

Post-Soviet steppe management causes pronounced synanthropy in the globally threatened Sociable Lapwing *Vanellus gregarius*

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Habitat associations and distribution of breeding Sociable Lapwings were examined in 2004–2008 in central Kazakhstan to develop and assess hypotheses relating to the species' decline and high conservation threat status. At a landscape scale, breeding colonies were strongly positively associated with villages and rivers. Habitat suitability models had very high predictive power and suggested that only 6.6–8.0% of the 30 000-km² study area was potentially suitable for Sociable Lapwings. Models developed to describe the spatial distribution of nests in one region of Kazakhstan in one year predicted well the distribution of nests in another region, suggesting good generality. At a colony scale, nests were most likely to be found in the most heavily grazed areas, with a high cover of animal dung and bare ground. Despite the low density of human settlements in the study area, most Sociable Lapwing nests were < 2 km from a village. Patterns of grazing were assessed by fitting GPS loggers to cattle. There was a strong positive correlation around villages between grazing intensity and the density of Sociable Lapwing nests, with clear evidence of a threshold of grazing density that needs to be reached before birds will breed. This high degree of synanthropy, perhaps unique in a critically endangered bird, is likely to result from post-Soviet changes in steppe management and offers both threats and opportunities to the species' conservation.

Keywords: agriculture, grazing, habitat suitability models, Kazakhstan.

The Sociable Lapwing *Vanellus gregarius* is a semi-colonial wader whose breeding distribution is confined to the Pontian (Eurasian) steppe belt. In common with other steppe species (e.g. Pallid Harrier *Circus macrourus* and Black-winged Pratincole *Glareola nordmanni*), its numbers have undergone a severe decline over the last 100 years. Sociable Lapwing numbers collapsed after the 1950s, and the decline accelerated in the 1990s (Ryabov 1974, Gordienko 1991, Eichhorn & Khrokov 2002). The species vanished from nearly half its former range during the 20th century, becoming

extinct in Ukraine in the 1960s (Dolgushin 1962) and west of the Ural River (including European Russia) in the 1980s (Tomkovich & Lebedeva 2004). Few quantitative data on the decline of the breeding population are available, but post-breeding maximum flock size on the breeding grounds decreased from several thousand birds around 1900 to rarely more than a thousand in the 1950s, and only tens of birds between 1969 and 2000 in Kazakhstan (Plotnikov 1898, Dolgushin 1962, Gordienko 1991). As a result of these declines and an assumed population size of 200–600 breeding pairs, the species' IUCN threat status was uplisted to Critically Endangered in 2004 (Birdlife International 2008). Within its current stronghold in

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Kazakhstan, breeding colonies are scattered across huge areas, making precise estimation of population size difficult. Surveys conducted in 2005–2008, however, suggest a larger world population than previously feared, with a current crude estimate of 5600 pairs (Sheldon *et al.* 2006).

Reasons for the decline remain unclear, but have been linked to low productivity on the breeding grounds (Watson *et al.* 2006), perhaps arising from changes in habitat suitability. The collapse of collectivist farming after the break-up of the Soviet Union has resulted in major changes in steppe use and management. Also, the hunting to near extinction of native grazers, especially the Saiga Antelope *Saiga tartarica* (Milner-Gulland *et al.* 2001), may have led to a reduction in the availability of grazed steppe favoured by many species. However, not enough was known about habitat use and distribution of Sociable Lapwings to assess the possibility that these changes have contributed to observed declines. Recent reports from the Middle East suggest that hunters kill significant numbers at stop-over sites (S. Jbour pers. comm.). This might have influenced population trends, and habitat changes in the wintering areas might also be implicated (Tomkovich & Lebedeva 2004).

We studied breeding habitat and nest-site selection of the species using a two-level habitat suitability modelling approach combined with spatial analysis of nest-site distribution and grazing patterns of domestic livestock. Our aim was to develop predictive models and link these with past and likely future changes in land use to assess the reasons for past declines and to forecast future population trends.

METHODS

Study areas

Data on Sociable Lapwing abundance and distribution were collected between 2004 and 2008 in a study area in the Lake Tengiz depression centred on the settlement of Korgalzhyn, 120 km southwest of Astana, Kazakhstan. The study area covered approximately 30 000 km² and stretched between 49°40′–50°55′ N and 68°38′–70°59′ E. Habitat suitability models were developed using nest-sites found and habitat data collected on 9000 km² of this study area in May and June 2006. The models were tested for spatial transferability in an area of approximately 12 000 km² in

the Irtysh region of northeast Kazakhstan's Pavlodar province, which was surveyed for Sociable Lapwing colonies in 2007. This area is situated between the lower Irtysh river at the settlement Akku (= Lebyazhe, 51°28′ N, 77°46′ E) and the Russian border (53°47′ N, 75°03′ E).

The Korgalzhyn study area is characterized by flat short-grass steppe and cereal fields in the north and hilly semi-desert in the south. Land use is restricted to livestock rearing and wheat cultivation, with about 80% of all arable fields having been abandoned since Kazakhstan's independence in 1991. The area holds hundreds of both fresh and saline lakes (*Solonchaks*), the largest being the saline Lake Tengiz with an area of 1380 km². The Pavlodar study area is dominated by the Irtysh river. The adjacent landscape on both sides of the river is characterized by herb-rich long-grass steppe and small birch forests (transition to west Siberian forest steppe).

