

Multi-temporal distribution modelling with satellite tracking data: predicting responses of a long-distance migrant to changing environmental conditions

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Summary

1. Despite the wealth of data available from satellite tracking (ST) studies, such data have rarely been used to model species distributions. Using a novel method, we show how to exploit satellite data to analyse whether and how a migratory species responds to fluctuating environmental conditions in its wintering area. This is particularly crucial for establishing comprehensive conservation measures for rare species in areas that are threatened by increasing land use and climate change.

2. We use ST data of Eleonora's falcon *Falco eleonora*, a long-distance migratory raptor that winters in Madagascar, and assess the performance of static species distribution models (SDM) as well as multi-temporal models. ST data were derived from seven falcons tracked during three consecutive wintering periods and for a total of 2410 bearings, of which 512 locations were used in SDMs. We employed environmental predictors (climate, topography and land cover) with a spatial resolution of 30 arc seconds (*c.* 1 km²) to match rigorously filtered ST data with an accuracy of ≤ 1 km.

3. We first created a model with low temporal but high spatial resolution (half-year). To predict suitable habitat for each month of the wintering season, we took advantage of the high temporal resolution inherent in ST data and employed temporally corresponding remote sensing data [Normalized Difference Vegetation Index (NDVI) 10-day composites] together with other variables to create monthly models.

4. We show that ST data are suited to build robust and transferable SDMs despite a low number of tracked individuals. Multi-temporal SMDs further revealed seasonal responses of the study species to changing environmental conditions in its wintering area.

5. *Synthesis and applications.* We present a transferable approach to predict the potential distribution of organisms as well as their dynamic response to changing environmental conditions. Future conservation management plans could include the prediction of a species' reaction to changing land-use practices or climate change based on the methodology proposed here. This would provide an early warning system for the decline of populations wintering in remote areas that underlie strong climatic fluctuations.

Key-words: Eleonora's falcon, Madagascar, MAXENT, migratory species, remote sensing, species distribution modelling, wintering area

Introduction

Satellite tracking (ST) has become a powerful tool to study long-distance migration of larger vertebrates (Cooke *et al.*

2004) and revealed novel aspects of spatial exploitation of the environment, such as stopover sites and wintering areas of birds, as well as migration of terrestrial and marine mammals, fish and reptiles (Ueta 2000; Hatase *et al.* 2002; Akesson *et al.* 2003; Yamaguchi *et al.* 2008). Satellite tracking data of migratory species have been mostly used in the form of points or vectors to determine the course, distance and speed of migrations, and to locate wintering areas (Hays *et al.* 2001).

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Furthermore, navigational strategies and migration patterns related to environmental conditions en route have been studied (Thorup *et al.* 2003, 2006; Gschweng *et al.* 2008; Mandel *et al.* 2008; Strandberg *et al.* 2008; López-López *et al.* 2010; Mellone *et al.* 2011; Kassara *et al.* 2012).

In recent years, numerous statistical methods to predict the potential distribution of species have been developed (Guisan & Zimmermann 2000; Elith & Leathwick 2009). By relating species presence and, where available, absence data to environmental predictors, such predictive models are created by inductively interpolating or extrapolating the potential distribution beyond locations where a species has been recorded. Species distribution modelling (SDM; Guisan & Thuiller 2005) has been used for macroecology, systematic conservation planning, invasive species, phylogeography and climate change impacts (see review by Elith & Leathwick 2009). Species occurrences required for SDMs are usually ground-based and opportunistically gathered data such as museum records, point counts or observations (Elith *et al.* 2006; Phillips, Anderson & Schapire 2006; Pearson *et al.* 2007), while the potential of satellite- or radiotracking data for distribution modelling has only recently been explored (Johnson & Gillingham 2008; Skov *et al.* 2008; Edrén *et al.* 2010; Smulders *et al.* 2010; Jiguet, Barbet-Massin & Chevallier 2011; Louzao *et al.* 2011; Razgour, Hanmer & Jones 2011; Van Toor, Jaberg & Safi 2011). Ground-based data are frequently biased by accessibility, that is, towards roads, rivers and human habitations (Reddy & Dávalos 2003; Boakes *et al.* 2010), whereas ST data are largely collected independently from such sampling constraints. Additionally, ground-based data sets usually vary in sampling intensity and methods across study areas (Anderson 2003; Phillips, Anderson & Schapire 2006).

Compared to occurrence data usually employed in SDMs, satellite tracking offers new potential to predict suitable habitat because data are collected with regular sampling intervals and largely independent from accessibility and environmental factors such as weather conditions (Hebblewhite & Haydon 2010). The high temporal and spatial accuracy of satellite locations further allow the use of environmental data in SDMs that precisely correspond to the conditions experienced by the tracked animal in space and time. The last decade has seen a dramatic increase in earth observation satellites and sensors, which provide remote sensing data over various spatial and temporal scales (Gillespie *et al.* 2008). Although ST delivers many point locations, these are usually obtained from only few individuals, hence possibly creating another sampling bias because of autocorrelation inherent in the behaviour of individuals. As a result, SDMs derived from ST data might reflect the idiosyncratic preferences of tracked animals rather than a general model transferable to entire populations or species.

In our study, we tested the potential of satellite tracking to predict suitable habitat of a highly mobile organism in its wintering area with seasonally variable environmental conditions. We applied various spatio-temporal filters to ST data with the aim of minimizing potential sampling bias because of autocor-

relation and evaluated transferability of models with a cross-validation approach. We further strived to optimally exploit the potential of satellite tracking data for SDMs by matching the high temporal resolution of remote sensing data with tracking locations, thus reflecting phenological fluctuations of the environment as they were experienced by the animals during the tracking period.

