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The relationship between population means and variances of reproductive success differs between local populations of white stork (*Ciconia ciconia*)

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Abstract We studied the size and productivity of white stork (*Ciconia ciconia*) populations in eight study sites in Poland. The number of nesting pairs and the average number of chicks fledged per pair fluctuated over time, and the studied populations differed in the variance of both breeding success and number of breeding pairs. The variance of breeding success (both for the mean number of chicks and the proportion of successful nests) and the variance of the number of breeding pairs was not correlated with the extent of stable habitats (pastures, meadows, wetlands), other habitats (farmland), or with local population trends over time. We found a nonlinear symmetrical relationship between annual mean reproductive success and its variance but only when considered as the proportion of successful nests (i.e., when individual nests are coded as a binary value: 0, no success; 1, success). No such relationship existed when success was expressed as the number of fledged chicks. Although a positive significant correlation occurred between fledgling numbers (discrete data) and the proportion of successful nests (binary data), we believe that the use of only binary data will be inadequate in more detailed analyses, such as population viability analysis.

Keywords Long-term studies · Life history · Population size · White stork · *Ciconia ciconia*

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Introduction

Individuals in populations differ in breeding success over both space and time. This fact has been used to produce models on population development, based on individual differentiation, and has a practical consequence for many aspects of population and conservation ecology (Łomnicki 1988; Lande et al. 2003). One important question to address, when developing such a model, is how differences in life-history characteristics affect population responses to temporal variation in demographic traits. Such temporal variation may be due to environmental stochasticity or may be density-dependent (e.g. Sæther 1997; Grant and Benton 2000). How the variance in individual success influences population structure and change over time is of interest (Conner and White 1999; Lande et al. 2003; Moreno et al. 2003). It is not, however, easy to predict the variance because, in many studies, authors focus only on the population mean and ignore the variance between individuals (for theoretical background, see Moreno et al. 2003). Recently, relationships between population means and variances in reproductive success were discussed by Moreno et al. (2003) who predicted consequences for life history in particular, and ecology in general. They focused mainly on between-species variation in the relationships. We want to add some theoretical background to their findings, as well as show the potential for a new way of understanding the problem using long-term data collected during intensive research on white stork (*Ciconia ciconia*) populations in Poland.

In this paper we consider aspects of the pattern of relationships between population means and variances in white stork populations in relation to differences in population size and changes in population size over time. We chose this species because (1) the white stork is traditionally presented as a long-term studied vertebrate species (Lack 1966); (2) establishing both population size and breeding success is relatively easy in the field, and therefore the obtained data are of good quality; and (3) in many parts of the white stork's geographical range, it is an endangered species and has been used to illustrate aspects of population ecology (e.g. Bairlein and Zink 1979; Engen and Sæther 2000). Moreover, Poland is host to about 25% of the world's white stork population (Jakubiec and Guziak 1998; Schulz 1998), and results can be applied to other populations across Europe.

Material and methods

The white stork builds large nests, mostly in human environments, and therefore nests are easy to find and to observe during the breeding period (e.g. Creutz 1985). The population size and breeding success of local populations were established by standard methods used during the International Census of White Storks (Creutz 1985; Schulz 1998).

Data were collected in the years 1973–2003, but not all data were collected in all study sites for the entire period (Table 1). The local white stork populations were studied in eight established long-term study sites located mainly in southern and western Poland (Fig. 1):

Klopot (Klo)—The study was conducted in 1974–2003, in Klopot, western Poland (52°07′N, 14°43′E). The site supports one of the largest white stork colonies in Poland (Jakubiec and Guziak 1998). The study site included ca. 50 small farms covering 9 km^2 located on the Odra river and comprised arable farmland (51%) and wetlands (32%) (for details see Radkiewicz 1992; Tryjanowski et al. 2005)

Wielichowo (Wie)—The study was conducted in 1983–2003. The study site (52°01′N, 16°22′E) covered