Habitat suitability modelling

Sampling design

Surveys for Sociable Lapwing colonies and nests were conducted throughout the Korgalzhyn study areas between April and June in 2004–2008, and in the Pavlodar study area in 2007. Habitat data were collected between 10 May and 16 June 2006 in the Korgalzhyn study area. In all years, all previously known breeding sites of Sociable Lapwing were surveyed, information on which was available from local databases and expert communication (Watson *et al.* 2006). Furthermore, we cold-searched large areas of pristine steppe and fallow fields. Observers regularly stopped at vantage points and surveyed the surrounding area using a telescope, and additionally searched for Sociable Lapwings when driving transects at low speed (c. 10–20 km/h) across all habitat types. In 2006, the total length of survey transects across the area was 1176 km. These transects connected 109 points chosen randomly across all habitat types and were surveyed at least once in the second half of May, when birds are most active. Using telescopes, Sociable Lapwings can be detected over large distances in the flat and uniform steppe landscape, up to some kilometres for flying birds and group-displaying males in good light conditions. After locating territorial birds, observations from a distant vantage point or car facilitated location of incubating females and nests.

In 2006, breeding habitat selection was studied at both landscape and colony scales across the Korgalzhyn study area. The sample unit at the landscape scale was the breeding colony. A colony was defined as a site with an aggregation (inter-nest spacing < 500 m) of at least two breeding pairs at least 3 km away from the next breeding site. The spatial extent of each colony was determined by buffering each nest-site cumulatively with $r = 500$ m in ARCVIEW 3.2a GIS. This distance was chosen because adults during the incubation period rarely moved more than 300–400 m away from the nest and thus this distance should represent the area used around a particular nest-site (see also Watson *et al.* 2006 for colony structure). Within 30 colonies, variables were measured at a randomly chosen nest-site representing 'presence'. These data were compared with habitat data collected at 109 points randomly selected (representing 'absence') across the whole study area for analysis at the landscape scale. Random points were automatically generated in the GIS using a random point generator and were constrained not to fall within colony borders or on open water.

The sample unit at the colony scale was the single nest. At 17 colonies across the Korgalzhyn study area, habitat data collected at nest-sites were compared with those at randomly chosen points within the borders of the colony representing habitat availability. Random points were constrained not to fall within 25 m of a nest. In total, habitat data were collected at 78 nest-sites and 262 randomly chosen absence points, resulting in a total sample size of 340 sample points for analyses of habitat selection at the colony scale. Nests found later than 25 May were excluded to avoid the inclusion of second clutches from breeders which failed during a first attempt and which might have differed in selected habitat and introduced pseudoreplication.

Recording of habitat variables

The choice of habitat variables was hypothesis-based and informed by the literature and our own experience with the species from 2004 and 2005 (Table 1). Plant composition and cover was recorded at 2×2 m sample plots, centred on each nest-site or random point. Cover was estimated to the nearest 5%. Vegetation height was measured at every nest-site and every random point on two scales. We distinguished between maximum vegetation height, defined as the height of the tallest plant within each plot, and modal vegetation height,

Table 1. Overview of all recorded habitat parameters.

Code	Description
elev ^a	Elevation above sea level (m)
slope ^a	Slope (°)
asp ^a	Aspect (arccos/arcsin-transformed)
dist.riv	Distance to nearest river (m)
dist.lake	Distance to nearest standing water feature (m)
dist.wat	Distance to nearest water feature (m)
dist.col ^a	Distance to nearest Sociable Lapwing colony (m)
dist.nest ^b	Distance to nearest Sociable Lapwing nest (m)
dist.rook	Distance to nearest rookery (m)
dist.sett	Distance to nearest settlement (m)
dist.veg ^b	Distance to the nearest vegetation patch of significantly different height (± 20 cm difference) (m)
vegH.max	Maximum vegetation height (mm)
vegH.mod	Modal vegetation height (mm)
cov.art	Cover of wormwood <i>Artemisia</i> spp. (%)
cov.stip	Cover of feather grass <i>Stipa</i> spp. (%)
cov.fest	Cover of fescue <i>Festuca</i> spp. (%)
cov.grass.tot	Total grass cover (%)
cov.herb	Cover of herbaceous plants (other than grasses) (%)
cov.ML	Cover of mosses and lichens (%)
cov.veg	Total vegetation cover (= cover of bare ground) (%)
cov.dung	Cover of dung (%)
dung.tot ^a	Dung abundance (strip transect count)
soil.type	Soil type
soil.surf	Soil surface structure

^aLandscape scale only.

^bColony scale only.

defined as the height of the majority of plants. Soil type and soil surface structure were recorded as one of seven substrate classes. As dung is a very good correlate of grazer density (Laing *et al.* 2003), each nest-site and random point was characterized by the cover of dung in the same way as the plant cover estimates. This proved an ineffective method at larger scales, as livestock is comparatively mobile and dung density low, so at the landscape scale, all livestock dung piles were counted over a strip transect of 25×2 m both to the west and east of each nest-site and random point. Altitude was recorded at every point from a handheld GPS unit, and slope and inclination were measured with a clinometer and a compass, respectively.

For spatial analysis, Soviet topographic maps (scaled 1 : 100 000) of the whole study area (last updated 1989) were rectified and stored in the

GIS. A rectified Landsat 7 ETM+ satellite image (issued 9 July 2002) was saved as an overlay to identify landscape changes after the map issue. Based on this data, a digital map was created containing information on the main land-use types, rivers, lakes and infrastructure. Values for distance variables were calculated using the extensions 'nearest features' and 'distance matrix' for ARCVIEW 3.2a (Jenness 2004, 2005).

