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Breeding ecology of the globally threatened Sociable Lapwing *Vanellus gregarius* and the demographic drivers of recent declines

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Abstract We assessed demographic rates and numbers of the globally threatened Sociable Lapwing *Vanellus gregarius* in central Kazakhstan from 2005 to 2012 to identify drivers of recent declines. Annual fecundity, estimated from a sample of over 1,000 nest histories, was highly variable. Nest survival was higher closer to human settlements, despite higher trampling rates, and when there were more neighbouring nests, but distance to settlements and colony density both varied systematically between years. Both overall nest survival and annual adult survival were on average lower than those estimated for congeneric species elsewhere, although daily chick survival was high. Breeding site fidelity and natal philopatry were low and colonies fluctuated greatly in size between years, making estimation of population trends and survival difficult. Estimates of productivity and survival suggest that the population is in slight to severe decline, with a mean annual estimate of population growth rate (λ) of 0.81 (95 % CL 0.64–0.98). This is reflected in changes in the number of nests found in our core study area, which after 5 years of relative stability declined rapidly after 2010. Of the three demographic rates, adult survival had the greatest influence on λ and only adult survival reached levels necessary for λ to achieve an annual mean of 1 in the absence of a change in any other rate, though only in 1 year. Our results suggest that low adult survival, perhaps resulting from known hunting pressure along the migration routes, is the most critical demographic rate and offers the most tractable conservation solution.

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Zusammenfassung

Brutbiologie und demografische Ursachen für den derzeitigen Rückgang des global gefährdeten Steppenkiebitzes *Vanellus gregarius*

In dieser Arbeit stellen wir Ergebnisse einer Studie zu Brutbiologie und demografischen Parametern des global bedrohten Steppenkiebitzes *Vanellus gregarius* vor, die zwischen 2005 und 2012 in Zentralkasachstan erhoben wurden. Die Fekundität (Anzahl geschlüpfter Küken pro Weibchen), bestimmt durch eine Analyse von über 1,000 Nestschicksalen, schwankte von Jahr zu Jahr stark. Überlebensraten von Nestern stiegen bei zunehmender Koloniedichte an und waren umso höher, je näher die Nestern an menschlichen Siedlungen lagen (trotz höheren Viehtrittrisikos). Beide Parameter variierten allerdings stark über den betrachteten Zeitraum. Die

Überlebenswahrscheinlichkeit von Nestern wie auch von Altvögeln war im Mittel niedriger als bei verwandtschaftlich nahe stehenden Arten, allerdings war die tägliche Überlebenswahrscheinlichkeit von Küken hoch. Brutorttreue von Altvögeln und natale Philopatrie waren niedrig, und die Größe von Brutkolonien fluktuierte stark, daher war die Abschätzung eines Populationstrends und von Überlebenswahrscheinlichkeiten schwierig. Unsere Werte deuten aber auf einen aktuell leichten bis ernsthaften Populationsrückgang hin, und wir schätzen jährliche Zuwachsraten der untersuchten Population (λ) auf 0.81 (95 % CL 0.64–0.98). Dies manifestierte sich auch in einer Abnahme der gefundenen Nester in unserem Kernuntersuchungsgebiet seit 2010 nach fünf Jahren vorhergegangener relativer Stabilität. Die Überlebensrate adulter Vögel hatte von den drei untersuchten demographischen Parametern den stärksten Einfluss auf λ, und nur dieser Faktor erreichte Werte, die bei gleichzeitig unveränderten Überlebenswahrscheinlichkeiten von Nestern und Küken im betreffenden Jahr für Populationsstabilität nötig wären, allerdings nur in einem Jahr. Vielmehr scheinen hohe Altvogelverluste, möglicherweise verursacht durch den bekannt gewordenen hohen Jagddruck entlang der Zugwege, kritisch für das Überleben der Art zu sein—gleichzeitig ist dieser Faktor durch Naturschutzmaßnahmen am ehesten zu beeinflussen.

Introduction

The disintegration of the Soviet Union in 1991 brought about profound changes in land management across the Eurasian steppe zone, including a redistribution of grazing animals to the immediate vicinity of villages and a contraction in the area of wheat cultivation (Robinson and Milner-Gulland 2003; Kamp et al. 2011). Many bird species are likely to have benefited temporarily from land use changes brought about by the removal of agricultural subsidies and rural depopulation, which led to lower intensity production systems and widespread agricultural abandonment, a process now in reverse (Kamp et al. 2011). An exception is the Sociable Lapwing *Vanellus gregarius*, a semi-colonial plover that breeds only on the steppes of central Asia and winters in northeast Africa, the Middle East and northwest India. With the loss of its steppe habitat to cereal cultivation, the species became extinct as a breeding bird in Ukraine before the 1960s (Dolgushin 1962) and west of the Ural River in the 1980s (Shevchenko 1998). The breeding range has therefore contracted eastwards to around half its former extent and is now largely restricted to northern Kazakhstan, with a tiny population in fringing regions of southern Russia (Sheldon et al. 2012) and perhaps in western China (Kamp et al. 2010). With the loss or reduction in numbers of native grazers and the concentration of domestic livestock around villages, closely grazed steppe is now found mostly within a kilometre or two of human habitation, and this is where most birds nest (Khrokov 1996; Kamp et al. 2009). Its requirement for closely-grazed steppe for nesting suggests that, like many other steppe species (Kamp et al. 2011), the Sociable Lapwing should have benefitted from the contraction of wheat cultivation and the concentration of grazing pressure that followed the collapse of the Soviet Union. However, severe declines since the 1950s (Gordienko 1991) apparently accelerated after 1990 (Eichhorn and Khrokov 2002), and the species was listed as Critically Endangered by the IUCN in 2004. The reasons for this decline are unclear. Research carried out in central Kazakhstan in 2004 suggested that nest survival rates were sufficiently low to explain the observed declines and that the main cause of nest failure was trampling by livestock (Watson et al. 2006). This is a plausible explanation given the species' confinement to the most heavily grazed areas around villages; declines in nesting success have also been implicated in population declines of a number of meadow-breeding waders in Europe (Roodbergen et al. 2012), the most likely reason being an increase in predation rates (MacDonald and Bolton 2008b). The population decline of the Sociable Lapwing's close relative, the Northern Lapwing *V. vanellus*, has been largely driven by low nest survival in Europe (Milsom 2005; King et al. 2008). However, the study of Watson et al. (2006) was based on a relatively small sample of nests found in a single year and used estimates of annual adult survival derived from other species in other habitats. Furthermore, the steppes of central Asia differ in many ways from the European agricultural habitats in which most studies of declining meadow wader populations have been undertaken. More recently, the Sociable Lapwing has been found to be the target of hunters where it gathers in major aggregations at traditional migration staging posts in Syria and Iraq (Sheldon et al. 2012), suggesting an alternative or additional driver of decline. An assessment of demographic rates would therefore help to assess whether recent declines can be explained by low productivity, low adult survival or both. This study extends the work of Watson et al. (2006) by collecting comparable data over a wider area and a longer span of time to understand better the breeding ecology and survival rates of this species, to assess recent population trends and to identify their demographic drivers. The paper also attempts to assess spatial and temporal patterns in the breeding distribution to inform future monitoring of the species.
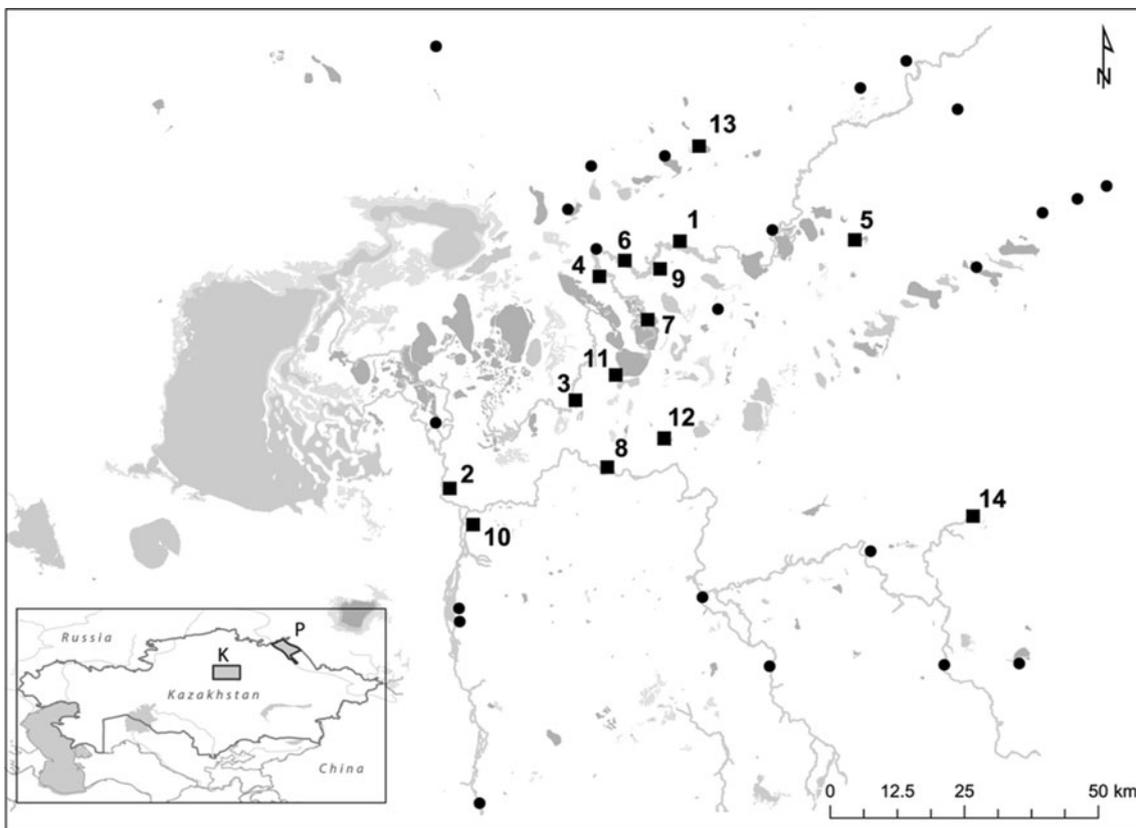
Methods

