Spatially explicit models for interacting populations in a changing landscape:
A case study on Namibian dragonflies (Odonata)

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Contents

1 Introduction

1.1 Aim of the work

Models, which are mostly abstractions of natural systems or processes, are useful to formulate hypotheses, to test the understanding of data survey and to make predictions about the future status of a system (Starfield & Bleloch 1991). Mathematical models of natural processes, and especially of population dynamics, are fundamental tools to develop and explore theories about processes that determine the structure of populations (Neuhauser 2001; Townsend et al. 2002).

Biological inquiries of animal populations are often limited to a relatively small spatial extent. Mathematical models may help to transfer the results of these detailed local descriptions of processes in the first place to situations with other internal or external environmental conditions and in the second place to a completely other spatial scale. Therefore, one target in population ecology is to understand and quantify the interactions of a population with its physical environment and with other species (Leibold 1995; McPeek & Peckarsky 1998).

The focal question of this work is how the population dynamics of local dragonfly populations and metapopulations, and consequently the biodiversity in arid regions may be altered by a change of the distribution and quality of their habitats. For that purpose I developed a spatially explicit model for the distribution of Odonata in the landscape. The components of this model are habitat suitability models, local population models, rules for the dispersal, and a dynamic landscape model. After a test of the model with certain theoretical scenarios, this model will be applied to different scenarios describing the dynamic change of the landscape under current and future climatic conditions. Using this model will make it possible to simulate certain trends and scenarios in the water balance and the reaction of the Odonata fauna to these changes.

This work is a part of the international project BIOTA (BIOdiversity Transect Analysis in Africa), which is funded by the German Federal Ministry of Education and Research. BIOTA has been initiated in 1999. Its aim is "a holistic scientific contribution towards sustainable use and conservation of the biodiversity of the African continent". My own research has been part of the subproject, which is entitled "Effects of anthropogenic changes on the diversity of Namibian Odonata: Modelling on different geographical scales". One of the aims of this subproject has been to develop the spatially explicit model mentioned above.

Note:

This work is dealing with models on different scales. The word "scale" is used for processes as well as for spatial resolution. Generally, the use of "large scale processes" means, that the resolution of the processes is taking place on a coarser spatio-temporal level. When speaking of "large scale" in the geographical context, the reference level normally is a finer spatial resolution – contrasting to the definition of "large scale" in the process context. I will use the term "large scale" for a coarser level and "small scale" for a finer level, regardless if the process or the geographical information is touched, to avoid confusion with the definition of "large" or "small" scales.

1.2 Modelling biodiversity

Biodiversity in its definition by the Convention on Biological Diversity of 1992 is described as "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems". Within the scope of this work, I will focus on some aspects of biodiversity. Gaston & Spicer (2004) provide an overview of the different aspects and scales, which are elements of biodiversity (Table 1.1).

Table 1.1:   Elements of biodiversity (adopted from Gaston & Spicer (2004)). Grey fields are subject of this work.

ecological diversity	genetic diversity	organismal diversity
biomes		domains or kingdoms
bioregions		phyla
landscapes		families
ecosystems		genera
habitats		species
niches		subspecies
populations	populations	populations
	individuals	individuals
	chromosomes	
	genes	
	nucleotides	

The central link between the three groups is the population level, which will be the main focus of this work. A population can be defined as a group of organisms of the same species with several typical properties, such as population density, birth and death rate, age distribution within the population and the dispersion (Jørgensen 1994). Another factor determining a population is the spatial contiguousness of its members (Akcakaya et al. 1999). One of the most important and most used measures for biodiversity is the species diversity, being described by the number of species (Hubbell 2001; Gaston & Spicer 2004). According to

Whittaker (1972), it can be distinguished in the alpha-, beta- and gamma-diversity. Alpha-diversity is simply defined as the number of species in a particular area or ecosystem, often determined at a patch-scale. Beta-diversity describes the change of species diversity between ecosystems and gamma-diversity refers to whole communities on a larger scale (Whittaker et al. 2001). To get information about the regional distribution of dragonfly species and consequently about the different levels of biodiversity, a modelling approach may help to understand existing patterns and analyse the impact of external changes on future distribution patterns.

The spatio-temporal distribution of species depends on a variety of factors. One the one hand, life-history parameters are responsible for the local pattern of the species' population dynamic. However, the traits of the organisms are bound to the resources, which the habitat provides. The variation of these resources on the other hand may cause feedback loops on the life-history parameters (Williams 1997; Johansson et al. 2001; Dmitriew & Rowe 2005). A potential for complex dynamics exists especially for multivoltine species under the influence of seasonally fluctuation (Kot & Schaffer 1984). Even long term adaptations of species due to selection towards better dispersers within one species may be a consequence of changes in the environment (van Dyck 1999; Hanski et al. 2004). One possible solution to combine internal processes with external forces, which may alter them, is a model that accounts for the local population dynamics as well as the regional distribution of potential habitats and consequently the information about the status of the metapopulation.

Coexistence between species sharing the same spatial resources becomes an important fact when considering the community structure in a given habitat. Communities are usually defined by spatial, functional or taxonomic relationships or by interactions within the food web (Schluter & Ricklefs 1993). The factors promoting their coexistence have to be identified (Yu et al. 2004). For interacting predators it is known, that predation affects survival, growth and behaviour (Wissinger 1988; Suhling & Lepkojus 2001; Stoks & McPeek 2003). Reference to a spatio-temporal level adds even more complexity to the problem: In temporary habitats the disturbance frequency or the duration, respectively, is known to exert influence on the community structure (Schneider & Frost 1996; Williams 1997). Furthermore, the effects of competition in a community model also have great influence on the stability of single populations (Nisbet & Onyiah 1994). Therefore the implementation of a multi-species model in the model approach is essential to seize processes influencing biodiversity on different scales.

1.3 Components of the spatially explicit dispersal model

To get information about potential impacts either of human action or of natural processes on dragonfly biodiversity, I will present a spatially explicit dispersal model. This model consists of different components, whose derivation will be shown in the following chapters of this thesis. To interpret information on biodiversity in its definition (cf. Chapter 1.1), a model system which deals with biodiversity issues has to analyse the species in their habitat, their interactions with each other and their dependency on external forces or resources (Huston 1994). Thus, the model must accomplish scale comprehensive requirements as the processes involved are taking place on different spatial scales. These different scales used in the model are depicted in Figure 1.1.
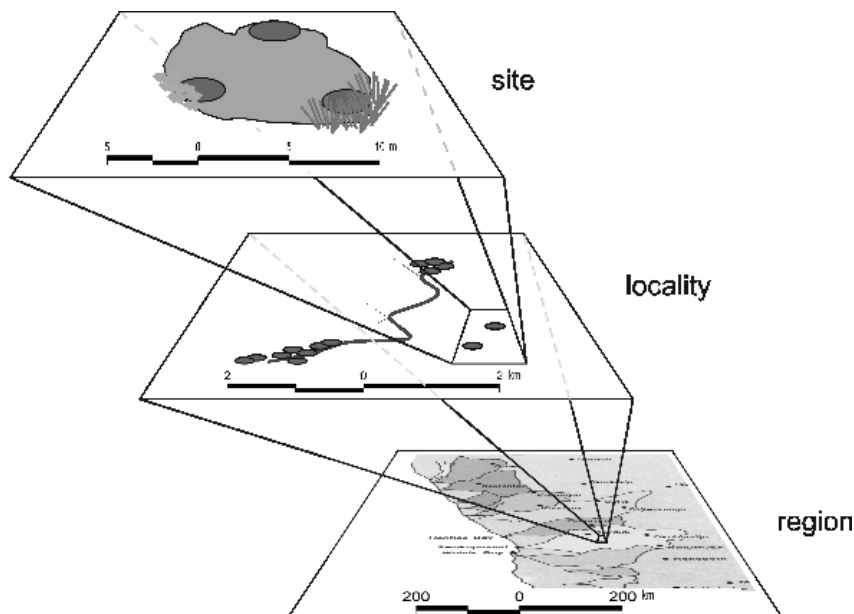
Figure 1.1: Different scales integrated in the spatially explicit model. The scale of the respective level is displayed in the different layers of the model.

The different submodels of the integrating approach will be presented in the following chapters. Figure 1.2 shows the modular concept of the model. In the second chapter, I will show the results of habitat suitability models (HSM). The HSM were calculated to gather knowledge about the habitat requirements of the dragonfly species, which are modelled. The scale on which the HSM are based is the site level. The third chapter still focuses on the habitat respective site scale and deals with population dynamic models for different Odonata species.

The information gathered in these two chapters will be integrated into the spatially explicit dispersal model. This model focuses on the regional scale with its smallest unit on the locality scale and therefore some abstractions of the real landscape are introduced. The basis of the

spatially explicit model is a model of a dynamically changing landscape, which will be described in Chapter 4.2 while the synthesis of all submodels can be seen in Chapter 4.3.
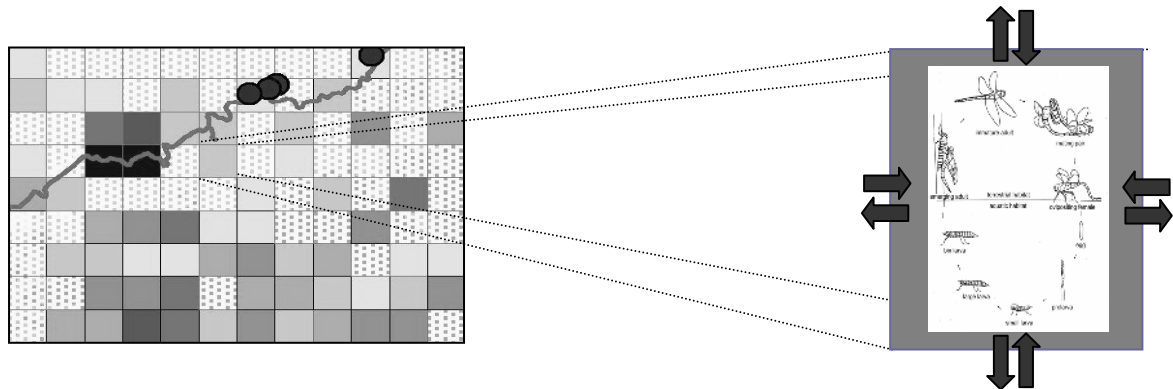

Figure 1.2: Model concept of the spatially explicit dispersal model. The map on the left represents the modelled landscape section, different colour of the cells stand for the different properties of the habitats. The image on the right is the zoomed view in one cell, where population dynamics are taking place dependent on habitat properties. The arrows indicate the dispersal of the adult dragonflies from their habitat.

One of the most important challenges when developing a model for the dispersal of highly mobile organisms like Odonata are the different scales on which the processes which determine the regional species composition are taking place (Mackey & Lindenmayer 2001). The egg and the larval part of the life cycle are taking place in the water while the emerged adult dragonfly is able to fly and to reach new habitats for further reproduction easily. Therefore dispersal between habitats, which are not directly connected, requires overland movement of the adults (Petersen et al. 2004). Processes at the local scale may be dependent on factors that cannot be displayed on a larger scale, so the information has to be transferred to another spatial scale. However, the same factor can have different consequences for species diversity on different scales (Chase & Leibold 2002). Factors, which may be perceived by one species as habitat heterogeneity can be interpreted as habitat fragmentation by another (Tews et al. 2004). Therefore landscape properties in the model have to be designed species-specific.

1.4 Area under investigation

Namibia can be described as a country with an arid climate (Leser 1982). An amount of 92 % of the country is defined as hyper-arid, arid or semi-arid (Tarr 1998). The land surface area covered by Namibia is approximately 823,680 km². The importance of the resource "water" becomes clear looking at the human population distribution in Namibia: About 58% of Namibia's population live in the northern regions Omusati, Oshana, Ohangwena, Oshikoto, Kavango and Caprivi (Mendelsohn et al. 2002), as the combination of water, soil fertility and

precipitation is best in these regions. However, the area of these regions is only about 18% of Namibia's total area.

During the summer in the southern hemisphere, the Intertropical Convergence Zone (ITCZ) is located north of Namibia and the Subtropical High Pressure Zone (SHPZ) lies south of Namibia. Tropical, moist air carries rain to the north of the country. In the winter situation, the ITCZ and the SHPZ move northwards, so the SHPZ build a kind of barrier for the tropical air. This results in the dry season for Namibia. In addition, the cold Benguela current at the coast of Namibia cools the air over the ocean so that the development of rain-bearing clouds is additionally reduced. This results in the extreme dry conditions of the Namib Desert.

The study area mainly consists of the ephemeral river catchments of western Namibia. The twelve major river catchments encompass about 20% of the area of Namibia (Table 1.2). They extend over a zone from approximately 17.5° to 25° southern latitude and approximately 12.5° to 17.5° eastern longitude. From north to the south the rivers are: Khumib, Hoarusib, Hoanib, Uniab, Koigab, Huab, Ugab, Omaruru, Swakop, Kuiseb, Tsondab and Tsauchab. Figure 1.3 shows the location of the western river catchments and the biomes covered by them.

Table 1.2:   Areas of the western river catchments

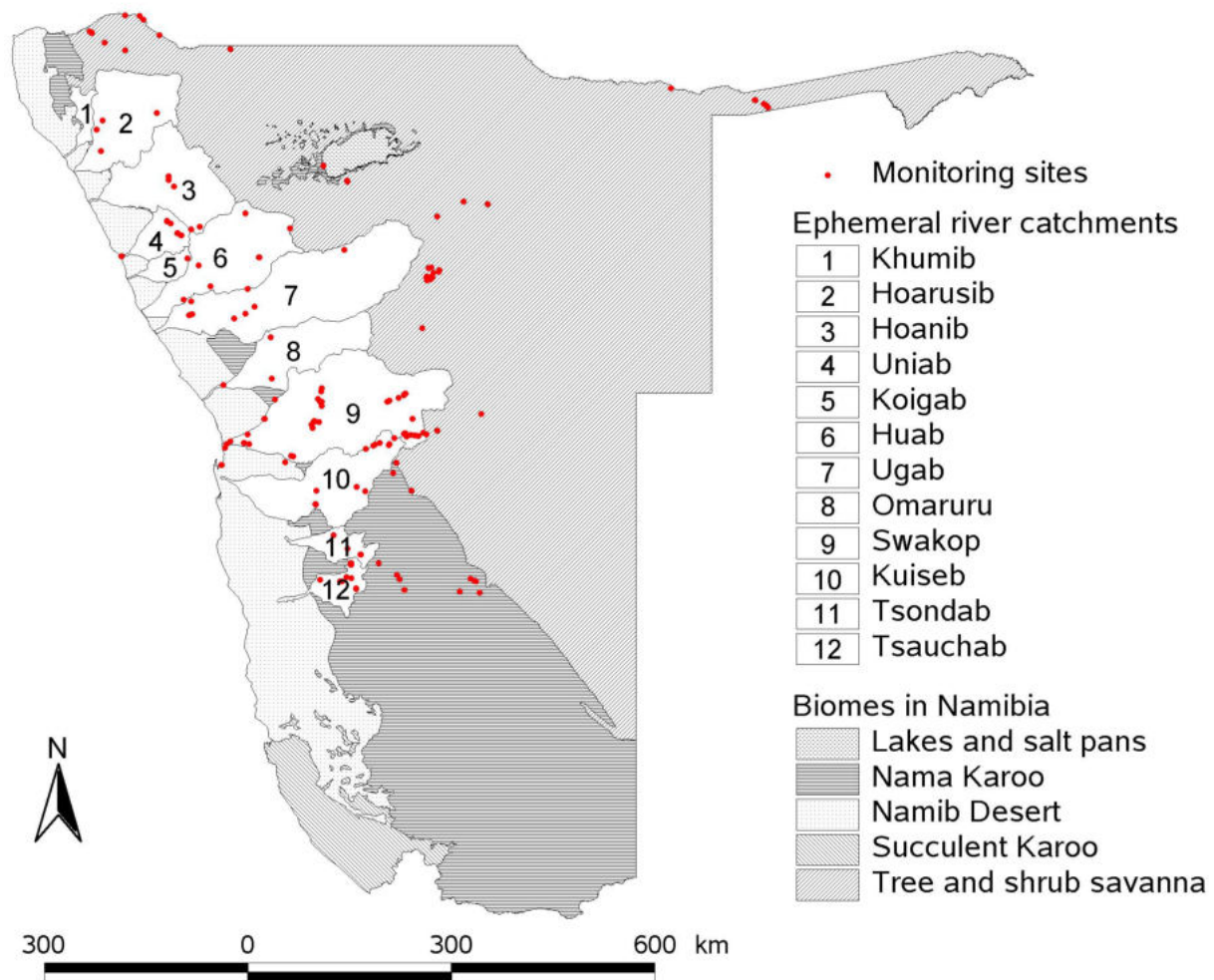| catchment	area [km²]
Khumib	2200
Hoarusib	15140
Hoanib	17200
Uniab	4500
Koigab	2400
Huab	14800
Ugab	28400
Omaruru	13100
Swakop	30070
Kuiseb	15500
Tsondab	3480
Tsauchab	3950
total	**150740**

Figure 1.3: Overview over the investigation area. Displayed are the ephemeral river catchments, the underlying biomes and the monitoring sites of the BIOTA project as at June 2003.

1.5 Biology and ecology of the species

According to Martens et al. (2003) 102 dragonfly species were recorded for Namibia. The model of the presented study mainly addresses questions on the patterns, which can be observed by interacting populations in the landscape. Therefore three common species belonging to different ecological types with different habitat requirements, flight and dispersal behaviours and life-history parameters have been chosen for modelling: *Pantala flavescens*, *Crocothemis erythraea* and *Paragomphus genei*. All three species belong to the group of widespread desert Odonata in Africa (Suhling et al. 2003). Additionally, the three species can be assigned to species groups, which are typical for the arid regions of Namibia (Table 1.3).

Table 1.3:   Ecological groups of dragonflies in Namibia (edited after Suhling, unpublished)

criteria	group 1	group 2	group 3
major habitat type	mainly ephemeral waters	from ephemeral to perennial waters	mainly perennial waters
habitat specificity*	low	low	high
dispersal mode	obligate migrants	good dispersers	reduced dispersal
phenology	seasonal (rainy season)	±a-seasonal	a-seasonal

* regarding the frequency of disturbances of the habitat and the duration of the hydroperiod of the habitat

One species type, which is typical for tropical-centred Odonata is described as "obligate migrant". It is carried by the winds of the ITCZ to areas where the rainy season produces temporary ponds (Corbet 1999; Corbet 2003). Representatives of this species type are for example the libellulid species *Sympetrum fonscolombii* (Selys, 1840) and *Pantala flavescens* (Fabricius, 1798). The presence of these species is dependent on the presence of water and probably the absence of predators (Suhling et al. 2003). Ephemeral waters usually provide these requirements and can therefore be considered as a typical habitat for group 1. In the following chapters *P. flavescens* is also described as "migrant" or "the migrant species".

As a representative of group 2, the libellulid *Crocothemis erythraea* (Brullé, 1832) was chosen. *C. erythraea* prefers vegetated wetlands, can be found in nearly all types of habitat in the area of investigation and has got medium dispersal abilities. A species which may be considered as a member of group 3 is the gomphid *Paragomphus genei* (Selys, 1841), which can mainly be found in ephemeral and permanent running waters, showing no preference for vegetation. This species seems to be confined to river valleys (Suhling et al. 2003). With respect to species belonging to group 2 (cf. Table 1.3) *P. genei* has restricted dispersal abilities. Therefore it was chosen as a representative of group 3. According to the phenology of the two species of group 2 and 3, they are in the following described as "resident 1" or "residential species 1" for *C. erythraea* respective "resident 2" or "residential species 2" for *P. genei*.

2 The habitat suitability models

2.1 Introduction

Habitat suitability models (HSM) in ecology are used for different purposes. On the one hand they may help to gain knowledge about the habitat-selective behaviour of certain species respectively to statistically ensure the expert knowledge obtained by observations and experiments. On the other hand, habitat suitability models serve as decisive tools in conservation management to make predictions of the presence or absence of some (key-) species in certain habitats or under certain habitat conditions (Fielding & Haworth 1995; Schröder & Reineking 2004a).

In this study the purpose of the habitat suitability models affects both sides: Basically, there is the need to identify the preferential habitat parameters for certain dragonfly species in western Namibia. Habitat selection is always closely related to dispersal of individuals (Stamps 2001) and therefore the knowledge of the habitat preferences is essential for the development of a dispersal model (cf. Chapter 4). However, the purpose of conservation management is also touched as the distribution of animals is one important aspect for the understanding of biodiversity (Huston 1994; Gaston & Spicer 2004). One of the major aspects in conservation management is to make predictions about the impacts of the change of the arrangement of habitats in space and time and especially about the relevance of habitats, which may serve as a refuge (Berg et al. 2004).

Habitat models are used to assess the impact of changes in the environmental conditions on the distribution of organisms (Guisan & Zimmermann 2000). They describe the optimal state of the habitat parameters for the species and therefore allow to give conclusions about a possible improvement of habitat quality (Lindenmayer et al. 1991). Temporary habitats, which supply a large fraction of the natural and artificial aquatic habitats in dry Namibia, are subject to a special dynamic. The pattern of disappearance of water respective the length of the hydroperiod leads to a dynamic change of biotic and abiotic habitat parameters like decrease in the habitat volume or an increase in insolation (Williams 1997). Disturbances of aquatic habitats either by desiccation of degradation are generally supposed to decrease species richness (Sada et al. 2005).

The suitability of habitats for certain species can be calculated with different statistical approaches, among others discriminant analysis, linear regression and logistic regression. These methods require good presence/absence data. For a detailed review see Schröder &

Reineking (2004a). A second group of methods for habitat suitability models is based on the ENFA (Ecological Niche Factor Analysis, (Hirzel et al. 2002; Brotons et al. 2004)), which is based only on presence data of the organisms. However, this approach requires the relevant parameters to be available in a geographical information system (GIS) and was therefore discarded in this work.

The aim of this chapter is to analyse the data, which were recorded during the monitoring programme of the BIOTA subproject for the three groups of dragonflies introduced in chapter 1 regarding the use of the aquatic habitats depending on the current set of habitat parameters and to identify key factors, which can be used in the dispersal model (Chapter 4).

2.2 Methods

2.2.1   Logistic regression as a tool for habitat suitability models

The statistical approach of the logistic regression was chosen to calculate the HSM. Regression models describe the relationship between a dependent variable (= outcome or response variable) and one or more independent variables (= predictor or explanatory variables), which are also called covariates (Backhaus et al. 2000; Hosmer & Lemeshow 2000). Logistic regression as a special case of Generalised Linear Models (GLM) differs from linear regression in the dependent variables, which are dichotomous. This is very advantageous for the modelling of presence/absence data, which are already binary coded with "0" for absence and "1" for presence. The independent variables can be both category variables and continuous variables (Dobson 1990; Backhaus et al. 2000).

The logistic distribution describes $E[Y \mid \vec{x}]$, the expectancy of Y under condition x (Equation 2.1).

$$E[Y \mid \vec{x}] = P(\vec{x}) = \frac{e^{\beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n}}{1 + e^{\beta_0 + \beta_1 x_1 + \ldots + \beta_n x_n}}$$

Eq. 2.1

with:

Y: dependent variable, explaining presence or absence of the species

$\vec{x}$:   independent variable, parameter vector of the habitat parameters

β_i: regression coefficients

This distribution yields that the expectancy is limited to the interval $[0,1]$. $P(\vec{x})$ can therefore be interpreted as the probability of occurrence for the investigated species in the parameter space described by the vector $\vec{x}$ or, spoken in terms of conservation biology, as habitat suitability. The parameters β_i of Equation 2.1 are estimated using the maximum likelihood method (Agresti 1996; Peeters & Gardeniers 1998). A likelihood function L is set up expressing the probabilities of the monitoring data as a function of the unknown parameters β_i. A prerequisite for the use of the logistic regression is the independence of the recorded data (Hosmer & Lemeshow 2000). The problem resulting from the demand on the independence of the data will be discussed in Section 2.4

After the estimation of the HSM an evaluation of the goodness of fit is needed to interpret the results of the statistical analysis in an ecological context. One measure for the goodness of a HSM is the confusion matrix, which compares the predicted presence/absence with the observed presence/absence data.

		observed data		
		1	0	sensitivity: a/(a+c)
prognosed	1	a	b	specificity: d/(b+d)
occurrence	0	c	d	% correct prognoses: a+d/(a+b+d+c)

Figure 2.1:   Confusion matrix and derived quality criteria. 0: absence, 1: presence

The entries b and c in Figure 2.1 are described as error type I (false positive, FP=b), which prognoses a presence with an observed absence, and error type II (false negative, FN=c), which prognoses an absence with an observed presence (Fielding & Bell 1997; Morrison et al. 1998).

The sensitivity represents the proportion of correct prognosed occurrences of all observed occurrences while the specificity describes the proportion of correct prognosed non-occurrences of all observed non-occurrences (Pearce & Ferrier 2000). These categories, which describe the discrimination of the model between presence and absence of the species can only be determined when applying a threshold value to the calculated probability of occurrence (Akcakaya & Atwood 1997).

The threshold value can take different values, depending on the intention of the model. Generally, a threshold value of 0.5 can be used and leads to a minimization of the total error of the model (Reineking & Schröder 2004). If the proportion of correct prognoses of occurrence has to be maximised, the threshold value p_{max} can be used. This threshold increases the type II error. Another possible threshold value, p_{fair}, leads to a same proportion

of wrong prognoses for absence as well as for the presence of the species and balances both error types (Schröder & Richter 1999). The results show the respective optimized p_{max} and p_{fair}-values for the single models, calculated with the program ROC & AUC (Schröder 2003).

Another measure for the discriminative power of the HSM is the use of the AUC-value (Area Under the ROC-Curve, ROC: Receiver Operating Characteristic). For a continuous variation of the threshold value in the interval between 0 and 1 every pair of sensitivity and specificity is calculated. The sensitivity (y-axis) is plotted against the value 1-specificity (x-axes). (Schröder 2000; Vogel 2002; Reineking & Schröder 2004). The AUC can reach values between 0.5, which is a complete random model and 1, which shows the perfect discrimination. Hosmer & Lemeshow (2000) provide a ranking of the AUC values:

$0.7 \leq AUC < 0.8$ = acceptable

$0.8 \leq AUC < 0.9$ = excellent

$0.9 \leq AUC$ = outstanding

Figure 2.2 shows an example for the ROC chart for *C. erythraea* and the parameter "aquatic vegetation diversity".
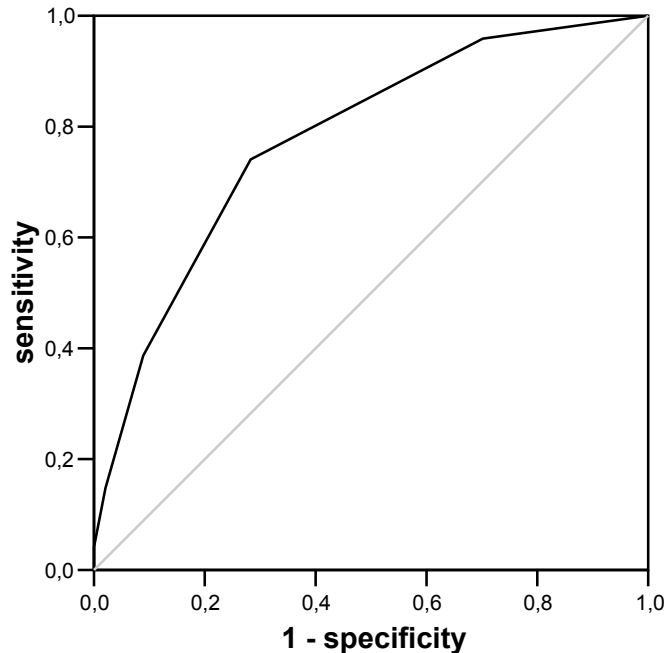

Figure 2.2:   ROC chart for *C. erythraea* and the parameter "aquatic vegetation diversity". The area under the curve (black line) is 0.778. The grey line shows a random model (AUC=0.5)

A value which is also of great importance for the interpretation of the results of the logistic regression analysis is the R²-value after Nagelkerke (1991), R^2_N. This measure quantifies the

proportion of the variance explained by the model (Sokal & Rohlf 1995). The higher the R^2_N-value, the better the model discriminates between presence and absence of the species.

2.2.2 Data basis

A one-year monitoring programme was carried out in the ephemeral river catchments of western Namibia (Suhling et al. 2005b, in press). A total of 279 sampling sites were visited, some of them more than once to record possible changes of temporally variable habitat parameters. In total 628 sites were used for the calculation of the HSM. The distribution of the sampling sites on the catchments is shown in Table 2.1. The Tsauchab River catchment, the Swakop River catchment, and the Uniab River catchment are outstanding with a total of 80 percent of all monitoring incidents respectively 69.2 percent of all monitoring sites. Table 2.2 gives an overview of the recorded habitat parameters and their coding (binary or metric). Generally, the presence of adult dragonflies at the aquatic habitat was recorded together with the biotic and abiotic factors.

Table 2.1: Distribution of the sampling sites on the catchments

catchment	# of sites (incl. repetitions)	% (incl. repetitions)	# of sites (no repetitions)	% (no repetitions)
Hoarusib	3	0.5	3	1.1
Hoanib	22	3.5	16	5.7
Uniab	113	18.0	41	14.7
Huab	28	4.5	17	6.1
Ugab	28	4.5	19	6.8
Omaruru	1	0.2	1	0.4
Swakop	192	30.6	91	32.6
Kuiseb	36	5.7	27	9.7
Tsondab	8	1.3	3	1.1
Tsauchab	197	31.4	61	21.9
total	**628**	**100.0**	**279**	**100.0**

Table 2.2:   Recorded parameters at the aquatic habitat during the monitoring and their coding

habitat parameter	coding
degree East	metric
degree South	metric
altitude a.s.l.	metric
length of habitat	metric
width of habitat	metric
area of habitat	metric
water depth	metric
chara/potamogeton	binary
algae / floating leaf plants	binary
rush / sedge	binary
reed / typha	binary
floating grasses	binary
herbaceous plants	binary
bushes / trees	binary
aquatic vegetation diversity	metric
no vegetation	binary
detritus	binary
mud	binary
sand	binary
gravel	binary
stones	binary
rock	binary
sediment diversity	metric
current velocity	metric
electrical conductivity	metric
pH-Value	metric
water temperature	metric
percentage riparian vegetation	metric
percentage riparian rocks	metric
percentage shadowed	metric

The parameters describing the aquatic vegetation and the sediment of the habitat were binary coded, as for many dragonfly species it appears that not the degree of the incidence of a parameter is important for habitat selection but simply the presence of the habitat parameter (Martens, pers. comm.).

The incidences of the parameters describing the different classes of vegetation growth heights (chara/potamogeton, algae/floating leaf plants, rush/sedge, reed/typha, floating grasses, herbaceous plants, and bushes/trees) at each site were summed up to the artificial parameter "aquatic vegetation diversity", characterising the complexity of the vegetation structure in the habitat. The same was performed for the sediment types (detritus, mud, sand, gravel, stones, rock) in the habitat, which were summed up to the parameter "sediment diversity".

Models were calculated for several common species in the investigation area. For rare species no significant models could be calculated due to the disparity of few presence data to a high amount of absence data (Backhaus et al. 2000). As the whole model system was set up in

order to model three species with different behaviour (Chapter 1.4) the results displayed in this chapter focus on *Crocothemis erythraea* and *Paragomphus genei* as representatives of the residential type and *Pantala flavescens* as representative of the migrant type.

2.2.3 Univariate habitat suitability models

As a preliminary analysis, a correlation analysis of the investigated habitat parameters against the presence of the focal species was conducted (Figure 2.3). Afterwards a univariate logistic regression analysis was performed for each single habitat parameter.

2.2.4 Multivariate habitat suitability models

The parameters, which yielded significant univariate models, were considered for the calculation of multivariate models. The logistic regression procedure was based on a forward stepwise regression taking the change of the likelihood ratio (LR) as a criterion for inclusion of a new parameter. For the conduction of a multivariate logistic regression it is recommended to investigate the correlation between the habitat variables in order to exclude those which are highly correlated (Fielding & Haworth 1995). Some of the variables were correlated with others by a correlation coefficient greater than 0.7. This holds especially true for the variables describing aquatic vegetation (e.g. reed and *Typha* was correlated with algae and floating leaves). Nevertheless, these parameters were included in the analysis because the presence of a certain vegetation structure may be important for the habitat selection of one species, even if another vegetation structure might be correlated with it. Additionally, the forward stepwise inclusion of covariates in the models creates some kind of bottleneck effect. This may prevent the inclusion of the correlated covariate because the likelihood ratio will not increase significantly after the first correlated covariate has been included in the model.

The parameter "no vegetation present" has been omitted in the regression procedure as it is included in the special case of aquatic vegetation diversity being zero and therefore it does not provide additional information in the multivariate model. Most of the habitat parameters were designed to explain the presence or absence of the species at the (micro-) habitat scale, except for the geographical coordinates, which have to be interpreted from a more regional point of view. Therefore these parameters were also excluded from the multivariate regression analysis.

2.2.5 Validation of the multivariate models

It is of special importance to know about the transferability of habitat models to other habitats, especially because the models often shall serve as a basis for decisions in

conservation planning (Schamberger & O'Neil 1986; Brooks 1997). For example, an error type II (prognosed absence with an actual presence at a habitat) may lead to a local extinction when this habitat is destroyed on the basis of (false) prognosis.

For a test of the validity of the models it seems reasonable to test the models on independent data from another area of investigation (Capen et al. 1986; Verbyla & Litvaitis 1989; Fielding & Bell 1997; Schröder 2000; Vogel 2002). This approach has been tested with the available data. The multivariate models have been calculated for one catchment while the test of their transferability has been done for another catchment. Unfortunately this procedure didn't lead to reasonable results as models from one catchment and for one species could not have been reproduced with the data from another catchment (see Chapter 2.4.2). Therefore the validation of the data has been conducted as an internal validation.

For the use of different internal and external validation techniques, Schröder & Reineking (2004b) provide an excellent overview. For the validation of the models the leaving-one-out technique, also known as Jackknife-procedure, a special case of the crossvalidation, has been chosen (Steyerberg et al. 2001). In the jackknife procedure only one sample site is taken for the testing of the validity while the remaining n-1 sample sites are used for the formulation of the HSM. This procedure is repeated until each of the sample sites has been used once. The confusion matrix of the validation procedure can be compared with the confusion matrix of the original model. The numbers of correct prognoses depending on the chosen threshold value serve for the evaluation of the transferability.

2.2.6   The habitat web – a semi-multivariate approach

The multivariate models for each of the three species led to the inclusion of different habitat parameters. Consequently, an approach was chosen to compare the habitat requirements based on the complete parameter space defined by the monitoring programme. For this, the R^2_N values of the univariate models, which act as a measurement for the explained variance of the model, are taken for all investigated parameters, regardless if a model can be calculated or not. A covariate for which no model can be calculated obtains a R^2_N value of zero. After sorting the R^2_N values from the highest to the lowest value, these values can be plotted as a net chart (see Figure 2.5.). To compare the species' habitat requirements in the investigated parameter space, Equation 2.3 calculates the area of the web spanned by the R^2_N values of the univariate models, normalized by the maximum area of all investigated habitat parameters.

Notation:

n: number of investigated covariates, sorted by the value of R^2_N

A: area of the habitat web

$$A_{max} = n \cdot 0.5 \cdot \sin\left(\frac{2\pi}{n}\right)$$

Eq. 2.2

$$A_{species} = 0.5 \cdot \sin\left(\frac{2\pi}{n}\right) \cdot (R^2{}_N(factor_n) \cdot R^2{}_N(factor_1) + \sum_{i=1}^{n-1} R^2{}_N(factor_i) \cdot R^2{}_N(factor_{i+1})) / A_{max}$$

Eq. 2.3

The maximum value of $A_{species}$ is 1. The higher the value of $A_{species}$ gets, the more specialized is the species regarding the parameters included in the monitoring programme.

2.3 Results

The calculations of the HSM were done with the complete set of all monitoring sites (cf. Chapter 1). The modelled species had the following number of occurrences in the data set: *C. erythraea* was observed in 243 out of 628 cases, *P. genei* in 117 and *P. flavescens* in 170 cases.

