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ORIGINAL ARTICLE

The potential distribution of the Red Kite in Germany

Christian Heuck · Roland Brandl · Jörg Albrecht · Thomas K. Gottschalk

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Abstract Central Europe has the responsibility to protect the Red Kite *Milvus milvus* as it holds the majority (>50 % of all breeding pairs) of the global population. This entails the need for comprehensive knowledge of the birds' ecology and distribution. Currently, only little is known about the factors limiting both the global occurrence of the Red Kite and its distribution on regional scales. In this study we analysed the effect of land use on the breeding distribution of Red Kites throughout Germany, the species' core distribution area, using a distribution model. For the first time, an extensive data set was used for modelling comprising a sample size of 2,625 Red Kite breeding sites, high-resolution land-use data (10 m × 10 m) and climatic as well as topographic variables. The model revealed a strong relationship between land-use patterns and the Red Kite's distribution. Furthermore, a comparison of the predicted habitat suitability map with the actual distribution of Red Kites showed that not all suitable habitats were occupied by the species and thus, the species' distribution seems not to be in equilibrium with its environment. The differences between actual and predicted distribution may stem from present or former high mortality rates which are not compensated for by current reproduction rates. Additionally, low juvenile dispersal of Red Kites reduces recolonisation of unoccupied patches.

Keywords Habitat-suitability map · Species distribution model · Spatial scale · Generalized linear model

Zusammenfassung

Die potentielle Brutverbreitung des Rotmilans *Milvus milvus* in Deutschland

Der Rotmilan besiedelt sein Verbreitungsgebiet mit sehr unterschiedlichen Dichten, wobei ein Großteil des Weltbestandes in Deutschland brütet (>50 % aller Brutpaare). Auch innerhalb Deutschlands kommt die Art sehr ungleichmäßig verteilt vor. Die Ursachen hierfür sind jedoch weitgehend unbekannt. Auf lokaler Ebene konnten mehrere Habitatanalysen zeigen, dass der Rotmilan eine reich strukturierte Landschaft mit Waldanteil und Offenflächen zur Nahrungssuche bevorzugt. Insgesamt scheinen also bestimmte Landnutzungstypen potentielle Brutplätze zu bestimmen. Mit einem logistischen Regressionsmodell haben wir untersucht, welche Landnutzungs-Muster einen geeigneten Brutplatz definieren und ob die Verteilung geeigneter Brutplätze für die ungleichmäßige Verteilung des Rotmilans in Deutschland verantwortlich sind. Das Modell basiert auf 2,625 Rotmilan-Horststandorten, einer hochauflösenden Landnutzungskarte sowie Klimadaten und einem digitalen Geländemodell. Die Horststandorte sind insbesondere durch hohe Grünlandanteile und eine hohe Landschaftsdiversität charakterisiert. Auf der Basis des Modells wurde eine Karte mit der potentiellen Verbreitung in Deutschland erstellt. Ein Vergleich mit der tatsächlichen Verbreitung des Rotmilans zeigt jedoch

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einige Abweichungen. Der Rotmilan besiedelt demnach nicht alle geeigneten Habitate. Als standorttreuer Vogel mit einer geringen Dismigration der Jungtiere könnte die Rekolonisation geeigneter Gebiete nach deren Räumung sehr langsam verlaufen. Wir nehmen daher an, dass dieser Prozess beim Rotmilan noch nicht abgeschlossen ist.

Introduction

Implementing effective conservation measures for a given species requires comprehensive knowledge of its ecology and the factors limiting its distribution (Rushton et al. 2004). While environmental conditions as temperature and water-availability usually control the large-scale distribution of biomes and associated species, we find additional mechanisms affecting distribution patterns on smaller spatial scales (Soberón 2007). For instance, on the landscape scale, factors such as topography and the occurrence of certain habitat types are important (Pearson and Dawson 2003). On the local scale, the abiotic environment and biotic interactions generally control the occurrence of species within their fundamental niche (Soberón 2007). Thus, allocation of individuals within a species' range is mainly influenced by the distribution of suitable habitat as well as the distribution of competitors, predators, and/or the dynamics of resources.

