Oikos

OIK-01294

Zurell, D., Eggers, U., Kaatz, M., Rotics, S., Sapir, N., Wikelski, M., Nathan, R. and Jeltsch, F. 2014. Individual-based modelling of resource competition to predict density-dependent population dynamics: a case study with white storks. – Oikos doi: 10.1111/oik.01294

Appendix 1

Detailed description of submodels and data used in individual-based model

Submodels of individual-based model (IBM)

The foraging components of the individual-based stork model basically follow the protocol provided by Johst et al. (2001). Our model is different from Johst et al. (2001) in that space is represented as a landscape grid, home range search is considered explicitly, and the entire stork populations (>1 breeding pair) can be simulated explicitly. Process overview is illustrated in Fig. 1 in the main article; parameters are listed in Table A1.

Resource allocation

Each grid cell is characterized by resource availability expressed as the potential energy intake rate *e*:

$$e = q * e_{max} \qquad (1)$$

where q is the relative resource productivity of the grid cell and e_{max} the maximum energy intake rate on a freshly mowed meadow.

Energy requirements

Adults need to fulfil their own energy requirements and those of the nestlings. The existence metabolism e_m of an adult includes the basal metabolism, the costs of thermoregulation, and limited locomotion activity. In the pre-hatching phase, we assume extra energy requirements e_x of the adults for nest building, egg laying and incubation (Djerdali et al. 2008). The energy requirements of the nestlings e_{nest} increase with body mass which is related to age:

$$e_{nest}(body\,mass) = 5.6(body\,mass)^{0.81} \qquad (4)$$

using a body mass of 70 g for the first day, 1500 g for the 20th day, 2600 g for the 30th day, and a saturation body mass of 2800 g for the 40th day (in between body mass is linearly interpolated).

The energy requirements e_{req} for the different phases are thus:

$$e_{req} = 2(e_m + e_x) \quad \text{for a pre-hatching pair}$$
$$e_{req} = e_m \quad \text{for a non-breeding individual} \qquad (5)$$
$$e_{req} = 2e_m + n_{nestlings} * e_{nest} \quad \text{for a nestling-rearing pair}$$

Patch selection

Storks use both random patch selection and optimal patch selection to select a foraging patch/grid cell within their home range, with proportion of random patch selection p_{rand}. With random patch selection, storks select a foraging patch randomly, independent of its quality, but prefer nearby patches ($d \leq 2.5$ km) with a probability p_{nearby}. With optimal patch selection, storks select the patch that yields the maximum food supply at lowest time and movement costs (depending on available resources and distance of patches), assuming a perfect knowledge of the environment.

Foraging time

As daytime foragers, white storks may use a maximum of 18 h day^{-1} for foraging during the nestling rearing period in Central Europe. Nestlings are brooded within the first 20 days of life because of insufficient thermoregulation. During this early nestling rearing phase, one adult always remains at the nest, and thus, by assuming that adults take turns, maximum daily foraging time per adult is only 9 h day^{-1}.

Our model considers time costs for flight and for foraging. Flight time is determined by the distance of the foraging grid cell:

$$flight\ time = t_f(d - 0.5) \qquad (2)$$

where t_f is the time cost of flight and d the distance.

The foraging time τ is the time spent for energy intake in the grid cell; it must at least cover the energetic costs of the outward and return flight which is determined by distance:

$$\tau(d) = 2de_f/e \qquad (3)$$

where e_f is the energy cost of a single flight. An additional constraint is that the foraging time cannot exceed a maximum (single) foraging time per trip τ_{max} which is determined by patch quality (relative resource productivity of the patch). $\tau_{max} = 2$ is set on high quality patches ($q \geq 0.65$) and $\tau_{max} = 1$ on low quality patches ($q < 0.65$). To capture the known behaviour of storks to forage longer on low-quality patches following repeatedly less successful flights, $\tau_{max} = 2$ is set also on low quality patches when six subsequent flights have been made to low quality patches. The actual foraging time τ from Eq. 3 is increased in small steps (0.01 h) until the energy intake is sufficient to cover the actual requirements or until the maximum foraging time τ_{max} is reached.

