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Landscape and climatic predictors of Kentish Plover (*Charadrius alexandrinus*) distributions throughout Kazakhstan

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Worldwide populations of shorebirds are declining, associated with a complex interplay of climate change, predation, human disturbance and habitat degradation. Comprehensive information on the distribution and breeding ecology of shorebird populations is crucial to understand and mitigate these threats. Kazakhstan, the largest country in Central Asia, comprises multiple flyways and breeding habitats for shorebird species, including the Kentish Plover *Charadrius alexandrinus*, but information on the population size and breeding distribution of shorebird species in the region is highly limited. We conducted a wide-scale survey of Kentish Plover across Kazakhstan during the breeding season and utilize species distribution modelling to outline key anthropogenic and environmental variables that determine Kentish Plover presence. Our results reveal widespread distribution of Kentish Plovers across Kazakhstan but indicate that breeding densities are generally low. Our distribution modelling stresses the primary importance of proximity to water bodies and climate as the main predictors of Kentish Plover presence, but reveals a weak association with indicators of human disturbance. We utilize our distribution modelling to provide the first quantitative estimate of the breeding population size of Kentish Plover in Kazakhstan, which indicates a modest number of individuals given the size of the country (between 12 000 and 32 000 individuals). Our results indicate the key routes via which climate change may impact on population-level distributions of Kentish Plover and provide a platform for future studies investigating species distributions across similarly vast and inaccessible regions.

Keywords: Central Asia, environmental drivers, habitat suitability, shorebird, species distribution.

Populations of shorebirds are facing a global decline, driven by climate change, antagonistic species interactions, human disturbance and habitat degradation (Sutherland *et al.* 2012, Pearce-Higgins *et al.* 2017, Kubelka *et al.* 2018, Amano *et al.* 2020). Understanding the causes and determining appropriate conservation interventions requires information on the distribution, density and breeding biology of shorebird populations (Haig 2019).

Central Asia comprises important flight paths and breeding habitats for multiple shorebird

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species (Gavrilov *et al.* 1998, Schielzeth *et al.* 2008, 2010, Pearce-Higgins *et al.* 2017). Kazakhstan is the largest country in Central Asia and hosts a broad range of habitats of high conservation importance suitable for shorebirds, including semi-desert, steppe and wetland, and falls within both the Central Asian and African-Eurasian flyways (Gavrilov *et al.* 1998, Yerokhov 2006, Schielzeth *et al.* 2008, 2010, Kamp *et al.* 2016, Pearce-Higgins *et al.* 2017). Moreover, Kazakhstan hosts a large number of globally threatened vertebrates and is understood to be a key breeding habitat for a number of globally threatened shorebird species, including the critically endangered Sociable Lapwing *Vanellus gregarius*, and is the population stronghold for the near threatened Black-winged Pratincole *Glareola nordmanni* (Watson *et al.* 2006, Kamp *et al.* 2009a, 2016, Venter *et al.* 2014, BirdLife International 2016a, 2018). Despite this, detailed information on the population size and breeding distribution of shorebird species in Kazakhstan, and Central Asia more generally, remains limited (Kamp *et al.* 2009a, Schielzeth *et al.* 2010, Sheldon 2017, Martin *et al.* 2018, Wetlands International, 2018).

Importantly, Kazakhstan provides some of the most conspicuous examples of recent land use change and degradation of habitats crucial to shorebirds (Kreuzberg-Mukhina 2006, Micklin 2007, Starodubtsev & Truskavetskiy 2011). For example, the Aral Sea basin, which also borders Uzbekistan and Turkmenistan, once hosted the fourth largest lake in the world (Gaybullaev *et al.* 2012). However, diversion of its two main tributaries for agricultural irrigation during the 1960s, in combination with a warming in climate, has resulted in a loss of up to 75–80% of its water surface (Bai *et al.* 2012, Gaybullaev *et al.* 2012, Klein *et al.* 2014), driving desertification of the region and a sharp increase in salinity (Micklin 2007). This dramatic change in habitat structure has been associated with a steep reduction in bird species diversity of approximately 50% and a decline in shorebird species of over 60% (Haig 2019). Similarly, the Caspian Sea, currently the world's largest inland water body, faces sustained environmental deterioration associated with climate change-related evaporation and industrial development (Nasrollahzadeh 2010, Chen *et al.* 2017). In other regions across Kazakhstan, agricultural expansion, increasing livestock concentrations and an increased frequency of droughts have been indicated as threats to shorebird populations (Morozov 2000, Watson *et al.* 2006, Kamp *et al.* 2009b, Pearce-Higgins *et al.* 2017). Kazakhstan thus represents a key area in which increased information on shorebird distributions, and the ecological drivers of their distributions, is urgently required.

The Kentish Plover C*haradrius alexandrinus* is a cosmopolitan shorebird species, and previous research indicates it is a widespread breeder across Kazakhstan (Martin *et al.* 2018, BirdLife International 2020a). Kentish Plovers typically nest and rear their offspring in open areas with little vegetation near salt pans, inland lakes and coastal shores (Cramp & Simmons 1983, Fraga & Amat 1996, Kosztolányi *et al.* 2009), and has emerged as model to study the evolution of mating system and parental care in behavioural ecology (Kosztolányi *et al.* 2006, Gómez-Serrano & López-López 2017, Székely 2019, McDonald *et al.* 2020). Although the conservation status of Kentish Plover is listed as Least Concern, estimates indicate that the global population is in decline (Delany & Scott 2006, BirdLife International 2016b). Throughout Europe, Kentish Plover breeding populations have seen historical contraction and face continuous challenges associated with human disturbance and habitat degradation (Schulz & Stock 1993, Lorenzo & Emmerson 1995, Montalvo & Figuerola 2006, Pietrelli & Biondi 2012, BirdLife International 2016b, Gómez-Serrano, 2020), increasing the importance of Central Asia including Kazakhstan as a breeding stronghold for the species. Despite this, however, there are currently no extensive surveys assessing the distribution and breeding ecology of Kentish Plover in the region (Gavrilov 1999, Gubin 2015, Sheldon 2017, Wetlands International, 2018).

To address this gap we conducted a wide-scale survey of Kentish Plover throughout Kazakhstan during the breeding season in 2019. Our study has three key aims: (1) to assess the frequency, distribution and breeding status of Kentish Plover throughout May–June; (2) to use species distribution modelling to outline the relative importance of key environmental variables in determining Kentish Plover presence, including vegetation density, climate, surface water geometry and human settlements; and (3) to use this modelling approach to predict potential Kentish Plover distributions across key habitat regions including Western Kazakhstan, the Aral Sea and Eastern Caspian

Sea, and to estimate the breeding population size for these regions and for the whole nation. Given that extensive, detailed surveys of Kazakhstan are particularly challenging due to its size and terrain, our modelling approach is well suited to assessing breeding population distributions across Kazakhstan. We predict that surface water geometry, vegetation density and indicators of human activity will exert the strongest influence on predictions of Kentish Plover presence.

METHODS

Survey data collection

Fieldwork was carried out between 8 May and 26 June 2019. The full extent of the survey across Kazakhstan ranged from continental Europe to Asia between 43°38′–53°01′N and 47°21′–84°29′E (Fig. 1, see Supporting Information Fig. S1 for detailed information on survey locations).

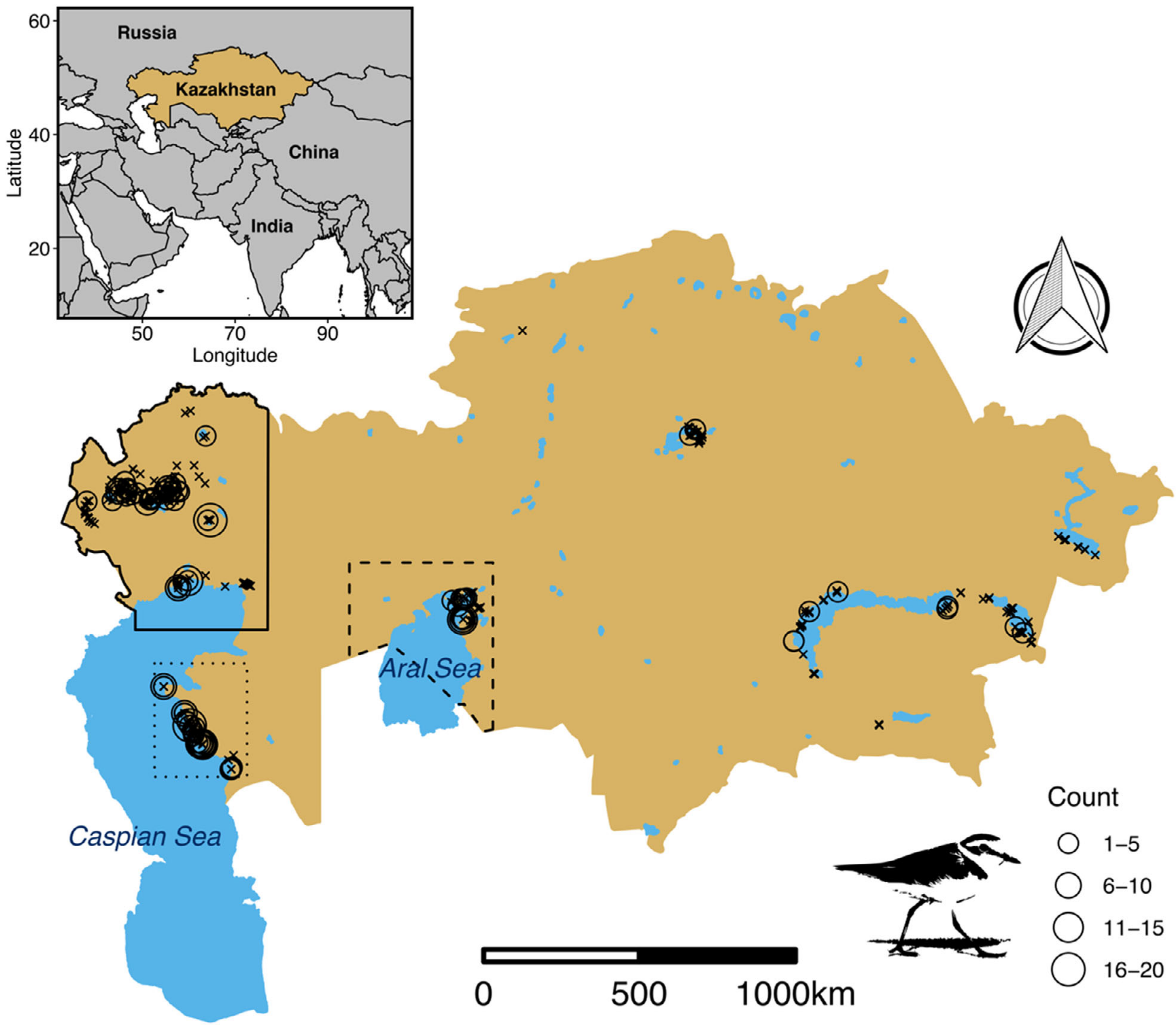

Figure 1. Map of Kazakhstan. The largest lakes (area ≥ 50 km^2) and reservoirs (storage capacity ≥ 0.5 km^3) are shown in light blue. Black crosses indicate the locations of sampling points where zero Kentish Plovers *Charadrius alexandrinus* were observed. Circles indicate the locations of sampling points where Kentish Plover were observed and the size of circles indicates the number of individuals counted. A total of 428 points are shown, excluding repeated visits to individual sites (73 excluded points). Three polygons show the Western Kazakhstan region (solid line) used for species distribution model training, and the Eastern Caspian Sea (dotted) and Aral Sea (dashed line) regions. Inset: illustration of a male Kentish Plover.

