

Solitude at periphery: lack of partners limits reproduction of the Black Stork (*Ciconia nigra*) at the margin of the distribution range

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Understanding the mechanisms forming species' ranges is a central ecological question, which could be answered by analysing factors limiting peripheral populations. In threatened species, such studies are essential for establishing effective conservation measures across the range. We analysed factors potentially influencing breeding in a declining peripheral population of a long-lived bird, the Black Stork (*Ciconia nigra*). We assessed reproductive success and the effects of intra- and interspecific competition, as well as predation by recording events at nests by remote cameras (camera traps and a webcam). Productivity of storks was low (1.1 fledglings per occupied nest) compared to the other parts of the range and resulted mainly from the lower proportion of successful nests (37% of occupied nests). The main reason for low breeding success was the occupancy of many nests (35%) by single non-reproductive birds. Breeders were often visited by non-local conspecifics, which harassed local birds but only seldomly caused direct damage. Impact of predators and interspecific nest-competitors on reproductive success was low. We suggest that many individuals have disappeared from the breeding population and shortage of mates is currently the most important factor lowering reproductive success of the Black Stork at its northern range margin. This mechanism could also limit the peripheral abundance and distribution in other long-lived birds.



1. Introduction

Species distributions are limited in space and understanding the factors shaping species' ranges is a central question in ecology (Holt & Keitt 2005). Various intra- and interspecific factors, acting via the main demographic parameters (births, deaths and movements) have been proposed to limit spa-

tial distributions of the species (Krebs 1978, Lawton 1993, Gaston 2003, Newton 2003, Gaston 2009, Sexton *et al.* 2009). However, often the negative effect of a limiting factor does not appear abruptly at the range limit, it rather increases gradually towards the margin (Gaston 2003, Holt *et al.* 2005).

Peripheral populations are predicted to have

stronger constraints on their abundance and well-being than central ones, explained by centre-periphery hypothesis (Brown 1984, Pironon *et al.* 2016). Ample studies have explored the validity of this hypothesis, but most have focused directly on abundance, whereas the importance of demographic parameters that shape abundance, or specific factors that influence demography (e.g., predation or individual behaviour) have been overlooked (Bridle & Vines 2007, Gaston 2009, Abeli *et al.* 2014, Pironon *et al.* 2016).

Yet in long-lived animals, changes in demographic parameters, e.g., reproductive success, reveal problems well before actual decline (Newton 1998). Therefore, determinants of population abundance should be defined in threatened marginal populations for their effective conservation. Indeed, not only central populations should be conserved, but also peripheral ones (Howe *et al.* 1991) as they may contribute to size and longevity of metapopulations (Howe *et al.* 1991, Lomolino & Channell 1995, Channell & Lomolino 2000) or harbour genetic diversity lacking in core populations (Hailer *et al.* 2006, Eckert *et al.* 2008, Pironon *et al.* 2016), for example in the context of future climate change (Rehm *et al.* 2015).

We analysed factors influencing a peripheral population of the threatened Black Stork (*Ciconia nigra*). This sensitive species has an unfavourable conservation status in Europe and is therefore listed in the Annex I of the EU Birds Directive (2009/147/EC). It is also listed in Annexes II of the Berne, Bonn and CITES Conventions respectively, and included in the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA). The Black Stork disappeared from the Western Europe in the first half of the last century and, although the populations are recovering, the species is still rare (BirdLife International 2015). The majority of the European population lives in eastern countries, where the numbers have been decreasing (Hagemeyer & Blair 1997, BirdLife International 2015). The decline has been particularly severe in the northern part of Eastern Europe (BirdLife International 2015). For example, the Estonian population, which occupied 100–120 breeding territories in 1990s (Sellis 2000) has fallen to half that (40–60 territories in 2010s; Elts *et al.* in prep.). Over the last decades, numbers have been declining similarly also in neighbouring

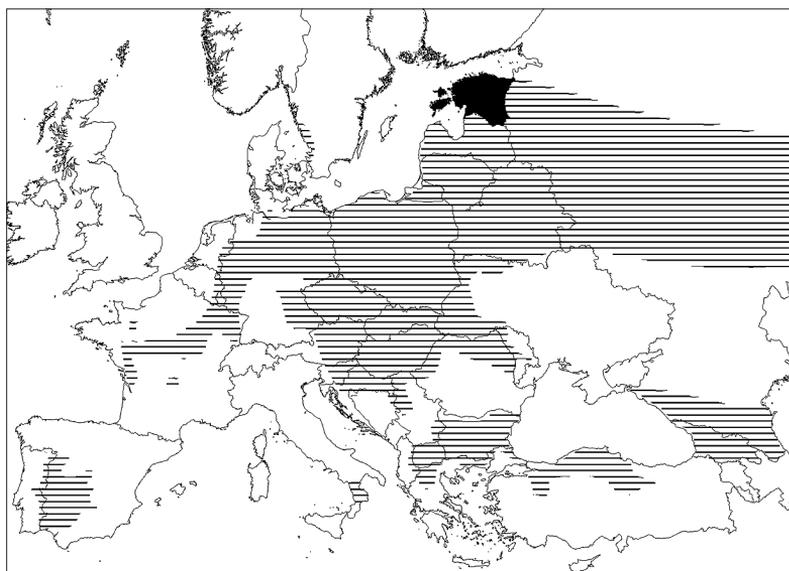
Latvia (decreased by 55%; Strazds 2011) and to a lesser extent in Lithuania (decreased by 20%; Treinys *et al.* 2008). The reasons behind these declines are unknown but identifying these are of utmost conservation importance.