Considering closely related and allopatric species with contrasting distributional range sizes, these factors get especially interesting. For example, we have little understanding of the factors explaining the limited distribution of the Red Kite *Milvus milvus* (Carter 2007; Bezzel 2010). In contrast, its closely related sister species, the Black Kite *Milvus migrans* (Schreiber et al. 2000), has a large distribution range across temperate and tropical regions (see Hagemeijer and Blair 1997). The Red Kite is endemic to the Western Palearctic and occurs mainly in the temperate and the western Mediterranean zones of Europe (Cramp and Simmons 1980; Ortlieb 1989; Nicolai 1997; Aebischer 2009; Knott et al. 2009). Furthermore, the abundance of the Red Kite varies considerably across its breeding range with Central Europe (in particular Germany) holding more than 50 % of the global population (Knott et al. 2009; Aebischer 2009). Even within the core of the species' range, there is considerable variation in abundance (Aebischer 2009). Some federal states of Germany like Bavaria and Brandenburg harbour a considerably low population size, whereas states like Mecklenburg-West Pomerania and Saxony-Anhalt harbour many breeding pairs. This restricted and mosaic-like distribution of the Red Kite attracted considerable attention by ornithologists and biogeographers. For example, Seoane et al. (2003) suggested that the distributional range of the species is determined by climatic factors. Furthermore, competition with other raptors occurs (Ortlieb 1989) but seems to be unlikely to drive its distribution and abundance across Europe, as a higher magnitude of intraspecific than interspecific competition has been identified for the Red Kite (Gelpke and Stübing 2010; Dobler 1990). Moreover, it has been suggested that historical changes in land use enabled the Red Kite's post-glacial expansion to Central Europe (Ortlieb 1989; Schreiber et al. 2000; Walz 2005).

On local and regional scales, the species prefers well-structured landscapes with woodlands and high amounts of grassland (Brown 1978; Del Hoyo et al. 1994; Carter 2007; Aebischer 2009; Nachtigall et al. 2010; Bezzel 2010). In particular, grassland is needed for effective foraging (Hille 1995; Schmidt 2009) and therefore might increase breeding success (Gelpke and Stübing 2010). Such observations suggest that certain land-use types determine the potential breeding areas as well as abundance of the Red Kite. Changes in land use with ongoing land-use intensification are among the main factors for the decreasing abundance and diversity of many bird species (e.g., Siriwardena et al. 2000; Chamberlain and Fuller 2000; Mason and Macdonald 2006; Jetz et al. 2007; Tryjanowski et al. 2011). Such changes in land use might also decrease breeding success, abundance and distribution of the Red Kite (Mammen 2000; Bauer et al. 2005). Furthermore, raptor species are known to have suffered from hunting pressure and the use of organochlorine compounds (Ratcliff 1967; Gomara et al. 2008). However, several species have expanded their breeding ranges after the legal protection in the 1950s, and the reductions in the use of organochlorine pesticides from around 1970 (Lensink 1997; Hauff 1998). Whether a combination of specific land-use types or other factors are responsible for the Red Kite's restricted distribution and variation of abundance throughout its range remains an unexplored issue (Bezzel 2010). Knowledge of the key factors determining the Red Kite's distribution, especially within its core distribution, is essential for the species' global conservation and management. Therefore, we assessed the effect of land use on the spatial distribution of breeding Red Kites within Germany. We generated a high resolution species distribution model to account for potential small-scaled habitat relationships and to reach high model performance (Gottschalk et al. 2011). We used data on Red Kite breeding sites with climatic, topographic and land-use variables in order to explore the factors explaining the distribution and abundance of this raptor across Germany. Thus, the aims of this study were to examine (1) whether the distribution of breeding sites of the Red Kite is related to land-use patterns and (2) which land-use factors determine habitat suitability and to analyse (3) whether land-use patterns explain the Red Kite's distribution within the species' core distribution area. In order to evaluate our predictive model results, we compared the habitat suitability map with the actual German breeding bird atlas data of the Red Kite.

Materials and methods

Sources of Red Kite and land-use data

We gathered locations for Red Kite breeding sites across 11 German federal states for the period 2000–2010. Due to the manifold sources of data, all data points were checked for plausibility (e.g., nest sites located in forests). The final analysis contained 2,625 records (Fig. 1). The Red Kite breeding records (presence data) were complemented by an equal number of "pseudo-absence" locations (Engler et al. 2004). The distance between these pseudo-absence points and presence points was at least 1 km.

All land-use data were derived from a high-resolution land-use raster map (10 m × 10 m) for Germany. The map is based on the geometry and land-use information of ATKIS (Amtliches Topographisch-Kartographisches Informationssystem) and on information on the European Union integrated administrative and control system (IACS). Corine Land Cover 2006 (CLC) information was used for forest type classifications. We attached the information on land use, topographic and climate conditions to each breeding record of the Red Kite as well as to the "pseudo-absence" locations. All GIS work was conducted using ArcInfo GIS 10.0 (Environmental Science Research Institute Inc., Redlands, CA, USA).