Data analysis

Habitat models were developed using binary logistic regression at both landscape and colony levels. Univariate models for all variables were built first using the 'logistf' package for S-PLUS 6.1 by Heinze and Schemper (2002). To avoid the inclusion of spurious variables in multivariate models, each univariate model was internally validated by bootstrapping with 300 iterations (Verbyla & Litvaitis 1989). For each boot-strap iteration (resampling of the dataset without replacement), deviance reduction compared to the non-boot-strapped model was recorded and a likelihood-ratio test (LRT) conducted. Variables were included in the further multivariate modelling process (see below) only if the boot-strap-LRT was significant ($P \leq 0.05$) for at least 95% of the boot-strap iterations. We included second-order terms in all univariate models to allow for unimodal relationships (Austin 2002). Where both sigmoid and unimodal responses were significant, we chose the one with the lower P -value for multivariate modelling, usually accompanied by better fit of the univariate model (Strauss & Biedermann 2006).

For multivariate modelling, we built models for all possible combinations of four, three and two variables in an automated process using a self-programmed script for S-PLUS 6.1. Including more than four variables in the same multivariate model would have led to over-parametrisation (Guisan & Zimmermann 2000). To reduce multicollinearity (Graham 2003), only combinations of variables with $r_s < 0.5$ were allowed to appear in the same model. As we intended to achieve parsimonious models, LRTs were conducted for every model to assess whether they were better than (or just as good as) any model with one less variable (Ferrier *et al.* 2002). Additionally, we assessed whether Nagelkerke's R^2 (R_N^2) of a boot-strapped model (mean of 300 iterations) was ≥ 0.3 (Strauss & Biedermann 2006). R_N^2 describes model calibration and refinement (Nagelkerke 1991). If both

requirements were fulfilled, the model was considered adequate.

Because many adequate models were obtained, an information theoretic approach (Burnham & Anderson 2002) was used to select those that were most informative. For each candidate model, the Akaike information criterion (AIC) was calculated to assess how well models performed in the trade-off between model fit and model complexity. We used the corrected value AIC_C , as recommended when sample size is small. Δ_i was calculated as the difference between AIC_C for a given model and AIC_C for the highest ranked model (i.e. that with the lowest AIC_C) for all candidate models. Models with $\Delta_i < 10$ were considered to have some support, and those with $\Delta_i < 2$ were considered to have strong support, for being the 'best models', i.e. those having the highest probability to be closest to reality (Burnham & Anderson 2002). Finally, model averaging was applied for all models qualifying as 'adequate' and relative variable importance evaluated. Standard errors were calculated as the square-root of the unconditional variance estimator (Burnham & Anderson 2002, Greaves *et al.* 2006).

To assess the predictive power of the achieved models, a set of three criteria describing model fit (calibration and refinement) and discriminant power was calculated: R_N^2 , AUC (area under the receiver operating characteristic curve), which evaluates discrimination (Hanley 1982), and CCR (overall correct classification rate) for discriminative power (Fielding & Bell 1997).

Model transferability and generality

Habitat preferences of a species can vary spatially and temporally (e.g. Whittingham *et al.* 2007). Poor model generality can lead to reduced spatial transferability of models and misleading management decisions (Gray *et al.* 2009). To test the spatial transferability of our results, we developed habitat suitability maps for both study areas (Austin 2002). Of the models containing only those variables with complete coverage for the study area (i.e. excluding variables such as vegetation height, which were collected only at sampling points), that with the lowest AIC_C was selected. In the GIS, grid themes were created describing the value of the considered variables for every grid cell for both study areas. The logistic regression equation for the referring model was then applied to each grid cell, and via a classifying process, areas of the same occurrence probability were ranked equally. Different

thresholds distinguishing between suitable and unsuitable habitat were tested, a widely used, but arbitrary level of $P = 0.5$ (e.g. Manel *et al.* 2001), and a threshold of $P = 0.22$ based on prevalence of the presences in the dataset (Liu *et al.* 2005). To externally validate the model on a spatial scale, we assessed the extent to which nest-sites in the NE Kazakhstan study area were situated within areas predicted as 'suitable' by the model from the central Kazakhstan study area used for prediction.

Spatial analysis of grazing patterns

Because previous work suggested a considerable influence of livestock grazing in habitat selection (Watson *et al.* 2006), we analysed grazing patterns of domestic livestock with a comparatively simple spatial approach to complement the rather mechanistic habitat modelling approach. Whereas horses are very mobile in the study areas and roam over distances of more than 100 km, cattle and sheep herds are now almost exclusively kept on steppe pastures immediately surrounding human settlements. The cattle and sheep of every household in the settlements are collected by shepherds in the early morning, driven radially out of the villages in different herds for grazing and herded back every evening. To quantify the spatial extent of diurnal domestic livestock movements and grazing patterns, GPS data loggers were attached to four cattle in two different villages of the Korgalzhyn study area using specially designed neck collars in May and June 2007. The loggers were programmed to fix the animals' position every 2 min from 6:00 until 18:00 h. These point data were downloaded and processed in the GIS. To estimate grazing intensity, the villages were buffered with concentric bands of 500 m width and the number of logger fixes falling into these distance categories was calculated, corrected for the area of each band. We assumed that the time spent in every distance band, and thus the number of fixes logged to the GPS per band, reflected grazing intensity. As the animals are kept in relatively tight herds all day long, the position of the tagged animal was considered representative of the whole herd. Maximum vegetation height was measured around two villages in the Korgalzhyn study area along eight 5-km transects radiating out at these villages in 45° sectors. Two sets of measurements were made at points along the transects (each 500 m apart), in May and in June 2007.

