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ORIGINAL ARTICLE

The Whiskered Tern *Chlidonias hybrida* expansion in Poland: the role of immigration

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Abstract The Whiskered Tern population in Poland has rapidly increased from 40 breeding pairs in 1990 to over 1,600 in 2007, with strongest local population in the Upper Vistula River Valley. Owing to rather low pre-breeding and adult apparent survival rates estimated for this population (0.54 and 0.80, respectively) and a delay in accession to reproduction (recruitment completed at age 3), matrix modelling indicated an intrinsic growth rate of $\lambda_{calc} = 1.02$. Observed growth rates of both the Polish and the Upper Vistula River Valley populations was $\lambda_{obs} = 1.29$. Using the deterministic population projection matrix including immigrant class, we estimated that, on average, 44 immigrants should enter the Upper Vistula River Valley population annually to match the observed growth. With survival rates increased ($\Phi_P = 0.63$, $\Phi_B = 0.90$) as to mimic no emigration and reduced dispersal, the estimated number of immigrants was only eight, indicating that substantial emigration rates are likely. A majority of the breeding sites were recorded in man-made water bodies. Colonisation has started in the southeast and proceeded towards the northwest. The strong, stable population in western Ukraine may explain high numbers of immigrants that could originate from there. Other factors favouring quick colonisation of Poland include availability of suitable breeding sites, the wide flexibility of the species with respect to breeding habitat, plentiful food, and high breeding success in the Upper Vistula River Valley. It also seems likely that westward shifts in both breeding and wintering ranges could add to the strong population increases in Eastern Europe.

Keywords Conservation · *Chlidonias hybrida* · Dispersion · Whiskered Tern · Metapopulation · Population dynamics · Population growth rate · Range expansion · Sternidae · Recruitment · Survival

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Zusammenfassung

Die Ausbreitung der Weißbart-Seeschwalbe (*Chlidonias hybrida*) in Polen: Rolle der Zuwanderung

Die Population der Weißbart-Seeschwalbe (*Chlidonias hybrida*) in Polen ist von 40 Brutpaaren (1990) sehr rasch auf über 1600 Brutpaare (2007) angewachsen, mit der stärksten örtlichen Population im oberen Weichseltal. Wegen der für diese Population geschätzten, ziemlich niedrigen Überlebensrate junger und adulter Vögel (0,54, bzw. 0,80) und der Verzögerung, mit der das Reproduktionsalter erreicht wird (mit 3 Jahren), legen Matrix-Modelle eine intrinsische Wachstumsrate von $\lambda_{calc} = 1{,}02$

nahe. Die beobachtete Wachstumsrate lag bei $\lambda_{obs} = 1{,}29$. Laut der Deterministischen Population Projection Matrix, müssten im Schnitt 44 Vögel pro Jahr in das obere Weichseltal einwandern, um das beobachtete Populationswachstum zu erreichen. Bei einer erhöhten Überlebensrate von ($\Phi_P = 0{,}63$, $\Phi_B = 0{,}90$) - unter der Annahme, dass keine Auswanderung und weitere Ausbreitung stattfindet, müsste die Zahl der Einwanderer bei 8 liegen, was recht hohe Auswanderungsraten vermuten lässt. Der größte Teil der Brutplätze wurde an künstlich angelegten Gewässern festgestellt. Die Besiedlung begann im Südosten und breitete sich nach Nordwesten aus. Die starke, stabile Population in der West-Ukraine könnte die hohe Zahl der Einwanderer von dort erklären. Andere, die rasche Besiedlung Polens unterstützende Faktoren sind die Verfügbarkeit geeigneter Brutplätze, die große Flexibilität dieser Vogelart bei der Wahl ihrer Brutplätze, das hohe Nahrungsangebot und der große Bruterfolg im oberen Weichseltal. Ferner scheint wahrscheinlich, dass das Verschieben der Brut- und Überwinterungsgebiete nach Westen zum starken Populationswachstum in Osteuropa beiträgt.

Introduction

Changes of breeding ranges coupled with population size changes are phenomena of central interest in ecology (Newton 1998). Birds can easily travel long distances and choose suitable habitats for colonisation far from current breeding areas, so are potentially more prone to exhibit spectacular range expansions (van den Bosch et al. 1992). Range expansion requires dispersal of individuals to occupy a new location. The identification of key factors affecting the expansion process is difficult, since it is usually caused by multiple interacting factors. Availability of new food resources (Duhem et al. 2008; Oro et al. 1999), and new, empty and suitable breeding habitat (Suryan et al. 2004; Kosciuch et al. 2006; Veech et al. 2011), or negative changes in the breeding habitats forcing the breeding population to leave (Danchin and Monnat 1992; Oro et al. 2004; Cadiou et al. 2010) represent environmental factors that may induce expansion. An even larger number of factors influencing expansion is associated with the characteristics of a species or population: range and population size, species tolerance (or flexibility) to potentially new environmental conditions, population genetics, morphological, physiological and ethological adaptations and demography (Kharintonov and Siegel-Causey 1988; Duckworth and Badyaev 2007; Gunnarsson et al. 2012).