Table 1 Minimum, maximum, mean ± SD, variance, and temporal trends in number of pairs/annum of locally breeding white storks over the study period

Study site	No. of years	Population size					
		Min.	Max.	Mean	SD	Variance	Trend
Kłopot (Klo)	30	16	33	25.8	4.09	16.76	−0.26
Wielichowo (Wie)	21	42	75	60.2	8.48	71.96	−0.76
Leszno (Les)	30	42	64	54.2	6.38	40.76	−0.16
Poznań (Poz)	21	52	70	60.3	5.78	33.44	0.38
Dzierżoniów (Dzi)	20	9	34	23.7	6.32	39.99	0.53
Żywiec (Zyw)	20	14	28	19.9	3.19	10.15	−0.46
Chyzne (Chy)	30	9	26	14.9	5.28	27.89	0.55
Nowy Targ (Nta)	30	11	52	27.1	13.19	173.98	1.41

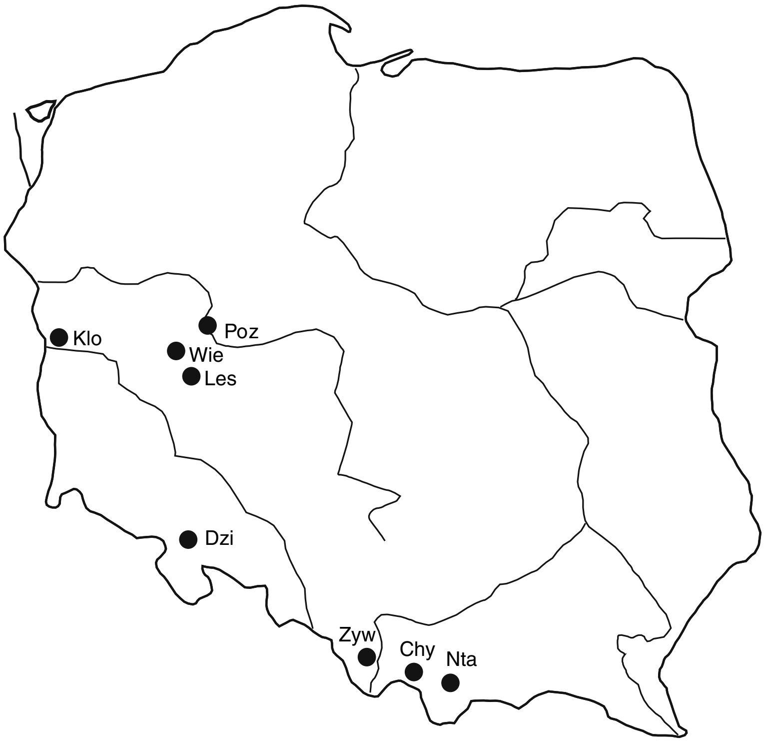


Fig. 1 Location of the eight study sites in Poland. For site abbreviations, see Table 1

417 km^2 and included arable fields (49%), and meadows and pastures (28%) (for more details see Kuźniak 1994; Tryjanowski and Kuźniak 2002).

Leszno (Les)—The study was conducted in 1974–2003, near Leszno in western Poland (52°51′N, 16°34′E). The study site covered 810 km^2 and included arable fields (68%), and meadows and pastures (6%) (for details see Kuźniak 1994).

Poznań (Poz)—The study was conducted in 1983–2003, near Poznań in western Poland (52°25′N, 16°58′E). The study site covered 1,483 km^2 and included arable fields (62%), and meadows and pastures (14%) (for details see Ptaszyk 1994; Ptaszyk et al. 2003).

Dzierżoniów (Dzi)—The study was conducted in 1984–2003, near Dzierżoniów in southwestern Poland (50°46′N, 16°43′E). The study site covered 793 km^2 and included arable fields (67%), and meadows and pastures (4%) (for details see Wuczyński 1997).