The Black Stork is a monogamous species, which in Eastern Europe breeds solitarily in remote old-growth forests (Lõhmus *et al.* 2005, Treinys *et al.* 2009, Strazds 2011). Atypically for a large long-lived bird, the Black Stork has high reproductive potential as it may breed every year and usually raises two to four (up to six) young (Janssen *et al.* 2004). In birds, high reproductive potential often compensates mortality (Newton 1998). Therefore, the current study mainly aims to identify determinants of reproductive success, following Gaston's (2009) recommendation to pay more attention to range limitation as a consequence principally of changing numbers of births rather than mortality.

Reproduction may be compromised at various breeding phases but pinpointing the time and cause of the failure is not easy in a sensitive bird species. For conservation reasons, monitoring of Black Stork nests is usually conducted only once in a breeding season, when nestlings are large enough to be ringed. Unfortunately, this precaution impedes identification of important characteristics of reproduction, such as occurrence of single birds or pairs at nests, estimation of clutch and early brood size, and detection of intra- and interspecific contacts. Novel technologies, such as various types of automated remote cameras (O'Brien & Kinnaird 2008, Rollack *et al.* 2013, Väli 2018) now enable us to overcome these obstacles, although potential effects of cameras on behaviour of study objects should not be forgotten (e.g., Larrucea *et al.* 2007, Meek *et al.* 2014).

We used motion-triggered cameras (known as camera traps), and a web-camera, to assess reproductive success, population structure, and intra- and interspecific relationships in a Black Stork population at the northern range limit for six breeding seasons. Firstly, we studied the ratio between single individuals and pairs occupying nests. We hypothesized that in a peripheral population many territories are occupied by single birds, which do not breed themselves but negatively influence reproductive success of pairs by destroying their eggs or killing their offspring, as has been ob-

Fig. 1. Breeding distribution of the Black Stork in Europe (shaded, according to BirdLife International 2015) and the location of the current study (Estonia) highlighted in black.



served in the closely related White Stork (*Ciconia ciconia*; Schüz 1944, Haverschmidt 1949). Secondly, we estimated the reproductive characteristics (number of pairs breeding, mean clutch and brood size, breeding success, productivity) with aims to detect the phase at which its reproductive success is affected and to compare the values with those obtained in other parts of the range. Thirdly, we recorded presence of potential nest competitors (both intra- and interspecific) and various predators to investigate their influence on breeding.

2. Material and methods

2.1. Study area and species

The study was conducted in Estonia (57.5°–59.6°N, 21.8–28.2°E; 45,227 km²), a flat lowland country located between nemoral and boreal environmental zones (Metzger *et al.* 2005) and at the northern border of European range of the Black Stork (Fig. 1). Approximately 50% of Estonia is covered by forests and the entire Estonian Black Stork population nests on large trees located in the forest interior (Löhmus *et al.* 2005). The most common tree species hosting nests are Scots Pine (*Pinus sylvestris*), Aspen (*Populus tremula*), European Oak (*Quercus robur*) and Silver and Downy Birch (*Betula pendula*, *B. pubescens*; Löhmus & Sellis 2003). Black Stork often use the

same nest for several years, which facilitates research on their nesting biology. New nests are usually built within a few kilometres of the previous one, but the longest recorded breeding dispersal movement amounts to 7.8 km (unpublished telemetry data of authors), which is approximately the same value as the mean distance between neighbouring pairs.

2.2. Recording activities at nests

In 2010–2015, we followed Black Storks at 41 different breeding territories (an area that contains one or more nests within the home range of a mated pair or a single individual) distributed throughout Estonia. The annual number of studied territories, occupied by storks, varied between 5 and 19 (17 in 2010, 19 in 2011, 17 in 2012, 13 in 2013, 7 in 2014 and 5 in 2015), resulting to the total of 96 studied “nest-years”.

We used camera traps (models *Moultrie I40*, *M45* and *M80*, in few cases also *Bushnell Trophy Cam 119435* and *Sunplus Spca 533*) that were mounted on the branch of the nesting tree, or on the neighbouring tree, 1–5 m (usually 2–3 m) from the nest. The minimum time between triggered photographs was 0.5–2 min. To reduce the potential negative effect of cameras, installation of cameras was done in the second half of March, before storks returned from wintering grounds to their nest sites.

Cameras were complemented with external batteries and operated throughout the breeding season. From nests remaining unoccupied, cameras were removed and moved to another nest during the ringing of nestlings in late June or early July to record the number of fledglings. We admit that cameras could still have influenced nest occupancy by storks and therefore no conclusions are made on occupancy rate.

However, once the camera-equipped nest was occupied by birds, we expected no further significant biases on reproductive success nor competition. In total, the number of analysed photographs was 31,179 in 2010, 106,126 in 2011, 86,151 in 2012, 64,977 in 2013, 72,990 in 2014 and 83,978 in 2015. As cameras were operating for various periods, the amount of data differed remarkably, but for most statistical analyses we included only data from cameras that recorded activities at nest for at least 50 days in spring. Additionally, each year we included data from a web-camera, which recorded activities continuously at nest and streamed live video to the web.

In each nest we registered its occupancy (a nest was considered occupied if it was renovated and decorated with moss by storks) and various reproductive parameters: breeding frequency (no. of nests where eggs were laid / no. of occupied nests), proportion of successful nests (no. of successful nests / no. of occupied nests and no. of successful nests / no. of nests where eggs were laid), brood size (mean number of large nestlings in successful nests) and productivity (brood size \times proportion of successful nests). In calculations only one nest per territory was considered.

