

A statistical habitat model for the Blue Winged Grasshopper (*Oedipoda caerulescens*) considering the habitat connectivity

Wilhelm Kuhn and Michael Kleyer

We used iterative statistical habitat models to predict the incidence of *Oedipoda caerulescens* (Orthoptera, Saltatoria). Our first model is derived from presence / absence data and habitat factors (temperature, vegetation cover and structure), all mapped on a landscape scale. It predicts a maximum incidence of 0.3, if the vegetation cover is about 50% and the "standardised vegetation height" is below 0.3 m. This habitat model produces the potential habitat map of the study area.

In a second model, presence / absence data are recorded from these potential habitats and their isolation and size are computed as independent variables. The predicted incidence is above 0.8, if the given patch is large and many other patches occupied by *Oedipoda caerulescens* are found in the neighbourhood. Even isolated patches are occupied, if their size is very large.

Key words: habitat model, *Oedipoda caerulescens*, Saltatoria, isolation, patch area, GIS, habitat network, conservation, logistic regression.

Introduction

During the past decades many authors emphasised the relevance of habitat size and isolation for the survival of animals in landscapes (Andrewarta & Birch 1954; Levins 1970; den Boer 1990; Fahrig 1991; Hanski & Gilpin 1991; Hanski 1994). Accordingly, species are the more in danger of becoming extinct the more their habitats are ephemeral or the more they are influenced by environmental variability (e.g. weather). However, if a sufficient spatial "network" of small habitats allows an exchange of individuals

between the local populations of a species, the regional population in a landscape can be stabilised. For evaluating the chances of species survival a habitat model should include a species-specific quantitative analysis of isolation (Adler & Wilson 1985). This can be achieved with successive statistical models based on presence/absence observations. The first model determines the decisive resources and environmental conditions that characterise the potential habitats. The second model specifies these results by

considering the spatial configuration of the habitats.

Very simple measures are often used to describe the spatial structure of habitats for analysing metapopulations (cf. Lefkovich & Fahrig 1985; Kareiva 1990). They do not exceed a determination of perimeter and size as well as of the distance between habitat centres (cf. Adler & Wilson 1985; Forman & Godron 1986; Fahrig & Paloheimo 1988; Poethke et al. 1996a; Settele et al. 1996; Veith et al. 1996). Since most insects move in a more or less random way through landscapes (Okubo 1980), the probability of immigration depends on the form of the habitat at right angles to the direction of migration (Forman & Godron 1986). It should therefore be considered for calculation.

In many models it is assumed that animals can move from any habitat to any other habitat, e.g., from a peripheral habitat across three other habitats directly to a central habitat (cf. Poethke 1996a). Animals migrating on the ground, however, certainly do not move from one habitat directly to another one, if there is a habitat between them. In that case it can be assumed that they will stay on the latter habitat for a while. Moreover, homogeneous inter-habitat areas are presumed for an assessment of the network degree (cf. Dunning et al. 1992). Different kinds of land use and different suitabilities of inter-habitat areas, however, may influence the migration of animals (Taylor et al. 1993). Therefore, the interspace should also be assessed for its possibly suboptimal to bad habitat quality, which should be taken into account for determining the distance measure.

In the present study the grasshopper *Oedipoda caerulescens* (Blue Winged Grasshopper) is used as an example to demonstrate, how highly resolved data on the habitat fac-



tors can be provided for an entire landscape. First, a regionally valid statistical habitat model is to be developed which quantifies the habitat quality of all single areas in a landscape (representing them as occurrence probability) and predicts potential habitats. The relationship between the presence of *O. caerulescens* and the spatial configuration of the habitats is presented in a second model considering those habitats exclusively.

■ Materials and methods

1. Biology of *Oedipoda caerulescens*

Oedipoda caerulescens (LINNAEUS 1785, Orthoptera, Saltatoria) is still frequently found in the southern Rhine valley. It is threatened in the other federal states of Germany and rare or partly extinct in North Germany (Detzel 1991). *O. caerulescens* lives on warm and dry soils covered by low and patchy vegetation (Blab 1993; Wallaschek 1995). The animals hibernate as eggs in the soil. In Central Europe the first larvae appear from May to June and pass through 4–5 larval stages. The adults appear in July and are found throughout October (Detzel 1991; Appelt 1996). They are able to actively reduce transpiration and thus survive severe droughts. While the intrapopular migration distance of most animals is very short (20–40 m), some individuals may well cover longer distances (up to 800 m, Appelt 1996). From his observations of the mode of locomotion Sanger (1977, in Wallaschek 1995) concludes that high and dense vegetation is avoided, because it impedes migration (low jump angle and flight path).

2. Study area

The study area "Hallesche Porphyrlandschaft" is situated in the Central German chernozem landscape and is passed by the river Saale. The region is rather arid as compared to other German regions (the annual precipitation is ca. 450–500 mm and the annual temperature is 8.4–9.9 °C; Meynen et al. 1962). The study area covers about 32 km²

(centre: 51° 33' North, 11° 53' East). In the northwest, deep valleys are directed towards the river Saale, which were formed during the Saale glacial period (Villwock 1981). The major part of the remaining area is plain or weakly undulating. More than 200 porphyry outcrops (Schopke 1992), most of which project from the surrounding farm land by a few meters only, are characteristic of the landscape. Apart from the porphyry outcrops, the soils consist of enormous layers of loess. Lithosols, Rankers and flat Cambisols (FAO 1988) are found where the loess soil has been eroded from the porphyry outcrops. Farm land, pastures, and herbaceous communities on fallow land cover ca. 75% of the area. Dry grasslands and heathlands only cover 5%, but show the highest fragmentation with 250 separate areas. The dry grasslands on the porphyry outcrops were used as sheep pastures in the past. Around 1990 grazing was drastically reduced. As a consequence, the fallow land is subject to intense ruderalisation (Bliss et al. 1996; Mahn & Partzsch 1996).