Our study species, the Eleonora's falcon (*Falco eleonorae* Géné 1839, Falconidae), is a long-distance migratory raptor, which colonially breeds on islands in the Mediterranean and off the Moroccan coast. Although Eleonora's falcon is widely distributed with regard to its breeding areas, it is concentrated in a few spatially restricted wintering areas in Madagascar (Gschweng *et al.* 2008; Mellone *et al.* 2011b; Kassara *et al.* 2012). In the first step, we modelled suitable habitat within its wintering area in Madagascar for the entire wet season ('half-year model'). In the second step, we assessed whether this highly mobile species shifts its distribution within its tropical wintering area in response to varying climatic and phenological conditions ('monthly models').

Our study focused on the following questions: (i) Is the temporal resolution of ST data suited to create temporally stratified models as to infer seasonal responses and corresponding shifts in habitat use? (ii) Are idiosyncratic habitat preferences of individuals mirrored in SDMs because they derive from many spatio-temporally precise locations but few individuals? (iii) Which opportunities arise from SDMs based on satellite data for the conservation of migratory species that overwinter in remote wintering areas?

Materials and methods

SATELLITE TRACKING

Details of capture and attachment methods as well as the origin of the birds are described in Gschweng *et al.* (2008). Solar-powered platform transmitter terminals (PTT; Microwave Telemetry Inc., 8835 Columbia, MD 21045, USA) were attached to the falcons as backpacks with harnesses. We mounted a total of 13 PTTs on six adult female and seven juvenile Eleonora's falcons between 2003 and 2005. Transmitters attached in 2003 and 2005 were programmed with duty cycles of 10/48 h (10 h switched on and 48 h switched off) and in 2004 with duty cycles of 6/16 h with a programmed inactivation of the tag after 1 year. Seven out of 13 tagged birds were used to generate SDMs from tracking data during their stay in Madagascar (three juveniles and four adults). The six other birds did not generate data suitable for the present study: Signal transmission terminated during the southward migration of two juveniles, for one adult at the time of arrival on Madagascar, and for one juvenile after two locations from the west coast of Madagascar. One adult migrated to Lebanon where signal transmission ended, and one juvenile wintered in the Democratic Republic of the Congo.

DATA FILTERING

We applied several criteria to maximize data quality of ST data for the purposes of our analyses (for details, Appendix S1, Supporting information). For all analyses, only location classes (LCs) 3, 2 and 1 with a spatial accuracy ≤ 1 km as indicated by

Argos were used, hence matching the grain of environmental data used in SDMs.

Because animals are foraging in a chronological order, tracking data potentially suffer from autocorrelation. To minimize such autocorrelation, we retained only the first bearing if a falcon was located more than once at the same position within a 2-h period and if the distance between these two data points was ≤ 1 km. We further excluded bearings subsequent to the falcon's arrival on the coast as well as all locations between sunset and sunrise except the first data point after sunset, leading to one remaining data point per night. The initial data set was thus reduced from 2410 to 512 locations, which we subsequently used in different partitions for the half-year model as well as for the monthly models (Appendix S1 and Table S1, Supporting information).

A final point concerned the unequal number of tracking points obtained from the seven falcons, which, if unaccounted for, could lead to unbalanced contributions of individuals to the SDMs. For this, we applied a random sampling procedure that was based on a trade-off between the number of individuals and the number of locations per individual feeding into the SDMs (Appendix S1, Supporting information and Table 1). While we retained all individuals irrespective of their number of locations, the data of those individuals with bearings exceeding a defined threshold were split by random sampling into training (SDM building) and test sets (internal SDM evaluation).

HALF-YEAR AND MONTHLY MODELS

We used the filtered data set for two modelling approaches: First, we modelled suitable habitat for the entire wet season in Madagascar ('half-year model') with tracking data of seven falcons that were split into 189 training and 323 test samples (Appendix S1 and Table S1, Supporting information). Environmental variables were derived for the entire half-year period and the model did not utilize the temporal information of falcon locations *within* this period. Second, we created models for each of the 6 months of the wet season. Tracking data were split by month and randomly sampled into training ($n = 369$) and test samples ($n = 143$), resulting in 71–76 training samples for the months December–March and 35 and 42 training samples for November and April, respectively (Table 1). In the monthly models, we utilized the temporal information of the ST data to match them with corresponding environmental variables (see below). Test samples were not further randomly sampled, hence individuals contributed unequally to internal model evaluation.

ENVIRONMENTAL VARIABLES

For all models, we used the following environmental variables that had no temporal component:

Topography

We considered both elevation above sea level and topographic roughness as potentially relevant, because falcons were observed during field surveys at higher elevations (> 600 m a.s.l.) and in topographically complex regions (M. Gschwend, unpublished data). Elevation was taken from the SRTM30 digital elevation model (version 2, <http://www2.jpl.nasa.gov/srtm>). Additionally, we derived two measures of topographic roughness from the SRTM30 data: Local roughness was derived with a moving window analysis that calculated the contrast for each grid cell in a 3×3 window (maximum–minimum elevation, subsequently log-transformed; 'SRTM30_{con}'). Topographic roughness over a larger extent was derived with a moving window analysis, calculating the variance for each grid cell in a 9×9 window (log-transformed; 'SRTM30_{var}').