Population dynamics depend on demographic rates—inflows into population (immigration and productivity) and losses (emigration and mortality; Clobert and Lebreton 1991), and this is true for a population exhibiting range expansion as well. The growth of an expanding population results from internal production of first colonisers (Pyk et al. 2013) and/or from immigration (Oro and Ruxton 2001; Skórka et al. 2005; Coulson and Coulson 2008; Doxa et al. 2013). While it may be difficult to tell which is more important at times, assessing the support for immigration effect is fairly easy (Pulliam 1988): the observed population size is plotted against the one expected without immigration (i.e. relying exclusively on local production of young by first colonisers), given the demographic parameters of the population studied (namely, productivity, pre-reproductive and adult survival). In some studies of terns and gulls, however, these parameters are not the ones specified for a given population, but rather are taken from estimates published for other populations (e.g., Gill and Mewaldt 1983; Skórka et al. 2005). Far more precise results can be achieved by using demographic parameters from the population of interest (i.e., Peery et al. 2006; Altwegg and Anderson 2009; Abadi et al. 2010; Szostek and Becker 2012; Doxa et al. 2013). Integrated population models (IPMs) represent a novel modelling framework that effectively uses count data (i.e., observed population size) and demographic (productivity and survival) data to achieve deep insights into the population dynamics (reviewed by Schaub and Abadi 2011, also Kéry and Schaub 2011).

Larids (gulls and terns) are frequently used species in various population-demographic studies (e.g., Nisbet and Cam 2002; Lebreton et al. 2003; Cam et al. 2004; Coulson and Coulson 2008; Szostek and Becker 2012; Doxa et al. 2013), but the marsh terns (the genus *Chlidonias*) remain poorly studied so far (Shealer 2007; Van der Winden and van Horssen 2008; Ledwoń et al. 2013). To fill this gap, in this paper we focus on the pattern of expansion of the Whiskered Tern *Chlidonias hybrida*, the marsh tern species that has been colonising Polish inland for the last four decades (Tomiałojć and Stawarczyk 2003; Betleja and Stawarczyk 2007). The first breeding was noted in the 1960s (Tomiałojć 1990), and following a spectacular population increase, the population size reached approximately 1,600 pairs in 2007 (Komisja Faunistyczna 2008). To assess the patterns of expansion of this tern species, we used annual census data of breeding colonies for 40 years (gathered by the Polish Rarities Committee) and the demographic data (i.e., productivity, offspring sex ratio, the apparent survival of both pre-breeding and adult age classes) estimated for the strongest Polish local population in the Upper Vistula River Valley. The effect of immigration on the increase in the number of breeding pairs could be assessed, and the annual number of immigrants could also be estimated via matrix modelling. We also describe Whiskered Tern habitat preferences, and discuss the factors responsible for its remarkable expansion.

Materials and methods

Study species

The Whiskered Tern is a medium-sized, socially monogamous marsh tern, with no sexual plumage dimorphism and a moderate size dimorphism (Cramp 1985; Ledwoń 2011). The species breeds across large areas of the Palearctic, Africa and Australia in a variety of wetland habitats. In the western and central Palaearctic, the Whiskered Tern breeds mainly in Spain and France, and in the area ranging from Eastern Europe, across the Black and Caspian Sea basins, to Kazakhstan, but it is rather localized and scarce over a majority of range (Mees 1977, 1979; Cramp 1985; Il'icev and Zubakin 1988; Gavrilov and Gavrilov 2005). The population from Western Europe winters mostly in tropical West Africa (Mees 1977, 1979). Eastern European birds winter in the Nile delta region in Egypt (Meininger and Atta 1994) and throughout the Nile valley (Cramp 1985). Birds from the central Palaearctic probably also winter in Iraq and India (BirdLife International 2013). Small numbers of birds (dozens) winter regularly in the Mediterranean (Cramp 1985; Isenmann 1972; Martinez et al. 1981; Rufray et al. 1998).

Strongest European populations breed in the east: in Russia (10,000–25,000 pairs), Romania (8,000–12,000), Ukraine (5,000–8,500) and Turkey (4,000–8,000; BirdLife International 2004). The species also breeds in southwestern Europe (Iberian Peninsula: 2,500–10,000, France: 2,300–2,400) and at a few more isolated sites in central Europe and Italy. In the south of Europe and in Russia, the population of the Whiskered Tern declined between 1970 and 1990 (Tucker and Heath 1994). In contrast, increases have been noted and new sites have been colonised in Romania, Ukraine, Belarus, central Russia, Lithuania, Latvia, Germany, the Netherlands, Poland, Slovakia and Hungary (Tucker and Heath 1994; BirdLife International/European Bird Census Council 2000; BirdLife International 2004).

Material

The data covered by this study were collected between 1968 (the first breeding attempt of the Whiskered Tern in Poland) and 2012. Up to and including 2007, all of the noted breeding attempts were verified by the Polish Rarities Committee. Data were collected by volunteers without any standardized protocols—observers sent reports to the Polish Rarities Committee with details of observed breeding. These details contained standard avifaunistic data, used in the analysis here: the date of observation, exact location, size of the colony (the number of pairs or nests) and habitat in which nesting was observed. Not all potential breeding sites were inspected every year, but we are unable to accurately assess the number of sites that were not monitored in some years at a national scale (this does not concern the Upper Vistula River Valley, where a complete censuses were undertaken each year, 1993–2012, see below). We analysed data from the whole of Poland on the basis of breeding records submitted to the Polish Rarities Committee over the period 1968–2007. The data from the Polish Rarities Committee archives contain information on about 10,952–11,472 (min–max) breeding pairs, which included 8,028 observed nests.