Our survey locations were selected based first on previously identified potentially suitable wetland and lake regions in past shorebird studies (Schielzeth *et al.* 2008, 2010, Lachmann *et al.* 2010, Martin *et al.* 2018). Secondly, as yet unsurveyed locations were selected via assessment of their potential suitability as Kentish Plover foraging and breeding sites based on Google satellite images, local expert knowledge and accessibility for observers. Areas of dense forest, high mountains and open water were not considered potentially suitable and were not sampled. Our screening approach thus focused on potentially suitable Kentish Plover breeding habitats including lakes, saltmarshes, salt pans, ponds and coastal shores. However, the final surveyed locations included a diversity of habitats, with a range of expected habitat suitabilities ranging from semi-desert regions, remote coastal shores, public beaches, freshwater reed beds and artificial reservoirs, thus including an assortment of habitats more or less suitable for breeding Kentish Plovers. Localities were surveyed for Kentish Plovers by counting the number of observable birds at selected vantage points. Counts were typically made from a vehicle using binoculars and/or scope; however, due to practicalities of accessibility, several sites were accessed on foot. We avoided overcounting of individuals by repeat scanning of previous counted sections to ensure birds had not flown and keeping track of bird movements to ensure counted birds did not travel to uncounted areas and thus were not double counted. Vantage points at localities were selected as a function of accessibility and to maximize visibility so that Kentish Plovers were likely to be observed if present. For several localities, multiple vantage points were surveyed. In such cases we aimed to separate vantage points by approximately 100 m.

We surveyed a total of 501 points. Four localities, including small water bodies or specific sections of larger water bodies (Lake Tlikshe, Lake Kambak, Lake Sorkol and Lake Alakol) were revisited on multiple days as part of a separate behavioural study (totalling 73 points). The majority of our sampling period was focused in Western Kazakhstan until 4 June, totalling 275 survey points (Figs 1 and S1). Subsequent survey data were collected in multiple regions across South-Western, Central and Eastern Kazakhstan, encompassing key water bodies and important bird areas (IBAs) including the Eastern Coast of the Caspian Sea, Aral Sea, Tengiz-Korgalzhyn, Lake Balkhash, Lake Alakol, Lake Zaysan and Lake Sorbulak (Sklyarenko *et al.* 2008, BirdLife International 2016b; Fig. S1).

At each survey point in which Kentish Plovers were observed we recorded evidence of active breeding at the site. A point was designated as an active breeding point if either active Kentish Plover nests, juveniles or chicks were observed, or if Kentish Plover courtship or distraction-displays, a behavioural response to predators specific to nesting or brood-rearing parents, were observed (Simmons 1951, Gómez-Serrano & López-López 2017).

Survey distributions

We summarized the total, median and mean number of Kentish Plover individuals observed per survey point as well as the proportion of survey points in which Kentish Plover was observed across the entire geographical extent of our survey. To avoid inflating counts due to repeat sampling of the same individuals, we also report mean values only for points sampled during the first visit to locations by excluding data sampled during repeat visits (73 visits).

We next assessed the seasonal frequency of breeding evidence recorded across the full survey period. For each day in which sampling occurred we created a binary variable indicating whether breeding was observed on that day or not. We again excluded repeat visits to the same locations (73 points) to avoid repeat identifications of the same breeding attempt on different days. We used a generalized linear model (GLM) with a binomial error structure. Explanatory variables included a linear and quadratic term for Julian date scaled to have a mean of zero and standard deviation of one (Schielzeth 2010) and the number of points sampled on each day, to control for differences in daily sampling effort. The significance of all predictor variables was assessed via likelihood ratio tests by removing the variable of interest, and the significance of linear terms was assessed from models without the inclusion of quadratic terms.

Regional species distribution modelling

Modelling framework

We next used a species distribution modelling approach to understand the main drivers of

Kentish Plover distributions and predict their distribution throughout Western Kazakhstan, the Aral Sea and Eastern Caspian Sea, i.e. projection of model findings in environmental space to the geographical space by extrapolation. To achieve this we conducted correlative modelling that correlates environmental variables ('predictors') with the occurrence of the species (Guisan & Zimmermann 2000, Pearson & Dawson 2003). The model assumes that the species is in equilibrium with its environment and that its distribution is mostly driven by abiotic predictors measured during the time of observation of the occurrences (Elith & Leathwick 2009, Heikkinen *et al.* 2016). Throughout, our occurrence data were treated as presence–absence data. We conducted the regional species distribution modelling in a regular, 300-m resolution, square grid. Hence, both presence data and the environmental predictors were resampled or calculated in this grid. We used the 300-m resolution, as this was one of the finest resolutions available for environmental predictors and to limit computational demands associated with finer resolutions. Furthermore, given visibility at vantage points typically allows for observations of Plovers within an approximate 150-m radius of the observer, our individual point counts are comparable with this scale (Dias *et al.* 2014).

Data preparation and distribution modelling were carried out in R statistical software (R Core Team 2019) using the packages 'corrplot' (Wei & Simko 2017), 'dismo' (Hijmans *et al.* 2017), 'raster' (Hijmans 2019), 'ROCR' (Sing *et al.* 2005), 'sf' (Pebesma 2018) and 'usdm' (Naimi *et al.* 2014).

Environmental predictors

We obtained environmental predictor variables based on *a priori* expectations of importance to breeding Kentish Plover (Table 1) across three key habitat regions: Western Kazakhstan, the Aral Sea and Eastern Caspian Sea (Fig. 1). Kentish Plovers typically breed on sandy shores surrounding inland water bodies and coastal shores (Lessells 1984, Kosztolányi *et al.* 2009, Pietrelli & Biondi 2012, Rocha *et al.* 2016) characterized by sandy beaches with little vegetation (Fraga & Amat 1996, Kosztolányi *et al.* 2009, McDonald *et al.* 2020). Due to the key importance of water bodies for Kentish Plover breeding, we calculated a number of environmental predictors describing the geometry of standing water bodies. We obtained details for both the permanent and temporary standing water bodies from the Global Lakes and Wetlands Database (Lehner & Döll 2004) at 30″ (~ 1-km) resolution. We then calculated the distance in metres of each grid point to the nearest permanent water body (PWB Dist) and the nearest temporary water body (TWB Dist). As Kentish Plovers typically feed at shorelines, we calculated the length of shoreline of each nearest permanent water body in metres (Shore length) and the size of the nearest permanent water body (PWB Size). In addition, we calculated the distance in metres between the nearest permanent water body and its closest neighbouring permanent water body, as an indicator of the connectivity of local water bodies (NPWB Dist).

We obtained vegetation density estimates for each grid square based on the Normalized Difference Vegetation Index (NDVI) for the period 21–30 May 2019 obtained from Copernicus Global Land Service (Copernicus 2020) at 1/336° (~ 300-m) resolution. This time slot was selected as a representative sample for the Western Kazakhstan surveys, which occurred mainly throughout May and encompassed the area with the most detailed sampling effort (8 May–4 June 2019, 275 survey points). NDVI values ranged from –0.08 to 0.92. Points without relevant NDVI values, e.g. due to cloud cover or shadow, were set to unknown (n = 139 811 of 5 356 473) and the points flagged as open water were set to be the minimum values, i.e. –0.1 (n = 914 217 of 5 356 473). Land cover data for the year 2015 were downloaded from Copernicus Global Land Service (Buchhorn *et al.* 2019) at 1/1008° (~ 100-m) resolution.

Ambient temperature and precipitation may modulate Kentish Plover breeding by impacting on parental behaviour and food availability (Kosztolányi *et al.* 2006, 2009, AlRashidi *et al.* 2011, Colwell & Haig 2019). We thus obtained climate data for the period 1970–2000 from the WorldClim database (Fick & Hijmans 2017) at 30″ (~ 1-km) resolution and calculated the mean temperature and mean precipitation for May (i.e. main period of Western Kazakhstan surveys).

Finally, to quantify the potential impact of human disturbance on Kentish Plover presence, we estimated the distance of each grid cell to the nearest human settlement in metres. Human settlements (populated areas) were located based on the HOTOSM Kazakhstan Populated Places dataset (HOTOSM, 2020). This contains both

Table 1. Name and description of the environmental predictors for species distribution modelling and the environmental dataset from which they were calculated. PWB Size was not included in the final species distribution model following assessment of collinearity between predictors.

Name	Description	Data reference
PWB Dist	Distance from nearest permanent standing water body (m)	Lehner & Döll (2004)
TWB Dist	Distance from nearest temporary water body (m)	Lehner & Döll (2004)
PWB Size	Size of nearest permanent standing water body (m^2)	Lehner & Döll (2004)
Shore Length	Shoreline length of nearest permanent standing water body (m)	Lehner & Döll (2004)
PWB Shape	Shape of nearest permanent standing water body (Shore Length/PWB Size)	Lehner & Döll 2004
NPWB Dist	Distance of nearest permanent standing water body to its closest neighbour (m). Indicates permanent water body isolation.	Lehner & Döll (2004)
Veg Dens	Vegetation density estimate	Copernicus 2020
Dist Sett	Distance from nearest settlement	HOTOSM (2020)
Wetland	Logical variable indicting whether a cell is covered by herbaceous wetland (i.e. 0 or 1)	Buchhorn *et al.* 2019
Frac Crop	Fraction of cell covered by croplands	Buchhorn *et al.* (2019)
Temperature	Mean temperature in May averaged over the period 1970–2000 (°C)	Fick & Hijmans (2017)
Precipitation	Mean precipitation in May averaged over the period 1970–2000 (mm)	Fick & Hijmans (2017)

settlements and isolated dwellings and is exported from the OpenStreetMap database, which is a crowd-sourced, volunteer geographical survey.