3. Mapping of habitat parameters

Habitat factors should be mapped with a justifiable expenditure of time, if all patches of a landscape are to be taken into account. It is known from the literature that the occurrence of *O. caerulescens* is determined by the soil surface temperature and vegetation structure (see above). A direct measurement of these quantities at a resolution corresponding to the spatial distribution of the animals is a very time-consuming procedure on an area of 32 km². Therefore, temperature is derived from the elevation of the landscape and the vegetation structure is derived from the vegetation units. All datasets can be downloaded from <http://www.uni-oldenburg.de/landeco/landeco.htm>.

4. Calculation of the insolation from a digital terrain model

Highly resolved digital terrain models (DTM) can be converted into maps of the potential insolation. Aerial photos were used to develop

the DTM. The points required for integration into the coordinate system had to be determined using a differential GPS in the field. Its validity is relatively high with mean deviations of less than 0.5 m and vertical offsets of less than 1 m. For development of the DTM grids were taken from aerial photos using an analytic stereoscope (Zeiss Planicomp P3). The coordinates of the measured points first yielded vector maps in the GIS, which were subsequently transferred into a raster of 5 m applying the kriging method (cf. Englund & Sparks 1988; O'Conaill et al. 1994). This serves as a basis for determining the insolation.

For every patch inclination and aspect were determined using standard GIS procedures. Depending on the geographic latitude, calendar day and hour of the day, the position of the sun (height of the sun, azimuthal angle) in the investigated area can be calculated. Insolation has been calculated for the 21st March (equinox) using an insolation model following Hetrick et al. (1993, for details see Kuhn 1998).

5. Conversion of a vegetation map into a map of vegetation structure

Several other authors have contributed to the vegetation map of the study area (Frank 1993; Mahn & Partzsch 1996; Siegle unpubl.; Vetter unpubl.). A total of 1,200 vegetation samples were classified to 112 units (cf. also Mahn 1957; Hilbig et al. 1972; Schubert 1973; 1974 a,b,c; Gutte & Hilbig 1975). Mapping of the vegetation units in the field was performed with the help of colour infrared aerial photos (scale 1:5,000). All of the vegetation samples and the vegetation map have been entered into a relational data bank and implemented into a GIS (Kuhn 1998).

Deduction of the vegetation structure from the vegetation map proceeds on the assumption that the vegetation structure of a landscape is determined by the growth forms of the plants. The "growth form" of a plant is interpreted as a complex set of characteristics, among them height, branching, distribution of leaves on the stem, size of leaves,

lateral extension and arrangement of shoots in clonal plants. Such information has been compiled for each species in a data base for biological traits of plants (Kleyer 1995). The horizontal component of the vegetation structure is described by the cover estimation of plants in the vegetation samples. Many parameters of the growth form, especially clonal extension, are correlated with the cover estimation and have therefore not been considered. The vertical component is described by the height of the plant and arrangement of leaves on the stem. Together they define the density of vegetation at different heights. Plants with a height of 20 cm and with leaves arranged as rosettes have a vertical structure different from that of plants with the same height but with leaves evenly distributed along the stem. For calculating the vertical structure simple geometrical models were used for the types "rosette", "half-rosette", "leaves evenly distributed" (Fig. 1). These geometrical models can be described by mathematical functions. This allows to calculate the decrease of the plant cover along with the height of the plants according to the database (see Kuhn 1998).

Then, referring to the cover at soil surface, the cover across all plant species of a vegetation type is determined for several heights (0–5 cm, 5–10 cm, etc.; Kuhn & Kleyer 1996; Kuhn 1998). Since the statistical analysis can best be visualised using only one independent variable, the values in the different height classes were aggregated to the height at which the cover of the stand is 25% of the cover estimated at the soil surface. This is the "standardised vegetation height". For a methodical comparison samples of the vegetation structure of

different plant communities were measured in the field (Sundermeier 1996). The differences between the measured values and the values derived from the growth form are very small in the layers between 0 and 40 cm. In high-growing plant communities (Arrhenatheretum, Convolvulo-Agrophyretum), deducing the vegetation structure from the growth form of plants overestimates the coverage in higher layers by 5–10% compared to measured values (Kuhn 1998).

6. Observation areas for *Oedipoda caerulescens*

Appelt (1996) selected some habitat types in which *Oedipoda caerulescens* can be expected to occur according to the literature (mainly dry grasslands). Those areas were carefully investigated in 1994 and 1995. However, this procedure emphasises sites with presence more than sites with absence because the latter are excluded from the survey. Thus, the entire gradient of habitat qualities in a landscape is condensed to the optimum which prevents a representative bell-shaped curve. Therefore, sample surveys in other land use types were performed in order to document the absences.

7. Statistical methods

Logistic regression analysis is used to relate the probability of occurrence of *O. caerulescens* to habitat factors (Trexler & Travis 1993; Jongman et al. 1995). Adjustment to the observed presence-absence patterns is performed by means of maximum likelihood functions. Two parameters, namely the share of concordant pairs and the rank correlation coefficient Somer's D (SAS Institute 1990) were used to

evaluate the quality of the model. In the following the term "incidence" is used for the probability of occurrence in areas with suitable and unsuitable vegetation structure and insolation during a given year ("spatial" incidence) as opposed to its common usage as a measure of the probability of occurrence in a given area over several years ("temporal" incidence).

In the regression model the incidences are continuously distributed on the gradients of vegetation structure and insolation. Visualising them on a map, cloud-like patterns of higher or lower incidences without distinct limitations would be obtained. If distances between habitats are to be calculated, however, a distinct limitation between habitats and inter-habitat areas is necessary. As the habitat model yields occurrence probabilities of maximally 0.3 (see results), all areas with predicted incidences higher than 0.1 are defined as habitats, the rest as inter-habitat areas ($P_{crit} = 0,1$; cf. Fielding & Haworth 1995).