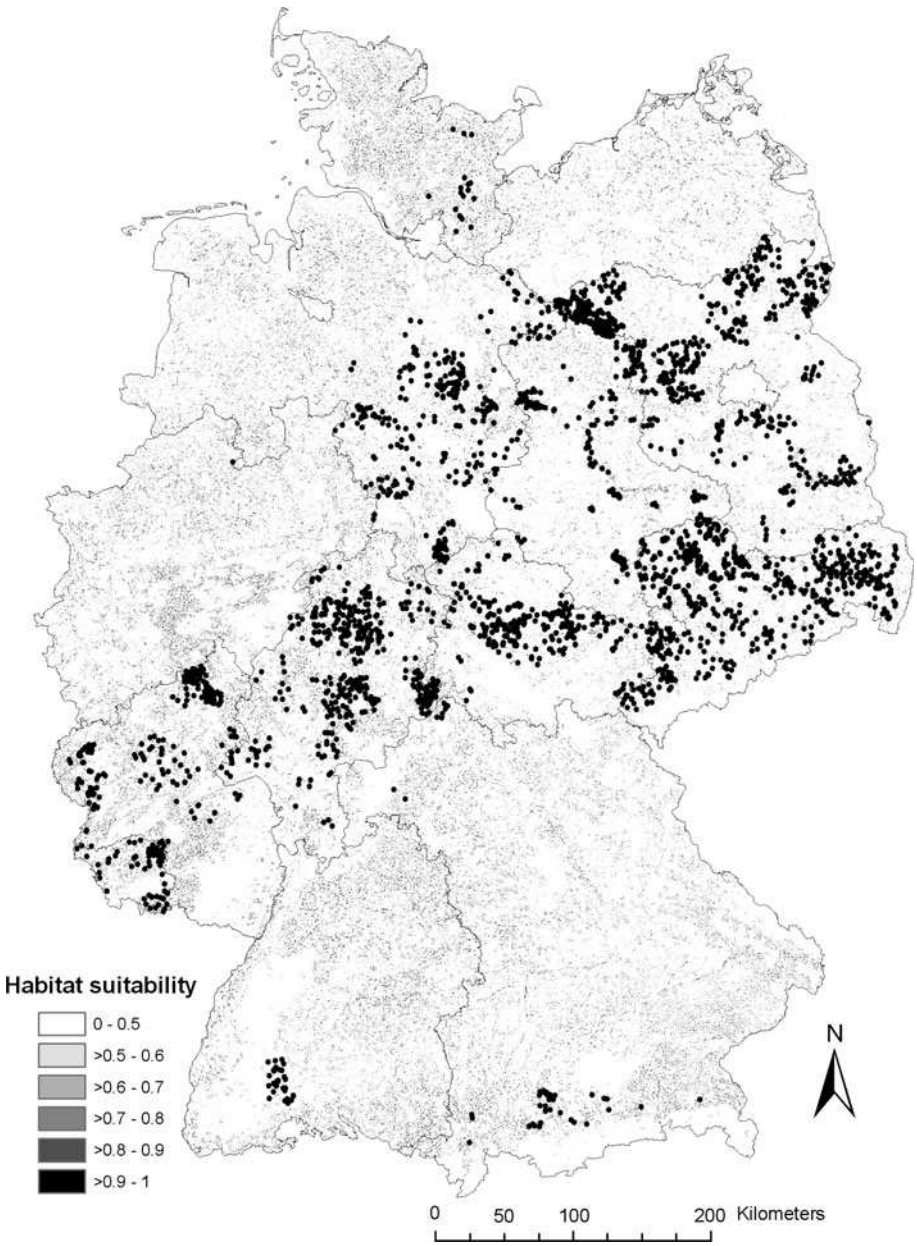

Fig. 1 Breeding habitat suitability map of the Red Kite. Values 0–0.5 show not suitable, 0.5—low and 1—high habitat suitability. Sample locations are indicated by *points* ($n = 2{,}625$)

Predictor variables

To model the characteristics of breeding sites we used local environmental variables at the breeding locations as well as characteristics within a buffer zone of the landscape matrix around breeding sites. Although the home-range size of the species differs within Germany (Porstendörfer 1994; Pfeiffer 1995; Newton et al. 1996; Norgall 2000; Walz 2005; Nachtigall et al. 2010) we used a radius of 1 km.

The original land-use map contained 31 land-use classes. For modelling the potential breeding habitats, we selected coniferous forest, deciduous forest, mixed forest, groves, hedges and single trees and merged all further land-use classes into "others" (Table 1). All variables of the surrounding landscape matrix were calculated using the Moving Window software SLICER (Gottschalk et al. 2008). Within the 1 km radius we calculated landscape diversity (Shannon-Index) and landscape fragmentation (Interspersion and Juxtaposition-Index; McGarigal and Marks 1995) as well as the percent cover of 12 land-use types known to be important for the habitat of the Red Kite (Brunken 2009; Nicolai and Mammen 2009) (Table 1). Additionally, we included the percent cover of all woody edge structures (proportion of forest edges, trees, hedges and groves). Further environmental variables examined for modelling were altitude (Vermessungsverwaltungen der Bundesländer und 2009), precipitation and temperature (Germany's Meteorological Service 2010).