The most important breeding area of the Whiskered Tern in Poland is the Upper Vistula River Valley (southern Poland, approx. 1,400 km^2); over 40 % of the national population breeds on 0.4 % of the country area. This is owing to its unique characteristics—the presence of carp ponds and high food availability (see Ledwoń et al. 2013). This area was treated separately, because complete censuses were performed there since 1993 (the early phase of expansion) up to and including 2012, and therefore, the data obtained for Upper Vistula River Valley are reliable and reflect the true number of nesting pairs. Breeding habitats in Upper Vistula River Valley were surveyed from late May to the late August to cover the whole, long breeding season of the Whiskered Tern. Nests were counted in breeding colonies in most cases, and only rarely was the colony size estimated on the basis of the number of adult birds flying over the colony. ML and JB recorded or co-recorded approximately 80 % of all the breeding pairs in the Upper Vistula River Valley and approximately 30 % of all breeding Whiskered Terns in Poland.

Some of the forms submitted to the Polish Rarities Committee contained an estimated range (min–max) of breeding pairs, rather than a single accurate number. In these cases, we used the geometric mean estimated from the minimum and maximum number of breeding pairs in the analyses, unless otherwise stated. The average differences between the minimum and maximum number of breeding pairs were small (6 % for the whole of Poland and 3 % for the Upper Vistula River Valley).

The type of habitat occupied by breeding Whiskered Tern was determined by observers and described in the form sent to the Polish Rarities Committee. These data were verified by TS and ML. Habitat types in the Upper Vistula River Valley were determined by ML and JB. Natural habitat types that were distinguished included flooded meadows in rivers valleys, natural lakes, oxbow lakes and lagoons, while man-made habitats were carp ponds, dam reservoirs, midfield ponds, mining areas and peat lakes. To assess potential changes in habitat preferences, we divided data into decades (10-year-long periods, see Habitat choice). The maximum number of pairs at a particular site was used to determine the percentage of pairs of Whiskered Terns nesting in the different types of habitats. To avoid pseudoreplication, each breeding site was included only once per decade.

Survival analysis

Apparent survival analysis was previously reported in detail (Ledwoń et al. 2013), so we present only the main points of this analysis here. Estimation was based on the capture–recapture data (403 adults and 1,484 chicks ringed) collected between 1993 and 2011 in the breeding population of the Upper Vistula River Valley. Like other tern species, the Whiskered Tern exhibits delayed maturity; there are very few breeders in the first year of life (second calendar year [cy]) when most of young birds stay in winter quarters, and the proportion of breeders increases until the fifth year of life. We used multistate models to account for the unobservable state that lasts until the first breeding. Estimated, model-averaged survival probabilities were 0.54 (SE = 0.28) for pre-breeders (Φ_P) and 0.80 (SE = 0.05) for breeders (Φ_B). Recruitment probability was defined here as the probability of entering the breeding population (i.e., the probability of first recruitment, the observable state), and was age-specific.

Population dynamics

Observed growth rate, λ_{obs}

The observed growth rates (λ_{obs}) were calculated from census data, separately for the Upper Vistula River Valley and for the whole Poland, as $\lambda_{obs} = N_{t+1}/N_t$ and averaged over all year pairs; where N_t is population size at time t, N_{t+1} is population size in the year next to t.

Intrinsic population growth (calculated growth rate, λ_{calc})

Population dynamics was modelled using a linear, female-based model $N_{t+1} = A \times N_t$, where A is the population projection matrix and N_t is the vector of population abundance at time t. The matrix A reflects a post-breeding census and has the form:

$f\,\Phi_P\,(\Psi_1)$	$f\,\Phi_P\,(\Psi_2)$	$f\,\Phi_P$	$f\,\Phi_B$	$f\,\Phi_B$
$\Phi_P\,(1-\Psi_1)$	0	0	0	0
0	$\Phi_P\,(1-\Psi_2)$	0	0	0
$\Phi_P\,(\Psi_1)$	0	0	Φ_B	0
	$\Phi_P\,(\Psi_2)$	Φ_P	0	Φ_B

where f is productivity (number of female fledgings per breeding female, see below). The matrix structure reflects juveniles, 1-year-old non-breeders, 2-year-old non-breeders, 1-year-old breeders, 2-year-old and older breeders. It has two survival probability parameters, taken from previous work (pre-breeding survival, $\Phi_P = 0.54$, adult survival, $\Phi_B = 0.80$, Ledwoń et al. 2013). To address delayed maturity and the presence of non-breeders in the population (Ledwoń et al. 2013), age-dependent recruitment term Ψ was included (see Fig. 1). Therefore, the probability that a pre-breeder enters the breeding population at a given age is a product of Φ_P and Ψ specific for a given age. For simplicity, we assumed that recruitment is completed after age 2 and that age-specific recruitment probabilities are 0.045 at age 1 (Ψ_1, second cy) and 0.508 at age 2 (Ψ_2, third cy) [calculated from Ledwoń et al. (2013), following Pradel and Lebreton (1999)].

