



# Do invasive species undergo metapopulation dynamics? A case study of the invasive Caspian gull, *Larus cachinnans*, in Poland

Magdalena Lenda<sup>1\*</sup>, Magdalena Zagalska-Neubauer<sup>2,3</sup>, Grzegorz Neubauer<sup>3</sup> and Piotr Skórka<sup>4</sup>

<sup>1</sup>Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland, <sup>2</sup>Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Kraków, Poland, <sup>3</sup>Ornithological Station, Museum and Institute of Zoology, Polish Academy of Sciences, Nadwiślańska 108, 80-680 Gdańsk, Poland, <sup>4</sup>Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71 C, 60-625 Poznań, Poland

## ABSTRACT

**Aim** The mechanisms of initial dispersal and habitat occupancy by invasive alien species are fundamental ecological problems. Most tests of metapopulation theory are performed on local population systems that are stable or in decline. In the current study we were interested in the usefulness of metapopulation theory to study patch occupancy, local colonization, extinction and the abundance of the invasive Caspian gull (*Larus cachinnans*) in its initial invasion stages.

**Location** Waterbodies in Poland.

**Methods** Characteristics of the habitat patches (waterbodies, 35 in total) occupied by breeding pairs of Caspian gulls and an equal sample of randomly selected unoccupied patches were compared with *t*-tests. Based on presence–absence data from 1989 to 2006 we analysed factors affecting the probability of local colonization, extinction and the size of local populations using generalized linear models.

**Results** Occupied habitat patches were significantly larger and less isolated (from other habitat patches and other local populations) and were located closer to rivers than empty patches. The proximity of local food resources (fish ponds, refuse dumps) positively affected the occurrence of breeding pairs. The probability of colonization was positively affected by patch area, and negatively by distances to fish ponds, nearest habitat patch, nearest breeding colony and to a river, and by higher forest cover around the patch boundaries. The probability of extinction was lower in patches with a higher number of breeding pairs and with a greater area of islets. The extinction probability increased with distances to other local populations, other habitat patches, fish ponds and to refuse dumps and with a higher cover of forest around the patch boundaries. The size of the local population decreased with distances to the nearest habitat patch, local population, river, fish pond and refuse dump. Local abundance was also positively affected by the area of islets in the patch.

**Main conclusions** During the initial stages of the invasion of Caspian gulls in Poland the species underwent metapopulation-like dynamics with frequent extinctions from colonized habitat patches. The results prove that metapopulation theory may be a useful conceptual framework for predicting which habitats are more vulnerable to invasion.

## Keywords

Birds, colonization, corridors, food resources, isolation, *Larus cachinnans*, local extinctions, patch occupancy, patch size, Poland.

\*Correspondence: Magdalena Lenda, Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Kraków, Poland.  
E-mail: lenda.m@vp.pl

## INTRODUCTION

Metapopulation theory states that local populations living in smaller and more isolated habitat patches will undergo extinctions more often than populations inhabiting large habitat patches located close to one another, which can be easily recolonized (Levins, 1970). This theory has been tested many times (Hanski & Gilpin, 1997; Hanski, 1998; Verbeylen *et al.*, 2003), modified (e.g. sink–source concept; Pulliam, 1988) and its dynamic has been considered in patch systems where colonization and extinction rates were at equilibrium, as stated in Levins' original model (Levins, 1970). The value of this concept is widely recognized in many areas of nature conservation since habitat fragmentation has become the major cause of extinction of local populations and of biodiversity loss in general (Saunders *et al.*, 1991; Gyllenberg & Hanski, 1997; Hanski & Ovaskainen, 2000; Lindenmayer & McCarthy, 2001).

Recently, the metapopulation concept has been successfully applied to research on species that are increasing and invading other patches, where the assumption of equilibrium does not hold (Marvier *et al.*, 2004; Seno & Koshiba, 2005). However, these are mostly theoretical studies; empirical examinations of metapopulation predictions for invasive species remain scarce, yet are crucial, especially during the initial stages of invasion (Puth & Post, 2005; Eraud *et al.*, 2007). Invasive species disperse easily and cause enormous damage to biodiversity and valuable natural systems as well as to the human economy (Byers *et al.*, 2002; Clavero & García-Berthou, 2005; McGeoch *et al.*, 2010). Invasive alien species can transform the structure and composition of species in ecosystems by repressing or excluding native species either directly, by out-competing them for resources, or indirectly, by changing the way in which nutrients are passed through the ecosystem. Additionally, invasive species adapt quickly and efficiently to new environmental conditions (Hänfling & Kollmann, 2002).

Knowledge on how species become invasive is urgently needed, as it is difficult to predict which areas may be invaded. If invasive species undergo metapopulation dynamics it would be possible to predict which habitat patches are more vulnerable to invasion and to undertake specific action that may minimize the negative effects of invasion.

The aim of this study was to examine if the application of metapopulation theory to invasive species is appropriate, and whether, based on the predictions of the theory, it is possible to recognize a mechanism of initial range spread and to predict which habitat patches are prone to further invasion. We used the invasive Caspian gull (*Larus cachinnans* Pallas, 1811), as a model species. Colonial waterbirds are excellent for research on metapopulation processes. They often occupy inland waterbodies and lakes, which are naturally isolated and easily identifiable habitat patches. Breeding colonies of waterbirds differ genetically (Burg *et al.*, 2003), which provides an argument for the examination of their population dynamics in the light of metapopulation theory (Esler, 2000; Burg *et al.*, 2003; Matthiopoulos *et al.*, 2005).