Habitat suitability model

Differences in numeric land-use variables between breeding sites and "pseudo-absence" locations were calculated with the LAMA-Tool 1.5 for ArcGIS (Aue and Ekschmitt 2010) and tested using a Mann–Whitney *U* test available in R (R Development Core Team 2011). *P* values were adjusted by a sequential Bonferroni correction to account for multiple testing (Rice 1989). Finally, all continuous variables were checked for intercorrelations using the Spearman rank correlation. In the case of two correlated variables ($|r| > 0.7$) the performance of univariate analyses was used to remove one of the variables from the final set of predictor variables (Fielding and Haworth 1995).

A generalized linear model (GLM) was developed with binomial error distribution and logit link function. For selection of meaningful variables we used the corrected Akaike information criterion (backward AICc; Burnham and Anderson 2002); AIC differences (Δ_i) and Akaike weights (ω_i). We show results for the three models with the greatest support, based on Akaike weights. For all further calculations we used the model with highest Akaike weights.

A spatially unbalanced sample design may cause artificial regional clusters of species records (Dormann et al. 2007). Thus, we extended the model formula described above by a thin-plate regression spline - containing the spatial coordinates of the breeding sites and "pseudo-absence" points–to capture the spatial structure within the data (Dormann et al. 2007). Hence, we extended the initially described GLM containing only the environmental predictors ("environment") to a generalized additive model (GAM), containing the environmental predictors and a spatial smoothing term to model broad scale spatial trends in the data ("trend + environment"). We calculated the proportion of the variance explained by the environmental predictor variables and by the spatial trend surface using Nagelkerke's R^2 (Nagelkerke 1991). With this model formulation we decompose the total variability of Red Kite breeding sites into variation explained by the environment and variation caused by the spatial structure within the data (Hothorn et al. 2011). Once the model has been fitted, the model term including the environmental variables can be used to predict the habitat suitability of the Red Kite in Germany accounting for spatial autocorrelation. We are aware that variable selection with the AICc should rather be done after minimising the effects of spatial autocorrelation, but the high number of variables caused a rather unrealistic high computation time and forced us to use this approximate approach. To evaluate whether inclusion of the spatial trend successfully captured the spatial structure in the data we used Moran's *I* to evaluate the spatial pattern in the residuals from the "environment" and the "trend + environment" models (see electronic supplementary material for details).

To compare different model approaches we quantified each model's prediction accuracy with AUC values estimated by cross-validation (Fielding and Bell 1997). We applied random data splitting with a proportion of 80:20 and 100 random splits (Huberty 1994). AUC values usually range from 0.5 indicating a random distribution of presence and absence points to 1.0 indicating a perfect discrimination between presence and absence (Engler et al. 2004; Hernandez et al. 2006). All model calculations were performed with the statistic package R (R Development Core Team 2011). Package dismo version 0.7-17 (Hijmans et al. 2012) was used for calculation of AUC-values, package mgcv version 1.7-9 (Wood 2003) was used for calculation of GAMs. Based on the resulting regression equation the breeding habitat suitability for the Red Kite was calculated for each pixel of the map. According to the equal number of presence and absence points, we used a probability threshold of 0.5 (Liu et al. 2005) to calculate the final habitat suitability map.

To evaluate our model results, we compared the generated habitat suitability map with abundance data of the German breeding bird atlas (Gedeon et al. unpublished data). We used linear regression to test for relationships

Table 1 Comparison of the mean (with standard deviation SD) of environmental variables for actual breeding sites of the Red Kite and "pseudo-absence" locations. The latter are randomly selected points with a minimum distance of 1 km to the nearest breeding site. All variables differed significantly between breeding sites and "pseudo-absence" locations (Mann–Whitney U-test with Bonferroni-correction). In the last column we also give z-values of the continuous variables of the final GAM "trend + environment" model as a standardized measure of effect size with a null-expectation of zero (no effect), i.e., a larger deviation from zero indicates a larger effect of the respective variable