Study sites

Fieldwork was undertaken from mid-April to early August in each year from 2005 to 2012 inclusive, although a very low number of birds returning to colonies in 2012 meant that sample sizes were low and only colony count data were included in the analyses for this year. Field teams were based around the town of Korgalzhyn (approx. 50.59°N, 70.05°E) some 120 km SW of Kazakhstan's capital city Astana. The study site covered an area of around 20,000 km², within which breeding aggregations (hereafter 'colonies') were found at 32 sites (Fig. 1), almost all of them close to villages. Of these, 14 colonies were covered with approximately the same fieldwork effort in each year (although 2 were not covered as intensively in the first year as the other sites; Table 1) and data from outside these core colonies were dropped from some analyses. In 2007, we also collected data around 26 villages in the Pavlodar region, around 500 km to the northeast of Korgalzhyn (Fig. 1), using identical methods to assess

geographical differences in breeding parameters. The main Korgalzhyn study site lies at the southern edge of the steppe belt and the southern limit of cereal cultivation in Kazakhstan. The habitat consists of *Festuca-Stipa* grass steppe, which around the widely spaced settlements becomes dominated by *Artemisia* because this is unpalatable to domestic grazers. Sociable Lapwings strongly select this heavily grazed *Artemisia* steppe, as a consequence of which most are found clustered around villages that maintain domestic cattle herds (Kamp et al. 2009). Also present in the area are extensive areas of active and abandoned agricultural land and a network of rivers and freshwater and saline lakes (Kamp et al. 2009, 2011) (Fig. 1).

Data collection

Nests

Nests were found by scanning suitable habitats, generally around settlements (Kamp et al. 2009), with binoculars and telescopes to find feeding birds or incubating females,

Fig. 1 Location of colonies of Sociable Lapwing *Vanellus gregarius* in the Korgalzhyn study area and the two study areas within Kazakhstan (*inset*, *K* Korgalzhyn region, *P* Pavlodar region). Core colonies (identified by *numbers* corresponding to those shown in Table 1) are shown as *squares*, colonies visited only in some years are marked as *circles*. Major water bodies and rivers are also shown. The large lake to the west of the study area is Lake Tengiz

Table 1 Number of nests of Sociable Lapwing *Vanellus gregarius* found in the 14 core colonies in the Korgalzhyn region, in other colonies in the Korgalzhyn region and in colonies in the Pavlodar region (only covered in 2007) in 2005–2012

Colony	2005	2006	2007	2008	2009	2010	2011	2012	Total
Core colonies									
1 Abai	4	0	0	8	3	3	4	1	23
2 Aktubek	31	22	33	13	27	34	15	13	188
3 Almas	0	0	0	0	1	4	4	9	18
4 Amangel'dy	8	17	12	7	0	7	18	2	71
5 Arykty	0	1	0	0	4	0	0	0	5
6 Birlik	9	6	10	0	4	5	0	0	34
7 Birtaban	0	0	1	0	0	2	0	0	3
8 Kaskatau	(0)	6	0	5	5	26	17	0	59
9 Korgalzhyn	10	25	21	6	25	12	15	2	116
10 Kulanotpes	3	16	7	13	12	9	0	0	60
11 Shalkar	15	14	10	9	12	8	14	9	91
12 Ushsart	3	7	19	12	3	0	1	0	45
13 Zhanteke	0	7	3	11	6	8	3	0	38
14 Zharaspai	(0)	5	10	21	3	5	0	0	44
Total (core)	(83)	126	126	105	105	123	91	36	
Other colonies									
Korgalzhyn region	2	42	66	32	17	8	14	8	189
Pavlodar region	–	–	138	–	–	–	–	–	138
Total	85	168	330	137	122	131	105	44	1,122

In 2005, the core colonies of Kaskatau and Zharaspai were not visited with the same frequency as other colonies so the absence of nests in that year may be an artefact of survey effort. Colonies are identified by numbers that show their locations in Fig. 1

which because of the species' selection of very short vegetation for nesting and its conspicuous white supercilium could be located through telescopes at distances of up to 2 km. Nest locations were recorded with GPS. At most nests, the length and width of all eggs in the clutch were measured with callipers to the nearest millimetre and weighed to the nearest 0.1 g on a portable electronic balance. We estimated first egg dates for most nests using changes in egg density from a linear regression of egg density on age from a number of nests of known age ($R^2 = 0.86$; Fig. S1), observed hatching dates or observations of nests found during the laying period (see below). We used the mean annual interval between these back-calculated first egg dates and the date of nest discovery as a "time-to-find" measure of our efficiency in finding nests each year. Nests were re-visited at intervals of around 3–4 days to record their fate and particular efforts were made to visit nests around the predicted hatching date to ring chicks. If an adult bird was incubating at the time of the visit, it was assumed that the clutch was still active and the bird was not disturbed. Nests were recorded as successful if at least one chick hatched and left the nest. Where chicks were not seen nearby with accompanying adults, success was assumed if the nest became empty at around the estimated hatching date and if it contained very small fragments of eggshell in the nest lining, indicative of

successful hatching in this (personal observation) and other lapwing species (Sheldon et al. 2007). Failure was assumed where the nest became empty before the estimated hatching date, when the nest was often damaged and large fragments of eggshell were present in or around the nest. The complete disappearance of the eggs, with no small eggshell fragments in the nest lining and often with no damage to the nest, was taken as evidence of predation, whereas the presence of crushed eggs and yolk in the nest and a damaged nest lining was assumed to result from trampling by livestock. In a smaller number of cases, nests were deserted or the parent killed (eggs recorded as cold on a number of visits, and no nearby adults). The condition of nests that were assumed to have failed or succeeded was confirmed by examination of nests whose fate was known from nest camera recordings (see below). Visits by fieldworkers to nests are unlikely to have influenced nest predation rates, since no effect of nest visiting were discernible in Northern Lapwings or across a range of other species (Galbraith 1987; Fletcher et al. 2005). Indeed, visiting nests of ground-nesting species might actually confer some degree of protection (Ibáñez-Álamo et al. 2012). After hatching, colour-ringed chicks were searched for every few days to estimate daily survival in the first days of life.