RESULTS

Breeding habitat and nest-site selection

At the landscape scale (breeding habitat selection), 16 variables were significant predictors of colony distribution in univariate binary logistic regression models ($P < 0.05$). A total of 61 multivariate models qualifying as 'adequate' were obtained. After the model selection process, five models remained with $\Delta_i < 10$ (Table 2a). The weights of the first three models summed to 0.96.

There was a single 'best' model (no other models had $\Delta_i < 2$), which revealed increasing probability of colony occurrence with decreasing distance to settlements and rivers, and decreasing vegetation height (Fig. 1). Occurrence probability fell to < 0.1 just 5.4 km away from settlements and 8.5 km away from rivers, and in areas with

Table 2. Modelling results at the landscape scale: (a) overview of all models with $\Delta_i < 10$; (b) averaged regression coefficients β with associated standard errors (se) and relative variable importance $w_+(j)$ for all models considered in model averaging.

(a)			
Model	AIC _C	Δ_i	w_i
vegH.mod + dist.riv + dist.sett	36.441	0.000	0.679
cov.art + cov.art (sqr) + cov.gras.tot + cov.gras.tot (sqr) + dist.wat + dung.tot	38.474	2.033	0.246
cov.art + cov.art (sqr) + vegH.mod + dist.riv + dist.wat	42.363	5.921	0.035
vegH.mod + dist.riv + dist.wat + dung.tot	43.013	6.572	0.025
cov.stip + dist.riv + dist.sett	46.281	9.840	0.005
(b)			
Variable	Averaged β	se	$w_+(j)$
Intercept	4.5861	12.1077	1.000
dist.riv	-0.0003	6.82E-08	0.749
vegH.mod	-0.0977	0.0025	0.744
dist.sett	-0.0009	2.19E-07	0.688
dist.wat	-0.0018	5.98E-07	0.311
cov.art	0.2540	0.0099	0.285
cov.art (sqr)	-0.0033	0.0211	0.285
dung.tot	0.4337	0.0601	0.277
cov.gras.tot	-0.2402	0.0118	0.246
cov.gras.tot (sqr)	0.0004	2.51E-07	0.246
cov.stip	-0.2413	0.0003	0.007
cov.veg	0.1690	0.0388	< 0.001
cov.veg (sqr)	-0.0023	1.94E-11	< 0.001
cov.herb	-0.1136	5.38E-08	< 0.001

For variable abbreviations, see Table 1.

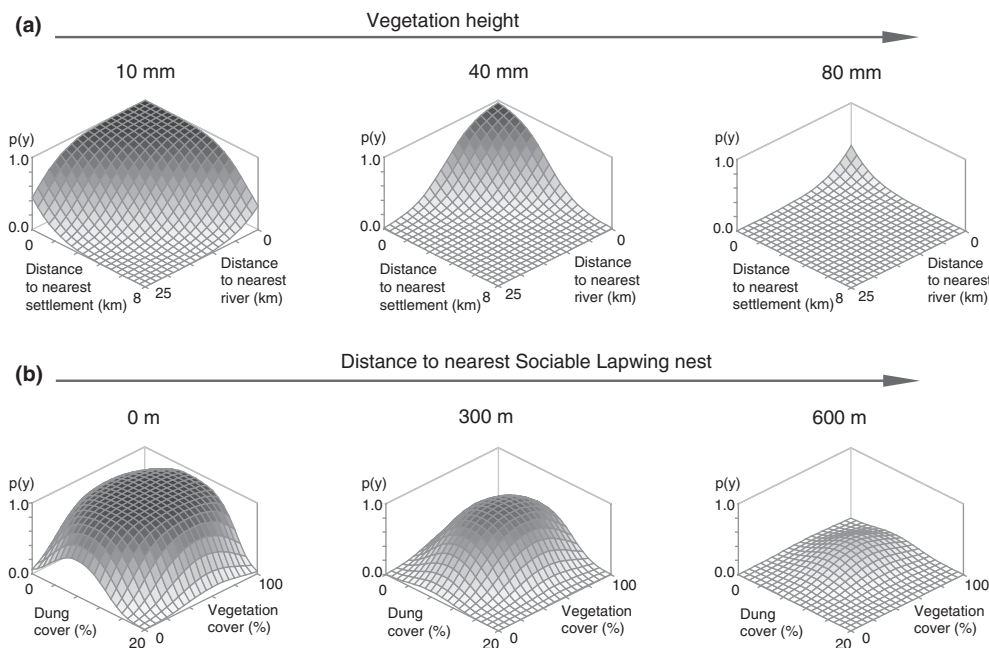


Figure 1. Visualisation of the habitat models with lowest AIC_C ('best models') at landscape (a, above) and colony (b, below) scales. Occurrence probability P is plotted against two variables on the x- and y-axes; diagrams represent different stages of a third variable.

vegetation taller than 8 cm. The model correctly classified 98.6% of data points; overall model performance was excellent ($R_N^2 = 0.916$, $AUC = 0.995$). Model averaging identified three variables with very high weights (Table 2b). The selection of colony sites in proximity to rivers was not an artefact of settlements being situated closer to rivers, as the spatial distribution of villages in the Korgalzhyn study area did not significantly differ from random points with respect to their distance to the nearest river (Wilcoxon rank sum test, $P = 0.176$, $n = 54$).