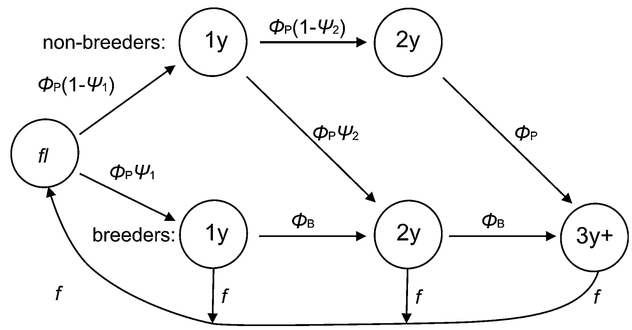


Fig. 1 Life cycle of the Whiskered Tern as constructed in the population projection matrix used in this study. *fl*—fledging (newborns), 1y (second cy), 2y (third cy) and 3y + (ad)—successive age classes, *f*—fecundity (productivity, the same for all age classes). A Whiskered Tern can either recruit at age 1 [enter the breeding population with probability $\Phi_P\Psi_1$], or remain a non-breeding individual [with probability $\Phi_P(1-\Psi_1)$]. Once an individual enters the breeding population and becomes a breeder, it survives to the next age class with probability Φ_B. If it remained a non-breeder at age 1, at age 2 it can either recruit [with probability $\Phi_P\Psi_2$] or, again, remain a non-breeding individual [with probability $\Phi_P\,(1-\Psi_2)$], and so on. The full recruitment is achieved at age 3 (fourth cy). All breeders produce offspring (*f*)

The mean number of female fledglings per pair (f) was also a known parameter ($f = 0.95$, SE = 0.09), estimated by molecular sexing of 47 chicks that were 10–21 days old from 25 nests in 2006 and 2007 from the Upper Vistula River Valley [for molecular methods, see Ledwoń (2011)]. This also fits earlier data on breeding success, when it was estimated as 1.9 chick per nest per year (Betleja 2003), which, assuming equal sex ratios among offspring, produces the same estimate of female offspring as the data from 2006–2007. We assumed that productivity remains the same over the rest of life (but see Nisbet et al. 1984; Ezard et al. 2007; Rebke et al. 2010). We calculated the first eigenvalue, λ_{calc}, of the matrix A, which is the asymptotic population growth rate, and thus reflects intrinsic population dynamics (i.e., population growth without immigration—caused by internal production of first colonisers, starting from four breeding pairs in 1991 for the Upper Vistula River Valley) (Caswell 2001).

In order to estimate the number of immigrants necessary to enter the population every year to match the observed population growth, in the next step, we added an immigrant class to the matrix, following Doxa et al. (2013). The number of immigrants was estimated in an iterative way, and all immigrants were assumed to be adult females, reproducing every year after entering the population. Calculations were performed in R 2.11 (R Development Core Team 2013). We used the R code proposed by Doxa et al. (2013), modified to reflect the three recruitment classes used in calculations (see ESM 1).

Both survival estimates we used from Ledwoń et al. (2013; $\Phi_P = 0.54$, $\Phi_B = 0.80$) were "apparent," since they accounted for both mortality and permanent emigration. To further assess the patterns in population dynamics, we also calculated intrinsic growth rate (λ_{calc}) in the above matrix with adult survival fixed at 0.90 (the value frequently seen in many tern species, see Table 4 in Ledwoń et al. 2013) to minimize the emigration process, and pre-breeding survival fixed at 0.63 (the estimate from the second-best model from Ledwoń et al. 2013) to increase the number of birds recruiting to the population. This enabled us to verify how much processes of both permanent emigration (breeding dispersal) and natal dispersal affect population growth patterns.

Estimation of the number of immigrants was performed for completely censused population in the Upper Vistula River Valley only.

Results

Population dynamics

In the 1970s and 1980s, the species was recorded approximately 20 times, including 16 times in eastern Poland and only four times in western Poland, apart from records at breeding sites. The first breeding case of the Whiskered Tern in Poland was in 1968, when four nests were found near Lublin (south-eastern Poland, Dyrcz et al. 1973). Over 22 years (1968–1989), Whiskered Terns bred only during 9 years, and the annual numbers of breeding pairs never exceeded ten (Fig. 2). Since 1985, the species has bred in Poland annually, and since 1990, the number of breeding pairs has increased rapidly from 38–40 to over 1,600 in 2007. During this time, the number of breeding sites increased from 1 to 41.

The first breeding of this species in the Upper Vistula River Valley was recorded in 1986, but before 1992 the annual numbers of breeding pairs did not exceed ten (Fig. 3). Between 1992 and 2012, the number of breeding Whiskered Terns rapidly increased from about 40 to nearly 800 pairs, and the number of breeding sites increased from 1 to 17.