8. Radial transect analysis

The spatial analysis proceeds on the assumption that the incidence in a target habitat is the higher the more animals immigrate from the outside. In our spatial analysis, each habitat is successively interpreted as the target with all of the other habitats as potential sources of the animals' dispersal. By programming appropriate GIS procedures, the habitat borders are marked by single dots which represent the starting and destination points (Fig. 2). The space around the destination points allows for an infinite number of possible directions of migration and an infinite extension. In order to reduce them, each destination point is surrounded by a circle (with a radius of 1000 m in this case) which is divided into sectors of equal angles. Destination and starting points of opposite habitat sides within a sector are connected by a linear transect, if it does not cross other habitat areas. Thus, only opposite sides of habitats are connected, while intervening habitat areas cause "shades". The length of each tran-



Fig. 1. Distribution of leaves along the shoot axis in different growth forms of plants (half rosette, leaves evenly distributed, rosette).

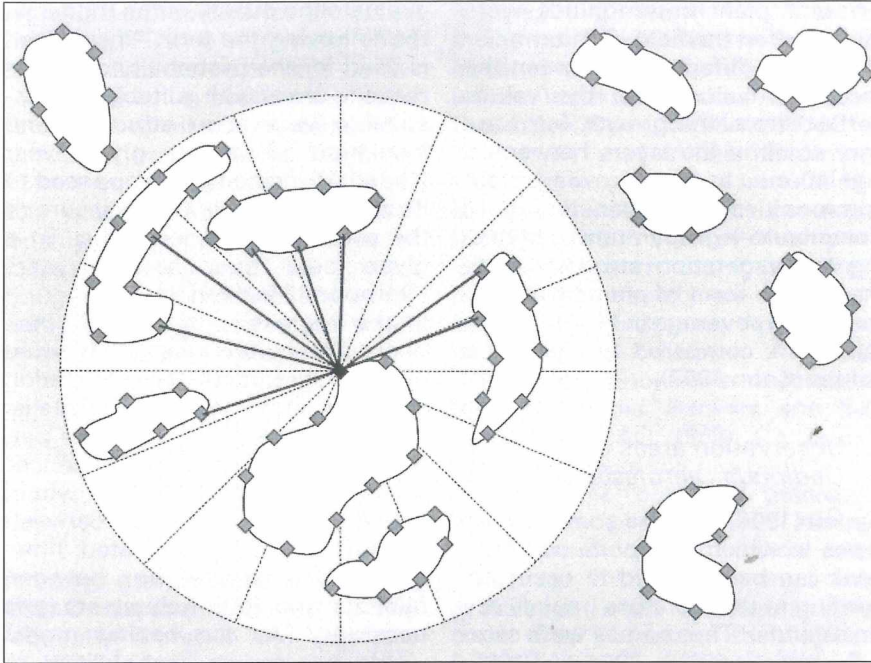


Fig. 2. Survey of the spatial structure between the border points of a habitat and neighbouring habitat areas by dividing them into sectors and description by radial transect lines.

sect line is determined (Fig. 2). Only one transect is admissible for each sector.

The number of transects between two habitats at a given sector width then depends on (i) the number of destination points in the target habitat, (ii) the "visible" (not shaded) width of the source habitat perpendicular to the direction of the transect, and (iii) the distance of the target habitat from the source (areas of equal size cover more sectors, if they are closer to the source habitat). Summing up the sector angles in which connection with a neighbouring habitat are possible from a starting point, the entire circle or "interaction angle" yields a measure for the orientation of the neighbouring habitat towards the destination point (cross side or front side).

The quality of the inter-habitat areas is assigned to the transects by overlaying them with the habitat suitability map. If inter-habitat areas consist of sites with different habitat qualities, the mean value of all partial qualities is calculated corresponding to the length of the transect. Connecting transects running through barriers (e.g. dense

spruce forests) are excluded from the further analysis. As a result of the radial transect analysis a set of connecting lines is available for every destination point within a pair of habitats. The transect lines of all habitats in the landscape are aggregated in a subsequent numerical analysis. Their representative angles and their lengths weighted with the partial habitat qualities of the interspaces they cross (see below) serve as parameters in the regression analysis.

9. Aggregation of spatial parameters

It is not sufficient to relate the incidence of the source habitat to the distances of potential neighbouring habitats. The effect of isolation on the incidence can only be determined, if the definition of the independent variable includes information about whether or not the neighbouring habitats are occupied. Therefore, the distance and size measures have to be weighted with the incidence of the neighbouring habitats.

Within the scope of a Markov model for explaining the incidence of

animal populations in fragmented landscapes Hanski (1994) combined number, size, and distance from neighbouring habitats to one term S . This expression is called connectivity S in the following:

$$S_i = \sum_{j=1}^{n_i} p_j e^{-\alpha d_{ij}} A_j$$

S_i : Connectivity S of the area i with "neighbouring" habitats

d_{ij} : Distance between habitats i and j [km]

α : Constant for the survival rate of migrating animals [1]

A_j : Size of habitat j [ha]

p_j : Probability of occupation (incidence) of neighbouring habitat j [0..1]

n_i : Number of habitats in the neighbourhood of area i

The connectivity S thus registers the sizes of all "neighbouring" habitats which are additionally weighted with their incidence and negative exponentially with their distance from the central habitat in question. The proximity to occupied neighbouring habitats gains a high importance, if the equation is formulated in this way. Contrary to Hanski's original version, not all habitats situated "anywhere" in the landscape are considered, but only the neighbouring ones in any given direction. The circle to search for neighboring habitats around the target point has a radius of 1,000 m. Thus, all habitats beyond the circle are excluded as well as those situated behind a habitat that neighbours the habitat in question. It is unlikely that *O. caerulescens* emigrates from such a far distant habitat, then misses out the next one and immigrates directly into the habitat in question.

In order to consider the extension and orientation of a target area at right angles to the migration direction of animals, the connectivity parameter T is applied to calculate the "interaction angle" of potential colonisation sources towards a target area (cf. Kuhn 1998).

$$T_i = \frac{1}{\sqrt{\frac{A_i}{\pi}}} \cdot \sum_{j=1}^{n_i} p_j \cdot \sin \beta_{ij}$$

A_i : Size of the target area i [ha]

T_i : Connectivity T of the area i

p_j : Incidence of the neighbouring area j [0 .. 1]

β_{ij} : Interaction angle of neighbouring habitat j in the direction of the target area i

As in the case of connectivity S , the sum factors are weighted with the incidences of neighbouring habitats. Both parameters increase with decreasing distances and thus with decreasing isolation of the target area i . Contrary to the connectivity S , however, the distances are not weighted with the size of the neighbouring areas. In order to consider the parameter "distances between neighbouring habitats" exclusively, Td was calculated as a further index.

$$Td = \sum_{j=1}^{n_i} p_j \cdot \frac{1}{s_{ij}}$$

s_{ij} : Distance between habitats i and j [km]

p_j : Incidence of the neighbouring habitat area j [0 .. 1]

n_i : Number of habitats within the neighbourhood of area i

In order to determine the interspace quality all areas of the landscape are classified into four logarithmically divided classes according to their calculated incidence values. Weight factors are then assigned to these classes. Areas with an incidence (P) > 0,1 are interpreted as potential habitats, those with $0,1 \geq P \geq 0,01$ are given the factor 1, those with $0,01 \geq P > 0,001$, the factor 2, those with $0,001 \geq P$, the fac-

tor 3, and small woods or settlements, the factor 10. The length of a source to target habitat transect that overlays a given interspace patch is multiplied with this weight factor according to the quality of this patch. Hence, the real distance between two neighbouring habitats counts three-fold, if the quality of the intervening areas is very low ($P \leq 0,001$). The mean weighted distance (effective distance) is then calculated across all transects connecting two habitats.

In a second study Appelt (1996) again examined the occurrence of *O. caerulescens* in 80 potential habitat areas predicted by means of the habitat model, so that there are also secure data available on the absence of the species besides the data on occupied habitats. 55 of those areas were occupied, while the species was not found on 25 areas. On the basis of these data the logistic regression analysis is performed using the following parameters which are also combined to complex models:

- The square root of the size of the target habitat (in m).
- The connectivity S following Hanski 1994 without considering the inter-habitat quality. Low values for the connectivity S are obtained, when the neighbouring habitats are small and larger habitats are very far away.
- The connectivity T (reciprocal distance and interaction angle with neighbouring areas) without considering the inter-habitat quality.

- The connectivity Td (reciprocal distance from neighbouring areas only) without considering the inter-habitat quality. High values for connectivity T and Td , respectively are suggestive of several close and occupied neighbouring habitats.
- The connectivity indices S and T considering the inter-habitat quality.

Results

1. The habitat model not considering the spatial landscape structure

The first habitat model does not yet include the spatial structure of the habitats in the landscape. It presents the occurrence of *Oedipoda caerulescens* in dependence on habitat factors such as insolation, vegetation coverage, and standardized vegetation height. The parameters for the stepwise introduction of these variables in the regression model are shown in Table 1. All of the three variables quite significantly contribute to the explanation of the incidence of *O. caerulescens* (cf. Models 1, 2, 3 in Table 1). According to the model fit, Model 3 yields the highest correspondence between the observed occurrence and predicted incidence. This model only includes the vegetation cover and the standardised vegetation height. Accordingly, an incidence of about 30% is to be expected, if the vegetation cover at the soil surface

Table 1. Stepwise logistic regression analysis for the habitat model without considering the spatial structure: Presence areas of *Oedipoda caerulescens* in dependence on habitat characteristics.

Model	Joint significance of independent variables	Association of predicted probabilities and observed responses		Estimated values for model parameters (confidence level of model parameters)									
		Concordant	Rank correlation	Intercept [kWh]	Insolation	Cover [%]	squared cover	Height [cm]	Height × cover	Height × squared cover	Cover × insolation	Height × insolation	
1	0.0001	63.9	0.442	-14.7987 (0.0001)	3.0407 (0.0001)	-	-	-	-	-	-	-	-
2	0.0001	83.7	0.816	-6.7799 (0.0001)	-	0.2286 (0.0001)	-0.00239 (0.0001)	-	-	-	-	-	-
3	0.0001	89.5	0.878	-2.6674 (0.0001)	-	0.1084 (0.0001)	-0.00132 (0.0001)	-0.2083 (0.0001)	0.00437 (0.0001)	-0.00003 (0.0001)	-	-	-
4	0.0001	88.6	0.867	-9.3193 (0.0001)	1.1202 (0.0001)	0.1997 (0.0001)	-0.00212 (0.0001)	-0.1130 (0.0001)	0.000432 (0.0001)	-	0.00384 (0.0001)	0.0109 (0.0001)	-

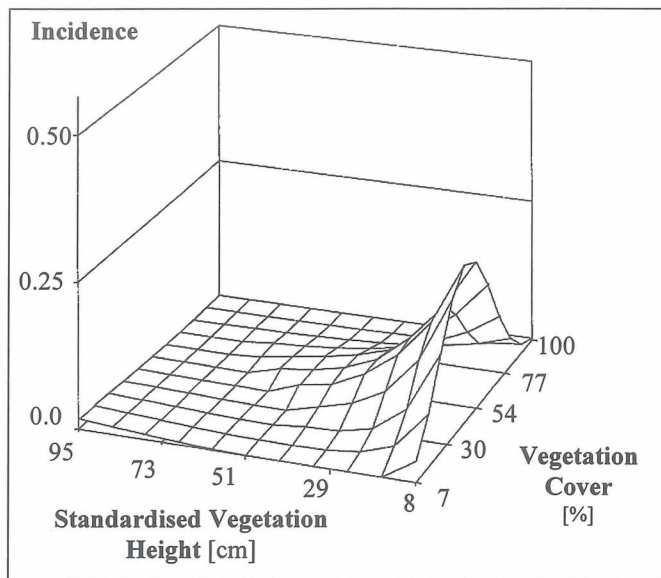


Fig. 3. The habitat model without considering the spatial structure (incidence: Probability of occurrence for *Oedipoda caerulescens* [%]; Standardised vegetation height: height at which the vegetation cover is 25% of the cover at the soil surface).

is around 50% and if the standardised vegetation height is below 30 cm (Fig. 3).

Although insolation alone also shows a significant relationship (Model 1), it does not yield a better model fit when combined with the above-mentioned parameters (Model 4).

2. Validation of the habitat model

For habitat models supposed to be valid on a regional scale, transferability is an essential requirement. Therefore, Model 3 is examined in a validation area that was not used for developing the model. The part of the study area south of the river Saale serves this purpose. The expected incidence of *Oedipoda caerulescens* can be calculated for every single area (except for small woods, waters, and settlements) by inserting the coverage and standardised vegetation height in these areas into the regression equation and resolving them for incidence. This was performed in the GIS. For evaluating the predicted occurrence, the incidence map is compared to the map of proved occurrence. Both datasets stem from observations in the same year.

Table 2. Stepwise logistic regression analysis for the habitat model with connectivity measures: Incidence of *Oedipoda caerulescens* in dependence on the landscape configuration (Models 14* and 15* with weighted habitat quality of the interspace) (n = 80).

Model	Joint significance of independent variables	Association of predicted probabilities and observed responses		Estimated values for the model parameters (confidence level of the model parameters)				
		Concordant [%]	Rank correlation	Intercept	Squared area size [m ²]	Connectivity S [m ² /km]	Connectivity T [1/km]	Connectivity Td [1/km]
5	0.0781	59.6	0.202	0.1930 (0.6492)	0.0263 (0.1146)	–	–	–
6	0.8485	46.5	0.028	0.7369 (0.0413)	–	0.0520 (0.8490)	–	–
7	0.0147	67.1	0.345	–0.6671 (0.3173)	–	–	0.0156 (0.0251)	–
8	0.0001	77.3	0.550	–1.7041 (0.0200)	–	–	–	0.0361 (0.0006)
9	0.1085	60.1	0.204	0.2763 (0.5316)	0.0407 (0.0645)	–0.4140 (–0.2484)	–	–
10	0.0019	73.4	0.471	–2.0541 (0.0230)	0.0415 (0.0326)	–	0.0201 (0.0061)	–
11	0.0003	76.4	0.530	–1.9040 (0.0151)	0.0142 (0.4286)	–	–	0.0345 (0.0012)
12	0.0509	67.5	0.351	–0.6752 (0.3347)	–	0.0106 (0.9696)	0.0156 (0.0263)	–
13	0.0001	79.1	0.585	–1.7548 (0.0199)	–	–0.6142 (0.0909)	–	0.0464 (0.0004)
14	0.0005	78.0	0.563	–2.6563 (0.0085)	0.0819 (0.0072)	–0.9605 (0.0260)	0.0274 (0.0019)	–
15	0.0001	82.3	0.647	–2.7724 (0.0035)	0.0614 (0.0340)	–1.4057 (0.0077)	–	0.0539 (0.0003)
14*	0.0011	76.9	0.540	–2.4324 (0.0126)	0.0665 (0.0110)	–1.0100 (0.0626)	0.0247 (0.0031)	–
15*	0.0001	81.7	0.636	–2.7906 (0.0035)	0.0496 (0.0522)	–1.7731 (0.0090)	–	0.0524 (0.0003)

Interpreting areas with a predicted incidence above 0.1 as habitats, the model yields 32 potential habitats covering an area of 12.5 ha in the validation area, however, *O. caerulescens* was found in 18 areas only.

15 of them were predicted as potential habitats by the model. *O. caerulescens* was also found on three areas which the model did not recognise as habitats. Fig. 4 shows a section of the area.

3. The habitat model considering the spatial landscape structure

Using the first habitat model all potential habitats were extracted from the landscape. Occurrences on

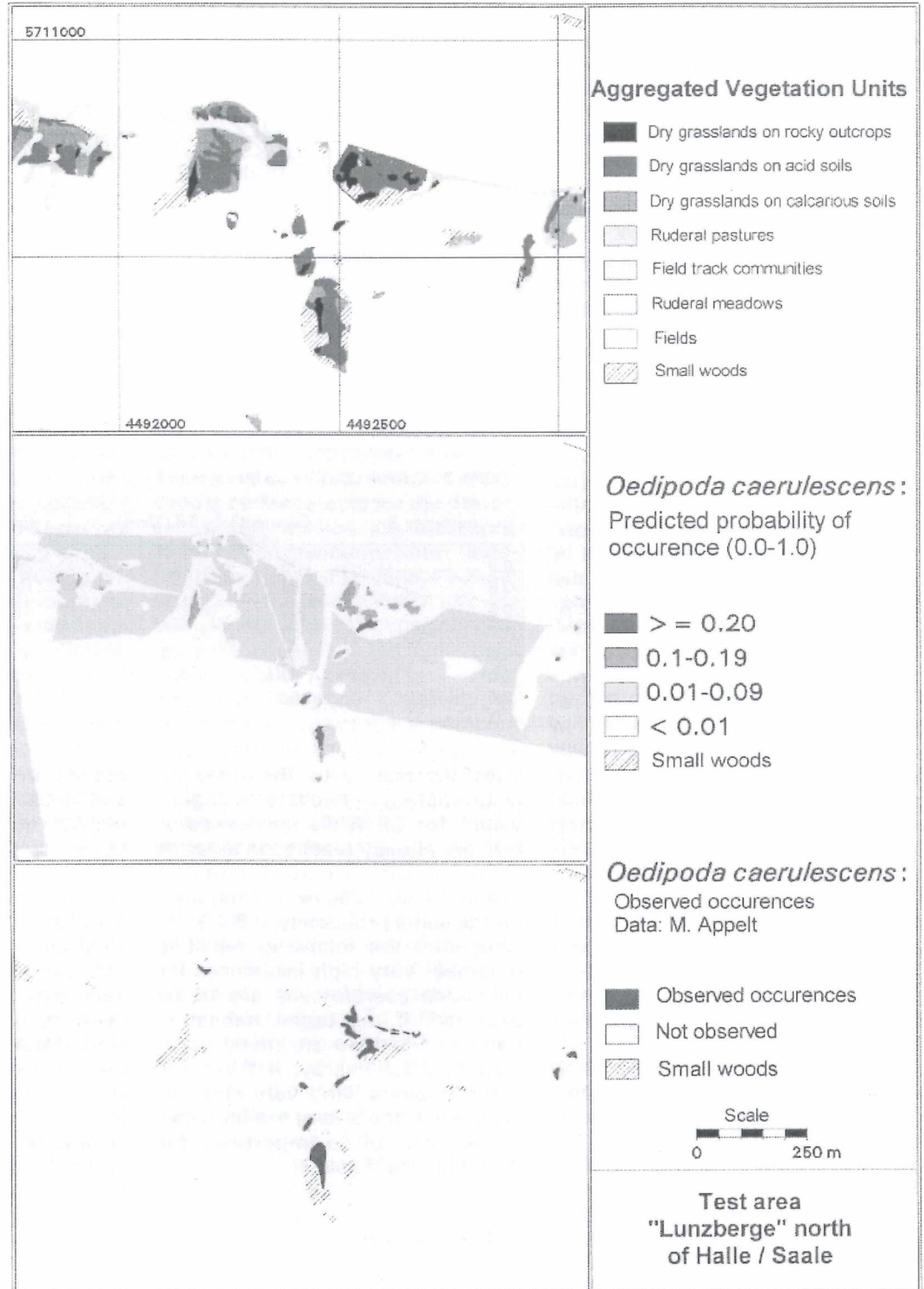


Fig. 4. Prediction of the occurrence of *Oedipoda caerulescens* within an independent test area.

these potential habitats are related to their sizes and distances in the following regression models (Table 2). Neither the sizes of potential habitats (transformed into the square root of the size, Model 5) nor the connectivities S or T (Models 6 and 7) alone show a significant relationship with the occurrence of *Oedipoda caerulescens*. A considerably improved significance level is obtained in Model 8. The sums of the reciprocal distances from the neighbouring areas weighted by incidences (connectivity Td) is positively correlated with the incidences of the target habitats.

If both size of target habitats and connectivity T are introduced in the model (Model 10), the fit does not reach the fit of Model 8, however, a combination of both parameters explains the incidence more significantly than each parameter alone (see Models 5 or 7). If connectivity S instead of connectivity T is combined with the size of the target habitats, the model is not significant (Model 9). Including size, connectivity S, and the distance Td in the model (Model 15) yields the best model fit and the highest significance. This means that the incidence increases with the size of the target habitat and with the proximity of neighbouring habitats. The result is shown in Fig. 5 for S = 1.0. In all models the connectivity S has either a weak positive or a negative effect on the incidence. Since S emphasizes the size of neighbouring habitats, this implies that the incidence increases, if the neighbouring habitats are rather small.

In the regression models 14* and 15* the distances are weighted with the quality of inter-habitat areas. Neither of the two models improves the quality of regression model 15.

Critical values still yielding an incidence of 75% for *Oedipoda caerulescens* can be derived from the regression model for distances (Td) and sizes (Table 3). In severely isolated habitats (S = 0,5, Td = 25) *Oedipoda caerulescens* only occurs with a probability of min 0.75, if their sizes exceed 2,800 m².

The negative correlation of connectivity S with the incidence is expressed by the fact that the critical

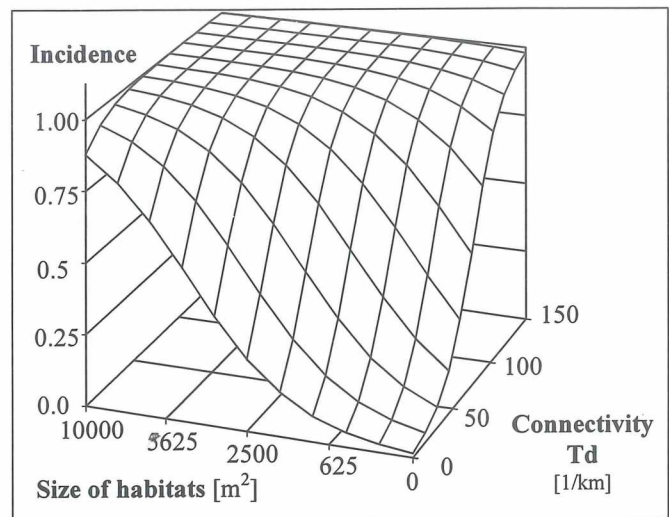


Fig. 5. Model 15 including size, connectivity S and the distance Td yields the best fit. The plot shows the incidence of *Oedipoda caerulescens* for S = 1.0 in relation to habitat size and Td which is a combination of distance and number of neighbouring habitats (low values of Td indicate long distances and / or low numbers of neighbouring habitats).

Table 3. Critical sizes for an incidence of > 0.75.

Connectivity S	Connectivity Td (1/km)	Critical Size [m ²] for I > 0.75
0.5	25	2800
0.5	50	950
0.5	100	no critical size
1.0	50	1750
1.0	100	no critical size
2.0	50	4100
2.0	100	400

sizes increase with the sizes of neighbouring habitats (higher values for S). While incidences of 0.75 are already reached in areas of 950 m² in the absence of large areas (S = 0.5), 1,750 m² are required for the same probability, if S = 1.

Altogether the following result is obtained: Very high incidences for *Oedipoda caerulescens* are to be expected, if the target habitat is large and if there are many occupied habitats nearby. If there are many habitats lying very close to each other, the size of the individual habitat is of no importance for the incidence (Table 3).

Discussion

With the first habitat model for *Oedipoda caerulescens* not considering the spatial structure, the land-

scape is divided into highly suitable and less suitable habitats. The highest quality of habitats is obtained with a vegetation cover around 50%. These values are higher than those stated in the literature (e.g. 33%, Appelt 1996; see Merkel 1980, cited in Blab 1993). These differences are due to the fact that our data stem from vegetation maps. Cover data in the vegetation tables were taken from (i) vegetation samples with areas larger than those of zoological samples in general and (ii) also from samples in which *Oedipoda caerulescens* was not found. It can therefore be assumed that the coverage rates are systematically higher in the vegetation samples than in detailed measurements of proved habitats.

Introducing the potential insolation into the logistic regression model does not yield an improvement, be-

cause vegetation cover and insolation are not uncorrelated on most sites such as dry grasslands on southern slopes. High insolation rates lower the water availability in the soil which in turn leads to lower vegetation cover and height.

The fit of the first habitat model is high, however, with 0.3 the predicted probability of occurrence is low. In our opinion this is due to the isolation and size of potential habitats. It should be realized, however, that this value might be improved by long-term observations throughout several years.

The transfer of the habitat model to the test area south of the river Saale should not be interpreted as a failure because the number of predicted habitats is distinctly higher than the proved occurrence. The respective areas may be considered potential habitats that will possibly be colonised at a later time. Other studies (Sternberg 1995; Geißler-Strobel 1998) emphasize the necessity to preserve unoccupied habitats even if they are less suitable. Correlated environmental variation may decrease the suitability of target habitats, while the quality of suboptimal habitats is temporarily improved. Such patches may then be colonized, if they are in suitable distance to occupied patches. If this is the case, the threatened populations of the target habitats can be supported by those of the suboptimal habitats (Sternberg 1995; Reich & Grimm 1996). The non-prediction of proved occurrences, however, is a decisive criterion for the usability of habitat models (Beier 1989). More than 80% of the proved occurrences were predicted as potential habitats.

With the second habitat model, which relates the occurrences on the potential habitats to their spatial configuration, the predicted incidence was drastically increased. The relationship between incidence and size is also known from other species groups (Adler & Wilson 1985; Thomas et al. 1992; Hanski 1994). It is explained by the facts that the sizes of habitats are correlated with their population numbers and that large populations will become extinct less frequently (Hovestadt 1990; Poethke et al. 1996a).

A high incidence can also be expected, if several small areas are connected with each other. According to the metapopulation theory, a network of small populations is stabilized via the exchange of individuals (Lefkovich & Fahrig 1985; Hanski 1994b; Thomas et al. 1992; Reich & Grimm 1996). Kleinert (1992) counts *Oedipoda caerulescens* among the grasshopper species eager for dispersal owing to its flying capability. It suits this picture that the species is frequently found in anthropogenic secondary biotopes (Küchenhoff 1994; Schreiber 1996). Veith et al. (1996) conclude a very high extinction and colonization dynamics of the species in the study area from the low inbreeding coefficients. Within the study area groups of small habitats are frequently occupied even if they are far away from other larger areas. Dispersal of the animals is possibly enhanced by intensive farming. Harvested fields have a vegetation structure in late summer which should be favourable for the dispersal of the species (cf. Meschede 1994). Unfortunately, our algorithms to include inter-space habitat quality in the connectivity calculation do actually not consider such temporal changes of the inter-space habitat quality. Hence, in view of the high dispersal capability of *Oedipoda caerulescens* a complex of populations lying close together will represent one single, but spatially heterogeneous population. There is a fluid transition to metapopulations colonising a weak network of strongly isolated habitats. Assuming a nondirectional dispersal of the animals it is to be expected that a consideration of the spatial orientation and form of habitats improves the model quality. Instead, connectivity T_d which only considers the number and distance of neighbouring habitats yields a higher fit than connectivity T . In the northwestern part of the study area there is a series of elongated habitats along southern slopes. Maybe the animals preferentially disperse there such that these slopes serve as connecting structures and a random dispersal can no longer be assumed.

According to Adler & Wilson (1985), Hanski (1994b), and Poethke et al.

(1996b) it would be expected that large occupied habitats positively affect the colonization of small neighbouring habitats ("mainland-island" type). A positive relationship between connectivity S and the incidence of small habitats would have to be assumed. Instead, separate small habitats in the vicinity of large habitats often remain unoccupied, while large groups of small areas at a greater distance are often occupied. Later surveys showed that *Oedipoda caerulescens* presumably migrates along waysides characterized by low and sparse vegetation (Appelt 1996; Wallaschek 1996; Fastnacht unpubl. data). Then certain sections of paths would be preferred lines of dispersal across the landscape. Distant groups of habitats would be colonized earlier, if paths went past them. Unfortunately, these narrow, linear landscape structures were neglected during the observation survey of *Oedipoda caerulescens*.

Large dry grasslands are the central habitats of *Oedipoda caerulescens*. Also small, spatially isolated habitat groups are occupied, if these areas form a network. Under the present land use of the interspaces (farm land, fallows) the populations are obviously not isolated. Since sheep grazing has been abandoned on the dry grasslands, succession will reduce the habitat quality. This will initially concern small and less steep areas. Populations distributed over groups of small areas are then expected to get extinct.

The study shows that parameters for the habitat network can be obtained from relatively simple presence / absence surveys in landscapes. Similar results were presented by Biedermann (1997) and Baumann (1997). This can be applied in planning processes such as the environmental impact statement. Based on the data presented here, Kuhn (1998) assessed not only the direct destruction of habitats by several alternative highway routes through the study area, but also their fragmentation effects.

Statistical habitat models imply the assumption that the observed occurrence is in an equilibrium with the environmental factors and their spatial arrangement. In a one- or two-year investigation this assump-

tion is impaired, if populations are affected by environmental changes. In fact, the dynamics of populations at different distances should be studied over a longer period of time. Such information cannot be obtained from pure presence / absence data. Since only relatively short study periods are possible in practical planning, the question arises of which conclusions can be drawn from habitat models considering the spatial structure for clarifying the population structure in landscapes. This can be done by means of the four criteria for the identification of metapopulations according to Reich and Grimm (1996): (1) Delimitation of local populations, (2) local extinction, (3) population interactions via dispersing individuals, and (4) colonization of unoccupied areas.

The first habitat model shows that *Oedipoda caerulescens* colonises limited habitats in the porphyritic landscape. Whether the respective populations are delimited or merge to a single, spatially heterogeneous population via high exchange rates, cannot be directly taken from the data. If all incidences are high in a group of habitats, i.e., if hardly a habitat is unoccupied, it is obviously a spatially heterogeneous population and not a metapopulation. Neither local extinction nor the exchange of individuals between local populations or recolonisation of unoccupied areas can directly be derived from presence / absence data. Assuming that all unoccupied areas can be colonised, local extinction could be presumed for the actually unoccupied areas (cf. Appelt & Poethke 1997). Several years' investigations would provide better evidence of a "turn-over". Finally, colonisation probabilities for habitats of different sizes and at different distances can be derived from the regression curve (Fig. 5) (cf. Hanski 1994b; Appelt & Poethke 1997; Settele 1998). In usual planning processes, several years' investigations of the abundance dynamics are not feasible. Then, statistical habitat models considering the spatial structure of habitats in landscapes can yield results on the habitat connectivity, which are, however, subject to certain assumptions.

■ Zusammenfassung

In dieser Studie haben wir zunächst ein qualitatives Habitatmodell für die Blauflügelige Ödlandschrecke (*Oedipoda caerulescens*) aufgestellt, das die potentiellen Habitate in einer Landschaft kennzeichnet. Ein zweites Habitatmodell verbessert dann die Prognose der Vorkommenswahrscheinlichkeit, indem es Größe und Isolation dieser Flächen berücksichtigt. Die Daten stammen aus einem 32 km² großen Untersuchungsgebiet in der Porphyirkuppenlandschaft nordwestlich von Halle/Saale. Die Landschaft besteht im wesentlichen aus Feldern, halbruderalen Trockenfluren, Halbtrockenrasen, Volltrockenrasen und verbuschten Flächen. Dem qualitativen Habitatmodell liegen flächendeckende Karten zur Besonnung der Standorte und zur Vegetationsstruktur zu Grunde. Die Besonnung wurde aus einem Höhenmodell, GIS-Funktionen zur automatisierten Ableitung von Exposition und Hangneigung und einem darauf aufbauenden Insolationsmodell berechnet. Die horizontale und vertikale Vegetationsstruktur wurde aus der flächendeckenden Vegetationskarte unter Berücksichtigung der Wuchsform und Architektur aller Pflanzenarten abgeleitet. Die logistische Regressionsanalyse ergab eine hohe Korrelation von Besonnung und Vegetationsstruktur, so daß die Berücksichtigung der Besonnung nicht zu einer Verbesserung der Modellgüte führte. Das Habitatmodell ergibt eine maximale Vorkommenswahrscheinlichkeit von 30%, wenn die Vegetationsdeckungsgrad bei 50% liegt und die "standardisierte Bestandeshöhe" unter 0,3 m liegt. Flächen mit diesen Eigenschaften wurden zu potentiellen Habitaten erklärt. Durch Nachsuche wurde dann von diesen die jeweils besetzten bestimmt. Zwischen allen potentiellen Habitaten ist die Distanz (bezogen auf die Habitatränder) und die Interhabitatqualität berechnet worden, außerdem die Größe und Form der Habitate. Für die Berechnung sind eigene GIS-Funktionen entwickelt worden ("radiale Transektanalyse"). Die Auswertung von Isolation und Größe der Habitate mit der logistischen Regression

konnte die prognostizierte maximale Vorkommenswahrscheinlichkeit auf über 80% steigern. Das Ergebnis zeigt, daß sehr hohe Inzidenzen (>75%) zu erwarten sind, wenn das jeweils betrachtete Habitat groß ist und wenn viele besetzte Habitate in der Nähe liegen.

■ Summary

For *Oedipoda caerulescens* (Orthoptera, Saltatoria), we first established a habitat model that shows potential habitats in a landscape. A second model based on the isolation and size of the habitats then improves the predicted incidence. The field data originated from a study region (32 km²) with porphyry hilltops northwest of Halle / Saale in Central Germany. The landscape mainly consists of large fields and rocky outcrops covered by ruderal grasslands, dry grasslands and shrubs. The habitat model is based presence / absence observations of *Oedipoda caerulescens* and on maps of insolation and vegetation structure covering the whole area. The insolation was computed from a digital terrain model providing data on slope and exposition. The vertical and lateral vegetation structure was derived from a vegetation map using data on plant growth form and architecture of all species in the study region.

Insolation and vegetation structure are highly correlated. Inclusion of insolation in the model therefore did not raise the predictive power of the habitat model.

The first habitat model predicts a maximum incidence of 0.3 for *Oedipoda caerulescens* if vegetation cover is about 50% and the "standardized vegetation height" is below 0.3 m. This parameter refers to the algorithm to compute the vertical vegetation structure from the vegetation map.

All patches with $P_{krit} < 0,1$ were declared to be potential habitats. We recorded presence or absence of *Oedipoda caerulescens* in these habitats and computed distance (with respect to habitat borders, not midpoints) and inter-habitat quality, also size and form of the habitats. The predicted maximum inci-

dence in this second model is above 0.8 if the given patch is large and many other patches occupied by *Oedipoda caerulescens* are lying in the neighbourhood.

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Authors' addresses:

Dr. Wilhelm Kuhn, Ecklenstr. 32, D-70184 Stuttgart; and

Prof. Dr. Michael Kleyer*, Landscape Ecology Working Group, Carl-von-Ossietzky-University of Oldenburg, PO Box 2503, D-26111 Oldenburg, Germany; e-mail: michael.kleyer@uni-oldenburg.de

* Corresponding author.