Distance to water

We reasoned that distance to the hydrological network might be related to resource availability and calculated distance to water in 1-km steps up to 10 km ('Hydro buffer') based on the hydrological network taken from the Digital Chart of the World (DCW). Distance values were inverted, that is, a value of 11 corresponded to a grid cell overlapping with water and a value of 1 to a grid cell 10 km distant from water. Grid cells beyond 10 km distance were set to zero.

Land cover

We included MODIS vegetation continuous fields (VCF; Hansen *et al.* 2003) for the year 2001 as structurally defined variables, which potentially correlate with resource availability as well as foraging and roosting habitat of falcons. These remote sensing data estimate per cent bare ground ('VCF bare'), per cent herb cover ('VCF herb') and per cent tree cover ('VCF tree').

For environmental variables that contained temporal information, we used two different approaches in the half-year and monthly models:

Table 1. Number of satellite tracking bearings of seven Eleonora's falcons used in training and testing of monthly species distribution models (SDMs) after random sampling to match the individual with ≥ 14 locations

Month	Individual (PTT No.), age and sex						Random sampling threshold	Training points	Excluded points used as test samples	
	40 532 ad. ♀	40 536 juv.	49 886 ad. ♀	49 887 ad. ♀	49 889 juv. ♀	49 890 ad. ♀				49 891 juv. ♂
Nov	7		16	14				$n = 14$	35	(2*)
Dec	18		31	36	19			$n = 18$	72	32
Jan	14	3	39	30	12		34	$n = 14$	71	61
Feb	23		29	31			4	$n = 23$	73	14
Mar	19		28	30		33		$n = 19$	76	34
Apr	15			15		12		$n = 15$	42	0

ad., adult; juv., juvenile; PTT, platform transmitter terminals.

*Not used because of small sample size.

Climate

Both temperature and precipitation are assumed to influence the distribution of organisms over larger extents, either directly as physiological constraints ('bioclimatic envelope') or indirectly via their effects on resource availability. For the monthly models, we used untransformed WORLDCLIM data (version 1.4; Hijmans *et al.* 2005) including minimum monthly temperature (T_{\min}), mean monthly temperature (T_{mean}), maximum monthly temperature (T_{\max}) and monthly precipitation ('Prec'). For the half-year model, we calculated from each set of monthly climate data (T_{\min} , T_{mean} , T_{\max} and 'Prec') corresponding to our observation period (Nov–Apr) the mean, minimum and maximum value for each grid cell with the Batch Grid Toolbox extension in ARCVIEW GIS 3.2a <http://arcscripits.esri.com/details.asp?dbid=14455>. This resulted in 12 variables ($T_{\min \text{ min}}$, $T_{\min \text{ mean}}$, $T_{\min \text{ max}}$, $T_{\text{mean min}}$, $T_{\text{mean mean}}$, $T_{\text{mean max}}$, $T_{\max \text{ min}}$, $T_{\max \text{ mean}}$, $T_{\max \text{ max}}$, 'Prec_{min}', 'Prec_{mean}' and 'Prec_{max}'). We also included total precipitation for the 6 months ('Prec_{sum}') and the standard deviation of monthly precipitation as a measure of seasonality ('Prec_{SD}').

Vegetation phenology

We employed the Normalized Difference Vegetation Index (NDVI) as a direct measure of vegetation greenness as it has been shown to correlate with the spatio-temporal occurrence of migratory birds (Tøttrup *et al.* 2008). Data matching our tracking periods were obtained from the SPOT VEGETATION programme (see Appendix S2, Supporting information). For the monthly models, we calculated the mean monthly NDVI ('mNDVI_{mean}') and its standard deviation ('mNDVI_{SD}'). For the half-year model, we calculated the mean, minimum, maximum and standard deviation of the NDVI ('NDVI_{mean}', 'NDVI_{max}', 'NDVI_{min}' and 'NDVI_{SD}') from the entire set of the six monthly means (November–April).

All environmental data were resampled and aligned with the digital elevation model (SRTM30) at a resolution of 30 arc seconds (*c.* 1 km²) using GIS (ARCVIEW 3.2a with SPATIAL ANALYST 2.0a extension; Esri, Redlands, CA 92373-8100, USA).

SPECIES DISTRIBUTION MODELLING

We modelled the distribution of Eleonora's falcons on their wintering grounds with the maximum entropy algorithm as implemented in MAXENT (version 3.2.19, <http://www.cs.princeton.edu/~schapire/maxent>, Phillips, Anderson & Schapire 2006). Compared to other SDM techniques, MAXENT has been shown to perform very well (Elith *et al.* 2006). It is a suitable modelling tool for our study because it requires presence-only data, it is robust to over-fitting in cases where environmental variables are correlated and performs well with a low number of occurrence points (Wisz *et al.* 2008).

Like most maximum likelihood estimation approaches, MAXENT *a priori* assumes a uniform distribution and performs a number of iterations in which the weights are adjusted to maximize the average probability of the point localities (also known as the average sample likelihood), expressed as the training gain (Phillips & Dudik 2008). These weights are then used to compute the MAXENT distribution over the entire geographical space.

We used MAXENT with standard settings except for the regularization multiplier that was set to 2.5 instead of one to minimize over-fitting given the relatively large number of predictor variables (Elith, Kearney & Phillips (2010), and the maximum number of iterations set to 1000 instead of 500 as to guarantee that the algorithm converged

on the threshold. The contribution of each environmental variable to model performance was evaluated with a jackknife procedure implemented in MAXENT, where variables are successively omitted and then used in isolation to measure their relative as well as their absolute contribution to the models.