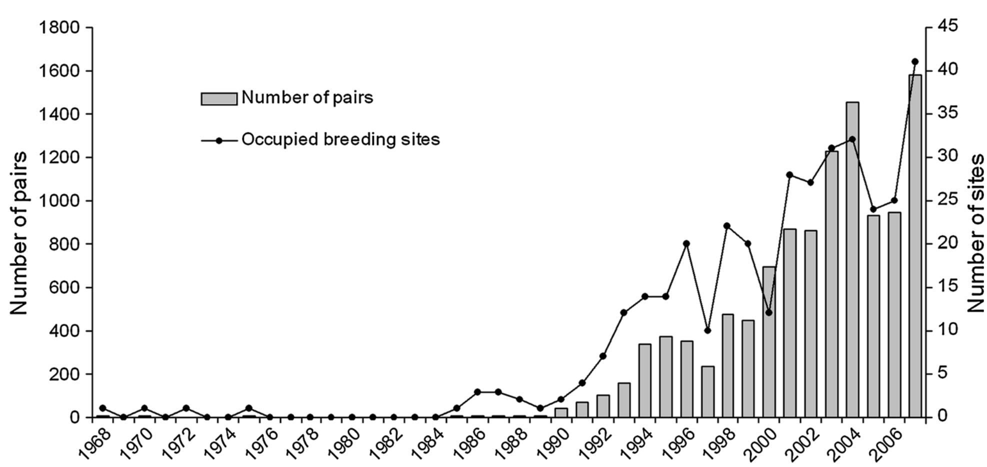
The increase in numbers of breeding pairs of the Whiskered Tern, both in Poland and in the Upper Vistula River Valley, follows an exponential model (Figs. 2, 3). During the period of annual breeding of the Whiskered Tern, the observed, average annual rate of population growth was $\lambda_{obs} = 1.29$ in both the whole of Poland (1985–2007) and in the Upper Vistula River Valley (1991–2012). This means that the population approximately doubled in 4 years.

The asymptotic population growth rate resulting from the matrix population model was $\lambda_{calc} = 1.02$. This suggests that the intrinsic growth rate was highly insufficient to match observed growth; it would explain just 1 % of the observed population size in 2012.

Immigration

With parameter values as used in this study (adult survival fixed at 0.80, pre-breeding survival at 0.54; see "Methods"), on average 44 immigrant females annually must have immigrated to the Upper Vistula River Valley to allow the observed population growth. A simulation performed to assess the importance of permanent emigration (a component of apparent survival parameter used in the study) and natal dispersal, with adult survival fixed at 0.90

Fig. 2 The numbers of breeding pairs and number of occupied breeding sites of the Whiskered Tern in Poland, 1968–2007



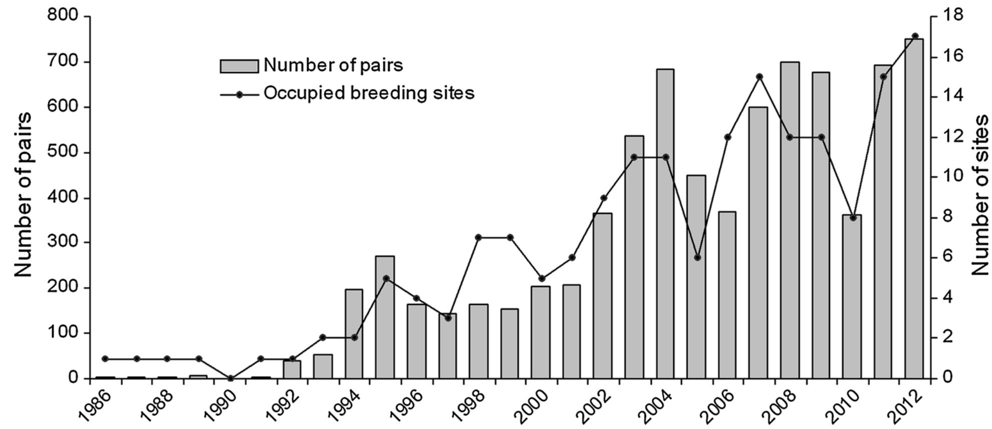


Fig. 3 The numbers of breeding pairs and number of occupied breeding sites of the Whiskered Tern in the Upper Vistula River Valley, 1986–2012

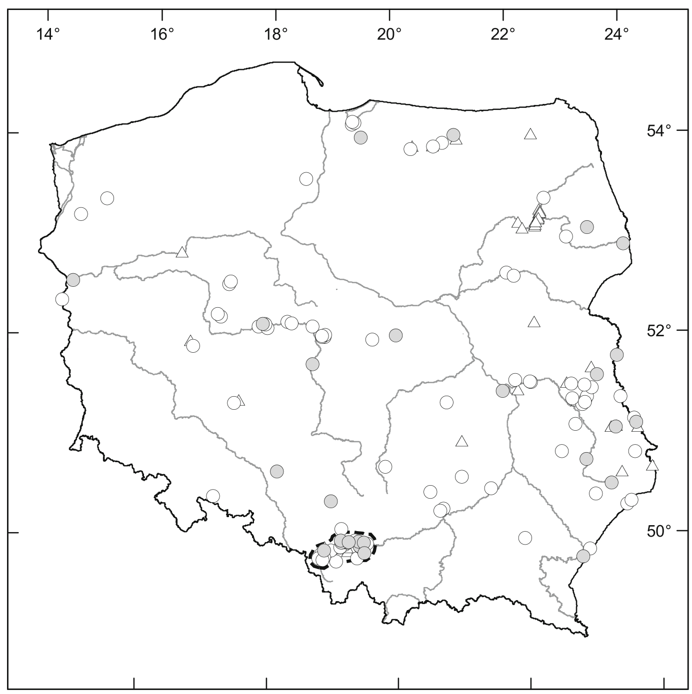


Fig. 4 Distribution of breeding sites of the Whiskered Tern in Poland, 1968–2007. *Open triangles*, sites occupied 1968–1999; *open circles*, sites occupied 2000–2007; *filled circles*, sites occupied in both periods. The Upper Vistula River Valley is marked by a *line*

and pre-breeding survival at 0.63 (see "Methods"), showed that only eight immigrant females would be needed annually, if parameters were fixed to these values. If only adult survival was fixed to 0.90, and pre-breeding survival was left unchanged at the value of 0.54, 16 immigrant females annually would be needed. First, this result stresses the importance of adult survival for population dynamics, and second, it clearly suggest that permanent emigration could be substantial and responsible for the large number of immigrants in the studied population.