In order to identify nest predators and to calibrate assessments of nest outcome, motion-triggered miniature

cameras fitted with an infrared spotlight device were deployed at a total of 29 nests in 2005–2008.

Survival

Adult birds were captured during incubation by placing wire mesh walk-in traps over the nest while the adults were off the nest and then rushing the nest when they returned after the eggs had sufficient time to warm. Adults were fitted with unique combinations of colour rings and released. All trapped and released females returned to the nest and continued incubation. Each year, all adult birds encountered in the field were checked for colour rings, both during nest-finding and during counts of flocks (see below). Nests were visited around the time of hatching to ring chicks, which were also fitted with unique colour ring combinations. Estimates of philopatry, indicative of the extent to which the study population is open or closed, can inform the interpretation of survival models (Cooch and White 2011). We therefore assessed rates of movement of individual birds between colonies and years using colour ring resightings and locations from a small number of birds fitted with 5-g or 9-g PTT satellite transmitters (Microwave Telemetry, locations downloaded through the Argos system) attached using a Teflon leg harness.

Flocks

At each encounter with Sociable Lapwings away from known nests, the number of adult birds present and their sex, the number of juveniles, the presence of colour-ringed birds, habitat and location were all recorded. Particular effort was made to find pre- and post-breeding flocks, to look for colour-ringed birds and to assess population size, but since these did not always gather at the breeding sites or use the same habitats as breeding birds, detection rates of such flocks were uncertain.

Population trend

Estimating the population trend of Sociable Lapwings was complicated by the fact that the area was used as a staging post before and after breeding by birds from outside the study area and also by the erratic occupancy of colonies in each year. We used the number of nests in the 14 core colonies that were covered with approximately equal effort in each year as a metric of annual population size, but the nest count could not be taken as a reliable index of wider population trends.

Data analysis

Nest phenology and survival

For around 10 % of nests, failure occurred before the eggs were measured, so first egg date could not be estimated directly from egg densities. Simply excluding these nests from models of age-specific survival would bias the resulting nest survival estimate, since most unmeasured clutches failed. We therefore imputed first egg dates for these nests by estimating the mean interval between first egg date and the date of discovery for each year across nests for which first egg date was estimated directly. This year-specific value was then added to half the number of days between the date of nest discovery and the date the nest was last recorded intact and the sum subtracted from the date of discovery to generate an approximate first egg date, in most cases accurate to within ±5 days. Egg volume was estimated as length $\times$ width^2 $\times$ 0.51 (Hoyt 1979).

We initially constructed nest survival models in program MARK (White and Burnham 1999; Rotella et al. 2004), which allowed us to account for age-specific nest survival rates and to fit covariates. Program MARK was accessed via the RMARK interface (Laake and Rexstad 2011) in R 2.13.1 (R Development Core Team 2011). Nest survival was modelled as a function of year, date and nest age. It is known from previous work on the study population that Sociable Lapwings are strongly associated with areas around human settlements (Kamp et al. 2009), and nests were on average around ten times closer to human settlements ($n = 940$, mean $= 1.24$ km, SE $= 0.033$) than points randomly distributed across the study area ($n = 1{,}000$, mean $= 10.29$ km, SE $= 0.27$; $F_{1, 1{,}938} = 1{,}020.5$, $P < 0.0001$). Therefore, distances from each nest to the nearest settlement were calculated in ArcGIS 10.0 and added as a covariate to models of nest survival. Because previous work on the closely related Northern Lapwing Vanellus vanellus has shown an effect of colony density on nest survival (MacDonald and Bolton 2008a), we also calculated for each nest the number of other nests in the same breeding season that fell within a radius of 500 m and added this as a covariate. The large number of candidate models resulting from the addition of covariates and their interactions with year and the difficulty of fitting models in MARK with complex interactions and random factors meant that we first assessed evidence of age-specific survival rates alone in MARK, and then modelled the environmental covariates using logistic regression in R. These latter models could only treat daily survival rate as constant, but because the inclusion of nest age in nest survival models received little support from the MARK models (see "Results"), this was considered adequate. We modelled a binary nest outcome (0 = success, 1 = failure), with exposure days fitted as the binomial denominator, as a function of colony (fitted as a random effect to reduce non-independence of nest outcomes within colonies), first egg date, year, distance to village, number of near neighbours and all two-way interactions between

them using mixed models implemented with the glmer function in the R package lme4 (Bates et al. 2011). Model selection was performed by comparing all possible models using the 'dredge' function in the R package MuMIn (Bartoń 2011). Log-likelihood was approximated with the Laplace method so competing mixed models could be compared using AIC$_c$ (Burnham and Anderson 2002). Because fieldwork was undertaken in Pavlodar only in 2007, models were initially restricted to nests found in the Korgalzhyn study area. A separate model assessed differences between nest survival in Korgalzhyn and Pavlodar in 2007, fitting region as a fixed factor. Finally, all nests were included in a model that fitted colony nested within region as a random effect. Models were ranked using the AIC$_c$ differences Δ_i between the best model and each other model and Akaike weights w_i calculated. The overall contribution of each covariate to the candidate model set was assessed by summing the Akaike weights of the models each covariate appeared in within the ranked subset of candidate models whose Akaike weights summed to 0.95. The parameter estimates of each covariate across the same set of best supported models ware averaged using the 'model.avg' function of MuMIn. Standard errors were calculated using the square root of the unconditional variance estimator (Burnham and Anderson 2002).

Re-nesting estimates and seasonal fecundity

Direct estimation of re-nesting probability was not possible because of the small number of colour-ringed adult birds present each year in the study site. We therefore assumed that the actual re-nesting rate fell somewhere between zero (i.e. treating all nests as first clutches) and a maximum that assumed that all nests that could have been second clutches were so. This was estimated by drawing up phenological plots of all nests in the core colonies. A small number ($n = 5$) of observations of re-nesting attempts by colour-ringed adults suggested a mean interval of 8.6 days between the end of the first nesting attempt and initiation of the second, and suggested that birds moved less than 10 km between consecutive breeding attempts (see "Results"). We therefore estimated the maximum number of second clutches in each year as the number of nests that were initiated 8 days or more after the end of any other nesting attempt within a 10-km radius in the same year, with the proviso that each earlier attempt could only give rise to a single 'second' nesting attempt. The maximum re-nesting rate for each breeding season was taken as the number of 'first' clutches divided by the total number of nests found in that season. Although we describe this as the 'maximum' re-nesting rate, the actual re-nesting rate could have been higher if birds moved further than 10 km between successive nesting attempts or if our detection rate of nests in

the core colonies varied systematically across the breeding season.

The number of chicks hatched by each breeding female in each breeding season was estimated using the fecundity model of Farnsworth and Simons (2001, 2005). For each year, we entered the length of the breeding season (date of completion of latest nest minus first egg date of earliest nest), nest survival rate, mean clutch size and mean number of chicks leaving successful nests. The interval between successive nesting attempts was fixed at the mean of the five observations of re-nesting (8.6 days). A range of fecundity estimates for each year was derived by fitting the lower 95 % confidence limit of the annual nest survival rate in a model with the re-nesting probability set at zero, defining the lower limit, and by fitting a model using the upper 95 % CL of the nest survival rate and the maximum re-nesting rate as described above, to define the upper limit.