All predictors were calculated for the three key study regions (Western Kazakhstan, the Aral Sea and Eastern Caspian Sea) separately, and the input datasets were clipped with a 50-km buffer around the study region before calculation. Buffer size was determined by computing limitations. Before selecting the final set of ecological predictor variables for our species distribution model, we assessed multicollinearity between predictors (Dormann *et al.* 2013). Predictor selection was based on pairwise Pearson's correlation coefficients ($|r| < 0.75$), and Condition Number (CN < 20) and variance inflation factors (VIF < 5) calculated on the entire dataset. The size of the nearest permanent water body (PWB Size) was highly correlated with the Shore length of the nearest permanent water body ($r > 0.9$). We therefore removed PWB Size, and replaced this variable with an estimate of water body shape (PWB Shape) calculated as Shore Length divided by PWB Size (Table 1). All remaining r-values were below 0.75 (Supporting Information Fig. S2) and VIFs were found to be < 3.6 and the CN < 6.

Modelling procedures

We conducted species distribution modelling in a two-step way. We first used maximum entropy modelling using MaxEnt ver. 3.4.1. (Phillips *et al.* 2006, 2020) for species distribution modelling to understand the relative importance and relationship between our different landscape and climatic predictors and potential Kentish Plover distributions. An advantage of MaxEnt is that it can be used to map distributions over large areas using low numbers of species presence data (Willis *et al.* 2015). It is one of the best performing methods (Elith *et al.* 2006, Phillips *et al.* 2006, Phillips & Dudík 2008, Shabani *et al.* 2016) and is widely used for modelling the distribution of birds (Suárez-Seoane *et al.* 2008, Yost *et al.* 2008, Tinoco *et al.* 2009, Young *et al.* 2009, Moreno *et al.* 2011). Secondly, to avoid reliance on a single model and to generate robust species distribution maps, we employed five additional modelling techniques [Gradient Boosting Machine (GBM), Random Forest (RF), Artificial Neural Network (ANN), GLM, generalized additive model (GAM)] with different parametrizations to produce a total of seven additional model predictions which we combined with the MaxEnt results to generate an ensemble species distribution prediction (Araújo & New 2007, Oppel *et al.* 2012, Kaky *et al.* 2020).

For our MaxEnt model we used Western Kazakhstan, the region with the most detailed sampling effort, for model training (Fig. 1); this consisted of 3 036 701 training points (272 820.83 km^2). Presence records were resampled within a 300-m resolution grid; that is, multiple occurrences within each 300-m grid cell were aggregated to the centroid of the cell ('grid point'). A total of 53 presence points and 100 000 randomly selected background points were used to train the model.

A known advantage of MaxEnt is that it performs well when the number of presence points is low, as in our dataset (Hernandez *et al.* 2006, Pearson *et al.* 2007, Phillips & Dudík 2008, Wisz *et al.* 2008). Hinge, product, threshold, linear and quadratic features were enabled during parametrization of the model and we used the default convergence threshold (10^{-5}). Environmental predictor importance (i.e. the regularized gain) was estimated by a leave-one-out jackknife algorithm, where each variable was excluded in turn, and also by conducting a model with each variable in isolation (Efron & Stein 1981). As MaxEnt models may be prone to transferability issues (Baldwin 2009), evaluation of the model requires an independent dataset. Eastern Caspian Sea and Aral Sea regions were used for independent evaluation of the trained model by the area under the receiver operating curve (AUC) goodness-of-fit measure (Hanley & McNeil 1982). These polygons include two of the largest water bodies in the region and encompass potentially key Kentish Plover habitats. The Eastern Caspian Sea region consists of 913 784 evaluation points (82 068.56 km^2) and Aral Sea region of 1 405 988 evaluation points (126 252.29 km^2). Subsequently, all three study regions were used for prediction. Raw prediction outputs were transformed to predicted probabilities between 0 and 1. For the transformation we applied the complementary log-log link function, which results in correct probability values if we assume that typical presences have a 1/point expected abundance (Phillips *et al.* 2017), which fits well with previous indicative surveys (Andrusenko & Dudenkov 1982).

For our ensemble species distribution modelling approach we generated a total of seven additional models intentionally ranging from a simple statistical method (i.e. GLM) through a complex statistical method (i.e. GAM) to simple and complex machine learning methods. Among the large and continuously increasing number of available machine learning methods, two main approaches were selected, neural network (ANN) and regression tree-based algorithms, one implementing bagging (RF) and the other boosting (GBM) to increase the predictive power of weak learners, i.e. small trees. This diversity of the selected methods, completed with some changes in parametrization, ensures the robustness of the ensemble approach (see Supporting Information Table S1 for model details). Each of the seven models was trained and evaluated in a way similar as described above regarding MaxEnt with only one exception: instead of randomly selected background points required by MaxEnt, all the absence points of Western Kazakhstan were downweighted (i.e. the weighted number of absences were equal to the number of presences) and used for training the other models. We then aggregated our individual model predictions to produce a robust ensemble prediction as a weighted average across all individual models (eight total models including our MaxEnt prediction), where models were weighted by goodness of fit (i.e. AUC–0.5; Oppel *et al.* 2012).

To quantify the proportion of habitat suitable for Kentish Plover in each region we classified each grid point into one of five habitat suitability categories (very highly unsuitable; highly unsuitable; moderately suitable; highly suitable; very highly suitable) based on its predicted probability of Kentish Plover presence (*pr*) from our weighted ensemble prediction. We categorized areas using criteria similar to those previously utilized in multiple studies, excluding grid points flagged as seawater by NDVI, where $0 \leq pr < 0.2$ is very highly unsuitable; $0.2 \leq pr < 0.4$ is highly unsuitable; $0.4 \leq pr < 0.6$ is moderately suitable; $0.6 \leq pr < 0.8$ is highly suitable; and $0.8 \leq pr \leq 1$ is very highly suitable (Convertino *et al.* 2014, Ma & Sun 2018, Zhang *et al.* 2019).

Population estimates

Western Kazakhstan

We first estimated the possible range of adult population sizes of Kentish Plover in the region with the most comprehensive sampling, Western Kazakhstan. To do so we calculated the mean density of adult individuals observed across all sampled grid cells within the Western Kazakhstan polygon with a habitat suitability (*pr*) threshold from our ensemble predictions of ≥ 0.8 (i.e. lower threshold of the 'very highly suitable' category; *n* grid cells sampled = 56). We chose this threshold of very highly suitable as it provides a reasonable yet conservative threshold above which Kentish Plover presence is highly likely (see Convertino *et al.* 2014, Ma & Sun 2018, Zhang *et al.* 2019 for similar categorizations). Mean density calculations excluded repeat visits to localities to avoid inflating counts due to repeated observations of the same individuals. We then estimated population size by extrapolating mean densities across all grid cells in

Western Kazakhstan for the respective habitat suitability (*pr*) threshold, excluding cells flagged as open water by NDVI. To ensure reliability we recalculated population size 10 000 times using non-parametric bootstrap resampling of grid cells to provide 95% percentile bootstrap confidence intervals around population sizes based on random samples of our observed data. For completeness and to provide estimates of population size uncertainty based on threshold choice we calculated predicted population sizes for a broader range of thresholds, i.e. $pr = 0.1$–0.95, where mean densities were recalculated for each respective threshold.

National level

To provide a range of national breeding population sizes, we repeated our regional modelling procedure at a 1-km resolution at the level of the nation. National-level modelling included all eight individual model procedures as described above and all individual model predictions were aggregated to produce a robust weighted ensemble prediction as described above. Beyond the larger scale and coarser resolution, the main differences compared with our fine-scale 300-m analysis were as follows: (1) the vegetation density predictor was calculated from 1-km resolution NDVI raster; (2) coarser resolution enabled an increase of the buffer used during predictor calculation to 100 km; (3) the number of presence points within the training dataset (Western Kazakhstan) was 41; and (4) predictions were made for all Kazakhstan (the Eastern Caspian Sea and Aral Sea regions were again used for evaluation, similarly to the 300-m resolution model). To calculate mean densities for the 1-km grid, we again summed point counts within grid cells with a predicted ensemble habitat suitability (*pr*) of ≥ 0.8, this time using all sampled cells across the country (n grid cells = 55). We then scaled these counts upwards from their intended 300-m grid resolution to a 1-km grid resolution (i.e. by a factor of 11.11) to avoid underestimation of abundances. We estimated population size by extrapolating mean densities across all grid cells in Kazakhstan for each respective habitat suitability (*pr*) threshold, excluding grid points flagged as seawater by NDVI (n = 87 324 of 2 969 052) and used the same non-parametric bootstrap approach as described above to estimate errors around our population size estimates. For completeness, we again provide estimates of population sizes based on a broader range of thresholds, i.e. $pr = 0.1$–0.95, where mean densities were recalculated for each respective threshold.

RESULTS

Survey distributions

Kentish Plovers were commonly observed throughout our detailed sampling of Western Kazakhstan (Fig. 1, Supporting Information Fig. S3). At the national level, Kentish Plovers were widely distributed; however, individual counts were generally low (Table 2, Figs 1 and 2). Kentish Plovers (including all adults, juveniles and chicks) were observed at 169 of the 501 sampled points with a mean (± se) of 1.112 ± 0.105 individuals and a median of 0 (interquartile range IQR: 0–1) individuals per point. Focusing only on adult Kentish Plovers across the 501 sampled points yielded a mean (± se) of 1.060 ± 0.102 individuals and a median of 0 (IQR: 0–1) individuals per point. Controlling for sampling effort (number of counts per day), breeding records of Kentish Plover were evenly distributed throughout the survey period, with the earliest record on 8 May and the latest on 20 June (n = 38 sampling days, Julian date: likelihood ratio test, $\chi^2_1 = 1.420$, $P = 0.233$; Julian date^2, $\chi^2_1 = 0.555$, $P = 0.456$; number points per day: $\chi^2_1 = 4.552$, $P = 0.033$; Fig. 2).