In our study we tested two hypotheses. The first is that population abundance, the probability of local colonization and patterns of patch occupancy are influenced by characteristics of landscape structure. That is, habitat patches occupied by the Caspian gull should be larger, less isolated from both other habitat patches and other local populations, closer to ecological corridors (Skórka *et al.*, 2009; Maciusik *et al.*, 2010), food resources and further from barriers (Harris & Reed, 2002) than unoccupied ones. Also, the occupied patches should have larger islets (nesting sites) than unoccupied habitat patches. The probability of local colonization, and local population abundance, should be influenced by these factors in the same way as for patch occupancy. The second hypothesis is that the probability of extinction of the local population depends on both landscape and population features, i.e. the extinction of a local population is expected to be higher in habitat patches that are small, isolated, surrounded by barriers and far from ecological corridors and food resources. The probability of local extinction should also be lower in more abundant populations.

## MATERIALS AND METHODS

### Study species

The Caspian gull is a colonial species that inhabits waterbodies, referred to as 'habitat patches' (we use both terms interchangeably throughout the text), especially in the breeding season. The native range of this species extends from the Black Sea eastwards through the steppe zones, reaching eastern Kazakhstan (Malling Olsen & Larsson, 2004). In recent decades the Caspian gull population has grown rapidly and expanded north and west, mainly along large river valleys (Filchagov, 1996; Jonsson, 1998). The main reasons for this extensive expansion were the availability of trawler discards from fishing boats, domestic refuse and a high breeding success in newly colonized areas (Fasola *et al.*, 1993; Jonsson, 1998; Skórka *et al.*, 2005). In fact, the availability of food resources from domestic refuse may be an important factor influencing the probability of winter survival and higher breeding success of some gulls (Oro *et al.*, 1999; Bertellotti & Yorio, 2000). Furthermore, in many countries the Caspian gull has become a species protected by law. The first breeding pairs in Poland were recorded in the Middle Vistula valley in the late 1980s, and inland waterbodies in southern Poland were colonized a few years later (Faber *et al.*, 2001). The significant, harmful effect of large, alien gulls on biodiversity is well known (Vidal *et al.*, 1998; Skórka *et al.*, 2005; Wójcik *et al.*, 2005). Caspian gulls breed in colonies that consist of up to a few thousand breeding pairs (along the coast or on marine islands) or a few hundred breeding pairs (on inland waterbodies). During the breeding season, from the end of March to the beginning of June, the colonies are mostly located on islets or shores (Skórka *et al.*, 2005) and the diet of this species at this time largely consists of fresh fish, mainly carp (*Cyprinus carpio*). The diet of some Caspian gulls includes other bird nestlings and



**Figure 1** Map of Poland with all breeding localities of the Caspian gull (*Larus cachinnans*) (grey circles) and the random sample of unoccupied habitat patches (black circles).

small mammals. After the breeding season, domestic refuse becomes a more important component of their diet (Skórka & Wójcik, 2008). The northern limit of this species' breeding range is in Poland and breeding localities within Poland are concentrated in the southern part of the country (Fig. 1) (Skórka *et al.*, 2005; Neubauer *et al.*, 2006).

## Data

Data on the waterbody breeding sites of Caspian gulls presented in this paper were collected by the authors and other local ornithologists as part of a national census for Poland. Most of the waterbodies in which we found breeding gulls were surveyed every year between 1989 and 2006. In the case of seven waterbodies, the surveys were irregular before gulls were found breeding there. However, after breeding gulls were found, all waterbodies were monitored every year. Note that this is not a problem for the analyses (see below) as the models we used allow for missing data (MacKenzie *et al.*, 2003, 2005). Waterbodies were surveyed during breeding seasons (April–May) and if observers found a Caspian gull breeding colony then the waterbody was monitored each year. It was assumed that breeding occurred where nests or adult birds with chicks were observed. In this study we only studied nest localities on inland waterbodies. This excluded breeding colonies on islands in the River Vistula due to the difficulty of defining and accurately measuring the area of the waterbody. However, colonies from the river were included in the analysis of the effects of distance to the nearest local population.

Habitat patches with breeding pairs (35 patches in total) were characterized from aerial photographs. An equal, random sample of habitat patches, where breeding gulls had never been

observed, was also chosen to compare with the occupied habitat patches. The sample of unoccupied waterbodies was obtained by a random selection of geographical coordinates within the species' range in Poland. We randomly selected a latitude and longitude position and then located the nearest unoccupied waterbody. Moreover, these waterbodies had to be visited every year by the observers in the study period. In the study we initially expected to include other known Caspian gull colonies in neighbouring countries. However, we only analysed data from Poland because colonies in Poland were much less isolated from one another and also formed a more complete system of local populations. An occupied habitat patch was defined as a waterbody where Caspian gull nesting was observed at least once between 1989 and 2006. Several characteristics (covariates) of occupied and unoccupied habitat patches were measured: the habitat patch area (ha), distance (km) to the nearest local population, distance (km) to the nearest waterbody larger than 5 ha, distance (km) to the nearest river that was longer than 100 km, distance to the nearest fish pond, distance to the nearest refuse dump, islet area (m<sup>2</sup>; also recorded in the field study), and forest coverage around the waterbody within 3 km from the edge of the patch.