Żywiec (Zyw)—The study was conducted in 1981–2000, near Zywiec in southern Poland (49°40′N, 19°13E). The study area covered 420 km^2 and included arable fields (60%), and meadows and pastures (4%).

Chyzne (Chy)—The study was conducted in 1974–2003, near Chyżne in southern Poland (49°25′N, 19°40′E). The study area covered 820 km^2 and included arable fields (59%), and meadows and pastures (3%) (for details see Profus and Mielczarek 1981; Profus and Cichocki 2002).

Nowy Targ (Nta)—The study was conducted in 1974–2003, near Nowy Targ in southern Poland (50°46′N, 16°10′E). The study area covered 950 km^2 and included arable fields (51%), and wetlands (1%) (for details see Profus and Mielczarek 1981; Profus and Cichocki 2002).

Analyses were done in two ways. First, the traditional analysis as described by Moreno et al. (2003), which is based, probably erroneously, on the least-squares methods was carried out, and secondly, a method based on maximum likelihood was performed.

Data on the variance of breeding success are presented in two ways: based on the numbers of fledglings and on nest success (a binary variable: 0, no success; 1, success, i.e. at least one fledgling was produced) as used by Moreno et al. (2003). Throughout the text, values are reported as means ± SD. Calculations were conducted using the SPSS for Windows package. All basic statistical analyses were applied according to the recommendations of Zar (1999).

Because some measures of variability in the number of pairs and in population productivity can be related to the duration of the study (Pimm 1991), we first checked the potential influence of the number of years by correlating the length of the study period with both the population mean and variance. However, none of the relationships were significant. The results were also recalculated for only the last 20 years at all study sites, to avoid gaps at some sites, but similar results to those presented below were found.

We then constructed generalised linear models (GLMs) of population size (number of breeding pairs at each site) and breeding success assuming Poisson and binomial distributions respectively. For the population size model, the previous year's population size (log-transformed) was included as an explanatory variable. We checked all single-term predictions added sequentially (site, year, and population size in the previous year) and potential interactions using analysis of deviance using the statistical language R (http://www.r-project.org; Ihaka and Gentleman 1996; R Development Core Team 2004).

Results

All basic biological information on the studied populations, based on a total of 7,066 nests, is presented in Table 1. The studied populations of white stork differed in mean number of fledglings ($F_{7,165} = 2.85$, $P = 0.008$), variance of the number of fledglings ($F_{7,164} = 7.15$, $P < 0.001$), mean proportion of nest success ($F_{7,165} = 8.29$, $P < 0.001$), variance of the proportion of nest success ($F_{7,165} = 8.10$, $P < 0.001$), and mean number of breeding pairs ($F_{7,165} = 155.89$, $P < 0.001$) (Figs. 2 and 3). The above results were determined using ANOVA based on annual means at sites, and after controlling for year effects. Under a Poisson model of fledgling number, means and variances are expected to be identical. Figure 2 reveals evidence that this is not always so. Overdispersion (variance > mean) seems apparent in some years and sites, for example Poznań, while underdispersion (mean < variance) is evident in high productivity situations, for example, Klopot.

Variance of breeding success (both the number of fledglings, and expressed as a binary value) and the number of breeding pairs in study sites did not correlate with the extent of stable habitats (pastures, meadows, wetlands), other habitats (farmland), or with local population trends over time ($P > 0.4$ for all correlations, quadratic relationships also not significant).

As predicted from statistical theory, we found a quadratic relationship between the annual mean and variance of the proportion of nest success ($y = 0.007 + 1.023x - 1.031x^2$; $r^2 = 0.992$; Fig. 4). However, only ca. 6% of all points (site/year combinations) were located below $x = 0.5$ (the shaded part of the figure), i.e., in years when less than half the nests at a site failed to produce at least one fledgling. For these cases, there exists a positive correlation between mean and variance of reproductive success but only when considered as the proportion of nest successes (Table 2). Correlations between the two measures of breeding success (i.e., between the mean of binary data and the mean number of fledglings) were significant at all study sites ($0.68 \le r \le 0.89$, $P < 0.001$ in all cases), as well as for the whole data set ($r = 0.79$, $n = 202$, $P < 0.001$).