Regional species distribution modelling

Our MaxEnt model provided fair model accuracy (Swets 1988) with an evaluated AUC of 0.771 (Suppporting Information Fig. S4). The three environmental predictor variables contributing the highest regularized gain when used in isolation in our MaxEnt model were distance to the nearest temporary water body (TWB Dist), distance to the nearest permanent water body (PWB Dist) and mean temperature for May (Temperature), indicating that these variables provide the highest predictive power in isolation (Fig. 3). Removal of TWB Dist while retaining all other predictors also resulted in the largest loss in training gain, indicating that this variable provides the most information not captured by other variables (Fig. 3), whereas PWB Dist provided the second highest training gain when in isolation. The modest decrease in training gain when excluding only PWB Dist suggests similar information is captured

Table 2. Summary of vantage points surveyed for Kentish Plover over key regions and water bodies in Kazakhstan. Data include 428 sampling points, excluding repeated visits to individual sites (73 excluded visits).

Region	Number of points sampled	Number of days sampled	Total number of individuals	Mean (± se) number of individuals per point
Aral Sea	36	2	68	1.889 (0.523)
Eastern Caspian Sea	81	3	184	2.272 (0.378)
Central Kazakhstan	1	1	0	0 (–)
Lake Alakol	34	2	6	0.176 (0.109)
Lake Balkhash	37	4	13	0.351 (0.143)
Lake Sorbulaq	2	1	0	0 (0)
Tengiz-Korgalzgyn	22	2	7	0.318 (0.195)
Lake Zaysan	12	2	0	0 (0)
Western Kazakhstan	203	22	163	0.803 (0.152)

across combinations of other variables. Excluding Temperature provided a comparably larger reduction in training gain, indicating that Temperature contributes comparably more unique explanatory power. All other variables provided relatively lower increments in training gain (Fig. 3). Response curves of the individual environmental predictors which had the highest training gain showed a reduction in the probability of Kentish Plover presence with increasing distance from both temporary and permanent water bodies (Supporting Information Figs S5 and S6). The probability of Kentish Plover presence provided a concave relationship with May temperatures, indicating a higher probability of presence between 17 and 18 °C (Figs S5 and S6).

Of our additional seven regional species distribution models, the Random Forest models (RF 1000 and RF 500) provided the best discriminative power (AUC: 0.776 and 0.678, respectively; Fig. S4). Our ensemble prediction had an AUC of 0.753 (Fig. S4) and our ensemble prediction indicated that a low proportion of the available habitat represents at least highly suitable Kentish Plover habitat combined across all three regions (Fig. 4). The Aral Sea region comprised the largest proportion of highly and very highly suitable habitat [3.724% (3899.79 km^2)], followed by the Western Kazakhstan region [0.823% (2035.08 km^2)] and the Eastern Caspian Sea region [0.003% (1.44 km^2)].

Population estimates

The mean observed density of Kentish Plover adults across sampled grid cells in all three regions (Western Kazakhstan, Eastern Caspian Sea, Aral Sea) excluding repeat visits was 1.425 per 300-m^2 grid cell (15.855 individuals per km^2). Using the mean observed density of Kentish Plover adults in Western Kazakhstan across all grid cells with habitat suitability (*pr*) from our regional ensemble model of ≥ 0.8 yielded a predicted population size [Estimate (upper–lower 95% range of bootstrap estimates)] of 6633 (3886–10 318; see Fig. S8a for the full range of predictions across multiple habitat suitability thresholds). At the national level, our best performing models included the Gradient Boosting Machine models (GBM 5000 and GMB 2000, AUC = 0.813 and 0.792, respectively) and the Random Forest model (RF 1000, AUC = 0.793; Fig. S7). Our national-level weighted mean ensemble model had an AUC of 0.773; using a habitat suitability threshold of ≥ 0.8 provided an estimated breeding population size for Kazakhstan of 20 800 (12 145–32 386) adult individuals (Fig. S8b).

DISCUSSION

We assessed the density and distribution of Kentish Plover throughout Kazakhstan during the breeding season of 2019 and used species distribution modelling to outline the importance of key environmental predictors in determining Kentish Plover presence. Our species distribution modelling stresses the importance of proximity to water bodies and climate as predictors of Kentish Plover presence and a relatively weaker impact of indicators of human disturbance. Our results provide an important appraisal of the status and breeding distribution of Kentish Plover across a perceived breeding stronghold for the species in the face of ongoing changes in climate and land use.

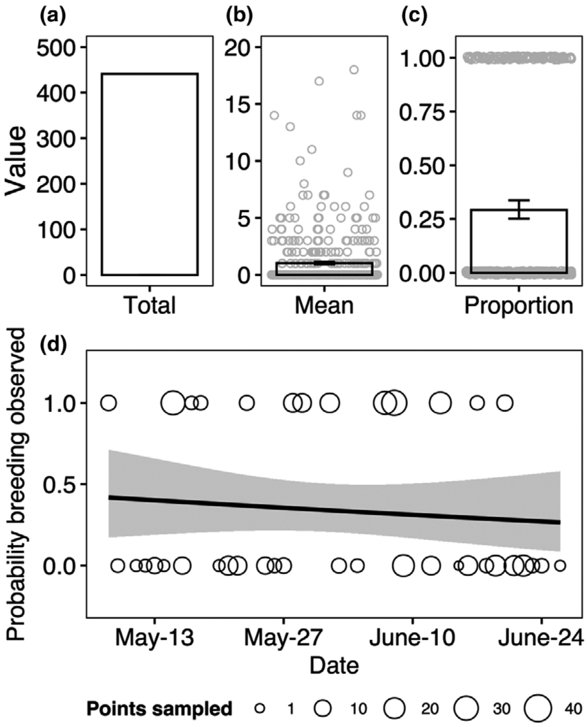

Figure 2. (a) Total counts, and (b) mean (± se) count per sampling point of individual Kentish Plovers over the full Kazakhstan survey. (c) The proportion of sampling points [± 95% confidence interval (CI)] in which individual Kentish Plover were observed over all survey points. Grey circles show data for individual vantage points. Data include 428 sampling points, excluding repeated visits to individual sites (73 excluded visits). (d) The relationship between the probability of observing evidence of actively breeding Kentish Plover across individual days over the entire survey period (8 May–26 June 2019). The size of circles indicates the number of sampling points sampled on each day.

Our results confirm previous indications that Kentish Plover is widespread across Kazakhstan (Martin *et al.* 2018) and considerably extends the results by capturing the distribution of Kentish Plover across Eastern Kazakhstan and poorly sampled regions, including the Aral Sea. Importantly, despite a widespread distribution, our results indicate markedly low densities of Kentish Plover. Previous reports in other regions indicate Kentish Plover breeding densities can vary widely, from three up to at least 1000 pairs per km^2 (Johnsgard 1981, Székely & Williams 1995, Székely *et al.* 1999, Pietrelli & Biondi 2012, BirdLife International 2020a). Our data suggest that breeding densities in Kazakhstan are typically at the lower range. The limited number of published assessments of Kentish Plover numbers across Kazakhstan restricts in-depth comparisons; however, limited historical accounts indicate that Kentish Plover densities may typically have been low (Gladkov 1951, Dolgushin 1962, Andrusenko & Dudenkov 1982). Although sampling effort and methodologies across studies probably vary, more recent localized surveys indicate appreciably higher numbers than reported in our study. For example, surveys of the Tengiz-Korgalzhyn region reported an average of 7.5 Kentish Plover individuals per point count in the months of June and July between 1999 and 2008 (Schielzeth *et al.* 2010), whereas for a similar time of the year in the same region, we report an average count of less than one individual per point count. Similarly, a more recent survey of Western Kazakhstan in 2010 reported a total of 460 Kentish Plovers over 43 observation sites (Lachmann *et al.* 2010). However, that study was conducted later in the season, spanning the post-breeding period (July–August), compared with our study (May–June), restricting direct comparisons. The low Kentish Plover densities we observed in Kazakhstan are mirrored by similar patterns in neighbouring Russia. In European Russia, bordering Western Kazakhstan, Kentish Plovers breed in Astrakhan and Volgograd regions as well as along the Asian regions of the Russian–Kazakhstan border (Hagemeijer & Blair 1997, Kubelka *et al.* 2019). The population of Kentish Plover in European Russia before 2000 was estimated to comprise between 1000 and 10 000 breeding pairs (Hagemeijer & Blair 1997, Heath *et al.* 2000). However, after 2000, population estimates were drastically reduced to between 150 and 1300 breeding pairs (Mischenko 2004). Current estimates indicate the total population size to comprise only 900–1100 breeding pairs (Mischenko 2017). Given the potential reductions in Kentish Plover in neighbouring European Russia, our results highlight the requirement for further detailed sampling in Kazakhstan as a key focus of future research. In particular, our prediction of Kentish Plover distributions indicates that regardless of exceptional ecological change over recent decades, the Aral Sea region may support the highest proportion of highly suitable Kentish Plover habitat compared with the Eastern Caspian Sea and Western Kazakhstan, and should thus be a focus of future population appraisals. In addition, our national distribution analyses indicate previously unsurveyed areas with a potentially high density of suitable Kentish Plover habitat in

