Breeding performance of the White-winged Tern (*Chlidonias leucopterus*) in two habitat types at the edge of their distribution range

Artur Goławski*, Emilia Mróz & Zbigniew Kasprzykowski

A. Goławski, E. Mróz, Siedlce University of Natural Sciences and Humanities, Faculty of Natural Science, Department of Zoology, Prusa 12, 08-110 Siedlce, Poland. * Corresponding author's e-mail: artur.golawski@uph.edu.pl

Z. Kasprzykowski, Siedlce University of Natural Sciences and Humanities, Faculty of Natural Science, Department of Ecology and Nature Protection, Prusa 12, 08-110 Siedlce, Poland

Received 6 August 2015, accepted 5 July 2016

Peripheral populations that are expanding their distribution often colonise habitats that are different from the centre of their distribution range. These less optimal areas could have an adverse effect on their breeding success. Consequently, the production of individuals in these populations must be high if the expansion is to continue. The Whitewinged Tern (Chlidonias leucopterus) is a good model for studying breeding parameters in peripheral populations, because in the last 20 years, a westward expansion of this tern has been reported in east-central Poland. We evaluate the breeding success of Whitewinged Tern's in two habitats. Data from the centre of this species' distribution range indicates that waterlogged sedges are the typical nesting habitat, whereas ox-bow lakes are less frequently occupied. In waterlogged sedges terns began breeding on average four days earlier than on ox-bow lakes. However, clutch size and the mean volume of eggs in a clutch were not explained by the habitat type. The hatching success was significantly higher and the number of hatchlings per pair of breeding terns was also higher (close to significance) in waterlogged sedges than on ox-bow lakes. The causes of nest losses differed by habitat type too. While there was no predation on the nests situated on ox-bow lakes, 30.8% of clutch losses in waterlogged sedges were due to predation. In contrast, 50.0% of clutches on ox-bow lakes failed because the nests sank into the water, whereas in waterlogged sedges this was the cause of just 1.9% of all brood losses. Waterlogged sedges are the preferred habitat, offering safer nesting sites than ox-bow lakes for terns nesting at the edge of their distribution range in east-central Poland.



1. Introduction

Populations of species living at the edge of their distribution range are often referred to as peripheral (Dias 1996). They tend to inhabit less optimal areas, and individuals are subject to different se-

lective pressures compared to central populations (Lawton 1993, Geber 2011). In general, the breeding output of peripheral populations is poorer than that of populations at the centre of their distribution range (Sanz 1998, Brewer & Gaston 2003, Vucetich & Waite 2003, Fargallo 2004, Sagarin *et*



al. 2006), because of the impact of weather or habitat quality (Bridle & Vines 2006, Paillisson et al. 2006, Gaston 2009, Arlettaz et al. 2010). However, most studies have been carried out on wellestablished or regressive peripheral populations. Little attention has been paid to the study of the breeding biology of peripheral populations that are in the process of range expansion, where a high production of individuals supporting the expansion is to be expected (Soutullo et al. 2006, Barrientos et al. 2009).

The White-winged Tern (Chlidonias leucopterus) in east-central Poland is a good model for studying breeding parameters in peripheral populations. First, the range of this species in Europe originally covered the eastern part of the continent, with isolated breeding sites in NE Poland, Hungary and Romania (Cramp 1985). The species' distribution range extends from Europe as far as the area around Lake Balkhash, then in a 1,000 km wide band from Lake Baikal up to the eastern coasts of Asia on the border between Russia and North Korea (Cramp 1985). In the last 20 years, a westward expansion of this tern has been reported in Europe, especially in countries like Germany and Denmark (Grell & Rasmussen 1997, Gruneberg & Boschert 2009, BirdLife International 2015); an increase in the breeding population has also taken place in Poland (Głowaciński 2001, Ławicki et al. 2011). Despite population fluctuations from one year to another, there has been a conspicuous increase in the number of pairs in east-central Poland, where the species has bred regularly since 1997. Initially a mere 30 pairs were reported, but now the number of pairs can exceed 1,000 in some years (Goławski et al. 2016). Second, the typical nesting habitat of the Whitewinged Tern is assumed to be naturally waterlogged grassland (Melnikov 1977, Kapocsy 1979, Cramp 1985, Tomiałojć & van der Winden 1997). Habitats used less frequently by this species are assumed to include fish ponds, lakes and ox-bow lakes (Cramp 1985). In east-central Poland, Goławski et al. (2015) found that when the water level in rivers was high and attractive shallow pools of water were in abundance, the preferred habitat was waterlogged sedge fields (70% of colonies), with only 30% of colonies being established on ox-bow lakes.