Adult and chick survival

We estimated apparent survival rates using Cormack–Jolly–Seber (C–J–S) live encounter models of resighting data of individually marked birds (Cooch and White 2011). As our marked sample consisted of birds ringed as chicks and birds ringed as adults, we specified two groups in the MARK models (Cooch and White 2011), with separate parameter information matrices (PIMs) for survival (Φ) and resighting (p) estimates for each group. For the birds marked as adults, we used U-CARE (Choquet et al. 2009) to assess evidence of transience (permanent emigration). For birds ringed as chicks, the survival estimate for the first year of life combined pre-fledging and post-fledging mortality. However, we also estimated the daily survival rate of chicks between hatching and fledging using C–J–S live encounter models to compare with similar estimates from congeneric species elsewhere.

The general model for goodness of fit testing was specified as that having age-group specific annual survival parameters in the year following ringing for birds ringed as chicks (Φ_c) and birds ringed as adults (Φ_a), to account for post-fledging and first-winter survival and for the adult transience detected in the U-CARE output, respectively, then shared year-specific survival parameters in all subsequent years as birds ringed as chicks became adults. The general model also had the same parameter structure for both age groups in the resighting matrices, with the exception that the resighting rate of birds ringed as adults was fitted as a standard time structure. Thus, three of the four PIMs (survival of birds ringed as adults, survival of birds ringed as chicks, resighting of birds ringed as chicks) had unique parameter values along their long diagonals, the two survival PIMs thereafter shared year-specific survival estimates and the two resighting PIMs shared year-specific

resighting estimates (Fig. S2). Subsequent refinement of this general model involved changing the PIMs to assess whether specifying different combinations of survival and resighting parameters improved the fit of the model, using AIC to assess the support for various models (Burnham and Anderson 2002). Because of the unusual PIM structure of the general model, the goodness of fit of this model was assessed using parametric bootstrapping in MARK (Cooch and White 2011).
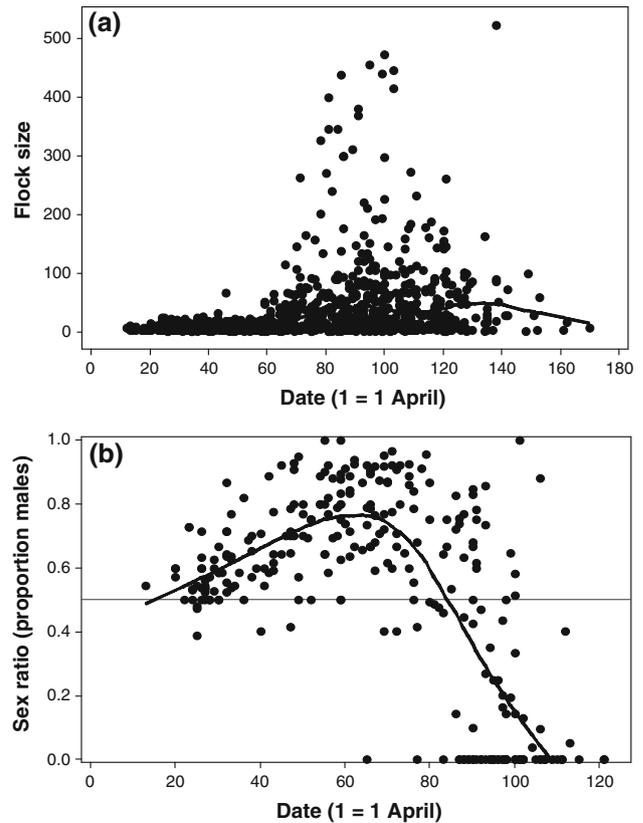
Population model

We used the estimates of fecundity (F), first-year survival (Φ_j) and adult survival (Φ_a) to estimate the population growth rate each year as $\lambda = (F/2 \times \Phi_j) + \Phi_a$ using annual estimates of Φ_j and Φ_a from the best supported model in Table 5a and dividing F by 2 to convert chicks produced to pairs produced. We then generated 10,000 estimates of λ for each year by which an estimate of F was randomly drawn from a uniform distribution within the range of extreme fecundity estimates (see above) and estimates of Φ_j and Φ_a drawn at random from a uniform distribution between the modelled 95 % CL of each. The 250th and 9750th ranked estimates of λ were taken as the 95 % CL of each annual estimate. Because of the low resighting rate of birds ringed as chicks after their first year, and hence uncertainty about the resulting adult survival estimates, we repeated the analysis using the mean adult survival rate across all years estimated only from birds ringed as adults, drawn from the best supported model in Table 5b.

Results

Arrival and departure patterns and colony occupancy

The earliest date birds were seen in the study area was 12 April, and the latest was 20 September. Birds arrived on the breeding grounds in pairs or small groups, but larger flocks started to form from the beginning of June as young birds and failed breeders started to gather in post-breeding flocks (Fig. 2a). These increased in size in late June and early July as more birds completed breeding and young birds joined the flocks, and then declined from mid-July as birds migrated away from the area. Large post-breeding flocks were not associated with the short-grazed *Artemisia* steppe of the type used exclusively by breeding birds, but foraged on active or abandoned arable land, on burnt ground or in taller steppe, and tended to rest during the heat of the day on the muddy edges of lakes. The adult sex ratio of flocks was temporally variable, indicating different migration strategies and a tendency of males to leave their mates after hatching of the chicks and gather in post-breeding flocks

Fig. 2 a Changes in flock size over the course of the breeding season and **b** changes in adult sex ratio over the course of the breeding season (*fitted lines* are locally weighted scatterplot smoothers)
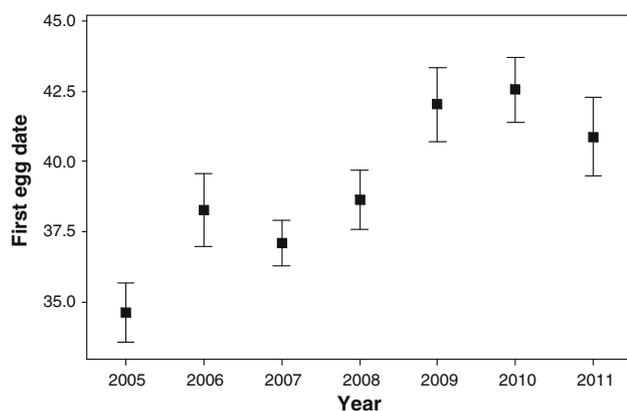
(Fig. 2b). On arrival, sex ratios in flocks were approximately balanced, but became increasingly male-skewed as females spread out to breed. However, as more females completed breeding and joined post-breeding flocks, the sex ratio reverted to equality around the end of June. As males started to depart, leaving many females with the young, the adult sex ratio became increasingly female-skewed, and most adult birds left at the end of the season were females (Fig. 2b).

Occupancy of the core colonies was highly erratic; only 3 held breeding birds in all years (Table 1). The number of nests found in core colonies generally declined over the study period, particularly in the last 2 years. Furthermore, the locations of breeding birds around a village could vary greatly between years (Fig. S3), so breeding aggregations were highly variable in both time and space. The return rate to a particular colony each year (expressed for each colony as the change between years in the percentage of nests held across all core colonies) was uncorrelated with either the absolute nest survival rate in that colony in the previous year, or with the nest survival rate relative to the average across all core colonies in the previous year ($r_6 < 0.2$, $P > 0.5$).

Nest distribution and phenology

In total, 1,078 nests were found over the 7 years of study (Table 1), for which the outcome could confidently be determined for 1,032. Although the mean interval between first egg date and nest discovery varied significantly between years in the core colonies ($F_{6,647} = 5.1$, $P < 0.001$, range 7.6–11.4 days), reflecting differences between years in numbers of fieldworkers and fieldwork start dates, this interval was less than half the incubation period (see below) in all years, suggesting a high rate of nest detection. The average interval between observations of nests was 3.4 days (SD = 1.54 days). First egg dates of individual nests ranged from 12 April to 17 June (median = 18 May), the first nests appearing almost synchronously with the arrival on the breeding grounds of adult birds, suggesting that mating might take place during return migration. Mean first egg dates in the core study area varied significantly between years and became later over the course of the study (Fig. 3). The synchrony of nests, measured as the standard deviation around the mean first egg date, also differed significantly between years in the core area (Bartlett's test, $P < 0.001$). Mean first egg date in each year was not correlated with nest synchrony or with mean March or April temperature or snowfall in that year (weather data for Astana, downloaded from http://rp5.kz). Mean egg volume (range 20,541–30,643 mm^3) did not vary systematically between years or with date, distance to settlements, number of near neighbours, clutch size or nest outcome (all $P > 0.1$).