At the colony scale, eight variables explained significant variation in nest distribution in univariate binary logistic regression models. Seven adequate multivariate models were obtained. After the model selection process, two models remained with $\Delta_i < 10$, their weights summing up to 0.99, although the second model had $\Delta_i > 2$, suggesting only a single 'best' model (Table 3a). This model predicted maximum probability of nest presence at around 10% cover of animal dung and around 50% cover of bare soil. Nest occurrence probability decreased quickly with increasing distance to neighbouring breeding pairs, as expected for a colonial species (Fig. 1). The model correctly classified 89.5% of the data points, and overall model performance was good ($R_N^2 = 0.596$, $AUC = 0.924$).

Removing the variable 'distance to nearest nest' reduced model fit considerably ($R_N^2 = 0.344$, $AUC = 0.820$), but the model still explained a high proportion of variation, suggesting a high influence of the cover of bare soil and dung in nest-site selection. Model averaging resulted in three variables (both linear and quadratic terms for each) with very high weights, and one with considerably less weight (Table 3b).

Spatial prediction and model generality

The model with the lowest Δ_i that included only variables available over the entire area of the study regions contained distance to nearest settlement and distance to nearest river as significant predictors. With $AIC_C = 49.8$ and $\Delta_i = 13.4$ it was less good than the overall best model, but overall model performance was still very good ($R_N^2 = 0.812$, $AUC = 0.979$, $CCR = 0.964$). Applying this model led to a prediction of apparently suitable habitat distributed patchily across both study areas (Fig. 2). Mean area of a predicted suitable habitat patch in the Korgalzhyn region was 4586 ha (± 397.4 se, range 458–9639, $n = 37$). The mean distance between neighbouring patches of suitable habitat was 4.72 km (± 0.78 se, range 0.1–24.1 km). The proportion of habitat predicated

Table 3. Modelling results at the colony scale: (a) overview of all models with $\Delta_i < 10$; (b) averaged regression coefficients β with associated standard errors (se) and relative variable importance $w_+(j)$ for all models considered in model averaging.

(a)			
Model	AIC _C	Δ_i	w_i
cov.dung + cov.dung (sqr) + cov.veg + cov.veg (sqr) + dist.nest	215.811	0.000	0.899
cov.dung + cov.dung (sqr) + cov.veg + cov.veg (sqr) + vegH.max + dist.nest	220.227	4.416	0.099
(b)			
Variable	Averaged β	se	$w_+(j)$
Intercept	-2.5592	3.3102	1.000
dist.nest	-0.0076	8.57E-06	1.000
cov.dung	0.6825	0.1465	0.998
cov.dung (sqr)	-0.0439	0.0010	0.998
cov.veg	0.1202	0.0058	0.998
cov.veg (sqr)	-0.0013	5.81E-07	0.998
vegH.max	-0.0118	5.72E-06	0.101
cov.grass	-0.0328	4.27E-06	< 0.001

For variable abbreviations, see Table 1.

as suitable in the Korgalzhyn study region was 6.6% applying a threshold of $P = 0.5$, and 8.0% using the prevalence approach with $P = 0.22$.

Spatial generality was good with 74.0% of all nest-sites found in the Pavlodar region in 2007 ($n = 146$) situated in areas predicted as suitable by the model developed in the Korgalzhyn area (threshold: $P = 0.5$). Patch occupancy was, however, low, with only 26.7% of all patches predicted as suitable being occupied by breeding Sociable Lapwings in 2007.

Spatial grazing patterns and Sociable Lapwing nest-site selection

The mean maximum daily distance covered by four cattle tracked with GPS-loggers in the Korgalzhyn study area was 4330 m (± 419 se, range 2100–8300 m, $n = 19$ track-days with 4076 GPS-fixes). Cattle always moved radially away from the villages during the day and returned along the same route. Grazing pressure decreased with increasing distance from the settlements with the exception of the 3000–3500-m band, which had a higher than expected density of GPS fixes because this is where cattle went to drink (Fig. 3). Vegetation height increased linearly with increasing distance

to the settlements (Fig. 3), although variation was high. Mean vegetation height per distance band was negatively correlated with cattle density (Spearman's $r = -0.72$, $P < 0.05$, $n = 11$ bands).

Most nest-sites were very close to villages, with a mean distance to the nearest village edge of 1164 m (± 36.0 se, range 10–6830 m, $n = 637$ nests in 2004–2008). Of all nests, 89% were situated closer than 2000 m to the nearest settlement, and thus in the areas with the highest grazer intensity (Fig. 3). The density of Sociable Lapwing nests per distance band was strongly positively associated with cattle density per distance band (Fig. 4), the relationship suggesting a threshold in grazing intensity needed to create a suitable habitat for the Sociable Lapwing.

DISCUSSION

Breeding habitat and nest-site selection

Breeding habitat selection of the Sociable Lapwing at a landscape scale appears to be driven by two key factors: proximity to rivers and the presence of grazing animals. The first of these might result from the species' migration strategy: birds often migrate along rivers, which serve as orientation strips and water supply in the monotonous steppe landscape (J. Kamp, R.D. Sheldon pers. obs. from colour-ringed and satellite-tagged birds 2006, 2007). Suitable habitat might thus simply be selected more often closer to rivers, because these areas are encountered first. Alternatively, the preference of breeding sites close to water might be driven by the fact that both adults and chicks visit water bodies to drink during hot days (Dolgushin 1962, J. Kamp, R.D. Sheldon pers. obs.).