Environmental variable		Unit	Red Kite breeding sites		"Pseudo-absence" locations		Effect size
			Mean	SD	Mean	SD	
Local variables							
A	Deciduous forest	Yes/no	–	–	–	–	–
	Coniferous forest	Yes/no	–	–	–	–	–
	Mixed forest	Yes/no	–	–	–	–	–
	Groves	Yes/no	–	–	–	–	–
	Single trees, trees in line	Yes/no	–	–	–	–	–
	Hedges	Yes/no	–	–	–	–	–
	Others	Yes/no	–	–	–	–	–
B	Mean temperature spring	°C*10	118.05	11.59	120.23	7.95	Rejected
C	Altitude	m	259.81	237.07	206.71	171.71	−2.11*
Variables of the surrounding matrix within 1000 m radius							
D	Landscape diversity	None	1.75	0.47	1.87	0.34	2.73**
E	Landscape fragmentation	None	70.46	9.07	72.05	5.94	Rejected
F	Arable land	%	40.48	25.53	38.48	27.31	Rejected
G	Pasture/meadows-unclassified	%	5.45	5.07	4.38	4.34	1.05
H	Discontinuous urban fabric	%	4.31	5.69	7.75	12.04	−6.39***
I	Deciduous forests	%	7.56	14.49	5.36	13.01	−8.01***
J	Coniferous forests	%	7.92	14.84	13.36	22.46	−11.0***
K	Mixed forests	%	8.98	11.04	10.18	14.90	−9.29***
L	Meadow	%	6.81	10.42	7.02	10.66	4.68***
M	Mowing meadow	%	9.79	13.44	5.50	11.18	6.11***
N	Groves	%	1.07	2.05	1.24	2.80	Rejected
O	Single trees and tree lines	%	0.99	1.00	0.63	1.01	−4.28***
P	Hedges	%	0.15	0.74	0.46	1.76	1.18
Q	Forest edges and woods	%	6.99	3.98	6.97	3.93	Rejected

* $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$

between the abundances of each raster cell of the atlas map and the mean habitat suitability of the respective raster cell of the habitat suitability map. This analysis was performed separately for the German Federal states, to depict differences among the Federal states. We excluded Berlin, Bremen, Hamburg and Saarland from the data set as these Federal states were too small (number of ordinance maps) to allow for rigorous statistical inference.

Results

Breeding locations of the Red Kite differed significantly from the "pseudo-absence" locations with respect to all selected land-use variables (Table 1). Compared to the absence points, the Red Kite preferred single trees and trees in a line as well as deciduous forest and mowing meadows (periodical change of mowing and pasturing) as well as meadows (frequent mowing) in the surrounding of the breeding sites. The birds avoided discontinuous urban fabric, coniferous forests and groves.

Habitat suitability model

The AUC-value of 0.96 of our model indicates outstanding discriminative power (Hosmer and Lemeshow 2000). This suggests an accurate discrimination rate between presence and absence. Five variables had almost no effect on the model performance, and were therefore rejected by the AICc (Table 2). The environmental variables explained 51 % of the variation in the Red Kite data (Fig. 2). Including the trend surface the model fit improved by 9 %. While

Table 2 Results of the three GLM models (only "environment") with the highest Akaike weights predicting the distribution of the Red Kite

Number	Model[a]	K[b]	AIC	Δ_i^c	ω_i^d
1	A, C, D, G, H, I, J, K, L, M, O, P	17	3551.60	0.00	0.44
2	A, B, C, D, G, H, I, J, K, L, M, O, P	18	3551.80	0.20	0.40
3	A, B, C, D, F, G, H, I, J, K, L, M, O, P	19	3552.64	1.04	0.26

[a] Abbreviations of model variables as given in Table 1

[b] Number of predictor variables

[c] AIC differences of the models in comparison to the best one

[d] Akaike weights

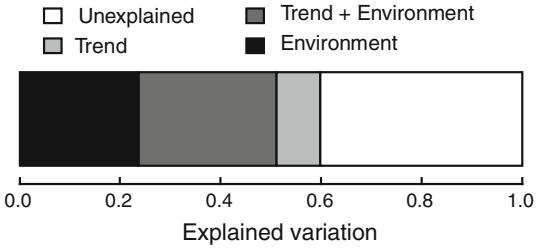

Fig. 2 Proportion of variation in Red Kite data in generalized additive models (GAM) explained by non-spatially structured environment (Environment), spatially structured environment (Trend + Environment), and trend (independent of environment). Spatial structure in the data was modelled by trend surface analysis using a thin-plate regression spline, and the explained variation was partitioned using partial regression analysis following Legendre (1993). The trend fraction is equal to the improvement in R^2 values from GAM trend + environment models over GAM environment models. The trend and trend + environment fractions combined are equal to the R^2 values from the trend surface models of Red kite distribution. The trend + environment and environment fractions combined are equal to the R^2 values from GAM environment models

27 % of the variation explained by the environmental variables was correlated with spatial structure, non-spatially structured environmental effects amounted to $R^2 = 0.24$. Examination of model residuals suggested that the trend surface successfully captured the spatial structure in the data (Fig. S1 in Electronic supplementary material).