In a first run of the half-year model, we used 25 environmental variables (three 'SRTM', one 'Hydro buffer', three 'VCF', 14 climatic and four 'NDVI'). For the final half-year model, we then chose a subset of 13 variables (Table 3) that substantially contributed to the first run and that were selected according to their ecological relevance for the falcons, which was based on the observations of wintering falcons in 2003 and 2004 (M. Gschwend, unpublished data).

The monthly models were created with a set of 13 variables comprising three topographic variables ('SRTM30', 'SRTM30_{con}' and 'SRTM30_{var}'), three land cover variables ('VCF herb', 'VCF tree' and 'VCF bare'), the variable 'Hydro buffer', three climatic variables (T_{\min} , T_{\max} and T_{mean}) and the NDVI and its standard deviation ('mNDVI' and 'mNDVI_{SD}'). We matched five environmental variables containing temporal information (temperature, NDVI) with those of the corresponding tracking data using the SWD format ('samples with data', see Appendix S2, Supporting information). Background points (10 000) were created within the coastline, but outside larger water bodies of Madagascar with the ARCVIEW extension 'Random Point Generator' (version 1.3, http://www.jennessent.com/arcview/random_points.htm) and grid values of every environmental variable were extracted at each point.

CROSS-VALIDATION OF HALF-YEAR MODEL

To test whether the comparatively low number of tracked individuals limits the transferability of our SDMs ('idiosyncratic habitat preferences'), we employed a cross-validation procedure for the half-year model. We partitioned the data set by individuals and ran seven models, each time excluding the tracking points of one individual from the training data and using the excluded individual as a test sample file to assess the performance of the models.

Results

HALF-YEAR MODEL

The half-year model predicted suitable habitat for the Eleonora's falcon on its wintering grounds in Madagascar for the complete wet season from November to April. Model performance as assessed by the area under the curve (AUC) was very high (0.947; Table 2), hence the model had a strong discriminatory power. Test AUC was high with 0.927. The variables 'Prec_{min}', 'SRTM30', $T_{\max \text{ min}}$ and 'Prec_{max}' contributed with more than 10% to the model (Table 3). The variable 'Prec_{min}' had the highest explanatory power when used in isolation, that is, this variable contained the most useful information by itself. The environmental variables that decreased the model most when omitted were $T_{\max \text{ min}}$ and elevation ('SRTM30'), which therefore had the most information not present in the other variables.

Areas of high habitat suitability predicted by the half-year model were in the northern part of Madagascar as well as in the central highlands (Fig. 1). Suitable habitat included two national parks (Marojejy NP and Anjanaharibe-Sud NP) and comprised, together with the Masoala NP, the last stretches of

Table 2. Number of training and test points, regularized training gain, training and test area under the curve (AUC) as well as standard deviation of the test AUC for the half-year model and for the monthly models

	Half-year model	Nov	Dec	Jan	Feb	Mar	Apr
Individuals (<i>n</i>)	7	3	4	6	4	4	3
Training points	189	35	72	71	73	76	42
Test points	323	0	32	61	14	34	0
Reg. training gain	1.640	2.799	1.186	1.341	2.475	2.676	1.895
Training AUC	0.947	0.984	0.918	0.925	0.982	0.986	0.976
Test AUC	0.927	–	0.929	0.919	0.990	0.959	–
Test AUC SD	0.008	–	0.020	0.017	0.004	0.019	–

AUC, area under the curve.

Table 3. Contribution of variables (percentage) to the half-year model for Eleonora's falcon in the wet season (November–April) in Madagascar

Variable	Percentage contribution
Prec _{min}	39.7
SRTM30	12.9
<i>T</i> _{max} min	10.8
Prec _{max}	10.1
<i>T</i> _{max} max	5.5
VCF bare	4.9
SRTM30 _{con}	4.2
SRTM30 _{var}	4.0
Hydro buffer	3.2
NDVI _{mean}	2.1
NDVI _{SD}	1.8
<i>T</i> _{min} max	0.5
<i>T</i> _{min} min	0.2

NDVI, Normalized Difference Vegetation Index; VCF, vegetation continuous fields.

closed forest covering *c.* 425 000 km² (Harper *et al.* 2007). On the central highlands, suitable habitat was predicted around the largest lakes of Madagascar at altitudes between 600 and 1200 m a.s.l. The dry south and west of Madagascar was largely predicted as unsuitable. In summary, Eleonora's falcons had a high probability of occurrence in topographically rugged regions at medium altitudes and with mesic climatic conditions.

CROSS-VALIDATION OF THE HALF-YEAR MODEL

Of the seven cross-validation runs, the models predicted five individuals well to excellent (AUC: 0.725–0.984), while two individuals were only moderately predicted by the models (Table 4). The low AUC (0.620) of individual 40 535 might be due to the extremely limited sample size of this animal (three tracking points) while the very low AUC (0.522) of individual 49 891 indicates that habitat suitability of this animal was not predicted by the other six falcons. These results indicate that the small sample size of seven individuals generally predicted overall habitat suitability of the wintering grounds of Eleonora's falcons rather well, hence suggesting

that habitat preferences of populations and their potential distributions can be modelled from few individuals with sufficient discriminatory power.