Data

Foraging parameters

Nine free ranging white storks were tagged with GPS transmitters (E-Obs GmbH; Munich, Germany) in the state of Saxony-Anhalt, Germany. GPS location was recorded in 5–20 min intervals between 26 July and 21 August 2011. For each location, distance from daily roosting place (usually the nest or a location nearby, see below) was calculated and used to generate a distribution of foraging distance from the nest. Home range radius – defined to encircle 95% of the records (Girard et al. 2002) – and the probability of nearby random patch selection were derived from this distribution. Only data between 5:00–19:00 (German time) were considered to exclude inactive periods. In approximately 19% of the records, a stork was in its nest or less than 50 meters away; in these cases, we assumed the stork was not foraging, and all such records were omitted from the foraging distance distribution. In approximately 13% of the days, the roosting place was over 400 meters from the nest or from the roosting location of the following day; all these cases were also removed from the analysis as they represent non local movement patterns of the post breeding phase. Altogether, a total of 169 foraging days and 27 679 records were analysed.

Long-term monitoring of white stork breeding performance

Data on white stork reproductive performance in the federal state of Brandenburg (Germany; excluding the former district Prenzlau) and in the former district Kalbe (Milde) in the federal state Saxony-Anhalt (Germany) were derived from the long-term monitoring scheme organized by the volunteer network '*LAG Weissstorchschutz'* of the Nature and Biodiversity Conservation Union Germany *(NABU*) (Eggers et al. submitted). The dataset comprises 38 195 observations from 1758 monitored locations with white stork nesting sites for the years 1956–2009. Brandenburg represents the federal state with the most white stork pairs in Germany: 1367 pairs were counted in 2012, compared to 5197 pairs throughout Germany (BAG Weissstorchschutz im NABU 2013).

Table A1. IBM parameters. Value sources are indicated by (++) for GPS-derived parameters, by (+) for parameters from Johst et al. (2001), and by (–) for assumptions.

Function	Parameter	Value	Unit	Description
Landscape grid	H	0.7 (-)	-	Hurst factor in fractal algorithm
	σ	15 (-)	-	Standard deviation in fractal algorithm
	p	0.85 (-)	-	Proportion of unsuitable patches in landscape grid
	x	0.5 (-)	km	Resolution of landscape grid
	n_x	33 (-)	-	Extent of landscape grid (Total area = n_x^2)
Resources	q	0..1 (+)	-	Relative resource productivity of landscape

	q_{high}	0.65 (+)	-	Minimum resource productivity defining high quality patches
	e_{max}	1330 (+)	kJ/h	Maximum energy intake rate per grid cell if q=1
Energy requirements	e_m	1613 (+)	kJ/day	Existence metabolism of adult stork
	e_x	1613 (-)	kJ/day	Pre-hatching extra energy requirements (for nest building, egg-laying, incubation etc.)
	e_{tol}	0.2 (-)	-	Adult tolerance rate against starvation
	$e_{nestling,tol}$	0.2 (-)	-	Nestling tolerance rate against starvation
Nestling rearing	$n_{nestling,init}$	4 (-)	ind.	Initial number of nestlings
	$mass_{nestling}$	70, 1500, 2600, 2800 (+)	g	Body mass of nestlings on day 1 (at hatching), day 20, day 30 and day 40
Patch selection	p_{rand}	0.25 (-)	-	Proportion of random patch selection
	p_{nearby}	0.72 (++)	-	Probability of nearby random patch selection
	d_{nearby}	2.5 (+)	km	Maximum distance of nearby patches
	d_{max}	5 (++)	km	Maximum distance for foraging (home range radius)
Foraging	τ_d	18 (+)	h	Maximum foraging time per adult per day
	$\tau_{d,early}$	9 (+)	h	Maximum foraging time per adult per day in brooding phase (first 20 breeding days)
	t_f	0.111 (+)	h/km	Time costs of flight
	e_f	40 (+)	kJ/km	Energy costs of flight
	τ_{max}	1 or 2 (+)	h	Maximum foraging time per trip (on low or high quality patches)
	Δ_τ	0.01 (+)	h	Step size of increase in foraging time τ

References

BAG Weissstorchschutz im NABU. 2013. Mitteilungsblatt 105/2013 105. Bundesfachausschuss Ornithologie, Bundesarbeitsgruppe Weissstorchschutz im Naturschutzbund Deutschland (NABU) e.V.