The modelling results identified a set of specific variables suggesting suitable breeding habitats of the Red Kite. Increasing altitude and percent cover of forests (all types) as well as discontinuous urban fabric within a 1 km radius around the breeding sites had significant negative effects on the occurrence probability of Red Kites (Table 1). Landscape diversity, hedges and the percent cover of the three grassland classes were positive predictors. In particular, increasing percent cover of mowing meadows (periodical change of mowing and pasturing), meadows (frequent mowing) and landscape diversity had significant effects, whereas the effects of hedges and unclassified pastures and meadows were not significant.

Approximately 10 % of the total area was predicted to cover suitable breeding habitat for the Red Kite (Fig. 1). The distribution map showed rather constant habitat suitability across Germany. Mountain ranges, densely populated areas and interior forest areas were less or not suitable. The predicted habitat suitability was positively correlated with the abundance of breeding Red Kite extracted from the breeding bird atlas of seven (Brandenburg, Baden-Württemberg, Bavaria, Hesse, Lower Saxony, North Rhine-Westphalia, Rhineland-Palatinate and Schleswig-Holstein) out of twelve analysed federal states (Fig. 3).

Discussion

According to Hosmer and Lemeshow (2000) and Swets (1988) the predictive power of our habitat suitability model was "outstanding". However, using land-use information of the surrounding breeding location based on a fixed radius for modelling comes along with some difficulties. Both size and shape of the used area can only approximate the natural variability of a species' foraging area. Telemetry studies revealed varying shapes and sizes of the home ranges of Red Kite breeding pairs (Newton et al. 1996; Nachtigall 1999). Nevertheless, from a theoretical point of view the shape of the Red Kite's home ranges should approximate a circle, as it offers optimal energy efficiency for a central place forager.

Selection of predictor variables

Our model revealed that breeding sites of the Red Kite within its core breeding area can be predicted by the diversity of surrounding land-use types and the proportion of grasslands. The general importance of grasslands for effective foraging has been shown by several earlier studies (Walz 2005; Schmidt 2009; Nicolai and Mammen 2009; Brunken 2009; Gelpke and Stübing 2010; Hothorn et al. 2011). Small mammals, which represent the Red Kite's main food source, cannot build up high population densities within frequently ploughed fields (Aebischer 2009) and therefore grasslands are the most important foraging areas.

Also landscape diversity was identified as a positive predictor of suitable habitats for the Red Kite. Increasing diversity of land-use types on farmland comes along with increasing numbers of edges, smaller landscape elements (e.g. hedges, groves and trees) and crop types. Although the birds can hardly hunt directly on these structures, they offer habitats for rodents and other prey species which can be hunted on adjacent open areas (Weber 2002; Aebischer