We also estimated the proportions of nests occupied by single non-reproductive birds and pairs, and counted the number of other Black Storks visiting the nest. Storks were assigned to a pair if they were recorded together at the nest for two weeks without fighting and/or they rebuilt the nest together and/or copulated. The same time limit for nest attendance, accompanied with nest decorating, was used for determining single local birds. Birds were considered “visitors” when they approached a pair, started fighting with or were intimidated by the birds at the nest. If possible, we also separated birds by their specific morphological characters and/or by observing them at the same time in different nests. GPS-transmitters and

colour rings with individual code facilitated separation of birds from others (in 11 cases).

We admit that only the minimum number of different birds were recorded, because we were unable to distinguish between unmarked individuals without specific characters that visited nests at different times. For the same reason, we were not able to detect single parents resulting from mortality or nest desertion during the breeding season.

We recorded also other species visiting nests and classified them as potential predators (Goshawk *Accipiter gentilis*, White-tailed Eagle *Haliaeetus albicilla*, Common Raven *Corvus corax*, Eurasian Jay *Garrulus glandarius*, Pine Marten *Martes martes*, Red Squirrel *Sciurus vulgaris*), competitors for nests (Common Buzzard *Buteo buteo*, Lesser Spotted Eagle *Clanga pomarina*, and Ural Owl *Strix uralensis*), and other species. These lists are not mutually exclusive as there are observations of White-tailed Eagles and Goshawks taking over Black Stork nests and the Common Buzzard and Ural Owl may potentially be a threat for small nestlings.

2.3. Statistical analysis

Reproductive success of Black Storks was described using common statistical parameters (mean, standard deviation). Generalized Linear Mixed Models (function *glmer* in the package *lme4* version 1.1-12; Bates *et al.* 2014) were used in the statistical environment R v. 3.3.3 (R Development Core Team 2017) to test for effects of visits of other storks, as well as competition and predation on reproductive parameters.

To analyse intraspecific interactions, we tested whether presence of “visiting” storks (binary categorical predictor) influenced occupancy of nests, proportion of breeding pairs among all occupied nests and proportion of successful pairs among pairs that started breeding (binary response variables in separate models). The identity of breeding territory was always included as a random factor. A likelihood-ratio test with chi-square approximation was used to test the significance of the models in comparison with null models (models without a predictor).

To test for the effect of potential interspecific competitors and predators, an information-theo-

Table 1. General linear mixed models describing relationships between the status of nests (response variable) and visits of non-local conspecifics (fixed factor). Breeding territory was always included as a random factor. Abbreviations: *SE* – standard error, *AIC* – Akaike information criterion, ΔAIC – difference of *AIC* values in the models with and without the fixed factor, χ^2 – value of the Chi-squared statistic, *P* – probability value.

Categorical predictor	<i>N</i>	Estimate \pm SE	<i>AIC</i>	ΔAIC	χ^2	<i>P</i>
Singles vs pairs	45	0.37 \pm 0.65	64.2	1.68	0.32	0.57
Eggs laid vs no eggs	44	5.62 \pm 7.51	53.2	-1.28	3.28	0.07
Successful vs unsuccessful breeding	15	0.67 \pm 1.65	23.2	1.73	0.23	0.63

retical approach for model selection and multi-model inference (Burnham & Anderson 2002) was used in the package *MuMIn* version 1.40.4 (Bartoń 2013). We used same response variables as in intraspecific analyses and presence of another species (listed above, both eagle species, whose visits were only occasional, were excluded) as binary categorical predictors. Null models were also ran. Given the small sample sizes and relatively many explanatory variables (7), only main effects were studied. We used the *dredge* function and Akaike information criterion corrected for small sample size (*AICc*) to select the best models. The relative importance of each model was estimated through ranking the models by the difference from the smallest *AICc* value ($\Delta AICc$) and the normalized Akaike weights. Top 2 *AICc* models ($\Delta AICc < 2$) were selected to calculate parameter estimates and relative importance values for explanatory variables.

3. Results

In 82 (85.4%) of the 96 nest-years we detected occupancy. Eggs were laid in 42 nest-years (51.2% of occupied nests) and at least one offspring fledged in 30 nest-years (36.6% of occupied pairs; 71.4% of pairs that laid eggs). The mean clutch size was 3.78 ± 0.63 eggs (\pm SD; $n = 18$), the mean brood consisted of 3.36 ± 0.63 ($n = 14$) hatchlings and 2.92 ± 0.81 ($n = 25$) fledglings. The overall productivity was 1.1 fledglings per occupied nest.

In 48 nest-years sufficient information was collected to distinguish between nests occupied by pairs or single birds. In 17 cases (35.4% of occupied nests) only single adult birds were recorded, with pairs (64.6%) occupying the remainder. In total, 55.8% of nests were visited by other Black

Storks ($n = 43$). These “visitors” were recorded mostly in April (45%; $n = 44$ visits) and May (36%), before breeding and during egg-laying and incubation. Although “visitors” were detected more often at nests of single birds (53%) than pairs (37%), the difference was not significant (Table 1). “Visitors” tended to visit nests more often where breeding had started (eggs laid in 69%, not laid in 57% of nests with “visitors”; Table 1).

Other storks also tended to visit nests of successful breeders more often (77% successful, 50% unsuccessful), but the difference among these was not significant (Table 1). Fights between local birds and visiting storks occurred at 13 nests *i.e.* 40% of visits ended up with fights. However, only in three cases did fights result in loss of eggs. Twice, a stranger destroyed a full clutch and once an egg was broken during a fight, and the remaining eggs were abandoned. Additionally, among nests visited by strangers, breeding was successful twice and not started in nine cases. In three of the latter cases, nests were occupied by a single bird.