All other variables with high weights in models pointed to the influence of grazing in habitat selection. Vegetation height and the density of dung piles were strongly correlated with the density of grazing livestock in the Central Kazakhstan study area, and the preference for habitat close to human settlements is linked to the fact that livestock grazing is currently concentrated there. The remaining variables with considerable weight (preference for a high wormwood *Artemisia* spp. cover and avoidance of a high cover of grassy plants and feather grass *Stipa* spp.) mirror vegetation characteristics of heavily grazed steppe communities: Grasses, especially feather grass, are positively selected by grazing livestock, as they are palatable, leading to an increased abundance and cover of the unpalatable *Artemisia* and other woody plants with increasing grazing

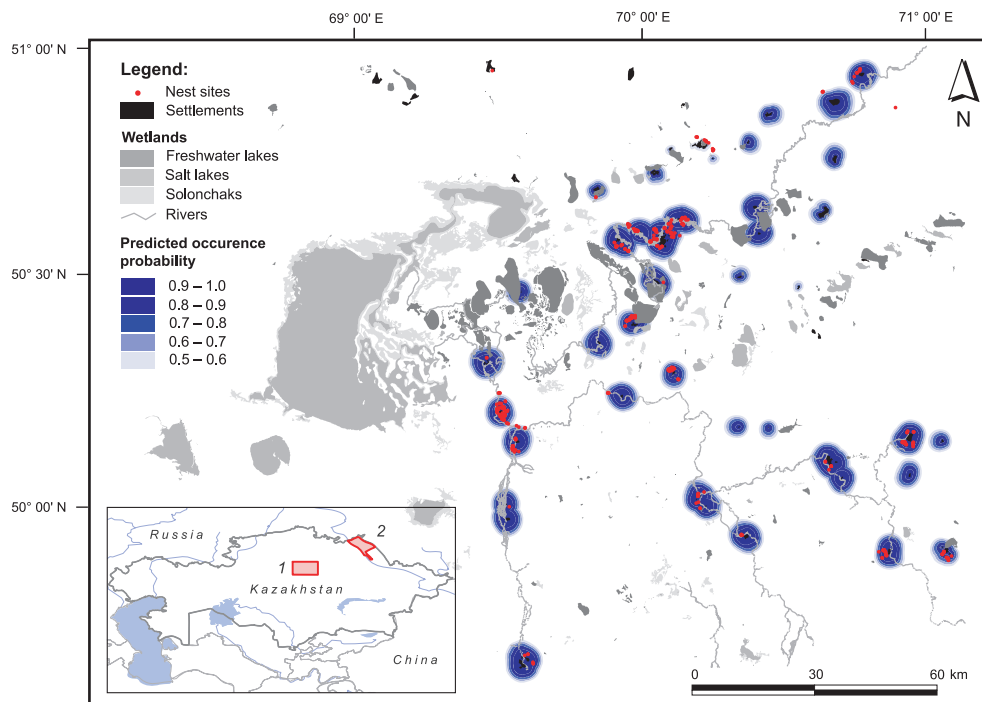


Figure 2. Habitat suitability map for the Korgalzhyn study area. The depth of blue shading indicates differences in occurrence probability. All nest-sites for the years 2004, 2005, 2007 and 2008 are plotted. Inset: Geographical position of the Korgalzhyn (No. 1) and Pavlodar (No. 2) study areas in Kazakhstan.

pressure (Bock *et al.* 1984, Baker & Guthery 1990, Yunusbaev *et al.* 2003).

The selection of colony sites near rivers was not an artefact of settlements being situated closer to rivers. However, cattle numbers might be higher in settlements situated at river shores (due to the unlimited availability of drinking water). This might lead to higher grazing pressure and thus more suitable habitat available closer to rivers.

In the Korgalzhyn study area we covered many areas previously known as breeding sites of Sociable Lapwings, which were often situated close to human habitation. This represents a source of possible bias when evaluating the influence of settlements on Sociable Lapwing distribution. However, we consider a systematic influence on the modelling results as very unlikely, as more than 1000 km of additional survey transects were covered in randomly chosen habitats when gathering distribution data for the models.

Within the colonies, the most influential variable in nest-site selection was distance to nearest nest, as to be expected for a colonial species. Removing this variable again suggested selection of more heavily grazed areas for nest placement, as both the cover of dung and the cover of bare ground generally increase with increasing grazing pressure by

domestic livestock (Bock *et al.* 1984, Yunusbaev *et al.* 2003). These results from the modelling approach were supported by the spatial analysis of grazing patterns, which revealed a strong relationship between grazing intensity and Sociable Lapwing nest density, and confirmed the suggestions of Watson *et al.* (2006) on nest-site selection.

The excellent transferability of a landscape model containing only the distance to rivers and settlements as covariates suggests that the availability of water and short swards around settlements are key factors in habitat selection across the whole breeding range. However, the number of patches occupied in the test area was very low. This indicates the absence of important covariates in the model used for prediction (e.g. vegetation height), suggesting that not all habitat predicted as 'suitable' is indeed suitable for Sociable Lapwing breeding. Low patch occupancy rates might also indicate that there is much more habitat available than currently used, particularly at this north-eastern limit of the species' range.