Waterbodies that were < 50 m apart were treated as a single habitat patch. Such a situation was commonplace at fish ponds grouped in complexes where ponds were separated only by embankments (width about 20–50 m), and were utilized by gulls as a single habitat patch. Distance to the nearest occupied patch was treated as an isolation index of local populations. Breeding colonies on islets in the River Vistula were included in this analysis, because coordinates of occupied islets were known.

The distance to the nearest waterbody over 5 ha was also used as an isolation index of the habitat patch. The choice of 5 ha is because this is the smallest area in which a breeding colony has been observed. The inclusion of other smaller waterbodies could lead to meaningless results. All calculations were made using the software program AUTOCAD (Autodesk Inc., 1988).

## Data processing and statistical analysis

### *Modelling factors affecting patch occupancy ( $\psi$ ), local colonization ( $\gamma$ ) and extinction ( $\varepsilon$ ) probabilities*

We compared features of occupied and unoccupied habitat patches (both  $n = 35$ ) using two-sample *t*-tests with equal variance. The Šidák–Bonferroni correction (Šidák, 1971) was applied to account for multiple testing and the significance level was thus set to  $\alpha = 0.005$ . Data were  $\log_e$  or arcsin transformed where necessary.

We used an approach introduced by MacKenzie *et al.* (2003, 2005), and the probabilities of local colonization  $\gamma$  (proportion of patches not occupied at time  $t$  which were occupied at time  $t + 1$ ) and extinction  $\varepsilon$  (proportion of occupied patches at time  $t$  which were not occupied at time  $t + 1$ ) were modelled using a generalized linear model with a logit link function. Presence–absence data and resulting estimates can be con-

founded by detection error, namely that a recorded 'absence' may in fact be a non-detection of nesting individuals rather than a true absence. Using such data with naive estimates will most likely result in underestimates of occupancy and colonization probabilities and overestimates of extinction probability (MacKenzie *et al.*, 2003, 2005). If a detection probability can be calculated, then unbiased estimators of colonization and extinction probabilities can be derived. Calculations were performed with the program PRESENCE 2.2. (Hines, 2006).

The Akaike information criterion corrected for small sample size (AICc) was used to identify the most parsimonious model from each candidate set. The model building procedure was as follows. First we built models to find out if  $\gamma$  and  $\varepsilon$  differed from zero (a null model). We then compared models in which  $\psi$ ,  $\gamma$  and  $\varepsilon$  were constant among years with models in which  $\psi$ ,  $\gamma$  and  $\varepsilon$  were year-specific. We also compared a model of metapopulation at equilibrium ( $\gamma = 1 - \varepsilon$ ) with a model where assumption of equilibrium was violated. We then included covariates that could affect  $\gamma$  and  $\varepsilon$ . We started with a saturated model, and in the next steps we removed covariates one by one based on an evaluation of standard errors (the covariates of  $\gamma$  and  $\varepsilon$  that had the largest standard errors were removed from the model). Finally, we ranked the models according to their  $\Delta$ AICc values and used the model with the lowest AICc together with associated weight values (probability that a given model is the best) as that best describing the data. Where there was support for more than one model ( $\Delta$ AICc < 4), we used the most inclusive model (the model that included the largest number of variables). We used model averaging for estimates of function slopes (betas) of parameters of interest (Burnham & Anderson, 1998). AICc values were also adjusted to allow for the extent of overdispersion measured by the variance inflation factor (*c-hat*) (Cooch & White, 2001). An important consequence of adjusting *c-hat* is that sampling variances are inflated, which leads to a lower risk of falsely identifying a model factor as important, i.e. of making a Type 1 error (Lebreton *et al.*, 2003). Recent literature has increasingly advocated the use of AIC values as a standard model selection procedure (Burnham & Anderson, 1998; Anderson & Burnham, 1999). Using information criteria to select amongst candidate models obviates problems associated with multiple testing in classical statistics (Burnham & Anderson, 1998). Likelihood ratio (LR) tests were additionally used to assess whether differences in fit between nested models were statistically significant.

#### *Including detection probability in the models describing local extinction and colonization*

The statistical procedures of MacKenzie *et al.* (2003, 2005) were deliberately proposed to include uncertainty in the detection probability of species. Calculation of detection probabilities requires that study sites (patches) were repeatedly surveyed (at least twice) in a given breeding season. However, we could not use data from all the waterbodies with Caspian gulls as many were surveyed only once per year during the

study period while others were surveyed several times. Instead, we used our own data from another project in which we studied metapopulation dynamics of the common gull (*Larus canus*) in southern Poland (P.S. *et al.*, unpublished). In that project 209 waterbodies were sampled three times during the breeding season every year from 1999 to 2007. The presence of breeding common gulls as well as the presence of other species from the Laridae family was noted. Breeding Caspian gulls were noted in 20 habitat patches at least once during the study period in that project. This allowed us to estimate the detection probability for this species. Details on the models built and compared are given in Appendix S1 in the Supporting Information. The estimated detection probability was very high: 0.95 (95% confidence intervals: 0.91–0.98). This is in line with our earlier experience: the Caspian gull is a large species and very noisy at its breeding site and therefore easy to find. Consequently, we fixed detection probability to unity in the aforementioned models estimating  $\gamma$  and  $\varepsilon$ .