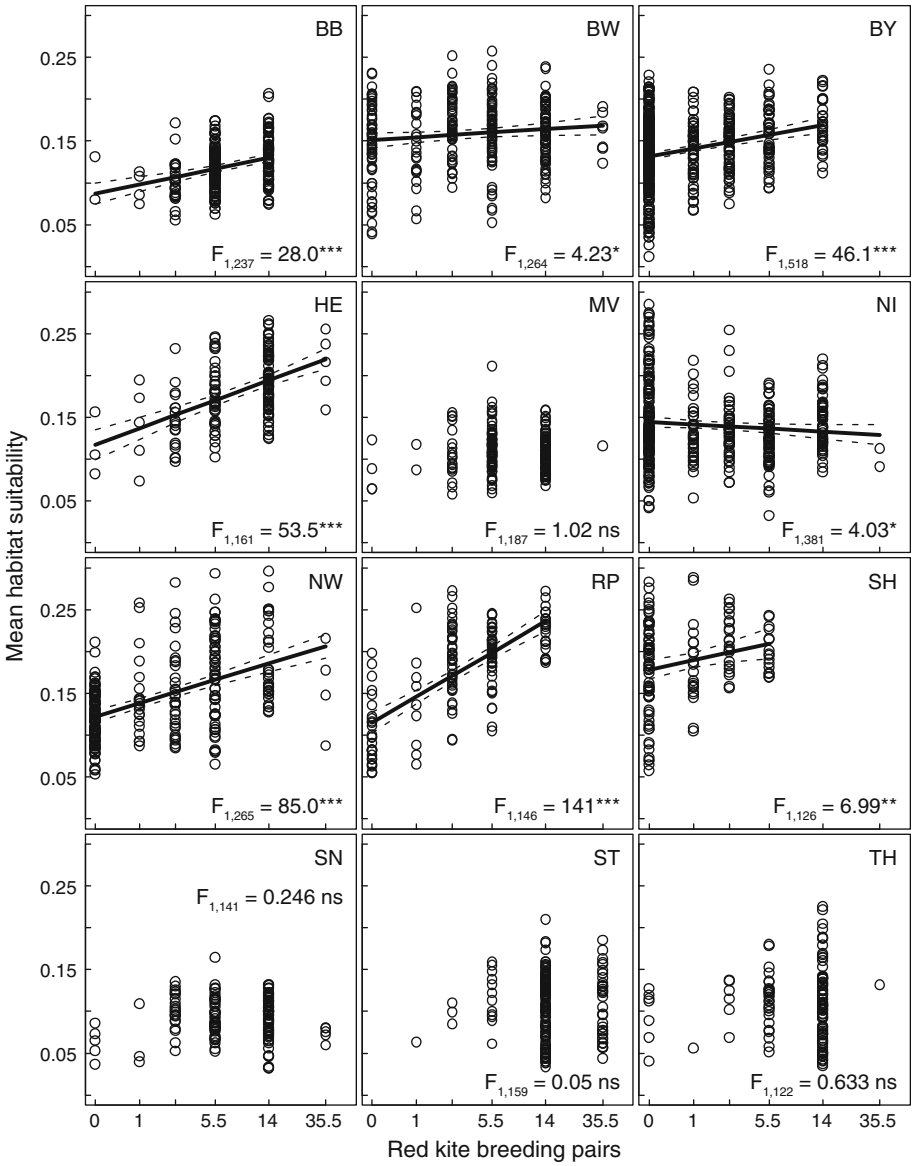

Fig. 3 Red Kite breeding pairs per ordinance map (DDA 2011) against mean habitat suitability for 12 of the 16 German federal states. Given are predictions from linear regression (*solid lines*) and 95 % confidence intervals of the regression. The federal states are depicted by the following labels: *BB* Brandenburg, *BW* Baden-Württemberg, *BY* Bavaria, *HE* Hesse, *MV* Mecklenburg-West Pomerania, *NI* Lower Saxony, *NW* North Rhine-Westphalia, *RP* Rhineland-Palatinate, *SH* Schleswig-Holstein, *SN* Saxony, *ST* Saxony-Anhalt, *TH* Thuringia. Note logarithmic scale for Red Kite breeding pairs

2009). Furthermore, a high number of different crop types increases the variability of vegetation height throughout the year and therefore increases prey availability as well as accessibility.

The revealed negative correlations between Red Kite breeding sites and percent cover of forests, altitude and discontinuous urban fabric is consistent with previous knowledge of the species. Previous knowledge suggests the species hunts in open areas (Carter 2007; Aebischer 2009), prefers lower altitudes for breeding (Ortlieb 1989; Bauer et al. 2005; Aebischer 2009; Ebenhöh et al. 2011) and only rarely forages (Porstendörfer 1994) or breeds within settlements (Ortlieb 1992; Walz 2005).

In addition, our model revealed that forest edges were suitable breeding habitats which is well in line with previous studies (Aebischer 2009; Nachtigall et al. 2010). To conclude, the species-habitat relationships observed in our study were similar to those reported in the literature. Therefore, we are confident that our model is suitable to predict the potential distribution of the Red Kite for Germany.

Distribution of the Red Kite

The comparison between existing abundance data of the Red Kite and our model results suggests that the distribution of Red Kites was predicted correctly for most German federal states (Fig. 3). Thus, the land-use pattern is able to explain the Red Kite's distribution within the species' core distribution area. This agrees with the suggested colonisation history of the Red Kite throughout Central Europe. It has been proposed that the mixture of forest patches and

open landscapes created by humans in the Middle Ages was the main driver for the post-glacial expansion from the Iberian Peninsula (Ortlieb 1989; Schreiber et al. 2000; Walz 2005).

However, comparing the predicted habitat suitability map with the actual distribution of the Red Kite (Grüneberg 2011) reveals a number of differences. A reason for these differences might be that we have not considered all important variables in the species' habitat-relationship. For example, some authors suggested a relationship between the distribution of the Red Kite and its favoured prey, the common hamster *Cricetus cricetus* (Nicolai 1997; Schmidt 2009). However, the known distribution of the hamster as well as that of other small mammal species does not correspond directly with the breeding range of the Red Kite (see Niethammer and Krapp 1978; Kryštufek et al. 2008). Moreover, the population densities of small mammals exhibit considerable fluctuations, affecting the birds' breeding success but not their distribution. However, the lack of large-scale abundance data on small mammals prevented us from clarifying this issue.