MONTHLY MODELS

The regularized training gain of the monthly models varied between 1.341 (January) and 2.799 (November). The training AUC was very high among the monthly models (0.918–0.986; Table 2), thus all monthly models had a strong discriminatory power. The test AUC, where available, had also high values (0.919–0.990).

Overall, one measure of topographic heterogeneity ('SRTM30_{var}') contributed strongly to all monthly models (15.5–38.3%) except for January (Table 5). Another important variable was 'VCF bare' (0.0–29.4%), which substantially contributed to the models of November, December and February, but not to March and April. The variables 'mNDVI' and 'Prec' had medium to high contributions in all monthly models ('mNDVI': 6.9–48.4%, 'Prec': 8.8–30.4%) except for November when their contribution was low ('mNDVI': 0.0%, 'Prec': 1.5%; Table 5).

The habitat suitability maps show conspicuous differences in the course of the 6 months of the wet season (Fig. 2). Areas of high habitat suitability were small in November, largest in December and January, and medium in the last 3 months. Throughout the wet season, areas of high suitability were predicted around the mountain massifs in the northernmost part of Madagascar. The central highlands as well as the mountain range along the east coast had higher predictions in December and January (see Appendix S3 and Figs S1 and S2, Supporting information).

RELEVANCE OF ENVIRONMENTAL VARIABLES IN MONTHLY MODELS

The variable with the highest contribution to five of the six models was a measure of topographic heterogeneity ('SRTM30_{var}'), indicating that Eleonora's falcons preferred rugged terrain. The variable mNDVI strongly contributed to four out of the six monthly models. While

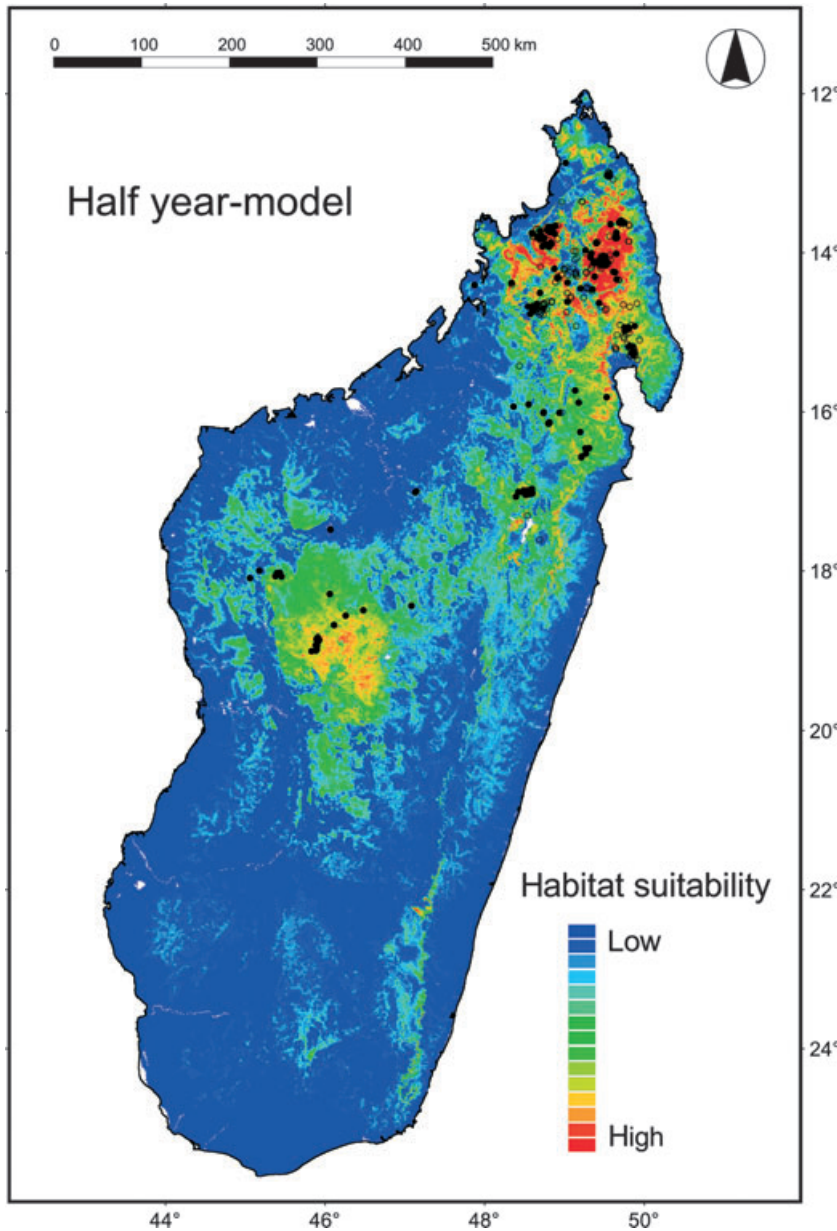


Fig. 1. Half-year model of habitat suitability for Eleonora's falcon on its wintering grounds in Madagascar during the wet season from November to April. Filled dots indicate satellite tracking (ST) points used for training, and circles indicate ST points that were used for testing the model.