The number of same-year nests within 500 m of any nest ranged from 0 to 12 in the core colonies (and up to 15 elsewhere) and differed significantly between years in the core study area ($F_{6,621} = 10.7$, $P < 0.0001$, uncorre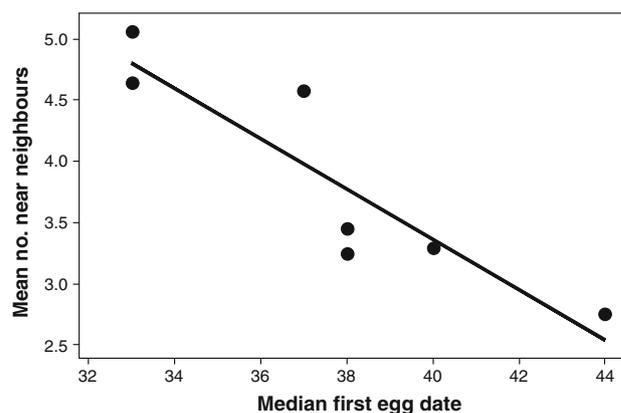cted for non-independence). There was a significant negative correlation in the core study area across years (Fig. 4) and across individuals ($r_{627} = -0.176$, $P < 0.001$) between first egg date and the number of near neighbours, indicating that breeding started later when densities of nests were lower, or vice versa. Mean distance of nests to the nearest human settlement also differed systematically between years ($F_{6,621} = 4.9$, $P < 0.001$), but did not vary systematically with first egg date.

The median and modal clutch size was four. It is likely that many of the recorded clutch sizes smaller than this resulted from the partial loss of eggs in clutches of four, since in 31.7 % of successful nests (those that produced at least one chick), one or more eggs were lost before hatching, resulting in the loss of at least 12 % of all eggs laid in ultimately successful nests. In most cases, this partial loss of eggs was thought to be due to trampling by livestock and this was supported by data from nest cameras (see below).

Re-nesting estimates

Only five colour-ringed females were seen to make two nesting attempts in a single season, in four cases following a successful first nest. The mean interval between the completion of the first nest and the initiation of the second was 8.6 days (range 5–14 days) and the average distance between successive nests was 2.5 km (range 0.94–6.85 km). The mean annual maximum re-nesting rate, which assumes that all nests that were initiated within 5 days and 10 km of the end of any other known nesting attempt were second clutches, was 1.17 (range 1.06–1.28), suggesting that between 0 % (assuming no re-nesting) and an average of 17 % (mean maximum re-nesting) of females laid second clutches, a rate comparable to that estimated for congeneric species elsewhere (Parish et al. 1997).

Fig. 3 Mean date of clutch initiation (first egg date: 1 = 1 April, ±1SE) of nests found each year at the Korgalzhyn study site. There was a significant difference in first egg date between years ($F_{6,888} = 5.13$, $P < 0.001$)

Fig. 4 Relationship between median first egg date (1 = 1 April) and mean number of near same-season neighbours (nests within 500 m) in the core study area across the 7 years of study. Birds were more dispersed in years when breeding started later ($r = -0.9$, $n = 7$, $P < 0.01$)

Estimated rates of re-nesting were uncorrelated across years with mean first egg date or nest survival.

Nest and chick survival and annual fecundity

The overall daily nest survival rate across all nests in all years ($n = 1,032$ nests with known outcome) was 0.956 (95 % CL 0.952–0.959), equating to an overall nest survival rate of 0.284 (0.252–0.309) across the 28-day laying and incubation period (mean incubation period = 25.4 days, SD = 1.02, $n = 24$ nests for which both clutch initiation date and hatching date were known to within 1 day; incubation commences on laying of last egg). There was little support from the MARK model for an effect of nest age, so more complex models were explored using logistic regression and assuming constant daily nest survival (Table 2). In models based on data from all nests and from
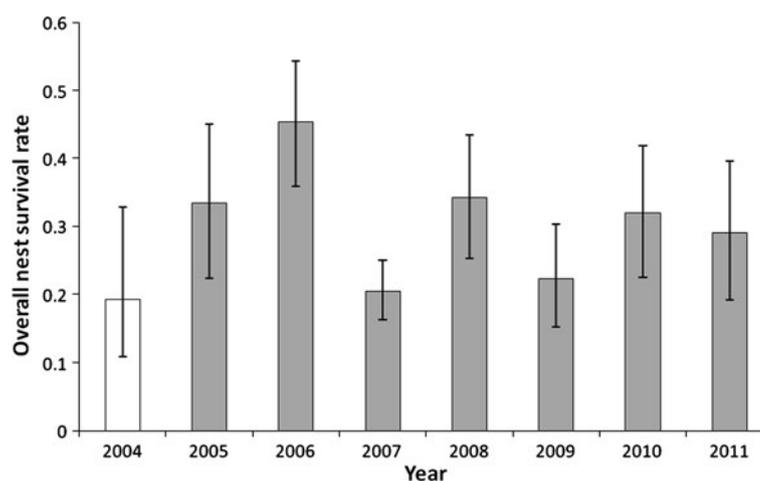
nests in the Korgalzhyn region only, all the models with greatest support included a factor relating to year, which was the most important variable across all such models (Table 3). Annual daily nest survival rates ranged from 0.945 (SE 0.004) in 2007 to 0.972 (SE 0.004) in 2006, equating to overall nest survival rates of 0.204 and 0.452, respectively (Fig. 5). The models also yielded support for an effect of the number of near neighbours (same-year nests within 500 m), for which the model averaged parameter was negative, indicating lower nest failure rates with increasing numbers of near neighbours. There was also some support for an effect of distance from nearest human settlement, the positive model averaged parameters indicating increasing nest failure with increasing distance from settlement. There was less evidence of an effect of date, the negative averaged parameters suggesting a poorly supported decline in nest failure as the breeding season progressed (Table 3). In the models of nests found in 2007, when the Pavlodar region was also covered, there was some support for an effect of region (Table 2), although

Table 2 Logistic regression models of nest survival, ranked in order of AIC$_c$

Model	df	ΔAIC$_c$	w_i	w_1/w_j
Data from 2007 only ($n = 327$)				
Neighbours	3	0	0.182	
Region + Neighbours	4	0.70	0.128	1.42
Intercept	2	1.41	0.090	2.02
Neighbours + FED	4	1.81	0.074	2.46
Region	3	1.88	0.071	2.56
Region × Neighbours	5	2.35	0.056	3.25
Korgalzhyn region only, all years ($n = 894$)				
Year	8	0	0.256	
Year + Dist_settlement	9	1.45	0.124	2.06
Year + FED	9	1.57	0.116	2.21
Year + Neighbours	9	1.84	0.102	2.51
Year × Dist_settlement	15	2.17	0.086	2.98
Year + FED + Dist_settlement	10	3.15	0.053	4.83
All nests and all years ($n = 1,032$)				
Year + Neighbours	10	0	0.208	
Year	9	0.06	0.201	1.03
Year × Neighbours	16	1.92	0.080	2.60
Year + Neighbours + FED	11	1.96	0.078	2.67
Year + Dist_settlement	10	1.99	0.077	2.70
Year + Neighbours + Dist_settlement	11	2.02	0.076	2.74
Year + FED	10	2.08	0.074	2.81