The generalised linear models of the number of breeding pairs and their productivity showed differences

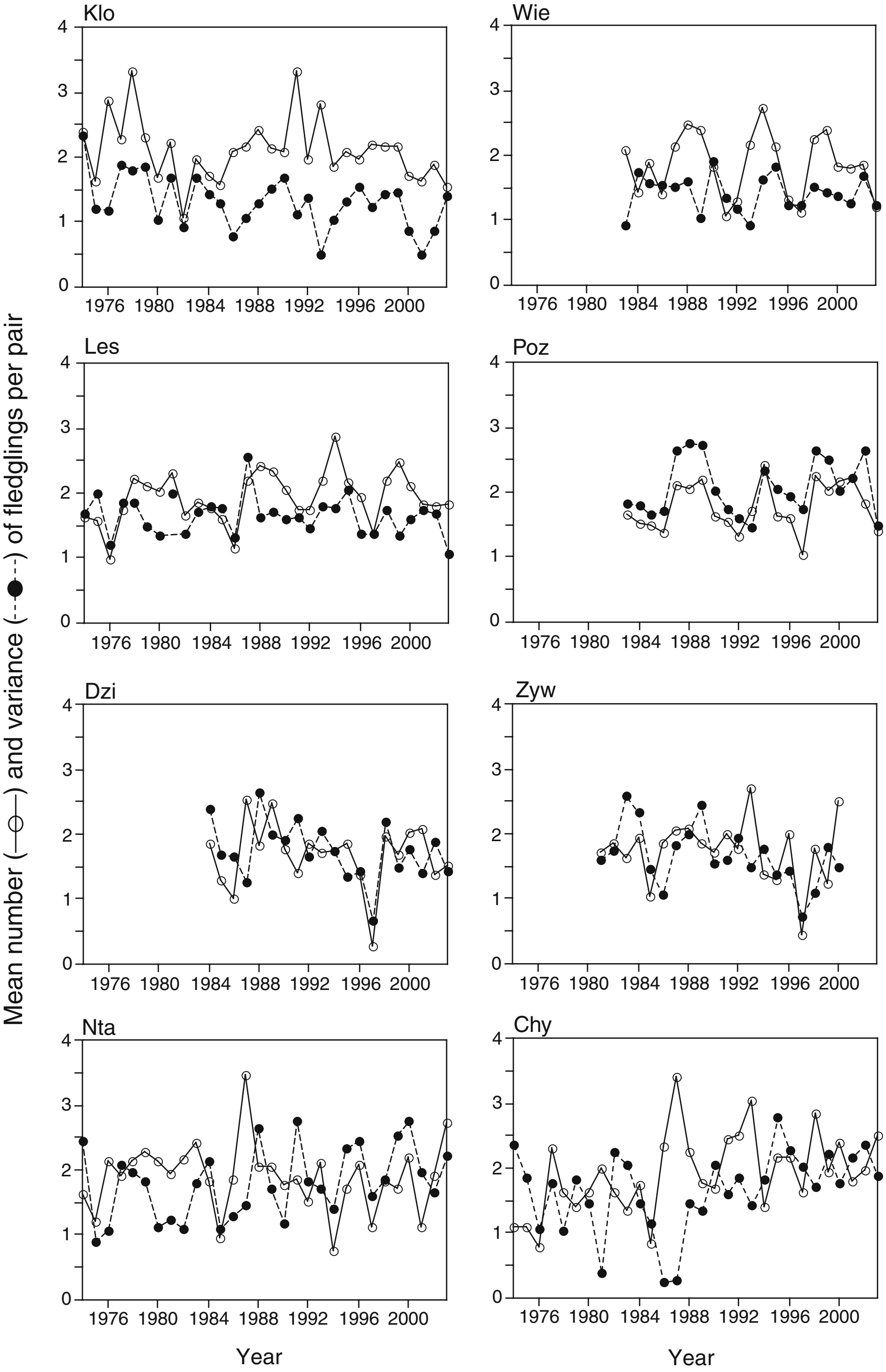


Fig. 2 Mean number (*solid line*) and variance (*dashed line*) of fledglings per pair (*y*-axis) of white storks in eight Polish study sites during