#### *Modelling the abundance of breeding pairs in habitat patches*

To analyse which factors affected the abundance of a local population we used a generalized linear model with a Poisson error distribution (Vincent & Haworth, 1983). We originally intended to use multiple regression with normal errors but their distribution was right skewed and none of the transformations improved them. In the models we included the number of years from 1989 to 2006 for which a given locality was occupied because habitat patches were colonized in different years and it is possible that the number of breeding birds was positively correlated with the number of years a patch was occupied. For example, if a patch was occupied between 1995 and 2000 we took 6 as the value of the covariate. Correlation analysis was also used to check how covariates were related to each other and if they were sufficiently independent to conduct the analysis (Appendix S2).

The AICc was used to identify the most parsimonious model from each candidate set. The procedure was the same as described above. We started with a saturated model, and in the next steps we removed covariates that had the largest standard errors until only a model with the intercept remained.

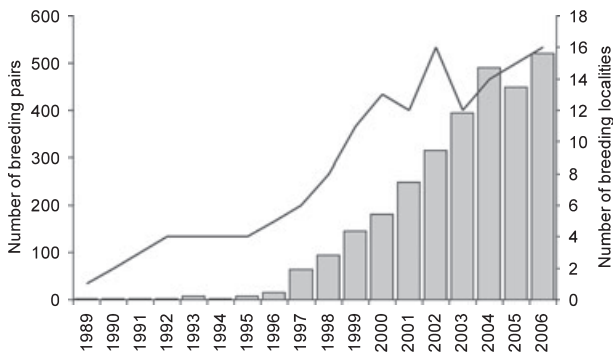
The significance level was set at  $\alpha = 0.05$ ; however, in some correlation analyses, where no specific hypotheses were tested, the Šidák–Bonferroni correction (Šidák, 1971) was applied and the significance level was thus set at  $\alpha = 0.002$ . We used JMP 7 software (SAS Inc., 2007) for statistical analysis.

All estimates of statistical parameters (means, betas) are given  $\pm 1$  SE.

## RESULTS

### **Nesting localities of invasive Caspian gulls on waterbodies in Poland**

From 1989 to 2006 there were 35 breeding localities for Caspian gulls on waterbodies in Poland (Fig. 1). The most stable colonies



**Figure 2** The increase in the number of breeding pairs (bars) and number of breeding localities (line) of the Caspian gull (*Larus cachinnans*) in Poland.

had existed for several years (17 years at Tarnawatka fish ponds and 15 years at sedimentation basins in Tarnów). The size of the largest occupied habitat patch was 6000 ha (reservoir in Włocławek) and the smallest 5 ha (sedimentation basin in Tarnów-Azoty). During the study the size of the Caspian gull population in Poland increased exponentially, with an annual average rate of increase of 33% (Fig. 2).

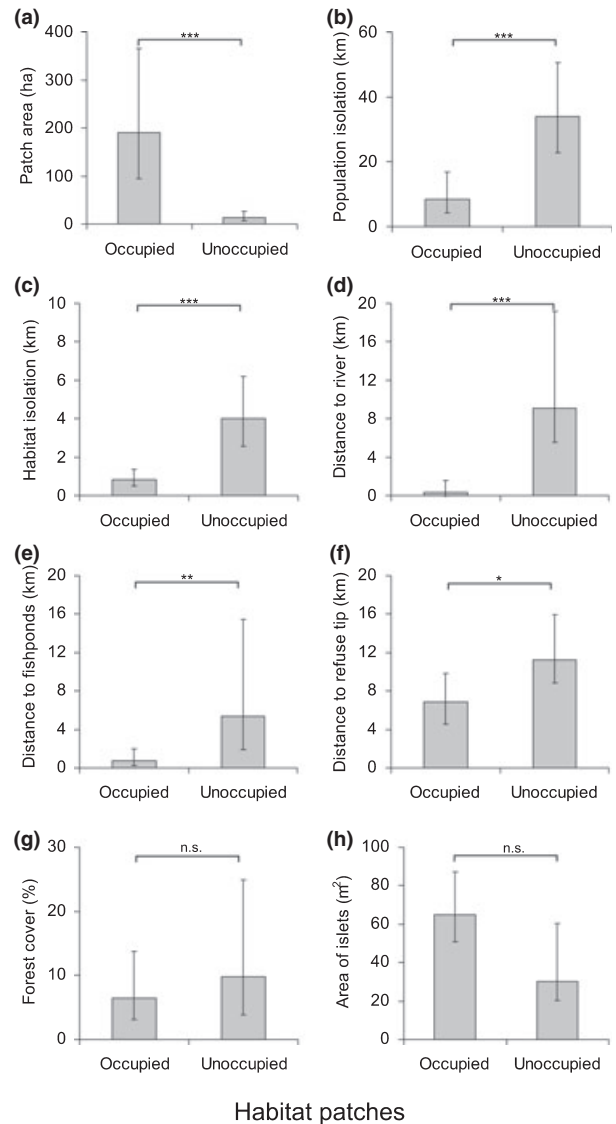
**Did the attributes of the occupied and unoccupied habitat patches differ?**