Djerdali, S. et al. 2008. Food supply and external cues limit the clutch size and hatchability in the white stork *Ciconia ciconia*. – Acta Ornithol. 43: 145–150.

Girard, I. et al. 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. – J. Wildl. Manage. 66: 1290–1300.

Johst, K. et al. 2001. Foraging in a patchy and dynamic landscape: human land use and the white stork. – Ecol. Appl. 11: 60–69.

Appendix B

Simulation results and sensitivity analysis of individual-based model

Table A2. Mean demographic rates obtained for different home range strategies. Presented are breeding density (breeding pairs per 100 km^2), per cent of unsuccessful pairs having lost their brood, number of fledglings per breeding pairs, early nestling mortality and absolute number of fledglings. Values are the mean numbers from n = 100 replicate simulations for populations at carrying capacity following an area-minimising home range strategy; the standard error is presented for the default landscape (±). Simulations were repeated in 10 replicate landscapes created with the same fractal parameters. The range of mean values for these replicate landscapes is presented in parentheses.

<table>
<tr><th rowspan="2">Parameter</th><th colspan="2">Breeding density</th><th colspan="2">% unsuccessful pairs</th><th colspan="2">Fledglings per breeding pair</th><th colspan="2">nestling mortality <20d (% of all deaths)</th><th colspan="2">Fledglings absolute</th></tr>
<tr><th>par --</th><th>par ++</th><th>par --</th><th>par ++</th><th>par --</th><th>par ++</th><th>par --</th><th>par++</th><th>par--</th><th>par++</th></tr>
<tr><td>Area-minimising with local aggregation</td><td colspan="2">9.95 ± 0.45
(6.97 – 9.85)</td><td colspan="2">19.4 ± 1.22
(9.44 – 28.22)</td><td colspan="2">1.36 ± 0.002
(1.26 – 1.48)</td><td colspan="2">83.85 ± 0.22
(86.94 - 92.77)</td><td colspan="2">36.52 ± 0.91
(24.28 - 35.86)</td></tr>
<tr><td>Area-minimising without local aggregation</td><td colspan="2">10.16 ± 0.51
(7.2 – 9.99)</td><td colspan="2">19.12 ± 1.39
(6.85 – 23.78)</td><td colspan="2">1.38 ± 0.002
(1.27 – 1.56)</td><td colspan="2">82.81 ± 0.23
(85.3 – 90.54)</td><td colspan="2">37.77 ± 1.07
(25.9 – 37.18)</td></tr>
<tr><td>Resource-maximising with local aggregation</td><td colspan="2">6.39 ± 0.56
(5.16 – 6.33)</td><td colspan="2">36.21 ± 1.52
(26.03 – 42.81)</td><td colspan="2">1.46 ± 0.004
(1.25 – 1.46)</td><td colspan="2">87.89 ± 0.18
(91.02 – 96.38)</td><td colspan="2">25.06 ± 2.45
(17.78 - 24.65)</td></tr>
<tr><td>Resource-maximising without local aggregation</td><td colspan="2">6.59 ± 0.35
(5.12 – 6.59)</td><td colspan="2">36.14 ± 0.95
(26.24 – 41.6)</td><td colspan="2">1.47 ± 0.002
(1.28 – 1.47)</td><td colspan="2">89.31 ± 0.14
(91.35 – 96.37)</td><td colspan="2">26.16 ± 1.43
(18.19 – 25.29)</td></tr>
</table>

Table A3. Sensitivity of mean demographic rates to changes in parameter values and landscape parameters. Presented are the mean numbers from n = 100 replicate simulations for populations at carrying capacity following an area-minimising home range strategy and actively forming local aggregations. The top row represents the baseline with default parameter values. IBM parameters were changed by –50% (par– – or +50% (par++) except p_{rand}, e_x and $e_{nestling,tol}$ which were changed by ±100%. p_{rand} proportion of random patch selection; p_{nearby} probability of nearby random patch selection; d_{max} maximum distance for foraging; d_{nearby} maximum distance of nearby patches; e_{max} maximum energy intake rate per grid cell; e_m existence metabolism of adults; e_x pre-hatching extra energy costs; $e_{nestling,tol}$ nestling tolerance rate against starvation; $n_{nestling,init}$ initial number of nestlings; t_f time costs of flight; e_f energy costs of flight; τ_{max} maximum foraging time per trip; n_x extent of landscape grid [number of cells] (total area = n_x^2); H Hurst factor controlling the degree of autocorrelation in fractal landscapes with higher H indicating higher clumping. For default parameter values see Table A1.