study period (*x*-axis). For abbreviations of the study sites, see Table 1

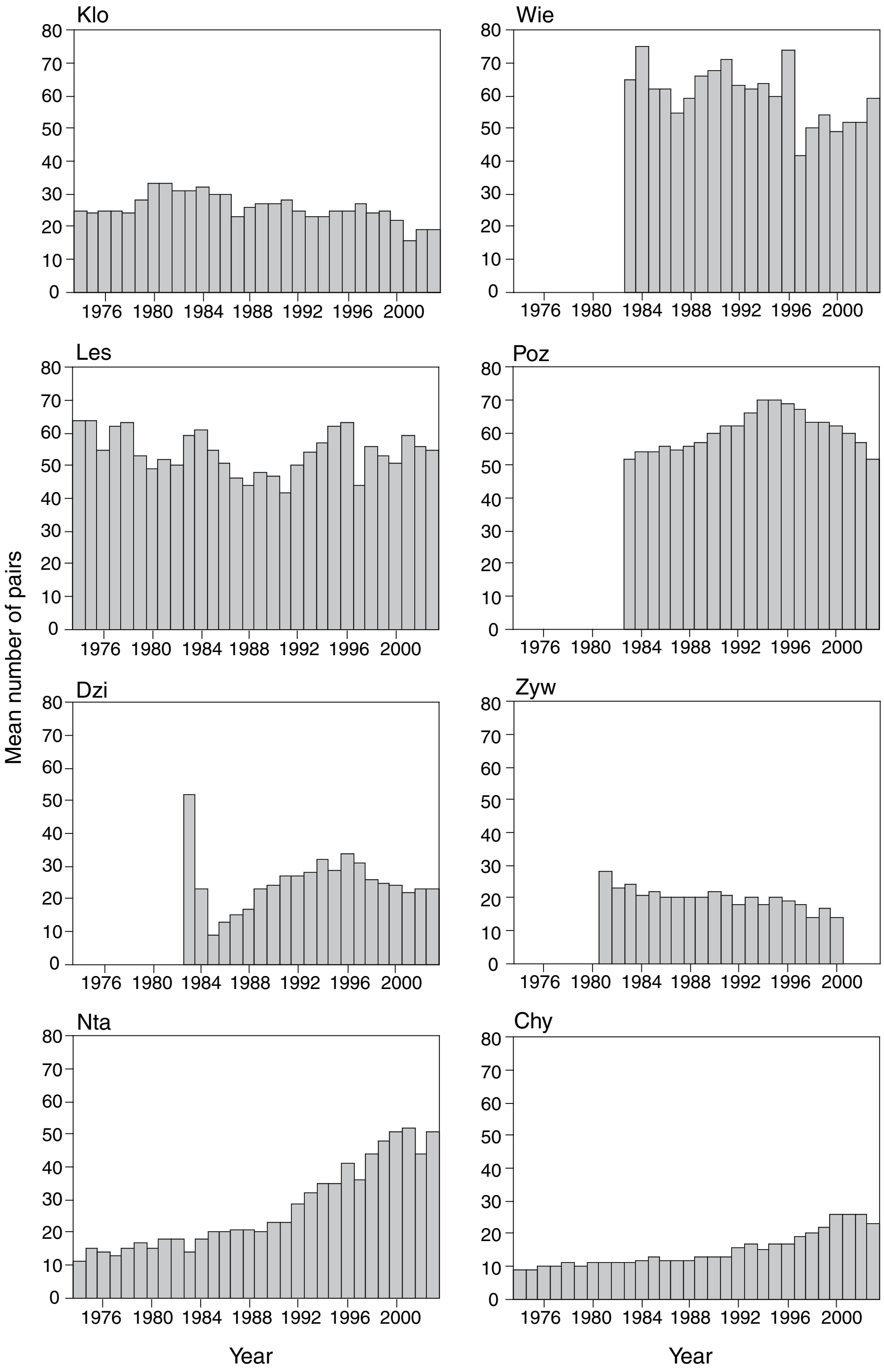
between study sites and years for both analysed variables. The numbers of breeding pairs were also significantly related to the log-population size of the previous year (Table 3).