Visits of other species were distributed throughout the breeding season. The most common interspecific visitors were the Eurasian Jay (recorded at 24.6% of nests), Pine Marten (20%), Common Buzzard (18.5%), Red Squirrel (17%) and Ural Owl (12.8%), while Common Raven (5.4%), Northern Goshawk (4.1%), White-tailed Eagle (2.8%) and Lesser Spotted Eagle (1.4%) were seldomly observed. Buzzards, Jays and Martens visited unoccupied nests more often than nests occupied by storks and the nests where storks did not start breeding; Goshawks and Ravens visited only occupied nests (Table 2). Among those nests where storks started breeding, Martens and Squirrels visited only successful nests while other species were seen only (Common Buzzard) or more often at unsuccessful nests (Table 2). Despite

several visits by potential predators, no actual predation events were recorded.

4. Discussion

4.1. Reproductive success

We found a very low proportion of successful nests in the Estonian Black Stork population. The recorded value (37%) is half the success observed during monitoring in southerly neighbouring countries Latvia and Lithuania (63% and 66%, respectively, calculated likewise from all occupied nests; Treinys *et al.* 2008, Strazds 2011) indicating the problems with reproduction only in the very northern margin of the range. Although no data on nest success are available from more southerly populations, higher values of productivity, compared to the one recorded in the current study (1.1 fledglings), have been observed in all studied southern regions (1.8 in Latvia; Strazds 2011, 1.9 in Ukraine; Horban & Bumar 2006, 1.9 in Spain; Cano-Alonso & Tellería 2013, 2.0 in Germany; Dornbusch 2006). The low productivity is not a result of small brood size, which is similar in Estonia to other countries (e.g., 2.7 nestlings in Latvia; Strazds 2011, 2.6 in Hungary; Tamás 2012, 3.0 in Lithuania; Treinys *et al.* 2008). This suggests that at least successful pairs do not have any problems associated with foraging, which causes smaller clutches or starvation of young (Newton 1998).

Our results on reproductive characteristics might have been biased because cameras were set preferentially at nests where breeding was detected recently. However, this means that we overestimated the reproductive success and the actual success is even lower. Indeed, regular monitoring of Estonian Black Stork nests suggests that only 29% (i.e. less than recorded in the current study) of the occupied nests are successful (R. Nellis, unpublished data).

Alternatively, cameras may interfere normal behaviour of animals (Larrucea *et al.* 2007, Meek *et al.* 2014) and thus influence the results of surveys. Although we attempted to reduce this effect by installing cameras before the breeding season, the presence of cameras may have affected nest occupancy, which was not the primary response used in our study. Estimation of reproductive character-

istics is probably much less biased, although variation of sensitivity towards cameras among birds might have a small effect.

The low proportion of the successful nests, causing the low productivity, could ultimately result from various factors. In addition to local limitations, such as unsuitable climate, birds at the northern range limit have longest migration route with highest expenditure of energy. Moreover, Estonian birds follow the eastern migration route (Bobek *et al.* 2008), where they are exposed to the poachers in the Middle East and to chemical contamination in East Africa (Strazds 2011, Strazds *et al.* 2015). Populations from western countries, where the numbers are increasing, use a different migration flyway to wintering grounds in West Africa (Bobek *et al.* 2008), which might be safer and thus increase their condition and reproductive potential. Negative factors in breeding grounds, such as disturbance at or lower quality of nest sites may also affect breeding success (Newton 1998).

For a species nesting in old-growth forest, forestry activities may have such an influence. Although forestry has been suggested as a significant threat in other countries (Horban & Bumar 2006, Kalocsa & Tamas 2006, Strazds 2011), no significant effect of forestry on the occupancy of nest sites by the Black Stork, nor on its reproductive success was found in Estonia (Rosensvald & Lõhmus 2003, Lõhmus *et al.* 2005). The range contractions may be caused by demographic factors also directly, not only through habitat destruction (Lawton 1996). Indeed, our most striking result is that currently about one third of nests are occupied by single birds, and this explains the low proportion of (successfully) breeding territories at the distributional margin.

4.2. Population structure

There is no comparative information from other parts of the range that could reveal the “normal” proportion of single storks in population. We could still ask, why are there so many single Black Storks at the northern European range margin? Although we were not able to identify sex of morphologically uniform Black Storks, the most plausible reason for such a bias is an unbalanced sex ratio (Donald 2007), previously recorded at species’

Table 2. Best generalized linear mixed models ($\Delta AICc < 2$) analysing the relationships between the occupancy of nests by Black Storks, proportion of nests with eggs laid and proportion of successful nests (response variables) and the presence of potential interspecific competitors and predators (fixed explanatory variables). Breeding territory was always used as a random factor. Abbreviations: R^2 – coefficient of determination, $AICc$ – Akaike information criterion, corrected for small sample size, $\Delta AICc$ – difference of $AICc$ values in the models, compared with the best model, RIV – relative importance values of the explanatory variables in all models.