In this paper we evaluate whether the White-

winged Tern's breeding parameters (clutch size, egg volume, hatching success and number of hatched nestlings) are related to habitat type. We have considered two types of habitats: waterlogged sedges, the typical habitat of these terns, and ox-bow lakes, which are less commonly occupied and a new breeding place for this species in eastern Poland (Goławski et al. 2015). Breeding success could be consistently different between habitats (e.g. Good 2002, McGowan et al. 2005, Amar et al. 2008) and particular habitats could be occupied at different times. Timing of breeding is known to impact reproductive output with earlier nesting individuals usually producing larger clutches, larger eggs, stronger nestlings and overall having higher breeding success (Ulenaers & Dhondt 1991, Sanz 1998, Minias et al. 2013). These breeding parameters determine the viability of the population and can limit species distribution (García & Arroyo 2001). High levels of local adaptation may constrain expansion into new locations, while the relative fitness of dispersing individuals will influence subsequent population growth (Gunnarsson et al. 2012). Knowledge of breeding parameters at the edge of species' ranges may thus indicate the traits involved in limiting species distributions (Lawton 1993, García & Arroyo 2001).

2. Material and methods

2.1. Study site

The study area covers the valley of the river Bug near the village of Morzyczyn (52°40'N, 21°54'E) in east-central Poland. The area incorporates the westernmost regular breeding sites of the White-winged Tern in Europe. The Bug is one of the largest rivers in Poland protected within the Natura 2000 framework, with abundant breeding sites like ox-bow lakes and waterlogged sedges and meadows (Goławski *et al.* 2015).

Nesting habitats of terns were divided into two types: ox-bow lakes and waterlogged sedges. All the ox-bow lakes supported similar vegetation — they were overgrown mostly by Water Soldier (*Stratiotes aloides*), White and Yellow Water Lilies (*Nymphaea alba* and *Nuphar lutea*) and Frogbit (*Hydrocharis morsus-ranae*). The ox-bow lakes were up to 33 ha in area and from 1.4 to 1.7 m

in depth. The waterlogged sedges were situated in depressions in the terrain and consisted mainly of sedges (*Carex* sp.); in addition, a wide variety of herbaceous plant species grew in their more elevated parts, which were hay meadows. Normally, they were inundated to a depth not exceeding 0.5 m. As the breeding season progressed, the water in these depressions gradually evaporated and became shallower, sometimes drying out altogether. Colonies of the White-winged Tern were located 0.6–6.1 km from each other in both habitats (the average distance between colonies was 2.1 km).

2.2. Data collection

The fieldwork covered the breeding seasons in 2007 and 2010. We tracked the terns nesting in the two habitats at the same time. In 2007 we recorded about 100 breeding pairs in the study area, which is about the normal abundance of this species in the area (Ławicki et al. 2011, author's data). In 2010, 220 pairs were nesting on the stretch of the Bug in the study area. In 2010, the highest-ever abundance of nesting White-winged Terns was recorded – about 1,000 breeding pairs were found along the whole valley of the River Bug in eastcentral Poland. We monitored six breeding colonies of the White-winged Tern: three in 2007 and three in 2010 in the localities described above. Three colonies were situated in waterlogged sedges (2007 – one colony, 2010 – two colonies) and three on ox-bow lakes (2007 - two colonies, 2010 – one colony).

During the two year study, 100 clutches of White-winged Tern were described. Every year the first inspection involved searching for nests in all or part (in colonies with more than 30 breeding pairs; two colonies) of the breeding colony. Two large colonies of more than 30 pairs were established on ox-bow lakes: the nests found in a 5 m wide belt of Water Soldier were monitored. Such a belt was selected at random, but always in such a way that it began in the middle of a patch of Water Soldier and ended at the edge of that patch, which coincided with the bank of the ox-bow lake. During every inspection in the season the observer moved along this belt, monitoring all the clutches/broods that appeared in the course of the season. It should be emphasised that most clutches were started at roughly the same time and were

found during the first inspection; only about 20% of clutches appeared later in the season and were first described during the second or some subsequent inspection. Nest inspections began on 20 May, when the first eggs were laid, and continued, normally once a week until early July, when the last hatchlings appeared. An inflatable dinghy was used to gain access to the nests on the ox-bow lakes. The positions of the nests were mapped, and a marker was placed in the field near each one. The fates of all the tern nests were monitored throughout the breeding season at roughly weekly intervals. We did not observe unusual nest desertion caused by our fieldwork. Some of the later clutches could have been repeat clutches, but since adult birds were not marked, this could not be confirmed.