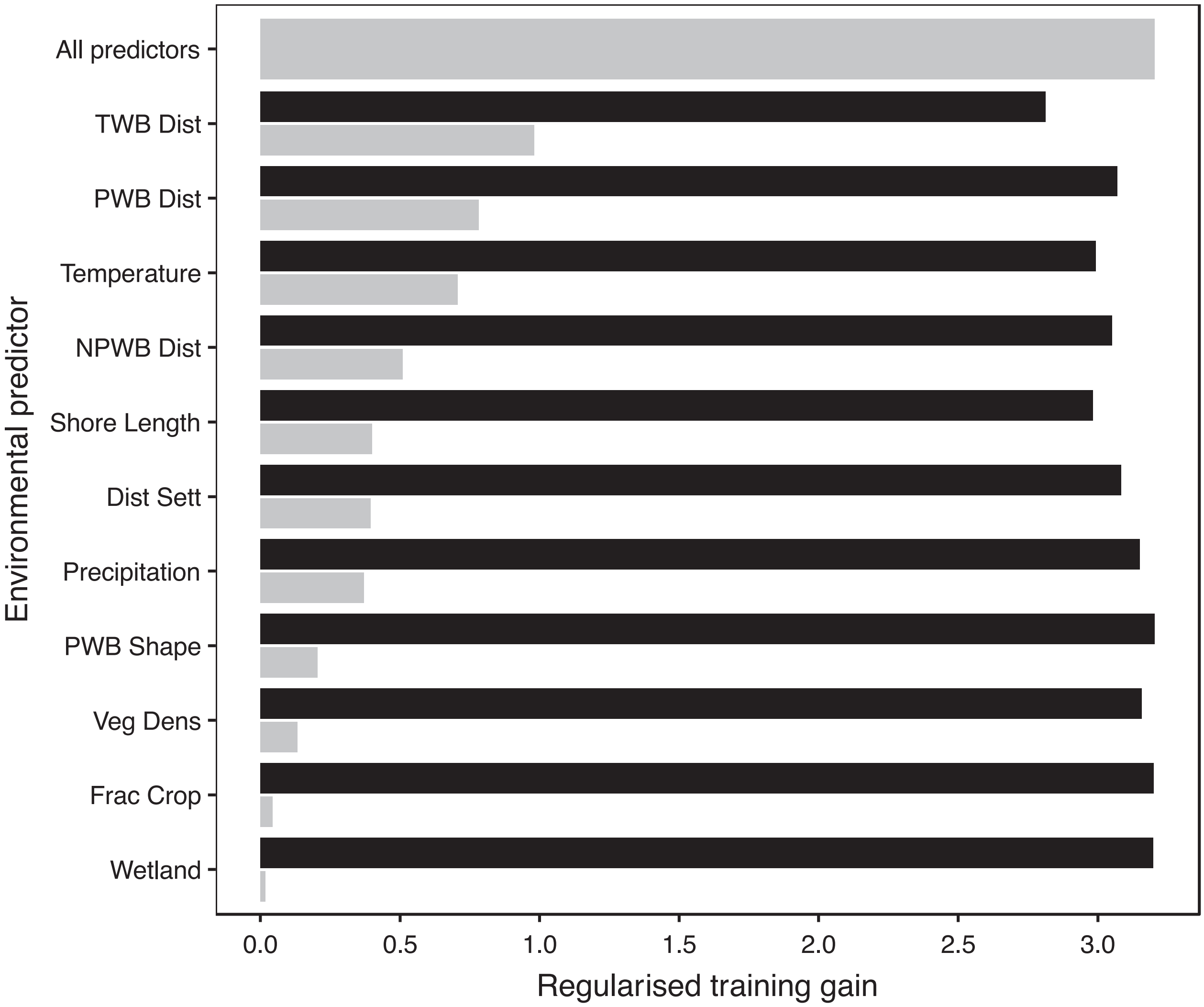

Figure 3. Jackknife regularized training gain for environmental predictors from regional MaxEnt species distribution modelling predicting Kentish Plover presence. Grey bars show training gain when only the indicated variable(s) are included and black bars show training gain when the indicated variable is excluded while controlling for all other predictors. Full names and details of predictors are provided in Table 1.

regions of the North and Northeast of the Aral Sea. We recommend that these previously unstudied regions should be targeted as a priority in future shorebird surveys and assessments of Kentish Plover populations.

Predictions from our species distribution model highlight the primary importance of temporary water bodies to the presence of Kentish Plover during the breeding season, as well as a secondary importance of coastal areas surrounding large permanent water bodies such as the Aral and Caspian Sea. The key role of proximity to transitory water bodies raises concerns in the context of the ongoing contraction of lake surface across Kazakhstan, particularly surrounding the Aral Sea and in Western Kazakhstan (Liu *et al.* 2019). Recent data suggest that the surface area of key water bodies in Western Kazakhstan has continued to decrease between 2001 and 2016, associated with climate warming and reduced precipitation (Bai *et al.* 2012, Klein *et al.* 2014, Liu *et al.* 2019). Crucially, due to their transient nature and smaller size, temporal water bodies may be at higher risk of severe size reduction and salinity increases as a result of climate warming and reduced precipitation. Such reductions may threaten suitable

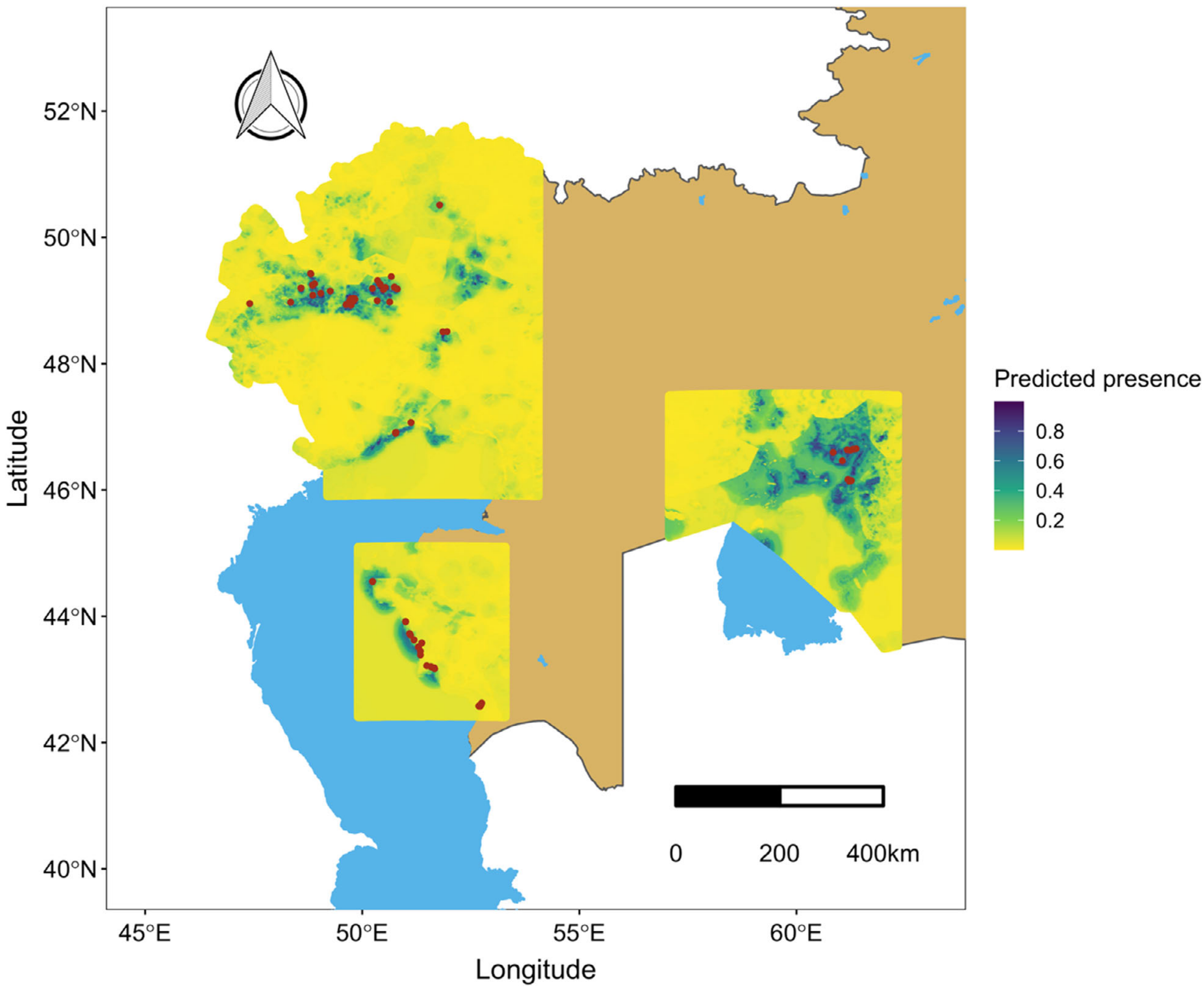

Figure 4. Localized map of Kazakhstan including the three study areas used in regional species distribution modelling. The largest lakes (area ≥ 50 km^2) and reservoirs (storage capacity ≥ 0.5 km^3) are shown in light blue. The distribution modelling regions are overlaid in coloured polygons, where the intensity of colour represents the probability of Kentish Plover presence from weighted mean ensemble model predictions. The largest NW polygon shows the Western Kazakhstan region used for model training and prediction, while the remaining two polygons show areas used only for prediction including Eastern Caspian Sea (SW smallest polygon) and Aral Sea (SE polygon). Red points show actual survey locations in which Kentish Plovers were observed. Observed absence points are not shown.

wading habitat and reduce foraging habitat quality for multiple shorebird species (Rubega & Robinson 1996, Kreuzberg-Mukhina 2006, Galbraith *et al.* 2014).

Importantly, patterns of environmental change are not homogeneous across Kazakhstan, and therefore predictions for distributional – or population density – changes of Kentish Plover at a national scale remain complex. For example, Eastern areas of Kazakhstan, and other more alpine lakes, have experienced opposing trends to the Southern Aral Sea and Western Kazakhstan, with a tendency for increased precipitation and reduced temperatures (Bai *et al.* 2012). In addition, more recent government-funded programmes to rehabilitate the Aral Sea have seen an increase in the surface area of Kazakhstan's North Aral sea in recent years (Micklin 2016). However, such increases in water levels may also negatively impact Kentish Plover habitats. For example, if the increased water volume of lakes is associated with sharp decreases in salinity, increases in vegetation density around shorelines or a reduction in the extent of shallow foraging grounds, then this can reduce the availability of foraging and nesting habitats. Such effects may be similar to the sea level rise-driven reduction in the extent of habitat suitable to the closely related Snowy Plover *Charadrius nivosus* in coastal regions of the USA (Aiello-Lammens *et al.* 2011).