Discussion

Breeding birds differed in their reproductive success between studied populations and between years. This produced a pattern in the relationship with variances, both in the number of breeding pairs, as well as in productivity. Because it is very easy to detect and record the number of pairs and the number of fledged chicks in the white stork, the observed changes are not associated with errors in detectability, but are derived from high quality data obtained during field studies. Therefore, it is possible to obtain data for all breeding pairs in the local populations and to study the variance between local breeders and between populations, both in one breeding season, as well as in the long-term.

In the studied populations, the number of pairs and breeding success varied from year to year, as in other

Fig. 3 Mean number of pairs of white storks in eight Polish study sites. See Table 1 for abbreviations of the study sites



areas where white storks were censused over long periods (Lack 1966; Creutz 1985; Schulz 1998; Barbraud et al. 1999). The variations are probably connected with changes in weather conditions and/or food supplies both in breeding areas and in migration and wintering grounds, and this affects both the number of pairs and their productivity (Creutz 1985; Dallinga and Schoenmakers 1987; Schulz 1998; Tryjanowski and Kuźniak 2002; Tryjanowski et al. 2004). However, not only the average values differed over the study period, but also the variances of breeding success. Moreno et al. (2003) suggested a relationship between population means and variances of reproductive success with species life-history traits, mainly with the mean lifespan of

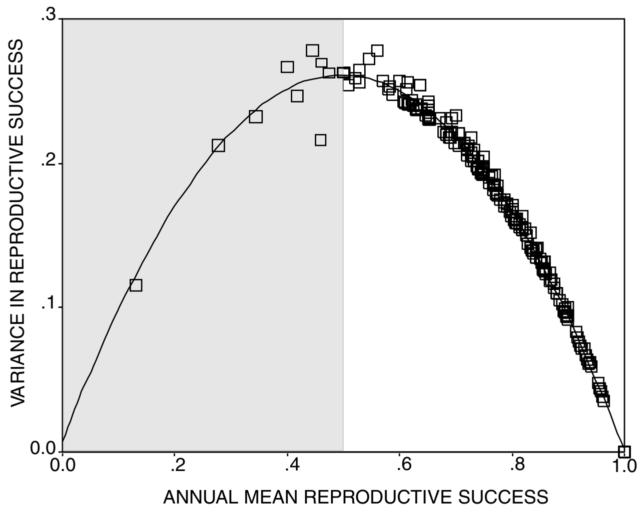


Fig. 4 Relationship between annual means and variances of breeding success (proportion of nests with at least one fledgling) for different white stork populations in Poland. *Shaded area* shows cases (population years) when less than half of local breeding pairs fledged young