During each inspection the number of eggs was recorded and the length and width of each egg were measured with slide calipers accurate to 0.1 mm. Egg volume was calculated using the formula $V = 0.5 \times \text{length} \times \text{width}^2$ (Hoyt 1979). Numbers of hatchlings (number of hatched eggs) and brood losses were also noted. A brood was regarded as lost if the nest or all the eggs disappeared, or had been abandoned or destroyed before the estimated hatching date (Mazzocchi et al. 1997). The causes of nest losses were: depredation by predators, abandoned or flooded. Depredation was classified as the cause when eggs were broken, probably by corvids (Corvidae) or mammalian predators, e.g. fox (Vulpes vulpes), or if the nest was found empty before the estimated hatching date. An additional pointer was the lack of anxious adult birds flying over the nest: the parent birds are extremely protective of their clutches/broods and attack the observer inspecting the nest in question. A clutch was considered abandoned if the eggs were cold on successive inspections. Flooded clutches included those that had been inundated or had sunk completely into the water together with the patch of Water Soldier on which the nest had been made. A complete clutch was one in which the number of eggs did not change during two consecutive inspections. A successful brood was taken to be one in which at least one chick hatched and was observed on or near the nest (the nestlings remain close to the nest for a few days after hatching). We did not attempt to count the number of nestlings that fledged, because it was impossible to follow

Table 1. Results of generalised linear model showing factors affecting the breeding parameters of the White-winged Tern in east-central Poland.

Factors	Estimate	SE	Wald statistic	P-value
Date of clutch initiation				
Intercept	1.888	0.066	325.445	< 0.001
Distance to nearest neighbouring nest	0.000	0.009	0.002	0.964
Habitat type	0.418	0.041	103.047	< 0.001
Year Habitat type × Year	0.171 -0.073	0.041 0.041	17.303 3.116	< 0.001 0.078
- Tablat type A Toui	0.070	0.041	0.110	0.070
Clutch size				
Intercept	1.009	0.105	92.047	< 0.001
Distance to nearest neighbouring nest	0.007	0.012	0.371	0.542
Habitat type	-0.006	0.073	0.006	0.937
Year Habitat type × Year	0.020 0.008	0.072 0.073	0.077 0.011	0.782 0.916
- real	0.000	0.073	0.011	0.910
Egg volume				
Intercept	2.443	0.010	543.537	< 0.001
Distance to nearest neighbouring nest	0.000	0.001	0.003	0.958
Habitat type	0.004	0.007	0.410	0.522
Year Habitat type × Year	-0.006 0.003	0.007 0.007	0.702 0.225	0.402 0.635
——————————————————————————————————————	0.003	0.007	0.225	0.633
Hatching success				
Intercept	1.505	0.326	21.302	< 0.001
Distance to nearest neighbouring nest	-0.166	0.038	18.915	< 0.001
Habitat type	0.691	0.225	9.426	0.002
Year	-1.206	0.224	29.006	< 0.001
Habitat type × Year	-0.202	0.223	0.826	0.363
Number of hatched nestlings				
Intercept	-0.593	0.224	7.003	0.008
Distance to nearest neighbouring nest	0.065	0.014	22.254	< 0.001
Habitat type	-0.373	0.192	3.785	0.052
Year	0.657	0.193	11.635	0.001
Habitat type × Year	0.198	0.194	1.047	0.306

the fate of nestlings without fencing the nest in. Nest inspection dates were chosen so as to include the hatching peak calculated from the estimated laying date and the average incubation period of 20 days, assuming that eggs were laid at 1-day intervals (Cramp 1985). The great majority of nests were found during the egg-laying period or at the start of incubation, so we could determine the date of hatching of nestlings accurate to ± 1 day; we calculated the clutch initiation date with a similar accuracy.

2.3. Statistics

We analysed the relationships between the breeding parameters of birds and habitat type (ox-bow lakes and waterlogged sedges) using Generalised Linear Models (GLZ) in the module provided by Statistica 10.0 (StatSoft 2012). We also included the study year (2007 and 2010) in the analysis. Habitat type and year were included as categorical factors, and the interaction between habitat type and year was introduced in the model. Because

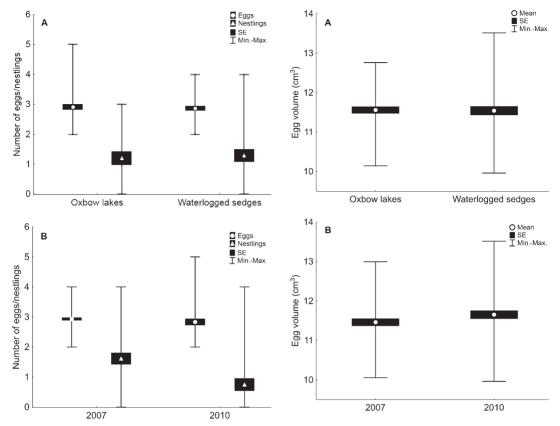


Fig. 1. Mean number of eggs and nestlings in two nesting habitats (panel A) and in the 2007 and 2010 breeding seasons (panel B) of the Whitewinged Tern (N = 100 nests).