Reasons for synanthropy

Breeding Sociable Lapwings are now almost wholly confined to short steppe swards close to human

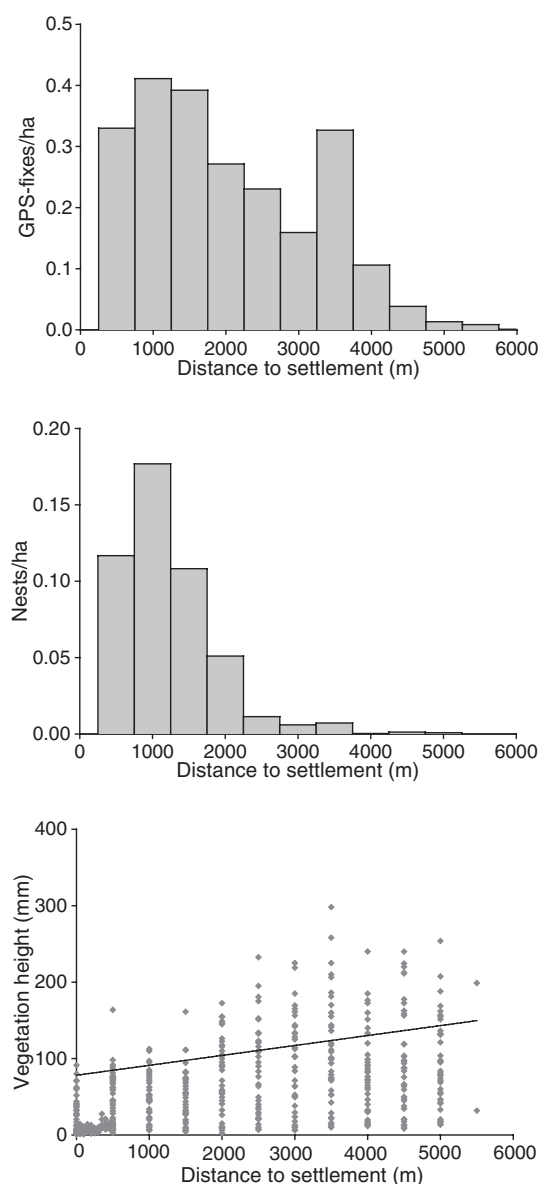


Figure 3. Grazing intensity of cattle ($n = 4976$ GPS-fixes), Sociable Lapwing nest density ($n = 673$ nests, years 2004–2008) and vegetation height around settlements. All density estimates are corrected for distance band area. Vegetation height increased with increasing distance from the nearest settlement (Generalised Linear Model (GLM) including month and site as fixed factors, $\chi^2_{478} = 93.22$, $P < 0.001$).

settlements. This type of habitat has been described previously in relation to this species, but only since 1990 (Khrokov 1996, Berezovikov *et al.* 1998, Eichhorn & Khrokov 2002, Bragin 2005, Watson *et al.* 2006). Sociable Lapwings were previously described as breeding in other habitats,

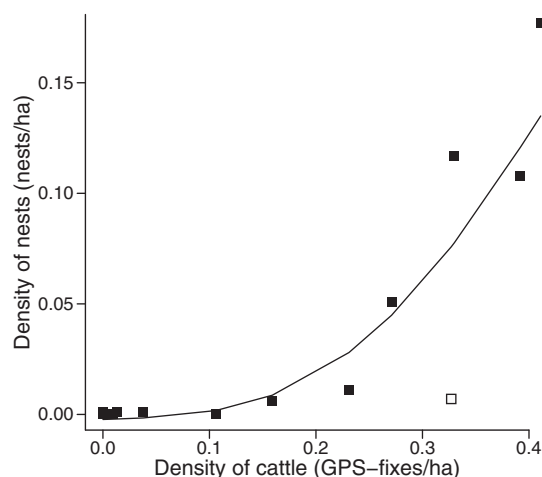


Figure 4. Relationship between cattle grazing intensity and Sociable Lapwing nest-site location ($n = 673$ nests, years 2004–2008). The line shows a spline smoothing function ($df = 3$). The outlier (open square) is the result of a water hole approximately 4 km from one village, where cattle spent much time drinking.

such as pristine fescue-feather grass steppe and semi-desert (Volchanetskiy 1937, Ryabov 1974, Khrokov 1977, Shevchenko 1999) as well as the shores of salt pans vegetated with short swards of halophytes ('solonchaks', Kuchin & Chekcheev 1987, Gordienko 1991, Shevchenko *et al.* 1993), but these seem to be virtually unused now. Arable fields have only ever been used rarely for breeding (Solomatina 1997, Karyakin & Koslov 1999). This current synanthropic relationship might be considered as a form of commensalism with domestic livestock. High dung densities are known to increase invertebrate abundance (Atkinson *et al.* 2004), and the pronounced preference for areas with a high density of dung might indicate the use of an improved food base on strongly grazed pastures. A high proportion of Sociable Lapwing nests (68% of 168 nests found in 2006, Korgalzhyn study area) were actually built in piles of cattle or horse dung. Sociable Lapwings choosing dung piles for nesting might profit from a camouflaging effect of dry dung, or insulation from the ground, which is often still frozen during the start of incubation in April. Away from the immediate vicinity of villages, the steppe is now largely ungrazed after the collapse of wild ungulate populations, such as wild ass *Equus hemionus* and Saiga Antelope (the latter declining by 95% in 1994–2002, Milner-Gulland *et al.* 2001), and because of the reduced mobility of livestock owners compared with Soviet times.

Land use change and population development: implications for conservation

Although the reasons for a population decline in Sociable Lapwing have not yet been clarified, there are suggestions that the population trend has matched land use changes on the breeding grounds. During Soviet times (c. 1930 until 1991), most livestock were owned by large state companies, and extremely low fuel prices and the widespread availability of machinery enabled farmers to distribute their livestock widely across the steppe pastures (Robinson *et al.* 2003, Milner-Gulland *et al.* 2006). After the collapse of the Soviet Union in 1991, livestock numbers crashed both in Russia and Kazakhstan due to a withdrawal of state subsidies and the use of animals as currency in times of economic hardship (Suleimanov & Oram 2000, Robinson & Milner-Gulland 2003). Since 2000, this negative trend has been reversed (Fig. 5).