Table 4. Model statistics of the cross-validation of the half-year model. Individuals were successively excluded from model training and used as test samples

Individual	Without 40 532	Without 40 536	Without 49 886	Without 49 887	Without 49 889	Without 49 890	Without 49 891
Training points	158	186	158	158	158	158	158
Test points	31	3	31	31	31	31	31
Reg. training gain	1.713	1.693	1.746	1.496	1.914	1.544	2.021
Training AUC	0.957	0.952	0.949	0.941	0.963	0.941	0.962
Test AUC	0.867	0.620	0.801	0.984	0.725	0.951	0.522
Test AUC SD	0.040	0.135	0.043	0.005	0.025	0.013	0.044

AUC, area under the curve.

the variable mNDVI did not contribute to the November model, that is, at the start of the wet season, the variable 'VCF bare' had its highest contribution in this month

(Table 5). Furthermore, the seasonally fluctuating variables precipitation and maximum temperature substantially contributed to the monthly models. The varying contributions

Table 5. Contribution of variables (percentage) to the monthly models for Eleonora's falcon in the wet season (November–April) in Madagascar. Variables are listed by their decreasing mean contribution to the monthly models

Variable	Nov	Dec	Jan	Feb	Mar	Apr
SRTM30 _{var}	27.3	29.4	7.3	34.2	15.5	38.3
mNDVI	0.0	17.9	29.4	26.9	48.4	6.9
Prec	1.5	10.4	9.1	8.8	13.0	30.4
VCF bare	29.4	14.4	3.7	21.9	1.1	0.0
T_{\max}	23.5	22.4	5.1	0.5	0.9	2.1
SRTM30	0.3	2.1	16.8	2.7	17.1	10.1
VCF tree	5.4	0.0	8.4	0.0	0.8	2.2
T_{mean}	0.0	0.7	10.4	1.4	0.2	0.0
Hydro buffer	3.5	0.7	3.3	1.2	0.6	3.1
SRTM30 _{con}	4.0	0.6	1.8	0.6	0.0	3.8
mNDVI _{SD}	3.7	1.2	1.0	0.3	1.0	1.9
VCF herb	0.7	0.1	3.7	1.2	0.5	1.4
T_{\min}	0.7	0.0	0.1	0.4	1.2	0.0

NDVI, Normalized Difference Vegetation Index; VCF, vegetation continuous fields;

of the variables 'Prec', ' T_{\max} ' and 'mNDVI' to the monthly models over the course of the wet season are illustrated in relation to the climatic conditions in the wintering area in Fig. 3.

The maximum temperature throughout Madagascar is highest in November and December (Hijmans *et al.* 2005). In these months, the contribution of ' T_{\max} ' to the monthly models is very high (Fig. 3). An even stronger effect is shown for precipitation. At the beginning of the wet season, precipitation contributed only marginally to the model, whereas its relevance steeply increased towards the end of the wet season when precipitation declines substantially throughout Madagascar (Hijmans *et al.* 2005). Thus, in April, when precipitation is lowest within the wet season, the variable precipitation contributed substantially to the model. From December to March, when the contribution of the variable precipitation was not exceeding 10.4%, 'mNDVI' (expressing a delayed response to precipitation) contributed substantially to the models (Fig. 3). This suggests that precipitation *per se* is not as important as the ecological conditions that result from precipitation, that is, the phenological response of vegetation.

Discussion

Our study demonstrated that satellite tracking data can be successfully utilized for species distribution modelling. Both model types (half-year and monthly) had high discriminatory power in the prediction of suitable habitat for Eleonora's falcon within its wintering area in Madagascar. The cross-validation of the half-year model further showed that SDMs based on a fairly low number of tracked animals do not suffer from idiosyncratic habitat preferences of individuals and probably generalize to larger populations or even the entire species (see below). The half-year model (Fig. 1) derived from seven individuals might better predict the occurrence of Eleonora's falcons from other breeding populations than the monthly models, which were based on lower samples (three to six individuals). However, the monthly models took

advantage of the high spatio-temporal resolution of ST data, which allowed a match with seasonally fluctuating variables such as climate (temperature and precipitation) and vegetation phenology (NDVI), thus resulting in a multi-temporal representation of habitat suitability over the course of the wet season. We believe that this novel approach has great potential for future tracking studies, especially when telemetry devices become more affordable and with increasing availability of multi-temporal environmental variables. Only then we can disentangle the dynamic responses of mobile animals to changing environments, both now and in the future, rather than predicting static habitat suitability with conventional applications of species distribution models.

HALF-YEAR MODEL

It has been assumed since 1913 that Eleonora's falcons overwinter in Madagascar (Rand 1936; Stresemann 1954) but until recently their distribution on the island remained largely unknown (Zefania 2001; Hawkins & Goodman 2003; Mellone *et al.* 2012; Kassara *et al.* 2012). Based on our ST data of seven individuals, the potential distribution of wintering Eleonora's falcon was mainly predicted in the northern part of Madagascar (the wider region around the Tsaratanana Massif and the Montagne d'Ambre) and the central highlands (Fig. 1). These predictions are supported by two recent ST studies of Eleonora's falcons from breeding colonies in Spain and Greece, respectively, where all individuals were found in the northern and north-eastern part of Madagascar (Mellone *et al.* 2011b; Kassara *et al.* 2012). The modelled range of Eleonora's falcon indicates a restricted, rather than a wide, wintering area on the island, suggesting particular habitat requirements that appear to be related to a combination of climatic factors and altitude (Table 3). Drier areas in the western and southern parts of Madagascar seem to be unsuitable for the falcons, which is supported by a 5-month survey during which not a single falcon was encountered in the western part of the island (M. Gschweng, unpublished data). Previous observations of