2.3.1   Univariate models

All three species show significant correlations for the area of the habitat, increasing from *P. flavescens* over *P. genei* to *C. erythraea* (Figure 2.3).
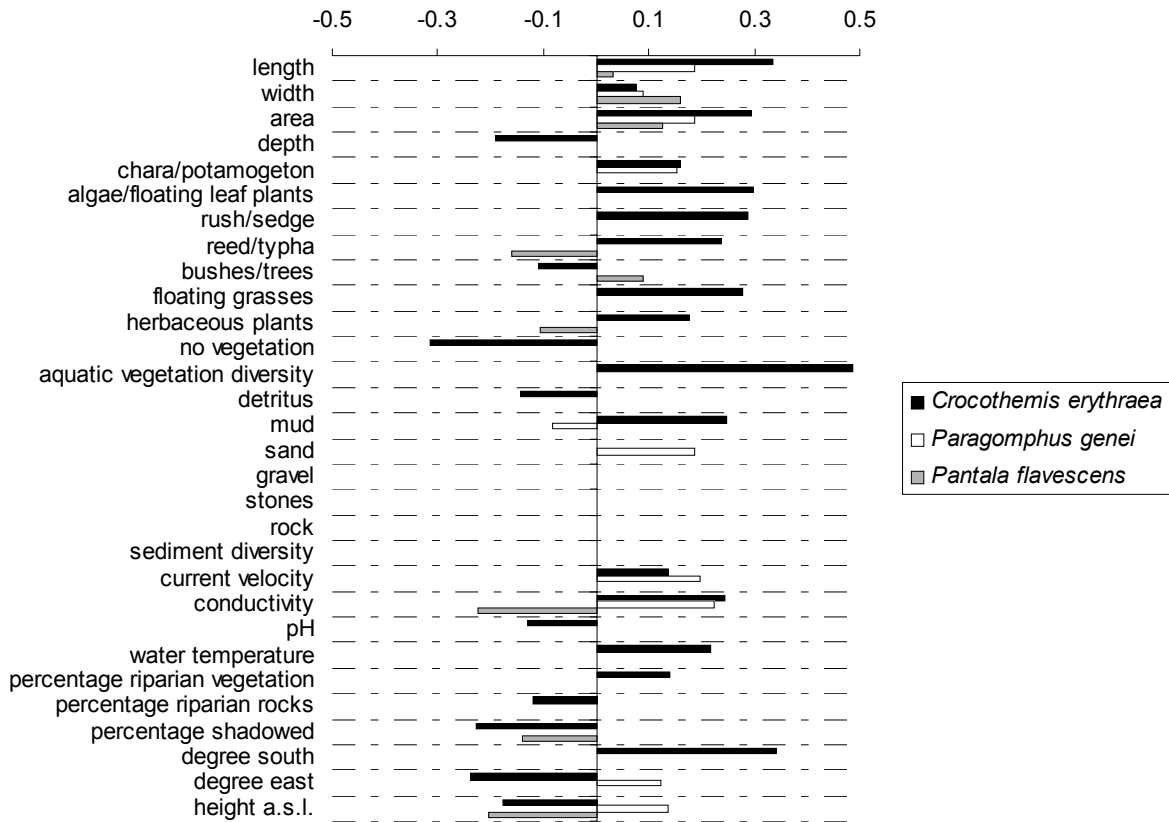
Figure 2.3: Spearman rank-correlation for *C. erythraea*, *P. genei* and *P. flavescens* for the investigated habitat parameters. Only significant correlations are shown (P<0.05)

C. erythraea was positively correlated with all habitat parameters regarding the vegetation in the aquatic habitat except for the presence of trees and bushes. The highest correlation can be seen for the artificial sum-parameter "aquatic vegetation diversity". The negative correlation with no vegetation in the habitat corresponds well with these findings. The abiotic parameters for *C. erythraea* showed significant positive correlation for presence of mud as a substrate in the habitat and also for current velocity, conductivity and water temperature, but negative correlation with detritus as substrate, percentage of the habitat in the shadow (at the time of monitoring), and the percentage of riparian rocks.

P. genei was positively correlated with the presence of *Chara* spp. and *Potamogeton* spp. but with no other habitat parameter associated with vegetation structure. Concerning abiotic parameters *P. genei* was positively correlated with sand as substrate, current velocity, and electrical conductivity, but negatively with mud as substrate.

For *P. flavescens* positive correlations for bushes and trees in the aquatic habitat can be stated, while negative correlations concerning reed/typha and herbaceous plants were calculated.

Regarding the abiotic habitat parameters, *P. flavescens* was negatively correlated with conductivity and the percentage of the habitat area that was shadowed.

The number and the quality of the univariate HSM differed much between the three species as already expected from the correlation analysis. Significant models and their quality criteria are displayed in Table 2.3 to Table 2.5.

Table 2.3: Univariate HSM for *C. erythraea* and their quality criteria. Bold numbers indicate high R^2_N-Values (above R^2=0.1) respectively at least "acceptable" AUC values according to Hosmer & Lemeshow (2000)

habitat factor	significance	R^2_N	regression coefficient	AUC	P_{fair}	P_{opt}
degree of latitude	***	**0.348**	0.718	**0.797**	0,340	0,395
degree of longitude	***	**0.154**	-0.638	0.659	0,308	0,585
altitude a.s.l.	***	0.066	-0.001	0.641	0,395	0,420
length	*	0.017	0.001	0.698	0,375	0,380
depth	***	0.044	-0.008	0.611	0,428	0,448
chara/potamogeton	***	0.033	1.003	0.552	0,485	0,485
algae/floating leaf plants	***	**0.115**	1.252	0.650	0,410	0,410
rush/sedge	***	**0.109**	1.215	0.647	0,398	0,398
reed/typha	***	0.072	1.222	0.594	0,480	0,480
bushes/trees	**	0.019	-1.283	0.525	0,280	0,703
floating grasses	***	0.099	1.428	0.613	0,493	0,493
herbaceous plants	***	0.040	1.074	0.559	0,488	0,488
no vegetation	***	**0.151**	-2.294	0.629	0,275	0,735
aquatic vegetation diversity	***	**0.302**	1.004	**0.778**	0,365	0,365
detritus	***	0.030	-1.027	0.548	0,305	0,708
mud	***	0.082	1.040	0.627	0,393	0,393
current velocity	**	0.020	0.032	0.560	0,370	0,505
electrical conductivity	*	0.020	0.000	0.642	0,430	0,435
pH	*	0.019	-0.273	0.576	0,453	0,480
temperature	***	0.062	0.111	0.626	0,440	0,450
percentage riparian vegetation	***	0.033	0.009	0.581	0,338	0,463
percentage riparian rocks	**	0.020	-0.006	0.570	0,370	0,720
percentage shadowed	***	0.060	-0.019	0.606	0,440	0,723

Table 2.4: Univariate HSM for *P. genei* and their quality criteria.

habitat factor	significance	R^2_N	regression coefficient	AUC	P_{fair}	P_{opt}
degree of latitude	**	0.020	0.159	0.559	0.278	0.180
degree of longitude	**	0.022	-0.255	0.600	0.298	0.170
altitude a.s.l.	***	0.076	-0.001	0.677	0.733	0.193
chara/potamogeton	***	0.032	1.006	0.562	0.678	0.260
sand	***	0.057	0.991	0.621	0.633	0.190
mud	*	0.011	-0.435	0.554	0.610	0.185
current velocity	***	0.039	0.042	0.607	0.460	0.180
electrical conductivity	*	0.021	0.000	0.659	0.228	0.195

Table 2.5:   Univariate HSM for *P. flavescens* and their quality criteria.

habitat factor	significance	R^2_N	regression coefficient	AUC	P_{fair}	P_{opt}
degree of longitude	**	0.019	0.231	0.588	0.673	0.295
altitude a.s.l.	*	0.014	0.001	0.556	0.32	0.285
width of habitat	**	0.016	0.015	0.605	0.42	0.255
bushes / trees	*	0.010	0.790	0.522	0.72	0.35
herbaceous plants	**	0.018	-0.867	0.539	0.645	0.215
electrical conductivity	**	0.025	0.000	0.642	0.34	0.315
pH-Value	*	0.022	0.322	0.554	0.368	0.27
percentage shadowed	**	0.034	-0.016	0.572	0.655	0.28

It is obvious that the presence of *C. erythraea* was determined by the presence of vegetation in the aquatic habitat except for the vegetation type "bushes/trees". The artificial sum parameter "aquatic vegetation diversity" yielded the highest R²-value except for the degree of latitude. With increasing vegetation diversity the predicted probability of occurrence increases. Figure 2.4 illustrates this model including the observed values for *C. erythraea, P. flavescens* and *P. genei*. An unimodal model (Gaussian-logit, (Peeters & Gardeniers 1998)) also did not yield significant models for *P. flavesencs* and *P. genei*.
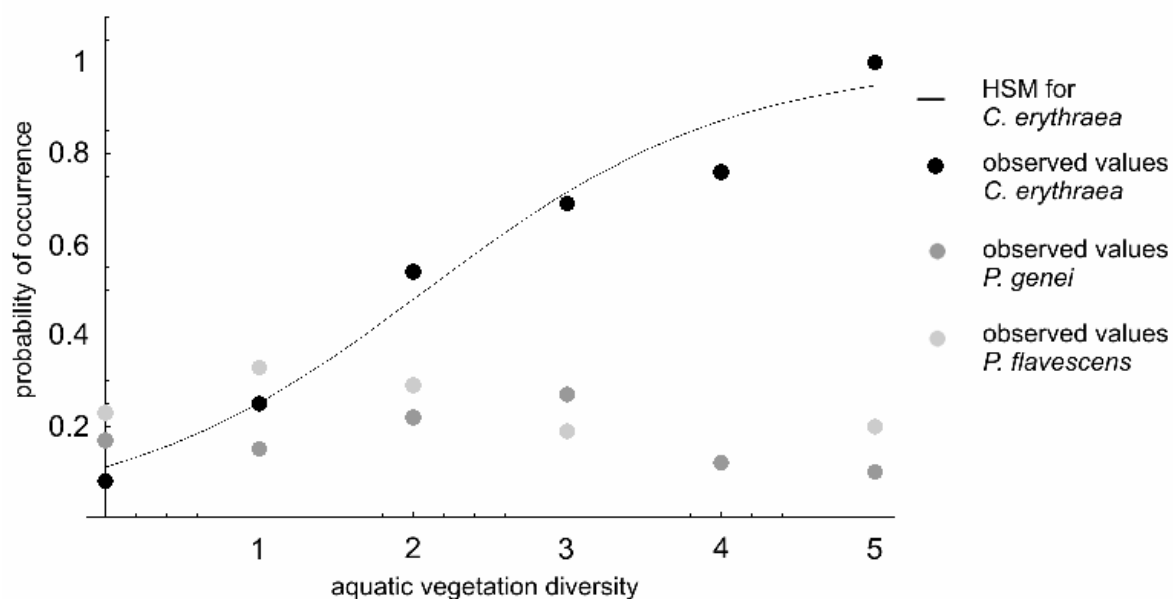
Figure 2.4:   Habitat suitablility model for the habitat parameter "aquatic vegetation diversity". The line is the fitted logistic regression model for C. erythraea and the dots represent the observed values. Also shown are the observed values for P. genei and P. flavescens, for which no significant models could have been calculated.

The univariate models confirmed the differences between the three species obtained from the correlation analysis. For *P. genei* as well as for *P. flavescens* none of the habitat parameters, which were included in the regression analysis, yielded R^2_N values comparable to those of *C. erythraea*. The regression coefficient, either with positive or negative sign was rather low

compared to the coefficients of the models for *C. erythraea*. The models for *P. genei* and *P. flavescens* showed great differences regarding the two different calculated threshold values, p_{opt} and p_{fair}, especially for those parameters, which were recorded as binary values. Only for *C. erythraea* the AUC values reached at least an acceptable value, and even here just for the covariates "degree of latitude" and "aquatic vegetation diversity"

2.3.2   Multivariate models

Various multivariate HSM were calculated for the three focal species (Table 2.6 to Table 2.8). Displayed are the results from the last step of the forward stepwise regression analysis for the inclusion of all parameters and the resulting criteria for the evaluation of the model's performance.

Table 2.6:   Multivariate HSM for *C. erythraea* and the quality criteria

habitat factor	significance of model	R^2_N	regression coefficient	AUC	P_{fair}	P_{opt}
	***	0.453		0.839	0.495	0.37
altitude a.s.l.			-0.002			
length			0.003			
bushes/trees			-2.318			
conductivity			-0.000			
aquatic vegetation diversity			0.875			

Table 2.7:   Multivariate HSM for *P. genei* and the quality criteria

habitat factor	significance of model	R^2_N	regression coefficient	AUC	P_{fair}	P_{opt}
	***	0.185		0.638	0.545	0.205
altitude a.s.l.			-0.001			
sand			1.168			
velocity			0.036			

Table 2.8:   Multivariate HSM for *P. flavescens* and the quality criteria

habitat factor	significance of model	R^2_N	regression coefficient	AUC	P_{fair}	P_{opt}
	***	0.123		0.662	0.440	0.25
altitude a.s.l.			0.001			
herbaceous plants			-1.317			
percentage shadowed			-0.012			

The models were highly significant for all three species. One factor, which all three species have in common, is the altitude a.s.l. of the habitat, but the regression coefficient for this parameter showed only a very low value in all three species.

For *C. erythraea* the 25 parameters for which univariate models were calculated were reduced to five parameters, which increased the explained variance of the model. The negative

regression coefficient for trees and bushes in the habitat and the positive for the aquatic vegetation diversity stand out from the other three parameters, which had regression coefficients near zero. The AUC value for the HSM for *C. erythraea* can be classified as an excellent value for the model's discriminative power (Hosmer & Lemeshow 2000). The R^2_N value of the multivariate model also increased from 0.302 for the univariate model regarding the covariate aquatic vegetation diversity to 0.453.

The eight habitat parameters from the univariate models for *P. genei* were reduced to three parameters in the multivariate model with sand showing the highest regression coefficient, followed by the covariate current velocity. The AUC value for the multivariate model was lower than the highest AUC value of all univariate models, while the explained variance increased to a still relatively low value of 0.185.

The eight univariate HSM for *P. flavescens* were also reduced to a multivariate model with three covariates. In this model the covariate that stood out regarding the regression coefficient was the negative value for the presence of herbaceous plants. The AUC value of the multivariate model did only slightly increase compared to the univariate model with the best AUC value.

2.3.3   Validation of the multivariate models

Results for the validation of the multivariate models were obtained with an internal jackknife validation (Table 2.9 to Table 2.14). For the models with the threshold value p_{opt} the percentage of total correct prognoses and the sensitivity and specificity are displayed as quality criteria. The models using the threshold value p_{fair} can be the compared by the percentages of correct prognoses as quality criterion due to the fact that p_{fair} optimizes the classification matrix regarding the same values for the number of correct prognoses, sensitivity and specificity. For all models, the quality criteria of the validated model did not differ very much from those of the unvalidated model.

Table 2.9:   Confusion matrices of the unvalidated and the jackknife-validated multivariate model for *C. erythraea*. Threshold value: p_{opt}

		unvalidated model			jackknife validated model	
		observed data			observed data	
		1	0		1	0
prognosed	1	118	32	1	114	39
occurrence	0	58	184	0	62	177
% correct prognoses|sensitivity|specificity		77.0|67.0|85.2			74.2|64.8|81.9	

Table 2.10: Confusion matrices of the unvalidated and the jackknife-validated multivariate model for *C. erythraea*. Threshold value: p_{fair}

		unvalidated model			jackknife validated model	
		observed data			observed data	
		1	0		1	0
prognosed occurrence	1	131	53	1	129	55
	0	45	163	0	47	161
% correct prognoses		75.0			73.3	

Table 2.11: Confusion matrices of the unvalidated and the jackknife-validated multivariate model for *P. genei*. Threshold value: p_{opt}

		unvalidated model			jackknife validated model	
		observed data			observed data	
		1	0		1	0
prognosed occurrence	1	13	6	1	12	14
	0	81	379	0	82	371
% correct prognoses| sensitivity|specificity		81.8|13.8|98.4			80.0|12.8|96.4	

Table 2.12: Confusion matrices of the unvalidated and the jackknife-validated multivariate model for *P. genei*. Threshold value: p_{fair}

		unvalidated model			jackknife validated model	
		observed data			observed data	
		1	0		1	0
prognosed occurrence	1	60	141	1	57	144
	0	34	244	0	37	241
% correct prognoses		63.5			62.2	

Table 2.13: Confusion matrices of the unvalidated and the jackknife-validated multivariate model for P. *flavescens*. Threshold value: p_{opt}

		unvalidated model			jackknife validated model	
		observed data			observed data	
		1	0		1	0
prognosed occurrence	1	36	13	1	35	15
	0	74	292	0	75	290
% correct prognoses| sensitivity|specificity		79.0|32.7|95.7			78.3|31.8|95.1	

Table 2.14: Confusion matrices of the unvalidated and the jackknife-validated multivariate model for *P. flavescens*. Threshold value: p_{fair}

		unvalidated model			jackknife validated model	
		observed data			observed data	
		1	0		1	0
prognosed	1	59	116	1	59	122
occurrence	0	51	189	0	51	183
% correct prognoses		59.8			58.3	

2.3.4   The habitat webs for the investigated species

Habitat webs for the three investigated species were combined in one net chart (Figure 2.5). It clearly shows the differences between the three species: *C. erythraea* has got the highest $A_{species}$ value ($A_{C.\ erythraea}$ = 0.00436), while *P. genei* can be found in the middle position with $A_{P.\ genei}$ = 0.00031 and *P. flavescens* with the smallest area, $A_{P.\ flavescens}$ = 0.00015.
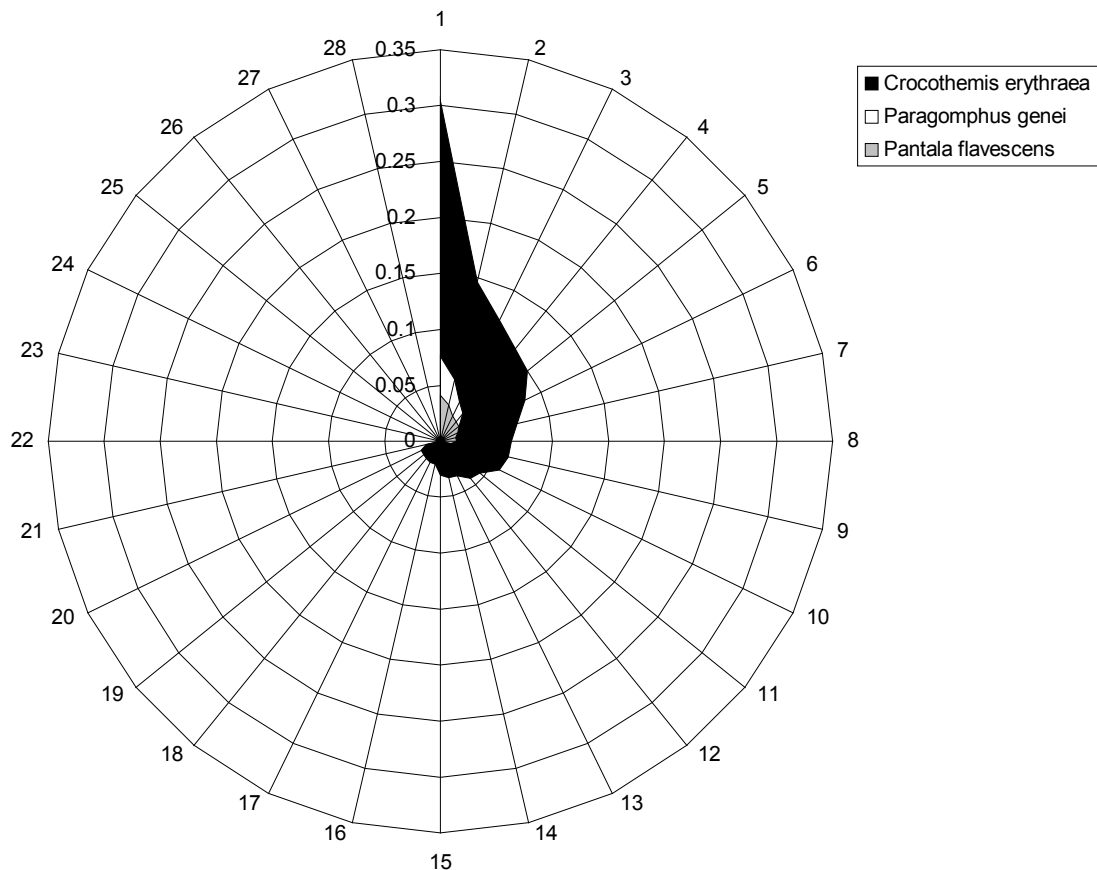
Figure 2.5: Habitat webs for *C. erythraea* (black web), *P. genei* (white web) and *P. flavescens* (grey web). The web for *C. erythraea* is located in the background, the web for *P. genei* in the middle and the web for *P. flavescens* in the foreground. The numbers on the spokes of the net are the positions of the sorted R²N values, descending from the largest to the smallest values. The values applied on the spokes are the R²N values of the univariate models.

2.4 Discussion

According to Hosmer & Lemeshow (2000) the independence of the recorded data is one prerequisite, which has to be kept by the logistic regression model. In ecological processes autocorrelation can often be found in cases when variables are recorded along an environmental gradient (spatial autocorrelation) or along a time series (temporal autocorrelation) (Koenig 1999). The sampling design of the monitoring data processed here may include temporal as well as spatial autocorrelation due to different facts.

Some of the habitats were visited more than once in order to be able to record possible changes concerning the habitat structure in the highly dynamic habitats in the area of investigation. Ephemeral ponds may not only be subject to a high risk of unpredictable disappearance of the water but also to the change of their habitat parameters (Williams 1996; Williams 1997; Fahd et al. 2000). These possible dynamic changes could have only been recorded by a repeated observation of these habitats. The minimum time span between two monitoring incidents at the same habitat was 30 days or greater. However, the larval development of some of the species inhabiting the ephemeral ponds in western Namibia is approximately as long as this time span for the migrant (Suhling et al. 2004) and only a little longer for the resident (Suhling et al. 2005a) and therefore the condition of temporal independence may be maintained. Additionally, the monitoring focused only on unmarked adults, so the possibility of different generations and associated with it different individuals being recorded at the same habitat was given.

Regarding the spatial independence of the data the monitoring design provided another problem. To be able to analyse parameters that are relevant for the presence of the species at the (micro-) habitat scale, adjunctive habitats with different structures were treated as different habitats at the expense of increasing spatial autocorrelation but with the advantage of a better discriminative power of the relevant parameters.

The cues for habitat selection are best to be concluded from the presence of larvae in the aquatic habitat or at least from successful oviposition (Corbet 1999). However, the monitoring programme focused on the observed presence of adults at the habitat due to a fragmentary larval identification key for some of the species at the time of the monitoring and only little data, which recorded reproductive behaviour. Therefore, the ability of adult dragonflies to fly may be one reason for the more or less poor results of the HSM in some cases. The presence at a microhabitat may have been recorded although it was only some kind of "stepping stone" on the way to a suitable oviposition site. Another possible explanation may be that the

(micro-)habitat scale had a resolution too fine for the determination of parameters which are responsible for the presence/absence of the common species regarded in the HSM (Roloff & Kernohan 1999).

Generally the calculation of significant HSM was only possible for the more common species, which can be considered to be less specialised regarding the habitat requirements. The reason for this limitation of the HSM to the generalists can be found in the disproportionality between few presences and many absences in the rare species (Backhaus et al. 2000). The result of this limitation to the less specialised species may also lead to poorer performance of the HSM, as it must be expected that generalists have lower habitat preferences. For the purposes of conservation management (Huston 1994) this limitation to the more common species imposes a problem as the focus of conservation lies more on the rare species which are hard to handle with this approach.

2.4.1   Univariate Models

The Spearman rank-correlation already shows the different habitat specifications of the focus species. The high amount of positive correlations and the resulting univariate habitat suitability models for *C. erythraea* regarding vegetation in the aquatic habitat allows drawing the conclusion that this species prefers habitats, which have a longer duration. Aquatic vegetation and especially the aquatic vegetation diversity, which describes the presence of vegetation types of diverse growth heights, needs time to develop. This time span with low disturbance is mainly available in perennial or at least temporary habitats. The negative correlation with the absence of vegetation strengthens this finding as it shows the general need of *C. erythraea* for vegetation structure in the habitat, which is also described by Suhling et al. (2003). Moreover, the development time of more than 40 days (Suhling et al. 2004) required by the species does not allow successful reproduction in waters existing very shortly (Johansson & Suhling 2004). Hence, vegetation may be a proximal cue for habitat selection.

In contrast to this, the habitat preferences regarding vegetation of *P. flavescens* are either not significant or have a negative correlation coefficient. For obligate migrants as defined by Corbet (1999) respectively the ecological group 1 (cf. Chapter 1), it seems reasonable to be able to make use of freshly established, even unvegetated habitats for reproduction. It is reported that *P. flavescens* oviposits even in discarded automobile tires filled with water (Corbet 1999). Competitive constraints are much smaller under these conditions because of the absence of residential species and predators in newly formed habitats (Suhling et al. 2003; Suhling et al. 2005a, see also Chapter 3).

Aggregation of the monitoring data from microhabitat to locality scale and a classification of the habitats into habitat types shows for *P. genei* a clear preference of habitats located in the river, mainly ephemeral rivers. 47.5% of all incidences recorded for *P. genei* were habitats, which can be characterized as being located in a river or at least a part of it, the main part of 31.9% were ephemeral river sections. This finding is confirmed by the positive correlation towards the presence of sand as substrate, which is typical for many ephemeral river sections in the area of investigation.

2.4.2 Multivariate models

The test of the spatial transferability conducted as an external validation of the models did not succeed. For the spatial validation, it has been tried to compare the catchments with a high amount of monitoring incidents, which were needed for the logistic regression procedure with each other. However, the models calculated for one catchment could not be reproduced with the data of another catchment. One reason for the failure of the external validation procedure can be found in the different compositions of the habitat types of the catchments (Figure 2.6).
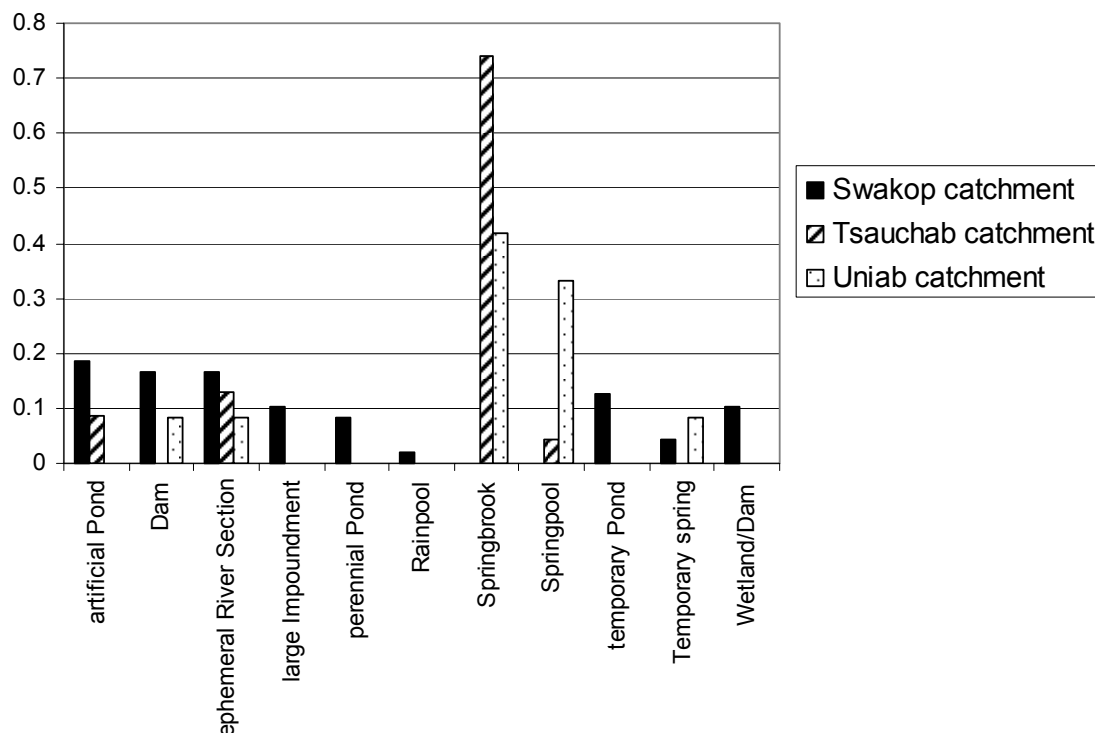
Figure 2.6:   Distribution of the monitoring sites assigned to classes of habitat types for the Tsauchab, the Swakop and the Uniab River catchment. Shown are the relative proportions of all habitats ocurring in the respective catchment.

While the Swakop River catchment is dominated by the habitat types "artificial pond", "ephemeral river section" and "dam" (in the sum about 52%), more than 73% of all localities monitored in the Tsauchab River catchment were classified as "springbrook". The Uniab River was dominated by the habitat types "springbrook" and "springpool" (in the sum about 75%). The distinction into different habitat types actually is a synopsis of certain habitat parameters: Temporary waters of course have a vegetation structure differing from permanent springs due to the frequency of disturbances in the habitat. Therefore the subsequent dragonfly communities of these habitat types also differ (Suhling et al. 2005a; Suhling et al. 2005b, in press) and therefore a spatial validation of habitat models obtained for one catchment was not possible for another.

The multivariate models, which were calculated for the three species, were best for *C. erythraea*. There are some possible explanations for this fact. In the first place, it is possible that the choice of habitat parameters were best suited for *C. erythraea* as on the one hand the number of covariates in the multivariate model was the highest and on the other hand, the R^2_N value was the highest of all three species, too. *P. flavescens* and *P. genei* with their relative low R^2_N values and only three covariates included in the models appear to react quite insensitively to the recorded parameters. This may be due to the recorded parameters, which were mostly based on the (micro-) habitat structure and the resulting possibility that the species choose their habitat on a larger spatial scale. Another explanation for the HSM with low quality criteria may be that *P. flavescens* is described as a species with low habitat specificity (Suhling et al. 2003) .

2.4.3   The habitat web

The habitat web may serve as a kind of linkage between the univariate and the "real" multivariate models. The results of the univariate models can be compared between the species while the multivariate models contain the species-specific habitat parameters, which lead to a significant improvement of the logistic regression model. Due to the fact that the multivariate models contain only species-specific parameters the species cannot be compared with each other. The habitat web with the usage of the R^2_N values of the univariate models allows the comparison between the species regarding the ecological niche, which is described by the monitoring parameters. Therefore the size of the area defined by the habitat web reacts sensitively to the parameters included in the sampling design. Adding more potentially relevant parameters can decrease the area of the habitat web for one species if this parameter

is irrelevant for this species while the same parameter can increase the area for another species.

However, the habitat web reveals in a more obvious way the differences between the three groups of Odonata, which will be modelled in the following sections. *C. erythraea* with the largest area of the habitat web is more dependent on explicit habitat parameters than *P. flavescens* and *P. genei*. The difference between the latter species is much smaller but also obvious. *P. genei* is therefore defined to be dependent on an implicit habitat parameter, the existence of rivers as guidelines. The derivation of this parameter will be shown in Chapter 4. *P. flavescens* with the lowest area in the habitat web will consequently be modelled mainly in dependence of the presence of water.

Overall, the habitat suitability models led to a satisfactory differentiation of the three focus species, which act as representatives of the ecological groups of Odonata in Namibia (cf. Table 1.3) to parameters that can be used in a slightly modified form in the spatially explicit dispersal model.

3 Population dynamics

3.1 Introduction

Models for the population dynamics of animals are common for analysis of processes determining the structure of populations and serve furthermore as tools in conservation management. They allow to draw conclusions on the present and future status of potentially endangered populations under different environmental conditions (Lindenmayer & Possingham 1995; Gurney & Nisbet 1998; Gotelli 2001). They also offer the possibility of reconstruction of experimental data and the setting up of "virtual" experiments.

In the arid and semi-arid regions of Namibia habitat discontinuity due to drought and the adherent risk of unsuccessful reproduction is one reason for the need of different behavioural strategies of different dragonfly species groups (cf Table 1.3). Obligate migrants, which colonize newly established, often ephemeral habitats during the rainy season, need a fast larval development to minimize the risk for their offspring of dying in a desiccating habitat (Wellborn et al. 1996; Williams 1997). The ephemeral habitats are often characterized by the absence of vertebrate predators like fish and therefore allow a more active behaviour in the foraging mode of the dragonflies (Johnson & Crowley 1980; Stoks & Johansson 2000; Johansson & Suhling 2004; Suhling et al. 2005a). Most of the ephemeral habitats have little or no aquatic vegetation due to their relatively short permanence, and therefore the species that colonize the newly formed habitats show little or no preference regarding the vegetation structure in the habitat ((Weir 1974), see also chapter 2).

The residential and more specialized species often need more structural diversity in the longer lasting or even perennial habitats (see chapter 2). These structures, either vegetation or sediment, can be used as ambush to avoid predation. This behaviour may lead to a slower larval development as a trade-off for the risk avoidance of being captured by a predator (Corbet 1999; Elkin & Baker 2000; Dmitriew & Rowe 2005; Suhling et al. 2005a). However, microhabitat structure and risk avoidance may also lead to increased proximity of larvae and consequently higher aggressive interactions (Elkin & Baker 2000). When modelling the population dynamics of the migrating and residential dragonflies, these behavioural strategies have to be taken into account and therefore the life-cycle parameters have to be adjusted to the ecological behaviour of the residents and migrants.

As there is normally more than one dragonfly species present at the aquatic habitat, the time of arrival of one species in relationship to the other species, so called priority effects, plays an

important role in the species composition of ephemeral habitats (Fincke 1999; Padeffke & Suhling 2003). Additionally, Odonata populations are structured by altering size-distributions and stabilizing population numbers through intraspecific competition respective cannibalism (van Buskirk 1992; Anholt 1994; Hopper & Crowley 1996; Fincke 1999; Suhling & Lepkojus 2001; Padeffke & Suhling 2003)

Different mathematical approaches exist to model stage-structured populations. Caswell (2001) and Tuljapurkar & Caswell (1997) provide a comparison between these approaches. One of the main differences is the way the time and the i-states are treated (cf. The i-state describes the state of the individual, which includes variables like size, maturity, the instar and the physiological condition. The i-state variables serve as a description of the population state, the p-state variable, if all individuals experience the same environment and if the influence of the population on the environment can be seen as the sum of the individual's contributions.

Table 3.1).

The i-state describes the state of the individual, which includes variables like size, maturity, the instar and the physiological condition. The i-state variables serve as a description of the population state, the p-state variable, if all individuals experience the same environment and if the influence of the population on the environment can be seen as the sum of the individual's contributions.