In contrast to our expectations, we found no evidence for a strong negative impact of proximity to human settlements on potential Kentish Plover distributions. This result suggests a contrast to research indicating that human disturbance can pose significant negative localized impacts on shorebird abundances, including Kentish Plovers (Martín *et al.* 2015, Colwell & Haig 2019). However, previous research has also indicated that the scale of such localized impacts (i.e. human intrusion and disturbance) during breeding seasons of other shorebirds may not be typically extensive enough to have population-level impacts (Pearce-Higgins *et al.* 2017). It may be that our measure of distance to human settlements does not accurately reflect land use practices with potentially negative consequences for shorebirds, e.g. recreation, development or local livestock densities. Instead, our individual predictor patterns suggest that closer proximity to human settlements was associated with a higher probability of Kentish Plover presence, a pattern recently identified in Sociable Lapwings (Kamp *et al.* 2009b). This may indicate that human settlements in our data are associated with a third latent variable not measured in the current study. Similarly, the fraction of grid cells designated as cropland provided little predictive power to our models, suggesting a low impact of agricultural practice on Kentish Plover distributions. This may be driven in part by the redundancy of the fraction of cropland measure compared with our estimates of vegetation density, as Kentish Plover prefer to nest in open areas with little vegetation (Kosztolányi *et al.* 2009).

We provide the first estimated range of breeding population sizes of Kentish Plover in Kazakhstan based on quantitative data (Sheldon 2017, Wetlands International 2018). We estimated population sizes for Western Kazakhstan of approximately 3886–10 318 adult individuals for a habitat suitability threshold of 0.8. At the national level, our estimated breeding population size ranged from 12 145 to 32 386 adult individuals. Although the AUC values of our models used to predict habitat suitability are within the range of values from species distribution models used to estimate population sizes in other species (Herrera *et al.* 2018), the relatively low AUC values may result in additional variation around our estimates, which could in principle result in under- or over-estimation of abundances (Lobo *et al.* 2008). Nevertheless, despite a large difference in area between the Western Kazakhstan region and the entire nation, the relatively small difference in the national and regional population size estimates indicates that the overall suitable habitat and the sampled abundance of Kentish Plover across the rest of Kazakhstan as a whole were both generally low. An important consideration when sampling breeding shorebird species is whether such low counts, as observed in this study, may be impacted by the low detectability of incubating adult individuals. Kentish Plover parents biparentally incubate their clutch, then care for their chicks either biparentally or uniparentally, leading them to feeding habitats typically near water edges (Kosztolányi *et al.* 2006, Székely *et al.* 2006). Thus, although the subset of incubating parents may be more difficult to detect, for every incubating parent a non-incubating partner is readily observable, and thus the presence of Kentish Plovers across sites in our study is unlikely to be underestimated as a result of a large number of unobserved incubating parents. Moreover, our identification of breeding behaviour included nesting birds, suggesting our methodology was able to identify incubating individuals in at least a subset of cases. Regardless, the possible underestimation by overlooking incubating birds can be approximated by assuming that every single non-incubating adult bird counted had a currently incubating unobserved partner. Although this is unlikely given that our counts included both courting pairs and parents caring for young, this potential underestimation of a factor of two would not qualitatively change our interpretation of a wide distribution but low density of Kentish Plover. Moreover, given the most recent estimates of the Kentish Plover global population range by four orders of magnitude (Callaghan *et al.* 2021) and previous estimates range by a factor of five (BirdLife International 2020a), where estimates are based on extrapolation of European population estimates at the global scale (BirdLife International 2016b), our population estimates provided here represent a qualitative improvement.

Nevertheless, we suggest that our estimates may instead represent an upper bound to the total number of Kentish Plover for two reasons: first, our sampling methodology probably over-represents high-density locations because we focused sampling on locations where occurrence of Kentish Plover was likely and, secondly, the abundance of Kentish Plover is unlikely to be uniform across even highly suitable habitat locations, given the species' tendency for spatially aggregated breeding (Stenzel & Page 2019). Our estimates should therefore be treated with caution. Despite this, our estimates represent the most detailed objective population estimates available for Kazakhstan, and stress the need for more sampling of breeding shorebird populations within the region.

Large-scale habitat suitability studies of shorebirds remain rare (Long *et al.* 2008). Our work here provides a pathway for future studies assessing the distribution of shorebirds across similarly large and isolated regions. For example, similar approaches may be utilized effectively to estimate Kentish Plover population sizes in regions neighbouring Kazakhstan. Such areas include both Russia and Central Asian countries such as Uzbekistan, which also contains regions of the Aral Sea that have undergone the most consistent size reductions in recent decades (Yang *et al.* 2020). Our work highlights several key aspects that can be further improved in such future studies. First, future studies may benefit from a greater depth of sampling both within areas of expected high habitat suitability but also habitats of expected low suitability, which may further improve parametrization of predictor variables. For example, while our analytical approach allowed us to disentangle distances from both permanent and temporary water bodies, studies that do not employ such a distinction may particularly benefit from targeted sampling across a diversity of distances from water bodies to determine more accurately the relationship between proximity to key water bodies and the presence of shorebird species.

Secondly, while our sampling resulted in a relatively low number of presence points, limiting our ability to model Kentish Plover densities, future studies with a greater number of positive counts may more effectively employ hierarchical modelling approaches (e.g. hurdle models) to predict species presence and subsequently estimate the density of individuals where they occur (Oppel *et al.* 2012, Herrera *et al.* 2018). Regardless, in cases similar to the current study where presence points are typically low, the threshold approach used here may provide a pragmatic approach to indicate a range of potential population estimates when direct modelling of densities is restricted.

Finally, future work should seek to capture a broader range of environmental predictors to assess more comprehensively the potential distribution of Kentish Plover. For example, while our study did not include information on the salinity of water bodies or the distribution of predation pressure, future studies should seek to assess how spatial and temporal variation in such variables may impact on breeding distributions and correlate with predictors used in this study (e.g. does water salinity relate to vegetation density), likely to be feasible on much more localized scales.

CONCLUSIONS

In summary, our results reveal widespread distribution but markedly low densities of Kentish Plover across Kazakhstan. Our results fill a critical gap in knowledge in an understudied region of high conservation importance and identify the key routes through which ongoing environmental change may impact Kentish Plover populations. Extensive ground-truthing using hundreds of additional survey sites, and more detailed confirmed absence data, would seem essential for robust population estimates for vast areas such as Kazakhstan, but our methodological approach provides a platform for future studies to assess the distributions of species across vast and inaccessible regions.

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ETHICAL NOTE

Requisite permissions were granted by the Territorial Inspectorate for Forestry and Animals Kazakhstan, the Committee for Environmental Regulation and Control Kazakhstan, and the Natural Resources and Environmental Management of the West Kazakhstan Region via the Charter of the Republican State Institution Ural Anti-Plague Station GGSV RK No.20.

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AUTHOR CONTRIBUTIONS

Grant C. Mcdonald: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Visualization (lead); Writing – original draft (lead); Writing – review & editing (lead). **Ákos Bede-Fazekas:** Formal analysis (equal); Writing – review & editing (equal). **Anton Ivanov:** Investigation (equal); Writing – review & editing (equal). **Lorenzo Crecco:** Data curation (equal); Formal analysis (supporting). **Tamás Székely:** Conceptualization (equal); Writing – review & editing (equal). **András Kosztolányi:** Conceptualization (equal); Investigation (equal); Writing – review & editing (equal).

CONFLICT OF INTEREST

None.

Data Availability Statement

Data is available via Figshare (https://doi.org/10.6084/m9.figshare.19672017.v1).

REFERENCES

Aiello-Lammens, M.E., Chu-Agor, M.L., Convertino, M., Fischer, R.A., Linkov, I. & Akçakaya, H.R. 2011. The impact of sea-level rise on Snowy Plovers in Florida: integrating geomorphological, habitat, and metapopulation models. *Glob. Chang. Biol.* **17**: 3644–3654.

AlRashidi, M., Kosztolányi, A., Shobrak, M., Küpper, C. & Székely, T. 2011. Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence. *Anim. Behav.* **82**: 235–243.

Amano, T., Székely, T., Wauchope, H.S., Sandel, B., Nagy, S., Mundkur, T., Langendoen, T., Blanco, D., Michel, N.L. & Sutherland, W.J. 2020. Responses of global waterbird populations to climate change vary with latitude. *Nat. Clim. Change* **10**: 959–964.

Andrusenko, N.N. & Dudenkov, N.A. 1982. Faunistic notes on waders of the Tengiz Lake. *Ornithology* **17**: 155. (In Russian).

Araújo, M.B. & New, M. 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**: 42–47.

Bai, J., Chen, X., Yang, L. & Fang, H. 2012. Monitoring variations of inland lakes in the arid region of Central Asia. *Front. Earth Sci.* **6**: 147–156.

Baldwin, R.A. 2009. Use of maximum entropy modeling in wildlife research. *Entropy* **11**: 854–866.

BirdLife International. 2016a. *Glareola nordmanni. The IUCN Red List of Threatened Species 2016*: e.T22694136A90086476. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22694136A90086476.en

BirdLife International. 2016b. *Charadrius alexandrinus. The IUCN Red List of Threatened Species 2016*: e.T22727487A86579835. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22727487A86579835.en

BirdLife International. 2018. Vanellus gregarius. *IUCN Red List of Threatened Species*.

BirdLife International. 2020. *Country profile: Kazakhstan*. Available from http://www.birdlife.org/datazone/country/kazakhstan (accessed 20 August 2020).

BirdLife International. 2020a. *Kentish Plover (Charadrius alexandrinus) – BirdLife species factsheet*.

Buchhorn, M., Smets, B., Bertels, L., Lesiv, M., Tsendbazar, N.-E., Herold, M. & Fritz, S. 2019. *Copernicus Global Land Service: Land Cover 100m: Collection 2: Epoch 2015: Globe (V2.0.2). ESA Living Planet Symposium 2019. (LPS2019)*. Milan: Zenodo. https://doi.org/10.5281/zenodo.3243509

Callaghan, C.T., Nakagawa, S. & Cornwell, W.K. 2021. Global abundance estimates for 9,700 bird species. *Proc. Natl Acad. Sci. USA* **118**: e2023170118.

Chen, J.L., Pekker, T., Wilson, C.R., Tapley, B.D., Kostianoy, A.G., Cretaux, J.-F. & Safarov, E.S. 2017. Long-term Caspian Sea level change. *Geophys. Res. Lett.* **44**: 6993–7001.

Colwell, M.A. & Haig, S.M. 2019. *The Population Ecology and Conservation of Charadrius plovers*, 1st edn. Boca Raton: CRC Press.

Convertino, M., Muñoz-Carpena, R., Chu-Agor, M.L., Kiker, G.A. & Linkov, I. 2014. Untangling drivers of species distributions: Global sensitivity and uncertainty analyses of MaxEnt. *Environ. Model. Softw.* **51**: 296–309.