Fig. 2. Mean egg volume in two nesting habitats (panel A) and in the 2007 and 2010 breeding seasons (panel B) of the White-winged Tern (N = 100 nests).

colony size has an effect on breeding success (Minias et al. 2015) the analysis included a parameter describing the distance between two nearestneighbour tern nests. While this continuous parameter is not equivalent to colony size, we consider the distance between adjacent nests to better measure the impact of neighbours in a specific part of the colony in contrast to a measure representing the whole colony. This is important, for example, when just the birds nesting in close proximity to one another jointly defend their broods against predators. The breeding parameters considered were: (1) clutch initiation date, standardised for each year, (2) clutch size, (3) volume of eggs, (4) hatching success, (5) number of hatched nestlings per breeding pair. To compare the hatching success of each egg we used a GLZ with logit-link function and binomial error distribution (0 failed, 1 – success). A GLZ with log-link function and Poisson error distribution was used to calculate the clutch size, number of hatched nestlings and clutch initiation date. To compare the mean volume of eggs in a clutch, a GLZ with log-link function and normal distribution error was used. In all GLZs, the model included the interaction between habitat type and year.

The relationships between the cause of clutch losses and season or habitat type were assessed with a χ^2 -test. The values are reported as mean \pm 1 SE. Only results with a probability of $\alpha \leq 0.05$ were assumed to be statistically significant.

3. Results

The clutch initiation date was explained by the type of habitat and year, but not the interaction between these two factors (Table 1). In the waterlogged sedges, terns began breeding on average

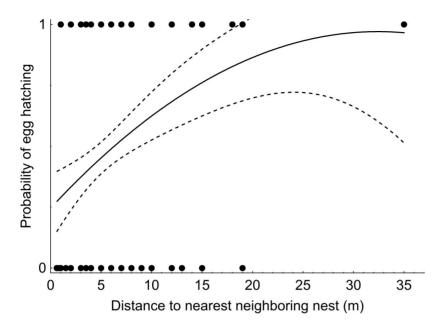


Fig. 3. Probability that an egg hatched as a function of distance to the nearest neighbouring nest (*N* = 228 eggs). Dashed curves represents 95% confidence interval around estimated values.

four days earlier (Median = 24 May, Range = 20 May–8 June, n = 52 clutches) than on the ox-bow lakes (Median = 28 May, Range = 21 May–10 June, n = 48 clutches). The clutch initiation date was earlier in 2010 (Median = 24 May, Range = 20 May–8 June, n = 47 clutches) than in 2007 (Median = 27 May, Range = 21 May–10 June, n = 53 clutches). The distance between two neighbouring nests did not affect the clutch initiation date (Table 1).

Neither habitat type nor year explained the number of eggs in a clutch (Fig. 1). Clutch size was not explained by the distance between nearest-neighbour nests either (Table 1). Clutches with three eggs were recorded most frequently (77.7%), while clutches consisting of two eggs made up 17.3%, and those of four eggs 3.7%. A single nest was found with five eggs. There were no significant differences between the mean volume of eggs in a clutch and the factors analysed (Table 1, Fig. 2).

The hatching success was significantly dependent on habitat type and year, but not on the interaction between these two factors (Table 1): it was 46.5% for birds breeding on the ox-bow lakes (n = 99 eggs) and 50.4% in the waterlogged sedges (n = 129 eggs). In 2007 the hatching success was 65.1% (n = 129 eggs), in 2010 it was 27.3% (n = 99 eggs). Nests with successfully hatched eggs were also significantly farther from the nearest-neigh-

bour nests than failed ones (Table 1, Fig. 3).

The number of hatchlings per pair of breeding terns was significantly dependent on year, and close to significance in the case of habitat type (p = 0.052, Fig. 1). The number of hatchlings was also significantly explained by the distance between the nearest-neighbour nests, increasing with distance between the nests (Table 1).

The causes of losses were dependent on habitat type (χ^2 -test: $\chi^2 = 34.54$, df = 2, p < 0.001). While there was no predation on the nests situated on the ox-bow lakes, in the waterlogged sedges, the mean value for the two years was 30.8% of clutch losses due to predation. In contrast, 50.0% of clutches on the ox-bow lakes failed because the nests were flooded, whereas in the waterlogged sedges this was the cause of just 1.9% of all brood losses (Fig. 4). The causes of brood losses differed between years (χ^2 -test: $\chi^2 = 65.64$, df = 2, p < 0.001). A greater percentage of nests was flooded in 2010 than in 2007, furthermore, in 2010 more nests were depredated in comparison to 2007 (Fig. 4).