The patches that were occupied by gulls at least once differed significantly from our random sample of unoccupied habitat patches. The occupied habitat patches were on average larger ( $t = 6.29$ , d.f. = 68,  $P < 0.001$ ; Fig. 3a), less isolated from the nearest local population ( $t = -4.06$ ; d.f. = 68;  $P = 0.001$ ; Fig. 3b), closer to the nearest habitat patch ( $t = -5.55$ , d.f. = 68,  $P < 0.001$ ; Fig. 3c), closer to the nearest river ( $t = -6.67$ , d.f. = 68,  $P < 0.001$ ; Fig. 3d) and fish ponds ( $t = -3.20$ , d.f. = 68,  $P = 0.002$ ; Fig. 3e) than the random sample of unoccupied habitat patches. The occupied habitat patches were closer to refuse dumps ( $t = -2.11$ , d.f. = 68,  $P = 0.038$ ; Fig. 3f) than unoccupied habitat patches but this relationship was not significant after Šidák–Bonferroni correction. The occupied habitat patches did not differ significantly from the random sample of unoccupied habitat patches in forest cover within 3 km from the borders of the patch ( $t = -1.21$ , d.f. = 68,  $P = 0.229$ ; Fig. 3g) or the area of islets ( $t = -1.75$ , d.f. = 68,  $P = 0.079$ ; Fig. 3h).

Within occupied habitat patches correlation coefficients between covariates were small, and none approached significance after Šidák–Bonferroni correction (Appendix S2). Within unoccupied habitat patches, no covariates were correlated at the significance level  $\alpha = 0.002$  (Appendix S2).

**Factors affecting colonization and extinction probabilities in local populations of invasive species**

We found that the null model with  $\gamma$  and  $\epsilon$  fixed at zero (no metapopulation dynamics) had the least support (model no.



**Figure 3** Comparison of characteristics of the habitat patches that were occupied ( $n = 35$ ) and those that were unoccupied ( $n = 35$ ) by the Caspian gull (*Larus cachinnans*) in Poland. Means with 95% confidence intervals are given (confidence intervals are asymmetrical because they were calculated on log-transformed data and then back-transformed). \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$ ; n.s.,  $P > 0.05$ .

17 in Table 1). The model describing a metapopulation at equilibrium ( $\epsilon = 1 - \gamma$ ; model 14 in Table 1) had less support than the model with independent estimates of  $\epsilon$  and  $\gamma$  (model 13 in Table 1) (LR test,  $\chi^2 = 82.670$ , d.f. = 7,  $P < 0.001$ ), which is to be expected in species with (meta)population growth. Accordingly, models with year-specific  $\psi$  and constant  $\epsilon$  and  $\gamma$  had generally higher support than models with  $\psi$  constant between years and year-specific rates of  $\epsilon$  and  $\gamma$  (Table 1). All models describing  $\epsilon$  and  $\gamma$  as a function of covariates had much more support than any other models (Table 1). Overall,  $\gamma$  and  $\epsilon$  were  $0.163 \pm 0.031$  and

**Table 1** Candidate models for patch occupancy ( $\psi$ ), colonization ( $\gamma$ ) and extinction ( $\varepsilon$ ) probabilities for the Caspian gull (*Larus cachinnans*) in Poland. Models are ranked according to the Akaike information criterion corrected for small sample size (AICc).

Models (ranked)	AIC	$\Delta$ AIC	AIC weight	K	$-2\log_e L$
1 $\psi, \gamma(\text{FPond}+\text{HIsol}+\text{PIsol}+\text{River}), \varepsilon(\text{ColSize}+\text{FPond}+\text{HIsol}+\text{Islet}+\text{Refuse}), P(.)^*$	410.03	0	0.34	13	384.03
2 $\psi, \gamma(\text{Area}+\text{FPond}+\text{HIsol}+\text{PIsol}+\text{River}), \varepsilon(\text{ColSize}+\text{Forest}+\text{FPond}+\text{HIsol}+\text{Islet}+\text{Refuse}), P(.)$	410.39	0.36	0.29	15	380.39
3 $\psi, \gamma(\text{FPond}+\text{PIsol}+\text{River}), \varepsilon(\text{ColSize}+\text{FPond}+\text{HIsol}+\text{Islet}), P(.)$	411.16	1.13	0.20	11	389.16
4 $\psi, \gamma(\text{Area}+\text{Forest}+\text{FPond}+\text{HIsol}+\text{PIsol}+\text{River}), \varepsilon(\text{ColSize}+\text{Forest}+\text{FPond}+\text{HIsol}+\text{Islet}+\text{PIsol}+\text{Refuse}), P(.)$	411.53	1.50	0.16	17	377.53
5 $\psi, \gamma(\text{Area}+\text{Forest}+\text{FPond}+\text{HIsol}+\text{PIsol}+\text{Refuse}+\text{River}), \varepsilon(\text{Area}+\text{ColSize}+\text{Forest}+\text{FPond}+\text{HIsol}+\text{Islet}+\text{PIsol}+\text{Refuse}), P(.)$	416.87	6.84	0.01	19	376.87
6 $\psi, \gamma(\text{Area}+\text{Forest}+\text{FPond}+\text{HIsol}+\text{Islet}+\text{PIsol}+\text{Refuse}+\text{River}), \varepsilon(\text{Area}+\text{ColSize}+\text{Forest}+\text{FPond}+\text{HIsol}+\text{Islet}+\text{PIsol}+\text{Refuse}+\text{River}), P(.)$	420.87	10.84	0.00	21	376.87
7 $\psi, \gamma(\text{PIsol}+\text{River}), \varepsilon(\text{ColSize}+\text{FPond}+\text{HIsol}), P(.)$	432.41	22.38	0.00	9	414.41
8 $\psi, \gamma(\text{PIsol}), \varepsilon(\text{ColSize}+\text{HIsol}), P(.)$	444.64	34.61	0.00	7	430.64
9 $\psi, \gamma(\text{PIsol}), \varepsilon(\text{HIsol}), P(.)$	456.28	46.25	0.00	6	444.28
10 $\psi(\text{year specific})^\ddagger, \varepsilon(.), P(.)$	485.37	75.34	0.00	20	447.37
11 $\psi(\text{year specific}), \gamma(.), P(.)$	692.75	282.72	0.00	20	652.75
12 $\psi(.), \varepsilon(.), P(.)$	766.68	356.65	0.00	4	726.68
13 $\psi, \gamma(.), \varepsilon(.), P(.)$	860.54	450.51	0.00	4	852.34
14 $\psi(.), \gamma(.), \varepsilon = 1-\gamma, P(.)$	941.01	530.98	0.00	3	935.01
15 $\psi(\text{year specific}), \gamma(\text{year specific}), P(.)$	963.35	553.32	0.00	36	891.35
16 $\psi(\text{year specific}), \varepsilon(\text{year specific}), P(.)$	994.91	584.88	0.00	36	922.91
17 $\psi, \gamma(\text{fixed} = 0), \varepsilon(\text{fixed} = 0), P(.)$	2955.11	2545.08	0.00	4	2947.11