Copernicus. 2020 *Normalized Difference Vegetation Index*. Downloaded from https://land.copernicus.eu/global/sites/cgls.vito.be/files/products/GIOGL1_PUM_NDVI300m-V1_I1.11.pdf (accessed 25 May 2020).

Cramp, S. & Simmons, K.E.L. 1983. *Handbook of the Birds of Europe, the Middle East, and North Africa: The Birds of the Western Palearctic*. New York: Oxford University Press.

Delany, S. & Scott, D. 2006. *Waterbird Population Estimates*, 4th edn. Wageningen: Wetlands International.

Dias, R.A., Blanco, D.E., Goijman, A.P. & Zaccagnini, M.E. 2014. Density, habitat use, and opportunities for conservation of shorebirds in rice fields in southeastern South America. *Condor* **116**: 384–393.

Dolgushin, I.A. 1962. *The Birds of Kazakhstan*, Vol **2**. Almaty: Institut Akademii Nauk Kazakhskoi SSR. [In Russian].

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**: 27–46.

Efron, B. & Stein, C. 1981. The jackknife estimate of variance. *Ann. Stat.* **9**: 586–596.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**: 129–151.

Elith, J. & Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **40**: 677–697.

Fick, S.E. & Hijmans, R.J. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**: 4302–4315.

Fraga, R.M. & Amat, J.A. 1996. Breeding biology of a Kentish Plover (*Charadrius alexandrinus*) population in an inland saline lake. *Ardeola* **43**: 69–85.

Galbraith, H., DesRochers, D.W., Brown, S. & Reed, J.M. 2014. Predicting vulnerabilities of North American shorebirds to climate change. *PLoS One* **9**: e108899.

Gavrilov, E.I. 1999. *Fauna and Distribution of the Birds of Kazakhstan*. Almaty (In Russian). Institute of Zoology.

Gavrilov, E.I., Erokhov, S.N. & Gavrilov, A.E. 1998. Between-year recapture rates of waders ringed on migration in south-eastern Kazakhstan: constancy in timing and location of flyway routes. *Int. Wader Stud.* **10**: 414–416.

Gaybullaev, B., Chen, S.-C. & Gaybullaev, D. 2012. Changes in water volume of the Aral Sea after 1960. *Appl. Water Sci.* **2**: 285–291.

Gladkov, N.A. 1951. *Waders. Birds of the Soviet Union*: **3**: 372. Moscow: Sovetskaya Nauka Press. [in Russian].

Gómez-Serrano, M.Á. 2020. Four-legged foes: dogs disturb nesting plovers more than people do on tourist beaches. *Ibis* **163**: 338–352.

Gómez-Serrano, M.Á. & López-López, P. 2017. Deceiving predators: linking distraction behavior with nest survival in a ground-nesting bird. *Behav. Ecol.* **28**: 260–269.

Gubin, B.M. 2015. *Birds of the Deserts of Kazakhstan – I*: 394. Almaty.

Guisan, A. & Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecol. Modell.* **135**: 147–186.

Hagemeijer, W.J.M. & Blair, M.J. 1997. *The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance*. London: T & A D Poyser.

Haig, S.M. 2019. Changing climates and challenges to *Charadrius* plover success throughout the annual cycle. In: Colwell, M.A. & Haig, S.M. (eds.) *The Population Ecology and Conservation of Charadrius plovers*: 245–276. Boca Raton: CRC Press.

Hanley, J.A. & McNeil, B.J. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* **143**: 29–36.

Heath, M.F., Borggreve, C., Peet, N. & Hagemeijer, W. 2000. *European Bird Populations: Estimates and Trends. BirdLife Conservation Series No. 10*. Cambridge: BirdLife International.

Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W. & Sykes, M.T. 2016. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Prog. Phys. Geogr.* **30**: 751–777.

Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* **29**: 773–785.

Herrera, J.P., Borgerson, C., Tongasoa, L., Andriamahazoarivosoa, P., Rasolofoniaina, B.J.R., Rakotondrafarasata, E.R., Randrianasolo, J.L.R.R., Johnson, S.E., Wright, P.C. & Golden, C.D. 2018. Estimating the population size of lemurs based on their mutualistic food trees. *J. Biogeogr.* **45**: 2546–2563.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. 2017. *dismo: Species Distribution Modeling. R package version 1.1-4*. Downloaded from CRAN.R-project.org/package=dismo

Hijmans, R.J. 2019. *raster: Geographic Data Analysis and Modeling. R package version 3.0-7.* Downloaded from https://CRAN.R-project.org/package=raster

HOTOSM. 2020. *HOTOSM. Kazakhstan Populated Places (OpenStreetMap Export)*. Downloaded from https://data.humdata.org/dataset/HOTOSM_kaz_populated_places (accessed 16 June 2020).

Johnsgard, P.A. 1981. *The Plovers, Sandpipers and Snipes of the World*. Lincoln: University of Nebraska Press.

Kaky, E., Nolan, V., Alatawi, A. & Gilbert, F. 2020. A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: a case study with Egyptian medicinal plants. *Ecol. Inform* **60**: 101150.

Kamp, J., Koshkin, M.A. & Sheldon, R.D. 2009a. Population size, breeding performance and habitat use of the Black-winged Pratincole *Glareola nordmanni*. *Bird Conserv. Int.* **19**: 149–163.

Kamp, J., Koshkin, M.A., Bragina, T.M., Katzner, T.E., Milner-Gulland, E.J., Schreiber, D., Sheldon, R., Shmalenko, A., Smelansky, I., Terraube, J. & Urazaliev, R. 2016. Persistent and novel threats to the biodiversity of Kazakhstan's steppes and semi-deserts. *Biodivers. Conserv.* **25**: 2521–2541.

Kamp, J., Sheldon, R.D., Koshkin, M.A., Donald, P.F. & Biedermann, R. 2009b. Post-Soviet steppe management causes pronounced synanthropy in the globally threatened Sociable Lapwing *Vanellus gregarius*. *Ibis* **151**: 452–463.

Klein, I., Dietz, A.J., Gessner, U., Galayeva, A., Myrzakhmetov, A. & Kuenzer, C. 2014. Evaluation of seasonal water body extents in Central Asia over the past 27 years derived from medium-resolution remote sensing data. *Int. J. Appl. Earth. Obs. Geoinf.* **26**: 335–349.

Kosztolányi, A., Javed, S., Küpper, C., Cuthill, I.C., Shamsi, A.A. & Székely, T. 2009. Breeding ecology of Kentish Plover *Charadrius alexandrinus* in an extremely hot environment. *Bird Study* **56**: 244–252.

Kosztolányi, A., Székely, T., Cuthill, I.C., Yilmaz, K.T. & Berberoglu, S. 2006. Ecological constraints on breeding system evolution: the influence of habitat on brood desertion in Kentish Plover. *J. Anim. Ecol.* **75**: 257–265.

Kreuzberg-Mukhina, E.A. 2006. The Aral Sea basin: changes in migratory and breeding waterbird populations due to major human-induced changes to the region's hydrology. In: Boere, G.C., Galbraith, C.A. & Stroud, D.A. (eds.) *Waterbirds around the World*: 283–284. Edinburgh: The Stationery Office.

Kubelka, V., Mlíkovský, J., Zavadilová, V., Frencl, M., Ivanov, A., Litvinov, K. & Šálek, M. 2019. Pilot study on nest predation in shorebirds breeding at the Caspian steppe lakes. *Wader Study* **126**: 142–150.

Kubelka, V., Šálek, M., Tomkovich, P., Végvári, Z., Freckleton, R.P. & Székely, T. 2018. Global pattern of nest predation is disrupted by climate change in shorebirds. *Science* **362**: 680–683.

Lachmann, L., Köhler, P. & Urazaliyev, R. 2010. *Report on ornithological data gathered during a Slender-billed Curlew search expedition in western Kazakhstan, July–August 2010*. Unpublished Report to RSPB and CIM.

Lehner, B. & Döll, B. 2004. Development and validation of a global database of lakes, reservoirs and wetlands. *J. Hydrol.* **296**: 1–22.

Lessells, C.M. 1984. The mating system of Kentish Plovers *Charadrius alexandrinus*. *Ibis* **126**: 474–483.

Liu, H., Chen, Y., Ye, Z., Li, Y. & Zhang, Q. 2019. Recent lake area changes in Central Asia. *Sci. Rep.* **9**: 16277.

Lobo, J.M., Jiménez-Valverde, A. & Real, R. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* **17**: 145–151.

Long, P.R., Zefania, S., Ffrench-Constant, R.H. & Székely, T. 2008. Estimating the population size of an endangered shorebird, the Madagascar Plover, using a habitat suitability model. *Anim. Conserv.* **11**: 118–127.

Lorenzo, J.A. & Emmerson, K.W. 1995. Recent information on the distribution and status of the breeding population of Kentish Plover *Charadrius alexandrinus* in the Canary Islands. *Wader Stud. Group Bull.* **76**: 43–46.

Ma, B. & Sun, J. 2018. Predicting the distribution of *Stipa purpurea* across the Tibetan Plateau via the MaxEnt model. *BMC Ecol.* **18**: 10.

Martín, B., Delgado, S., de la Cruz, A., Tirado, S. & Ferrer, M. 2015. Effects of human presence on the long-term trends of migrant and resident shorebirds: evidence of local population declines. *Anim. Conserv.* **18**: 73–81.

Martin, T.E., Dubos, J., Riviere, T., Loubon, M., Fleureau, J., Martineau, A., Guillemin, M. & Nivet-Mazerolles, M. 2018. Bird records from arid and semi-arid areas in southern Kazakhstan, 2009–2017. *Sandgrouse* **40**: 53–74.

McDonald, G.C., Engel, N., Ratão, S.S., Székely, T. & Kosztolányi, A. 2020. The impact of social structure on breeding strategies in an island bird. *Sci. Rep.* **10**. http://dx.doi.org/10.1038/s41598-020-70595-w

Micklin, P. 2007. The Aral Sea disaster. *Annu Rev. Earth Planet Sci.* **35**: 47–72.

Micklin, P. 2016. The future Aral Sea: hope and despair. *Environ. Earth Sci.* **9**: 1–15.

Mischenko, A.L. 2004. *Estimation of Numbers and Trends for biRds of the European Russia ('Birds of Europe II')*. Moscow: Russian Bird Conservation Union. (In Russian).