Table 3.1:   Different types of population dynamic models

	discrete-state	*continuous-state*
discrete-time	matrix population models	integrodifference equations
continuous-time	delay-differential equations	partial differential equations

Time in natural processes is generally a continuous variable. However, the life-cycle of Odonata can be divided into several distinct stages (Figure 3.1). The egg stage and the larval stages take place in the water and the adult stage is being spent as a terrestrial insect. The larval stage itself can be differentiated into distinct stadia, defined by successive molts. Corbet (1999) reports that 86% of all observations include 10 to 14 molts, while the total number of molts lies between 8 to 17 (counting the prolarva as stadium 1). The adult stage can be divided into the prereproductive (immature), the reproductive (mature) and the putative postreproductive period.
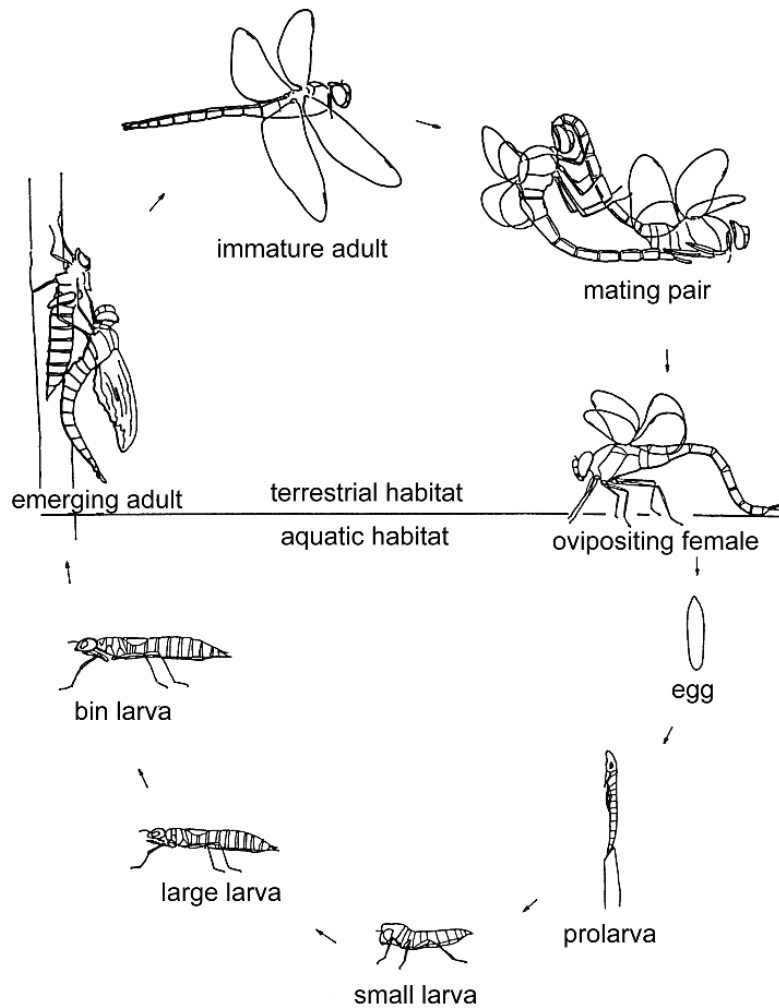
Figure 3.1: Life cycle of dragonflies (adopted from (Wildermuth 1981))

Within the scope of the BIOTA-Africa subproject S08 a study has been done where the mathematical formulation of the life-cycle was based on delay-differential equations (Schroeder 2001). This approach appears to fit best to the situation of dragonflies with discrete stages and a continuous time scale. An already existing model for dragonflies in temperate regions (Crowley et al. 1987) has been customised and fitted for tropical Odonata. Additionally, competition between two species and cannibalism respectively has been implemented. One of the main problems of this model was that it reacted highly sensitively to slight changes in the parameters due to its complexity. Therefore it has been discarded for further use in the dispersal model.

Due to the existence of discrete stadia in the larval part of the life-cycle, the time scale is also discretised and the population dynamics is modelled with a matrix approach, which will be described in detail in this chapter. However, the choice of the mathematical tool to solve the problem and the adjunctive extension of the models to continuous time and infinite

dimensions may not lead to new biological insights (Metz et al. 1992). Caswell (2001) states, that the use of a certain mathematical technique often is a matter of personal taste.

The main task of this part of the work is to develop a model that describes the effects, which are essential for the population structure of dragonflies in the arid regions of Namibia. These effects have been demonstrated in field experiments (Padeffke & Suhling 2003) and therefore the focus of the simulation will be on the replication of these results. The model can be used for migrants as well as for the residential species (cf. Table 1.3). Later it will be integrated into the spatially explicit dispersal model (Chapter 4), serving as the basis for the local population dynamics before the adult dragonflies disperse over the landscape. Furthermore the model shall offer the possibility to simulate different colonization sequences with regard to a possible coexistence of species with different life-history traits.

3.2 Methods

3.2.1   From the life-cycle to the model

Generally, the life-cycle implemented in the model consists of an egg-stage, three larval stages and two adult stages describing the prereproductive and the reproductive phase. The prolarva and the bin larva (Figure 3.1) are omitted in the model as the experimental data (see below) which served as base for parameter estimation also focused on the free-living larval stages. The stage "bin larva" is especially important for conditions where hibernation or aestivation is essential in the life-cycle. In temperate regions a diapause in the development may be useful to achieve synchronised emergence, especially in partivoltine species (Corbet 1999, p. 230 ff.), which is not true for the Namibian Odonata.

Figure 3.2 shows the conceptual model for the transfer of the life-cycle of a dragonfly into a matrix model. The horizontal layers represent the different stages of the life cycle while the vertical arrangement of the stages represents the transition between the stages.

The reduction of the larval stage to three distinct stages is on the one hand accomplished in order to ease the implementation of intraspecific competition and on the other hand due to lack of knowledge and high variation of the actual numbers of larval stages in the modelled species. However, the distinction between the larval stages is important as the main cannibalistic effects responsible for the population structure occur between different sized larvae (Hopper & Crowley 1996).
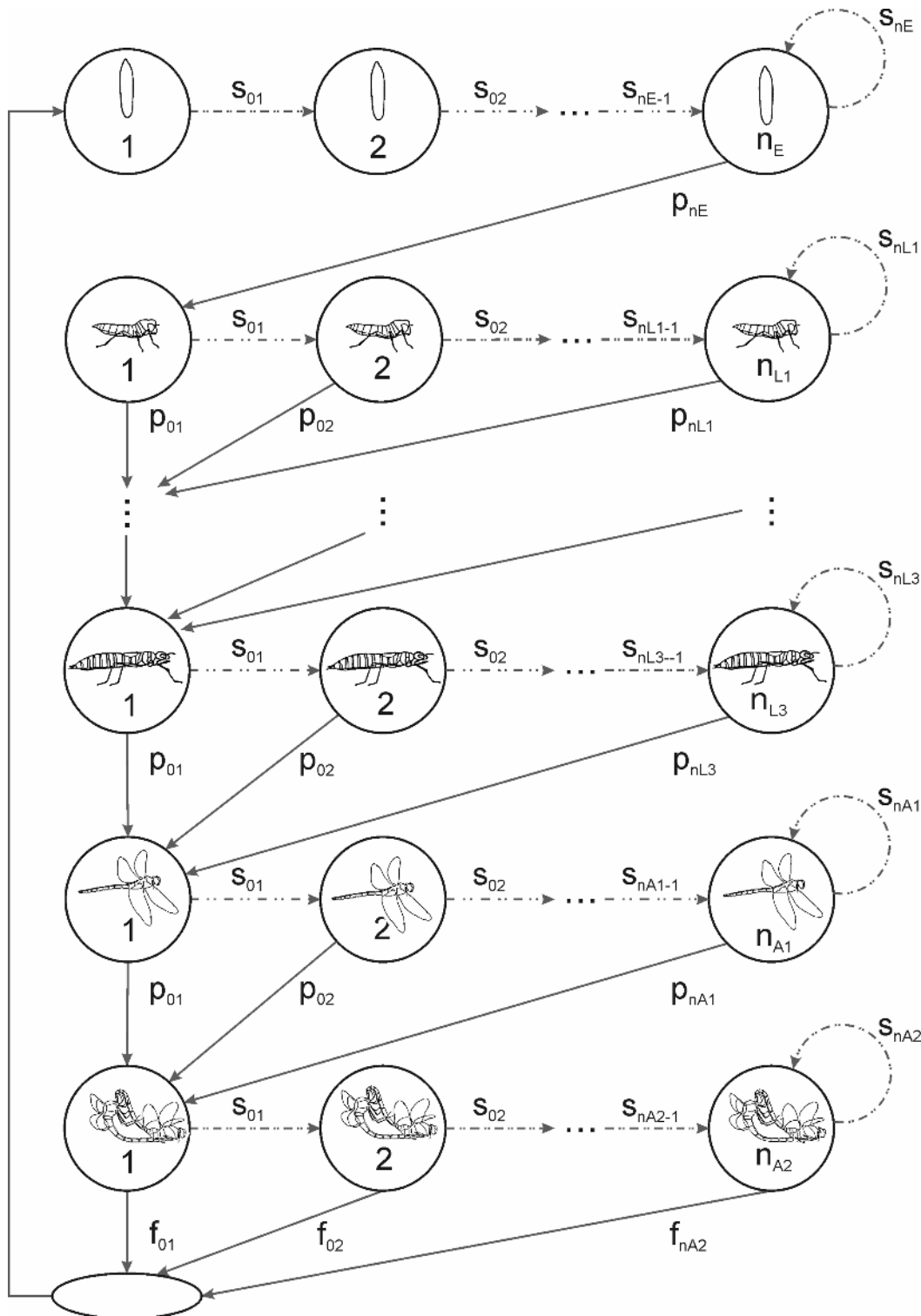
Figure 3.2: Conceptual model of the life-cycle. **s**: suvival probabilities, **p**: transition probabilities, **f**: fertility rates, **nE**: number of age classes in egg-stage, **nL1**: number of age classes in small larval stage, **nL3**: number of age classes in large larval stage, **nA1**: number of age classes in immature adult stage, **nA2**: number of age classes in mature adult stage

As an extension to the classical approach by Leslie, the model's projection matrix was constructed as an extended Leslie-Matrix (Richter & Söndgerath 1990; Söndgerath & Richter 1990; Söndgerath & Müller-Pietralla 1996; Vogel 2002). This approach takes into account the

age-structure within a stage and allows modelling the population dynamics in a more detailed way. The model uses different types of transitions: The survival-probabilities describe the transition within one stage, i.e. the ageing process and the transition probabilities describe the transitions from one stage to the next, i.e. the development process. The different transitions are elements of the submatrices (Eqs. 3.4-3.6) of the extended Leslie-matrix (Eq. 3.3). The population at time-step t+1 is calculated by the multiplication of the Leslie-matrix with the population vector both at time step t (Eq. 3.1). The population vector itself consists of the vectors of the different stages incorporated into the model (Eq. 3.2).

Notation:

$\vec{x}$:	population vector
M:	Leslie matrix
L_1:	small larvae
L_2:	medium larvae
L_3:	large larvae
A_1:	immature adults
A_2:	mature adults
S:	submatrix describing the survival probabilities within one stage
T:	submatrix describing the transition probabilities between the stages
F:	submatrix describing the fertility rates in the mature adult stage
p:	transition probabilities of the age classes in the respective stage
s:	survival probabilities of the age classes in the respective stage
f:	fertility rates
n:	maximum number of age classes in the respective stage
t:	timestep

$$\vec{x}_{t+1} = M_t \cdot \vec{x}_t \qquad\qquad \text{Eq. 3.1}$$

$$\vec{x}_t = \left(\vec{E}, \vec{L}_1, \vec{L}_2, \vec{L}_3, \vec{A}_1, \vec{A}_2 \right)^T \qquad\qquad \text{Eq. 3.2}$$

$$M_t = \begin{pmatrix} S_E & 0 & 0 & 0 & 0 & F_{A_2} \\ T_E & S_{L_1} & 0 & 0 & 0 & 0 \\ 0 & T_{L_1} & S_{L_2} & 0 & 0 & 0 \\ 0 & 0 & T_{L_2} & S_{L_3} & 0 & 0 \\ 0 & 0 & 0 & T_{L_3} & S_{A_1} & 0 \\ 0 & 0 & 0 & 0 & T_{A_1} & S_{A_2} \end{pmatrix} \qquad\qquad \text{Eq. 3.3}$$

$$T = \begin{pmatrix} p_1 & \cdots & \cdots & p_n \\ 0 & & & 0 \\ \vdots & & & \vdots \\ 0 & \cdots & \cdots & 0 \end{pmatrix}$$ Eq. 3.4

$$S = \begin{pmatrix} 0 & \cdots & & \cdots & & 0 \\ (1-p_1)s_1 & & & & & \\ 0 & & \ddots & & & \vdots \\ \vdots & & & \ddots & & \\ 0 & & \cdots & (1-p_{n-1})s_{n-1} & (1-p_n)s_n \end{pmatrix}$$ Eq. 3.5

$$F = \begin{pmatrix} f_1 & \cdots & \cdots & f_n \\ 0 & & & 0 \\ \vdots & & & \vdots \\ 0 & \cdots & \cdots & 0 \end{pmatrix}$$ Eq. 3.6

The derivation of the matrix' parameters is described in the following. The larval stages are named according to their size to ease the reading of the text. The larval stage 1 is named "small larvae", larval stage 2 is named "medium larvae" and larval stage 3 is named "large larvae".

3.2.2   Duration of the stages

As each stage has its own age structure and the duration of one age class is determined to be one day (= timestep of the model), it is necessary to know the average duration of the stages. Suhling et al. (2004) have calculated the development time from hatching to the emergence of the immature adult to be 33 days for *Pantala flavescens,* 56 days for *Crocothemis erythraea,* and 60 days for *Paragomphus genei*. However, the total development times in the model are set to 34 days for the migrant species and to 60 days for the resident species as not only minimum development times are regarded.

The larval stage is split into three distinct sub-stages, therefore the total development time of the larvae of the experiments is split into three parts assuming that the later larval stages have a longer duration with an approximatively linear trend (Corbet 1999). Experiments for the development time of the eggs and the first two free-living larval stages of Namibian species were conducted (Johansson & Suhling 2004; Schenk & Söndgerath 2005; Schenk & Suhling 2005, submitted). According to these studies, the durations of the first two free-swimming larval stages resemble the small larval stage in the model. The durations for the medium and

large larvae have been adjusted to the small stage duration using the assumption of a linear increase in the stage duration (Corbet 1999). As no species-specific data for the adults has been available, the durations are estimated from data available for other species (Corbet 1999, p. 261 ff.). Averages for the durations of the stages of the migrant and the resident type are displayed in Table 3.2.

3.2.3   Survival probabilities

The survival probabilities of the larvae, which describe the transitions within one stage, are being modelled as a linear combination of a basis survival rate and a food- and density dependent mortality.

The daily survival rate (DSR) has been taken from experimental data collected in Namibia in 2001 (Schenk, unpublished data). In laboratory experiments eggs of different Namibian Odonata were reared in single containers to exclude them from externally driven mortality like predation or cannibalism. After hatching, the larvae were supplied with food ad libitum, hence starvation can be excluded as a reason for mortality. The survival rates and the development times for the larval stages of these experiments have been acquired for the calculation of the base daily survival rates (base DSR), assuming constant rates within one larval stage. The investigated species represent the "migrant" type (*Pantala flavescens* and *Sympetrum fonscolombii*) and the "resident" type (*Orthetrum chrysostigma* and *Trithemis kirbyi*) (cf. Table 1.3, see also Schenk et al. 2004).

Experimental data is implemented as follows into the model: the averaged daily survival rates of the first two free-living stadia are set as base-survival rate for the small larval stage. Due to the lack of experimental data on survival rates of larger larval stages, the DSR of the second free-living stadium is used to set the parameters for the stages "medium larvae" and "large larvae" of the model. These data led to the following fixed parameters (Table 3.2).

Table 3.2: Fixed parameters for the population dynamic model derived from literature reviews and experimental data, DSR: daily survival rate

	migrant	*resident*
duration of egg stage [d]	5	9
duration of 1st larval stage [d]	10	15
duration of 2nd larval stage [d]	11	20
duration of 3rd larval stage [d]	13	25
duration of immature stage [d]	13	13
duration of mature stage [d]	50	50
base DSR of egg stage	0.974	0.922
base DSR of 1st larval stage	0.896	0.969
base DSR of 2nd larval stage	0.961	0.974
base DSR of 3rd larval stage	0.961	0.974
DSR of immature adults	0.944	0.944
DSR of mature adults	0.944	0.944

3.2.4   Transition probabilities

For modelling it is assumed that transition between stages mainly depends on the amount of ingested food. This can be seen equivalently to the temperature-dependent development known from other population dynamic models (Curry et al. 1978; Söndgerath & Müller-Pietralla 1996; Vogel 2002). This approach has been chosen because food can be expected as one of the most limiting factors for the larval development of Odonata in the ephemeral habitats in Namibia.

In temperate regions, the development of insects is mainly associated with temperature limits (Curry et al. 1978; Mathavan 1990; Krishnaraj & Pritchard 1995; Briere et al. 1999; Griebeler & Gottschalk 2000). The long-term average daily temperatures in the area under investigation have lower seasonal variation along the coast than in the inland areas. However, even for Windhoek, which can be seen as representative for the region around the S. von Bach Dam, the lowest monthly average temperature is about 13° C (Mendelsohn et al. 2002). Therefore the inhibition of development through temperature can be supposed to be significantly lower than in temperate climates and is discarded in the model.

The concept realized in the model is the following: The development is directly dependent on the proportion of available food in the aquatic habitat. Each larvae in stadium n (n=1 to 3) can obtain up to one development unit per time unit (=day). If the larval density is higher than the available food units, the development speed decreases. The function describing the development speed in dependence of the available food was fitted from modified data from Hassan (1976). The development time of the larvae under optimal food supply in Hassan's

experiments was set to a development rate of 1. Lower food availability resulted in longer larval development. The ratio between optimum development time to prolonged development time was set equal to the fraction of development rate. Linear regression led to Equation 3.7.

Table 3.3:   Food supply, duration of larval stages and development rate per day under optimum food conditions (Data from Hassan (1976))

food supply [%]	average larval development [days]	development rate
100	40.000	1.000
50	57.200	0.699
25	74.600	0.536
12.5	118.500	0.338

$$develop(food) = 1.0119 \cdot food^{0.5084}, r^2 = 0.988 \qquad \text{Eq. 3.7}$$
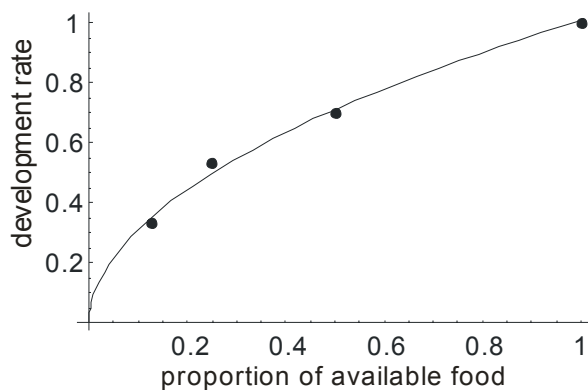
Figure 3.3:   Estimated function for the dependency of the development rate of the available food

For the calculation of the needed food of the whole dragonfly population at time t, it is assumed that the unspecific prey pool represents a size-structured population. Therefore each larva can obtain up to one food unit per time step, where larger larvae consume a larger food unit than smaller larvae. Corbet (1999, p. 111) states, that in most studies on dragonfly larvae the size of the late stadium larvae corresponds with the size of the prey, although this has not been proven for small larvae. Hence, this correlation was assumed for all three larval stages.

The numbers of the larvae in all three stages are summed up, as each larva can obtain only one food unit per time step. This number is set equal to the needed food units at time-step t (Equation 3.8). If the number of unspecific food units is higher than the needed ones, the available food at time step t is set to one (=optimum food supply), otherwise the proportion of unspecific food to needed food is considered as available food (Equation 3.10).

Notation:

food$_{needed}$:   needed food

food$_{unspec}$:   total food in the unspecific food pool

food$_{avail}$:   available food

L$_i$:   Number of larvae in stage i

P: Number of prey units in unspecific prey pool

$$food_{needed}(t) = \sum_{i=1}^{i=3} L_i(t)$$ Eq. 3.8

$$food_{unspec}(t) = P(t)$$ Eq. 3.9

$$food_{avail}(t) = \begin{cases} \dfrac{food_{unspec}(t)}{food_{needed}(t)}, & food_{needed}(t) > food_{unspec}(t) \\ 1, & food_{needed}(t) \leq food_{unspec}(t) \end{cases}$$ Eq. 3.10

This leads to a density dependent development: at high larval densities the development speed decreases as stated by McPeek & Crowley (1987). When there is food ad libitum, either due to low larval densities or due to a habitat containing enough unspecific prey, the larval stages get the benefit in the form of an optimal development.

However, this approach is simplified as it assumes that all of the consumed food is transferred directly into growth although Lawton (1971) reports that only 42.4 percent of consumed energy are transferred into growth in *P. nymphula*. Furthermore, other predators preying on the unspecific prey pool are neglected. The total larval development of each age class is the sum of the obtained development units from entering the stage up to the considered time.

In order to take the natural variability of the transition probabilities into account, the latter are modelled by a distribution function of a Weibull type for each age class (equation 3.11) (Söndgerath & Müller-Pietralla 1996). The transition probability is dependent on the sum of development units from entering the stage up to the current time-step. The threshold value develop$_{crit}$ is the mean development, which is needed to complete one stage under optimum food conditions, whereas the shape parameter β determines the steepness of the distribution.

Notation:

trans   transition probability

develop   sum of development units

develop$_{crit}$ threshold value

β   shape parameter

$$trans(develop) = 1 - Exp\left(-\left(\frac{develop}{develop_{crit}}\right)^{\beta}\right)$$

Eq. 3.11

3.2.5   Additional mortality induced by competition

One factor which structures Odonata populations by altering size-distributions and stabilizing population numbers is intraspecific competition respective cannibalism (van Buskirk 1992; Anholt 1994; Hopper & Crowley 1996; Padeffke & Suhling 2003). The food web describing the situation of the larvae for a one-species model with intraspecific competition is shown in Figure 3.4.
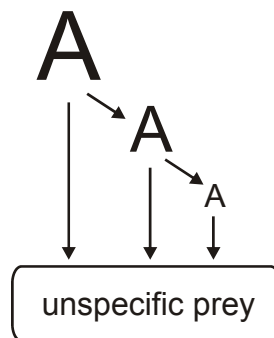
Figure 3.4:   Food web for a one-species model. Size of the letters reflects the larval stages.

The following approach is used to incorporate the effects of cannibalism into the model: It is presumed that in a habitat containing enough unspecific food for the dragonflies, the need for cannibalism is very low. With increasing deficiency of unspecific prey, the medium larvae will prey upon the small larvae and the large larvae will prey upon the medium larvae. The influence of the large larvae on the small larvae can be assumed as rather low due to inefficient handling time and is therefore discarded to ease the implementation in the model. The intraspecific predation leads to higher mortalities. The following equations (Eqs. 3.14-3.16) describe the additional mortality rates induced by food deficiency and presence of larger conspecifics. They are used to adjust the survival rates.

Notation:

addmort: additional mortality

1:              small larvae

2:              medium larvae

3:              large larvae

DR: density ratio

$$DR_{21} = \frac{\sum medium\ larvae}{\sum small\ larvae}$$
<div align="right">Eq. 3.12</div>

$$DR_{32} = \frac{\sum large\ larvae}{\sum medium\ larvae}$$
<div align="right">Eq. 3.13</div>

$$addmort_1(food_{avail}) = 0.1 \cdot Exp\left(-6 \cdot food_{avail}^{(1+2 \cdot DR_{21})}\right)$$
<div align="right">Eq. 3.14</div>

$$addmort_2(food_{avail}) = 0.05 \cdot Exp\left(-6 \cdot food_{avail}^{(1+DR_{32})}\right)$$
<div align="right">Eq. 3.15</div>

$$addmort_3(food_{avail}) = 0.025 \cdot Exp(-6 \cdot food_{avail})$$
<div align="right">Eq. 3.16</div>

Transforming the equations 3.14 and 3.15 leads to the equations 3.17 and 3.18.

$$addmort_1(food_{avail}) = 0.1 \cdot Exp\left(-\left(\frac{food_{avail}}{\frac{1}{6}^{\frac{1}{(1+2DR_{21})}}}\right)^{(1+2 \cdot DR_{21})}\right)$$
<div align="right">Eq. 3.17</div>

$$addmort_2(food_{avail}) = 0.05 \cdot Exp\left(-\left(\frac{food_{avail}}{\frac{1}{6}^{\frac{1}{(1+DR_{32})}}}\right)^{(1+DR_{32})}\right)$$
<div align="right">Eq. 3.18</div>

These functions are of a Weibull-Type with a density-dependent shift in the threshold value. The first factor at the right hand side of the equations is the maximum value of additional mortality per time unit. This value is higher for small larvae than for medium and large larvae (van Buskirk 1989), but does not increase any more at very high larval densities due to constraints imposed by the increase of handling time. With an increasing density of the larger

larvae, the threshold value, at which the additional mortality decreases, moves towards the value of 1. This represents the situation that even in habitats with very good availability of unspecific food the pressure of competition on the smaller stages is higher when there are higher numbers of larger conspecifics. The steepness of the threshold also increases with increasing density ratio.

In the special case, when there are no larger larvae, the density-ratio becomes zero and the equations describe an exponential course. For the small larvae, the density ratio medium vs. small larvae is doubled to put more emphasis on the higher vulnerability of small larvae towards aggressive encounters (van Buskirk 1989).

Figure 3.5 shows the additional mortality of small larvae induced by insufficient food without predation pressure by medium sized larvae (A), by a density-ratio of 0.5 (B), by a density-ratio of one (C), and by a density-ratio of ten (D). The additional mortality increases rapidly. The presence of only a few larger conspecifics (density-ratio 0.5) has a significant effect on the additional mortality at low food levels.
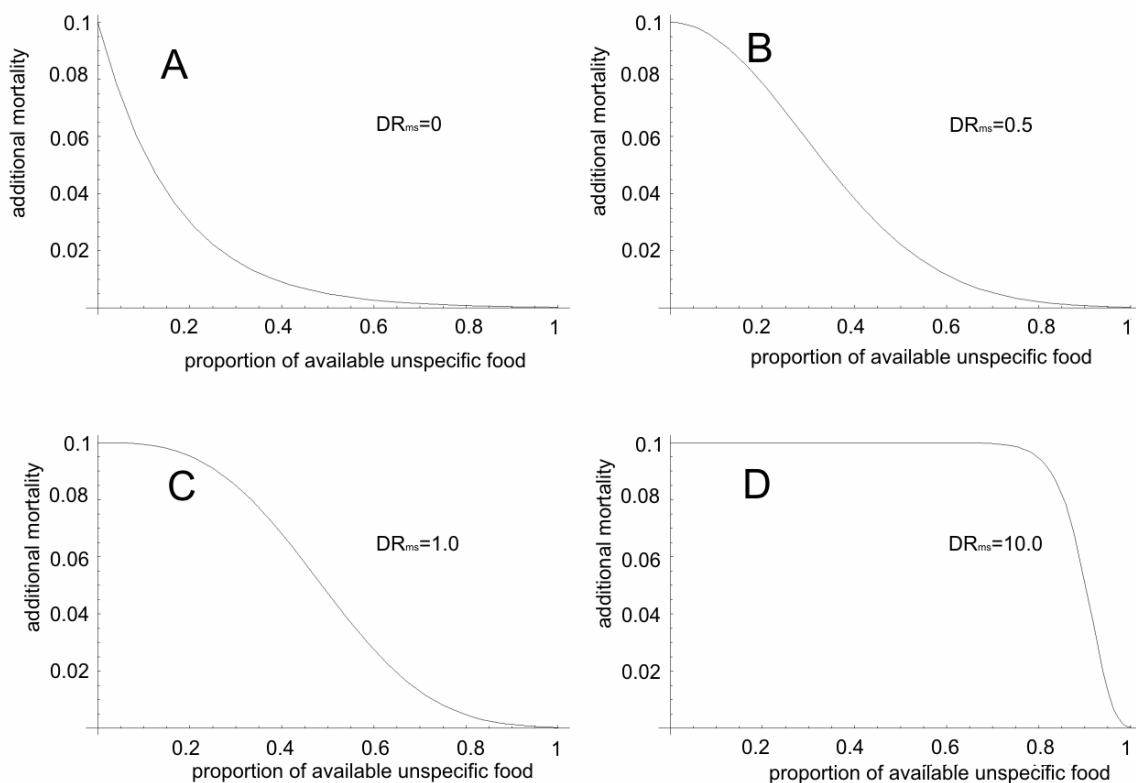
Figure 3.5:   Additional mortality for small larvae influences by different density ratios of medium larvae/small larvae. A: Density ratio (DR)=0, no bigger conspecifics present, B: DR=0.5, twice as much small larvae as medium larvae, C: DR= 1, same number of small and medium larvae, D: DR=10, 10 times more medium larvae as small larvae.

The equation for the large larvae does not incorporate density-dependence as they are not preyed upon by larger conspecifics. Possible effects of mortality induced by within-stage cannibalism are not included in the model.

The total daily survival probabilities, which are used in the projection matrix, are calculated as the difference between the basis survival rates and the additional density- and food-dependent mortality.

$$s_{L1} = DSR_{L1} - addmort_1(food_{avail}) \qquad\qquad \text{Eq. 3.19}$$

$$s_{L2} = DSR_{L2} - addmort_2(food_{avail}) \qquad\qquad \text{Eq. 3.20}$$

$$s_{L3} = DSR_{L3} - addmort_3(food_{avail}) \qquad\qquad \text{Eq. 3.21}$$

$$s_{A1} = DSR_{A1} \qquad\qquad \text{Eq. 3.22}$$

$$s_{A2} = DSR_{A2} \qquad\qquad \text{Eq. 3.23}$$

The adult stages (immature and mature) are modelled without dependency on food or competition as it can be supposed that they are able to get sufficient food in the terrestrial environment (Suhling, personal communication).

After calculation of the additional mortalities, the proportion of the killed smaller conspecifics is added as available food resource for the respective larger stage and the development rates are calculated using Equation 3.7. In this way the model takes into account that the larger conspecifics are able to replenish a food deficiency in an environment with sub-optimal food supply by eating smaller individuals. This results in a thinning effect, in a faster development of the larger stage and an additional feedback by the smaller number of conspecifics (Brodin & Johansson 2002).

3.2.6   Depletion of unspecific prey

In the model it is assumed that the larvae in the habitat are not able to deplete the unspecific prey pool entirely. Therefore, one parameter which is very important in the model is the so called "predation efficiency", which represents the part of the unspecific prey which is available as food. For instance, a value of 0.8 means, that the dragonfly larvae can make use of 80% of the unspecific food resource in their habitat. This factor prevents the unspecific food resource from a total depletion by the larvae. One possible factor promoting the

"predation efficiency" in nature is predator avoidance, a behaviour of dragonfly larvae which leads to reduced foraging activity (Corbet 1999; Stoks 2001).

To model the import of unspecific food into the habitat, on average every 7th day a random number of food units in the range from 100 to 1000 are added to the unspecific prey pool. At high population densities this additional food may be quickly used, while at low larval densities it offers the unspecific food pool the possibility to recover more quickly. This import of unspecific food can be interpreted as a "colonisation" of the habitat, which is reported by Padeffke & Suhling (2003).

3.2.7 Fertility rates

In the model, oviposition is realised with a stochastic approach: On average the individuals of every 5th age class lay clutches of 500 eggs at each time step. This represents an average interval between two ovipositions of 5 days (Corbet 1999). The clutch size of 500 eggs corresponds with data of Schenk & Söndgerath (2005).

3.2.8 Stochastic rounding

The approach realised in the population dynamic model is deterministic. However, a deterministic model includes fractional parts of the single age classes, which does not make sense from the biological point of view. The problematic issue, which accompanies with the use of real numbers, becomes even more apparent referring to dispersal of animals, where only "whole" individuals from the age classes are able to disperse over the landscape. Therefore a stochastic rounding procedure has been implemented after the calculation of the population vector $\vec{x}_{t+1}$. An equally distributed random number determines whether the real number is rounded up or down (Böttcher 2003). If the random number is smaller than the fractional part the real number is rounded up to the next integer, otherwise it is rounded down. By this means small fractions are more likely to be rounded down while bigger fractions are rounded up.

The model, which includes the stochastic rounding, was compared to the model that calculated the real numbers using Monte Carlo simulation techniques. No obvious changes in the characteristics of the population dynamics were detected. The numbers of generations per year and the population sizes were in the same range as in the simulations without stochastic rounding; therefore the following models are calculated with the stochastic rounding to avoid biological confusion.

After estimating the fixed parameters from experimental and literature data, a sensitivity analysis for the one species model has been conducted to investigate in which way the capacity of the unspecific food and the predator efficiency have influence on the population dynamics. The sensitivity analysis has only been done for the one species models of the migrant and the residential species because the food web for the two species model (Figure 3.6) shows, that the only difference to the one species model is that the amount of additional food obtained by competition is divided between the two species. The capacity of unspecific prey as well as the predator efficiency does not differ from the one species model. For the ease of computation and due to lack of empirical data, the predator efficiencies of migrants and residents in the two species model have identical values.

3.2.9   Two species model

So far the model contains only one species in a local habitat. Analysis of monitoring data (cf. Chapter 1) has shown that the case of a single species present in a habitat was observed in 16.7% of the observations. In 8.3% of the observations no dragonfly was recorded at all. This means that a total of 75% of all observations recorded more than one dragonfly species. In addition, the population dynamic model is intended to be integrated into the spatially explicit dispersal model among others to analyze the spatial effects of the colonisation sequences of different species. The sequence of arrival and of oviposition, so called priority effects, are of great importance for the success or failure to establish a population at a habitat (Fincke 1999; Padeffke & Suhling 2003) Therefore, the one-species model is extended to the situation of two species making use of the same habitat and the same food resources. The projection matrix is doubled, with the life-history parameters adjusted to the second species. One interface in the model is the unspecific prey pool, which is used by both species. Equation 3.8 was adjusted to the 2-species situation with N_1 and N_2 describing the species 1 and species 2, respectively (Equation 3.24).

$$food_{needed}(t) = \sum_{i=1}^{i=3} \left(L_{1i}(t) + L_{2i}(t) \right)$$
Eq. 3.24

Each larval stage preys upon the unspecific prey pool, which is supposed to be size-structured for the ease of the calculation of the needed food. The medium larvae of each species are able to prey upon the small larvae of either the same species (intraspecific competition) or the other species (interspecific competition). The same applies to the large larvae, which prey

upon the medium larvae. Figure 3.6 illustrates the food dependencies for the two species model.
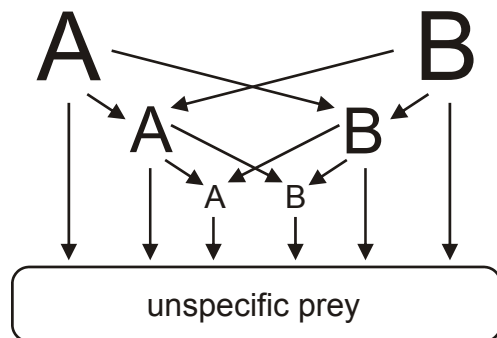
Figure 3.6:   Food web for the two-species model. Size of the letters reflects the larval stages. Different letters indicate different species. The arrowhead indicates that the pointed compartment of the food web is used as food by the composite compartment.

The model presumes that inter- and intraspecific competition is not different between the species but between different larval stages. Therefore the density- and food-dependent survival rates (Equations 3.14-3.16) are also adjusted to the two-species-situation as the numbers of killed individuals in the smaller stage serve as additional food for species 1 as well as for species 2. The proportion of individuals in the larger stage of each species is used to distribute the eaten individuals of the smaller stage as additional food for the larger larvae of each species. Again, the development of the respective larger larvae is calculated afterwards.

The focus of the analysis of the two-species model lies on the first 100 days of a simulation with different initial conditions for the settlement as the colonisation sequence is one of the major questions which have to be analysed with the model. The results of a one species population dynamic model can therefore be left out.

The results display the situation in a habitat with an unspecific food capacity of 10^5 food units and an initial food unit number of 10^3 units. This initial food density has been chosen to be able to produce competitive effects from the beginning of the simulation.

The simulations have been done as a 100-fold repetition with same initial conditions. This repetition was necessary because there are stochastic elements in the population dynamic model: oviposition rates and colonisation of the unspecific prey include stochasticity. Both of them reflect natural processes that are difficult to describe with a deterministic approach. However, in order to obtain more general statements about the effects of colonization sequence, mean values over the replicates are necessary.

Four different scenarios have been simulated with the model (Table 3.4). The first three scenarios can be seen as a simulation study according to the experiments conducted at Tsaobis Leopard Reserve Park in 2001 (Padeffke & Suhling 2003). Eggs of a migrant species (*Sympetrum fonscolombii*) and a residential species (*Trithemis kirbyi*) were used to simulate different colonisation sequences. Apart from two control groups, the study design was the following: 90 eggs of each species were used. For one experiment, *S. fonscolombii* laid eggs 11 days before *T. kirbyi*, another experiment reversed this situation and a third experiment was carried out with both species ovipositing at the same time. The time gaps between the colonisation events therefore are chosen in analogy to this experiment. However, the model is a simplification of the life-cycle of the dragonflies with fewer stages than in reality. Therefore another simulation study is also included in this work, especially focusing on the influence of the population size on the competitive success of the residents and on another colonisation gap.

Table 3.4:   Simulated scenarios with the two-species model. Shown are initial egg numbers and colonisation sequences.

scenario	colonisation sequence	number of eggs (resident)	number of eggs (migrant)
S-11	resident oviposits 11 days before migrant	1000	1000
S±0	resident and migrant oviposit at the same time	1000	1000
S+11	migrant oviposits 11 days before resident	1000	1000
S-24	resident oviposits 24 days before migrant	5000	500

3.3 Results

3.3.1   Sensitivity analysis

The sensitivity analysis varied the two parameters "predation efficiency" and "capacity of unspecific food". Predation efficiency was altered in steps of 0.1 from 0.1 to 1 and the capacity of unspecific food was varied between 10^4 and 10^5 food units in the habitat. For each parameter combination a three-year simulation for the population dynamics was calculated, each with a 100-fold repetition. Mean values for the single stages of the life-cycle and for the development of the unspecific food pool were calculated.

Furthermore the sensitivity analysis was done for resident species as well as for the migrant. The results displayed in Figures 3.7 and 3.8 are chosen for the medium sized larvae as they can be found in a middle position of the aquatic food web – preying upon the smaller

conspecifics and being prey for the larger larvae. As initial population for each simulation 1000 larvae in both the first and the second stage were used, initial food capacity was 10^4 food units for each simulation.

Figure 3.7 shows the results for the migrant species at a maximum food capacity of 10^4 food units on the left and 10^5 food units on the right, varying in predation efficiency (displayed are the values 0.1, 0.3, 0.6, 0.7 and 0.8). For the values of the predation efficiency from 0.1 to 0.6, nine distinct generations can easily be identified. The simulations with ten times higher capacity of unspecific food yielded a population density which was also about ten times higher. The numbers of individuals increased from predation efficiency values 0.1 to 0.3, while for the following predation efficiency values the numbers decreased. Predation efficiency values bigger or equal to 0.7 led to a more or less constant but low population density in the case of 10^4 food units and an irregular population fluctuation in the case of 10^5 food units, but also with lower population densities.

The same parameter combinations of the sensitivity analysis have been modelled for the residential species (Figure 3.8). For the predation efficiency values 0.1, 0.3 and 0.6 seven distinct generations can be identified. In contrast to the migrating species, each generation showed a smaller sub-peak. This sub-peak increased with increasing simulation time, while the main peak decreases. The sub-peaks can be explained due to the longer duration of the larval stages and the fact that the simulation started with 1000 small and medium larvae. For predation efficiency values of 0.7 and 0.8 again, after the initial population, no distinct generations could be identified in the low food capacity scenario and the number of larvae decreased. For the model version with higher food capacity the population fluctuation was more evenly than for the residents with the same food capacity, but still without separated generations.
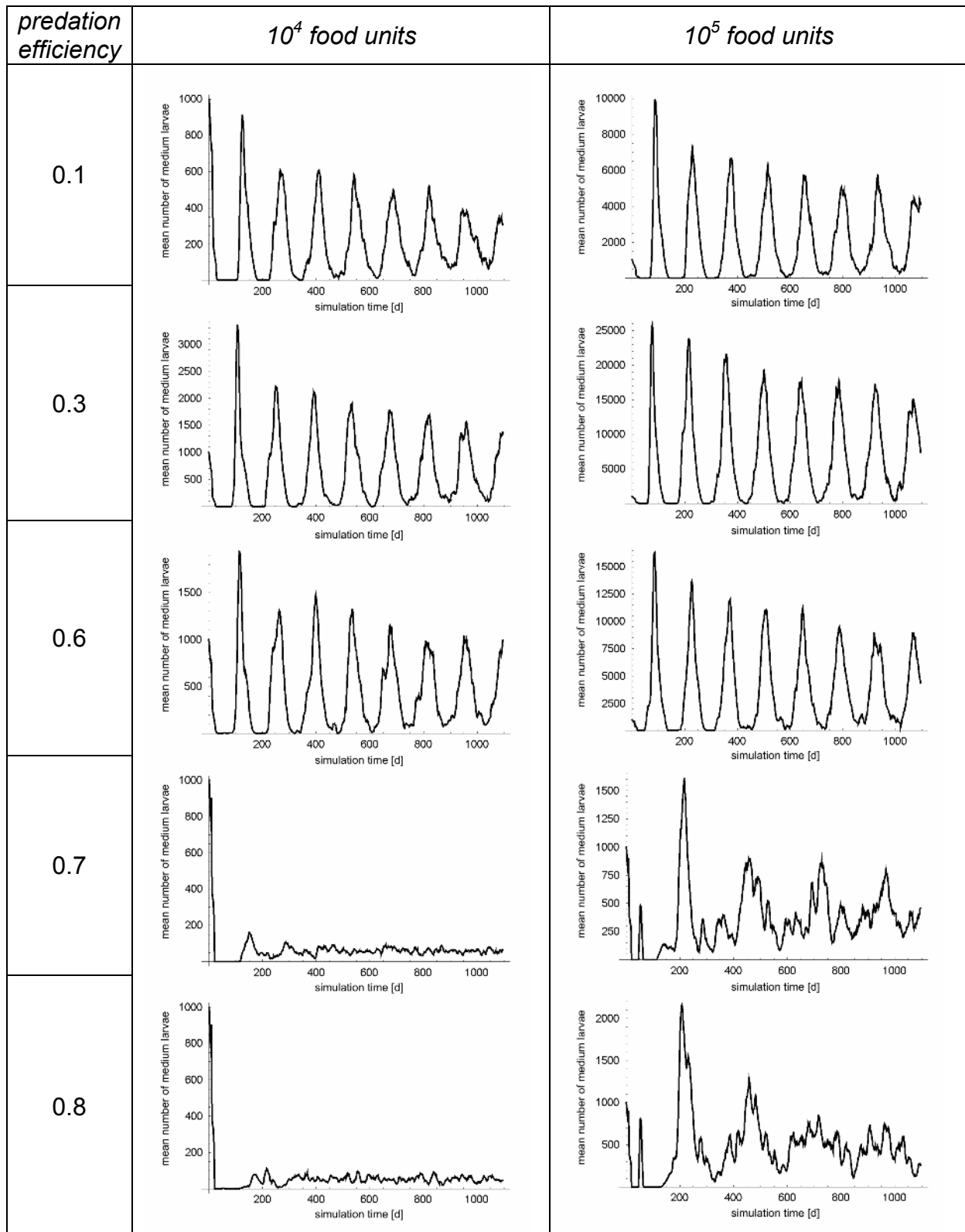
Figure 3.7:   Results of the sensitivity analysis for the migrant species. Displayed are mean numbers of medium larvae. Simulation time: 3 years, number of repetitions: 100.
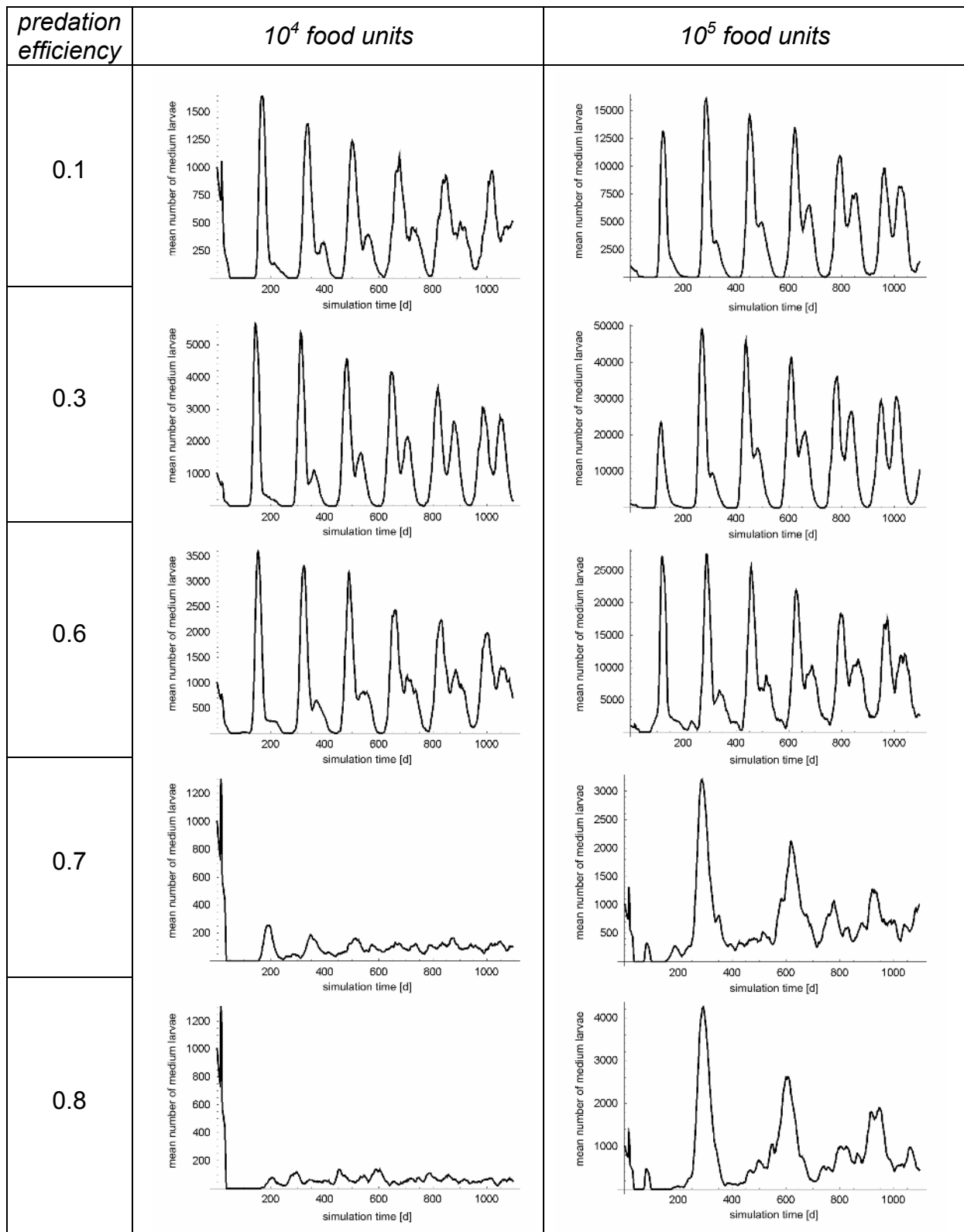
Figure 3.8:   Results of the sensitivity analysis for the resident species. Displayed are mean numbers of medium larvae. Simulation time: 3 years, number of repetitions: 100.

3.3.2   Two-species model

Scenario S±0

The first scenario assumes that migrants and residents oviposit at the same time with a number of 1000 eggs of the migrant species vs. 1000 eggs of the residential species. Differences between the two interacting species were revealed by this simulation (Figure 3.9 and 3.10).
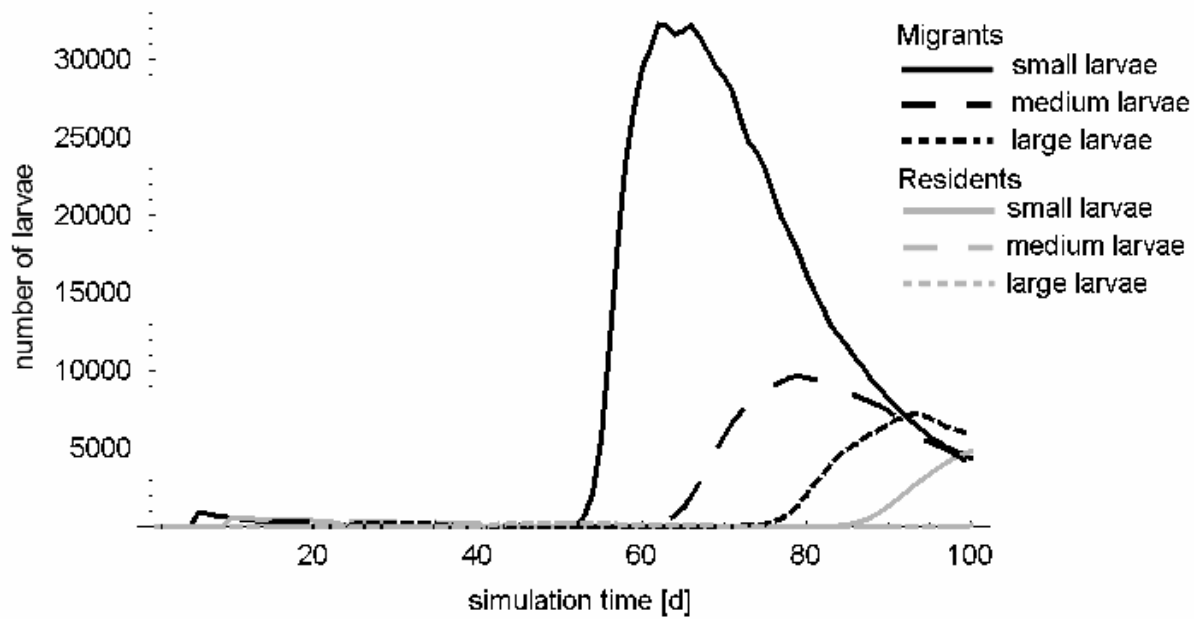
Figure 3.9: 2-species model, Simulation study: S±0. Displayed are mean larvae numbers of a 100-fold repetition.
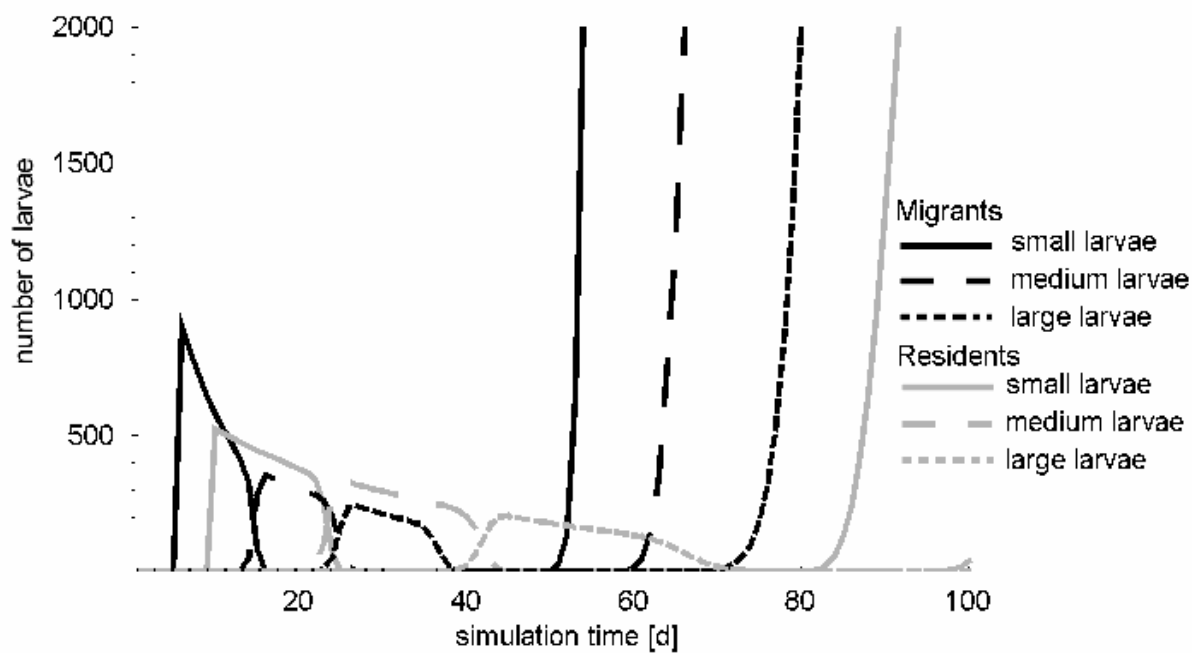
Figure 3.10: Zoomed up view of the simulation study S±0. Displayed are mean larvae numbers of a 100-fold repetition.

The migrant species began to develop the second generation, indicated by the high peak after about 50 days, much earlier than the residential species, which reached the second generation after about 85 days with a peak of a much lower slope than the migrant species. The second stage of the migrants was in-phase with the first stage of the residents. The same holds true for the third stage of the migrants and the second stage of the residents.

In the second generation of the migrants, the remaining residents in the third stage were not able to affect the first stage larvae of the migrants negatively, so this stage was able to develop without interspecific interaction.

However, these results are mean values. Therefore the coefficient of variation for the number of larvae in the small stage is displayed in Figure 3.11. The coefficient of variation is calculated as the ratio between the standard deviation and the mean values from the single simulations, displayed in percent (Equation 3.25).

$$CV = \frac{\sigma}{\mu} \cdot 100$$ Eq. 3.25

For both species the peaks of the coefficient of variation were at about the same level, indicating a relatively high variability between the single simulations. The first peak can be explained by the transition of the small larvae into the next stage. The second peak increased

in both species at the time when the second generation rose. This effect can be explained because oviposition was modelled as a stochastic process and therefore the number of offspring in the second generation varied between the simulations.
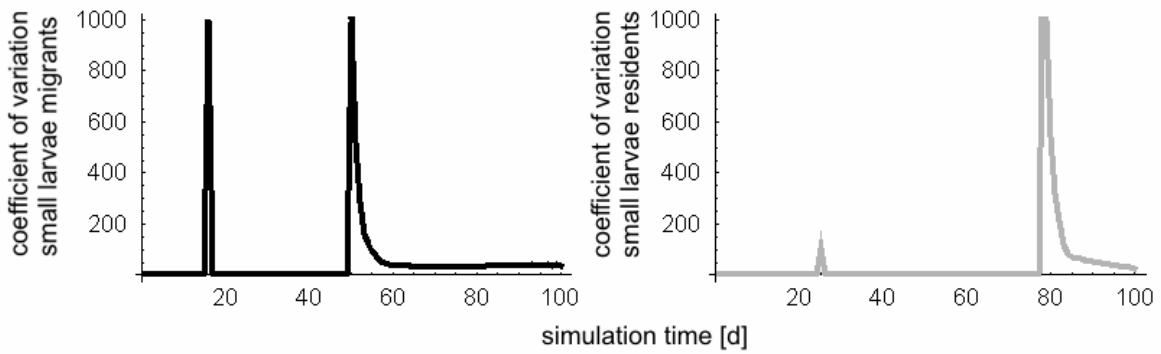
Figure 3.11: Coefficient of variation for the number of small larvae for the simulation: S±0, residents (right) and migrants (left)

Scenario S+11

The initial condition for this study was that the migrant species oviposits 11 days before the oviposition of the residential species occurred (Figure 3.12 and Figure 3.13).
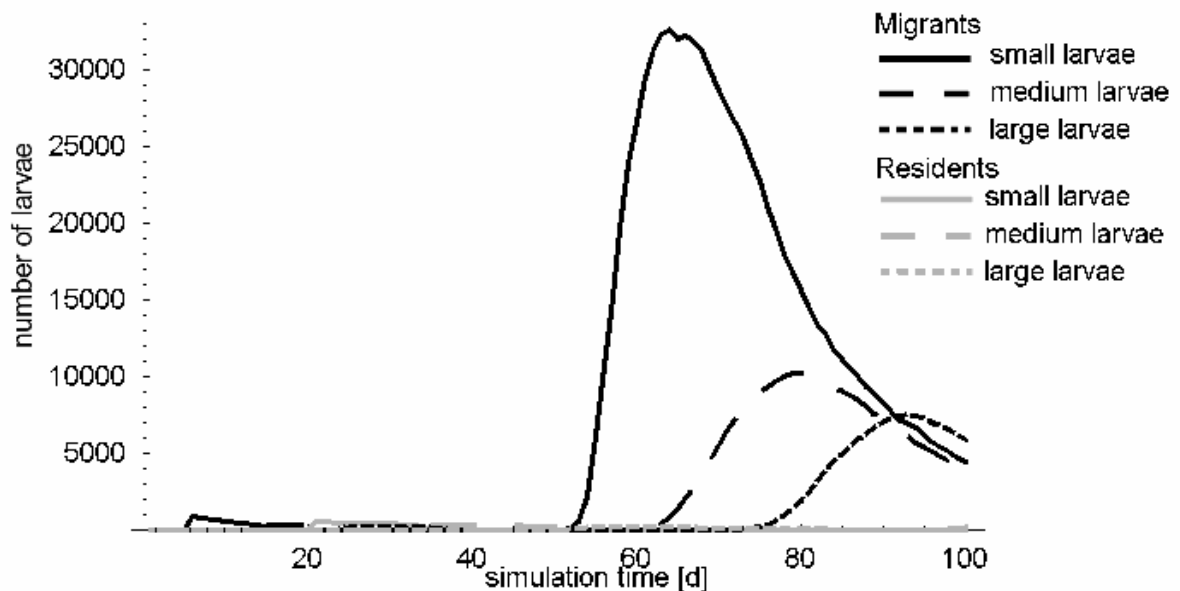
Figure 3.12: 2-species model. Simulation study: S+11. Displayed are mean larvae numbers of a 100-fold repetition.
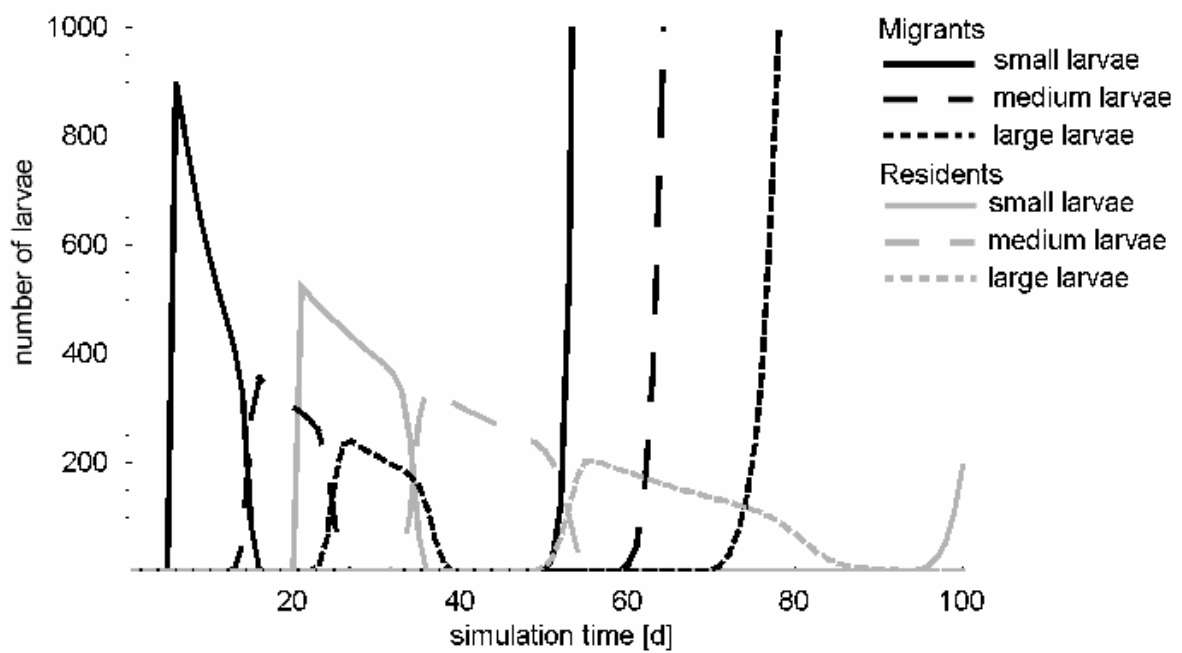
Figure 3.13: Zoomed up view of the simulation S+11. Displayed are mean larvae numbers of a 100-fold repetition.

The number of larvae of the migrant species in the second generation was about the same amount as in S±0, while the second generation of the residents began to rise on day 95 of the simulation. Again, the coefficient of variation of the simulations was calculated (Figure 3.14). It can be seen that the coefficient of variation for the migrants at the rise of the second generation was only about half of the coefficient of variation for the residential species. Additionally, the resident showed a little peak at day 40 of the simulation. This peak cannot be observed for the migrant species.
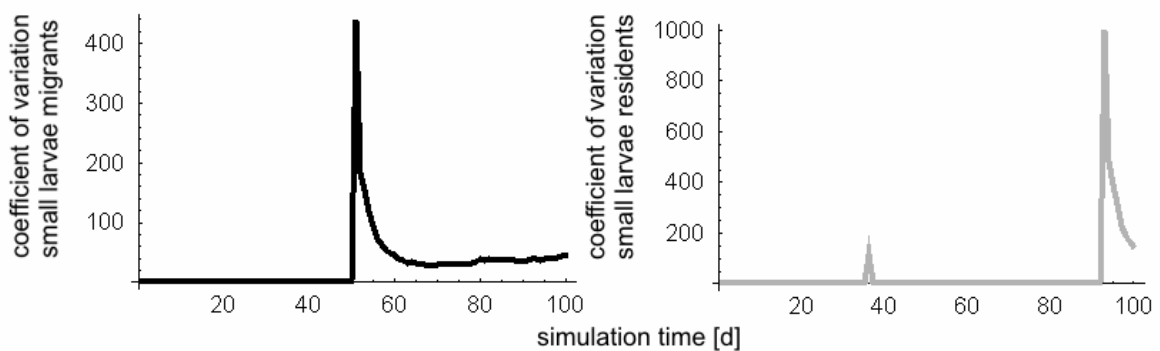
Figure 3.14: Coefficient of variation of the number of small larvae for the simulation S+11.

Another effect of this scenario was that the number of adults in the second generation of the migrant was twice as high as the number of adults of the residents in the same generation (Figure 3.15).
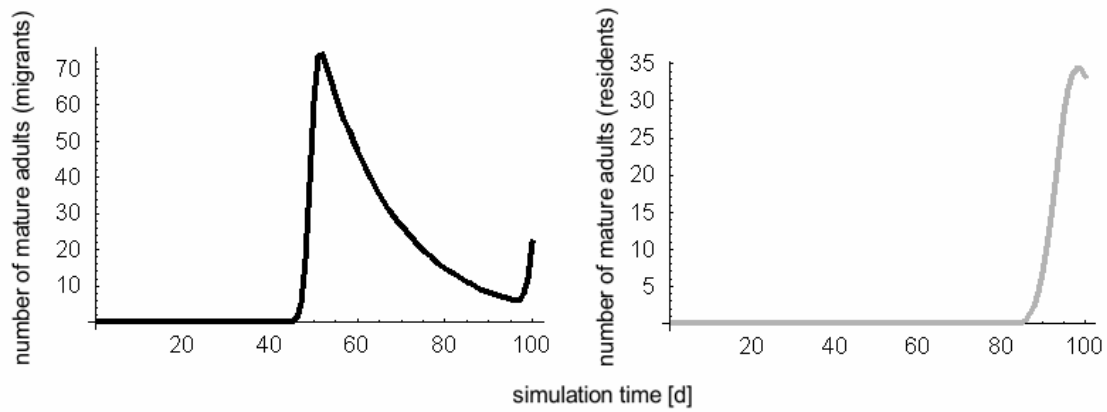
Figure 3.15: Mean number of mature adults for the both simulated species. Simulation study: S+11.

Furthermore, the coefficient of variation of mature adults of the first migrant generation resulted in a narrow peak with a subsequent slow increase until reaching the second generation at the end of the simulation (Figure 3.16). In contrast to this, the coefficient of variation for the resident's mature adults reached a peak about 5 times higher than that of the migrants with a slower decline from the maximum.
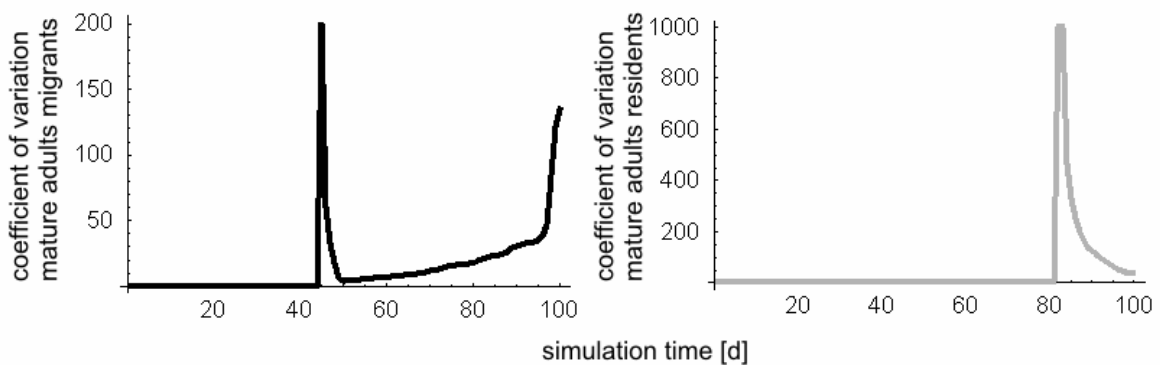
Figure 3.16: Coefficient of variation for the number of mature adults. Simulation study: S+11.

Scenario S-11

This simulation study inverts the situation described above. Here, the resident starts with 1000 eggs and the oviposition of 1000 eggs of the migrant species takes place 11 days later (Figure 3.17 and Figure 3.18).
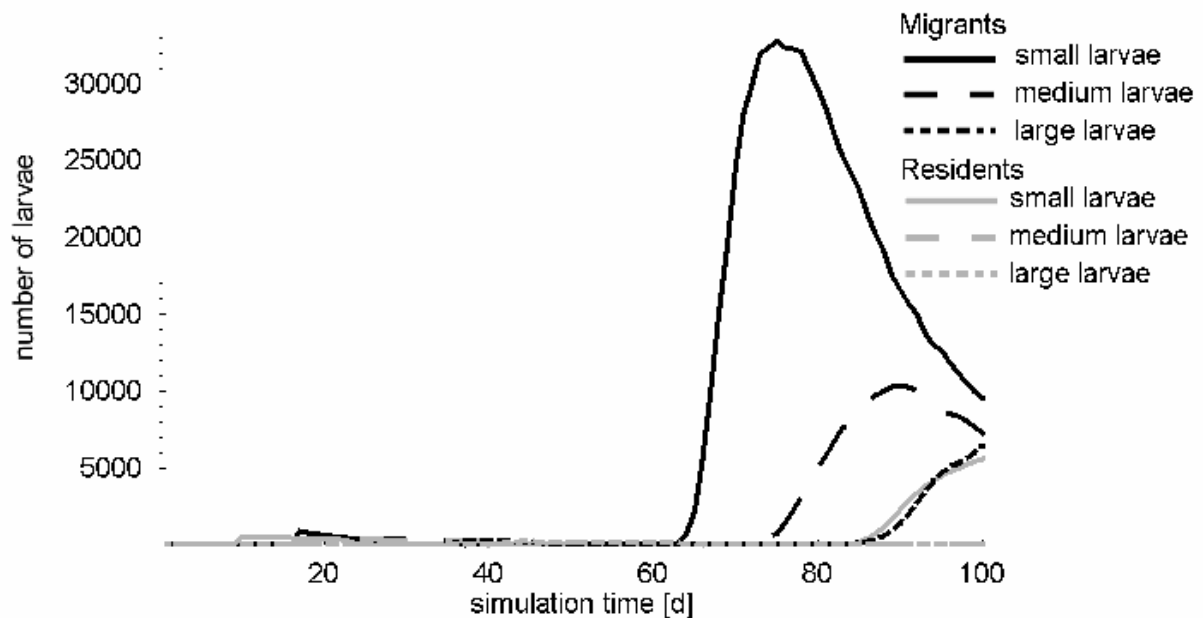
Figure 3.17: 2-species model. Simulation study: S-11. Displayed are mean larvae numbers of a 100-fold repetition.
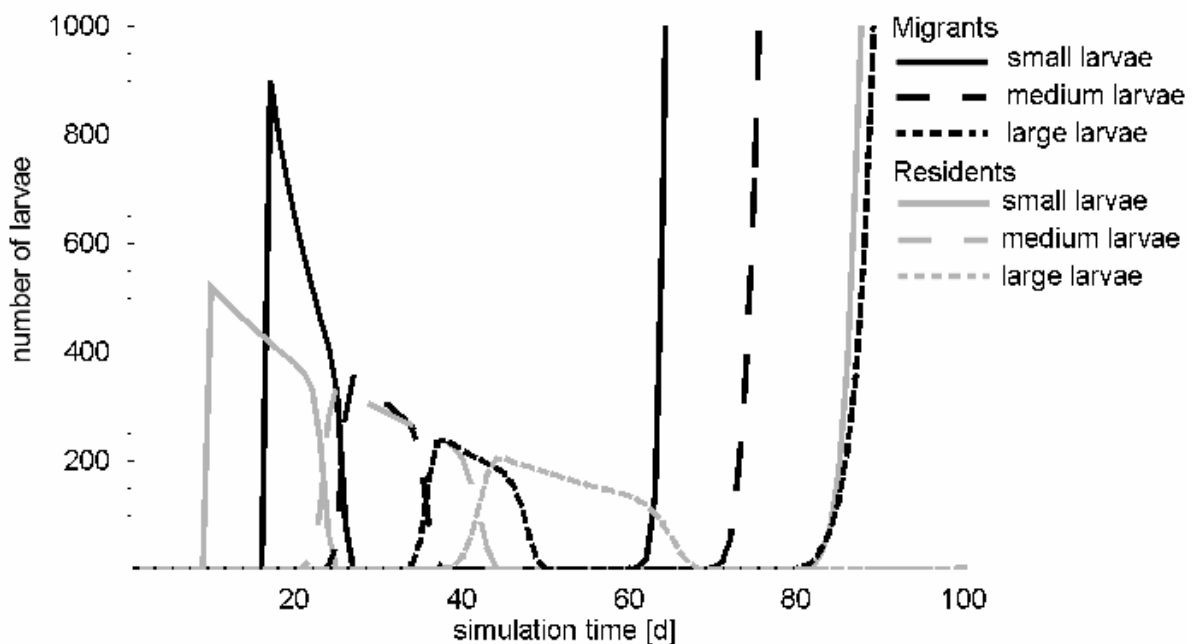
Figure 3.18: Zoomed up view of the simulation S-11. Displayed are mean larvae numbers of a 100-fold repetition.

The advantage of the earlier oviposition of the residential species was levelled out when reaching the medium larval stage. At the beginning of this stage the migrating species was almost synchronized with the resident. Consequently the migrant reached the large larval stage even before the resident. In the second generation, the small larvae of the resident were following the dynamics of the large larvae of the migrant – avoiding interspecific competition effects.
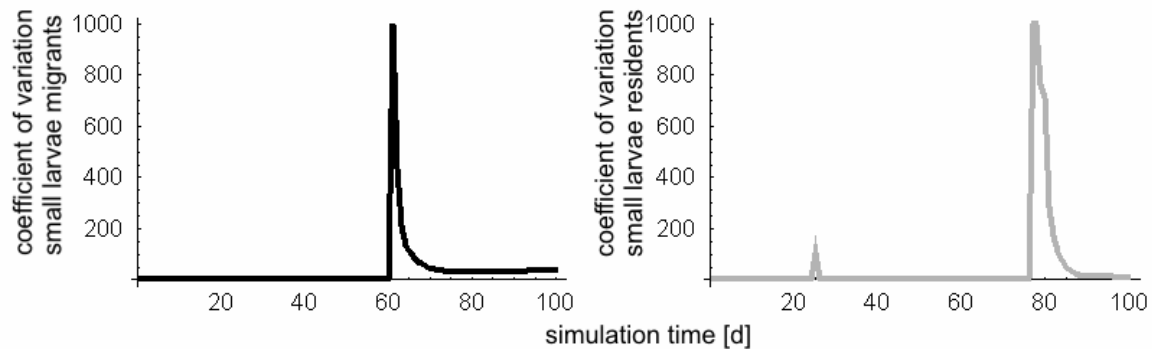
Figure 3.19: Coefficient of variation for the number of small larvae for the simulation: migrants arriving 11 days after the residents.

The calculation of the coefficient of variation for the small larvae for this simulation (Figure 3.19) showed that both species reached a peak of about the same height when they entered the second generation, but the level of the coefficient of variation after that peak was remaining at a higher level for the migrant species.

b) Scenario S-24

This simulation study was conducted due to the parameter setting of the population dynamic model. The model distinguishes only between three larval stages and incorporates cannibalistic effects just between the stages large/medium and medium/small. Therefore differences to the field experiments can be expected. The time gap of colonization of 24 days realised in this simulation therefore reflects the situation that eggs of the residential species have the possibility to develop into larvae of the second stage while the migrant species is just entering the first larval stage. In order to construct a situation of a permanent habitat occupied by residents and a supposed colonisation of migrants, the initial egg number of the residents was chosen at 5000 eggs while the migrants entered the simulation with only 500 eggs (Figure 3.20 and Figure 3.21). The migrant species reached the second generation before the residential species but with lower density. Figure 3.22 shows the coefficient of variation for

the small larval stages of this simulation. The peak of the coefficient of variation was higher for the resident species but the migrants' coefficient of variation stayed at a higher level than that of the resident.
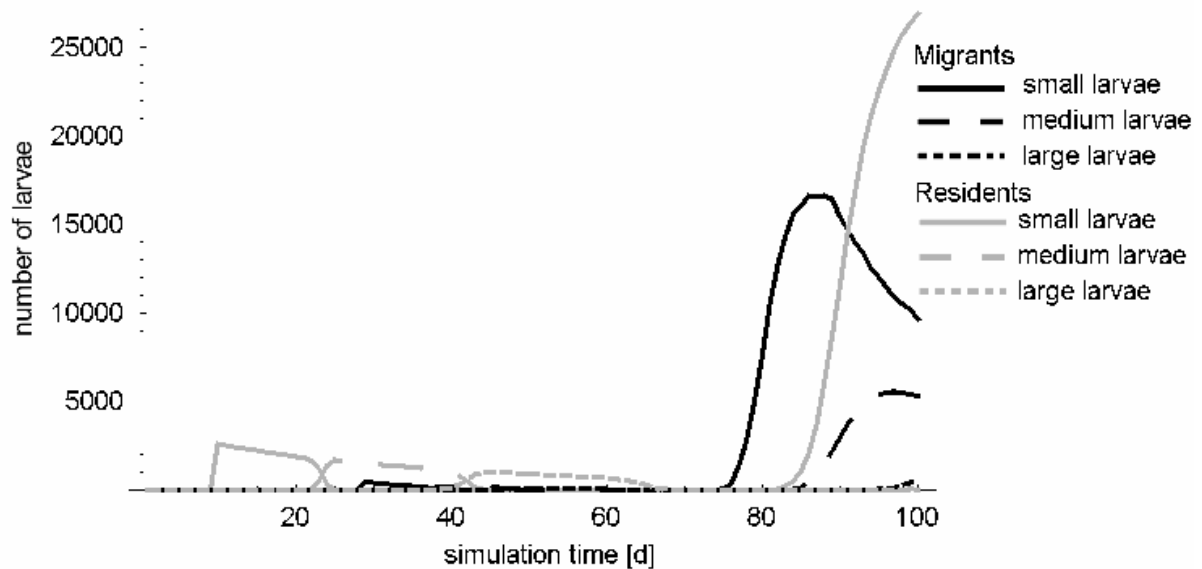
Figure 3.20: 2-species model. Simulation study: S-24. Displayed are mean larvae numbers of a 100-fold repetition.
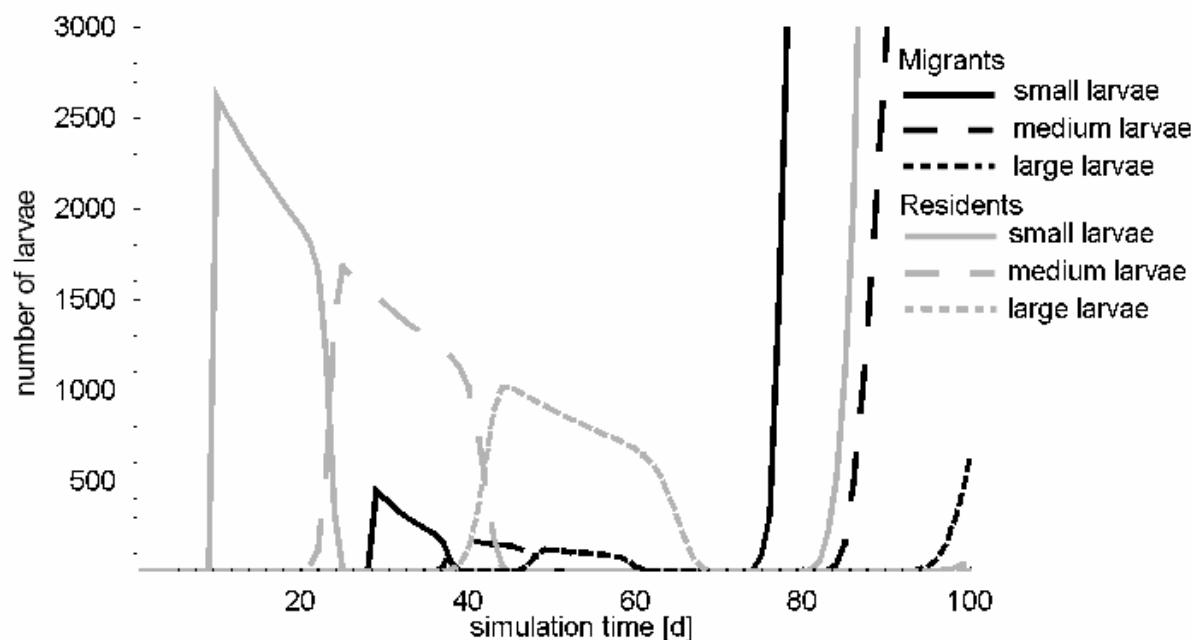
Figure 3.21: Zoomed up view of the simulation S-24. Displayed are mean larvae numbers of a 100-fold repetition.
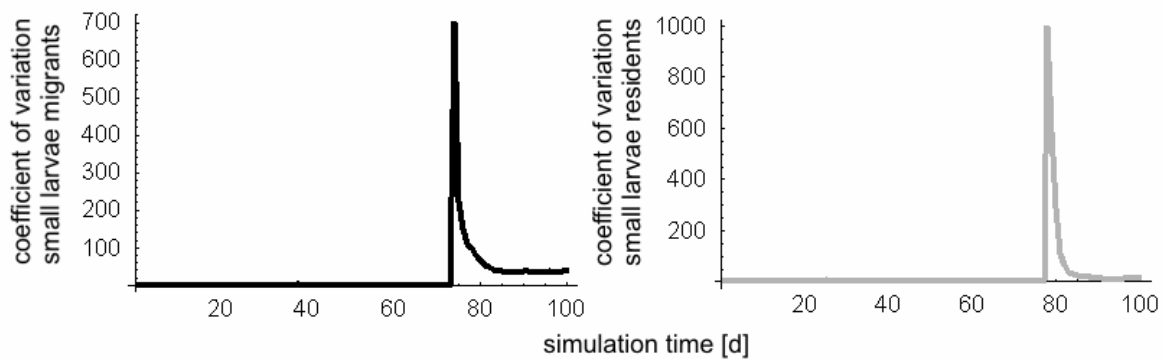
Figure 3.22: Coefficient of variation for the number of small larvae for the simulation S-24.

3.4 Discussion

3.4.1   One-species model

Overall the model reproduces the typical pattern of multivoltinism for the two modelled species types. It produces reasonable results for different levels of prey density and the efficiency by which the prey can be used as a food resource.

The results of the sensitivity analysis clearly show the effect of the different life-cycle traits between migrants and residents. The migrant species is able to complete up to two generations more during the three years of the analysis compared to the residential species. One important factor for the classification of dragonfly species regarding their life-cycle is the voltinism, the number of generations per year (Corbet 1999). Tropical-centred species complete mostly less or at least one generation per year (multi- and univoltinism). In contrast to this, the majority of temperate-centred species need at least one year or more to complete their life-cycle (partivoltinism) (Figure 3.23). More than 60% of tropical-centred dragonfly species complete more than one generation per year, a pattern that is well reproduced by the model for the residents as well as for the migrants.
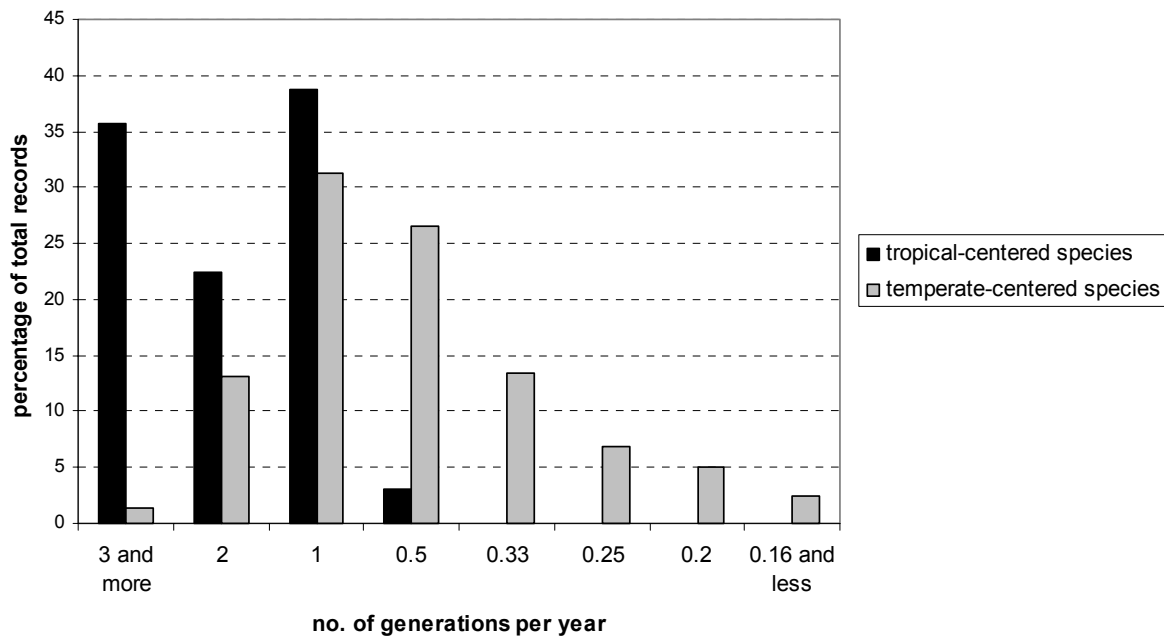
Figure 3.23: Patterns of voltinism for tropical- and temperate-centred dragonfly species (data from Corbet (1999))

Univoltinism in the tropical-centred species can be explained by seasonal constraints, which limit the species in spite of their general ability of a fast development. Highest voltinism is likely to occur in migratory species, which are able to make use of ephemeral habitats (Corbet 1999).

A parameter on which the model reacts very sensible is the predation efficiency (Figure 3.7 and Figure 3.8). Low values of predation efficiency lead to the situation that the population can only make use of a small part of the unspecific food. This situation results in the development of distinct generations. The amount of available food is always low and so the additional mortality induced by intraspecific competition (described by Equations 3.14 and 3.15) is higher. Elkin & Baker (2000) described that predator avoidance may lead to increased intraspecific interactions, which agrees with the simulation results. Additionally, at higher population densities of larger larvae a higher degree of cannibalism on smaller larvae is the result to replenish the needed food.

Higher predation efficiency stronger depletes the food resources. This results in a faster development due to more available food and may therefore lead to overlapping generations. The maximum population density decreases in the simulations with high predation efficiency but the minimum densities seem to be buffered. This is another clue that generations overlap in these simulations. The lower maximum densities may be explained by the fact that the

unspecific food pool cannot recover from low values as fast as at low predation efficiency values. Therefore the overall food situation in these simulations is worse than in the case of lower predation efficiency.

The model excludes seasonal effects, which can potentially be induced either by aridity or by lower temperatures. These effects may dampen the numbers of generations per year (Corbet 1999; Corbet 2003; Suhling et al. 2003). The laboratory experiments which served as basis for the calculation of the survival rates were conducted with unregulated temperature (Schenk et al. 2004; Schenk & Söndgerath 2005) but to a certain extent the outdoor temperatures were buffered by the indoor situation. However, the experiments covered only a part of the year so that no information about seasonal variation was available. The field experiments also covered a time interval of 75 days only and therefore contain no sufficient information about seasonal variation (Suhling et al. 2004). If seasonal effects induced by changes in the temperature regime play an important role in the phenology of the investigated species, more experimental data would be necessary to implement the effects in the model.

The parameters of the density- and food-dependent functions, which describe the additional mortality, lack empirical data for fitting. Nevertheless, these equations are based on literature reviews and reflect the main processes taking place in competitively structured dragonfly communities. Feedback loops exist and are described as thinning effects. They result in an advantage on the respective larger larval stage by reducing smaller potential food competitors and the uptake of additional food (Polis 1981; de Roos 1997; Brodin & Johansson 2002). Additionally the conspecifics which are killed in an encounter event may also serve as food (van den Bosch & Gabriel 1997). These functions also model the effect that cannibalism occurs earlier at a higher density (De Block & Stoks 2004). The level of additional mortality induced by these functions is based on experiments on competition between dragonfly larvae (van Buskirk 1989). Another effect of interaction between dragonfly larvae is also included into the model. It has been observed that competing dragonfly species kill conspecifics but do not use them as a food resource (Corbet 1999). When the number of killed conspecifics, which is added as additional food resource and the proportion of unspecific food, exceeds the amount of food that is needed by the larvae, the odd part of the food is discarded. This behaviour increases the thinning effect by removing other competitors. Additionally it has been observed in experiments dealing with larval cannibalism that the cannibalism rate does not increase linearly with density (van Buskirk 1989). In the model this is achieved by a limitation of the additional mortality term. Hence, the functions describing the additional mortality reflect inter- and intraspecific competition effects well.

3.4.2   Two-species model

One important requirement before the model can be implemented into the spatially explicit dispersal model is that it has to reproduce the patterns of different colonisation patterns for the two modelled species types. The simulations therefore have to rebuild the field experiments conducted in Namibia (Figure 3.24).
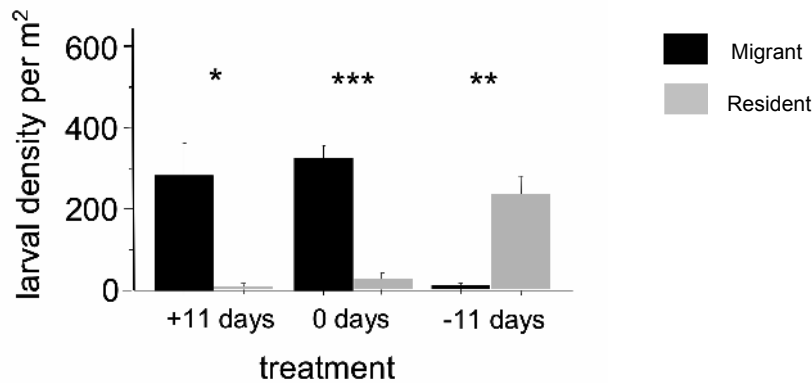
Figure 3.24: Results of the field experiment investigating the colonization sequence. Edited after Padeffke & Suhling (2003). Displayed are remaining larvae at the end of the experiments. +11 days: migrant oviposits first, 0 days: migrant and resident oviposit at the same time, -11 days: resident oviposits first. For pairwise comparisons, t-tests were used. * P<0.05, ** P<0.01, *** P<0.001

This study showed for the situation that the migrant oviposits first or at the same time as the resident, larval densities of the migrant at the end of the experiment were significantly higher than those of the resident. In contrast to this, in the situation where the resident oviposits before the migrant, the larvae of the resident reached significant higher densities.

The patterns reproduced by the model are very similar to these findings. The mean values, which are displayed in Figure 3.9 (S±0) and Figure 3.12 (S+11), show much higher densities for the migrant species. The results of the simulation with the migrants arriving after the residents (Figure 3.18) show similar densities, which seems to be in contrast to the experiments studying the priority effects. However, a relatively high variation in population size of the small larvae for both species between the single simulations is indicated by the coefficient of variation for the situation of migrants arriving at the same time as the residents (S±0). When the migrants arrive before the residents (S+11), the coefficient of variation for the residents is more than twice as high as for the migrants. Therefore a very high variability between the simulations can be stated which may even lead to an extinction of the residential species. The high extinction risk of the residents can also be seen when looking at the numbers of mature adults (Figure 3.15 and Figure 3.16). The first generation of the migrants has a much lower coefficient of variation than the resident. This shows that the problems for

the residents to establish a population, which is capable of surviving, are enhanced in a habitat where the migrant species has already oviposited.

In the reversed situation, when residents oviposit first (S-11), a high variation for the results of the migrant species and a very low variation for the resident species can be found in the simulations. This can be seen as evidence that the establishment of a local population of residents is much easier if there is a temporal advantage. However, the simulation study, which was intended to amplify the advantageous effects for the resident species (S-24), did not produce very different results compared to the situation adopted from the experimental design. The number of larvae of the resident species in the second generation is about 5 times higher than in the simulation depicted in Figure 3.17, but this may be due to the fact that the initial egg number is also 5 times higher. The same applies to the number of small larvae of the migrant species, which is about half the size of the simulation with the 11 day advantage of the resident. Here the number of eggs introduced in the habitat was only 500 (in contrast to 1000 eggs in the 11 day advantage simulation). The effect of the temporal and density-dependent advantage of the resident was not enhanced in this simulation. One possible explanation is that the initial food density, which was set at the level of the other simulations, inhibits a more rapid development of the larvae of the resident and increases the additional mortality induced by food deficiency.

Overall the two species model produces reasonable results similar to the conducted experiments investigating the priority effects (Padeffke & Suhling 2003). Repeated simulation runs and the calculation of mean values for the single stages of the life-cycle led to an advantage of the migrant species in the most cases, but the coefficient of variation, which shows that the extinction of the species is possible in single simulation runs, leads to the conclusion that the model reproduces the patterns observed in reality. Further experiments investigating the priority effects in dependence of the available food and different initial densities of the competing species would possibly serve for a further validation of the model.

Other species can also be implemented in the model, given the appropriate life history parameters, under the assumption that food dependence is the factor, which mainly drives the population dynamics.

4 The spatially explicit dispersal model

4.1 Introduction

Landscape structures are generally of great importance for the survival of populations. For instance, patchiness of habitats may enhance the overall population survival (Fahrig & Paloheimo 1988). The distribution and variation of resources in the spatial context is known to directly and indirectly effect the distribution of animals as it may lead to concentration of species at certain localities (Mackey & Lindenmayer 2001).

To show how landscape structures and climate change are supposed to alter the population dynamics of dragonflies, the spatially explicit dispersal model contains the information and submodels described in Chapters 2 and 3. They are integrated into a model dealing with the landscape, the habitats provided by the landscape at the current time step and rules for the dispersal of the dragonflies over the utilisable parts of the landscape. The aim of this chapter is to show the development and application of this model for three different landscape sections in Namibia as well as for four theoretical scenarios with an artificial landscape. The model can be used to show the importance of certain landscape structures on the persistence of populations of the species types modelled in Chapter 3 under current and future climatic conditions.

The task of developing a model, which describes the landscape in the investigation area in a realistic way, requires an abstraction of the real landscape. The processes described so far – habitat choice, larval interactions and mating – are basically taking place at the habitat or locality scale (cf. Chapter 1, 2 and 3). At larger spatial scales, especially in the case of a patchily distribution, the local populations may be connected by migration between the habitats (Hansson et al. 2002). To model these effects, an extension of space is needed in order to add more complexity and realism (Caswell & Cohen 1993). Models which are commonly used for this purpose are metapopulation models (Hanski 1999; Hanski & Gaggiotti 2004).

Additionally, the arid environment in Namibia and the patchy distribution of the partially sparse distribution of the aquatic habitats, which are necessary for Odonata to complete their life-cycle, can be compared with the opposed situation of islands being located in a surrounding matrix of water (Angelibert & Giani 2003; Hanski & Gaggiotti 2004). This follows the metapopulation concept by Levins (1969) as well as the theory of island

biogeography by Mac Arthur and Wilson (1967) with a discrete space concept and the distinction between habitat patches and the rest of the environment, the landscape matrix.

Although closely related with each other (Hovestadt & Poethke 2005), one of the main differences between these two approaches is that island biogeographical models focus on the community level or – in other words – species richness, while the metapopulation models usually treat individual species (Hanski & Simberloff 1997). However, there also exist metapopulation models for two species (Nee et al. 1997; Hanski 1999). One approach to close the gap between island biogeography and metapopulation models and to add complexity and realism into the models is the development of metacommunity models (Leibold et al. 2004; Leibold & Miller 2004). The metacommunity is being defined as a set of local communities linked by dispersal of multiple interacting species (Wilson 1992). The model presented in this chapter can be defined to be located between the metapopulation and the metacommunity approach as it deals with pairs of interacting species being dependent on the same food resources (cf. Chapter 3), which is defined as a third population having great influence on the population structure of the focus species.

Originally, a metapopulation is defined as a population of local populations which are connected via dispersal and colonization (Levins 1969). The simplest assumption is that the metapopulation size, P(t), is being measured by the fraction of patches which are occupied at time t. P(t) in the classical Levins' formulation depends only on colonization and extinction rates. However, this approach is spatially implicit and especially for the purpose of modelling effects of habitat destruction in a specific part of a landscape a spatially explicit approach is necessary (Hanski 1999; Hanski & Gaggiotti 2004). One method to achieve this aim is the use of a regular lattice model or a cellular automaton for the description of the landscape properties and the integration of the habitat suitability models and the population dynamics (Hogeweg 1988; Schröder 2000; Britton et al. 2001; Vogel 2002; Hanski & Gaggiotti 2004).

In the first part of this chapter (Chapter 4.2), the development of the landscape model is described. The parameters, which describe the landscape, are derived as static in the first approximation. Afterwards, a dynamic change of the landscape is implemented into the model. The impact of this dynamic on the metapopulation structure will be analysed. Closely connected to the landscape dynamic is the following derivation of scenarios describing the climate change in the dispersal model. Four theoretical scenarios are constructed and described to test the dispersal model and to get first insights into the importance of certain landscape structures.

In the second part of this chapter (Chapter 4.3), the rules for the dispersal of the dragonflies are described and the impact of dispersal is analysed using landscape metrics. In the following, the effects of the dispersal rules will be discussed. Subsequently, the spatially explicit model will be applied to the theoretical scenarios, to scenarios under current climatic conditions and under climate change conditions, each directly followed by a discussion of the results.

4.2 The landscape model

To model the dispersal of animals in the landscape it is necessary to be aware of the processes that lead to the distribution of the species. The landscape must be reduced to characteristics that are of relevance for the species which are chosen as focus organisms (Turner et al. 1995). The results of the habitat suitability models (cf. Chapter 2), literature review and expert knowledge were used to minimize the number of these factors.

The simplification of the landscape and its parameters leads to the fact that a single landscape unit has to be considered as homogeneous in its properties. Additionally, the sum of landscape units located in one region (the landscape section) has to be simplified concerning regional properties of the landscape like climate etc. Therefore it will be necessary to take these regional differences into account for the landscape composition, as there might be factors, which influence the persistence of populations on this large scale.

4.2.1 Choice of the modelled sections

The ephemeral river catchments of western Namibia cover three different biomes (Mendelsohn et al. 2002): The tree and shrub savannah, the Nama Karoo and the Namib Desert. As biomes are defined by their different climatic conditions amongst others (Schultz 1995), I therefore have decided to locate the regions for the implementation of the dispersal model in these biomes to be able to integrate the influence of the climate on the spatial population dynamics into the model. Due to the availability of LANDSAT satellite images and a huge amount of information from the monitoring (cf. chapter 1), I have focused on the Swakop river catchment.

In the eastern part, the region around the S. von Bach Dam and the Swakoppoort Dam, both reservoirs, which are used for the water supply of Windhoek, provide large areas with open water. So the first landscape sector is referred to as "von Bach" and includes the S. von Bach Dam in the northeastern corner and the Swakoppoort Dam in the southwestern corner. The Nama Karoo biome is taken into account in the second landscape sector, referred to as

"Tsaobis". It is located around the Tsobis Leopard Nature Park south of Karibib where the field experiments and some of the laboratory experiments of the BIOTA subproject were conducted. The third landscape sector covers the biome Namib Desert and is located around Swakopmund. This section is referred to as "Swakopmund" (cf. Figure 4.1)
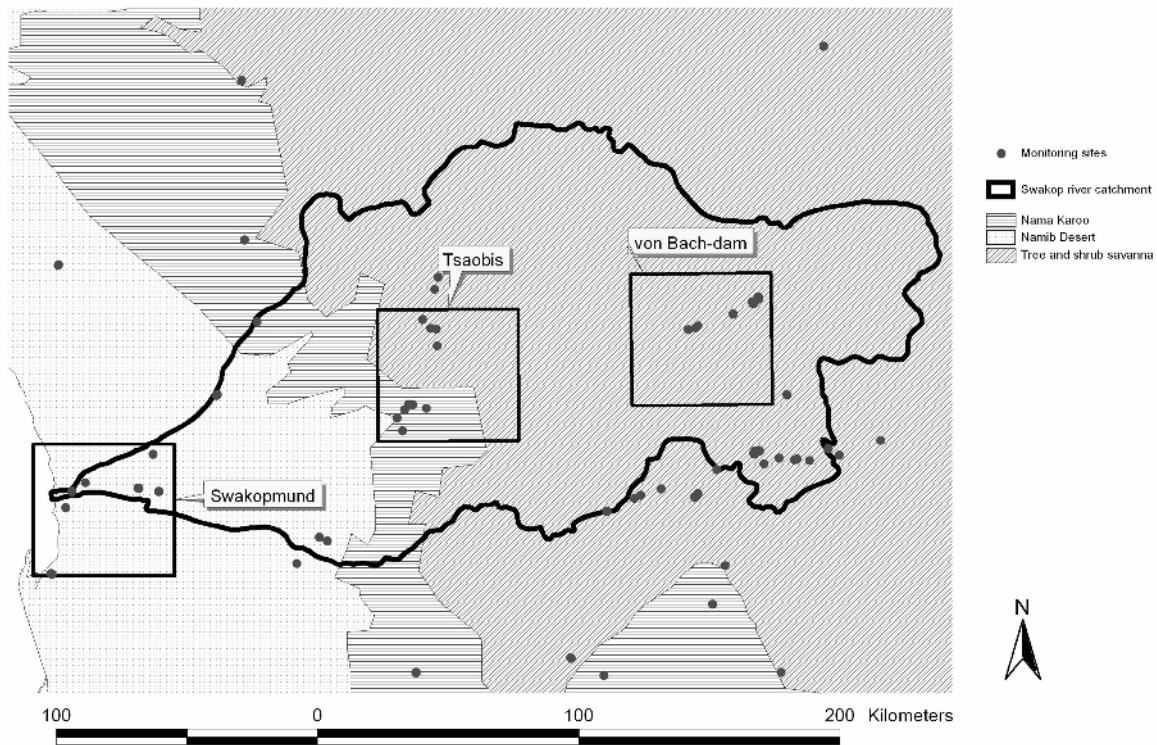
Figure 4.1:   Location of the modelled landscape sectors in the Swakop river catchment

4.2.2   Landscape properties

Movement of organisms can generally be distinguished into several taxonomic "movement behaviours" (Dingle 1996). The first category is the "station keeping" (containing the movements for kinesis, foraging, commuting and territorial behaviour). Station keeping is mostly focused on movements within the habitat (Hassell & Southwood 1978). The next movement category is ranging, often also described as dispersal, which includes movement to explore an area. Both, station keeping and dispersal are movements, which are home range or resource directed. As the dispersal movements of dragonflies, being highly mobile organisms, are taking place mostly at a larger spatial scale than the station keeping movements, the model focuses on a grid cell with a size of 1 km².

The landscape is modelled as a lattice model with identical cell sizes. Each modelled landscape section (Figure 4.1) has a size of 50*50 km to enable comparability between the sections. The properties of the landscape are reduced to three parameters which are results of

behavioural observations of the focus species and the habitat suitability models and which are of ecological relevance for the presence of the Odonata species (cf. Chapter 1).

Presence of water

The first parameter, which describes the landscape, is the presence of open water. It is essential for dragonflies as they spend the egg and the larval stages of their life cycle in freshwaters. Furthermore, this parameter distinguishes between temporary and permanent waters, which will be important for the construction of a dynamic landscape model (cf. Chapter 4.2.3).

Per definition the lattice cells with permanent water cannot get dry in the run of a scenario, while the temporary cells dry out and can be rewetted. The landscape matrix has been defined as cells, which are not able to contain sufficient water to provide an aquatic habitat. In addition to this it was not reasonable to define the whole lattice as potentially temporary waters to reduce the calculation time. Therefore existing LANDSAT 7 ETM+ satellite images taken in spring 2000 were analysed for the presence of open water using ERDAS Imagine 8.5. An automatic classification of spectral criteria was conducted with a manual correction of pixels, which were erroneously classified as "water". This classification was based on the fact that the band 4 (near infrared) is useful to locate water bodies (Avery & Berlin 1992). It led to binary maps containing only the pixels with open water. These maps were transformed into ArcView shape files and were used for further analysis.

The final properties of each cell in each landscape sector were adjusted manually. Cells for which the remote sensing analysis yielded the presence of water were at least defined as cells with temporary water. However, permanence of water cannot be estimated by a single snapshot of the landscape, therefore permanent waters were defined due to knowledge from the monitoring programme in 2001 and from maps, which described the location of larger reservoirs in the respective landscape sectors.

The satellite images were taken near the end of the rainy season and the starting point for the modelling of the scenarios was assigned at the climax of the rainy season. Therefore additional temporary waters had to be added in comparison to the date where the satellite image was taken. Again, the rules were based on the knowledge from the monitoring programme. Most of the additional waters were placed in the riverbed, as at the climax of the rainy season it can be supposed that there are many temporary ponds fed by influx from the slopes of the riverbed, even if the river does not flow constantly. The result is a snapshot of the landscape at the maximum of an average rainy season, when most of the temporary waters

are filled up with water. Figure 4.2 to Figure 4.4 show the maps for the three landscape sections.
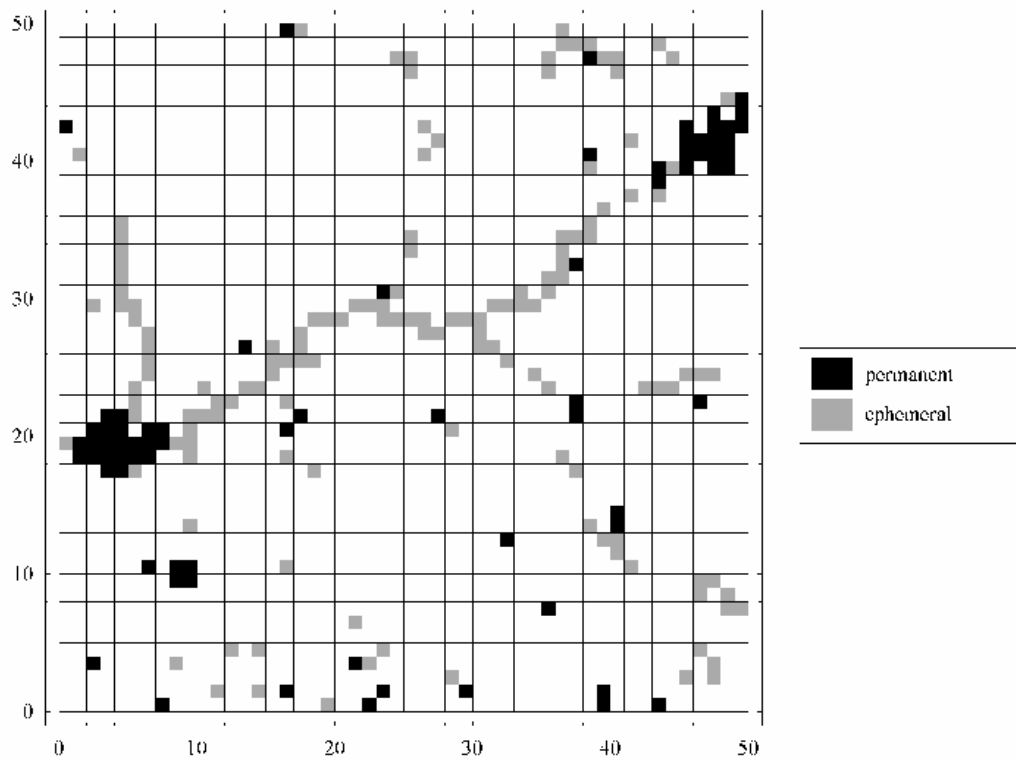
Figure 4.2:   Landscape layer "presence of open waters" for the landscape section "von-Bach". Depicted is the climax of the rainy season under current climatic conditions. Black cells: permanent waters, grey cells: temporary waters.
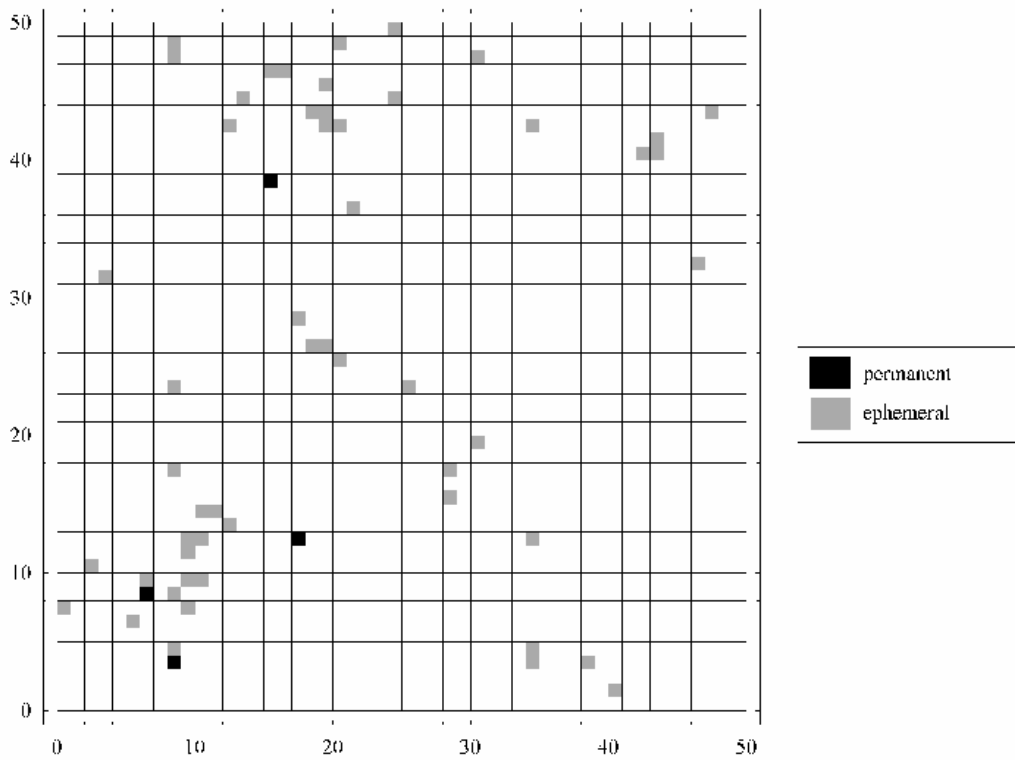
Figure 4.3: Landscape layer "presence of open waters" for the landscape section "Tsaobis". Depicted is the climax of the rainy season under current climatic conditions. Black cells: permanent waters, grey cells: temporary waters.
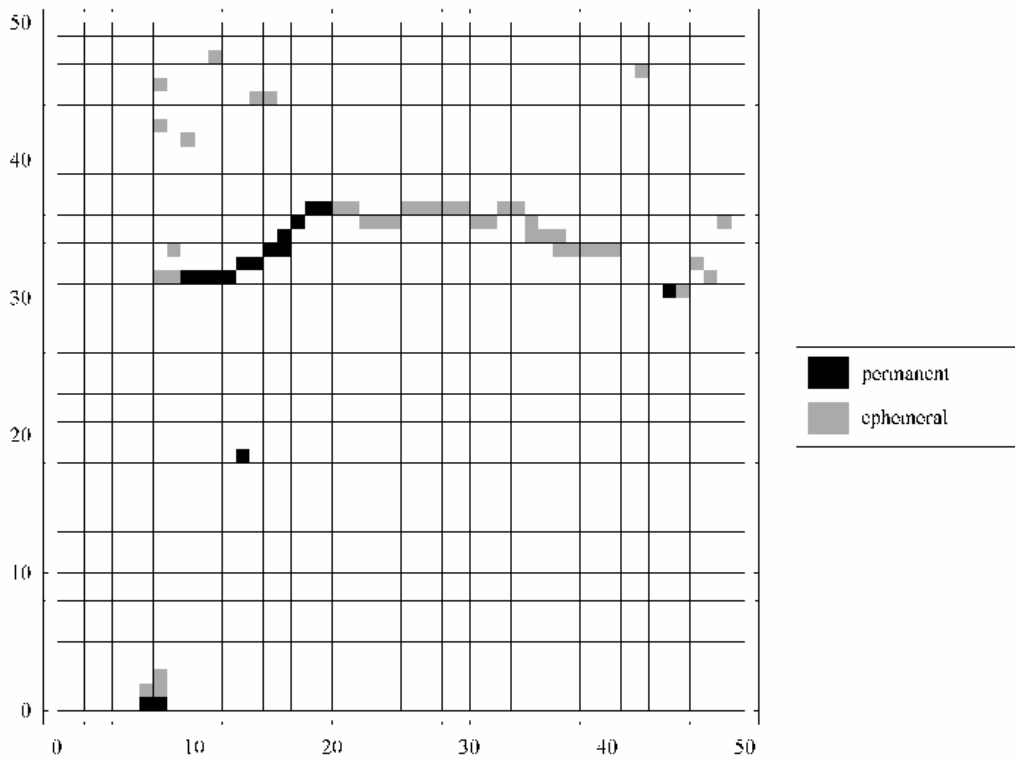
Figure 4.4: Landscape layer "presence of open waters" for the landscape section "Swakopmund". Depicted is the climax of the rainy season under current climatic conditions. Black cells: permanent waters, grey cells: temporary waters.

Aquatic vegetation diversity

The introduction of the second landscape parameter was done to convert the habitat parameter "aquatic vegetation diversity" (cf. Chapter 2) from the local habitat scale to the cell size of 1 km². The LANDSAT satellite images again were used as a base to get information about the vegetation structure. The images were processed with the image analyst extension of ArcView.

One measure for the photosynthetic activity, which is strongly correlated with the density and vitality of the vegetation, is the NDVI (Normalized Difference Vegetation Index, equation 4.1). It uses the spectral information of the red spectral band (band 3, bandwidth 0.63-0.69 μm) and the near infrared band (band 4, bandwidth 0.75-0.90 μm) and provides a method to compare the vegetation greenness stored in the band information in the satellite images (Avery & Berlin 1992; Schmidt & Karnieli 2000). The NDVI can take values between -1 and 1. The higher the NDVI value of the pixel of the satellite image, the "greener" is the vegetation.

$$NDVI = \frac{near\ IR\ band - red\ band}{near\ IR\ band + red\ band}$$ Eq. 4.1

According to Chapter 2 the aquatic vegetation diversity was of special interest to model the habitat requirements of the residential species *C. erythraea.* The results of the NDVI calculations alone did not allow distinguishing between the different classes of vegetation diversity, especially at the coarser scale of the cellular automaton. Therefore additional expert knowledge from the monitoring was used to create a map of the landscape layer "aquatic vegetation diversity". Only habitats, which were at least defined as temporary habitats in the first landscape layer (presence of open water) were considered. A set of rules was applied to these grid cells in addition to the NDVI information: Cells, which are placed in the riverbed of the Swakop River, are subject of high disturbances through flooding of the river and were therefore only able to get low aquatic vegetation diversity values. Permanent habitats, which are used as cattle watering tank are also subject of high disturbances through the animals and were only able to obtain low vegetation diversity values. Only permanent habitats with low supposed disturbance were able to get the highest observed value of 5. The results of the NDVI analysis were additionally considered by comparison of the results of the applied rules with the NDVI maps. Cells with high NDVI values, which were disregarded by the rules, were classified with higher vegetation diversity as solely by the application of the rules. The maps resulting from this procedure for all three landscape sectors for the scenario with the

current climatic conditions based on data from Mendelsohn et al. (2002) are depicted in Figure 4.5 to Figure 4.7. The maps for the scenarios based on the prognosis of the IPCC for climate change and for the theoretical scenarios (see Chapter 4.2.4) can be found in the Appendix (Figures A.1 to A.3 and Figures A.9 to A.11).
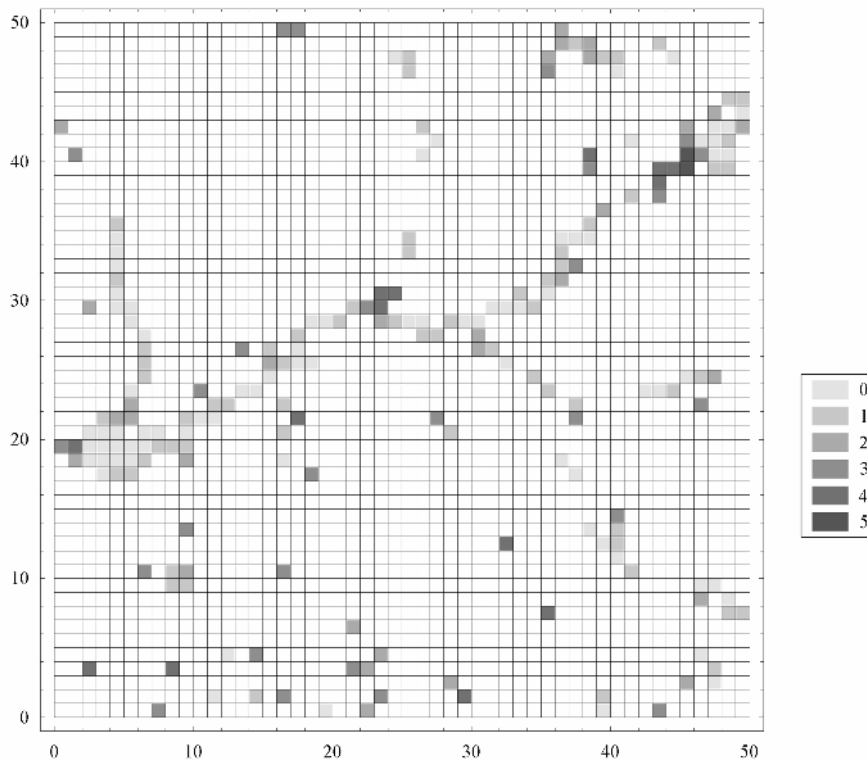
Figure 4.5: Landscape layer "aquatic vegetation diversity", scenario "von Bach". Numbers on the axis represent the internal program addresses of the cells. Different grey shades represent values for aquatic vegetation diversity.
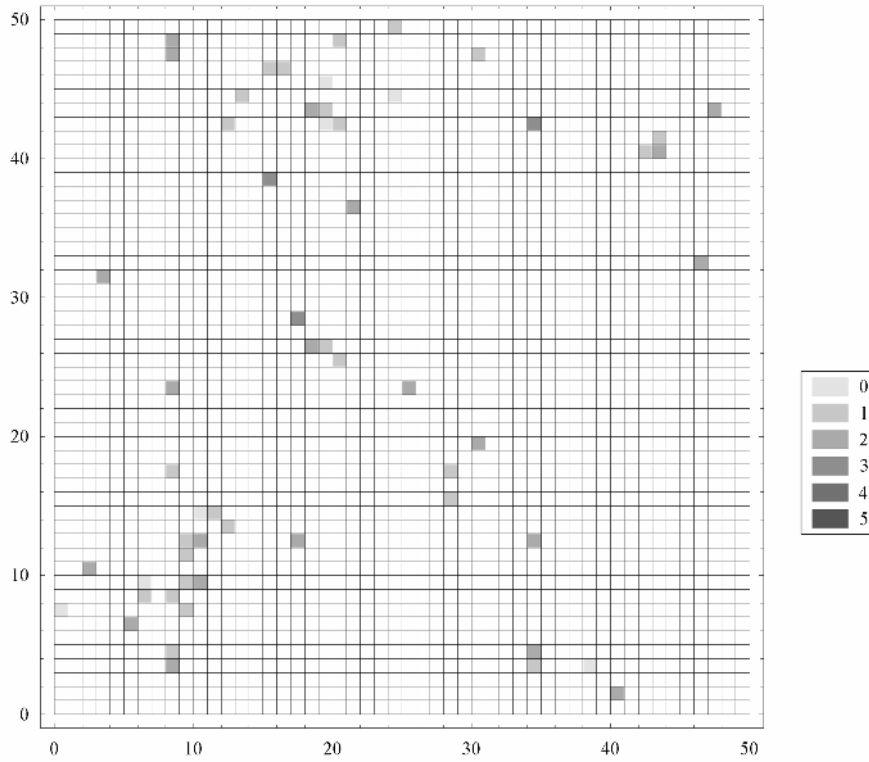
Figure 4.6:   Landscape layer "aquatic vegetation diversity", scenario "Tsaobis". Numbers on the axis represent the internal program addresses of the cells. Different grey shades represent values for aquatic vegetation diversity.
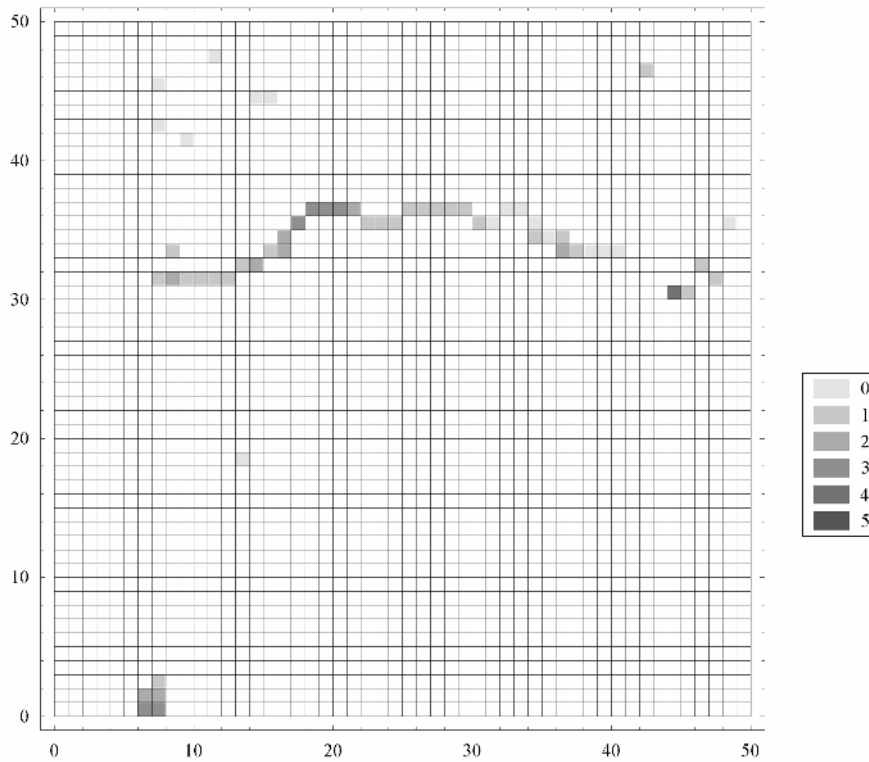
Figure 4.7:   Landscape layer "aquatic vegetation diversity", scenario "Swakopmund". Numbers on the axis represent the internal program addresses of the cells. Different grey shades represent values for aquatic vegetation diversity.

Rivers as guidelines

The third landscape parameter was introduced as a result of the assumption that *P. genei* seems to prefer habitats located in a riverbed (cf. Chapter 2, see also Suhling et al. 2003). Therefore a map describing the "existence of rivers as guidelines" would have to meet the requirement that it reproduces the linear structure of the rivers in the landscape, but it must also make a distinction between other linear structures like roads or railroads. This approach follows the filter model of habitat selection (Wildermuth 1994) as the first step of biotope selection.

The rivers in the area of investigation can be characterized by a poorly vegetated riverbed and gallery forest, usually formed of acacia trees (e.g. camel thorn tree) and/or tamarisk shrubs at the riverbank (Jacobson et al. 1995). One possibility to identify these structures from a satellite image is the use of the NDVI, as it is shows this contrast. The widely barren riverbed has got a low NDVI value while the gallery forest has got a high NDVI value. This contrast in addition to the apparently linear structure of the river course may be one of the criteria, which can be used by species like *P. genei* for navigation on the search of a new habitat meeting the requirement of being located in a river. However, there is no direct evidence for such a dispersal mechanism.

To enhance this contrast an edge detection convolution kernel has been applied to the NDVI map. As a kind of "moving window" it is applied to each pixel of the original data. The kernel uses the matrix depicted in Figure 4.8 to recalculate the values of the NDVI. The value of the central pixel is multiplied with 24 whereas the adjacent 24 pixels are multiplied with -1. The sum of the values after applying the matrix on the central and its contiguous pixels determines the new value for the central pixel.

-1	-1	-1	-1	-1
-1	-1	-1	-1	-1
-1	-1	24	-1	-1
-1	-1	-1	-1	-1
-1	-1	-1	-1	-1

Figure 4.8:   Edge detection matrix for determination of "rivers as guidelines", applied to NDVI maps.

By application of this method differences of adjacent pixels and therewith the contrasts between areas covered with vegetation and barren areas are sharpened. The resulting map was viewed in the GIS at a scale of 1:150,000. Grid cells were defined whether they were containing rivers as guidelines or not for the three modelled landscape sections under current

climatic conditions (Figure 4.9 to Figure 4.11). Displayed are all cells for which the analysis yielded the presence of "rivers as guidelines", whether they actually contain water or not. The maps for the theoretical scenarios can be found in the Appendix (Figures A.4 to A.5).
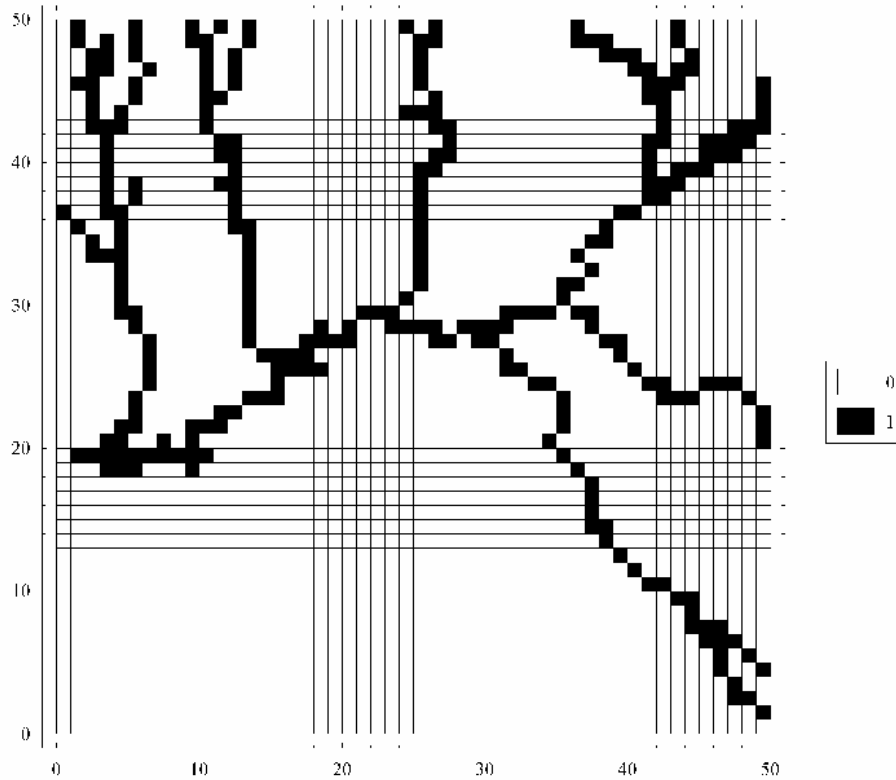
Figure 4.9: Landscape layer "rivers as guidelines" for the landscape section "von Bach". Black cells were identified as containing linear structures representing the riverbed.
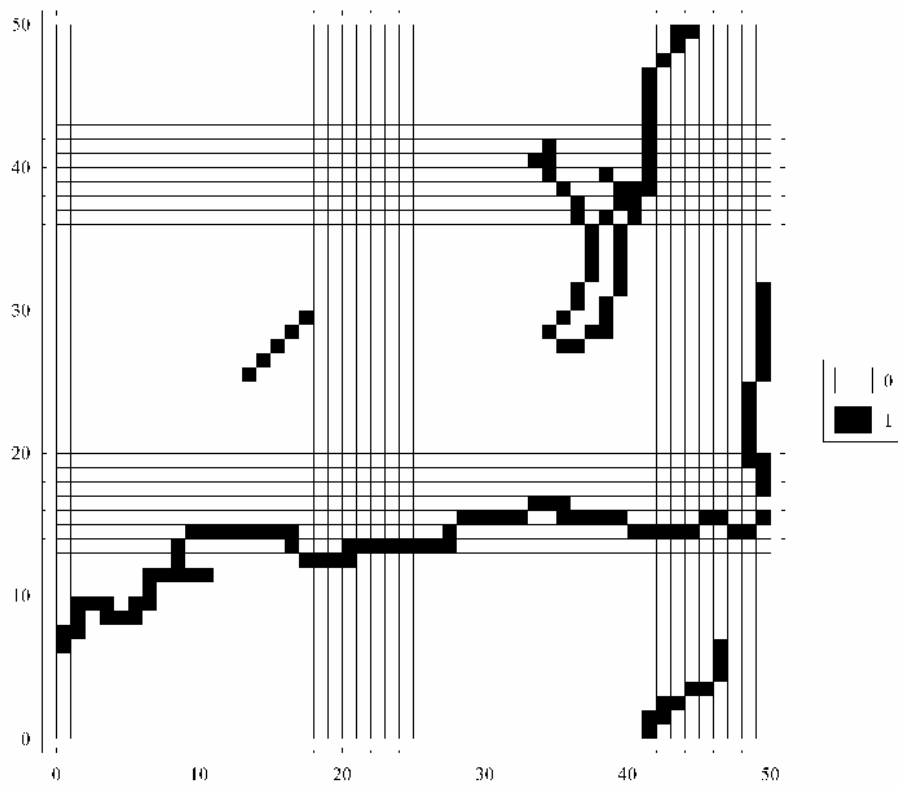
Figure 4.10: Landscape layer "rivers as guidelines" for the landscape section "Tsaobis". Black cells were identified as containing linear structures representing the riverbed.
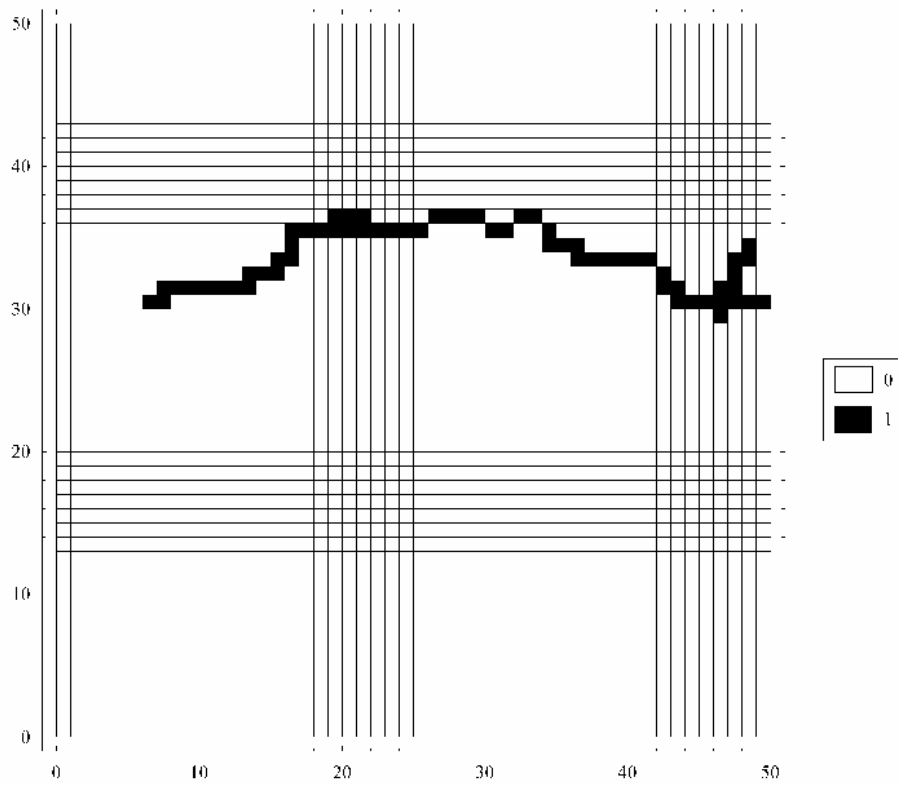
Figure 4.11: Landscape layer "rivers as guidelines" for the landscape section "Swakopmund". Black cells were identified as containing linear structures representing the riverbed.

Other properties of the aquatic habitats, which have to be set up in the landscape model, are the capacity of cells for unspecific prey and the value for predation efficiency in the habitat. These have shown to be relevant factors in the population dynamic model (cf. Chapter 3). The capacity of the unspecific prey was set to 10,000 food units in temporary and to 100,000 food units in permanent habitats. These values resulted from the fact that permanent waters are in most cases bigger than temporary rainfed ponds with a small spatial extension. Therefore the permanent waters are able to provide a higher capacity of unspecific prey.

Predation efficiency is coupled with the aquatic vegetation diversity in the habitat. Firstly, denser vegetation gives more possibilities for reduced activity behaviour in the presence of predators, which often can be found in permanent habitats. Secondly, denser vegetation may lead to more hiding places for the unspecific prey. Both processes lead to reduced consumption of prey and a lower predation efficiency value. Therefore higher vegetation diversity has been defined to lead to lower predation efficiency. However, the predation efficiency in the landscape model was limited to values from 0.6 to 0.8 as this was the range at which the different generations of the larvae began to overlap (cf. Chapter 3, sensitivity analysis).a

4.2.3   Dynamic change of the landscape

A dynamically changing landscape can be compared with a continuous fragmentation of the freshwater habitats induced by drying up of the water (and defragmentation in the case of re-wetting). These processes are essential for the distribution and density of insects in the landscape (Thomas et al. 1992; Hanski 1994; Biedermann 2004). Therefore it is necessary to build up a scenario with a dynamically changing landscape for modelling the dispersal of Odonata. Due to the aridity of the region, the processes of waters getting dry and the following re-flooding of the waters with the start of the rainy season determine the large-scale population dynamics of the dragonflies being dependent on open waters. The persistence of temporary ponds may be of special importance for the survival of a metapopulation of the focus species in the landscape.

To build up the standard scenarios, average monthly rainfall data of the respective landscape sectors were used and set as "standard scenario" under current climatic conditions (Mendelsohn et al. 2002). These scenarios serve as a base for modelling changes in the climatic boundary conditions or different management strategies for water use. Precipitation is the most important source of water in the runoff cycle, which forms temporary waters (Williams 1987).

The number of temporary waters in the landscape sector at the climax of the rainy season as defined by the landscape parameter "areas with open water" (cf. chapter 4.2.2) was standardized to 100 percent. The relative differences in the amount of the monthly rainfall from one month to another were equated with the proportional change in the numbers of temporary waters and the number of temporary waters for each month was calculated (Figure 4.12 to Figure 4.14).
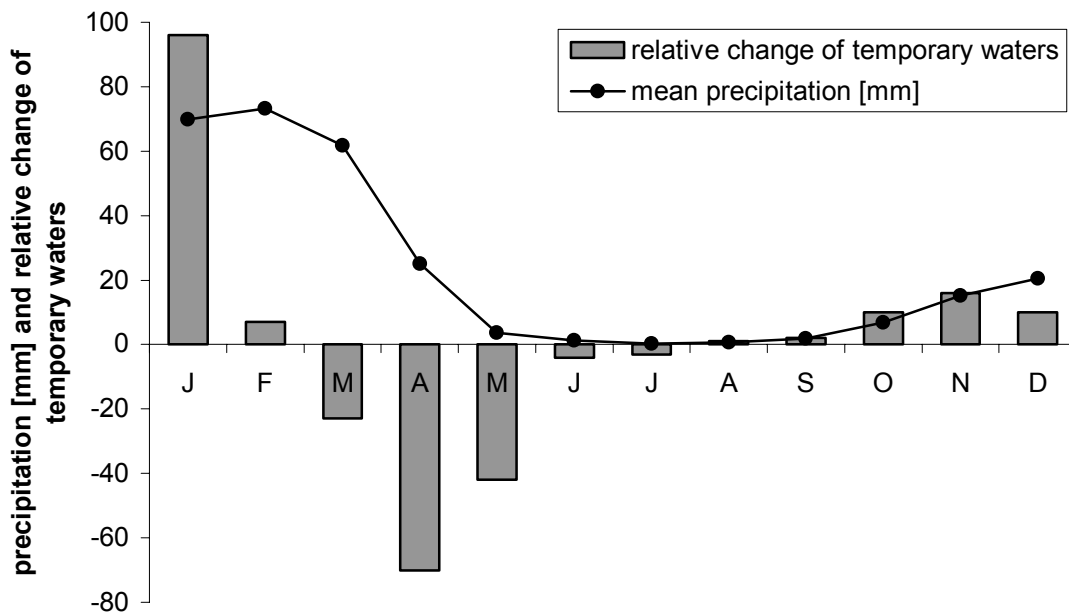
Figure 4.12: Construction of the standard scenario from mean monthly precipitation data (landscape section: "von Bach").
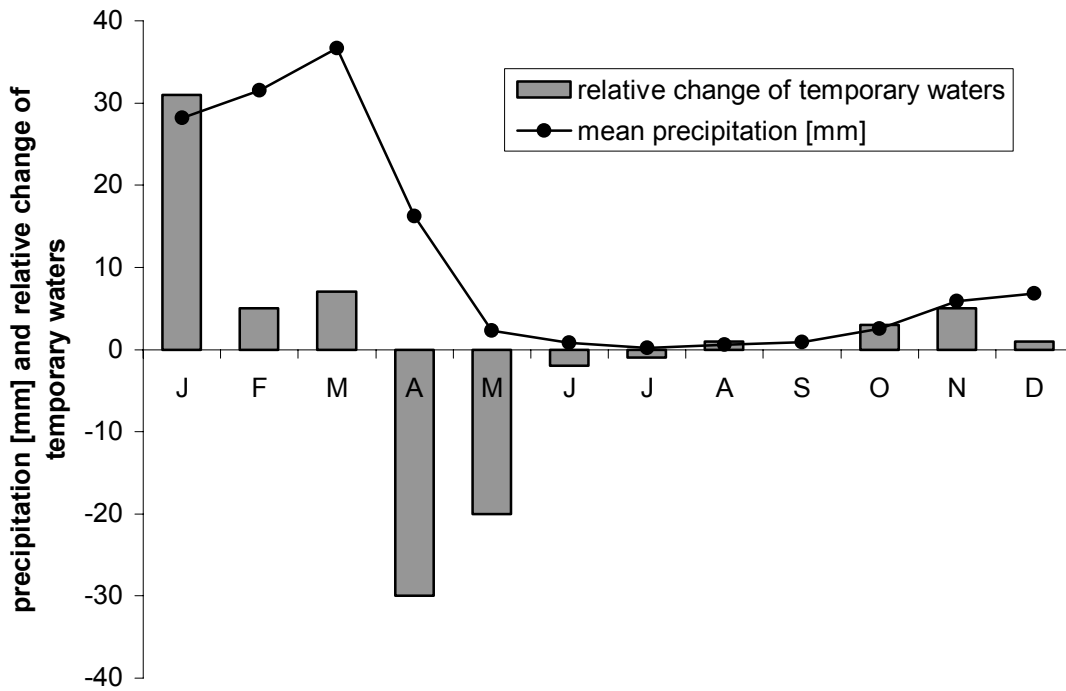
Figure 4.13: Construction of the standard scenario from mean monthly precipitation data (landscape section: "Tsaobis").
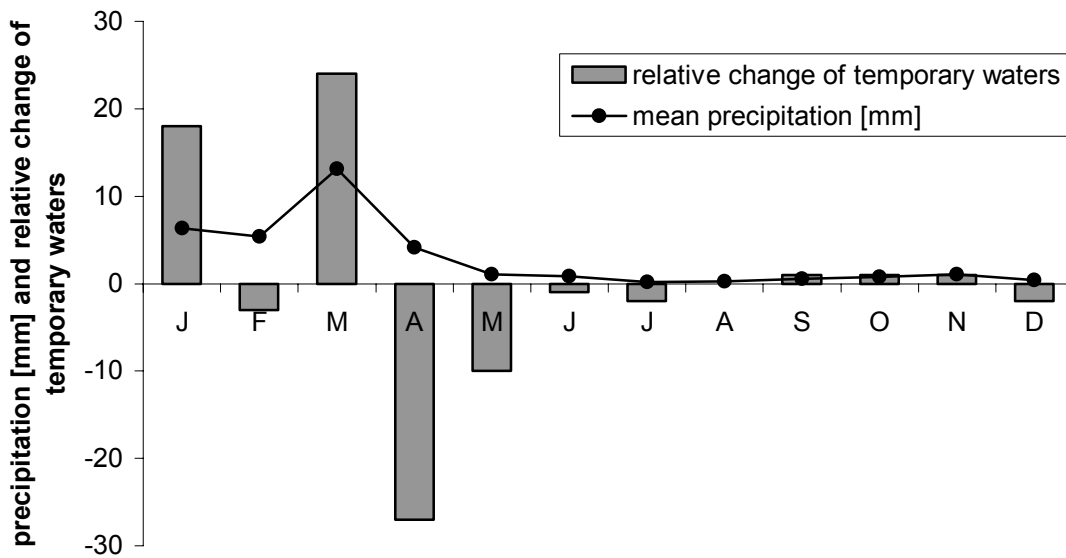
Figure 4.14: Construction of the standard scenario from mean monthly precipitation data (landscape section: "Swakopmund").

The "von Bach" section receives the highest precipitation of all three landscape sectors. The slope of the decrease of precipitation at the end of the rainy season is lower in the tree and shrub savannah as in the Nama Karoo ("Tsaobis" section). The relative change of temporary waters in the "Swakopmund" section is more irregular than in the other sections. A first

climax of the rainy season is followed by a lower average precipitation in February while the main precipitation falls in March. This results in a phase of drying waters in February despite the fact that the rainy season is about to begin.

To increase the temporal resolution of the changes in the landscape at the time scale, the monthly drying and re-wetting cells are equally divided into weekly subsets. In the dispersal model (cf. Chapter 4.3) the layer describing the presence of open water with its differentiation into temporary and permanent habitats is imported every 7th time step.

The drying respective re-wetting cells for each week are randomly determined as no further information about the persistence of the single cells like the permeability of the ground substrate for example is included in the model. Furthermore, the allocation of rainfall in the real landscape in Namibia is almost randomized (De Bruine et al. 1998). Hence, a random choice of the desiccating or rewetting cells is able to create this "patchiness" of the landscape. The result of this implementation of the landscape dynamics is that in the first approximation a cell, which is filled during the rainy season, persists as long as the cell dries out during the time of drying of the habitats (negative bars in Figure 4.12 to Figure 4.14).

Temporary waters are defined as "bodies of fresh water that experience a recurrent dry phase of varying length that is sometimes predictable in both its time of onset and duration" (Williams 1997). After Jacobsen et al. (1995) ephemeral is defined as "lasting only a few days; when applied to rivers, describing a river that only flows for a few days each year after localised rainfall".

According to these definitions the difference between temporary and ephemeral waters is obvious: Ephemeral habitats have an even shorter duration than temporary habitats and temporary habitats are more predictable regarding their duration. The landscape dynamic is determined by the amount of precipitation but the variability of rainfall can also be supposed to have a high influence on the persistence of aquatic habitats. The consequence of these definitions for the landscape model is that in a landscape section with high variability of rainfall it can be supposed that the number of ephemeral habitats is higher than in landscapes with low rainfall variability.

One measure that describes the variability of the precipitation is the coefficient of variation. It describes the standard deviation of annual totals as a percentage of average annual rainfall and increases in Namibia from east to west (Mendelsohn et al. 2002). To emphasise the ephemeral character of the modelled landscape sectors the "degree of variability" in the ranges "low variability", "medium variability" and "high variability" has been introduced. However, the

simulation time in the dispersal model is set to one year and the coefficient of variation refers to interannual variability. Therefore the coefficient of variation in the landscape sectors is set equal to the degree of variability for the standard scenario and is applied to the respective landscape sectors (Table 4.1 and Figure 4.15).

Table 4.1:   Degree of variability in the modelled landscape sectors (standard scenario).

landscape sector	coefficient of variation	degree of variability
von Bach	30%-50%	low
Tsaobis	50%-80%	medium
Swakopmund	>100%	high
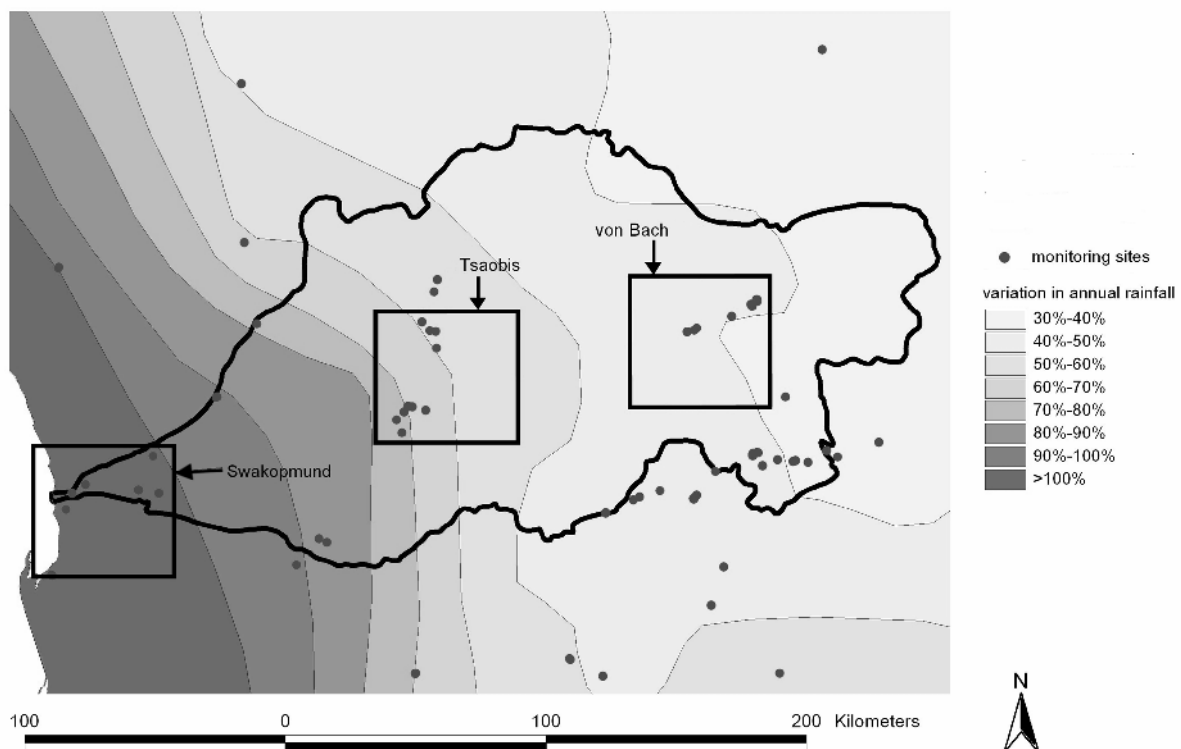
Figure 4.15: Coefficient of variation of precipitation in the Swakop River catchment.

This parameter leads to an additional random dynamic behaviour of the ephemeral waters: A cell, which is filled during the rainy season, can get dry even during the rainy season but it can also be refilled again before the onset of the dry season. The higher the degree of variability, the more temporary cells are subject to this algorithm – they get an ephemeral character. Generally, the model implies that when a temporary cell gets dry the larvae inhabiting this cell are dying because of the desiccation of the habitat. An increasing number of ephemeral habitats (= increasing degree of variability) consequently leads to gaps in habitat continuity and therefore to aggravation of the conditions to complete the life-cycle.

To measure the influence of the degree of variability on the modelled species, a simulation was conducted, which varied the degree of variability in each landscape sector. The number of habitats, which last at least as long as the duration of the aquatic stage of the species under optimum food conditions (cf. Chapter 3) was calculated (Table 4.2). As the landscape model was modelled in a one-year cycle, the longest duration of a temporary cell was defined from the filling of the cell in the rainy season to the drying of the cell in the dry season, although the starting point of the simulations was set to the climax of the rainy season.

Table 4.2:   Number of temporary habitats, which may provide completion of the larval stages for the residential and the migrating species in the modelled regions in the "standard" scenario. Results are mean values from 50 simulations of the random drying and rewetting of the cells

variability	migrants				residents			
	no	low	medium	high	no	low	medium	high
Von Bach	140	140	139	139	134	112	102	98
Tsaobis	50	50	49	49	44	38	31	26
Swakopmund	30	29	24	21	20	15	7	4

Consequently the number of cells, which may serve as potential habitats for completion of the larval life cycle, decreased with increasing variability in each landscape sector. In the "von Bach" section and the "Tsaobis" section the number of habitats in which the migrants may complete their life cycle was only marginally diminished, whereas the number of habitats for the residents was highly affected by the increasing variability. For the "Swakopmund" section even the number of habitats for the migrant species was noteworthy reduced. For the residential species the number of habitats was seriously minimised in the "Swakopmund" section.