4. Discussion

The breeding parameters of White-winged Terns nesting at the edge of their range in east-central Poland were similar to those in the centre of the range (Cramp 1985). This applies in particular to clutch size and mean egg volume, which were almost

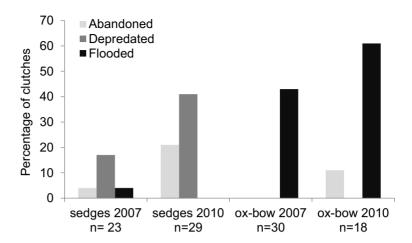


Fig. 4. Causes of brood losses in the White-winged Tern in two nesting habitats in 2007 and 2010, (*N* = 100 clutches).

identical with the results of other studies (Borodulina 1960, Melnikov 1977). Hatching success, and thus the number of hatchlings, varies a great deal from one locality to another, but the figures from east-central Poland did not diverge significantly from those documented elsewhere in Europe and Asia (Borodulina 1960, Melnikov 1977, Kapocsy 1979). Therefore, the breeding parameters at the edge of this species' range were not worse than in the centre of its range, but we documented an impact of habitat on breeding in our peripheral study population.

Our study shows that some of the White-winged Tern's breeding parameters differed between the two types of habitat in which they nested. The terns initiated nesting in the water-logged sedges four days earlier than on the ox-bow lakes. In the former habitat they achieved a better hatching success and consequently they also tended to have more hatchlings in the colonies in the sedge in comparison to those established on the ox-bow lakes. We did not find any differences in clutch size or mean egg volume in clutches between individuals in these two habitats. The differences between the two habitats were due to the rates and nature of nest losses.

Predation was the main cause of losses in the waterlogged sedges, whereas this did not occur on the ox-bow lakes. In this latter habitat most nests were built on patches of Water Soldier, and the water there was often more than one metre deep. These clutches were thus more secure from predators. In contrast, the water depth in the waterlogged sedges was not normally more than 50 cm, and could fall quickly during the course of the sea-

son. In our study plot it was infrequently the case that a nest, originally constructed on shallow water, was lying on dry land just a week or two later. Every single one of these nests was predated, the marks on the egg shells pointing to corvids and mammalian predators as the culprits. On the other hand, clutches laid on the ox-bow lakes perished mainly because they sank along with the patch of Water Soldier on which the nest had been made. This was probably due to wind-driven wave action during thunderstorms causing whole carpets of Water Soldier to shift and then sink. Losses caused by wind increased significantly as the terns' breeding season progressed, because the number of thunderstorms with their accompanying strong winds also increased in this period (author's data). Strong winds were also responsible for losses of up to 15% among Black Terns (Chlidonias niger) (Chapman Mosher 1987, Goławski et al. 2014).

A greater distance between neighbouring nests favoured greater hatching success and a larger number of hatchlings. However, it was expected that a shorter distance between active nests should increase the safety of broods, as shown in other studies (Hernandez-Matias et al. 2003, Minias et al. 2013). In eastern Poland, larger distances between nests of White-winged Terns probably prevented predators from locating clutches too easily. Nest aggregations may be either more conspicuous (Clode 1993) or more attractive to predators (Stokes & Boersma 2000) than sparse nests. More important is the fact that the bigger distance between neighbouring nests reduced the number of nests that sank with fragments of the Water Soldier patch. It was the central sections of Water Soldier

patches that sank or were displaced; those closer to the bank of the ox-bow lakes provided safer nesting sites for the terns (author's data). The higher hatching success in nests situated in greater distances could probably be the result of specific features of this habitat.

Our documented higher breeding success in the waterlogged sedges compared with the oxbow lakes matches the habitat preference shown by the terns. Waterlogged sedges are the preferred habitat in this part of Poland (Goławski et al. 2015), and are the characteristic nesting habitat in Europe and Asia (Cramp 1985). During an increase in geographical range, species often occupy different habitats in comparison to previously used areas. Expansion is also connected with differences in breeding parameters – use of novel habitats could result in higher breeding success (e.g. data for the American Oysterchater *Haematopus* palliatus; McGowan et al. 2005). However, in White-winged Terns nesting in eastern Poland, new and less preferred habitat influenced a small reduction in breeding parameters in comparison with preferred habitats.

Breeding parameters of White-winged Terns were also explained by the study year, likely caused by different weather and habitat conditions in the two study years. The amount of rainfall just before the terns arrived at their breeding grounds (April-May) in 2007 was 50 mm, but in 2010 far more rain fell, 137 mm (weather for the nearest weather station in the town of Ostrołęka; www. tutiempo.net). That is why in the latter year much larger areas of sedges were waterlogged, providing an appropriate habitat for breeding. In 2010, when a large number of nesting White-winged Terns were recorded (Ławicki et al. 2011), they started nesting earlier than in 2007. Despite this, hatching success and number of hatchlings were higher in 2007, probably due to the more stable habitat conditions in this year in comparison with 2010. In 2010, conditions were more changeable as a consequence of the rainfall, which contributed to nest flooding; on the other hand, there were also periodic falls in water levels, especially in the sedges, which led to increased predation pressure. The water level also governed the breeding effects in other Chlidonias species (Gilbert & Servello 2005, Paillisson et al. 2006).