Parameter	Breeding density		% unsuccessful pairs		Fledglings per breeding pair		nestling mortality <20d (% of all deaths)		Fledglings absolute	
	par --	par ++	par --	par ++	par --	par ++	par --	par++	par--	par++
Area-minimising with local aggregations	9.95 ± 0.45		19.4 ± 1.22		1.36 ± 0.002		83.85 ± 0.22		36.52 ± 0.91	
p_{rand}	13.11	5.57	0	47.18	1.66	1.18	83.03	86.85	58.62	17.86
p_{nearby}	7.7	11.58	36.19	9.71	1.22	1.48	85.39	84.89	25.36	46.01
d_{max} (d_{nearby})	11.72	8.01	8.38	34.99	1.49	1.23	84.86	84.95	46.88	26.68
e_{max}	0.74	25.67	38.41	13.68	1.10	1.36	80.70	82.47	2.39	94.4
e_m	18.7	5.56	19.29	20.44	1.16	1.57	84.03	84.78	58.89	23.37
e_x	5.55	4.01	85.59	1.35	1.01	2.71	98.13	45.75	15.29	28.8
$e_{nestling,tol}$	6.18	1.61	51.00	87.29	1.09	3.99	93.26	44.4	18.33	17.45
$n_{nestling,init}$	10.09	10.05	17.64	20.08	1.34	1.35	54.61	91.00	36.6	36.52

t_f	10.04	9.93	18.09	22.26	1.38	1.32	83.24	84.72	37.21	35.41
e_f	12.91	8.49	4.51	25.36	1.57	1.26	87.47	83.12	54.5	28.91
τ_{max}	6.61	11.72	34.27	14.12	1.23	1.41	85.12	84.35	21.91	44.71
brooding	10.96	8.31	13.9	34.34	1.35	1.11	40.81	78.12	39.96	25.02
no brooding	10.83		14.82		1.35		33.73		39.5	
equal sex numbers	11.10		24.77		1.25		86.86		37.85	
n_x = 65	8.23		24.62		1.33		90.92		115.01	
H = 0.1	6.49 – 8.71		15.29 – 33.11		1.23 – 1.41		85.31 – 91.30		21.93 – 33.09	
H = 0.3	6.65 – 8.9		13.8 – 34.52		1.22 – 1.37		87.32 – 93.14		21.80 – 31.21	
H = 0.5	7.45 – 10.86		15.48 – 24.11		1.27– 1.40		84.05 – 90.38		26.26 – 39.94	
H = 0.9	6.19 – 9.65		14.07 – 31.06		1.25 – 1.41		86.69 – 91.56		21.81 – 35.21	

Table A4. Local (per cell) demographic rates for different home range strategies. Presented are the highest per cell values found within any one landscape grid (averaged from n = 100 replicate simulations) for populations at carrying capacity. For more details see Table A2 and for default parameter values see Table A1.

Parameter	Fledglings per breeding pair (max. of all cells)	Fledglings absolute (max. of all cells)	Breeding pairs absolute (max. of all cells)	Unsuccessful pairs absolute (max. of all cells)	Solitary storks absolute (max. of all cells)	Number of cells occupied by breeding pairs
	par -- par ++	par -- par ++	par -- par ++	par-- par++	par-- par++	par-- par++
Area-minimising with local aggregation	1.25 (0.75 – 1.75)	22.42 (6.5 – 14.89)	17.94 (5.0 – 9.73)	5.91 (0.78 – 3.0)	0.56 (0.5 – 1.88)	64 (65 – 88)
Area-minimising without local aggregation	1.64 (1.44 – 2.3)	5.68 (1.63 - 4.4)	3.33 (1.38 – 3.0)	0.82 (0.52 – 1.03)	0.91 (0.28 – 1.0)	76 (72 - 102)
Resource-maximising with local aggregation	1.76 (0.73 – 1.52)	8.0 (3.0 11.0)	5.5 (1.5 – 7.5)	2.0 (1.0 – 3.38)	0.5 (0.5 – 2.5)	183 (145 – 220)
Resource-maximising without local aggregation	1.66 (1.02 – 1.58)	2.32 (1.03 – 2.09)	1.13 (0.78 – 1.55)	0.75 (0.5 –0.75)	0.66 (0.25 – 0.88)	226 (159 - 279)