	Common Buzzard	Ural Owl	Northern Goshawk	Common Raven	Eurasian Jay	Pine Marten	Red Squirrel	R^2	$AICc$	$\Delta AICc$	Weight
<i>Occupied vs. unoccupied nests</i>											
Model 1	-1.88					-1.61		0.12	45.2	0	0.20
Model 2	-2.09		34.84			-1.82		0.14	45.7	0.54	0.15
Model 3	-2.13							0.08	46.2	1.02	0.12
Model 4	-1.92		31.27		-1.29	-1.59		0.17	46.2	1.05	0.12
Model 5	-1.83				-1.30			0.11	46.3	1.13	0.11
Model 6	-1.70				-1.00	-1.39		0.14	46.3	1.16	0.11
Model 7	-1.89		31.06		-1.59			0.13	46.7	1.52	0.09
Model 8	-1.78			32.88		-1.64		0.13	47	1.79	0.08
Full average estimate	-1.91		12.02	2.71	-0.57	-1.09					
RIV	1.00		0.37	0.08	0.44	0.67					
<i>Breeding started vs breeding not started</i>											
Model 1	-2.16							0.09	90.6	0	0.32
Model 2	-1.98					-1.29		0.12	90.8	0.15	0.30
Model 3	-2.08	-0.74						0.10	92.4	1.78	0.13
Model 4						-1.44		0.06	92.5	1.93	0.12
Model 5	-2.05				-0.44			0.10	92.6	1.96	0.12
Full average estimate	-1.81	-0.09			-0.05	-0.56					
RIV	0.88	0.13			0.12	0.42					
<i>Successful breeding vs unsuccessful breeding</i>											
Model 1							31.33	0.09	38.3	0	0.169
Model 2	-36.54							0.09	38.5	0.15	0.157
Null model									38.62	0.32	0.14
Model 3								0.00	38.6	0.32	0.144
Model 4	-36.45								35.51	0.16	0.143
Model 5						35.09		0.14	39.4	1.08	0.098
Model 6						34.05		0.05	39.8	1.47	0.081
Model 7	-40.71					32.70		0.13	40	1.65	0.074
Model 8	-67.7					43.06		0.20	40.1	1.83	0.068
Model 9					-38.84	73.72		0.20	40.1	1.83	0.068
Full average estimate	-18.51				-2.63	16.52			23.39		
RIV (Success)	0.44				0.07	0.39	0.54				

range margins (Woolfenden *et al.* 2001). There are no data on the adult sex ratio in the Black Stork nor in its close relatives. However, male-biased sex ratios in monogamous birds may lead to increased competition for partners and harassment of other individuals (Ewen *et al.* 2011). This is consistent with what we observed in our study. We have shown earlier that sex ratio of Black Stork nestlings is balanced in most of Europe, including Es-

tonia (Konovalov *et al.* 2015). Hence, if the bias exists, it must develop after fledging either via sex-specific dispersal or mortality (Gowaty 1993, Székely *et al.* 2014).

Dispersal is considered as a key process in the occurrence of range limits and shaping the distribution of population performance (Bridle & Vines 2007). In Central Europe, mean natal dispersal of Black Storks is 140 ± 132 km (Tamás 2011). There

is no data on sex-specific dispersal distances in this species, but in the closely related White Stork, characterised by similar mean natal dispersal distances (94 ± 132 km), females settle significantly farther from natal sites (in average 177 km) than males (15 km; Chernetsov *et al.* 2006). Breeding dispersal has not been estimated for the Black Stork, but adults usually return to the same nest in consecutive years (Tamás 2011), which is typical also for the White Stork exhibiting short mean breeding dispersal (18 km; Itonaga *et al.* 2010). Unfortunately, sex-specific differences in breeding dispersal have not been evaluated even in the White Stork.

Survival rates of female birds appear to be systematically lower than those of males (reviewed in Donald 2007). The mean annual survival rate of adult Black Storks is estimated as 84% (Tamás 2012), but there is no published data on sex-specific mortality. Ring recoveries of Estonian Black Storks suggest equal survival during the first year of life, but higher mortality rates among females thereafter (R. Nellis and Ü. Väli, unpublished data). This should be taken with caution because in the well-studied White Stork, no effect of sex was found in survival models for various European populations; the re-sighting rate was higher in males instead, supposedly because of differences in nest attendance (Kanyamibwa *et al.* 1993). Hence, both sex-specific dispersal and mortality should be considered as potential factors influencing sex ratio and thereby lack of mates in the Black Stork, but both require further studies.

In saturated populations of long-lived birds, surplus non-territorial birds exist (Newton 1998). Such “floaters” quickly replace disappeared individuals at breeding territories and compensate for mortality in breeding population. After strong decline, the Estonian Black Stork population could not be considered saturated and many territories are vacant. We recorded many “visiting” storks, which often harassed local birds, but only rarely caused the actual damage on eggs. It is likely that “visitors” approaching birds at nests are not “floaters” looking for mates and nests, but instead are single birds having left their own territories to compete only for mates. Indeed, this is also supported by the tracking data from territorial individuals, which in years when they have skipped breeding, have moved over large areas and visited sev-

eral nests of other Black Storks (U. Sellis, unpublished data).

4.3. Predation and interspecific competition

Predators can have diverse roles at range limits and do so in concert with competition (Holt and Barfield 2009). In temperate and boreal forests, corvids frequently prey on eggs of forest birds (Andren 1992, Weidinger 2009) and their nestlings are threatened by Pine Martens and raptors (Newton 1979, Strazds 2011). Previously, predation by Pine Marten was considered as a significant and increasing threat for the Black Stork (Strazds 2011). We found low predation pressure by the Pine Marten, despite rather frequent visits at nests. As Martens visited mostly nests without breeding, they probably were just looking for the suitable site for resting. Other potential predators, Raven and Goshawk, were probably targeting eggs and nestlings, but they were recorded only infrequently at stork nests.