K is the number of parameters estimated. In each model the detection probability (P) was fixed at 1.

Abbreviations for covariates: Area, the habitat patch area; ColSize, Caspian gull colony size; Forest, forest coverage within 3 km from the edge of the patch; FPond, distance to the nearest fish pond; HIsol, distance to the nearest waterbody; Islet, islet area; PIsol, distance to the nearest local population; Refuse, distance to the nearest refuse dump; River, distance to the nearest river that is longer than 100 km.

\*Denotes that a given parameter had a constant value between years.

†(year specific) denotes that a given parameter was allowed to vary between years.

0.036 ± 0.006, respectively. The probability of colonization was positively affected by patch area (beta = 0.412 ± 0.209), and negatively by distances to fish ponds (beta = -0.440 ± 0.223), nearest habitat patch (beta = -0.415 ± 0.200), nearest breeding colony (beta = -0.331 ± 0.162) and river (beta = -0.384 ± 0.184), and by forest cover around the patch boundaries (beta = -0.300 ± 0.147).

The probability of extinction was significantly lower in patches with a higher number of breeding birds (beta = -5.561 ± 2.205) and with a greater area of islets (beta = -0.892 ± 0.293). The extinction probability increased with distances to other local populations (beta = 0.531 ± 0.263), habitat patches (beta = 1.203 ± 0.451), fish ponds (beta = 1.117 ± 0.394) and refuse dumps (beta = 0.846 ± 0.351) (Table 1). The extinction probability was also higher in patches with higher cover of forest within 3 km of the patch boundary (beta = 0.549 ± 0.243) (Table 1).

### Factors affecting local population abundance

The median number of breeding pairs in a habitat patch (after taking into account the number of years a habitat patch was occupied) was positively affected by the islet area available for gulls (beta = 0.409 ± 0.122) (Table 2). The number of breed-

ing pairs was negatively affected by an increase in distance to the nearest breeding locality (beta = -1.316 ± 0.617), habitat patch (beta = -0.291 ± 0.115), fish pond (beta = -0.135 ± 0.062), refuse dump (beta = -0.204 ± 0.097) and river (beta = -0.480 ± 0.142) (Table 2). The model with these covariates has the greatest support and was significantly different from the null model containing the intercept only (LR test,  $\chi^2 = 317.656$ , d.f. = 7,  $P < 0.001$ )

## DISCUSSION

### Factors affecting patch occupancy, local colonization, extinction and abundance in the initial stages of invasion

The spatial spread of a species is influenced by its successful establishment, which is a step driven by the processes of colonization and extinction. With (2002) stressed the role of environmental heterogeneity, which may influence the initial stages of an invasion process, such as dispersal and colonization. Our study confirms the role of environmental heterogeneity and it underlines the fact that not every local colonization is a successful event during the invasion process.

**Table 2** Candidate models for factors affecting local population abundance of the Caspian gull (*Larus cachinnans*) in Poland. Models are ranked according to the Akaike information criterion corrected for small sample size (AICc).

	Models (ranked)	AIC	$\Delta$ AIC	AIC weight	K	$-2\log L$
1	$a_0, b(\text{FPond}+\text{HIsol}+\text{Islet}+\text{PIsol}+\text{Refuse}+\text{River}+\text{Years})$	419.86	0	0.84	8	403.14
2	$a_0, b(\text{Forest}+\text{FPond}+\text{HIsol}+\text{Islet}+\text{PIsol}+\text{Refuse}+\text{River}+\text{Years})$	424.12	4.26	0.10	9	405.21
3	$a_0, b(\text{FPond}+\text{HIsol}+\text{Islet}+\text{PIsol}+\text{River}+\text{Years})$	425.96	6.10	0.04	7	411.40
4	$a_0, b(\text{Area}+\text{Forest}+\text{FPond}+\text{HIsol}+\text{Islet}+\text{PIsol}+\text{Refuse}+\text{River}+\text{Years})$	427.23	7.37	0.02	10	406.12
5	$a_0, b(\text{HIsol}+\text{Islet}+\text{PIsol}+\text{River}+\text{Years})$	451.75	31.89	0.00	6	439.34
6	$a_0, b(\text{Islet}+\text{PIsol}+\text{River}+\text{Years})$	516.74	96.88	0.00	5	768.20
7	$a_0, b(\text{PIsol}+\text{River}+\text{Years})$	557.65	137.79	0.00	4	549.45
8	$a_0, b(\text{PIsol}+\text{Years})$	601.72	181.86	0.00	3	595.60
9	$a_0, b(\text{Years})$	682.69	262.83	0.00	2	678.63
10	$a_0$	722.82	302.95	0.00	1	720.80