Distribution

A total of 148 breeding sites of the Whiskered Tern were distributed throughout the whole of Poland, but the majority (86 %) of all recorded pairs were nesting in eastern and southeastern Poland (Fig. 4). The Upper Vistula River Valley concentrated on average 42.4 % (SD = 23.4) of the Polish population. Range expansion started in southeastern Poland, and Whiskered Terns settled in northwestern Poland just after 2001.

Habitat choice

For 146 of the 148 known breeding localities, we were able to determine the type of habitat (Table 1). Among nine predefined habitat types, only four were occupied in the 1980s, six in the 1990s and all nine in the 2000s. Most frequently occupied habitat type were carp ponds (35 % and 41 % of occupied sites, respectively, during 1990s and

Table 1 The type of wetlands occupied by breeding Whiskered Tern *Chlidonias hybrida* in Poland in consecutive decades

Type of breeding sites	Number of occupied breeding sites (%)			Percent of pairs		
	1980s	1990s	2000s	1980s	1990s	2000s
Carp ponds	1 (14)	22 (35)	43 (41)	3	26	31
Dam reservoirs	4 (57)	13 (21)	14 (13)	86	45	32
Natural lakes	0	1 (2)	8 (8)	0	2	14
Midfield ponds	0	4 (6)	4 (4)	0	7	7
Flooded meadows in rivers valleys	1 (14)	14 (22)	12 (12)	8	12	6
Oxbow lakes	1 (14)	9 (14)	13 (13)	3	7	5
Mining areas	0	0	5 (5)	0	0	4
Lagoons	0	0	1 (1)	0	0	1
Peat lakes	0	0	4 (4)	0	0	1

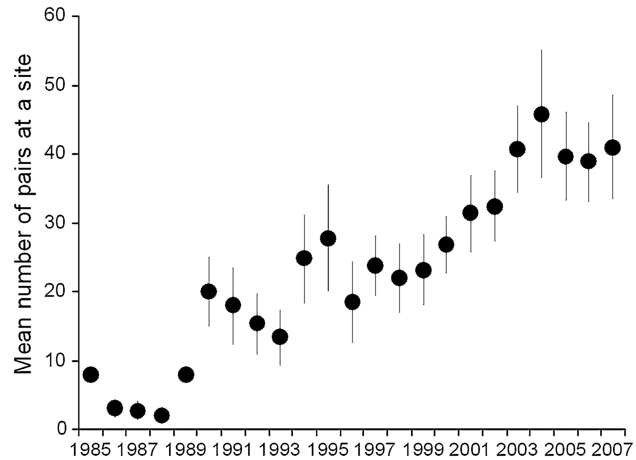


Fig. 5 Numbers of pairs of Whiskered Tern per site in Poland, 1985–2007. Only occupied sites in a given year used to calculate means and the outlying, large colony of 415 pairs from the year 2000 was omitted. *Points* are yearly means, *bars* denote 1 standard error

2000s) and dam reservoirs (21 and 13 %, respectively). These two habitats concentrated the biggest fraction of the population: during the 1990s and 2000s, respectively, 26–31 % of pairs bred at carp ponds and 45–32 % at dam reservoirs. Other habitat types were occupied at a lower rate and had much smaller numbers of pairs. Most Whiskered Terns (79 and 75 % in the 1990s and 2000s, respectively) bred at man-made habitats. In the Upper Vistula River Valley alone, breeding Whiskered Terns were recorded at 34 sites: 32 carp pond complexes and two dam reservoirs. Whiskered Terns build nests on floating or emergent vegetation, mainly on Water Fringe (*Nymphoides peltata*), Knotweed (*Polygonum* sp.), Water Soldier (*Stratiotes alloides*), Yellow Water Lily (*Nuphar lutea*), European White Water Lily (*Nymphaea alba*), sedges (*Carex* spp.), Reed Mannagrass (*Glyceria maxima*), and Water Chestnut (*Trapa natans*).

Sizes of colonies and local populations

Whiskered Terns breed in Poland either in single pairs or in colonies. Most data gathered by the Polish Rarities Committee contain the total number of breeding pairs at the level of locality (e.g., carp pond complexes, reservoirs). For most localities, the sizes of particular colonies are unknown, and therefore, we show the numbers per locality rather than sizes of particular colonies. In 48 % of the sites, the maximum number of breeding pairs did not exceed ten. The largest breeding colony—containing 436 nests distributed in five subcolonies—was found at Goczałkowice Reservoir in southern Poland in 2004. Between 1985 and 2007, the mean number of pairs per occupied site clearly increased from below ten to about 40 (Fig. 5). This was mostly due to the increase of size in biggest colonies, although the number of small colonies increased simultaneously. It is, however, difficult to assess bias in these data, as smaller colonies are more difficult to detect, but clearly, large colonies (i.e., colonies of 100 and more pairs) have been noted since 1994, and annually—only after 2000. Whiskered Terns breed both in mono-specific colonies and with other species, e.g., with Black-necked Grebe (*Podiceps nigricollis*), Great Crested Grebe (*P. cristatus*), Black-headed Gull (*Chroicocephalus ridibundus*) and Black Tern (*C. niger*).