Thus, our studies corroborate the recent review paper concluding low impact of corvids on populations of other bird species (Madden *et al.* 2015), and even complement this review where forest-dwelling storks and raptors were poorly represented. Common Jays and Squirrels were recorded more often, but these predators are usually a threat only for birds smaller than the Black Stork. Also, the increasing negative influence of the White-tailed Eagle, along with the rapid growth of its population, has been suspected (Strazds *et al.* 2017) and there is evidence of White-tailed Eagles killing Black Storks (Langgemach & Henne 2001, Strazds 2011, Strazds *et al.* 2017).

We observed this species only in one nest where no breeding occurred, but outside the current study period we have recorded two attacks of White-tailed Eagles on juvenile Black Storks at nests. In summary, although we probably underestimated the number of predators at nests, because the cameras were not recording events continuously, the effect of predation on the Black Stork was low. This corroborates the earlier study in Hungary located at the centre of European range (Tamás 2012).

Large and medium-sized forest birds often exchange their nests (Newton 1979, Skuja & Budrys

1999, Hakkarainen *et al.* 2004, Horban & Bumar 2006), but previous studies on the effect of nest site competition have been focusing on hole-nesting passerines (reviewed in Newton 1998). Horban & Bumar (2006) have suggested Black Stork nest usurpation by the Great Grey Owl (*Strix nebulosa*). We recorded only few potential competitors for nests (Common Buzzard and Ural Owl), but these species mostly visited unoccupied nests or those without breeding. Probably these smaller competitors did not pose any influence on the nest occupancy nor breeding of the Black Stork. On the other hand, larger species such as the White-tailed Eagle (at least twice) and the Lesser Spotted Eagle (*Clanga pomarina*; once recorded by web-camera) usurped Black Stork and bred in the nest. Still inter-specific competition for nests had no detectable effect on the reproduction in the population level.

4.4. Conclusions

Our results confirmed that decline in a peripheral population may be linked to poor reproductive performance. Reproductive problems may emerge only at the very edge of the distribution. Although occupancy of nest sites and presence of individuals may be detected by regular monitoring activities, it does not necessarily mean that all conditions for reproduction are fulfilled. We showed that single individuals of a territorial species may occupy nest sites, but still not find partners for breeding. This would have been unnoticed in the course of normal monitoring, but was detected here because automated cameras were used at nests. Obviously, all novel applications should be taken into use with caution and potential additional threat for studied species should be avoided. If this is done, pinpointing threats and planning conservation actions is much more effective than traditionally used indirect methods.

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Yksin periferiassa: partnerien puuttuminen rajoittaa mustahaikaran lisääntymistä levinneisyysalueen reunalla

Lajien levinneisyysalueiden määräytyminen on tärkeä ekologian kysymys, ja sen mekanismeja voidaan selvittää tutkimalla levinneisyysalueiden reunaopulaatioita. Erityisesti uhanalaisilla lajeilla tällaisia tutkimuksia tarvitaan tehokkaiden suojelutoimien mahdollistamiseksi. Tutkimme vähenevän mustahaikarapopulaation lisääntymisparametreihin vaikuttavia tekijöitä. Selvitimme lajinsisäisen ja -välisen kilpailun, sekä pesäpredaation vaikutusta lisääntymismenestykseen riistakameroiden ja web-kameroiden avulla.

Haikaroiden poikastuotto oli alhainen (1.1 len-
topoikasta/aktiivinen pesä) verrattuna muuhun levinneisyysalueeseen. Tämä johtui pääosin alhaisesta onnistuneiden pesintöjen määrästä (37 % aktiivisista pesistä). Pääsyy alhaiselle lisääntymismenestykselle oli se, että 35 % :ssa pesistä oli vain yksi emo ja tämä yksilö ei ollut lisääntymisaktiivinen. Muut saman lajin yksilöt vierailivat usein häiritsemässä pesiviä lintuja, mutta aiheuttivat harvoin suoraa vahinkoa. Täten petojen ja lajitoverien vierailujen vaikutus lisääntymismenestykseen oli vähäinen.

Esitämme, että lisääntymiskumppaneiden vähyys on tärkein alhaista lisääntymismenestystä se-
littävät tekijä levinneisyysalueen pohjoisrajalla esiintyvissä mustahaikarapopulaatioissa. Tämä mekanismi voi rajoittaa levinneisyysalueiden reunaopulaatioiden kokoa ja levinneisyyttä muillakin pitkäikäisillä lajeilla.

References

- Abeli, T., Gentili, R., Mondoni, A., Orsenigo, S., Rossi, G. 2014: Effects of marginality on plant population performance. — *Journal of Biogeography* 41: 239–249.
- Andren, H. 1992: Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. — *Ecology* 73: 794–804.
- Bartoń, K. 2013. MuMIn: Multi-model Inference. R package version 1.9.13.
- Bates, D., Maechler, M., Bolker, B.M., Walker, S. 2014:

- lme4: Linear mixed-effects models using Eigen and S4. — ArXiv e-print; <http://arxiv.org/abs/1406.5823>.
- BirdLife International 2015: *Ciconia nigra*. — The IUCN Red List of Threatened Species 2015: e.T22697669 A60167006. Accessed 11 November 2017.
- Bobek, M., Hampl, R., Peske, L., Pojer, F., Somek, J., Bures, S. 2008: African Odyssey project – satellite tracking of black storks *Ciconia nigra* breeding at a migratory divide. — *Journal of Avian Biology* 39: 500–506.
- Bridle, J.R. & Vines, T.H. 2007: Limits to evolution at range margins: when and why does adaptation fail? — *Trends in Ecology and Evolution* 22: 140–147.
- Brown, J.H. 1984: On the relationship between abundance and distribution of species. — *American Naturalist* 124: 255–279.
- Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. — New York, Springer-Verlag.
- Cano-Alonso, L.S. & Tellería, J.L. 2013: Breeding productivity in relation to nesting substrate and nest site accessibility to humans in the Black Stork *Ciconia nigra*. — *Ardeola* 60: 357–363.
- Channell, R. & Lomolino, M.V. 2000: Dynamic biogeography and conservation of endangered species. — *Nature* 403: 84–86.
- Chernetsov, N., Chromik, W., Dolata, P.T., Profus, P., Tryjanowski, P. 2006: Sex-related natal dispersal of White Storks (*Ciconia ciconia*) in Poland: how far and where to? — *Auk* 123: 1103–1109.
- Donald, P.F. 2007: Adult sex ratios in wild bird populations. — *Ibis* 149: 671–692.
- Dornbusch, G. 2006: The Black Stork *Ciconia nigra* in Germany. — *Biota* 7: 25–30.
- Eckert, C.G., Samis, K.E., Loughheed, S.C. 2008: Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. — *Molecular Ecology* 17: 1170–1188.
- Ewen, J.G., Thorogood, R., Armstrong, D.P. 2011: Demographic consequences of adult sex ratio in a reintroduced hihi population. — *Journal of Animal Ecology* 80: 448–455.
- Gaston, K.J. 2003: The structure and dynamics of geographic ranges. — Oxford University Press, Oxford.
- Gaston, K.J. 2009: Geographic range limits of species. — *Proceedings of the Royal Society B: Biological Sciences* 276: 1395–1406.
- Gowaty, P.A. 1993: Differential dispersal, local resource competition, and sex ratio variation in birds. — *American Naturalist* 141: 263–280.
- Hagemeyer, W.J.M. & Blair, M.J. 1997: The EBCC Atlas of European breeding birds: their distribution and abundance. — Poyser, London.
- Hailer, F., Helander, B., Folkestad, A.O., Ganusevich, S.A., Garstad, S., Hauff, P., Koren, C., Nygard, T., Volke, V., Vilá, C., Ellegren, H. 2006: Bottlenecked but long-lived: high genetic diversity retained in white-tailed eagles upon recovery from population decline. — *Biology Letters* 2: 316–319.
- Hakkaraainen, H., Mykrä, S., Kurki, S., Tornberg, R., Jungell, S. 2004: Competitive interactions among raptors in boreal forests. — *Oecologia* 141: 420–424.
- Haverschmidt, F. 1949. The life of the White Stork. — E.J. Brill, Leiden.
- Holt, R.D. & Barfield, M. 2009: Trophic interactions and range limits: the diverse roles of predation. — *Proceedings of the Royal Society B: Biological Sciences* 276: 1435–1442.
- Holt, R.D. & Keitt, T.H. 2005: Species' borders: a unifying theme in ecology. — *Oikos* 108: 3–6.
- Holt, R.D., Keitt, T.H., Lewis, M.A., Maurer, B.A., Taper, M.L. 2005: Theoretical models of species' borders: single species approaches. — *Oikos* 108: 18–27.
- Horban, I. & Bumar, H. 2006: Conservation biology of Black Stork *Ciconia nigra* in Ukrainian Polissya. — *Biota* 7: 37–46.
- Howe, R.W., Davis, G.J., Mosca, V. 1991: The demographic significance of “sink” populations. — *Biological Conservation* 57: 239–255.
- Itonaga, N., Köppen, U., Plath, M., Wallschläger, D. 2010: Breeding dispersal directions in the white stork (*Ciconia ciconia*) are affected by spring migration routes. — *Journal of Ethology* 28: 393–397.
- Janssen, G., Hormann, M., Rohde, C. 2004: Der Schwarzstorch. — Westarp Wissenschaften, Hohenwarsleben.
- Kalocsa, B. & Tamás, E.A. 2006: An analysis of nesting data of Black Storks *Ciconia nigra* in the Gemenc region of the Danube Drava National Park (1992–2003). — *Biota* 7: 47–50.
- Kanyamibwa, S., Bairlein, F., Schierer, A. 1993: Comparison of survival rates between populations of White Stork *Ciconia ciconia* in Central Europe. — *Ornis Scandinavica* 24: 297–302.
- Kononov, A., Kaldma, K., Bokotey, A., Brossault, P., Chapalain, F., Dmitrenko, M., Dzyubenko, N., Sellis, U., Strazds, M., Strenna, L., Treinys, R., Zielinski, P., Väli, Ü. 2015: Spatio-temporal variation in nestling sex ratio among the Black Stork *Ciconia nigra* populations across Europe. — *Journal of Ornithology* 156: 381–387.
- Krebs, C.J. 1978: Ecology: the experimental analysis of distribution and abundance, 2nd edn. — Harper and Row, New York.
- Langgemach, T. & Henne, E. 2001: Storks *Ciconia nigra*, *C. ciconia* and common cranes *Grus grus* as prey of the white-tailed eagle *Haliaeetus albicilla*. — *Vogelwelt* 122: 81–87.
- Larruca, E.S., Brussard, P.F., Jaeger, M.M., Barrett, R.H. 2007: Cameras, coyotes, and the assumption of equal detectability. — *Journal of Wildlife Management* 71: 1682–1689.
- Lawton, J.H. 1993: Range, population abundance and conservation. — *Trends in Ecology and Evolution* 8: 409–413.
- Lawton, J.H. 1996: Population abundances, geographic