Mischenko, A.L. 2017. *Estimation of Numbers and Trends for biRds of the European Russia ('European Red List of Birds')*. Moscow: Russian Society for Bird Conservation and Study (BirdsRussia) (In Russian).

Montalvo, T. & Figuerola, J. 2006. The distribution and conservation of the Kentish Plover *Charadrius alexandrinus* in Catalonia. *Catalan J. Ornithol.* **22**: 1–8.

Moreno, R., Zamora, R., Molina, J.R., Vasquez, A. & Herrera, M.Á. 2011. Predictive modeling of microhabitats for endemic birds in South Chilean temperate forests using Maximum entropy (Maxent). *Ecol. Inform.* **6**: 364–370.

Morozov, V.V. 2000. Current status of the southern subspecies of the Whimbrel *Numenius phaeopus alboaxillaris* Lowe 1921 in Russia and Kazakhstan. *Wader Stud. Group Bull.* **92**: 30–37.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. 2014. Where is positional uncertainty a problem for species distribution modelling? *Ecography* **37**: 191–203.

Nasrollahzadeh, A. 2010. Caspian Sea and its ecological challenges. *Caspian J. Env. Sci.* **8**: 97–104.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A.F., Miller, P.I. & Louzao, M. 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biol. Conserv.* **156**: 94–104.

Pearce-Higgins, J.W., Brown, D.J., Douglas, D.J.T., Alves, J.A., Bellio, M., Bocher, P., Buchanan, G.M., Clay, R.P., Conklin, J., Crockford, N., Dann, P., Elts, J., Friis, C., Fuller, R.A., Gill, J.A., Gosbell, K., Johnson, J.A., Marquez-Ferrando, R., Masero, J.A., Melville, D.S., Millington, S., Minton, C., Mundkur, T., Nol, E., Pehlak, H., Piersma, T., Robin, F., Rogers, D.I., Ruthrauff, D.R., Senner, N.R., Shah, J.N., Sheldon, R.D., Soloviev, S.A., Tomkovich, P.S. & Verkuil, Y.I. 2017. A global threats overview for *Numeniini* populations: synthesising expert knowledge for a group of declining migratory birds. *Bird Conserv. Int.* **27**: 6–34.

Pearson, R.G. & Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **12**: 361–371.

Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* **34**: 102–117.

Pebesma, E. 2018. Simple features for R: Standardized support for spatial vector data. *R J* **10**: 439.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**: 231–259.

Phillips, S.J. & Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**: 161–175.

Phillips, S.J., Anderson, R.P., Dudik, M., Schapire, R.E. & Blair, M.E. 2017. Opening the black box: an open-source release of Maxent. *Ecography* **40**: 887–893.

Phillips, S.J., Dudík, M. & Schapire, R. 2020. *Maxent software for modeling species niches and distributions (Version 3.4.1)*. Downloaded from biodiversityinformatics.amnh.org/open_source/maxent (accessed 29 June 2020).

Pietrelli, L. & Biondi, M. 2012. Long term reproduction data of Kentish Plover *Charadrius alexandrinus* along a Mediterranean coast. *Wader Stud. Group Bull.* **119**: 114–119.

R Core Team 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rocha, A.D., Fonseca, D., Masero, J.A. & Ramos, J.A. 2016. Coastal saltpans are a good alternative breeding habitat for Kentish Plover *Charadrius alexandrinus* when umbrella species are present. *J. Avian Biol.* **47**: 824–833.

Rubega, M.A. & Robinson, J.A. 1996. Water salinization and shorebirds: emerging issues. *Int. Wader Stud.* **9**: 45–54.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**: 103–113.

Schielzeth, H., Eichhorn, G., Heinicke, T., Kamp, J., Koshkin, M.A., Koshkin, A.V. & Lachmann, L. 2008. Waterbird population estimates for a key staging site in Kazakhstan: a contribution to wetland conservation on the Central Asian flyway. *Bird Conserv. Int.* **18**: 71–86.

Schielzeth, H., Kamp, J., Eichhorn, G., Heinicke, T., Koshkin, M.A., Lachmann, L., Sheldon, R.D. & Koshkin, A.V. 2010. Wader, gull and tern population estimates for a key breeding and stopover site in Central Kazakhstan. *Bird Conserv. Int.* **20**: 186–199.

Schulz, R. & Stock, M. 1993. Kentish Plovers and tourists: competitors on sandy coasts? *Wader Stud. Group Bull.* **68**: 83–91.

Shabani, F., Kumar, L. & Ahmadi, M. 2016. A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent area. *Ecol. Evol.* **6**: 5973–5986.

Sheldon, R.D. 2017. *Estimates of breeding waterbird populations in Central and South-west Asia, The Caucasus and the Arabian Peninsula*. Wageningen: Wetlands International.

Simmons, K.E.L. 1951. Distraction-display in the Kentish Plover. *Br. Birds* **44**: 181–187.

Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. 2005. ROCR: visualizing classifier performance in R. *Bioinformatics* **21**: 7881.

Sklyarenko, S., Welch, G. & Brombacher, M. 2008. *Important bird areas in Kazakhstan: priority sites for conservation*. Astana: Association for the Conservation of Biodiversity of Kazakhstan (ACBK).

Starodubtsev, V.M. & Truskavetskiy, S.R. 2011. Desertification processes in the Ili River delta under anthropogenic pressure. *Water Resour.* **38**: 253.

Stenzel, L.E. & Page, G.W. 2019. Breeding biology of *Charadrius* plovers. In: Colwell, M.A. & Haig, S.M. (eds.) *The Population Ecology and Conservation of Charadrius plovers*: 91–125. Boca Raton: CRC Press.

Suárez-Seoane, S., García de la Morena, E.L., Morales Prieto, M.B., Osborne, P.E. & de Juana, E. 2008. Maximum entropy niche-based modelling of seasonal changes in Little Bustard (*Tetrax tetrax*) distribution. *Ecol. Modell.* **219**: 17–29.

Sutherland, W.J., Alves, J.A., Amano, T., Chang, C.H., Davidson, N.C., Finlayson, C.M., Gill, J.A., Gill, R.E., González, P.M., Gunnarsson, T.G., Kleijn, D., Spray, C.J., Székely, T. & Thompson, D.B.A. 2012. A horizon scanning assessment of current and potential future threats to migratory shorebirds. *Ibis* **154**: 663–679.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. *Science* **240**: 1285–1293.

Székely, T. 2019. Why study plovers? The significance of non-model organisms in avian ecology, behaviour and evolution. *J. Ornithol.* **160**: 923–933.

Székely, T., Cuthill, I.C. & Kis, J. 1999. Brood desertion in Kentish Plover: sex differences in remating opportunities. *Behav. Ecol.* **10**: 185–190.

Székely, T., Thomas, G.H. & Cuthill, I.C. 2006. Sexual conflict, ecology, and breeding systems in shorebirds. *Bioscience* **56**: 801–808.

Székely, T. & Williams, T.D. 1995. Costs and benefits of brood desertion in female Kentish Plovers, *Charadrius alexandrinus*. *Behav. Ecol. Sociobiol.* **37**: 155–161.

Tinoco, B.A., Astudillo, P.X., Latta, S.C. & Graham, C.H. 2009. Distribution, ecology and conservation of an endangered Andean hummingbird: the Violet-throated Metaltail (*Metallura baroni*). *Bird Conserv. Int.* **19**: 63–76.

Venter, O., Fuller, R.A., Segan, D.B., Carwardine, J., Brooks, T., Butchart, S.H.M., Di Marco, M., Iwamura, T., Joseph, L., O'Grady, D., Possingham, H.P., Rondinini, C., Smith, R.J., Venter, M. & Watson, J.E.M. 2014. Targeting global protected area expansion for imperiled biodiversity. *PLoS Biol.* **12**: e1001891.

Watson, M., Wilson, J.M., Koshkin, M., Sherbakov, B., Karpov, F., Gavrilov, A., Schielzeth, H., Brombacher, M., Collar, N.J. & Cresswell, W. 2006. Nest survival and productivity of the critically endangered Sociable Lapwing *Vanellus gregarius*. *Ibis* **148**: 489–502.

Wei, T. & Simko, V. 2017. *R package "corrplot": Visualization of a Correlation Matrix (Version 0.84)*. Downloaded from github.com/taiyun/corrplot

Wetlands International. 2018. *Report on the Conservation Status of Migratory Waterbirds in the AEWA Agreement Area*. 7th ed. Agreement On The Conservation Of African-Eurasian Migratory Waterbirds (AEWA). Downloaded from https://www.unepaewa.org/sites/default/files/document/aewa_mop7_14_CSR7_with_annexes_en_corr1_0.pdf

Willis, K.J., Seddon, A.W.R., Long, P.R., Jeffers, E.S., Caithness, N., Thurston, M., Smit, M.G.D., Hagemann, R. & Macias-Fauria, M. 2015. Remote assessment of locally important ecological features across landscapes: how representative of reality? *Ecol. Appl.* **25**: 1290–1302.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. & Guisan, A. 2008. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **14**: 763–773.

Yang, X., Wang, N., Chen, A., He, J., Hua, T. & Qie, Y. 2020. Changes in area and water volume of the Aral Sea in the arid Central Asia over the period of 1960–2018 and their causes. *Catena* **191**: 104566.

Yerokhov, S.N. 2006. Past and current status of *Antidae* populations in Kazakhstan. In: Boere, G.C., Galbraith, C.A. & Stroud, D.A. (eds.) *Waterbirds around the World*: 269–274. Edinburgh: The Stationery Office.

Yost, A.C., Petersen, S.L., Gregg, M. & Miller, R. 2008. Predictive modeling and mapping Sage Grouse (*Centrocercus urophasianus*) nesting habitat using Maximum Entropy and a long-term dataset from Southern Oregon. *Ecol. Inform.* **3**: 375–386.

Young, B.E., Franke, I., Hernandez, P.A., Herzog, S.K., Paniagua, L., Tovar, C. & Valqui, T. 2009. Using spatial models to predict areas of endemism and gaps in the protection of Andean slope birds. *Auk* **126**: 554–565.

Zhang, J., Jiang, F., Li, G., Qin, W., Li, S., Gao, H., Cai, Z., Lin, G. & Zhang, T. 2019. Maxent modeling for predicting the spatial distribution of three raptors in the Sanjiangyuan National Park, China. *Ecol. Evol.* **9**: 6643–6654.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary material