

Reproductive success of a reintroduced population of Eagle Owls *Bubo bubo* in relation to habitat characteristics in the Eifel, Germany

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Eagle Owls *Bubo bubo* were successfully reintroduced in the Eifel (Germany) in 1974 – 1999. Here we analyse whether reproductive success was related to habitat characteristics and if the patterns of habitat use and reproduction changed during the population increase. Microclimatic as well as mesoclimatic conditions influenced reproductive success. Owls nesting in basin-shaped enclosed rocky areas and on poriferous volcanic rocks were more successful than those breeding on other rock- and stone types. Additionally, reproductive success declined with elevation; at lower elevations climate was milder and drier, and pairs were breeding earlier in the season. In cold years pairs were breeding later and reproductive success was lower. Reproductive success decreased with the proportion of wooded area around the nest, probably due to a decrease of open hunting area. Although there was no long-term trend in the average reproductive success, a conspicuous decrease in the number of young per successful brood was detected, which was compensated by a decrease in the proportion of total breeding failures. An interpolation of the reproductive potential in the Eifel showed areas of high reproductive value for Eagle Owls, predominantly in low altitude areas. Only a small proportion of these sites were actually occupied.



Key words: *Bubo bubo*, conservation biology, habitat selection, reintroduction program, reproductive success, timing of breeding

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INTRODUCTION

In view of the world-wide reduction of biodiversity, nature conservation has to utilise all possibilities, including reintroduction, to save species from extinction (Scherzinger 1994). Temporary rearing

programs with consecutive reintroduction are increasingly important to conserve species that are mainly endangered due to rapid changes of their demographic structure (Ebenhard 1995) but that are not endangered due to a lack of suitable habitat or due to persecution. A closely monitored rein-

roduced population gives the opportunity to analyse aspects of the biology of a species which are otherwise difficult to follow in natural populations, e.g. settlement decisions in an increasing 'founder' population, or density-dependent trends in reproductive success.

After complete eradication in north-western Germany and neighbouring countries, the Eagle Owl *Bubo bubo* was successfully reintroduced by a conservation project started in 1964 (Herrlinger 1973). After the first successful breeding attempts in the Harz mountains (1973) and in the Eifel (1975), an increasing and expanding population established in north-west Germany, Belgium, eastern France and Luxembourg. This re-establishment was supported during the 1980s and early 1990s by further release of captive-bred owls (Dalbeck & Heg submitted). The number of released Eagle Owls was reduced during the early 1990s and abandoned afterwards (Dalbeck & Heg submitted). Since 1978, the European Group of Experts on Conservation and Biology of Owls (EGE) follows the development of the population in the Eifel, which is one of the centres of the reintroduction program. Today, the population of Eagle Owls in the Eifel is stable at a level of 70–90 occupied sites including c. 60–80 successful breeding pairs (Dalbeck & Heg submitted).

The aim of this study was to investigate (1) long-term changes in reproductive success after the re-introduction of Eagle Owls; (2) the relationships between climate, the timing of breeding and reproductive success, (3) effect of micro-and macro-habitat characteristics on reproductive success and (4) future prospects for the population based on the current use of the Eifel area and the availability and distribution of suitable breeding sites not yet occupied by the owls.

METHODS

Study area

Data were collected in the Eifel region in western Germany, a typical central European hillside landscape of c. 9500 km² with elevations ranging from

60 m to 750 m above sea level. The major part of the study area lies on an old Palaeozoic plateau, separated by steep river valleys and with scattered extinct volcanoes. Large forests are restricted to uplands in the west of the study area with unfavourable climate and poor soils, covering up to 50% of the land. At lower elevations, land use is dominated by agriculture and forests are restricted to hill slopes and valleys. The climate is sub-Atlantic i.e. temperate with cool summers and mild winters. The average summer temperature decreases, and winter temperature increases from west to east, modulated by altitude (average annual temperature is 6°C at high elevations and > 9°C in lowland areas). Mean annual precipitation is > 1100 mm in the upland central and western parts and < 550 mm in the lowlands of the south-east of the study area (Deutscher Wetterdienst 1957).

Population monitoring and reproductive success

A detailed description of Eagle Owl monitoring is given in Bergerhausen & Willems (1988). In hillside areas Eagle Owls mainly breed in rocky formations (Bergerhausen & Willems 1988). All rocky formations ($n = 421$) within the study area were assumed to be potential breeding sites. In the Eifel area, the majority of these sites were natural rock formations of the larger valleys and quarries (Bergerhausen *et al.* 1989b, Dalbeck & Heg submitted). Only seven breeding sites were in trees ($n = 2$) and buildings/ruins ($n = 5$).

To assess population growth and reproduction, potential breeding sites were visited at least three times per season. If courtship behaviour was recorded, sites were visited up to twelve times to determine reproductive parameters such as breeding success and – if any – number of young. Between 1985 and 1994, all known 421 potential breeding sites were visited yearly. Before 1985 and after 1994, only sites occupied at least once in any year were checked regularly.

Breeding behaviour was monitored until chicks reached four weeks of age (Bergerhausen & Willems 1988, Dalbeck & Heg submitted); chick number alive at this age was used as a measure of

reproductive success. Total breeding failure was common and therefore analysed separately. To avoid disturbance, no attempt was made to determine clutch size. We determined laying date from a sub-sample of broods for 1983–93 by estimating chick age from wing length (i.e. maximum wing chord, based on a calibration growth curve of Eagle Owl hatchlings in captivity provided by W. Bergerhausen, pers. comm.) and subtracting 35 days for the average incubation duration (Glutz von Blotzheim & Bauer 1994). All laying dates were expressed in days since the first of February (1 = 1st of February).

Timing of breeding, reproductive success and weather

To assess the effects of weather conditions on laying date and reproductive success, we calculated the following weather parameters for the winter period November–March: average temperature, number of days with the minimum temperature below 0°C ('frost-days'), number of days with the maximum temperature below 0°C ('ice-days'), total precipitation, number of days with snow coverage ('snow-days'), and total hours of sunshine (converted in 'sun-days'). These data were obtained from the meteorological station Sistig/ Eifel (at 505 m elevation) for each month separately for the years 1983 – 1998 (Deutscher Wetterdienst 1983–1998). The average temperature was highly associated with the number of snow-days (Pearson $r = -0.82$, $P < 0.001$, $n = 16$ years), frost-days (Pearson $r = -0.95$, $P < 0.001$, $n = 16$) and ice-days (Pearson $r = -0.93$, $P < 0.001$, $n = 16$). Since temperature, snow-days, frost-days and ice-days were highly correlated, a compound measure of these four variables was created (Principal Component, PC), using Factor Analysis (Eigenvalue: 3.56, Component Matrix/ Communalities: average temperature: $-0.98/0.96$, frost-days: $0.96/0.92$, ice-days: $0.93/0.86$, snow-days: $0.90/0.82$). However, since PC-values will not be comparable across study populations except when e.g. the original data-sets of two populations would be analysed in conjunction, the results will also be presented for average temperature only (which

had the highest loading on the PC, see above). Only the sub-sample of nests with known laying dates could be used for these analyses.

Reproductive success and habitat quality

Reproductive success was known for all territorial pairs. To assess the effects of habitat characteristics on reproductive success, the following abiotic habitat parameters were recorded for each of the nesting sites (see also Dalbeck & Heg submitted): (1) micro-habitat characteristics i.e. (a) habitat type: rocky slope, slope, heap, quarry, clay or gravel pit, building, (b) stone type: clay, limestone, sandstone, schist, volcanic stone, sand/gravel, others), and (c) type of ledge: secluded basin, cliff or slope, (d) ledge characteristics such as height and breadth (in metres), and exposure in five classes (north to east, east to south, south to west, west to north or all directions). (2) Macro-habitat features i.e. percentage of land covered by wood, open landscape, watercourses and human settlements (villages, towns and suburban areas) in a perimeter of 2.0 km around potential breeding sites (these four variables sum up to 100%, and the percentage coverage by watercourses were omitted from the analyses to avoid redundancy), and distances to nearest roost (forest edge or group of trees), nearest road and nearest human settlement (in metres). A perimeter of 2.0 km around the nest sites was used, because a radio-telemetry study during breeding showed Eagle Owls in our study population gather the majority of their food within this perimeter (Dalbeck *et al.* 1998, see also Leditznig 1996). However, since the analyses on the timing of breeding, climate and reproductive success showed a considerable effect of temperature and elevation via laying date on reproductive success (see Results), it became pertinent to include also some general climatic condition effects. This allowed us to assess whether macro- and micro-habitat features affected reproductive success independent of general climate. The general climatic conditions we determined for each nest site were: (3) elevation (in metres) and (4) annual average temperature (in °C, both from isoclines in Deutscher Wetterdienst 1957).

Statistical analyses

Statistical analyses were done with SPSS 11.0 and R1.0.8 (Crawley 2002). All tests are two-tailed with the *P*-level of significance set at 0.05. We used General Linear Models (GLM) or General Linear Mixed Models (GLMM) in the majority of analyses. For the general modelling procedures, when and how to use link-functions and correct for over-dispersion, see Crawley (2002). GLMM uses a Restricted Maximum Likelihood Method (REML) to decompose variances and allows incorporation of continuous and categorical fixed variables, and random effects. Nest site identity (random factor) was added in the GLMMs where appropriate. Average annual reproductive success in relation to laying date and weather was analysed with a General Linear Model (GLM). Nest site dependent reproductive success was related to habitat characteristics and average climatic conditions using a GLMM. As total breeding failure seemed an important determinant of reproductive success, we separately assessed the effects of habitat characteristics and climatic conditions on the 'breeding success' per site ('no fledglings' coded 0 and 'at least one fledgling' coded 1) with a GLM, using a weighted logit-link function (analysis on proportions, i.e. the number of successful breeding events per the number of successful plus unsuccessful breeding events, see Crawley 2002). For this analysis, only active territorial pairs where the female was seen to incubate eggs were selected.

To assess whether Eagle Owls settled first on breeding sites with the highest expected reproductive success, and re-used those sites more frequently, expected reproductive success on 259 of the 421 potential breeding sites was computed using the model presented in the Results (Table 3). Of the remaining 162 sites not all the relevant habitat parameters had been measured. The occupation rate of never used sites could be calculated using the data 1985–1994 only, therefore sample size is 10 per site. For the other sites the sample sizes varied between 1 and 21. To analyse whether the re-use of sites depends on the first year of settlement, the yearly occupation rate for each site at least used once was calculated from the first year

of settlement onwards. The same model was used to calculate the expected reproduction at each as yet unoccupied site for the total study area. Since reproductive success could only be assessed on sites used at least once, only 138 sites were available to compute a geographical contour map of the expected average reproductive success. However, this would overestimate the suitability for reproduction of a region with a relatively high number of unoccupied low quality sites, since non-used sites are excluded in the assessment. Therefore, we calculated the expected reproductive success, instead of reproductive success, for all the sites where the relevant habitat parameters were measured. For some never used sites the percentage wood coverage was not determined, and we assumed a value of 30.23%, which is the median value of the non-used sites. This increased the sample size to 393.

We identified 'geographical hotspots' in the area by kernel estimations, i.e. to identify areas with sites frequently used by Eagle Owls, areas with sites with a high expected reproductive success, and areas both highly frequented and with a high expected reproductive success. This allowed us to identify areas particularly valuable for the persistence of the population as a whole. Finally, we used the expected reproductive success to assess sites not used at the end of study period (1998), but which might be valuable to the owls. Unless otherwise stated averages are given \pm SE.

RESULTS

Population dynamics

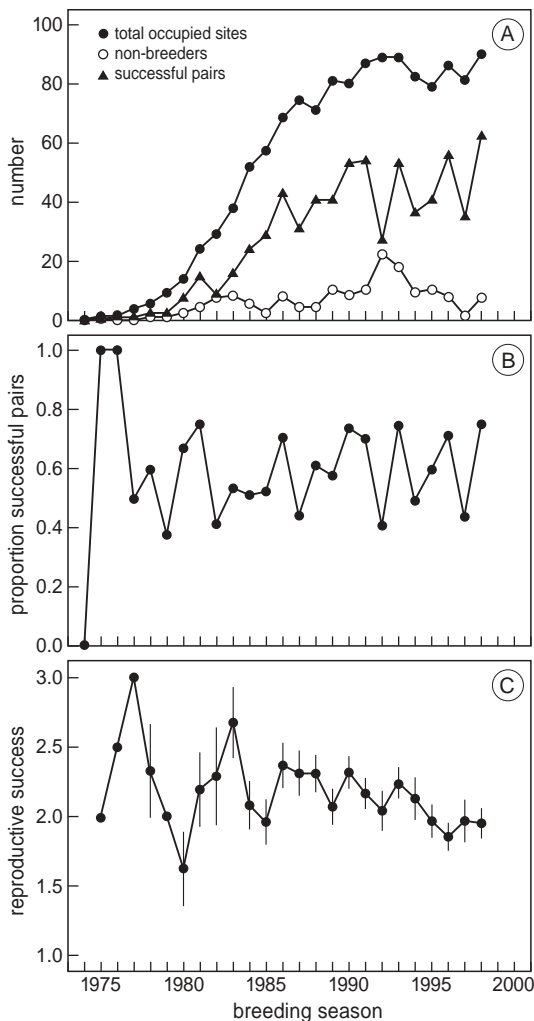
Between 1974 and 1998, 138 sites were occupied at least once by a single adult or a pair, and in any given year, the majority were occupied by territorial pairs (Table 1). The majority of territorial pairs tried to reproduce (nesting activity, eggs or chicks, 88.8%), but only 67.2% of these breeder pairs successfully fledged at least one chick (Table 1). The number of occupied sites steadily increased over the years and levelled off around 1991 (Fig. 1A). By then, the majority of sites were occupied by

Table 1. Occupancy and average reproductive success of Eagle Owls at 138 nest sites between 1978 and 1998, separated for all occupied sites (single individuals, breeder pairs or unknown individuals), sites occupied by a pair ('territorial pairs'), sites occupied by a pair with a nest ('breeder pairs'), and sites occupied by a pair with at least one chick at an age of 4 weeks or older ('successful pairs'). Sample sizes are the number of nest site years.

Number of sites occupied by	Sample size	% All occupied sites	Average reproductive success ^a
All occupied sites ^b	1271	100.0	1.13 ± 1.23 (0 – 5)
Territorial pairs	1130	88.9	1.27 ± 1.24 (0 – 5)
Breeder pairs	1003	78.9	1.43 ± 1.22 (0 – 5)
Successful pairs	674	53.0	2.13 ± 0.86 (1 – 5)

^a Number of chicks alive at four weeks of age, means ± SD (range).

^b In 15 additionally occupied sites, the reproductive success could not be determined with certainty.



pairs. Single adults were omitted from all subsequent analyses on reproductive success.

There were no long-term changes in the proportion of successful breeding pairs over the years (Fig. 1B, GLM with weighted logit-link function, $\chi^2_1 = 2.08$, $P = 0.15$, $n = 25$ years), but there was a decline in the average number of young fledged through the years for successful pairs (Fig. 1C, GLMM corrected for random nest site identity, effect of year: $F_{1,438.0} = 8.3$, $P = 0.004$, $n = 674$, with coefficients: intercept 41.75 ± 13.76 , year -0.020 ± 0.007).

Effects of timing of breeding, elevation and climate

We used the sub-sample of broods with known laying dates to assess the relationships between climate, elevation, laying date and reproductive success. In years when clutches were produced early in the season, the proportion of breeding failures was low (Fig. 2A, GLM with weighted logit-link, $\chi^2_1 = 6.77$, $P = 0.026$, $n = 12$ years; constant = -0.508 ± 0.321 , coefficient for laying date effect = 0.019 ± 0.007) and reproductive success was

Figure 1. (A) Number of occupied sites for 1974 – 1998 (total, non-breeders, and successful pairs), (B) proportion successful breeding pairs of all territorial pairs (at least one chick fledged), and (C) reproductive success of successful breeding pairs (mean number of fledged chicks ± SE), (sample sizes see (A)). Note that no chicks fledged in 1974.

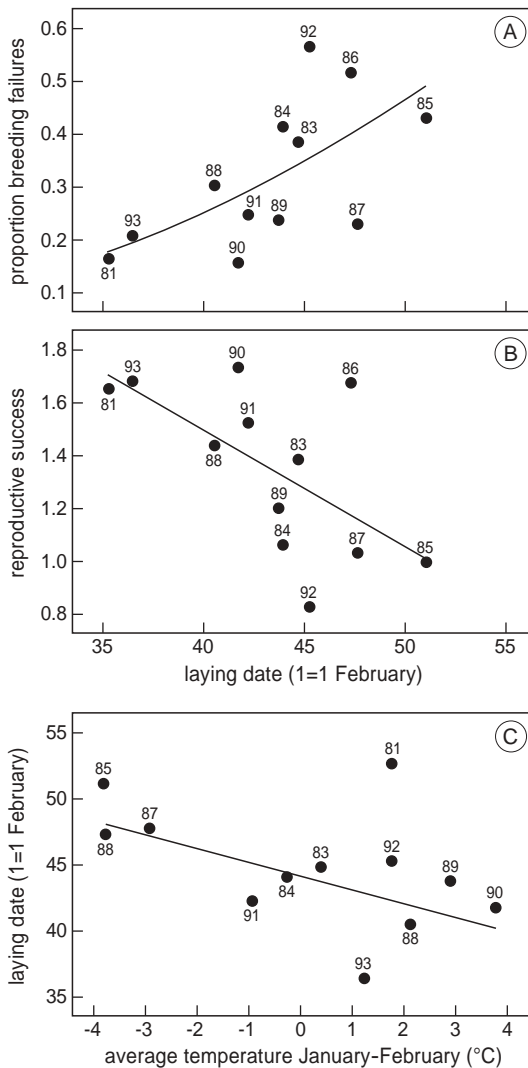


Figure 2. Relationship between the average laying date and (A) the proportion of breeding failures and (B) average reproductive success. (C) Laying date advanced with the average temperature in January and February. The years and regression lines are indicated in the figures (see text for statistics). Note that for 1982 no weather data were available.

high (Fig. 2B, GLM $F_{1,11} = 6.21$, $P = 0.032$, constant = 3.222 ± 0.756 , coefficient for laying date effect = -0.043 ± 0.017). A major determinant of differences in average laying date and subsequent

reproductive success seemed to be the weather in January and February, which is just before and during clutch initiation. Onset of laying was delayed when breeders experienced bad weather in late winter (GLM on the Principal Component PC of the four weather variables, $F_{1,10} = 8.90$, $P = 0.015$), e.g. laying was delayed under low late winter temperatures (Fig. 2C, GLM $F_{1,10} = 8.30$, $P = 0.018$; constant = 44.141 ± 0.897 , coefficient for temperature effect = 1.021 ± 0.354). When the PC was fitted first to a regression model, no additional effects of precipitation or sun-days on the timing of breeding could be detected.

At higher elevations pairs experience lower temperatures than pairs breeding at lower elevations, a 3°C gradient was similar in magnitude to year-to-year differences in average temperatures. Hence, we expected a positive relationship between elevation of a nest site and timing of breeding. This was confirmed by the analysis (Table 2). To give an example, average laying date at elevations below 300 m was 40.53 ± 0.96 ($n = 202$) compared with 45.54 ± 0.83 above 300 m ($n = 226$). Both climatic conditions in January and February, and elevation were significantly associated with the timing of breeding (effects of PC and laying date in Table 3, illustrated with average temperature in Fig. 3A). Apparently, pairs breeding at higher altitudes showed a lower reproductive success via delayed breeding (Fig. 3B, Table 2). However, independently of laying date reproductive success and elevation were inversely related, suggesting that there might be additional negative effects of breeding at high altitudes beyond delayed breeding (Table 2).

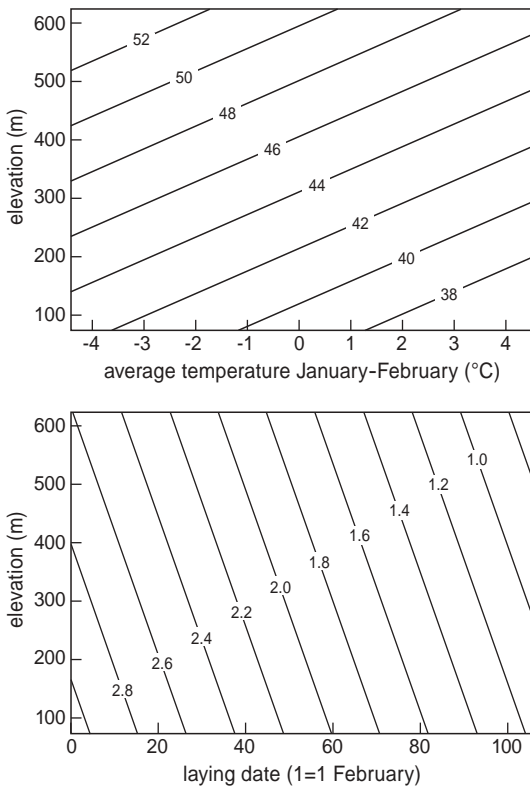
Effects of micro- and macro-habitat quality

Reproductive success varied across years. Exceptionally low productivity was recorded in 1992, when an earthquake occurred on the 13th of April (5.9 Richter), destroying many broods. GLMMs were used to assess fixed categorical, fixed covariates and the random effect of nest site identity simultaneously on reproductive success (Table 3). This allowed us to test for effects of micro- and macro-habitat characteristics on reproductive

Table 2. Results of two GLMMs on the effect of climate (Principal Component, A) or average temperature (B), and elevation on the laying date of territorial pairs. (C) The effect of laying date and elevation on reproductive success ($n = 409$ of 98 nest sites). Models corrected for random nest identity effects.

Parameter	<i>F</i>	<i>df</i>	Error <i>df</i>	<i>P</i>	Coefficients \pm SE
A Laying date ($n = 409$)					
Constant	290.07	1	57.2	<0.001	37.31 \pm 2.19
Climate PC ^a	16.09	1	285.7	<0.001	2.02 \pm 0.51
Elevation	11.16	1	56.3	0.001	0.021 \pm 0.006
B Laying date ($n = 409$)					
Constant	292.98	1	57.8	<0.001	37.51 \pm 2.19
Temperature	14.25	1	288.5	<0.001	-0.813 \pm 0.215
Elevation	11.26	1	56.6	0.001	0.021 \pm 0.006
C Reproductive success ($n = 1064$)					
Constant	251.05	1	95.3	<0.001	3.14 \pm 0.198
Laying Date	23.79	1	257.4	<0.001	-0.018 \pm 0.004
Elevation	3.73	1	64.2	0.058	-0.00085 \pm 0.00044

^aPrincipal component of four January–February weather variables: average temperature, snow-days, frost-days, and ice-days.



success, while ‘controlling’ for confounding effects of annual differences and nest sites.

Nest sites located on volcanic rocks produced the highest number of offspring, followed by schist, sandstone, limestone, sand/gravel and clay (Fig. 4A, Table 3). Note that there were only five breeding sites located on buildings, and although they seemed to do equally well as birds breeding on volcanic rocks, larger sample sizes are needed to establish this. Relatively high productivity was also reached in basins, followed by cliffs compared to rock-slopes (Table 3, Fig. 4B). As before, there were general climatic effects on reproductive success. First, success tended to increase with average annual temperature (Table 3, Fig. 4C). Second, sites at higher elevations above sea level were sig-

Figure 3. Contour plots representing interrelationships between laying date, elevation, average annual temperature in January and February, and reproductive success. (A) Laying date was associated with the combined effect of elevation ($P = 0.001$) and average temperature ($P < 0.001$). (B) Reproductive success was associated with the combined effect of elevation ($P = 0.058$) and laying date ($P < 0.001$). Plots based on results in Table 2.

Table 3. Effects of habitat characteristics on reproductive success of territorial pairs ($n = 1076$ of 123 nest sites). Results are depicted for a GLMM, corrected for the random effect of nest site identity.

Parameter	<i>F</i>	<i>df</i>	Error <i>df</i>	<i>P</i>	Coefficients \pm SE
Constant	10.99	1	89.5	0.001	2.579 \pm 0.533
Year	4.66	20	945.1	<0.001	^b
Stone type	5.20	6	102.8	<0.001	
Volcanic stone					0 ^a
Limestone					-0.353 \pm 0.137*
Sandstone					-0.693 \pm 0.196***
Schist stone					-0.487 \pm 0.193*
Building					0.567 \pm 0.488
Sand					-1.236 \pm 0.523*
Clay					-1.363 \pm 0.398***
Placement	3.15	2	88.5	0.048	
Basin					0 ^a
Cliff					-0.206 \pm 0.176
Slope					-0.501 \pm 0.207*
Average temperature (°C)	3.00	1	83.2	0.087	0.146 \pm 0.084
Elevation (m)	9.81	1	89.3	0.002	-0.0023 \pm 0.0007
% Wood within 2 km	5.51	1	92.5	0.021	-0.0077 \pm 0.0033

^a Reference category. Symbols denote categories significantly different from the reference category: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

^b For clarity coefficients for the different years not depicted (see also Fig. 1).

All interactions and the following fixed effects were not significant: habitat type; ledge height and breadth; exposure; percentage of open landscape and human settlements; distances to nearest roost, nearest road and nearest human settlement.

nificantly less productive than those at lower elevations (Table 3, Fig. 4D). Finally, offspring production decreased with the percentage of continuous woodland area around the nest site (Table 3, Fig. 4E). There was a tendency for a curvilinear relationship with percentage woodland, but the effect of percentage woodland squared failed to reach significance in the final model ($P > 0.1$).

An important component of reproductive success was total breeding failure. Almost all complete breeding failures were caused by nests being abandoned during incubation or shortly after hatching following human disturbance or severe weather conditions like prolonged rain, low temperatures or snowfall. We computed the number of successful breeding attempts (at least one chick fledged) and the total number of breeding attempts (territorial pairs showing breeding activity) per nest site and entered these as the depen-

dent variable in a GLM with a weighted logit-link function (Table 4). The same variables affecting reproductive success of territorial pairs were also responsible for general breeding success, i.e. stone type (better at volcanic rocks), placement of the rock (better in basins), elevation (better at lower elevations), and percentage woodland area (better when less cover). The only exception was average annual temperature, which was non-significant for breeding success ($P > 0.16$).

Effects of site occupancy

The number of years a particular breeding site had been occupied varied between 1 and 21 years (Fig. 5A). This large variation is partly due to the population expanding during the study period. We expected the reproductive success to increase with the number of years the site had been occupied, e.g. due to released birds gaining breeding experi-

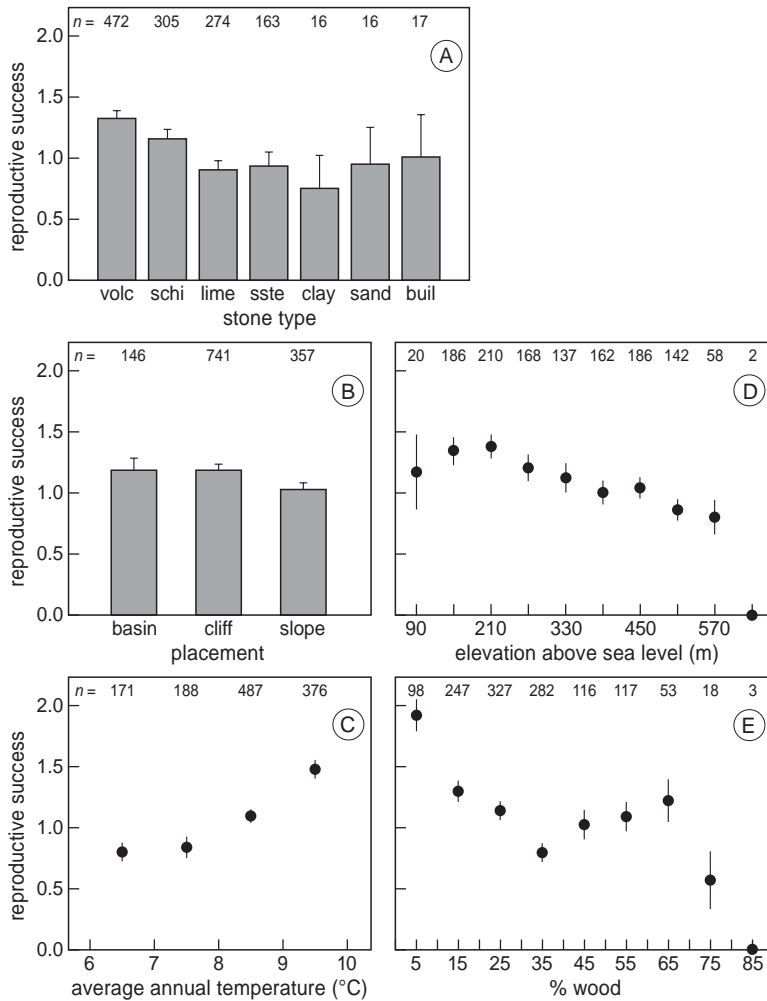


Figure 4. Reproductive success differed by (A) stone type of the nest site, (B) placement, (C) temperature, (D) elevation, and (E) percentage continuous woodland around the nest site. See Table 2 for statistics. Sample sizes are indicated.

ence or getting older, assuming some degree of site-fidelity. However, although reproductive success significantly increased in the first nine years, it decreased significantly afterwards (Fig. 5B, GLMM with random nest site identity, $n = 1271$, effect of year: $F_{20,1049.7} = 4.15$, $P < 0.001$; effect of years site occupied: $F_{1,850.0} = 29.17$, $P < 0.001$; effect of years site occupied squared: $F_{1,1139.4} = 25.38$, $P < 0.001$).

Above, we showed that habitat characteristics related to Eagle Owl reproductive success (Table 3), and therefore one would expect Eagle Owls to preferentially use and re-use sites where they can expect the highest reproductive success. To compare both occupied and unoccupied sites, we derived a measure of reproductive success comparable across all sites. We calculated the expected reproductive success for all sites both occupied

Table 4. Effects of the habitat characteristics on the probability of successful breeding per nest site (number of broods with at least one offspring fledged / total number of incubated broods, calculated per site; $n = 118$ sites). Only breeding attempts were selected, i.e. the territorial pairs showed breeding activity and the female was incubating eggs. Results are depicted for a GLM, with a weighted logit-link function.

Parameter	<i>F</i>	<i>df</i>	<i>P</i>	Coefficients ± SE
Constant				3.535 ± 0.477
Stone type	3.97	6	<0.001	
Volcanic stone				0 ^a
Limestone				-0.430 ± 0.195*
Sandstone				-1.022 ± 0.295***
Schist stone				-0.408 ± 0.306
Building				0.932 ± 1.120
Sand				-1.830 ± 0.768*
Clay				-1.695 ± 0.709*
Placement	2.39	2	0.09	
Basin				0 ^a
Cliff				-0.423 ± 0.276
Slope				-0.958 ± 0.306**
Elevation (m)	34.65	1	<0.001	-0.0042 ± 0.0008
% Wood within 2 km	8.13	1	0.004	-0.014 ± 0.005

^a Reference category, symbols denote categories significantly different from the reference category: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Due to overdispersion (null deviance = 261.7, $df = 117$, residual deviance = 190.3, $df = 107$), F -test instead of deviance χ^2 was used (see Crawley 2002).

All interactions and the following fixed effects were not significant: habitat type; ledge height and breadth; exposure; percentage of open landscape and human settlements; distances to nearest roost, nearest road and nearest human settlement; average temperature.

and unoccupied, based on the habitat effects on reproduction depicted in Table 3:

$$\text{Expected reproductive success} = \alpha + \beta_{\text{stone type}} + \delta_{\text{placement}} + \gamma \times \text{temperature} + \lambda \times \text{elevation} + \mu \times \text{percentage wood cover within 2km around the site.}$$

Where α is the overall intercept (constant + average year coefficient = $2.579 - 0.242 = 2.337$), β are the seven coefficients for each of the 7 different stone types, δ are the three coefficients for each of the 3 different placements (basin, cliff or slope) and γ is 0.146, λ is -0.0023 and μ is -0.0077 (see Table 3). The expected reproductive success could also be used to assess the prospects for as yet unused sites (see below).

Eagle Owls preferentially used sites with the highest expected reproductive success (Fig. 6A,

GLM with weighted logit-link, $n = 259$, constant = -1.193 ± 0.094 ; effect of expected reproductive success = 0.586 ± 0.075 and F -test used due to overdispersion: $F_1 = 61.6$, $P < 0.0001$), and sites occupied in the early years were more frequently occupied compared to sites used first in later years (1975: ca. 85% occupied, 1994: ca. 60% occupied, Fig. 6B, GLM with weighted logit-link, $n = 117$, null model $\Pi^2 = 836.3$; final model $\Pi^2 = 814.9$, constant = 139.2 ± 30.0 , effect of first year = -0.070 ± 0.015 with $\Pi^2 = 21.5$, $df = 1$, $P < 0.0001$. Sites used first since 1995, $n = 8$, were excluded from the analysis, since no accurate occupation rates could be calculated for them. Thus, we expected sites with the highest reproductive success to be occupied first. However, of the sites used at least once, there was no relationship

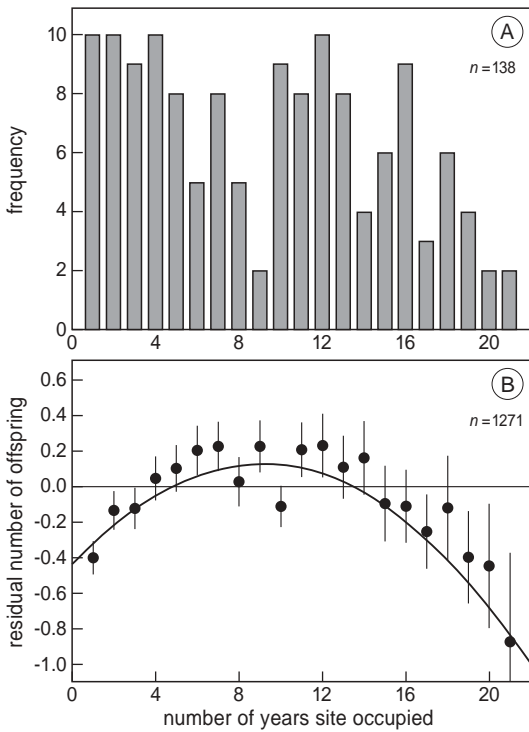


Figure 5. (A) Frequency distribution of the number of years a nest site was occupied by single adults or pairs. (B) Residual reproductive success in relation to the number of years the site was occupied. Residuals are offset against the annual mean reproductive success. See text for statistics.

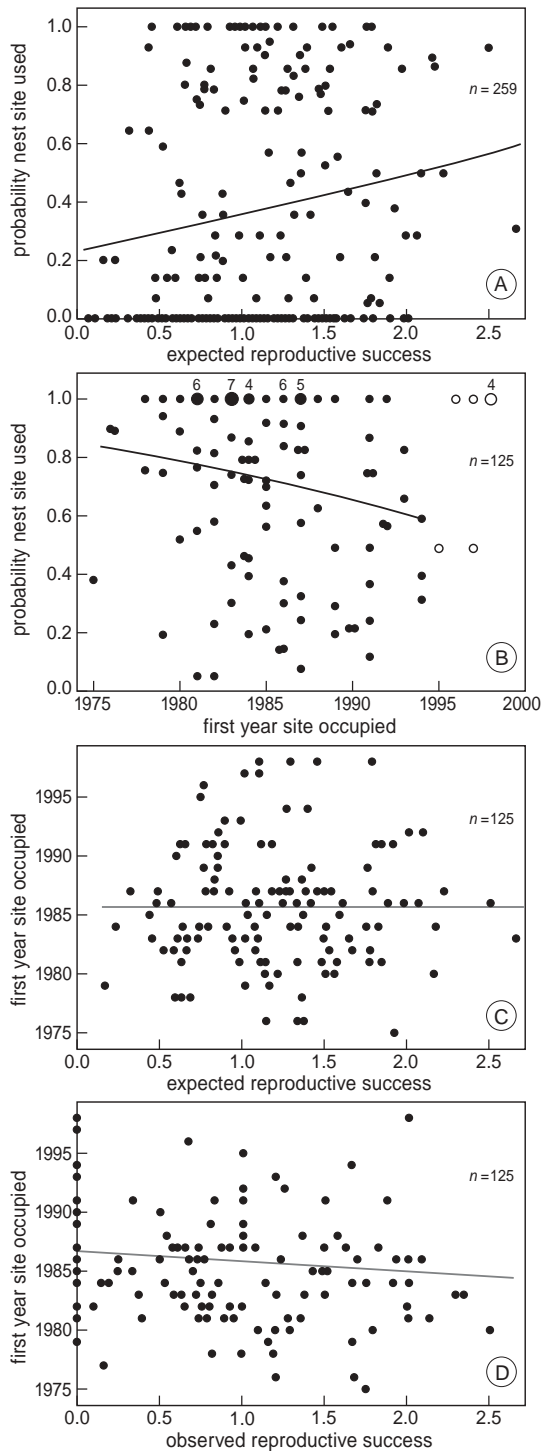


Figure 6. Relationships between the probability a site was used, the first year of settlement and expected reproductive success. (A) Sites with a higher expected reproductive success were more likely to be occupied. (B) The occupation rate since first settlement of sites first used in the early years was higher compared to sites used in their sample years. Multiple occurrences are depicted with their sample sizes. Sites used first since 1995 (open symbols, $n = 8$) were excluded from the statistical analysis (see text). Of the sites used at least once, no relationship was apparent between (C) the expected reproductive success and (D) the observed reproductive success, versus the year of first settlement.

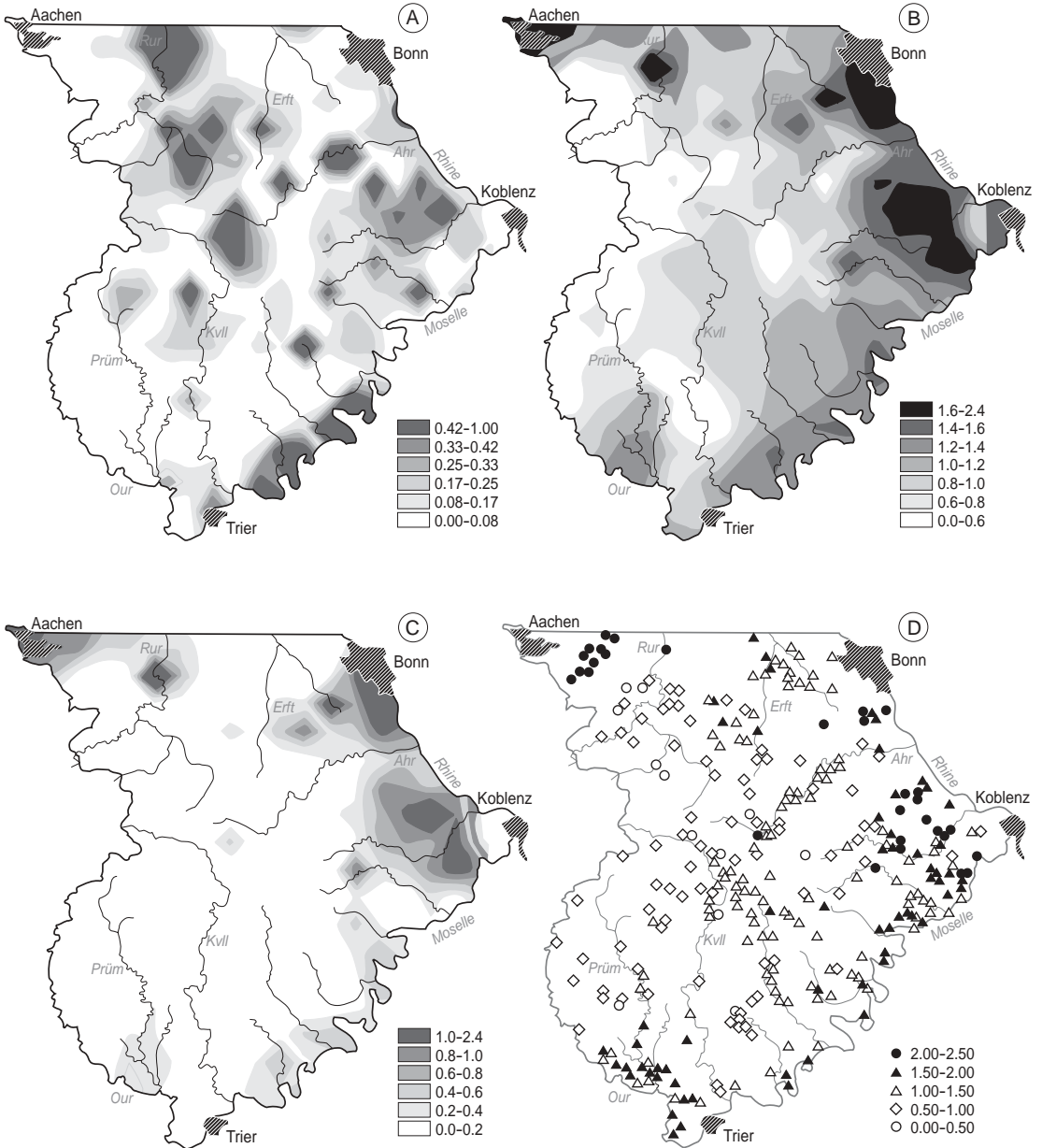


Figure 7. Interpolated contour maps of the Eifel of (A) the probability a site was used by Eagle Owls (based on $n = 417$ sites), (B) expected annual reproductive success (based on $n = 393$ sites), (C) settlement probability multiplied by the expected annual reproductive success (based on $n = 393$ sites). (D) Expected reproductive success of all non-used sites in 1998 ($n = 311$). See text for statistics.

between expected or observed reproductive success and the year of first occupation (Fig. 6CD, $n = 125$, expected: GLM $F_{1,124} < 0.001$, $P = 0.99$; and observed: GLMM with random nest identity and fixed year effects, effect of first occupation: $F_{1,170.4} = 3.18$, $P = 0.076$), although for observed reproductive success the relationship tended towards the predicted direction of early sites being more productive (Fig. 6D, coefficient first year of occupation: -0.024 ± 0.014).

Future development of the population

A relatively high site occupancy rate was apparent in the eastern Eifel, in the Rur-Eifel, parts of the northern and central Eifel and the valleys of the rivers Ahr and Moselle (Fig. 7A). These were also the areas with the highest densities of Eagle Owls (see Dalbeck & Heg submitted).

If we calculate the expected reproductive success for used and non-used sites (see above), hotspots of expected offspring productivity were located in the eastern Eifel, in the Rur valley (northern Eifel) and parts of the valley of the river Moselle (Fig. 7B). The eastern Eifel and the Moselle valley are low elevation areas, and show a relatively high occupation rate and high likelihood of reproductive success (Fig. 7C). Particularly the area west of Koblenz (eastern Eifel) has high breeding numbers as well (see also Dalbeck & Heg submitted).

To calculate whether prospecting juvenile Eagle Owls have still non-occupied high quality breeding sites available to colonise, the expected reproductive success of all sites not yet used in 1998 was calculated (Fig. 7D). As expected, high quality sites were only available at the lower elevations along the perimeter of the Eifel region, particularly in the areas where Eagle Owls have already reached considerable densities (Fig. 7D). The only two exceptions are the Moselle valley, particularly just south-west from Koblenz, and around Trier. These two areas provide a large number of high quality breeding sites, in regions with relatively low owl densities.

DISCUSSION

Climate, timing of breeding and reproduction

Timing of breeding is an important determinant of reproductive success in birds (e.g. Siikamäki 1998, Heg 1999). For owls, early breeding generally seems to be beneficial. In Ural Owls *Strix uralensis* of southern Finland early breeding females had a higher annual (Pietiäinen 1988, 1989) and lifetime reproductive success (Brommer *et al.* 1998). Korpimäki & Lagerström (1988) found a strong negative relationship between laying date and clutch and brood sizes in Tengmalm's Owl *Aegolius funereus*, the same was stressed for Barn Owl *Tyto alba* in Burgundy (Baudvin & Jouaire 2001). Leditznig *et al.* (2001), Penteriani *et al.* (2002) and Marchesi *et al.* (2002) found a clear relationship between laying date and productivity in Eagle Owls of pre-alpine Austria, Mediterranean France and in the north Italian pre-Alps. Therefore, our results on reintroduced Eagle Owls are in agreement with findings in Eagle Owl- and other Palaearctic owl populations. For the conditions of temperate Europe, it can be expected that winter severity and pre-breeding food availability will affect the accumulation of body reserves, and timing of laying and clutch size. Therefore, early breeding can be assumed as a response to good physical condition of the Eagle Owls (Penteriani *et al.* 2002). Eagle Owls need c. 30 weeks for breeding and raising the young (Glutz von Blotzheim & Bauer 1994), so an important benefit of early laying might be the prolonged time available to raise owlets to independence before the following winter. Hence, early breeding may improve offspring survival, as it does in other raptors and owls (e.g. Houston 1989, Daan *et al.* 1990, Sergio & Newton 2003).

Whatever the causal chain of factors, laying date and reproductive success were associated with weather conditions during the pre-breeding period. Weather conditions at nest sites depended on (1) annual variations in average temperature during the previous winter and (2) regional variations in weather conditions related to elevation (up to 3°C lower temperatures at higher elevations)



Figure 8. High-quality habitat of Eagle Owl in the valley of the river Moselle, Germany (photo L. Dalbeck). Rocks surrounded by open, mixed landscapes in climatically favoured lowland areas permit the highest reproductive success in the Eifel. Traffic, badly constructed power pylons along railroads and plot realignment are typical problems and dangers in the study area.

and the west-east seasonal temperature gradient (east: colder in winter, warmer in summer, less precipitation). Comparing reproductive success of European Eagle Owl populations, Donázár (1990) found an effect of average latitude (and therefore climate) on average brood size.

We have circumstantial evidence that adverse weather might directly lead to losses of broods due to cooling of the eggs or hatchlings, as indicated by the increase of complete breeding failure with elevation. A direct influence of elevation seems to be negligible in Mediterranean populations such as in southern France (Penteriani *et al.* 2002). Nevertheless, weather conditions might also indirectly affect timing of breeding and reproductive success

in the Eifel area e.g. via prey abundance and prey accessibility (Olsson 1997).

Reproduction and habitat quality

In mountain- and hillside areas of Europe Eagle Owls are considered to be typical cliff-nesting raptors (Mikkola 1983, Glutz von Blotzheim & Bauer 1994). The breeding distribution in the study area was also closely linked to the distribution of rock formations, and particularly cliffs with an eastward exposure at low elevations were highly preferred (Dalbeck & Heg submitted). Sites with cliffs or basins were more productive than nests at slopes. Nests on volcanic stone were more productive than all other nests. Clay and sand/gravel

(mainly pits) were of especially poor quality for successful breeding, providing few if any potential nesting ledges. Furthermore (potential) nest cups in clay pits tended to be soaked with water after rainfall and during snow melt. In contrast, volcanic rocks warmed up more quickly in the sun, and basins and cliffs provided warmer habitats in early winter than slopes due to temperature inversions. Olsson (1997) also specified drainage and shelter (and therefore microclimate) as factors of critical importance for quality of the nest site, and therefore Eagle Owl breeding success in south-eastern Sweden.

Differential microclimatic conditions of rock types might be the reason for differences in reproduction. Slope type rock formations often are situated near the bottom of the valleys, where during temperature inversions cold air is accumulating at night. This may affect suitability of a rock especially during incubation in late winter when steep drops in temperature and snow gales still regularly occur. Slope type rock formations are generally smaller than other rock types and therefore may also be accessible to predators (e.g. Wild Boar *Sus scrofa*), an important factor of breeding failure in south-east Sweden (Olsson 1997) and parts of Germany (Görner, pers. comm.).

The negative correlation between the proportion of forested area and reproductive success suggests that besides climate also food availability may play a major role. Forests used for wood production are generally considered too dense to be successful hunting grounds for large raptors like Eagle Owls and are clearly avoided as stressed by many authors (Olsson 1979, Leditznig 1996, Penteriani *et al.* 2001, Marchesi *et al.* 2002, Martinez *et al.* 2003) – with the exception of very old, mature forests, one of the preferred hunting grounds in Austria (Leditznig *et al.* 2001). A combination of Eagle Owls large wingspan and high wing loading (Eagle Owl 0.71 g cm^{-2} , all other owls of Europe $<0.40 \text{ g cm}^{-2}$; Mikkola 1983) leads to limits in manoeuvrability. In the study area, the diet of Eagle Owls is dominated by Hedgehog *Erinaceus europaeus*, a species which prefers a mixed landscape, Hare *Lepus europaeus* and Rabbit

Oryctolagus cuniculus, both typical species of open land, *Columba* pigeons and Brown Rats *Rattus norvegicus* which are typical for open, human altered landscapes and settlements (Dalbeck 2003) and – in the case of the Brown Rat – of riverbanks (Dalbeck 1996). Assuming that a majority of pairs predominantly rely on these species for feeding their chicks, and that hunting grounds close to the nest increase prey delivery rate, the decline in reproductive success with increasing forest area is to be expected. Similarly, negative relationships between distance to the nearest non-forested plot and reproductive success were also found in southern Sweden (Olsson 1979), Saxony (August 2000), Austria (Leditznig 1996) and in southern France (Penteriani *et al.* 2001).

Reproductive success and site occupancy

In a sense, the reintroduction project can be considered a large-scale habitat selection experiment. We predicted that during the re-establishment stage, Eagle Owls would first choose the high quality sites allowing a high productivity, and when the population reached saturation progressively low quality sites would be occupied (following 'the ideal free distribution' paradigm, Fretwell & Lucas 1970). This pattern of non-random territory occupancy has been observed in a number of bird species (Sergio & Newton 2003) including Eagle Owl (Marchesi *et al.* 2002). Our results were ambiguous: on the one hand, Eagle Owls preferably used and re-used sites with a higher than expected reproductive success, supporting the prediction of non-random habitat choice. On the other hand, there was no relationship between expected reproductive success and the year a site was occupied for the first time, which is in contrast to predictions of the ideal free distribution. In this reintroduced population, only young owls were released, leading to a continuous change in demographic structure of the growing population with an increasing number of older, experienced owls (Radler 1991). On the other hand, the study area is relatively large (nearly $10\,000 \text{ km}^2$). Therefore owls settling in the high Eifel, an area of poor chick productivity but where owls have

reached high densities in the late 1980s (Dalbeck & Heg submitted), probably have imperfect knowledge of the quality of non-occupied sites still available elsewhere. Alternatively, moderate breeding opportunities at selected sites might be compensated by absence of disturbance by humans or by a high survival rate of adults. Furthermore, Eagle Owls may have difficulties in predicting whether a site is suitable for breeding, especially if unpredictable factors, like recreational activities as rock-climbing in spring and summer, influence the breeding success.

