasz 2000), it is possible that the habitat quality was not suitable initially to support breeding. However, we have no evidence that habitat quality or availability have changed considerably over the last two decades. This is a general problem because immigrants are more likely to be adapted to their natal habitat than to new ones outside their normal range. Our results show that in the Tarnów population, the habitat has characteristics of a typical source despite the net immigration. It is possible that Yellow-legged Gulls inhabiting inland areas had to adapt to local environmental conditions to enable them to breed there successfully. For individuals that have adapted to sink habitats, this has made range-edge habitats available. Thus, the inversion of the sink populations of Yellow-legged Gulls into sources could also occur. As the proportion of sink habitats is greater at the range boundary, such adaptation could allow rapid colonization and a high rate of population increase. However, more studies in different parts of the range of the Yellow-legged Gull are necessary to understand fully the range-size changes.

Impact on native species

Our results indicate that the Yellow-legged Gull is a strong competitor, and that it may cause the populations of some species to decline in future. In the study colony, the Black-headed Gull population has declined rapidly. So far, in southern Poland, Yellow-legged Gulls have bred almost exclusively in man-made reservoirs (gravel pits, sedimentation basins and artificial reservoirs). Of the total population of Black-headed Gulls in southeastern Poland (estimated at 20 000–30 000 pairs, Walasz & Mielczarek 1992) about 6000 (20%) breed in industrial reservoirs. Thus, if the population growth of the Yellow-legged Gull continues, it might cause a decline in Black-headed Gull numbers of about 20%. We might also ask why Yellow-legged Gulls do not breed in fishponds, which are the dominant freshwater habitat in southeastern Poland. Other studies have also shown that Yellow-legged Gulls might exclude other species from their breeding grounds, mainly through predation and their earlier breeding (Fasola *et al*. 1989, Vidal *et al*. 1998). In the Tarnów colony the predation of Yellow-legged Gulls on other locally nesting birds was probably not significant. The exclusion of Black-headed Gulls was caused mainly by the earlier breeding of Yellow-legged Gulls, which hold breeding territories from February, thus making them inaccessible for smaller and later-breeding species. For a smaller species to remove a larger one from a breeding site, it has to be more numerous and more aggressive (Quintana & Yorio 1998). Although aggressive encounters were often observed on the ground between these gull species in the Tarnów colony, the Yellow-legged Gulls were always able to exclude Black-headed Gulls.

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Appendix. Food found at nests of Yellow-legged Gulls during incubation and chick-rearing stages and its quantitative composition.

	Incubation stage		Chick-rearing stage	
Food item	*n*	%	*n*	%
Fish				
Cyprinus carpio	12	21.1	211	65.9
Rutilus rutilus	10	17.5	23	7.2
Alburnus alburnus	1	1.8	8	2.5
Tinca tinca	–	–	4	1.3
Barbus barbus	–	–	2	0.6
Abramis brama	–	–	2	0.6
Carassius carassius	–	–	1	1.3
Leuciscus cephalus	5	8.8	1	1.3
Unidentified fish	2	3.5	3	0.9
Birds from the colony				
Larus ridibundus – chicks	–	–	10	3.1
L. ridibundus – eggs	2	3.5	7	2.2
L. ridibundus – adults	–	–	2	0.6
Gallinula chloropus – chick	–	–	1	0.3
Refuse	22	38.6	34	10.6
Other				
Talpa europaea	1	1.8	2	0.6
Microtus arvalis	1	1.8	2	0.6
*Lumbricidae**	–	–	2	0.6
Gryllotalpa gryllotalpa	–	–	1	0.3
Rana sp.	1	1.8	1	0.3
Hirundo rustica	–	–	1	0.3
Turdus merula	–	–	1	0.3
Mustela nivalis	–	–	1	0.3
Total	57	100	320	100

*At two nests 50 specimens in total.