Table A5. Sensitivity of local (per cell) demographic rates to changes in parameter values. Presented are the highest per cell values found within any one landscape grid (averaged from n = 100 replicate simulations) for populations at carrying capacity. IBM parameters were changed by ±50% except p_{rand}, e_x and $e_{nestling,tol}$ which were changed by ±100%. For more details see Table A3 and for default parameter values see Table A1.

Parameter	Fledglings per breeding pair (max. of all cells)		Fledglings absolute (max. of all cells)		Breeding pairs absolute (max. of all cells)		Unsuccessful pairs absolute (max. of all cells)		Solitary storks absolute (max. of all cells)		Number of cells occupied by breeding pairs	
	par --	par ++	par --	par ++	par --	par ++	par--	par++	par--	par++	par--	par++
Area-minimising with local aggregation	1.25 (0.75 – 1.75)		22.42 (6.5 – 14.89)		17.94 (5.0 – 9.73)		5.91 (0.78 – 3.0)		0.56 (0.5 – 1.88)		64 (65 – 88)	
p_{rand}	2.17	0.63	44.76	3.0	32.57	3.0	0.0	1.5	0.26	1.0	22	49
p_{nearby}	0.81	1.13	14.71	27.15	12.33	19.46	3.39	1.1	0.5	1.16	67	71
d_{max} (d_{nearby})	1.41	0.86	35.41	13.67	24.1	12.12	2.59	5.58	1.0	0.25	63	66
e_{max}	0.50	1.30	0.50	73.75	0.50	56.51	1.0	10.81	0.5	0.88	16	89
e_m	0.87	1.03	18.04	12.1	18.04	7.94	6.51	1.94	0.31	0.53	87	43
e_x	0.73	2.09	9.25	15.02	9.25	5.96	30.21	0.06	1.5	0.53	64	35
$e_{nestling,tol}$	1.05	3.19	9.91	14.81	8.96	3.7	9.78	0.0	0.51	1.52	51	26
$n_{nestling,init}$	1.1	0.81	18.55	14.05	12.64	11.3	1.82	2.58	1.5	0.75	66	67
t_f	1.06	0.98	17.22	11.07	13.11	9.05	1.05	1.52	2.06	1.0	64	73
e_f	1.07	1.17	21.57	19.51	10.05	14.38	0.38	2.0	5.0	1.0	79	58
τ_{max}	0.98	1.08	5.51	28.75	4.01	19.54	3.0	2.39	1.0	1.5	45	73
brooding	1.15	0.73	17.8	10.42	13.97	8.83	1.57	6.34	0.52	0.75	74	65
no brooding	0.98		14.13		10.27		1.01		2.0		75	
equal sex numbers	1.09		18.25		15.09		5.76		0.0		89	
n_x = 65	0.93		33.47		25.16		3.5		1.5		259	
H = 0.1	1.0 – 1.25		3.52 – 13.64		3.0 – 10.8		1.25 – 3.9		0.38 – 1.02		59 - 149	
H = 0.3	0.73 – 1.02		6.0 – 12.4		4.5 – 10.64		1.13 – 3.13		0.5 – 1.01		89 - 127	
H = 0.5	0.63 – 1.25		6.5 – 17.5		5.0 – 12.94		1.06 – 3.64		0.51 – 1.63		55 - 113	
H = 0.9	0.75 – 1.41		6.0 – 14.75		4.0 – 12.3		0.81 – 5.0		0.52 – 1.13		60 - 94	