4.2.4   Building scenarios

4.2.4.1   Climate change

Scenarios of climate change published by the Intergovernmental Panel on Climate Change (IPCC) suppose that in southern Africa the average runoff and water availability will decrease in connection with a global warming (McCarthy et al. 2001). Average temperatures will also increase with the climate change. Interrelated with climate change is a fragmentation of the landscape regarding areas with open water.

During the 20th century a warming of approximately 0.7°C has been recorded. The models of the IPCC predict a further warming of 0.2° C per decade in the low effects scenario and a warming of 0.5° C in the high effects scenario. The impact of this increase on rainfall is not defined as well as the temperatures themselves (Hulme et al. 2001). In intermediate warming

scenarios, which will serve as basis for modelling climate change impacts, precipitation will decrease about 10% in the interior of southern Africa. Additionally the variability of rainfall is supposed to increase. Directly connected to the change of climatic conditions, the desertification process is supposed to accelerate including potential feedback loops because of CO_2 release from dead vegetation.

The forecasts of the IPCC concerning climate change in Namibia serve as basis for the adaptation of the landscape model to build climate change scenarios for the three landscape sectors. The dynamic of the landscape in the model is dependent on the precipitation data in the modelled biomes. Therefore the predicted consequences of the intermediate warming scenario by the IPCC – 10% decrease of precipitation – is applied to existing precipitation data.

The variability of precipitation is supposed to increase. Therefore the degree of variability introduced in Chapter 4.2.3 is shifted towards the northeast of Namibia (cf Table 4.1 and Figure 4.15). The "Swakopmund" section already has a high variability in the standard scenario and is therefore not affected in terms of increasing variability. The "Tasobis" section shifts from medium variability to high variability and the "von Bach" section shifts from low variability to medium variability. Consequences of this change on the local population dynamics can be seen from the analysis presented in Figure 4.16. The number of suited temporary habitats for the migrants is not as much diminished as for the residents due to longer duration of the larval stage. Therefore the latter have fewer habitats available for reproduction with an increasing degree of variability.
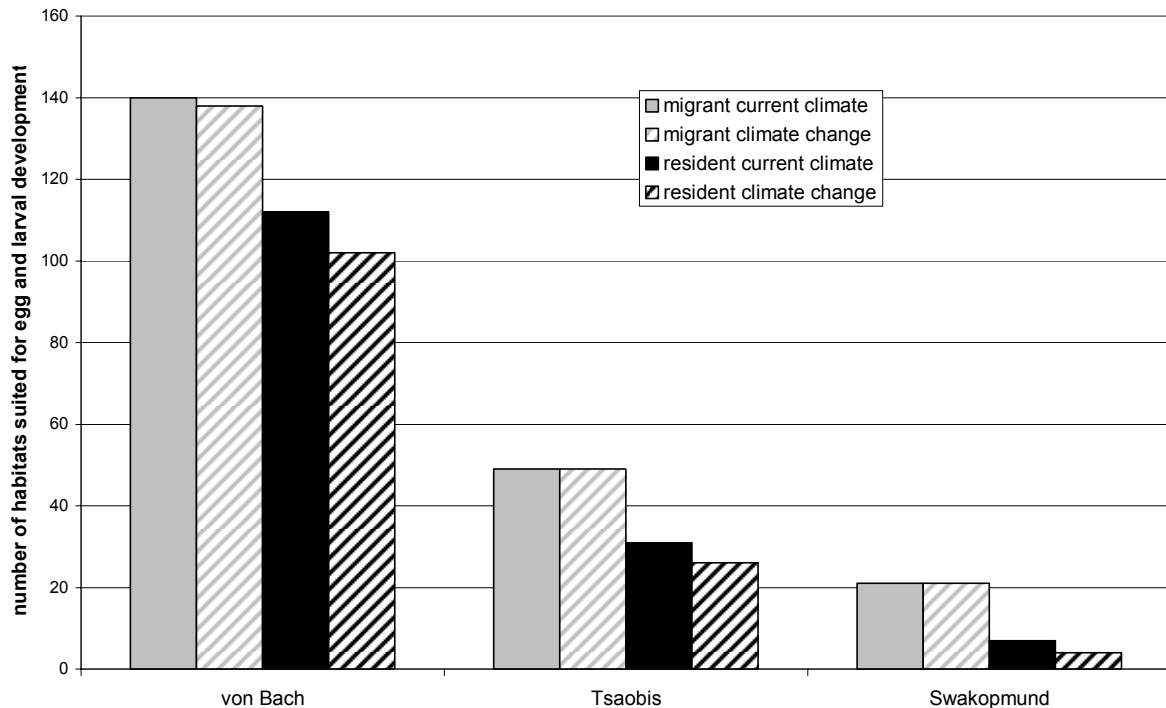
Figure 4.16: Number of temporary habitats suited for egg and larval development in the three landscape sections. Comparison between current climate and climate change scenarios (based on Table 4.2).

Many habitats, especially rainfed farmdams that collect water from the slopes of the riverbed, are situated at the threshold between longer lasting temporary and ephemeral habitats at existing climatic conditions (Suhling, pers. comm). To take this into account, the number of permanent habitats is reduced by 20%, particularly those located in the riverbed. In the first step of the scenario building, these habitats are transformed into temporary habitats. Connected with decreasing precipitation is a decrease of the numbers of habitats themselves as they are mostly supplied by rain. Hence, not only the monthly average precipitation rate but also the number of temporary habitats in the landscape at the climax of the rainy season is diminished by 10%, which is calculated in a second step.

These considerations serve as the basis for the scenarios, which describe the modelled landscape sections in the Swakop River catchment under the influence of climate change. The different landscape layers that were used for the simulation study in the dispersal model can be found in the Appendix (Figures A.6 to A.11). For the following simulations one of the 50 repetitions of the dynamics for each landscape sector has been chosen as the "standard scenario". The scenario, which was chosen, had to meet the requirements to provide the mean number of habitats with the minimum duration for larval development for the migrant species as well as for the resident species (Table 4.2).

4.2.4.2 Theoretical landscapes as a test of the model

Four different types of artificial landscapes have been constructed to investigate effects of certain landscape structures on the distribution of the dragonflies. Connectivity between habitats and the resulting landscape pattern as well as the dispersal abilities of a species play a relevant role in the persistence of a (meta-)population in the landscape (Wiegand et al. 1999; Söndgerath & Schröder 2002). The bases of all four scenarios are two clusters of four cells arranged in a square of 2*2 cells. These clusters have been located in the upper right and lower left corner of the cellular automaton with a distance of 3 cells from the border (Figure 4.17.). The dynamics of the scenarios containing temporary water are modelled in accordance with the standard scenario of the "von Bach" section under current climatic conditions.

Scenario T1 consists of only the two clusters of 4 cells in each corner. With this structure it is proposed to study whether different species types stay isolated because of the relative high distance between the two localities. The scenario T2 consists of a chain of temporary habitats working as stepping-stones across the diagonal between the two permanent localities. The chain of habitats is defined as habitats being located in a riverbed with the consequences of being subject of disturbance on the one hand and having the property "river as guideline" on the other hand. The distance between the two permanent habitats therefore is diminished depending on the seasonal existence of temporary waters. Scenario T3 is similar to scenario T2 with the difference that the temporary habitats are located at the opposite diagonal of the cellular automaton. This scenario has been set up to investigate the importance of stepping stone habitats on the one hand and the mechanism of dispersal along a river course for the residential species 2 on the other hand. This is directed in opposite direction of the permanent habitats in this case. The fourth theoretical scenario, T4, has the same structure as T2 with the difference, that the permanent localities are now defined as being temporary. Consequently, in the dry season a period exists where absolutely no water is in the landscape and consequently also no larvae can survive.
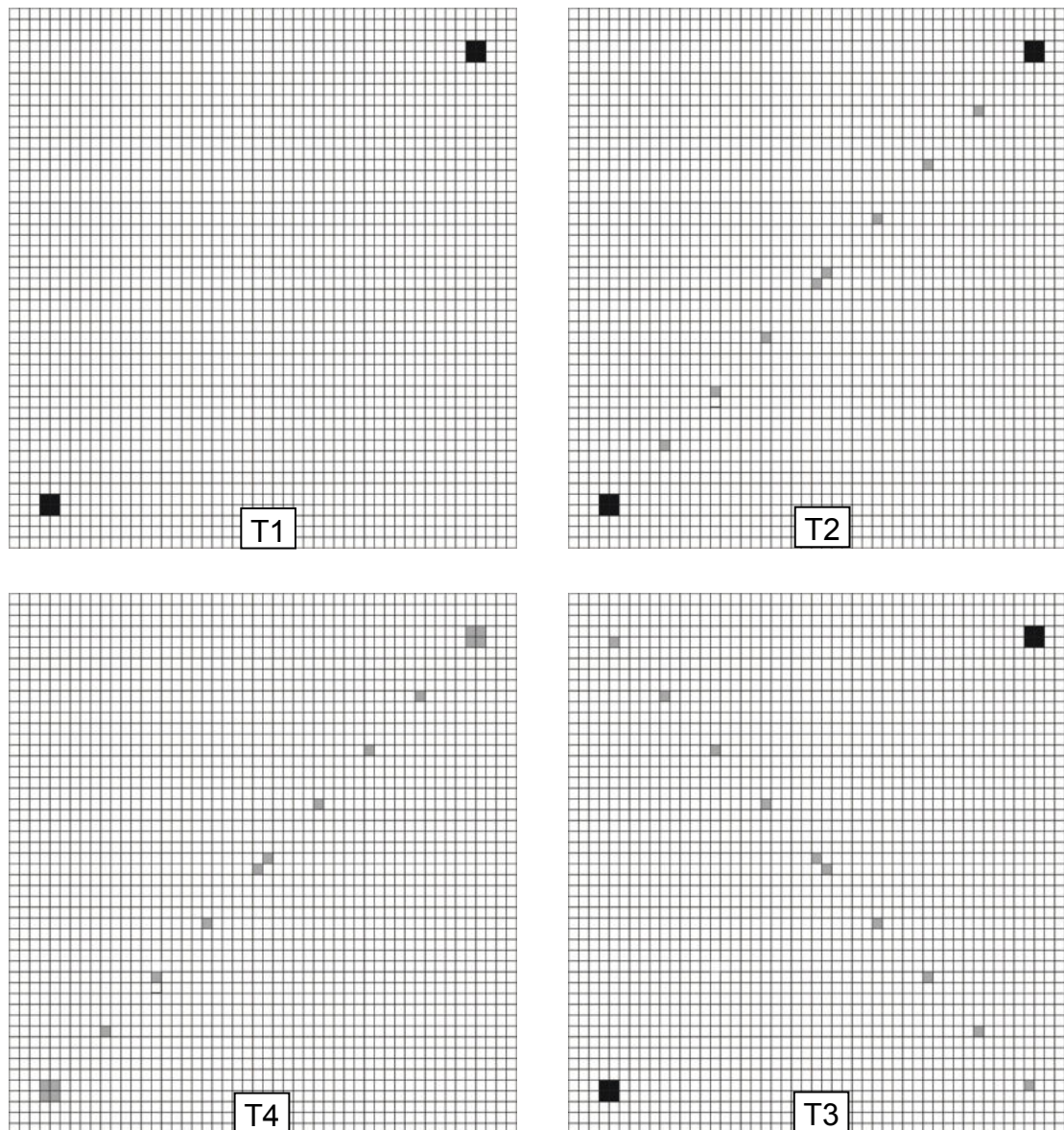
Figure 4.17: Theoretical scenarios. Depicted is the starting point of the simulation (climax of rainy season). Black fields: permanent waters, grey fields: temporary waters. Scenario shortcuts clockwise from upper left corner: T1, T2, T3 and T4.

4.2.5 Discussion

The concept of the dynamically changing landscape pre-determines the patterns of the regional population dynamics of the species (Mackey & Lindenmayer 2001). Residential species with a longer lasting larval stage are naturally more affected by the variability of the habitats than migrating species with shorter larval duration. Certainly, there are much more factors such as temperature, evapotranspiration, wind, geomorphology and geology determining the duration of temporary waters (Williams 1987), but the approach realized here is sufficient to simulate the annual circle of the desiccation respective re-flooding of the waters.

The scale definition is a crucial aspect in the landscape model. As it has been shown in the chapters 1, 2 and 3 of this work, the main processes and factors that determine the local population dynamics are taking place at the habitat scale or, in the case of the habitat suitability models, even at the microhabitat scale. The size of one lattice cell with 1 km² was chosen because the dispersal ranges of the modelled species exceed the scale of the habitat. The disadvantage which results in this change of the model's scale is that each cell in a regularly lattice can only have the state 0 or 1 regarding the presence of water. In fact there may be more than one habitat placed in one km², information that gets lost in the reduction of the scale. The landscape matrix, which is defined as empty, may also comprise resources for the animals as it has been shown for other insects (Dennis 2004) and in simulation studies (Wiegand et al. 2005). This aspect had to be neglected in this modelling approach to keep the model's calculation time in a reasonable range on the one hand and due to lack of further empirical data on the other hand.

4.3 The dispersal model

The spatial distribution of animals depends on a variety of factors. Some of these factors, which promote the presence of the modelled species at a local scale, have been described in Chapter 2. However, habitat choice of dragonflies does not only depend on micro-habitat factors like the aquatic vegetation diversity. Different steps in habitat selection of adult dragonflies have been identified in a so called filter model and set in correlation with a certain flight height (Wildermuth 1994). The first filter is responsible for the biotope selection at a flight height of 5-20 m. The next step is the habitat selection at flight heights of 0.5-5 m while oviposition site selection is correlated with low flight heights of 0-0.5 m. Jonsen and Taylor (2000) emphasise that the movement behaviour of Odonata is dependent on the broader landscape structure. Additionally, the choice of the oviposition site cannot be set equivalent to the assured survival of the larvae in the habitat (Corbet 1999).

Corbet (1999) distinguishes four different types of spatial displacement by flight of Odonata (cf. Table 4.3). Considering the spatial extension of the landscape model, the dispersal in the model belongs mainly to the flight types "commuting", "seasonal refuge" and "migration". With these flight types approximate distances between 10m for the commuting flight and even thousands of kilometres for the migration flight can be reached. The latter is characterised by a lower boundary of the approximate distance of some tens kilometres.

Table 4.3:   Flight types of Odonata (after Corbet 1999)

flight attribute	flight type			
	Maiden flight	Commuting	Seasonal refuge	Migration
approximate distance	<1m to 500 m	10 m to several km	100 m to tens of km	Tens to thousands of km

In addition to these different flight types, dragonflies as well as other terrestrial invertebrates and vertebrates are highly mobile, so their spatial distribution always includes a certain degree of stochasticity (Mackey & Lindenmayer 2001). These two facts have to be incorporated into a function describing the dispersal of the modelled species at the spatial resolution of the cellular automaton as follows.

4.3.1   The dispersal function

The classical approach to measure the dispersal of animals is the mark-release-recapture method, from which dispersal parameters as mean and maximum dispersal distance can be derived (Schneider 2003). However, this approach is difficult to realize when the study object is such a highly mobile organism as an adult dragonfly. Dispersal of animals is always closely

connected with the exchange of genetic information between the local populations (Loxdale & Lushai 2001; Mallet 2001; Whitlock 2004). Both dispersal and gene flow are known to affect long-term survival and evolution of species (Simpkin et al. 2000). To estimate differences between the model species regarding the distance they are able to cover by different flight types according to Table 4.3, it is therefore useful to take genetic data as a measurement of dispersal ability (Watts et al. 2004).

As there is only little empirical data available about the dispersal modes of the three model species at the resolution of the cellular automata, I decided to use a simple mathematical approach, an exponential function (Petersen et al. 1999; Briers et al. 2002), which has also been used for estimation of dragonfly dispersal (Conrad et al. 1999). This function satisfies the requirements of a distribution with an abundance of short dispersal distances and only little long distance dispersal events (Nathan et al. 2003), which is reasonable with regard of the spatial extension covered by the cellular automaton. Other possible distributions especially for the description of long-distance dispersal may be normal distributions for example, which can be combined by using weighted sums (Nichols & Godfrey 1994).

The landscape sectors in the landscape model are limited to a size of 50*50 km (cf. Chapter 4.2.1). Therefore the probability functions that determine the maximum dispersal distance from the cell of origin for each time step are normalized to the extension of the cellular automaton (Figure 4.18 and Equation 4.1). The highest probability of dispersal is given for the nearby cells and it decreases with increasing distance.

The slopes of the functions for the different species were interpolated from population genetic data (Giere 2002; Habekost 2002). These population genetic analyses were conducted on a larger scale, therefore the Hamming distances for the localities (as far as available from the Swakop catchment) were chosen for the comparison of the species. The lower the value of the genetic distance, the higher is the dispersal ability of the observed species. Due to lack of further empirical data, the species-specific dispersal factor for *C. erythraea* was normalized to one, while the parameters of the other species were calculated in relation to *C. erythraea*, resulting in Equation 4.1 for the dispersal-functions. This equation gives the probability of the maximum dispersal-distance for each time-step.

$$p(x) = Exp\left(-\frac{x}{\alpha \cdot \sqrt{\dim}}\right)$$

Eq. 4.1

with:

x   distance from cell of origin

α   species-specific dispersal parameter

dim   dimension of the cellular automaton

For *C. erythraea* α = 1 (0.005/0.005), for *P. flavescens* α = 0.005/0.003 and for *P. genei* α = 0.005./0.009. For the modelled landscape sectors dim = 50.
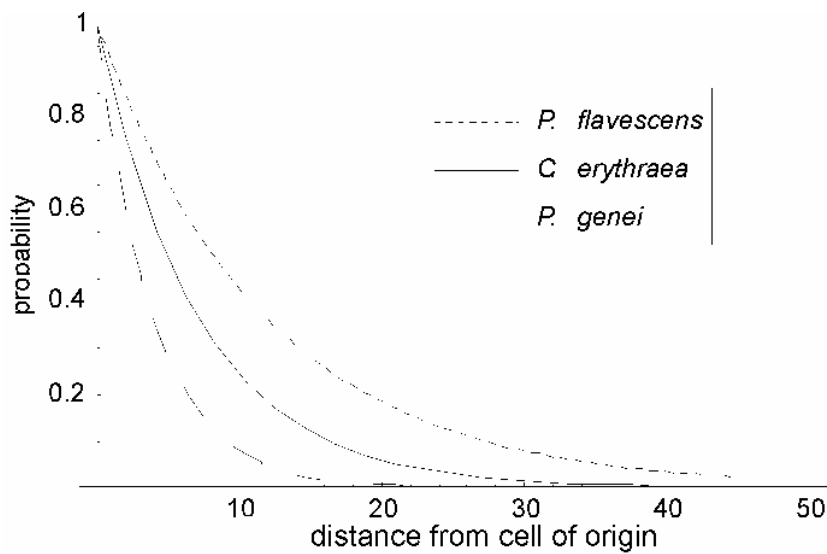
Figure 4.18: Dispersal functions for the three species *P. flavescens*, *C. erythraea* and *P. genei* based on Equation 4.1.

The dispersal distance is determined by an equally distributed random number assigning the probability to travel a specific distance. There are no proofs for a density-dependent dispersal rate of adult dragonflies from their current habitat and also no assured data for a difference of dispersal behaviour between immature and mature adults (Corbet 1999, p. 395). Therefore a random proportion of each age class of immature and mature adults, respectively, is chosen to disperse in the respective time step. The random numbers are equally distributed and the numbers of the migrants are rounded down to the next integer. However, dispersal may increase the risk of mortality (Weisser 2001; Purse et al. 2003). Therefore the proportion of dispersing individuals is reduced by 10% when reaching the destination cell to implement a trade-off between successful colonisation of a new habitat and the risk of dying during dispersal.

4.3.2   The dispersal modes

The dispersal procedure in the model distinguishes two different dispersal modes for each species. Species have the ability to choose between two of the landscape layers realized in the landscape model for the choice of the destination cell.

Generally, all cells within a circle with the radius of the dispersal distance around the cell of origin are analysed with regard to their suitability for immature and mature adults. The destination cell is randomly drawn from all suited cells within the maximum dispersal distance. Depending on the results of the habitat suitability models (HSM) (Chapter 1), for *C. erythraea* and *P. flavescens* the habitat parameter "presence of open water" and "aquatic vegetation diversity" are regarded.

To be able to compare the different dispersal modes of the species a fraction of 70% was defined for the respective major parts of the dispersal while the minor fraction has a probability of 30%. Different combinations of these proportions have been tested and the 70:30 combination has reproduced reasonable results. The important fact of this ratio is that the contrary use of the landscape layers is consistent with the behaviour of the species: The migrant type is known to use habitats regardless of its quality (Corbet 1999; Suhling et al. 2003). With regard to the aquatic vegetation diversity the probability of occurrence of the residential species *C. erythraea* increases with increasing values of the parameter, giving the clue that the quality of the habitat is more important than the solely presence of water.

As for *C. erythraea* the univariate HSM considering the aquatic vegetation diversity led to a R² value of 0.302 this parameter was chosen to determine the main part of the dispersal events of this species. All cells within the radius of the dispersal distance are analysed with regard to a vegetation diversity value at least as high as in the cell of origin. One cell out of the cells with the best suitability is chosen randomly as destination cell.

However, there is more than one factor, which determines the habitat choice of a species as the filter model for habitat selection proposes (Wildermuth 1994). Therefore the choice of a habitat, which is generally suited for reproduction, that means a cell containing water, is also implemented into the model. Due to the relative high R^2_N value for aquatic vegetation diversity the second landscape layer is only regarded to exert influence on a minor fraction of the dispersal events.

For *P. flavescens* no significant model exists concerning aquatic vegetation diversity. However, at least a non-significant HSM for *P. flavescens* could have been calculated.

Therefore for *P. flavescens* a minor part of the dispersal events refers to the landscape parameter aquatic vegetation diversity, again choosing the destination cell in accordance with the HSM. The major fraction of dispersal events takes place only in cells where open waters can be found irrespective of the explicit habitat parameter.

As already stated in Chapter 2, for *P. genei* no HSM concerning aquatic vegetation diversity could be calculated, but the species prefers habitats located in a river. Therefore the landscape parameter "existence of rivers as guidelines" has been chosen to be responsible for the major fraction of the dispersal events for *P. genei*, the minor part is orientated along habitats without special habitat characteristics. Again, the ratio 70:30 has been chosen for reasons of comparability with the other two species.

4.3.3   Landscape metrics: distance of the nearest cell containing water

One important measure for the potential survival of a metapopulation in the landscape is the ability to reach suited habitats in a certain distance from the habitat of origin during the dispersal process (Fahrig & Paloheimo 1988; Hanski & Gaggiotti 2004; With 2004). One value that can be used to describe this fact is the proportion of habitats, which are difficult to reach for the focal species. The distance at which habitats are defined as "hard to reach" is determined by the dispersal function.

For each weekly snapshot of the landscape layer "presence of open water" the distance of each cell containing water to the nearest cell that also contains water has been determined. This results in the number of cells whose next neighbour can be found in a certain distance for each week of the simulation. The proportion of more distant neighbourhood cells increases through the drying of the habitats due to the decline of the rainy season. This process can be seen in analogy to fragmentation by habitat destruction in the landscape.

The distance at which maximally 10% of all dispersal events are taking place, D_{10} (distance travelled by 10%), has been chosen at the basis of the dispersal functions (Equation 4.1) (Kovats et al. 1996; Petersen et al. 1999; Petersen et al. 2004). The proportion of cells whose neighbours are further away than this distance has been calculated for each species, each weekly snapshot and each landscape (Figure 4.19 to Figure 4.21).
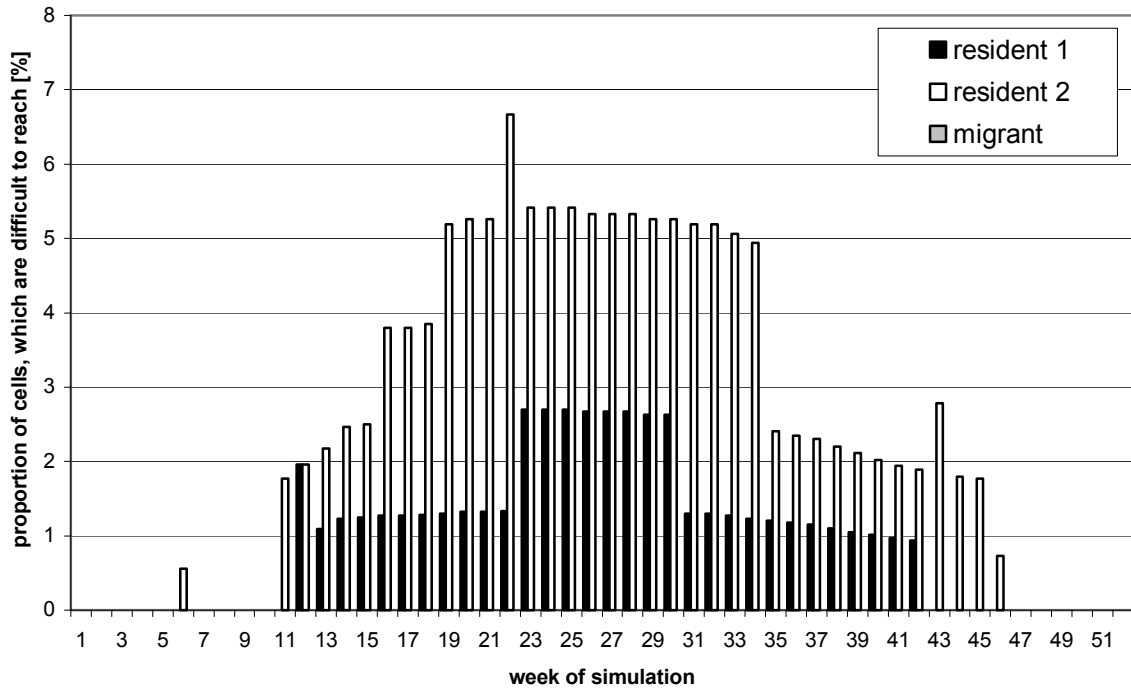
Figure 4.19: Proportion of cells, which can be reached in only 10% of all dispersal events. Scenario: standard climatic conditions, landscape section: "von Bach". The values for the migrant were zero for the whole simulation time.
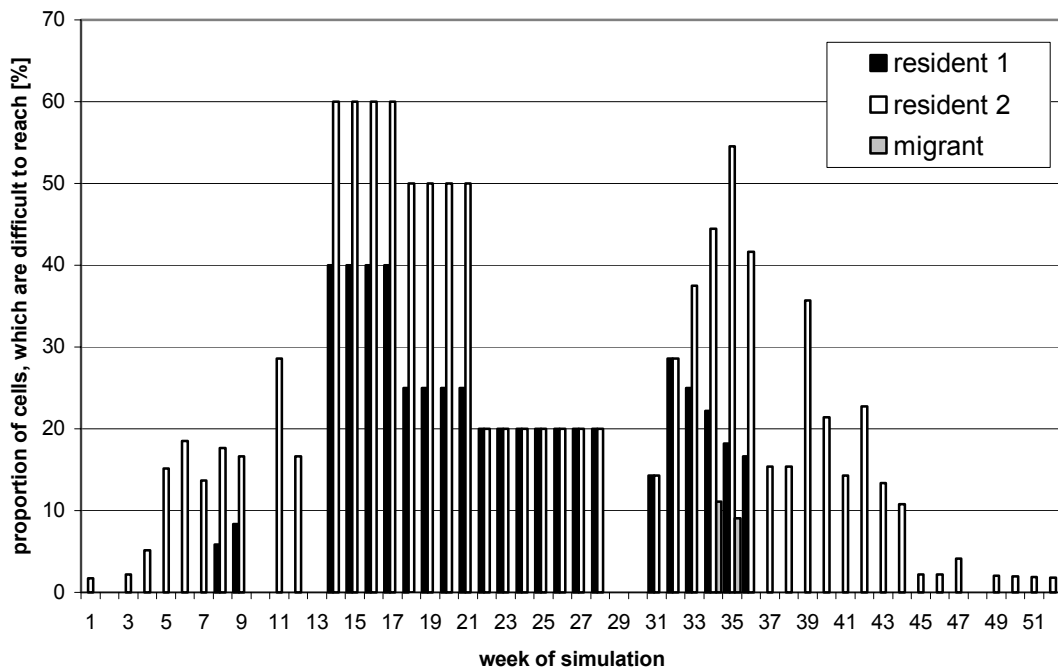
Figure 4.20: Proportion of cells which can be reached in only 10% of all dispersal events. Scenario: standard climatic conditions, landscape section: "Tsaobis"
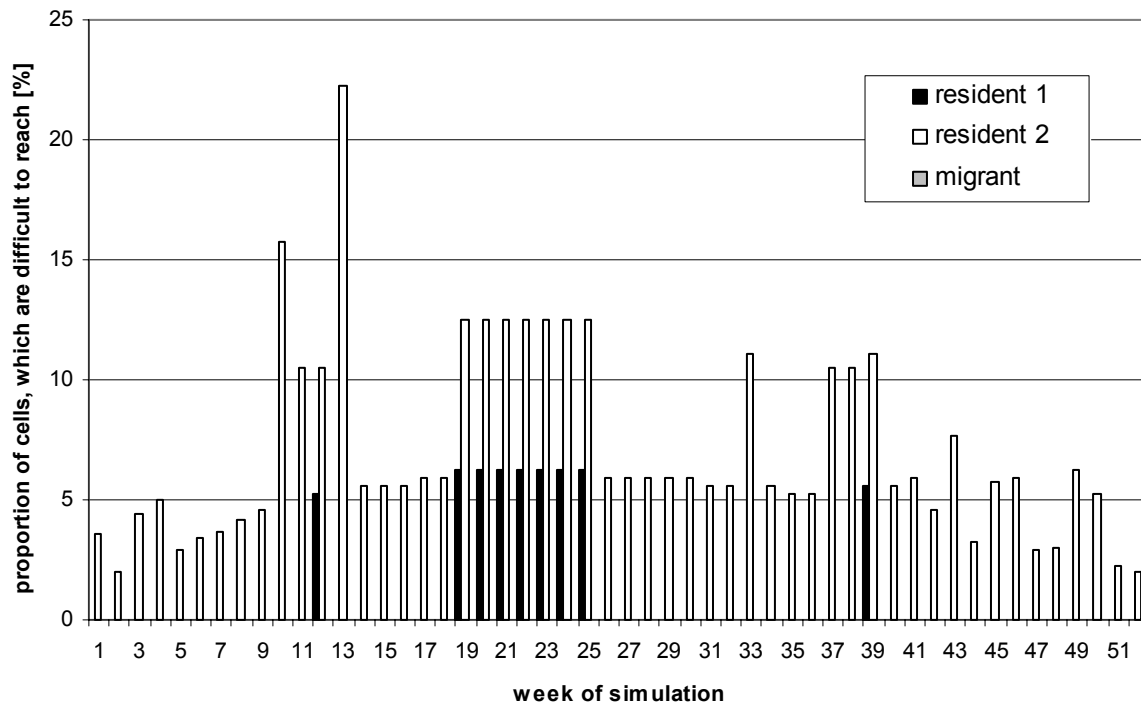
Figure 4.21: Proportion of cells which can be reached in only 10% of all dispersal events. Scenario: standard climatic conditions, landscape section: "Swakopmund". The values for the migrant were zero for the whole simulation time.

The proportion of cells, which were difficult to reach by the definition of 10% of all dispersal events, was low throughout the year in the von-Bach scenario. The migrant species therefore was not affected at any time of the simulation, while for the resident 2 with the poorest dispersal ability values up to 7% of all cells occurred. The time span in which the resident 1 was impaired by its dispersal abilities was a little lower than that of the resident 2. In the "Tsaobis" landscape section for resident 2 there existed a high proportion of cells, which were difficult to reach throughout the simulation year, while the resident 1 was only affected in the dry season. Even for the migrant a short time span (2 weeks) existed in which a proportion of about 10% of the cells were difficult to reach. In the "Swakopmund" section the relative values were lower than in the "Tsaobis" section and again the migrant was not affected at all while some cells were hard to reach for the resident 2 throughout the year.

Discussion

Even by neglecting potential habitat preferences, which may additionally limit the distribution of the species, the combination of landscape dynamics and dispersal abilities showed that the residential species with the most limited dispersal capability was highly affected by the seasonal fragmentation of the landscape accompanied by the desiccating waters.

Fragmentation generally is supposed to have high influence on the habitat specialists while habitat generalists are not much affected by fragmentation (Biedermann 2004).

The scenario for the Nama Karoo has got the highest proportion of cells, which were difficult to reach, although it could have been expected that the Namib Desert scenario would be the section with the most difficult spatial arrangement of habitats for the poorer dispersers. This can be explained by the more linear structure of the habitats in the "Swakopmund" section compared to those in the "Tsaobis" section and consequently a smaller distance between the habitats.

Another factor, which may strengthen this effect, is the increasing variability of the ephemeral habitats. This variability may lead to cells which only exist for a very short time but which may be located in a better spatial arrangement regarding the distance from one habitat to each other. This may also explain the 2 week gap in the "Tsaobis" section at simulation week 29 and 30 (cf. Figure 4.20).

The dispersal model focuses only on three 50*50 km sections of the landscape and no sufficient information to quantify the long-distance dispersal beyond the extension of these sections has been available. Therefore the borders of the cellular automata were considered as closed for adult dragonflies. This reflects the situation of an equilibrium between adults which emigrate from one sector and adults which immigrate in the same time step from outside the sector.

However, one mechanism that is supposed to promote coexistence of competing species is a trade-off in the life-history of the species. Superior competitors have to be limited in some way in comparison with the inferior competitor (Amarasekare 2003). The migrating species *P. flavescens*, belonging to the ecological group 1 is supposed to follow the Intertropical Convergence Zone (ITCZ) (Corbet 2003), resulting in a seasonal phenology (cf. Table 1.3). These migration movements are beyond the scale of the modelled sections. One solution of this problem would be a linkage between the single cellular automata by far distance dispersal. However, this could not have been implemented due to the lack of empirical data. Therefore an indirect implementation of the seasonal phenology has been chosen. A reduction of the number of offspring of the migrant species has been introduced in the dispersal model by coupling the fertility of the migrant with a factor determined by a sine function with its maximum of one at the climax of the rainy season. The minimum of the sine function is at zero at the climax of the dry season. However, there is also no empirical evidence for this function but the number of adults of *P. flavescens* in the rainy season is much higher than in

the dry season (Suhling, pers. comm.) and therefore this approach is useful to reproduce the observed patterns.

4.3.4   Simulations based on the theoretical scenarios

The theoretical scenarios (Chapter 4.2.4) serve as a test of the model's plausibility and may help to answer questions regarding the importance of certain spatial structures and isolation effects on the persistence of the species in the landscape. In all modelled theoretical scenarios the initial population was 200 adults of each species positioned in the permanent habitats clusters (respective temporary habitat clusters in scenario T4) in the upper right and lower left corner of the cellular automaton (Table 4.4). Simulation time has been one year with a 20fold repetition of each simulation. The simulations started at the climax of the rainy season. Displayed are mean results from the repeated runs.

Table 4.4:   Modelled variations for the theoretical scenarios. R1: resident 1, R2: resident 2, M: migrant. The entries indicate the interacting species pair

T1	T2	T3	T4
R1_R2	R1_R2	R1_R2	R1_R2
R1_M	R1_M	R1_M	R1_M
R2_M	R2_M	R2_M	R2_M

Scenario T4

In this scenario all species combinations (R1_R2, R1_M, and R2_M) led to the extinction of all species due to a relatively long phase in the dry season with no habitat present at all in the cellular automaton. This result can be seen as a kind of plausibility test of the model as the number of initial adults was too low to survive the drought.