Climate variables were not significant drivers of the Red Kites breeding distribution within Germany. Although Seoane et al. (2003) showed a significant effect of temperature on the distribution of the Red Kite for the Iberian Peninsula, temperature was rejected in our modelling procedure. Due to a lower temperature range in Germany, we suggest that temperature might not control the distribution of Red Kites within Germany, but could control Red Kite distribution on the continental scale. The Red Kite is supposed to avoid rainy climates (Seoane 2003; Aebischer 2009) as rains decrease hatching success and increase nestling mortality (Newton et al. 1994; Lovegrove 1990 cited in Seoane 2003). In our data set the mean spring precipitation correlated with the mean spring temperature. As precipitation was neither selected in our initial models nor in the model of Seoane et al. (2003) it was excluded from our final analysis. Nevertheless, our data on precipitation only depict mean values and not frequencies or the duration of precipitation events, which might affect breeding success and might limit species distribution.

A fundamental assumption in species distribution models is that the current range of a given species is in equilibrium with the limiting environmental variables (Zimmermann et al. 2010). This means that all suitable habitats are occupied by the species. This is obvious, as additional factors limiting its distribution (e.g., former hunting pressure, poisoning, pesticides) are not involved in the model. By considering actual breeding sites against randomly selected pseudo-absences this assumption is of minor importance for our model but it is of essential importance for using the model to predict the potential range (i.e. generating a habitat suitability map). Within the last centuries human persecution caused considerable fluctuations in the occurrence of the Red Kite (Collar and Andrew 1988; Walz 2005) suggesting that the species failed to recolonise all suitable habitats. The colonisation of abandoned breeding locations by juveniles can take considerable time as the Red Kites' juvenile dispersal distance is low (2–43 km, Pfeiffer 2009). A further reason for this slow range expansion could be the strong philopatry (Ortlieb 1989) with adults generally returning to last year's breeding sites. Similar patterns of slow recovery combined with a strong philopatry have been observed for the Osprey *Pandion haliaetus* (Lohmus 2001; Krummenacher et al. 2009). Overall, these considerations suggest that the Red Kite needs considerable time to recolonise former breeding areas after legal protection (Lensink 1997). To confirm our hypothesis that the discrepancy between actual and predicted breeding distribution is due to the behavioral characteristics of this species, we need more detailed information on Red Kite juvenile dispersal and its influence on the Red Kites' population dynamics. Thus we recommend the tagging of nestlings within all parts of the Red Kite's current distribution.

However, it is still unclear why low population sizes occur in Saarland and Rhineland-Palatinate as well as exceptionally high population numbers in Saxony-Anhalt and Mecklenburg-West Pomerania. We can only speculate whether these patterns result from regional variability of natural conditions or stem from different mortality rates between breeding areas or between different wintering grounds. Hirschfeld (2011) estimated that 250–500 individuals are killed illegally every year in Germany, and an unknown but serious number are killed during migration and during overwintering (Knott et al. 2009). Furthermore, an increasing number of individuals are reported to be killed by wind turbines (Dürr 2009; Langgemach et al. 2010). We conclude from our model and the current state of knowledge on the species that the distribution of the Red Kite is at present not in equilibrium with its environment.

Conclusion and outlook

Based on land-use data and a large number of Red Kite breeding records, this study identified significant and plausible relationships between breeding sites of Red Kites and specific land-use variables. Thus, the availability of suitable habitat determines the distribution on the local scale. Furthermore, the generated habitat suitability map generally fits to the known actual distribution of the species within Germany. Accordingly, the extensive occurrence of suitable land-use types affects the distribution on the landscape scale. A further step in unravelling the reasons for the Red Kite's restricted global distribution is a Europe-wide modelling approach based on the complete Corine Land Cover data-set.

The generated habitat suitability map shows that land-use variables are not sufficient for explaining habitat occupancy by the species nor for explaining all variation in abundance within Germany. As a consequence of our results and because of the mentioned biological traits of the species, we argue that the colonisation of suitable habitats is still in progress. A future challenge is to collect detailed spatial information on reproduction, mortality and dispersal of juveniles and adults and its influence on distribution and abundance.

We revealed evidence for unoccupied but suitable habitat for the Red Kite. Therefore factors limiting the population and its dispersal, like human persecution and high mortality rates, e.g., due to improper placement of wind turbines, have to be taken into account for efficient species conservation. Concerning wind turbine planning, planners have to keep in mind that an unoccupied habitat might be still suitable for the Red Kite and might be colonised in the next few years. Therefore, knowledge on the potential distribution and of potential suitable habitats of the Red Kite revealed by high-resolution modelling might be very useful in future environmental impact assessment studies.

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