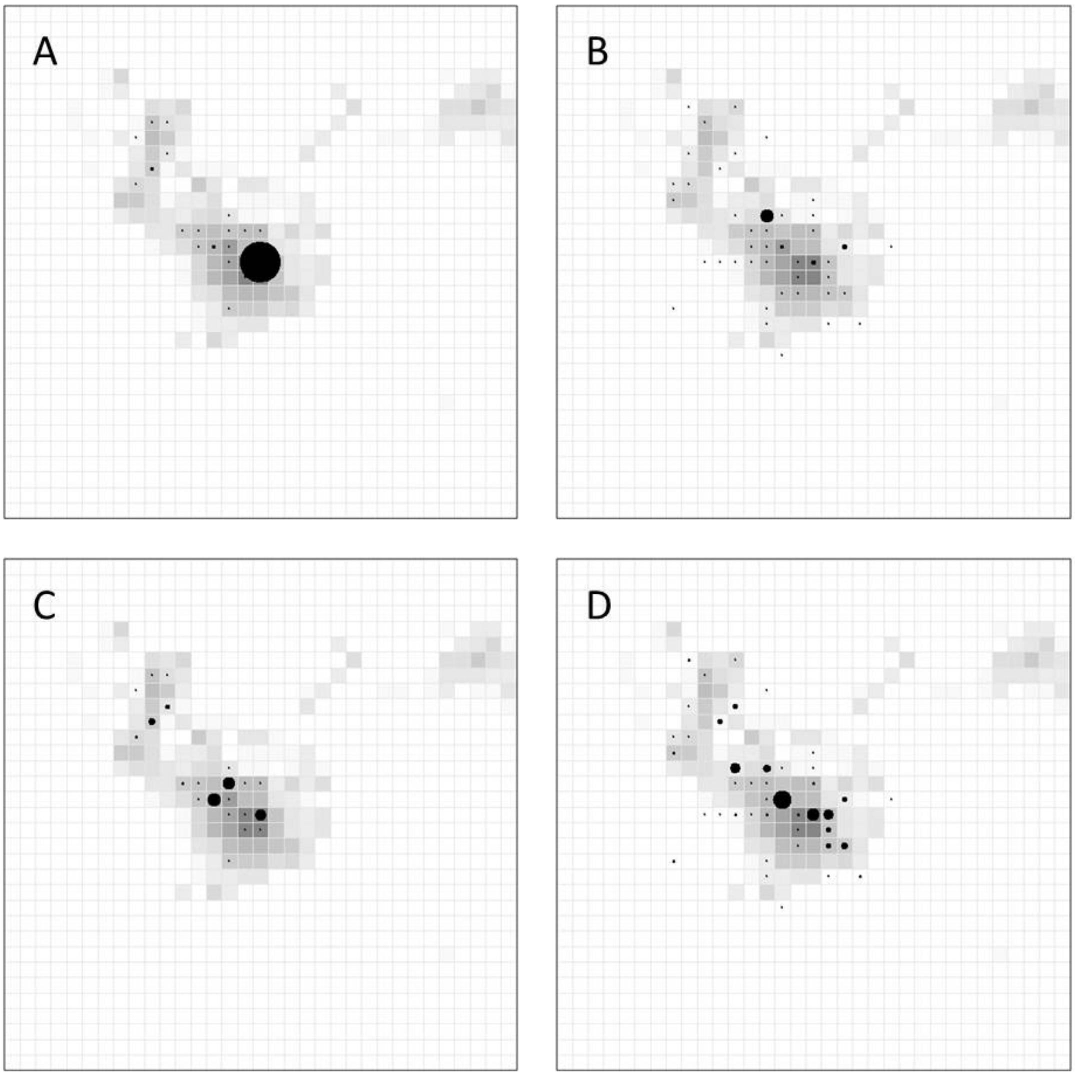

Figure A1. Spatial population structure of white stork breeding populations actively forming local nest aggregations in the default landscape. Left panels depict a stork population following an area-minimising home range strategy (A, C), right panels a stork population following a resource-maximising home range strategy (B, D). Grey shading indicate resource levels [kJ h^{-1}]. Points in the upper panels show mean numbers of breeding pairs for n = 100 simulations, and points in the lower panels show mean number of fledglings per breeding pair. Point size is proportional to the relative numbers, scaled for each row separately, and corresponds to a maximum of (A) 17.94 and (B) 5.5 mean breeding pairs, and to a maximum of (C) 1.25 and (D) 1.76 mean fledglings per breeding pair.