Waterlogged sedges are the preferred habitat,

offering safer nesting sites than ox-bow lakes for terns nesting at the edge of their distribution range in east-central Poland. Perhaps, owing to their habitat preferences, terns breed here earlier than on ox-bow lakes. In other *Laridae* species, too, e.g. Common Tern (*Sterna hirundo*), hatching success was lower and nest destruction greater in suboptimal habitats than in optimal ones (Safina *et al.* 1989). Similarly, in the Yellow-legged Gull (*Larus michahellis*), some reproductive parameters were higher for birds breeding in better-quality habitats (Oro 2008). Differences in breeding success in relation to the habitats occupied were also found in Black Tern (van der Winden *et al.* 2004).

In conclusion, it seems that the most suitable type of habitat for the White-winged Tern, both in the centre and at the edge of its distribution range, are waterlogged sedges (Borodulina 1960, Melnikov 1977, Goławski et al. 2015), which are a better nesting site for this species than other habitats like ox-bow lakes. Waterlogged sedges are densely occupied relatively seldom, however, only when rivers carrying exceptionally high waters subsequently overflow their banks and inundate large areas of land. In years with lower water levels, terns nest on the ox-bow lakes, where the breeding parameters (hatching success) achieved are slightly worse. Abiotic and biotic interactions thus take place at the range limits (Sexton et al. 2009). In our opinion, the lesser breeding results on oxbow lakes could therefore limit the rate of the species' expansion, which corresponds with the conclusions of other studies on different species e.g. harriers (García & Arroyo 2001). It is nonetheless expected that there will be a gradual adaptation to the suboptimal ox-bow lake habitat, e.g. breeding will start earlier, before the advent of stronger winds, which will be reflected in better breeding results, in accordance with the dynamics of the expansion model described by Sutter and Kawecki (2009).

Acknowledgements. We would like to thank to Ewa Droś and Paweł Żmińczuk who carried out the surveys. We also thank to three anonymous referees and Andreas Lindén for very constructive suggestions and to Peter Senn, Marzena Stańska and Shelley Hinsley for the language corrections. This study complies with current Polish laws and was financially supported by the Siedlce University of Natural Sciences and Humanities.

Valkoposkitiiran pesimämenestys kahdessa eri elinympäristössä levinneisyysalueensa rajamailla

Levinneisyysalueidensa rajamailla lajit kolonisoivat usein uusia ja hieman erilaisia ympäristöjä kuin levinneisyysalueidensa keskellä. Nämä uudet ympäristöt voivat olla huonompia pesinnän kannalta. Lajin leviäminen vaatii kuitenkin hyvän poikastuoton. Valkoposkitiira (Chlidonias leucopterus) on hyvä mallilaii reunapopulaatioiden pesimämenestyksen tarkasteluun, koska laji on levinnyt Puolassa voimakkaasti länteen päin viimeisten 20 vuoden aikana. Tutkimme valkoposkitiiran pesinnän onnistumista kuvaavia parametrejä kahdessa eri elinympäristössä. Veden tulvima saraikko on valkoposkitiiran tyypillistä pesimähabitaattia Puolassa. Tiirat pesivät harvemmin jokien meanderoinnin seurauksena syntyneillä lammilla eli juoluoilla. Juoluoissa vesi on syvempää ja niiden kasvillisuuteen kuuluu mm. lummekasveja.

Pesintä alkoi saraikoissa neljä päivää aikaisemmin kuin juoluoissa. Munamäärä ja munien koko eivät eronneet elinympäristöjen välillä. Pesien säilyvyys ja kuoriutuneitten poikasten määrä per pesä olivat parempia saraikoissa kuin juoluoissa. Myös pesien tuhoutumisen pääasiallinen syy erosi habitaattien välillä. Juoluoissa pesiä ei saalistettu lainkaan, mutta saraikoissa saalistus oli syynä 30,8 % tuhoutuneista pesistä. Juoluoissa puolestaan 50,0 % pesistä upposi veteen. Saraikoissa vain 1,9 % epäonnistuneista pesistä tuhoutui uppoamalla. Suositumpana pesimäympäristönä tunnettu veden tulvima saraikko tarjoaa siis turvallisemman pesimäpaikan valkoposkitiiroille, jotka pesivät Puolassa levinneisyysalueensa reunoilla.