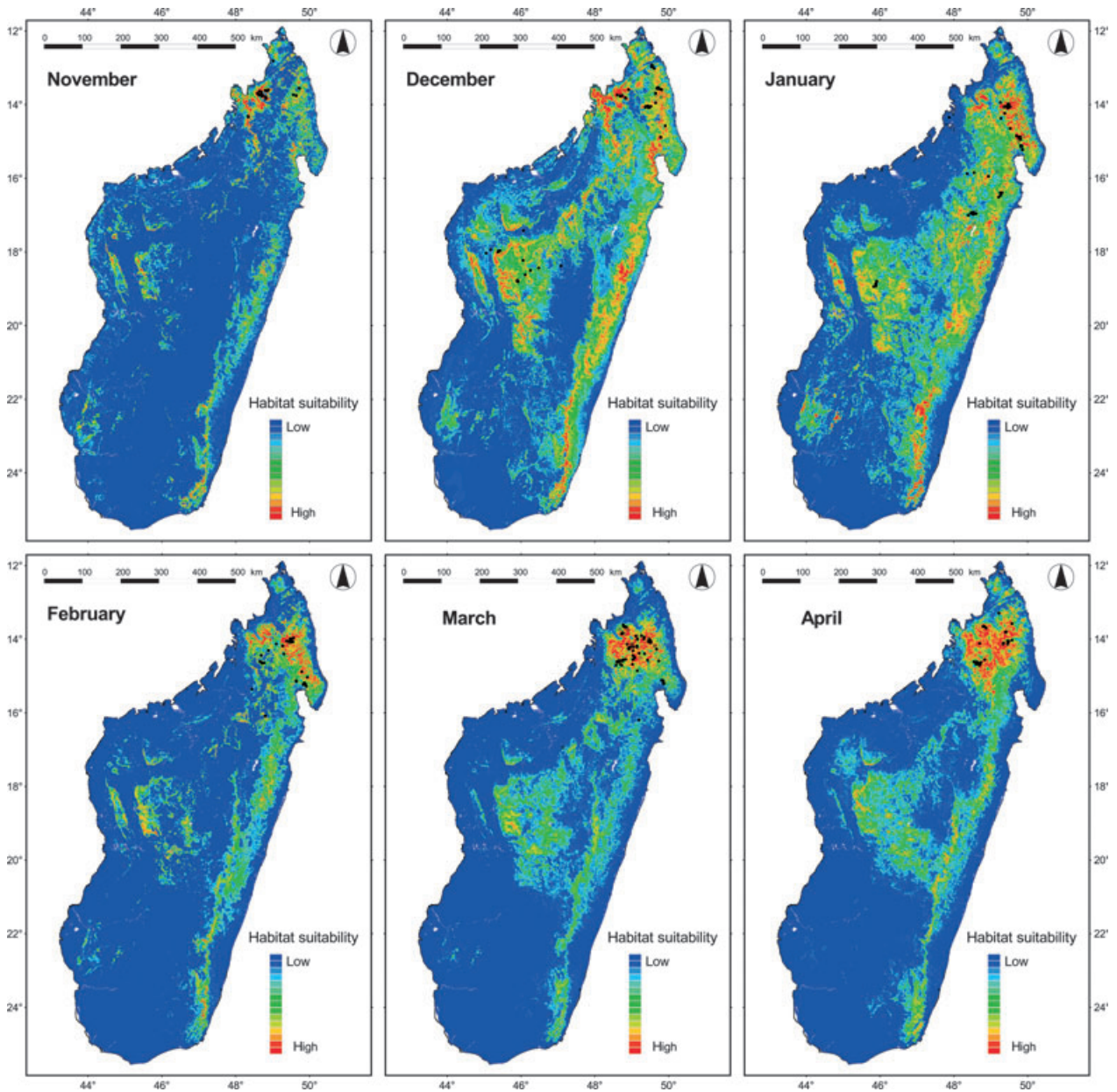


Fig. 2. Monthly models of habitat suitability for Eleonora's falcon on its wintering grounds in Madagascar during the wet season from November to April. Black dots show satellite tracking points used for model training.

Eleonora's falcons near the west coast of Madagascar (Walter 1979; Thiollay & Meyburg 1981) are probably due to the arrival of migrating individuals in November and December (Gschwend *et al.* 2008) and are unlikely to reflect suitable wintering habitat for the falcons.

Despite the excellent discriminatory power of our half-year model, the southern part of the eastern ridge was predicted as suitable, although Eleonora's falcons have never been reported there. Inferential SDMs such as MAXENT predict the potential distribution of species while the actual distribution might be more restricted. Discrepancies between potential (modelled) and actual ranges can be due to several factors such as interspecific interactions (e.g. competition), biogeographic barriers or missing

environmental variables in the model (Svenning & Skov 2004; Munguía, Peterson & Sánchez-Cordero 2008). It is unlikely that geographical barriers play a role for the distribution of the highly mobile Eleonora's falcon within Madagascar. Interspecific competition is likewise improbable given the high abundance of insects during the wet season. Another reason for a restricted occurrence within the modelled distribution could be that falcons use population-specific areas. As shown for other migratory bird species, populations from different parts of the species' range show fidelity to both their particular breeding and wintering areas (see review by Webster *et al.* 2002; Paxton *et al.* 2011). Thus, parts of the potentially suitable habitat may remain uninhabited by our study animals originating