Degrees of freedom and Akaike weights (w_i) are also shown. In all models, colony was fitted as a random effect (nested within region in the case of 'all nests'). In models of data from 2007, region was fitted as a fixed effect to assess differences in nest survival between Korgalzhyn and Pavlodar. Only those of the 35 candidate models in each case that had Akaike weights (w_i) > 0.05 are shown. Sample sizes differ from those shown in Table 1 as nests with unknown outcome were not included in the survival models. The evidence ratio (w_1/w_j) is given with reference to the best supported model. *FED* first egg date, *Neighbours* number of same-season nests within 500 m

Table 3 The relative importance [$w_+(j)$] and covariate parameter estimates of the variables included in one or more of the subset of models of nest failure whose combined AIC$_c$ weight summed to 0.95

Variable	$w_+(j)$	Model-averaged parameter (SE)
Data from 2007 only ($n = 327$)		
Neighbours	0.603	−0.0494 (0.031)
Region	0.527	
FED	0.385	0.0017 (0.0077)
Dist_settlement	0.163	0.00007 (0.00012)
Region × FED	0.095	
Region × Neighbours	0.091	
Region × Dist_settlement	0.082	
Korgalzhyn region only, all years ($n = 894$)		
Year	0.985	
Dist_settlement	0.432	0.0003 (0.0004)
FED	0.301	−0.0025 (0.004)
Neighbours	0.276	−0.0063 (0.019)
Year × Dist_settlement	0.173	
All nests and all years ($n = 1,032$)		
Year	1.000	
Neighbours	0.575	−0.0254 (0.0347)
Dist_settlement	0.290	0.000093 (0.00024)
FED	0.251	−0.00081 (0.00356)
Year × Neighbours	0.146	
Year × Dist_settlement	0.038	
Year × FED	0.000	

Covariate parameters are estimated from model averaging

FED first egg date, *Neighbours* number of same-season nests within 500 m

Fig. 5 Overall nest survival rate in each year with 95 % CL. The figure for 2004 indicates the nest survival rate reported by Watson et al. (2006)

this had less importance in competing models than the effect of the number of near neighbours (Table 3), and nest survival rates in Korgalzhyn and Pavlodar in 2007 were more similar to each other than they were to nest survival rates in other years (Fig. 5). In most cases, the standard errors of the covariate parameters spanned zero, suggesting weak effects of the covariates on nest survival.

Of 331 recorded nest failures in the core colonies for which a cause of failure could be inferred, predation accounted for the greatest number of losses across the study period, followed by trampling and desertion (Table 4). Causes of nest failure differed significantly between years, with a higher than expected proportion of losses to trampling in 2008 (the year in which nests were on average closest to settlements) and a lower than expected proportion in 2010 and 2011 (Table 4). Across all study sites, nests that were trampled were significantly closer to human settlements than nests that were predated ($F_{1,461} = 11.6$, $P < 0.001$).

Of the 29 nests at which cameras were deployed, 7 were predated, 3 were trampled and 1 was deserted (the eggs later taken by Rooks *Corvus frugilegus*), a ratio of causes of failure similar to that inferred for the main sample. One nest

that went on to produce two chicks lost two eggs to trampling by livestock. Of the 7 predation attempts, the predators comprised Red Fox *Vulpes vulpes* (2), Little Souslik *Citellus pygmaeus* (2), Long-eared Hedgehog *Hemiechinus auritus* (2) and Steppe Polecat *Mustela eversmanii* (1). All except the sousliks predated nests at night.

Estimates of mean annual fecundity ranged from 0.75 to 1.55 chicks hatched per breeding female (Fig. 6). Variation in fecundity between years was almost entirely explained by the strong annual variation in nest survival rate (linear regression, $R^2 = 0.96$), other factors such as re-nesting probability, first egg date, clutch size and partial clutch loss having little influence. Daily chick survival, estimated from 752 chicks ringed at the age of 5 days or less, was estimated at 0.983 (95 % CL 0.979–0.986), an estimate almost identical to that of Watson et al. (2006), so survival from hatching to fledging at 20 days was around 0.71 (0.65–0.75).
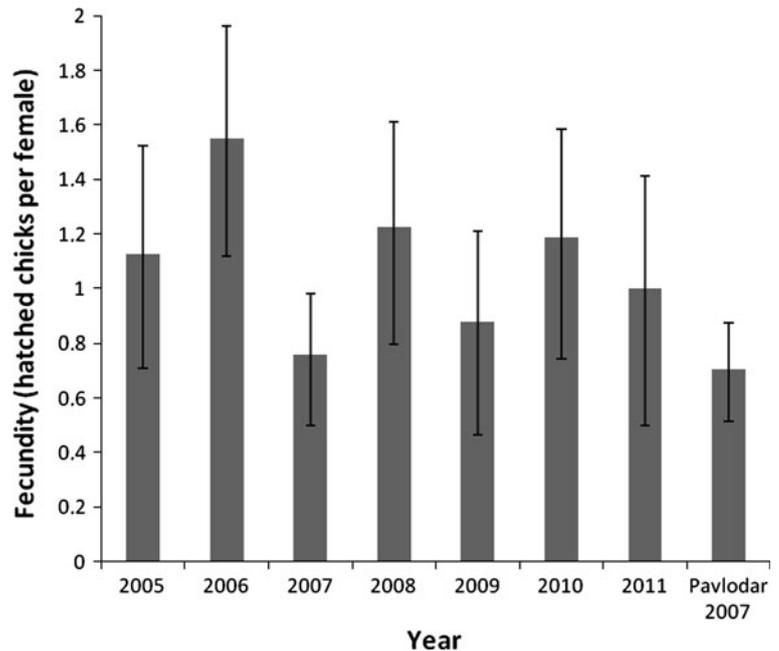
Annual survival

Over the 7 years of study, 1,310 chicks and 132 adults (mostly females caught at the nest) were fitted with unique colour ring combinations. Of these, 98 birds ringed as chicks (7.5 %) and 35 birds ringed as adults (26.5 %) were resighted in one or more subsequent years. The U-CARE output suggested significant transience (permanent emigration) in the set of birds ringed as adults. The general model fitted the data well (bootstrapped goodness of fit test, $P > 0.2$) and there was no suggestion of overdispersion (bootstrapped $\hat{c} = 0.85$). The model with the greatest support was that in which birds ringed as chicks had annually variable first-year survival and birds ringed as adults had constant survival in the year after ringing, after which annual survival of birds ringed as chicks and as adults shared common annual survival estimates (Table 5a). Post-hatching survival to the following year ranged from 0.11 (95 % CL 0.05–0.23) in 2007–2008 to

Table 4 Causes of nest failure by year in the 14 core colonies

Years	Deserted	Predated	Trampled	Weather	Unknown	Total
2005	3	24	5	0	6	38
2006	4	*11*	*16*	5	5	41
2007	3	53	14	0	10	80
2008	1	*8*	*24*	0	10	43
2009	2	51	10	0	2	65
2010	2	51	*3*	0	0	56
2011	6	33	*2*	0	3	44
Total	21	231	74	5	36	367

Known causes of failure varied significantly between years ($\chi^2_{18} = 133.7$, $P < 0.0001$), the values italicized contributing a value of over 5.0 to the overall χ^2 score

Fig. 6 Annual estimates of fecundity (chicks produced per female) from a model incorporating nest survival, partial clutch loss and re-nesting probability. *Error bars* represent the likely extremes rather than specific confidence limits (see text)

0.59 (0.23–0.88) in 2009–2010 (mean across all years: 0.27, 95 % CL 0.16–0.42). Adult annual apparent survival ranged from 0.19 (0.08–0.39) in 2010–2011 to 0.82 (0.25–0.98) in 2009–2010 (mean across all years: 0.55, 95 % CL 0.47–0.62). All the best supported models indicated far lower resighting rates for birds ringed as chicks than for birds ringed as adults, even when birds ringed as chicks had reached adult age, suggesting that for birds ringed as chicks, mortality and permanent emigration were poorly separated. Because these birds contributed data to the estimation of adult survival rates, we also estimated adult survival using only data from birds ringed as adults (Table 5b). For this analysis, the general model was that in which survival and resighting were both time dependent. There was no evidence of a lack of goodness of fit (bootstrapped $P > 0.1$) or overdispersion (bootstrapped $\hat{c} = 0.66$). The best supported model indicated constant survival (corrected for transience) and resighting rates and yielded a higher mean annual apparent survival rate (mean = 0.66, 95 % CL 0.52–0.77) than that obtained from models including birds ringed as chicks.