Table 3 Analysis of deviance table for the number of pairs and breeding success, showing effects of sequential addition of variables in generalized linear models. Test statistics are based on chi-square approximation

	df	Deviance	Residual df	Residual deviance	*P*
Variable: number of pairs					
Null			160	1,531	
+ Study site	7	1,300	153	231	< 0.0001
+ Year	20	34	133	197	0.025
+ Log-no. of pairs in previous year	1	135	132	62	< 0.0001
Variable: breeding success					
Null			201	654	
+ Study site	7	181	194	472	< 0.0001
+ Year	29	149	165	323	< 0.0001

studied birds. They reported that in short-lived birds, such as the blue tit *Parus caeruleus* or the pied flycatcher *Ficedula hypoleuca*, correlations between breeding success and its variance had a negative sign, but in long-lived species, such as two species of the albatross, *Diomedea melanophris* and *D. chrysostoma*, the correlation had positive sign. However, our results suggest this could just be the consequence of the statistics used. When binary data are used, long-lived species that lay only one egg, such as albatross, appear less sensitive than small passerines that lay several eggs (see Sæther 1988). Our study reported that even different populations of the same species can differ in that relationship. However, we suggest that this is not a product of the biology of the species, but just a similar relationship predicted by the linkage between mean and variance in reproductive success when expressed as a binary value (see also Zar 1999). By definition that relation is a non-linear function, but in practice we more often noted only the right part of that symmetric function in the field (white area in Fig. 4, where breeding success exceeds 50%) and hence a negative correlation between means and variance. In fact, during field study it is relatively difficult to find populations where more than 50% of pairs do not have breeding success in a given year, i.e. do not produce fledglings at all (see Figs. 2 and 4). Note that this relationship does not exist when success is expressed as the mean number of fledglings.

Although there is a correlation between the mean number of fledglings and the proportion of nest successes, the use of binary data (success or failure) will be inefficient in more detailed analyses, such as population viability analysis (Conner and White 1999; Brook 2000). We agree with the conclusion of Moreno et al. (2003) that, at least in long-term studies, not only should the average annual data be presented, but measures of variability as well. We think that differences in particular population dynamics could be the effect of differences in the condition of birds, survival pattern and age structure (see Engen and Sæther 2000). However, lack of such data in all of our study sites renders such a detailed analysis impossible. The obtained findings are easy to use in constructing predictive models for nature conservation because the relationships between population parameters (including population means and variances) provide the background for population viability analysis, modelling extinction time of both local populations and species as a whole (Lande et al. 2003). We believe

Table 2 Evidence for relationships between annual breeding success and breeding success variance in several white stork populations

Study site	Correlation of means and variances		Range in mean number of fledglings	Correlation of means and variances (binary data)		Range in mean binary success
	r	*P*		*r*	*P*	
Kłopot (Klo)	0.24	0.20	1.06–3.33	−0.94	< 0.001	0.47–0.96
Wielichowo (Wie)	0.14	0.54	1.07–2.75	−0.99	< 0.001	0.74–0.93
Leszno (Les)	0.39	< 0.04	0.98–2.87	−0.97	< 0.001	0.50–0.89
Poznań (Poz)	0.75	< 0.001	1.02–2.42	−0.85	< 0.001	0.41–0.77
Dzierżoniów(Dzi)	0.35	0.12	0.29–2.53	−0.34	0.13	0.13–0.93
Żywiec (Zyw)	0.27	0.23	0.44–2.70	−0.76	< 0.001	0.27–0.90
Chyzne (Chy)	−0.20	0.28	0.80–3.41	−0.92	< 0.001	0.40–1.00
Nowy Targ (Nta)	0.14	0.44	0.77–3.46	−0.87	< 0.001	0.34–1.00

that underdispersion in fledgling number occurs when mean fledgling numbers are high and a large proportion of the population is performing well. There is a biological limit to the number of chicks that white storks can produce, resulting in, effectively, a truncated Poisson distribution. Overdispersion may well be a feature of poor breeding performance or of a population that consists of a mixture, possibly a bimodal one, of good and poor breeders, thus inflating the variance above that expected from the statistical model. Thus, in a more stable habitat/environment underdispersed populations may be the norm, but in changeable situations this may no longer be true. The first step to understanding some processes in ecology better, as well as to applying these results to conservation, is to conduct studies that are more detailed than the traditional measures of population size and productivity. We have tried to emphasise that in this paper.

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