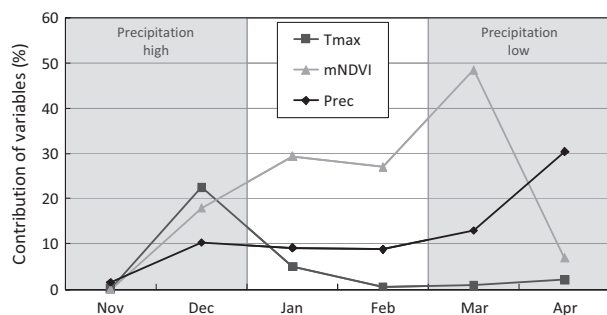


Fig. 3. Percentage contribution of variables maximum temperature (T_{\max}), precipitation (Prec) and Normalized Difference Vegetation Index (mNDVI) to the monthly models of Eleonora's falcon during the wet season on its wintering grounds in Madagascar. Precipitation is higher at the beginning of the wet season (November and December) and declines towards the end of the wet season, mainly in March and April.

from Sardinia, while populations from other parts of the breeding range of Eleonora's falcon might winter in these areas. Because juvenile falcons migrate independently from adults and arrive about 1 month later in Madagascar (Gschweng *et al.* 2008; Kassara *et al.* 2012), population-specific preferences for certain regions within the potential distribution in Madagascar, if they exist, would need to be inherited rather than learned. Ongoing tracking studies of Eleonora's falcon will provide interesting and independent tests of the generality of our model, which should be also checked with field surveys in areas predicted as suitable.

MONTHLY MODELS

The monthly models revealed a seasonal response of the tracked individuals to climatic variables such as precipitation and temperature, but also to phenological vegetation signal (NDVI). Predicted regions differed substantially among the monthly models (Fig. S2 and Appendix S3, Supporting information) and indicate pronounced habitat shifts of Eleonora's falcon over the course of the wet season. These findings are supported by the observations of peregrinating falcons during the wet season (Hawkins & Goodman 2003). The predicted habitat suitability of Eleonora's falcon in Madagascar was strongly related to NDVI for five of the 6 months (with the exception of November). This measure of greenness of vegetation is a delayed phenological response to precipitation in seasonal biomes (Brown, de Beurs & Vrieling 2010). In highly seasonal regions, rainfall is known to trigger sharp increases in insect abundance such as swarming termites (Korb & Salewski 2000). Thus, the high contribution of NDVI might also indicate that the falcons follow resource abundance within suitable habitat.

Our approach of multi-temporal models has broad potential to reveal spatial shifts of habitat suitability in response to seasonally changing environments. Such models might be better suited to identify areas essential for a given species in space and time compared to a temporally coarse model such as our half-

year model. However, if factors such as topography and land cover types primarily determine habitat suitability of a species, a temporally coarse model will be more appropriate to highlight areas most relevant for conservation and management interventions. In Madagascar, the central highlands are intensively farmed for rice, whereas deforestation is still rampant in the northern and eastern forest regions. Considering that 90% of the global populations of Eleonora's falcon are estimated to winter in Madagascar (Gschweng *et al.* 2008), thorough knowledge is required to pinpoint those areas that are most suitable for this period of their life cycle.

Against the background of increasing land use and climate change on Madagascar, suitable habitat for Eleonora's falcon is likely to decline on the long term. Our models thus provide a baseline for the potential distribution of this species under current conditions in its wintering area. The causes of population declines of migratory species are frequently unclear as various factors can operate on the breeding grounds, wintering grounds and in the migration corridors between the two. Changing habitat conditions on the wintering grounds are particularly problematic because sufficiently dense monitoring networks are frequently lacking. Comparing habitat suitability models derived over several generations might offer an efficient tool to evaluate whether population declines in the breeding grounds are correlated with a concomitant reduction in the extent of suitable habitat in the wintering areas. This would be essential to inform management interventions aimed at protecting or restoring critical habitat for migratory species.

Outlook

The predictive power and transferability of models created with a low number of individuals, as in our study, should still be carefully checked with independent data. In addition to the encouraging results of our cross-validation, a recent study modelled the wintering range of Black Storks in West Africa based on nine individuals and demonstrated a good match between the predicted range and the previously reported wintering range (Jiguet, Barbet-Massin & Chevallier 2011). Their nine-bird model was further supported by a second model based on only six birds, which showed a close match with the nine-bird range. Thus, we are confident that our SDMs, despite the low number of individuals, predict the actual wintering area of Eleonora's falcon in Madagascar.

These results allow an optimistic forecast for future SDM based on ST data of few individuals. We believe that modelling ST data with multi-temporal remote sensing data provides untapped potential in the future because new tracking devices will not only become more affordable but also directly record variables in addition to the location and time, for example weather, light or behaviour (Cooke *et al.* 2004). Tracked animals could essentially become 'biosensors' that measure environmental conditions in their environment, information that could be then used in conjunction with corresponding environmental variables covering larger spatial extents. Such an approach would help to bridge the gap between inferential

(phenomenological) and mechanistic models and allow an improved forecasting of the effects of land cover or climate change, which will be essential for informed conservation measures aimed at threatened species.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Data filtering.

Appendix S2. Processing of NDVI data used in monthly and half-year models.

Appendix S3. Mean monthly model and seasonal changes in habitat suitability.

Table S1. Data set used for random sampling of model training and testing.

Table S2. Temporal coverage of data used to calculate monthly NDVI data.

Fig. S1. Mean habitat suitability averaged across six monthly models.

Fig. S2. Seasonal changes in habitat suitability.

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