K is the number of parameters estimated.  $a_0$  is the intercept and  $b$  is the slope.

Years, number of years that each locality was occupied by birds. For definition of other abbreviations see Table 1.

In our study, habitat patches occupied by Caspian gulls, as predicted, were larger than unoccupied habitat patches. Also, larger patches had a higher probability of being (re)colonized. Patch-size-dependent variation in rates of emigration and immigration of individuals is expected to moderately increase the speed of invasion, as it does for metapopulation persistence (Day & Possingham, 1995; Hill *et al.*, 1996; Guadagnin & Maltchik, 2007). Large sites are then more rapidly colonized and act like invasion pools (Lockwood *et al.*, 2005). In our study, the positive effect of habitat patch area on the presence and colonization probability of the Caspian gull may also arise from the fact that the larger waterbodies may be easier to find for migrants/dispersers in the landscape. It seems that abundant food resources in larger waterbodies might also be the reason for this observed pattern (Skórka *et al.*, 2005). On the other hand, the size of occupied waterbodies did not significantly influence extinction probability and the size of local populations. This is an interesting result, because in other studies it was one of the most important factors affecting extinction probability (Crooks *et al.*, 2001; Ferraz *et al.*, 2007). Moreover, one might expect that in larger areas it is possible to find many appropriate places to breed and establish a larger colony. The local breeding populations of Caspian gull had probably not achieved the habitat carrying capacity at the time of this study. Thus, at the initial stages of invasion of the Caspian gull, the patch size affects the probability of colonization and the presence of the species but does not limit its abundance.

As expected from metapopulation theory, both habitat isolation (distance to the nearest habitat patch) and population isolation (distance to the nearest local population) had a negative influence on the probability of colonization, and increased the extinction rate, of local populations on the waterbodies. Also, habitat patches in which breeding pairs had been found and were most numerous were less isolated from other habitat patches and nesting localities in comparison with unoccupied habitat patches. As shown by several authors (e.g. Jansson & Angelstam, 1999), dispersal may be distance dependent, i.e. individual dispersal was positively correlated with the

number of appropriate habitats in the vicinity. It is understood that isolated habitat patches are difficult to detect for animals, which can spend too much time searching for them, so they choose closer sites instead. The waterbodies located close to one another may provide an additional source of food for chicks, thus the reduced cost of travelling for food may positively affect the nest attendance of adult gulls and therefore increase breeding success (Bukacińska *et al.*, 1996). Higher nesting success may in turn positively affect local population (re)colonization and abundance. Birds move mostly between water habitats while foraging in the breeding season (Skórka *et al.*, 2009). Consequently, the proximity of other habitat patches may cause the inflow of new immigrants (rescue effect) and increase the likelihood of breeding colonies persisting in the target patches. Hastings *et al.* (2005) also found that the distance between suitable habitat patches, and their quality were the main factors affecting the spread of invasion.

Similarly, the proximity of the source of dispersing individuals (other occupied habitat patches) has been shown to increase the likelihood of a given site being colonized (Lockwood *et al.*, 2005). The proximity of a source of dispersing migrants increased the probability of site colonization by the invasive Eurasian collared dove (*Streptopelia decaocto*) (Eraud *et al.*, 2007). Our study suggests that the situation with the Caspian gull might be similar and thus we believe that the invasion process may be greatly affected by sources of individuals successfully colonizing habitat patches.

Waterbodies located close to large rivers were more likely to be colonized by Caspian gulls, and colonies were larger than in habitat patches located further afield. This is probably connected with the fact that the main migration routes for this species are large, long river valleys with an abundant supply of fish (Skórka *et al.*, 2009). If the birds migrate along rivers, then more migrants should find waterbodies that are closer to their travel routes.

In the diet of the Caspian gull, fresh fish (mainly carp) and domestic food refuse predominate (Skórka *et al.*, 2005; Skórka & Wójcik, 2008). Thus, the dispersal and size of local populations of the gull should strongly depend on human

activity, which is confirmed in our study. The colonization probability was positively related to the proximity of fish ponds, and habitat patches located further from fish ponds and refuse dumps underwent frequent extinctions. Moreover, breeding local populations were more abundant in habitat patches near fish ponds and refuse dumps. Certainly, the waterbodies where carp are bred are an extra source of attractive food for adult birds as well as for chicks. Duhem *et al.* (2007) stressed that easily available food from human activity affected the local population abundance and density of a closely related species, the yellow-legged gull (*Larus michahellis*). Skórka *et al.* (2005) emphasized that the Caspian gull often feeds on refuse dumps. Therefore, refuse dumps may provide extra food when fish are temporarily unavailable (e.g. when fish ponds are drained) and may allow birds to breed in an otherwise unsuitable environment. Moreover, this species winters in numerous flocks at refuse dumps that are often located near human settlements in Poland (Meissner & Betleja, 2007). Such refuse may also enhance the winter survival of birds and attract individuals from distant populations, and thus have a rescue effect. As such, refuse dumps may be regarded as buffers against local population size fluctuations/extinctions.