Site fidelity

The low rate of breeding site fidelity suggested by the annually fluctuating colony counts (Table 1) was confirmed by resightings of colour-ringed birds and by satellite tracking of a small number of birds. Of 464 resightings of colour-ringed birds in breeding seasons after the year of ringing, only 41.3 % were made in the same colony in which the birds were ringed. Birds ringed as chicks were significantly less likely to be resighted in later years in their

colonies of ringing (28.9 % of resightings) than birds ringed as adults (54.6 % of resightings; $\chi^2_1 = 14.1$, $P < 0.001$). There was no difference between the sexes in natal colony philopatry of birds ringed as chicks and resighted in subsequent years ($\chi^2_1 = 0.5$, ns). Three birds fitted with satellite tags returned to the breeding grounds in Kazakhstan in one or more years after the year of tag attachment. A male fitted with a tag in 2007 in the Korgalzhyn study site spent the 2008 breeding season nearly 900 km west of the site of capture. In the 2009 breeding season, this bird returned to the study area, but in 2010 it summered around 300 km to the southwest. Two breeding females fitted with tags in the Korgalzhyn study area in 2010 spent the following breeding season 280 km southeast and 300 km northwest of their 2010 breeding sites. The population was therefore extremely open.

Population growth rate

Estimates of population growth rate (λ) in each year of study, and the average across all years, were always less than 1.0, suggesting that the population is currently in decline (Fig. 7). However, estimates of λ based upon adult survival estimates derived only from birds ringed as adults were higher, and the 95 % CL spanned $\lambda = 1.0$ in four of six between-years intervals, although the 95 % CL of the mean did not quite span 1.0 (Fig. 7), indicating that, if productivity and survival estimates were estimated accurately, the population trajectory lies somewhere between stability and severe decline. Plots of randomised estimates of each demographic parameters on λ indicate the extent to which, in the absence of a change in the other rates, each

Table 5 Competing models of survival

Ringed as chicks		Ringed as adults		Params	ΔAIC_c	w_i	w_1/w_j
Φ	p	Φ	p				
a. All ringed birds							
$\Phi_{.1= t,\, t}$	$p_{c./.}$	$\Phi_{.1=./.,\, t}$	$p_{a./.}$	16	0	0.65	
$\Phi_{.1= t,\, 2=./.,\, t}$	$p_{c./.}$	$\Phi_{.1=./.,\, t}$	$p_{a./.}$	16	1.89	0.25	2.60
$\Phi_{c.1= t,\, t}$	$p_{c./.}$	$\Phi_{a.1=./.,\,./.}$	$p_{a./.}$	17	6.15	0.03	21.67
$\Phi_{c.1= t,\,./.}$	$p_{c./.}$	$\Phi_{a.1=./.,\,./.}$	$p_{a./.}$	12	7.17	0.02	32.50
General model							
$\Phi_{.1= t,\, t}$	$p_{c.1=t,\, t}$	$\Phi_{.1= t,\, t}$	$p_{a.t}$	32	17.38	<0.0001	
b. Birds ringed as adults							
$\Phi_{1=./.,\,./.}$	$p_{./.}$			3	0	0.69	
$\Phi_{1=./.,\, t}$	$p_{./.}$			8	1.95	0.26	2.65
$\Phi_{1=./.,\,./.}$	p_t			8	5.44	0.05	13.80
General model							
$\Phi_{1=./.,\, t}$	p_t			14	10.63	<0.0001	

Apparent survival (Φ) and resighting (p) parameters for birds ringed as chicks and birds ringed as adults are shown. Annual estimates either may vary by time (t) or are fixed (./.). The first and second long diagonals of the survival PIMs were permitted to contain different parameter values to those in the rest of the matrix, and could themselves vary by time ($1 = t$), or be fixed ($1 = ./.$). Where the survival PIMs of the two groups shared the same parameters (other than in the first or second long diagonals, as indicated), a common Φ is indicated without a subscript; where the two survival PIMs shared no common parameters, separate estimates were generated for birds ringed as chicks (Φ_c) and birds ringed as adults (Φ_a). The same subscripting protocol applies to the resighting estimates. The evidence ratio (w_1/w_j) is given with reference to the best supported model

parameter would need to increase to achieve population stability ($\lambda = 1.0$). Levels of adult survival necessary for λ to reach an annual mean of 1 in the absence of a change in any other demographic rate were reached in 1 year of the study, but the mean rate of first-year survival and fecundity required for population stability exceeded that recorded during any year of study (Fig. 8). Regression of each of the three demographic parameters on 10,000 randomly generated estimates of λ indicated that of the three demographic rates, adult survival had the greatest influence on population growth rate ($R^2 = 0.62$, compared to $R^2 = 0.22$ for first-year survival and $R^2 = 0.14$ for fecundity). For λ to reach an annual mean of 1 in the absence of a change in any other demographic rate, fecundity or first-year survival would need to more than double (+125 %), whereas adult survival would need to increase by 30 %.
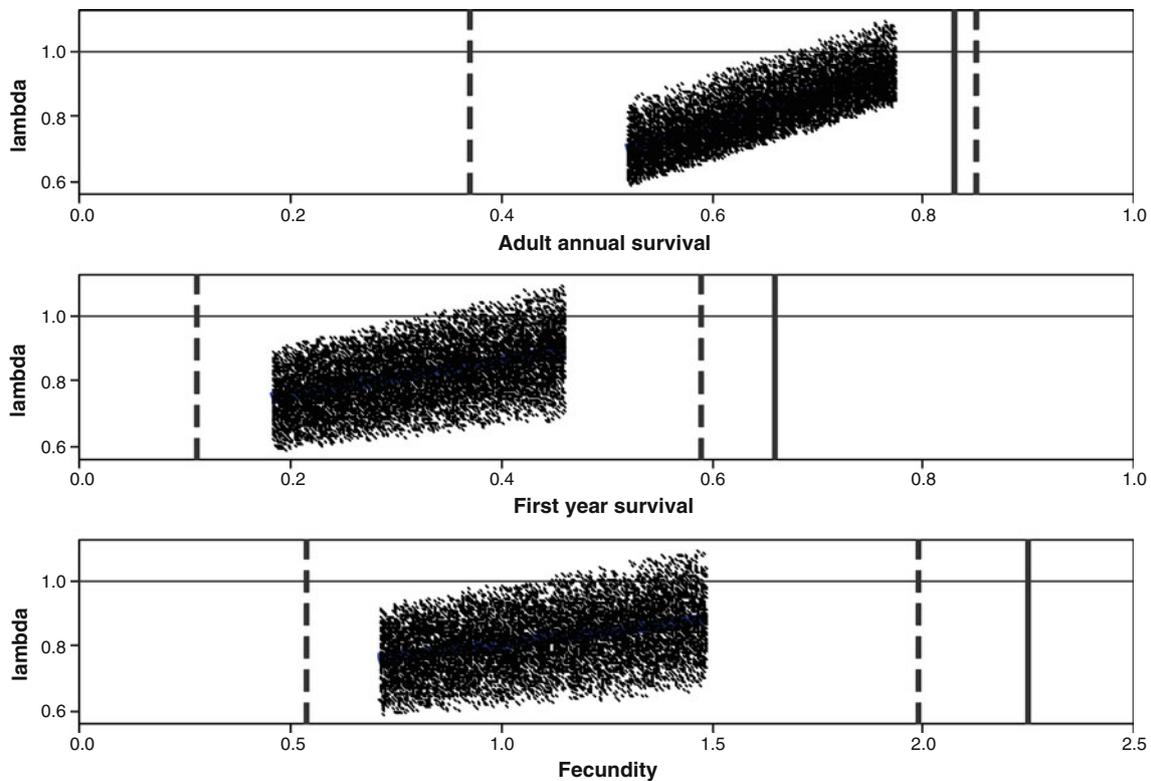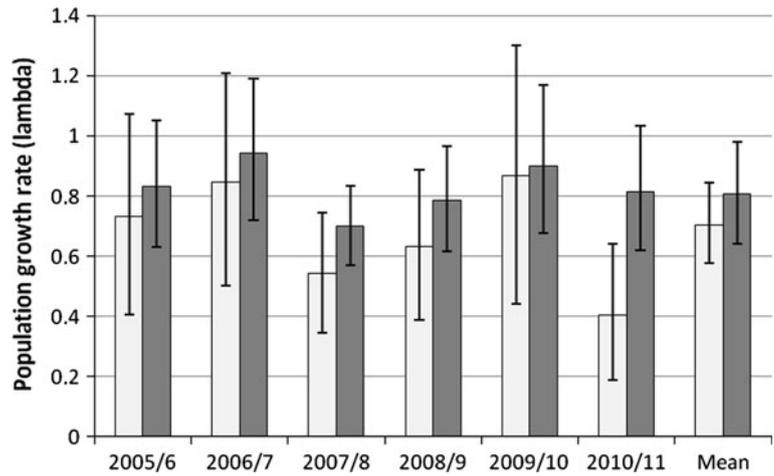
Discussion