Large-scale wheat farming was introduced in Kazakhstan during the 'Virgin Lands Campaign' 1953–60, when 25.4 million ha were ploughed in the steppe belt. After 1991, huge areas of arable land fell fallow (De Beurs & Henebry 2004). The area used for crop-growing was reduced by nearly 40% during the 1990s (Suleimanov & Oram 2000). This trend has been reversed since around 2000: in the eight districts of Kazakhstan situated in the steppe belt, the area sown for cereal crops steadily increased by an average of 31% (± 6.3 se, range -8.5 to 45.4%) during the period 2000–2008.

Population trends of the Sociable Lapwing seem to be strongly correlated with the changing avail-

ability of short-grazed habitat. The highest breeding numbers were reached around 1900, when post-breeding flocks of 8000–10 000 birds were observed (Plotnikov 1898) and the species was a 'common breeder' in Eastern Kazakhstan and Russia (Finsch 1879). The range contraction and severe decline observed in the 1930s and 1950s (Dolgushin 1962, Ryabov 1974) coincide with agricultural intensification. Further declines during the Soviet period might have been linked to an intensification in farming and an increased livestock mobility leading to lower grazing pressure in steppe habitat. A strong decline of Sociable Lapwing numbers after 1991 has been linked repeatedly to the cessation of grazing in many areas following the collapse of livestock numbers (Tomkovich & Lebedeva 2004).

After 2000, however, the livestock concentration effects increased the suitable breeding area for Sociable Lapwing at least in Central and Northern Kazakhstan and are mirrored by a positive population trend. Numbers in our Korgalzhyn study area increased by 48% between 2005 and 2007 (R.D. Sheldon, J. Kamp, M.A. Koshkin unpubl. data), in the Pavlodar study area by approximately 23% between 1991 and 2007 (Solomatin 1997, J. Kamp, M.A. Koshkin pers. obs.), and also in other regions of Kazakhstan, e.g. the Naurzum region, N Kazakhstan, between 2000 and 2008 (Eichhorn & Khrokov 2002, Bragin 2005).

However, two recent developments mean that the current situation might change soon. First, there is likely to be an increase in the reclamation of fallow land and agricultural intensification of steppe land. A doubling of grain prices since 1999

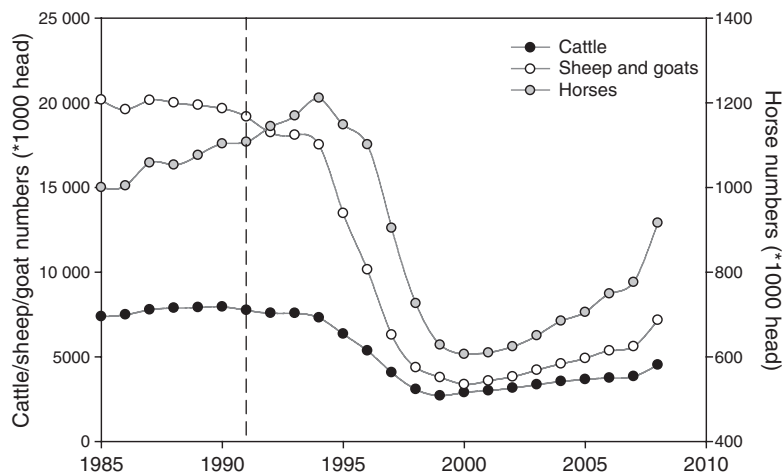


Figure 5. Trends in livestock numbers for the districts ('oblasts') of Kazakhstan situated in the steppe belt ($n = 8$), between 1985 and 2008 (Kazakhstan State Statistics Agency 2008). The Soviet Union collapsed in 1989 and Kazakhstan gained independence in 1991.

(FAOSTAT 2008) and a record harvest in 2007 (Kazakhstan State Statistics Agency 2008) have enabled farmers to buy expertise and equipment and return to large-scale farming in many parts of the northern steppes. Cereal yield has increased by 41.5% since 2000 (Kazakhstan State Statistics Agency 2008). World food demand has been predicted to double by 2050 (Tilman *et al.* 2002), and the production of bioethanol is rapidly increasing (IAE 2007), so increasing quantities of cereals will be demanded on the world markets. Kazakhstan opened its first bioethanol plant in 2008, with a capacity of 350 000 tons of cereal products, and a rapid increase of this business is expected (Biohim 2008).

Secondly, there are likely to be significant changes in livestock management. A stable economic growth in Kazakhstan since 2000 has led to a steady improvement of living standards, accompanied by a tendency for rural migration to the cities. It thus seems likely that the current livestock management system characterized by village-based herding of self-sustaining communities might soon give way to more intensive systems with animals kept concentrated day and night in large stables, and an increasing tendency to give up small-scale animal husbandry. Both processes would result in a decrease of suitable habitat for the Sociable Lapwing and other steppe species such as Black-winged Pratincole *Glareola nordmanni* and White-winged Lark *Melanocorypha leucoptera*.

Whereas habitat availability and low breeding success seem currently not to be limiting factors in Sociable Lapwing populations (R.D. Sheldon, J. Kamp, M.A. Koshkin unpubl. data), future developments in steppe land use, especially changes in grazing patterns and expansion and intensification of agriculture, should be monitored closely. A continued monitoring of Sociable Lapwing numbers and productivity across the distribution range would be highly desirable. Important stopover sites have been discovered recently, but distribution, habitat use and threats at the migration routes as well as on the wintering grounds are largely unknown. More insight could lead to better conservation in the whole life cycle of this charismatic, yet much depleted, species.

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