Habitat preferences of the reintroduced Eagle Owls do not generally differ from those of autochthonous populations of hillside areas, by preferring rock formations for breeding with sufficient open landscapes in the surroundings. Furthermore, reproductive success is comparatively high (Bergerhausen *et al.* 1989, Dalbeck & Heg submitted). Therefore we do not have indications of an influence of the origin of the breeding stock (mainly owls imported from surrounding countries, like Check Republic, Poland, Sweden and zoo-animals from the former population) on habitat preferences. However, reintroduced Eagle Owls increasingly use habitats other than rock formations for breeding, e.g. tree nests, artificial nesting platforms in trees, buildings, or simply bare ground (Hamann 2004, Görner 2005), especially in lowland areas. This indicates tradition to play a role as a factor of habitat choice of Eagle Owl. Therefore, as the released captive-bred birds had no experience with natural nests, nest site choice of these birds may have been rather 'simplified'.

The increasing local densities following the re-establishment of the population may also have made unoccupied high quality sites unsuitable, due to density-dependence (Newton 1998). At hotspots of Eagle Owl occupation in the east of the study area, nests are now close together, often less than 1000 m, and in some cases less than 400 m apart. The recent decrease in the proportion of large broods (Fig. 2) may also have been a density-dependent effect by a reduction of food supply, resulting in smaller clutch sizes as in Tengmalm's Owl (Korpimäki & Hakkarainen 1991). Disturbance

caused by neighbours or non-breeders during the mating and early breeding season may impact reproductive success, as in Great Horned Owls *Bubo virginianus* in Canada (Rohner 1996), and as indicated by a telemetry study on Eagle Owls in our study area (Dalbeck *et al.* 1998). This interference among individuals may be the reason for the surprising decrease in reproductive success of sites being occupied for more than fourteen years. The initial increase in reproductive success at such sites can be explained by new settlers gaining breeding experience (Fowler 1995), as known in captive breeding female Eagle Owls (Radler 1991). Long-term changes of the environment, e.g. afforestation, changing abundance of important prey species, climate, disturbance by man, are less likely to provide an explanation, since they would affect the majority of the sites. This was not the case, however, because the average reproductive success did not change between 1978 and 1999.

Conservation measures

The Eagle Owl is endangered in many parts of Europe, including some of the strongholds of the species, e.g. Russia (Tucker & Heath 1994), Finland (Valkama pers. comm.) or – as a consequence of direct persecution, electrocution and rabbit haemorrhagic disease – Spain (Martinez & Zuberogoitia 2001, Martinez *et al.* 2003). The Eagle Owl is listed in Annex I of the EEC Birds Directive (79/409/EEC, Heath & Evans 2000). Therefore the most suitable areas in number and size need to be declared as Special Protection Areas (SPA) on a European scale (Dalbeck & Breuer 2002). In Germany conservation measures and reintroduction lead to a continued increasing population of 800 (Mebs & Scherzinger 2000) – 1000 pairs (Mebs, pers. comm.), and therefore the Eagle Owl population in Germany is of an increasing importance for the conservation of this species in Europe.

From the start of the reintroduction program onwards, scientific work on the population was dedicated to an application in the field of nature conservation. For this reason, we wish to make some proposals concerning the conservation of

Eagle Owl. To us it is of major importance to use the high level of knowledge on Eagle Owls in Europe to realise conservation measures in terms of the Birds Directive. Measures to address should include general issues, like electrocution, as one of the largest problems all over Europe (Radler & Bergerhausen 1988, Bevanger 1994, Bergerhausen 1995, Negro & Ferrer 1995, Sergio *et al.* 2004), road construction, afforestation, persecution, poisoning due to rodenticides as well as special demands of the given area (Boillot *et al.* 1997). The choice of most suitable protected sites should include knowledge on the ecological requirements of the species:

(1) General distribution patterns of Eagle Owls are similar in many of the observed populations: preference for low altitudinal areas, importance of rock formations for nesting, and of open, mixed landscapes for hunting. However, regional differences among populations should be considered in developing conservation measures.

(2) In many Mediterranean areas, natural cliffs and therefore Eagle Owls are rather regular distributed (Martinez *et al.* 1992), whereas in the Eifel area and other parts of central Europe, suitable nesting sites might be a limiting resource. Therefore all these sites are of major importance, and applicable schemes of Eagle Owl protection must be developed, e.g. concerning quarries and the problem of tourism, especially rock-climbing in the relatively few natural habitats of the owls.

(3) The Eagle Owls in the study area need a variety of different prey species in order to be less prone to fluctuations of single prey species e.g. after the breakdown of the Rabbit population. Therefore conservation of open, mixed cultural landscapes and wetlands is of prime importance for Eagle Owl conservation.

(4) Direct persecution is of less importance in Germany at the moment but legalisation of hunting of this species is being discussed (N.N. 2006). Obviously, legal hunting would jeopardise the entire reintroduction scheme, and the long-lasting efforts and investments by many individuals, non-governmental and governmental authorities to save this fascinating owl species would be spoilt.

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SAMENVATTING

Oehoes *Bubo bubo* zijn succesvol geïntroduceerd in de Eifel in de jaren 1974–1999. Tegenwoordig broeden ongeveer 90 Oehoe-paren in het gebied, waarvan ongeveer 60 jaarlijks één of meerdere jongen grootbrengen. Het voortplantingssucces is echter variabel en wisselt van jaar tot jaar. In dit stuk analyseren we welke factoren het succes beïnvloeden en hoe dat veranderd is door de jaren. Nestelplaatsen in de beschutting van ronde of halfronde rotswanden, en vooral op rotsen van vulkanische oorsprong, hadden meer succes dan andere nestelplaatsen. Dit komt waarschijnlijk omdat het microklimaat op deze plaatsen gunstiger is. Daarnaast was het succes het hoogst in de dalen en nam geleidelijk af richting de heuveltoppen (tot 750 m boven zeeniveau). Hoe hoger de broedplek lag, hoe later in het seizoen de Oehoes tot broeden kwamen. Dit laat zien dat ook op deze schaal klimaat een sterk effect op succes had. Deze conclusie wordt gestaafd door de vergelijking tussen jaren: Oehoes broeden later in jaren met een koude nawinter, en hebben dan ook minder succes (de eieren worden gelegd in februari-maart). Het voortplantingssucces bleek ook achteruit te gaan met toenemende bedekking van bos binnen 2 km rondom het nest, waarschijnlijk omdat Oehoes open gebied nodig hebben om voldoende prooi te kunnen vinden voor de jongen. Het gemiddeld succes per nestplek (1.13 jongen) en per succesvol paar (2.13 jongen) was vergelijkbaar met andere Oehoe-populaties, en bleef redelijk constant door de jaren. Echter, het gemiddeld aantal jongen per succesvol broedsel nam duidelijk af, wat gecompenseerd werd door een afname in het aantal paren dat helemaal geen jongen groot bracht. Omdat alle potentiële broedplaatsen jaarlijks gecontroleerd werden op Oehoes (totaal 421 rotswanden), bleek het mogelijk om (1) een schatting te geven van het verdere uitbreidings-potentieel van de Eifel-populatie, (2) een schatting te geven welke plekken naar verwachting veel jongen opleveren (op grond van ligging en habitat). Het blijkt dat vooral in de dalen veel rotswanden voorhanden zijn met naar verwachting een hoog voortplantingssucces. Slechts een deel van deze wanden wordt ook daadwerkelijk door Oehoes benut, de grootste leegstand treedt op in het Moezeldal. Deze informatie kan gebruikt worden om gedetailleerde voorstellen te maken ter bescherming van de soort en de meest waardevolle nestelplaatsen.

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