- ranges and conservation: 1994 Witherby Lecture. — *Bird Study* 43: 3–19.
- Lõhmus, A. & Sellis, U. 2003: Nest trees – a limiting factor for the Black Stork population in Estonia. — *Aves* 40: 84–91.
- Lõhmus, A., Sellis, U., Rosenthal, R. 2005: Have recent changes in forest structure reduced the Estonian black stork *Ciconia nigra* population? — *Biodiversity and Conservation* 14: 1421–1432.
- Lomolino, M.V. & Channell, R. 1995: Splendid isolation: patterns of geographic range collapse in endangered mammals. — *Journal of Mammalogy* 76: 335–347.
- Madden, C.F., Arroyo, B., Amar, A. 2015: A review of the impacts of corvids on bird productivity and abundance. — *Ibis* 157: 1–16.
- Meek, P.D., Ballard, G.A., Fleming, P.J., Schaefer, M., Williams, W., Falzon, G. 2014: Camera traps can be heard and seen by animals. — *PLoS ONE* 9: e110832.
- Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Múcher, C.A., Watkins, J.W. 2005: A climatic stratification of the environment of Europe: a climatic stratification of the European environment. — *Global Ecology and Biogeography* 14: 549–563.
- Newton, I. 1979: Population ecology of raptors. — Poyser, Berkhamsted.
- Newton, I. 1998: Population limitation in birds. — Academic Press, San Diego and London.
- Newton, I. 2003: Speciation and biogeography of birds. — Academic Press, London and San Diego.
- O'Brien, T.G. & Kinnaird, M.F. 2008: A picture is worth a thousand words: the application of camera trapping to the study of birds. — *Bird Conservation International* 18: 144–162.
- Pironon, S., Papuga, G., Villellas, J., Angert, A.L., García, M.B., Tompson, J.D. 2016: Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm: The centre-periphery hypothesis. — *Biological Reviews* 92: 1877–1909.
- R Development Core Team 2017: R: A language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>.
- Rehm, E.M., Olivas, P., Stroud, J., Feeley, K.J. 2015: Losing your edge: climate change and the conservation value of range-edge populations. — *Ecology and Evolution* 5: 4315–4326.
- Rollack, C.E., Wiebe, K., Stoffel, M.J., Houston, C.S. 2013: Turkey Vulture breeding behavior studied with trail cameras. — *Journal of Raptor Research* 47: 153–160.
- Rosenthal, R. & Lõhmus, A. 2003: Nesting of the black stork (*Ciconia nigra*) and white-tailed eagle (*Haliaeetus albicilla*) in relation to forest management. — *Forest Ecology and Management* 185: 217–223.
- Schüz, E. 1944: Nest-Erwerb und Nest-Besitz beim Weißen Storch. — *Zeitschrift für Tierpsychologie* 6: 1–25.
- Sellis, U. 2000: Will the black stork remain to breed in Estonia? — *Hirundo* 13: 19–30.
- 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.
- Skuja, S. & Budrys, R.R. 1999: Nesting sites of Black Stork, Lesser Spotted Eagle and Common Buzzard and their nest exchange in the forests of north, northeast and central Lithuania. — *Baltic Forestry* 5: 67–73.
- Strazds, M. 2011: Conservation ecology of the black stork in Latvia. — PhD dissertation, University of Latvia.
- Strazds, M., Bauer, H.G., Väli, Ü., Kukare, A., Bartkevičs, V. 2015: Recent impact of DDT contamination on Black Stork eggs. — *Journal of Ornithology* 156: 187–198.
- Strazds, M., Kuze, J., Ose, L. 2017: Impact of growing White-tailed eagle population on declining Black Stork population in Latvia. — The collection of Abstracts and Short Notes of the SEAEAGLE 2017 conference: 113. http://www.kotkas.ee/seaeagle2017/files/WTSE2017_abstracts-and-short-notes.pdf. Accessed in 22. November 2017.
- Székely, T., Liker, A., Freckleton, R.P., Fichtel, C., Kappeler, P.M. 2014: Sex-biased survival predicts adult sex ratio variation in wild birds. — *Proceedings of the Royal Society B: Biological Sciences* 281: 20140342.
- Tamás, E. 2011: Longevity and survival of the black stork *Ciconia nigra* based on ring recoveries. — *Biologia* 66: 912–915.
- Tamás, E.A. 2012: Breeding and migration of the Black Stork (*Ciconia nigra*), with special regard to a Central European population and the impact of hydro-meteorological factors and wetland status. — PhD dissertation, University of Debrecen.
- Treinsys, R., Lõhmus, A., Stončius, D., Skuja, S., Drobelis, E., Šablevičius, B., Rumbutis, S., Dementavičius, D., Naruševičius, V., Petraška, A., Augutis, D. 2008: At the border of ecological change: status and nest sites of the Lithuanian Black Stork *Ciconia nigra* population 2000–2006 versus 1976–1992. — *Journal of Ornithology* 149: 75–81.
- Treinsys, R., Stončius, D., Augutis, D., Skuja, S. 2009: Breeding habitat of the Black Stork *Ciconia nigra* in Lithuania: Implications for conservation planning. — *Baltic Forestry* 15: 33–40.
- Väli, Ü. 2018: Timing of breeding events of the Lesser Spotted Eagle *Clanga pomarina* as revealed by remote cameras and GPS-tracking. *Ardea* 106: 51–60.
- Weidinger, K. 2009: Nest predators of woodland open-nesting songbirds in central Europe. — *Ibis* 151: 352–360.
- Woolfenden, B.E., Gibbs, H.L., Sealy, S.G. 2001: Demography of Brown-headed Cowbirds at Delta Marsh, Manitoba. — *Auk* 118: 156–166.