Discussion

Between 1985 and 2007, the breeding population of the Whiskered Tern in Poland increased sharply from eight pairs to approximately 1,600 in 2007, and the same growth rate was seen in the strongest Polish population in the Upper Vistula River Valley; the exponential model fits the observed growth. It is evident that most of the population increase resulted from immigration and could not be achieved by intrinsic dynamics exclusively (production of young by first colonisers). Also, other studies of terns and gulls have shown that immigration represents the key demographic parameter associated with large increases in local populations (Oro and Ruxton 2001; Suryan et al. 2004; Skórka et al. 2005; Coulson and Coulson 2008; Doxa et al. 2013). Our data suggest that the number of breeding Whiskered Terns in Upper Vistula River Valley have stabilized after 2004 (Fig. 3). Owing to the lack of data from the area of the whole Poland in the last 5 years (breeding of the species is no longer considered by the Rarities

Committee since 2008), the changes in the size of Polish population in last few years unfortunately remain unknown.

Estimates of pre-breeding and adult survival for the Whiskered Tern used in this study were rather low when compared to values published for other terns (Table 4 in Ledwoń et al. 2013), most likely because they accounted for permanent emigration and natal dispersal. Indeed, when survival rates in the population matrix were increased as to mimic no emigration and reduced dispersal, the estimated number of immigrants appeared three to five times lower. This suggests that the studied population can experience substantial emigration. As showed previously at the small scale (Upper Vistula River Valley), both emigration processes may be enhanced by the human-induced disturbance of the main breeding habitat (fish ponds, dam reservoirs) related to farming (Ledwoń et al. 2013). The high turnover rate in this population may thus result from emigration rates (emigration of adults and natal dispersal of young resulting in low recruitment) on the one hand, and from annual immigration, which must balance emigration to ensure observed, rapid growth. Both these processes seem to fit population conditions observed around Poland: a strong, stable population in Ukraine (a possible source of immigrants to the Upper Vistula River Valley) and increases in, e.g., Germany (a sink for emigrants from the Upper Vistula River Valley).

Our population model is based on productivity obtained only in 2006–2007 and only in the Upper Vistula River Valley. However, it seems, that our assumptions—0.95 female fledglings per pair (1.9 fledglings per pair) are relevant at least for this area (concentrating over 40 % of the national population), because the same high breeding success—1.9 fledglings per pair—was noted here in 1999–2001 ($n = 58$ nests) (Betleja 2003). We used this value of the fecundity parameter for modelling growth, assuming it would not bias the results much.

The high rate of breeding success and good quality of the breeding habitats may attract immigrants from other populations, and may enhance high breeding site fidelity (Oro et al. 1999; Oro and Ruxton 2001; Suryan et al. 2004; Doxa et al. 2013). Also, high rates of breeding success may have an effect on the population growth rate (Oro et al. 1999; Oro and Ruxton 2001; Szostek and Becker 2012). The Whiskered Tern population in the Upper Vistula River Valley is characterised by high rates of breeding success, low predation pressure, high food abundance in carp ponds (Betleja 2003; Ledwoń 2010), and relatively high adult and pre-breeding survival rates in comparison with the declining populations of other *Chlidonias* and *Sterna* terns (Shealer 2007; Szostek and Becker 2012; Ledwoń et al. 2013). The good quality of the breeding habitats, which caused the high breeding success of the Whiskered Tern in the Upper Vistula River Valley, has influenced expansion in range and population growth of this species in Poland.

The range expansion and increase in size of the Whiskered Tern population in Poland could also be related to newly established man-made reservoirs and ponds. Only about 20 % of Whiskered Tern breed in natural habitats (such as natural lakes, flooded meadows), while approx. 80 % of pairs breed in carp ponds and dam reservoirs. However, the numbers of breeding birds on flooded meadows in river valleys could be underestimated because of incomplete data from the Biebrza Marshes in north-eastern Poland. Numerous reservoirs that were built in the second half of the 20th century in Europe, as well as the much older carp ponds in Eastern and Central Europe, became the equivalent of natural habitats for the Whiskered Tern. Furthermore, other studies have shown the importance of man-made reservoirs and carp ponds for the expansion of the Whiskered Tern (Gorban and Dzyubenko 1995; Dzyubenko 2001; Danko et al. 2002; Cazacu 2006; Atamas 2011), as well as for other tern and gull species (Suryan et al. 2004; Skórka et al. 2005; Zielińska et al. 2007; Becker and Sudmann 1998; Lenda et al. 2010). The colonisation of these new, empty and suitable habitat patches by Whiskered Tern was an important step that enabled its rapid range expansion in Eastern and Central Europe.