The high temporal variation in demographic rates suggests that even in species-poor and structurally simple ecosystems such as the Eurasian steppe, lengthy studies are needed to estimate population processes. Annual estimates of fecundity, first-year survival and adult survival all varied by a factor of at least two over the 7 years of study. This high temporal variation and uncertainty around estimates of annual survival, the result of very low rates of

philopatry, precluded confident identification of the demographic drivers of recent declines and the demographic model of population trajectory should, as always (Beissinger and Westphal 1998), be treated with caution. However, both productivity and survival appeared low in most years compared with estimates from congeneric species, particularly the Northern Lapwing, although higher than many survival rates reported for other wader species (Sandercock 2003).

Most wader nest failures are due to predation, particularly by nocturnal mammalian predators (Teunissen et al. 2008) as in our study, and high levels of nest predation may be driving declines in many European populations (King et al. 2008; MacDonald and Bolton 2008b; Roodbergen et al. 2012). Mean nest survival for Northern Lapwings across Europe fell from 0.43 before 1980 to 0.32 in 1996–2006, when most populations were in decline (Roodbergen et al. 2012). The latter figure is higher than the mean annual nest survival rate of 0.28 recorded over the 7 years of our study. However, chick survival was high and the total of 0.83 fledged chicks per pair, the minimum number estimated by (Peach et al. 1994) to be necessary to maintain populations in Northern Lapwings, lay within the range of estimates of productivity in all but one study year. Although trampling by livestock was a significant cause of nest failure in some years, overall it was greatly exceeded by predation, and there was evidence that overall nest survival was higher closer to human settlements, where

Fig. 7 Estimates of population growth rate (λ) in each annual interval with 95 % CL derived from randomisation. *Light bars* estimates based on adult survival rates from birds ringed as adults and birds ringed as chicks (after their first year) from the best supported model in Table 5a; *dark bars* estimates of λ based on adult survival rates estimated only from resightings of birds ringed as adults (see text)

Fig. 8 Plots of 10,000 estimates of population growth rate, lambda (λ), with regression, generated from estimates of adult survival, first-year survival and fecundity drawn at random from a uniform distribution between the 95 % CL of the mean across years of the two survival rates and the range of mean annual fecundity (see "Methods"). The estimated values of λ are plotted against each of the three demographic rates separately. In the *upper two plots*, the *vertical dotted lines* indicate the lowest and highest annual survival rates recorded in any year of study, in the *lower plot* they represent the lowest minimum and highest maximum fecundity rates recorded in any year. In each graph, the *solid vertical line* represents the value at which the regression crosses λ = 1. Only in the case of adult survival did this fall between the *vertical dotted lines*, indicating that only this demographic rate reached sufficient levels during one or more years of the study to achieve population stability in the absence of a change in the other two demographic rates

trampling accounted for a higher proportion of nest failures. Our results therefore do not support the suggestion of an earlier study (Watson et al. 2006) that increased trampling rates from nesting near villages are the driver of recent declines, and suggest instead that birds may obtain some benefit from nesting close to human settlements, where populations of the main predators identified in this study may be lower.

Mean annual adult survival for Northern Lapwings in Europe ranges across studies from 0.71 to 0.83

(Roodbergen et al. 2012), a range that excludes our mean estimate of annual adult survival of Sociable Lapwings across all years (0.66) but includes annual estimates from 3 of our 6 annual intervals. Adult survival had the greatest influence on estimates of λ. The very low degree of philopatry renders it difficult to distinguish between permanent emigration and mortality, and so estimates of survival must be treated with caution. The low degree of philopatry, with some individuals settling hundreds of kilometres apart in consecutive breeding seasons, was unexpected, since elsewhere the closely related Northern Lapwing shows high philopatry (Thompson et al. 1994), but may indicate an adaptation to settling on the grazed land in the wake of unpredictably migrating herds of native grazers (Kamp et al. 2009). The same degree of flexibility appears to apply to the species' coloniality, since, in years with early arrival, birds settled in greater concentrations. A pattern of later arrival over the study period, in marked contrast to patterns of earlier arrival in Northern Lapwing populations in Europe (Both et al. 2005), has therefore led to a pattern of declining coloniality over time. Given the high annual variation in colony occupancy, it is likely that the severe declines documented by previous surveys, most of them based on only a few years of observation, were imprecisely estimated. It is uncertain whether the severe drop in numbers of nests at core colonies in later years of the current study represents a real population decline or instead a redistribution of birds through the species' large area of occupancy, although the demographic models support the former. A coordinated survey of all known breeding sites throughout the range is urgently needed to assess the trajectory of the wider population.

Conservation intervention does not necessarily need to address only the demographic factor driving the decline, since an increase in one demographic rate might compensate for a fall in another (Green 2002). Even if reduced fecundity were identified as the driver of decline in Sociable Lapwing populations, nest protection through predator control or other methods is not a practicable conservation option for a nomadic species with a huge and fragmented range. Furthermore, studies of the impacts of controlling or excluding predators on nest survival rates in ground-nesting birds are equivocal, some showing no effect (Bodey et al. 2011), some suggesting a general positive effect (Donald et al. 2002; Rickenbach et al. 2011), some showing an effect only where predator densities are particularly high (Bolton et al. 2007), and others suggesting species-specific impacts (Isaksson et al. 2007) and potential impacts on adult survival (Smith et al. 2010). Reducing grazing pressure around villages to reduce trampling would be problematic and might result in changes in grassland structure that have negative effects on breeding waders (Sabatier et al. 2010). Furthermore, with current levels of first-year and adult survival, increasing fecundity to the level required to achieve population stability would require rates of nest success considerably higher than that recorded in any year of our study, or in most studies of congeneric species. In contrast, adult survival, which had the greatest influence on λ, achieved the level required to maintain populations with current levels of fecundity and first-year survival in one study year, and fell within the range of adult survival rates of congeneric species elsewhere. The population model suggested that population stability could be achieved by increasing adult survival by 30 % to a mean of around 0.84 (or less, if first-year survival increased commensurately), at the upper limit of that recorded for Northern Lapwing in Europe. In contrast, fecundity and first-year survival would need to more than double to achieve the same effect. Therefore, addressing survival appears to be the most tractable way of protecting this species. The recent discovery of concentrated hunting pressure at traditional migration stopover sites in Syria and Iraq (Sheldon et al. 2012), where a high proportion of the world population gathers each year at predictable times, provides a likely mechanism of decline and conservation efforts should concentrate on reducing this.

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