References

- Amar, A., Arroyo, B., Meek, W., Redpath, S. & Riley, H. 2008: Influence of habitat on breeding performance of Hen Harriers Circus cyaneus in Orkney. — Ibis 150: 400–404.
- Arlettaz, R., Schaad, M., Reichlin, T.S. & Schaub, M.
 2010: Impact of weather and climate variation on Hoopoe reproductive ecology and population growth.
 — Journal of Ornithology 151: 889–899.
- Barrientos, R., Barbosa, A., Valera, F. & Moreno, E. 2009: Breeding parameters of the trumpeter finch at the periphery of its range: A case study with mainland ex-

- panding and island populations. Journal of Arid Environments 73: 1177–1180.
- BirdLife International 2015: IUCN Red List for birds. Downloaded from http://www.birdlife.org on 26/07/2015.
- Borodulina, T.L. 1960: Biological and economic importance of *Laridae* in aquatic ecosystems of southern part of SU. Trudy Instituta Morphologii Zhivotnykh Akademii Nauk SSSR, Moscow, SSSR. (In Russian)
- Brewer, A.M. & Gaston, K.J. 2003: The geographical range structure of the holly leafminer. II. Demographic rates. — Journal of Animal Ecology 72: 82–93.
- Bridle, J.R. & Vines, T.H. 2006: Limits to evolution at range margins: when and why does adaptation fail?—
 Trends in Ecology and Evolution 22: 140–147.
- Chapman Mosher, B.-A. 1987: Factors influencing reproductive success and nesting strategies in Black Terns.
 Ph. D. Thesis, Simon Fraser University, Burnaby, Canada.
- Clode, D. 1993: Colonially breeding seabirds: predators or prey? — Trends in Ecology and Evolution 8: 336– 338
- Cramp, S. 1985: The Birds of the Western Palearctic, vol. 4. Oxford University Press, Oxford, UK.
- Dias, P.C. 1996: Sources and sinks in population biology.

 Trends in Ecology & Evolution 11: 326–330.
- Fargallo, J.A. 2004: Latitudinal trends of reproductive traits in the Blue Tit *Parus caeruleus*. — Ardeola 51: 177–190.
- García, J.T. & Arroyo, B.E. 2001: Effect of abiotic factors on reproduction in the centre and periphery of breeding ranges: a comparative analysis in sympatric harriers. — Ecography 24: 393–402.
- Gaston, K.J. 2009: Geographic range limits of species. Proceedings of the Royal Society of London B 276: 1391–1393.
- Geber, M.A. 2011: Ecological and evolutionary limits to species geographic ranges. — The American Naturalist 178: S1–S5.
- Gilbert, A.T. & Servello F.A. 2005: Water level dynamics in wetlands and nesting success of Black Terns in Maine. — Waterbirds 28: 181–187.
- Głowaciński, Z. 2001: Polish Red Data Book of Animals, Vertebrates. — PWRiL, Warszawa, Poland. (In Polish with English summary)
- Goławski, A., Kasprzykowski, Z., Ledwoń, M., Mróz, E. & Morelli, F. 2016: Brood sex-ratio in expansive and non-expansive tern species in east-central Poland. — Bird Study 63: 31–36.
- Goławski, A., Kasprzykowski, Z., Mróz, E., Rzepała, M. & Chmielewski, S. 2015: The differences in habitat selection in two sympatric species of eastern Poland: the White-winged Tern (*Chlidonias leucopterus*) and the Black Tern (*Chlidonias niger*). Wilson Journal of Ornithology 127: 52–58.
- Goławski, A., Mróz, E., Kasprzykowski, Z., Słupska, K., Droś, E. & Żmińczuk, P. 2014: Breeding ecology of