In other areas of Eastern and Central Europe during the 20th and 21st centuries, populations of Whiskered Tern increased in size and expanded in range, thus indicating an expansion in the northwestern direction (BirdLife International/European Bird Census Council 2000, BirdLife International 2004; Tucker and Heath 1994; Sellin and Schirmeister 2005; Dvorak et al. 2010). The German population increased from several pairs in 2001 to nearly 250 in 2008 (Grüneberg and Boschert 2009), in Slovakia, the population increased from several to approx. 200 pairs between 1970 and 1993 (Danko et al. 2002). In the Czech Republic, there has been no increase in the breeding population and the species is still a very rare breeder; this seems to be related to the lack of suitable breeding habitats in carp ponds (M. Vavrik, in litt). The west Ukrainian population increased from several to approximately 1,000 breeding pairs between the 1940s and 1980s, and then stabilised until the early 2000s (N. Atamas and N. Dzyubenko, in litt; but see Gorban and Dzyubenko 1995; Kinda and Potapov 1998; Dzyubenko 2001), and the total number of breeding pairs in the whole of Ukraine increased from 200–300 breeding pairs in the 1940s to 8,000–9,000 in the 1990s (BirdLife International/European Bird Census Council 2000, BirdLife International 2004). The most distinctive wave of expansion in the western part of Ukraine took place in the 1980s, (Gorban and Dzyubenko 1995; Dzyubenko 2001). Strong expansion of this species in Poland started a decade later. Coupled with the northwestern direction of expansion in Poland and the rest of Europe, this strongly supports the view that southeastern populations of the species (i.e., the Ukrainian one) are the source of colonisers.

Some authors suggest that range expansion of the Whiskered Tern is linked to the dramatic changes in landscape that took place during the mid-20th century in the centre of the Whiskered Tern breeding range (Gorban 1991; Tucker and Heath 1994; Van der Winden 1997). Large areas of steppe wetlands in Russia and Kazakhstan (roughly between the Volga River, the Ural f and the Aral Sea) were drained and designated for agriculture. This, in turn, resulted in a drastic decline in wetland bird species, such as the Sociable Lapwing *Vanellus gregarius* (Shevchenko 1988; Sheldon et al. 2013). Despite scarce data on Whiskered Tern numbers in this area, some authors have suggested it could be the most important refugee for the species in this part of the Palearctic (Gorban 1991; Tucker and Heath 1994; Van der Winden 1997). Assuming this to be true, Whiskered Terns could have moved from an area where their breeding habitats were destroyed, and colonised respective habitats westwards: in Eastern and Central Europe where they had not bred before. Therefore, the centre of the breeding range could shift towards the north and west from the Russian and Kazakh steppes (Tucker and Heath 1994). Also other studies showed that catastrophic and unpredictable events can trigger massive dispersal of colonial waterbirds (Oro et al. 1999; Martinez-Abrain et al. 2001).

Another factor influencing the expansion in range and increase in size of the Whiskered Tern populations in Eastern and Central Europe could be a change in wintering areas. In recent decades, almost the whole western Palearctic population wintered in Manzala and Burullus lakes in the Nile delta in Egypt. More than 43,000 birds wintered there in 1989/1990 and 10 years earlier, up to 25,000 birds were present in winter (Meininger and Atta 1994). At the same time, the Mesopotamian Marshes, once considered an important wintering place for this species (Il'icev and Zubakin 1988; Snow and Perrins 1998), have been heavily dried and polluted (Stattersfield et al. 1998). Despite no existing detailed data on changes of Whiskered Tern numbers in these areas, the simultaneous destruction of habitats in the breeding grounds in central Asia and wintering grounds in the Middle East could lead to a shift in the species (both breeding and wintering) range to the west. Enhanced by numerous factors favouring settlement and high productivity in central Europe, this process likely resulted in the permanent settlement of the species in Central and Eastern Europe. As suggested for the Slender-billed gull *Larus genei* in Mediterranean France (see Doxa et al. 2013), when seen from a wider perspective, regional increases (such as the Whiskered Tern in Poland and adjacent areas) may not necessarily reveal good population conditions, but could indicate population problems elsewhere.

Last, but not least, an important factor helpful in exploiting the new area is the ability of Whiskered Tern to build nests on the open water surface or on floating leaves, unlike the other two *Chlidonias* species, which need a foundation for their nests. As a nest base, they usually use floating islands of dead plants, abandoned grebes' nests, clumps of sedges, quagmire, or hard plants on deeper water (e.g. Water Soldier), which are scarce and dispersed in Poland, especially in fish pond habitats (ML, JB, unpublished data). Therefore, this ability enabled the Whiskered Tern to build nests in a large spectrum of wetland habitats, including almost every site with abundant food, even with limited abundance of soft water plants.

To summarize, our results are in line with the conclusions of Doxa et al. (2013), who claimed that any population with adult survival < 0.9 would rely on immigration to maintain its numbers, rather than on intrinsic dynamics. In the case of the Whiskered Tern in Upper Vistula River Valley, the population is likely to experience a substantial emigration rate (as shown by relatively low apparent adult survival) and high natal dispersal (as shown by low apparent pre-breeding survival) on the one hand, and annual immigration on the other. Both these processes seem to fit population trends observed around Poland: a strong, stable population in Ukraine (a possible source of immigrants to the Upper Vistula River Valley) and increases in, e.g,. Germany (a sink for emigrants from the Upper Vistula River Valley).

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