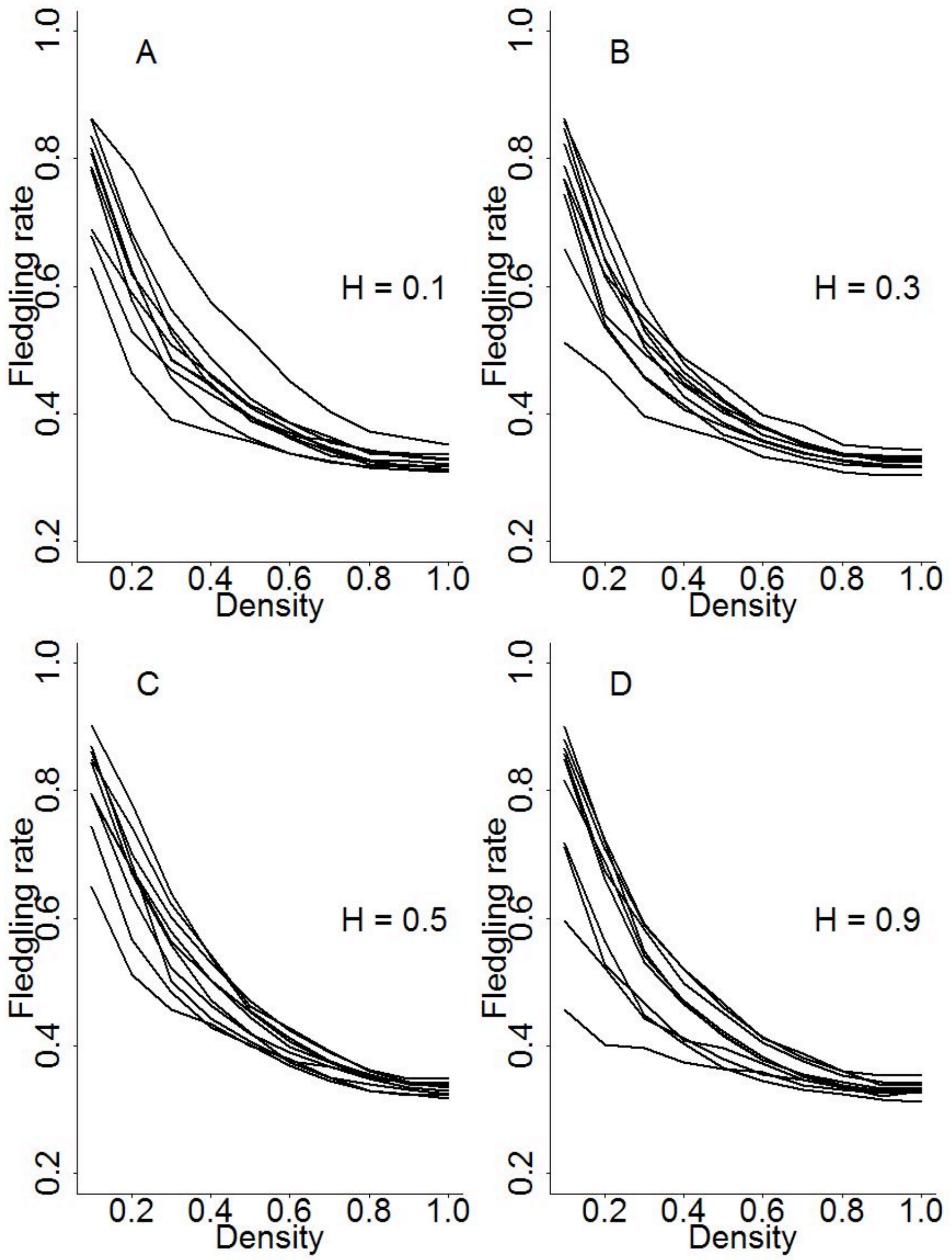

Figure A2. Mean proportion of nestlings surviving the breeding season plotted as a function of density for landscapes with different degrees of fragmentation. Storks follow an area-minimising home range strategy and actively form local nest aggregations. Fragmentation levels are expressed by the Hurst factor *H* determining the degree of spatial autocorrelation with stronger habitat clumping for increasing *H*. For each fractal dimension we simulated 10 replicate landscapes and ran n = 100 replicate simulations for each.