- the Black Tern *Chlidonias niger* in the Bug Valley. Ornis Polonica 55: 162–172. (In Polish with English summary)
- Good, T.P. 2002: Breeding success in the Western Gull × Glaucous-winged Gull complex: the influence of habitat and nest-site characteristics. — Condor 104: 353–365.
- Grell, M. & Rasmussen, L.M. 1997: First breeding of the white-winged black tern in Denmark. Dansk Ornitologisk Forenings Tidsskrift 91: 121–124. (In Danish with English summary)
- Gruneberg, C. & Boschert, M. 2009: Weisbart- und Weisflugelseeschwalben in Deutschland: Bestandsentwicklung und aktuelle Brutverbreitung. DDA-Monitoring-Rundbrief 1: 9–13.
- Gunnarsson, T.G., Sutherland, W.J., Alves, J.A., Potts, P.M. & Gill, J.A. 2012: Rapid changes in phenotype distribution during range expansion in a migratory bird. — Proceedings of the Royal Society B 279: 411– 416
- Hernandez-Matias, A., Jover, L. & Ruiz X. 2003: Predation on Common Tern eggs in relation to sub-colony size, nest aggregation and breeding synchrony. Waterbirds 26: 280–289.
- Hoyt, D.E. 1979: Practical methods for estimating volume and fresh weight of birds eggs. Auk 96: 73–77.
- Kapocsy, G. 1979: Weßflügel- und Weißartseechwalbe.
 A. Ziemsen Verlag. DDR Wittenberg, Lutherstadt, Germany.
- Lawton, J.H. 1993: Range, population abundance and conservation. Trends in Ecology & Evolution 8: 409–413
- Ławicki, Ł., Niedźwiecki, S., Sawicki, W., Świętochowski, P., Goławski, A., Kasprzykowski, Z., Urban, M., Wylegała, P., Czechowski, P., Prange, M., Janiszewski, T., Menerski, S., Lenkiewicz, W. & Jantarski, M. 2011: Numerous nesting of the White-winged Tern Chlidonias leucopterus in Poland in 2010. Ornis Polonica 52: 85–96. (In Polish with English summary)
- Mazzocchi, I.M., Hickey, J.M. & Miller, R.L. 1997: Productivity and nesting habitat characteristics of the Black Tern in northern New York. — Colonial Waterbirds 20: 596–603.
- McGowan, C.P., Simons, T.R., Golder, W. & Cordes, J. 2005: A comparison of American Oystercatcher reproductive success on barrier beach and river island habitats in costal North Carolina. — Waterbirds 28: 150–155.
- Melnikov, J.I. 1977: Ecology of White-winged Tern in eastern Siberia. In Ecology of birds in eastern Siberia, Irkutsk (ed. Skryabin, N.G.): 59–92. Irkutsk Univ. Publ., Irkutsk. (In Russian)
- Minias, P., Janiszewski, T. & Lesner, B. 2013: Center-periphery gradients of chick survival in the colonies of Whiskered Terns *Chlidonias hybrida* may be explained by the variation in the maternal effects of egg size.

 Acta Ornithologica 48: 179–186.

- Minias, P., Włodarczyk, R. & Janiszewski, T. 2015: Opposing selective pressures may act on the colony size in a waterbird species. Evolutionary Ecology 29: 283–297.
- Oro, D. 2008: Living in a ghetto within a local population: an empirical example of an ideal despotic distribution.

 Ecology 89: 838–846.
- Paillisson, J.-M., Reeber, S., Carpentier, A. & Marion, L. 2006: Plant-water regime management in a wetland: consequences for a floating vegetation-nesting bird, whiskered tern *Chlidonias hybrida*. — Biodiversity and Conservation 15: 3469–3480.
- Safina, C., Witting, D. & Smith, K. 1989: Viability of salt marshes as nesting habitat for Common Terns in New York. — Condor 91: 571–584.
- Sagarin, R.D., Gaines, S.D. & Gaylord, B. 2006: Moving beyond assumptions to understand abundance distributions across the ranges of species. — Trends in Ecology & Evolution 21: 524–530.
- Sanz, J.J. 1998: Effects of geographic location and habitat on breeding parameters of Great Tits. — Auk 115: 1034–1051.
- Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. 2009: Evolution and ecology of species range limits. — Annual Review of Ecology, Evolution, and Systematics 40: 415–436.
- Soutullo, A., Liminana, R., Urios, V., Surroca, M. & Gill, J.A. 2006: Density-dependent regulation of population size in colonial breeders: allee and buffer effects in the migratory Montagu's harrier. — Oecologia 149: 543–552.
- StatSoft Inc. 2012: Statistica, data analysis software system, version 10.0. www.statsoft.com.
- Stokes, D.L. & Boersma, P.D. 2000: Nesting density and reproductive success in a colonial seabird, the Magellanic Penguin. — Ecology 81: 2878–2891.
- Sutter, M. & Kawecki, T.J. 2009: Influence of learning on range expansion and adaptation to novel habitats. — Journal of Evolutionary Biology 22: 2201–2214.
- Tomiałojć, L. & van der Winden, J. 1997: White-winged Black Tern *Chlidonias leucopterus*. — In The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance (eds. Hagemeijer E.J.M. & Blair M.J.): 366–367. T & A D Poyser, London.
- Ulenaers, P. & & Dhondt, A.A. 1991: Phenology, habitat choice and reproduction of the Great Crested Grebe *Podiceps cristatus* L., on a fish farm. — Ardea 79: 395–408.
- van der Winden, J., Beintema, A.J. & Heemskerk, L. 2004: Habitat-related Black Tern *Chlidonias niger* breeding success in The Netherlands. — Ardea 92: 53–61.
- Vucetich, J.A. & Waite, T.A. 2003: Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. Conservation Genetics 4: 639–645.