Forest cover in the vicinity of waterbodies constituted a barrier in the colonization process of habitat patches by the Caspian gull and local populations that were breeding in the patches surrounded by forests have a higher rate of local extinction. Forests, however, had no significant effect on the abundance of birds in habitat patches. The influence of forests on metapopulation processes is somehow surprising because gulls are mobile birds. Our other study indicates that forests may be a barrier for the gulls during foraging in habitat patches (Skórka *et al.*, 2009) and, therefore, large forest cover may increase the cost of foraging during the breeding season because birds have to forage in more distant patches (Skórka *et al.*, 2009). Harris & Reed (2002) have shown that forests may be a physical barrier for smaller and less mobile bird species; our study indicates this is also true for large and quite mobile species. We believe that no predator inhabiting Polish forests is able to hunt Caspian gull.

Our results suggest that habitat patches with larger islets might be more attractive to the Caspian gull as a breeding site than patches with small islets. The patches with larger islets had a lower probability of local population extinction. This may be explained in part by the fact that the size of islets is an important factor limiting colony size (de León *et al.*, 2006).

Local populations are significantly more likely to persist if they also are larger. Our findings are in agreement with other studies indicating that small populations are more vulnerable to environmental stochasticity leading to a higher probability of extinction (Pimm *et al.*, 1993; Crooks *et al.*, 2001; Barbraud *et al.*, 2003), which seems to be true for invasive species as well (Fagan *et al.*, 2002). Moreover, smaller local populations are more exposed to predators, so reducing breeding success (Serrano *et al.*, 2005), which may be important in the case of waterbirds.

## Metapopulation dynamics of invasive Caspian gull in Poland

Our study suggests that metapopulation theory makes it possible to characterize the present pattern of occurrence, but also to predict successive stages, of Caspian gull expansion in Poland. The expansion of gull immigrants from distant south-eastern European populations (Skórka *et al.*, 2005) has resulted in an increase in the number of breeding pairs in the study area. The colonization and population development of the Caspian gull in Poland could therefore result from a population explosion in the Black Sea basin (Fasola *et al.*, 1993; Filchagov, 1996; Skórka *et al.*, 2005). A high density in source populations is an important reason for undertaking migration, because such conditions may generate considerable competition for food and suitable nest sites and, as a result, may force some individuals to disperse (Brown & Rannala, 1995; Oro *et al.*, 1996). In source populations of Caspian gull in south-eastern Europe, where the species lives in higher densities and competition may be significant, seeking new habitats and colonizing them may be beneficial, as was shown for other gull species (Oro & Ruxton, 2001). The high breeding success that was observed in Polish colonies (Skórka *et al.*, 2005) suggests that this species has found suitable breeding and foraging habitats in Poland. Additionally, the availability of new habitats suggests that the metapopulation in Poland will certainly grow. Caspian gulls are likely to successively colonize large waterbodies in river valleys. Large waterbodies are potential breeding sites for many other endangered native bird species. Consequently, the invasion of this opportunistic predatory species on a wider scale may strongly negatively influence biodiversity, abundance and also the nesting success of native water bird species (authors' unpublished data). Moreover, an expanding Caspian gull population may also bring negative economic effects due to their impact on the number of fish raised in fish ponds (Skórka *et al.*, 2005). The possible impact of an expanding population of this gull on human health should also be considered. Large gulls, often foraging on refuse dumps and in the proximity of human settlements, may be vectors of many diseases, e.g. possibly bird flu (Hatch, 1996).

## CONCLUSIONS

In the present study we tested the predictions of metapopulation theory with regard to patch occupancy and local extinctions in a waterbird, the Caspian gull, which has become invasive in eastern Europe. Puth & Post (2005) underline that mechanisms of initial phases of invasion are poorly understood and need more attention from researchers, as only a small percentage of studies have analysed them. These authors suggest that initial dispersal is the stage during which it is possible to predict further invasion and appropriately direct management efforts. Our results, based on the initial stages of invasion of Caspian gull in Poland, imply that this species undergoes metapopulation-like dynamics during colonization of new habitat patches. This is quite an



unexpected result as it was believed that invaders occupied all potential habitat patches, regardless of their area or isolation. Moreover, our results clearly show that local extinctions in habitat patches were frequent. This again contradicts the view of invaders as species that successfully occupy almost all potential habitat patches. This study also confirms and stresses the role of human activity in the spread of non-native species.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Modelling the detection probability of Caspian gulls in habitat patches.

**Appendix S2** Correlations among attributes of occupied and unoccupied patches.

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## BIOSKETCH

**Magdalena Lenda** is a researcher in the Institute of Nature Conservation in Poland. She is interested in the biology of invasive species, spatial ecology and behavioural ecology. Her present research focuses on the invasion of alien walnut and goldenrods in Europe.

Author contributions: M.L. conceived the idea and led the writing; G.N. and M.Z-N. collected the data; M.L. and P.S. analysed the data; G.N., M.Z-N. and P.S. commented on the manuscript.

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