Scenario T1

In this scenario, the question was to what extent the dispersal of the species was responsible for potential isolation by distance. The results clearly show that both of the residential species were not able to establish a population in the opposed habitat cluster due to their low dispersal ability. The migrant species was able to reach this locality in both simulations R1_M and R2_M, but in both cases only with low population density (Figure 4.22).

a)

b)

c)
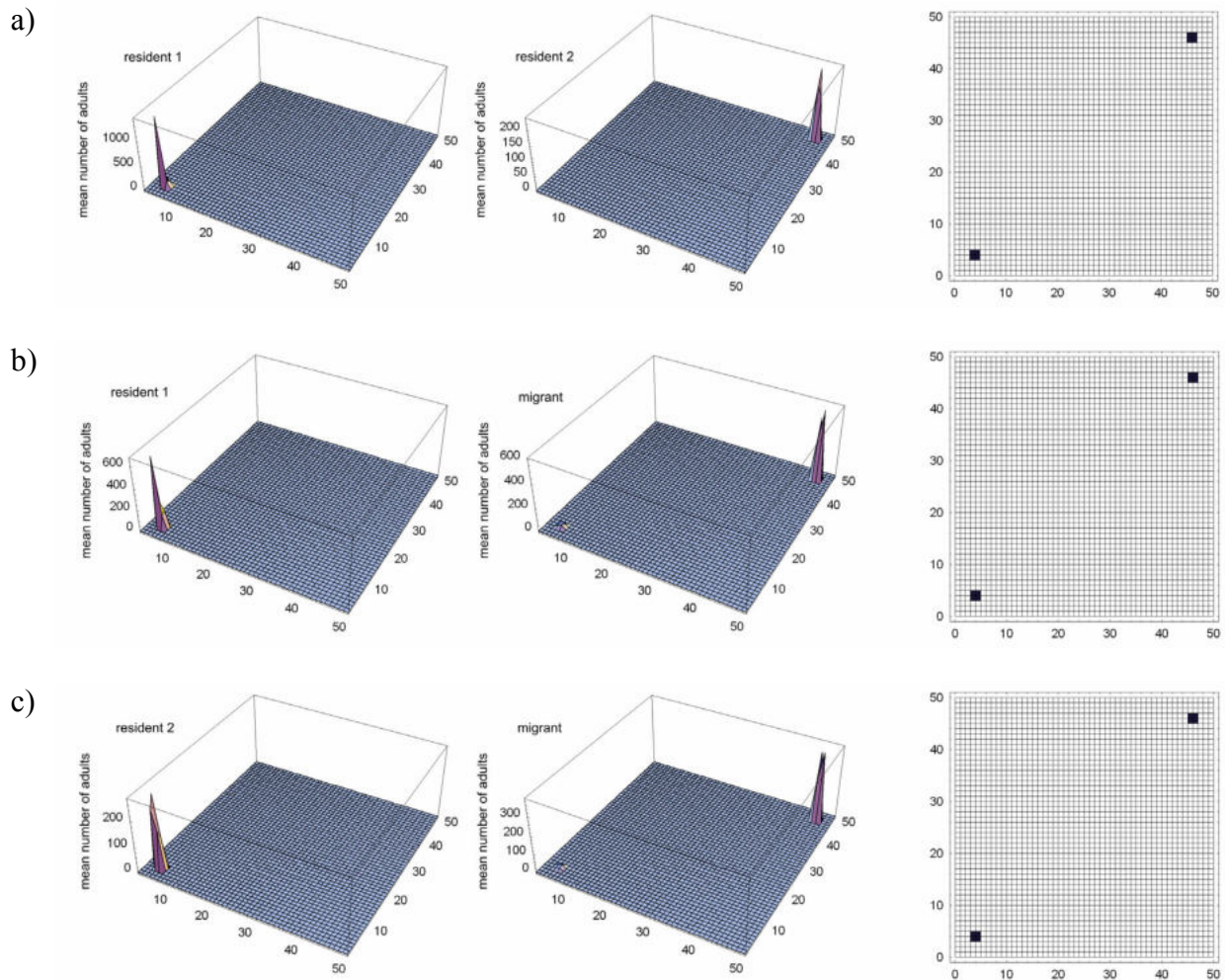
Figure 4.22: Simulation results for the T1 scenario. a) R1_R2 b) R1_M c) R2_M. Displayed are mean numbers at the end of the simulation.

Scenario T2

This scenario emphasised the importance of well vegetated permanent habitats for the resident 1. Despite the existence of temporary habitats along the chain of stepping stones the residential species was concentrated in the cell with the highest aquatic vegetation diversity in the south-western corner (Figure 4.23). This concentration may be explained by the species' medium dispersal ability, which enabled the resident 1 to reach habitats with better properties according to the habitat preferences even from habitats located in a greater distance. Hence, this cell can be seen as a kind of refuge for resident 1. The resident 2 was not able to use the habitats along the chain of stepping stones for reaching the second permanent cluster in the opposite corner of the cellular automaton in both simulations (R1_R2 and R2_M) despite the fact that the stepping stone habitats were defined as preferred habitats. This seems to be a combination of low dispersal ability and a relative long phase of dry ephemeral habitats in the dry season. The migrant's focus population stayed in the cluster of origin but due to high

dispersal abilities this species was able to reach the opposite habitat cluster and to establish a population especially in the scenario R1_M.

a)

b)

c)
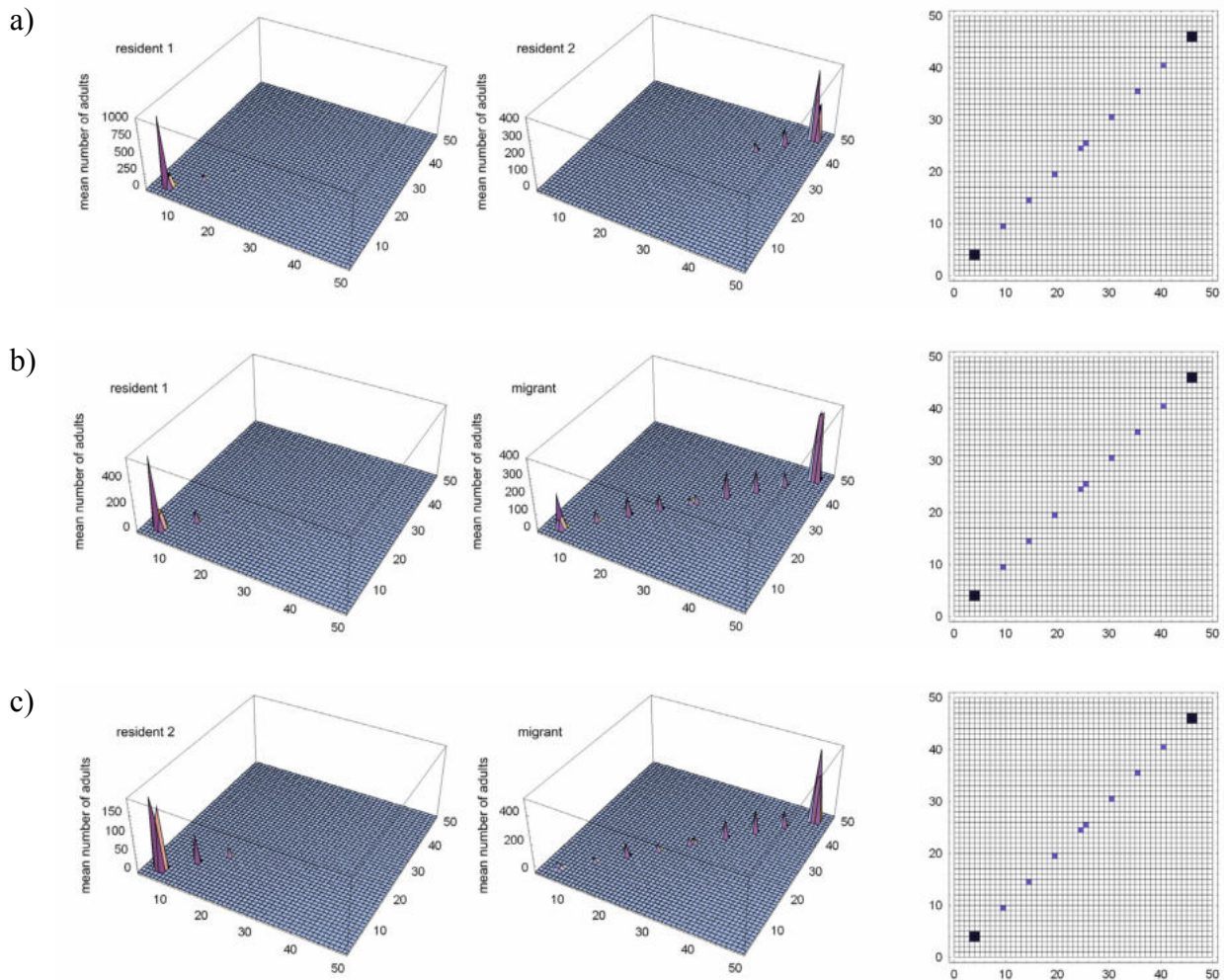
Figure 4.23: Simulation results for the T2 scenario. a) R1_R2 b) R1_M c) R2_M. Displayed are mean numbers at the end of the simulation

Scenario T3

The intention in setting up this scenario has been to investigate if the residential species 2 is able to use a river with ephemeral habitats, which is located orthogonal to the axis between the two permanent habitat clusters. The results of the simulation study T2 have shown that even the ephemeral habitats along the axis between the permanent cells are not sufficient for the resident 2 to reach the other permanent cluster, therefore the results of this study are not displayed further.

4.3.5 Simulations based on the landscape sections

For each of the three landscape sections and each pair of species a 20-fold repeated simulation with the scenario based on the current climatic conditions was conducted. The initial

population of these simulations was the result of a one-year simulation with the same scenario as the repeated simulation. For each species 200 mature individuals were equally distributed over cells, which were known as a habitat of the species from the monitoring programme. The distribution of the species at the end of the initial year was taken as initial population for the repeated runs. The simulation started at the climax of the rainy season. Mean sums of the egg stage, the larval and the adult stages for each simulation week were recorded. Additionally to the spatial pattern, the overall average density of individuals per cell and the metapopulation size were calculated to get knowledge of the total population of the species in the respective landscape sector. Table 4.5 provides an overview of the modelled variations for the spatially explicit dispersal model. The given shortcuts for the scenarios will be used in the following sections, for example "von Bach_R1_R2_s" refers to the scenario in which the two residential species were modelled under the standard scenario in the "von Bach" region.

Table 4.5:   Modelled variations of the dispersal model in the three landscape sections. R1: Resident 1, R2: Resident 2, M: Migrant. The first two entries denote the interacting species pair, the last entry denotes the climatic boundary scenario: s: standard scenario, cc: climate change scenario.

von Bach		Tsaobis		Swakopmund	
R1_R2_s	R1_R2_cc	R1_R2_s	R1_R2_cc	R1_R2_s	R1_R2_cc
R1_M_s	R1_M_cc	R1_M_s	R1_M_cc	R1_M_s	R1_M_cc
R2_M_s	R2_M_cc	R2_M_s	R2_M_cc	R2_M_s	R2_M_cc

The focus of the analysis will be on the landscape sections "von Bach" and "Tsaobis" as they were supposed to change in their variability according to the climate-change simulation procedure and were therefore suited well for a comparison. For each simulation the situation at the climax of the dry season and at the end of the rainy season (= after a one year simulation) will be displayed. For "von Bach" the climax of the dry season with no ephemeral waters left was reached in the 23rd simulation week and for "Tsaobis" in the 18th simulation week. The same holds true for the simulations with the climate change scenarios described later.

4.3.5.1   Standard scenarios

Scenario R1_R2_s

For the "von Bach" section the spatial distribution of the adults in the landscape showed a clear preference of the resident 1 towards the well-vegetated permanent habitats, represented

by the outlets of the dams in the north-east and south-west corner of the cellular automaton, especially during the rainy season (Figure 4.24). In both displayed situations the residential species 2 reached lower densities. The focus of this species was in the area of the S. von Bach dam in the north-east corner in the dry season and a second focus in the area of the Swakoppoort dam in the rainy season with the river bed serving as stepping-stone habitats with lower density. In permanent waters located away from the river course no population of the resident 2 worth mentioning was able to establish.

Generally, the same pattern can be seen for the simulation of the "Tsaobis" scenario. The relatively well-vegetated habitats, which were located away from the Swakop river course, were preferred by the resident 1 in the rainy season. Resident 2 mainly could be found in habitats located near the river course in the southern part of the section (Figure 4.25).

In both simulations the resident 2 reached lower densities in the dry season as well as in the rainy season, but the difference between the two species seemed to increase with advancing simulation time.
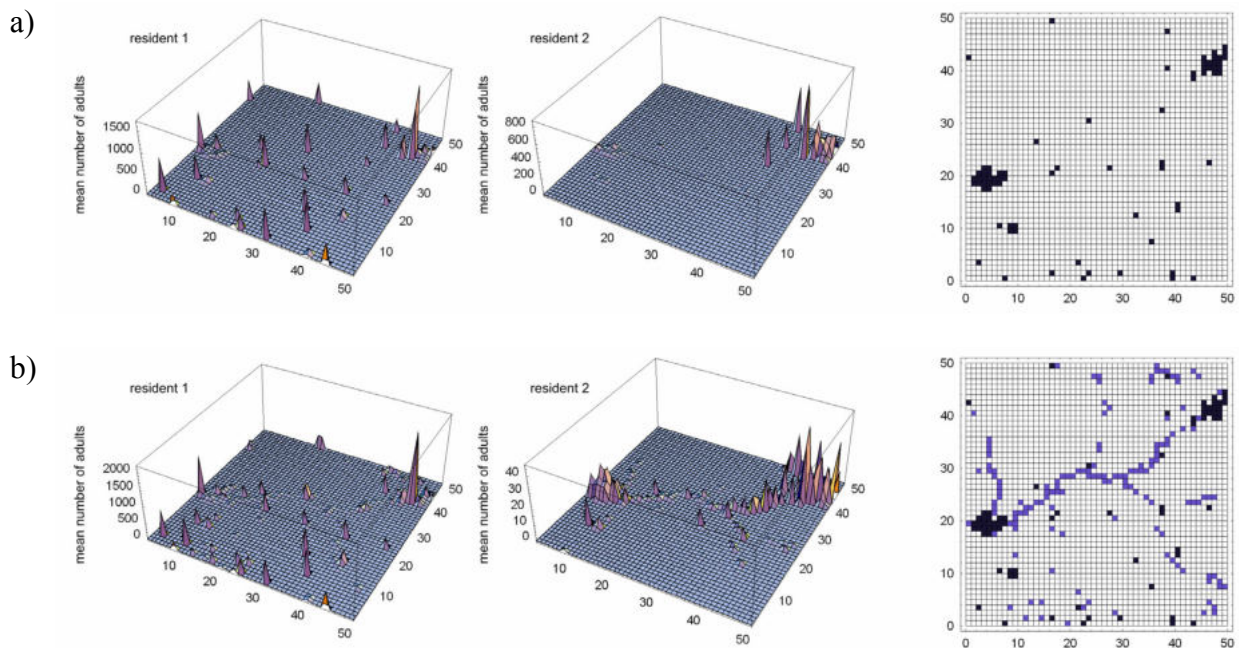
Figure 4.24: Results for the von Bach_R1_R2_s simulation. a) climax of dry season b) climax of rainy season (end of simulation).

a)

b)
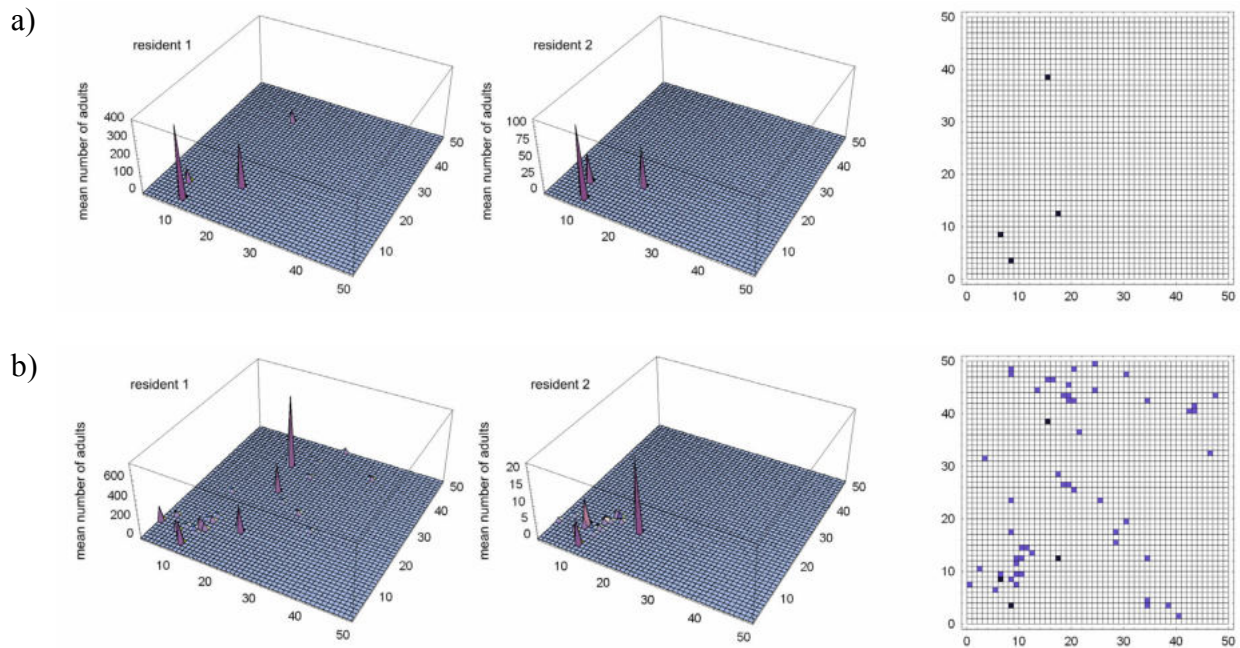
Figure 4.25: Results for the Tsaobis_R1_R2_s simulation. a) climax of dry season b) climax of rainy season (end of simulation).

To describe the difference between the species' densities, the mean densities of each stage of the metapopulations in the respective landscape sector for the whole simulation time were calculated (Figure 4.26 and Figure 4.27). While the density of the residential species 1 in the von-Bach scenario increased relatively constant, the resident 2 experienced a continuous decrease in the metapopulation density. In the "Tsaobis" section the temporal pattern of increasing and decreasing densities was the same but with more distinct peaks during the year. Common to both landscape sections was the much higher density of the resident 1 in each stage.
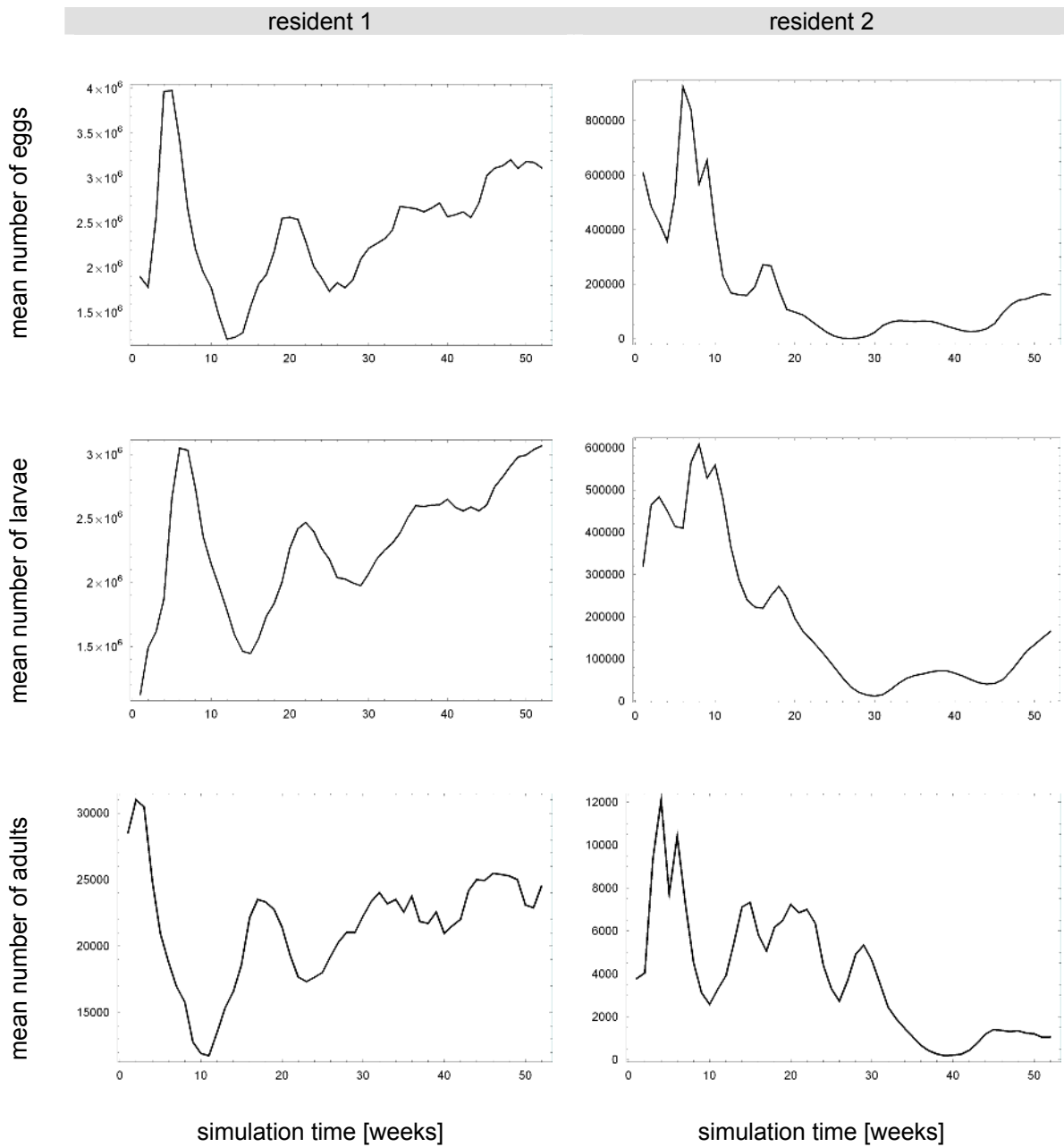
Figure 4.26: Mean numbers of individuals in the different stages during the simulation. Scenario: von Bach_R1_R2_s.
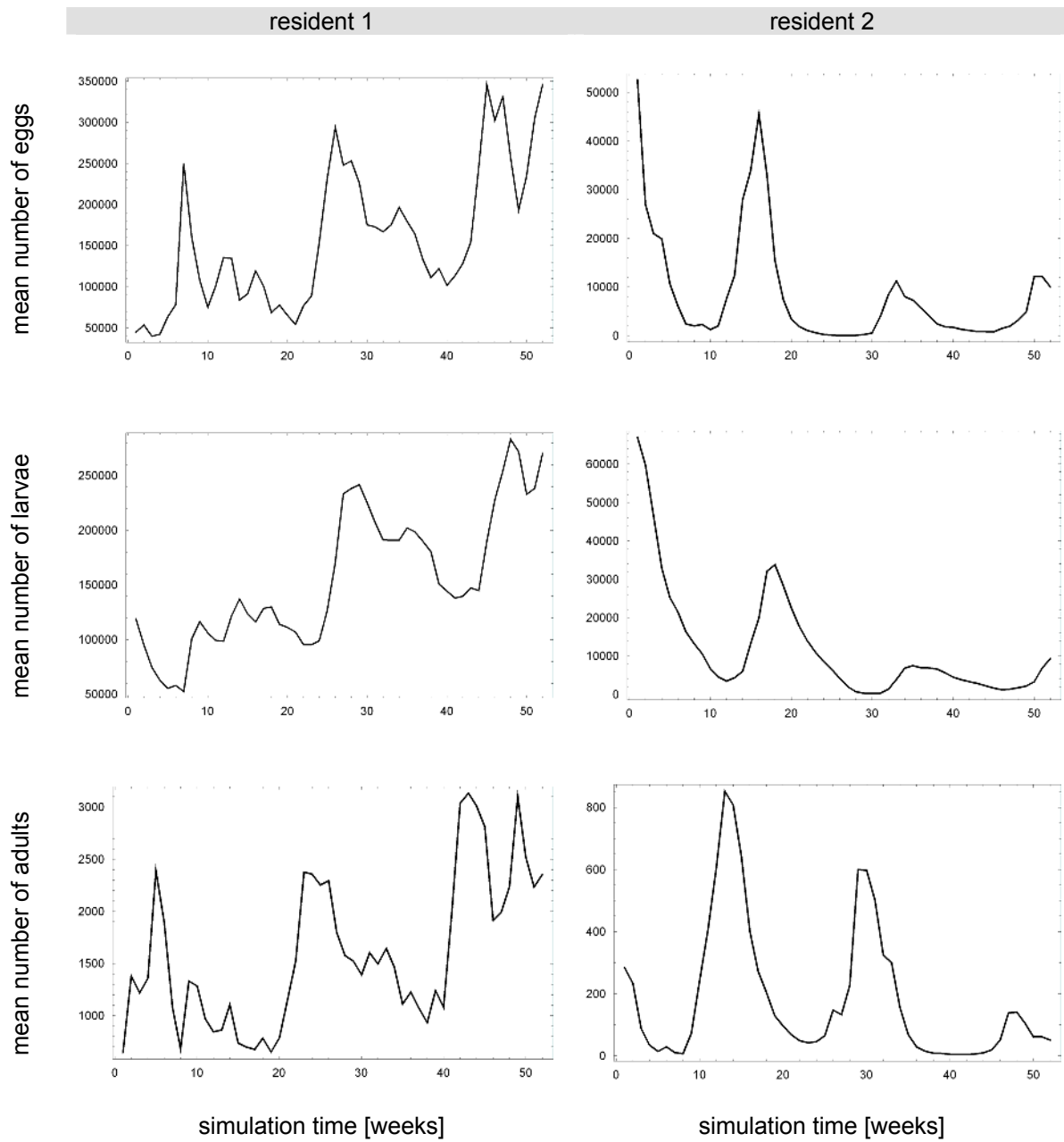
Figure 4.27: Mean numbers of individuals in the different stages during the simulation. Scenario: Tsaobis_R1_R2_s.

Scenario R1_M_s

For this scenario, in the "von Bach" section the resident 1 developed peaks with high adult population densities in the permanent habitats with high aquatic vegetation diversity in both displayed situations (Figure 4.28). Even in the rainy season when habitats were provided along the river course the main areas of distribution of the adults were permanent habitats. The migrant species was more or less equally distributed over the landscape in the dry season as well as in the rainy season. In the rainy season the migrant was able to make use of the ephemeral habitats existing along the Swakop River. The "Tsaobis" scenario also showed a similar pattern for the resident 1 as in the scenario R1_R2_s, but with lower densities (Figure 4.29). The migrant species was able to disperse over the whole landscape section and used even the habitats located in the north-east corner, which were not used by any of the local populations of the residential species 1.
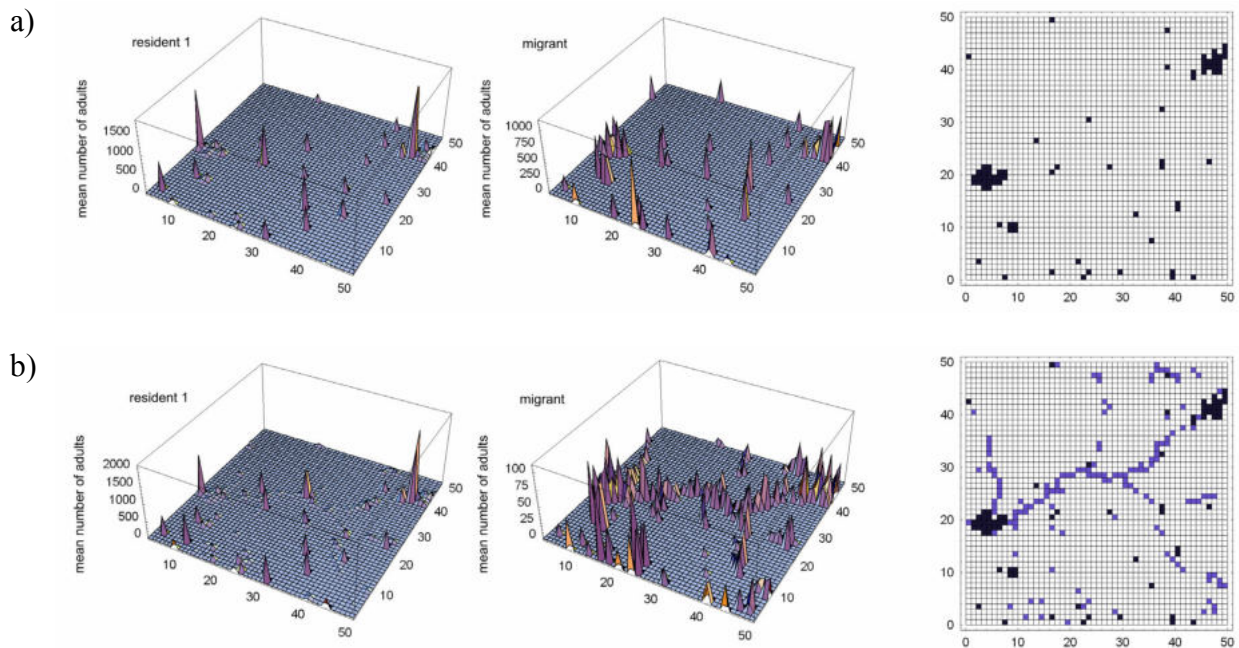
Figure 4.28: Results for the von Bach_R1_M_s simulation. a) climax of dry season b) climax of rainy season (end of simulation).

a)

b)
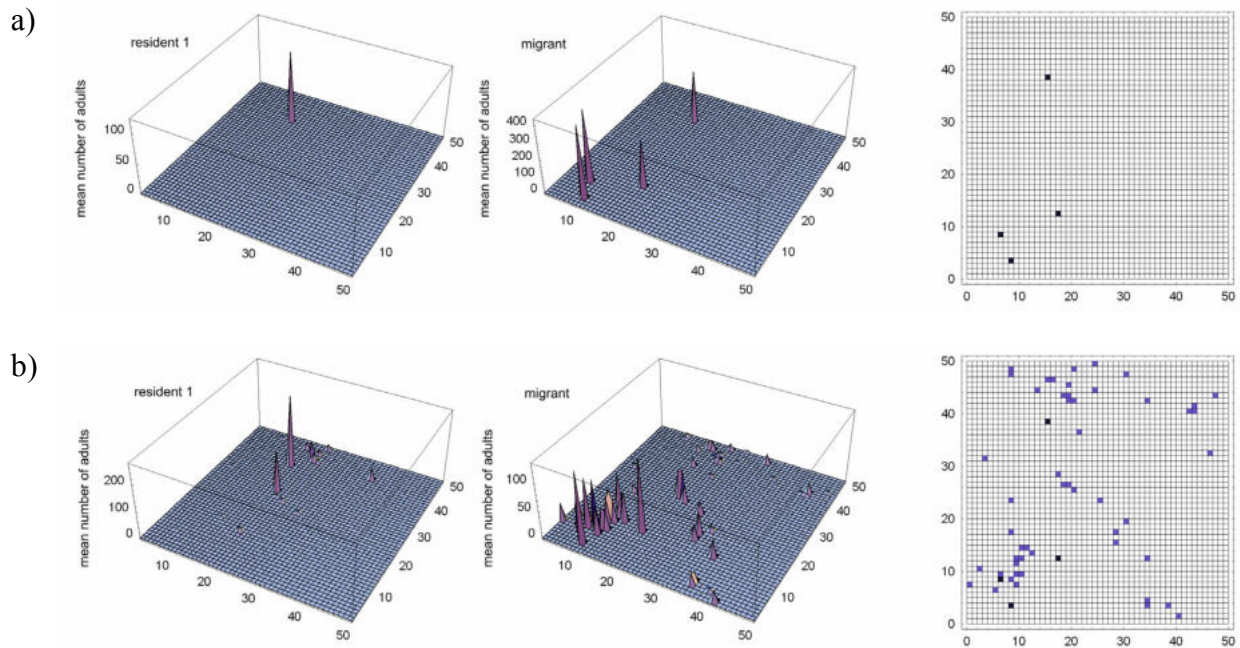
Figure 4.29: Results for the Tsaobis_R1_M_s simulation. a) climax of dry season b) climax of rainy season (end of simulation).

The analysis of the metapopulation structure throughout the simulation year showed that the fertility reduction of the migrant (cf. Chapter 4.3.3) led to a decrease from relative high population densities at the beginning of the simulation during the dry season in both landscape sectors. The resident 1 without implementation of this fertility reduction was able to reach higher population densities in the dry season (Figure 4.30 and Figure 4.31). The main difference between the two landscape sections was that in the "von Bach" section the migrant was not able to recover as good from the decrease in population density as in the "Tsaobis" section.
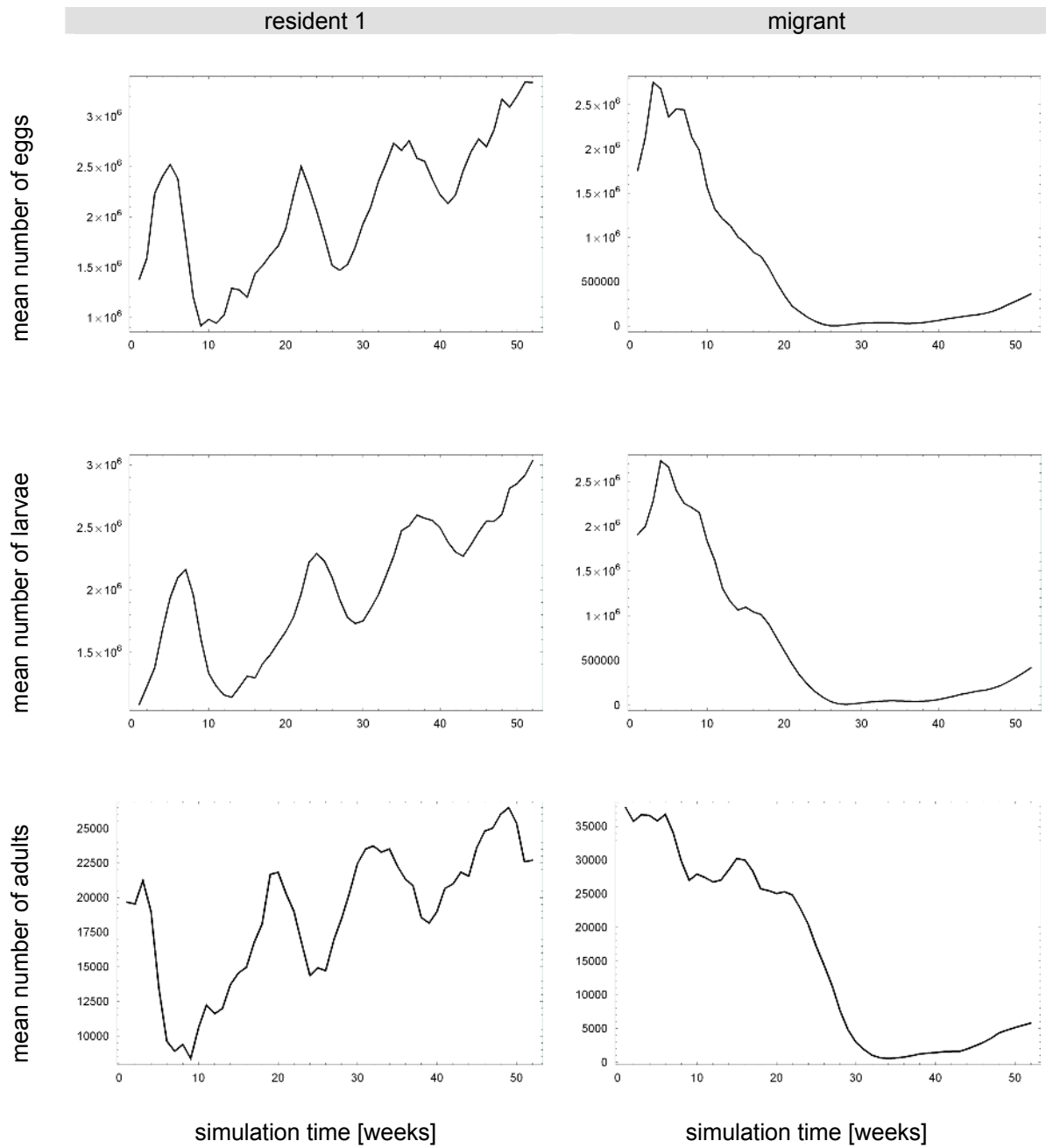
Figure 4.30: Mean numbers of individuals in the different stages during the simulation. Scenario: von Bach_R1_M_s.
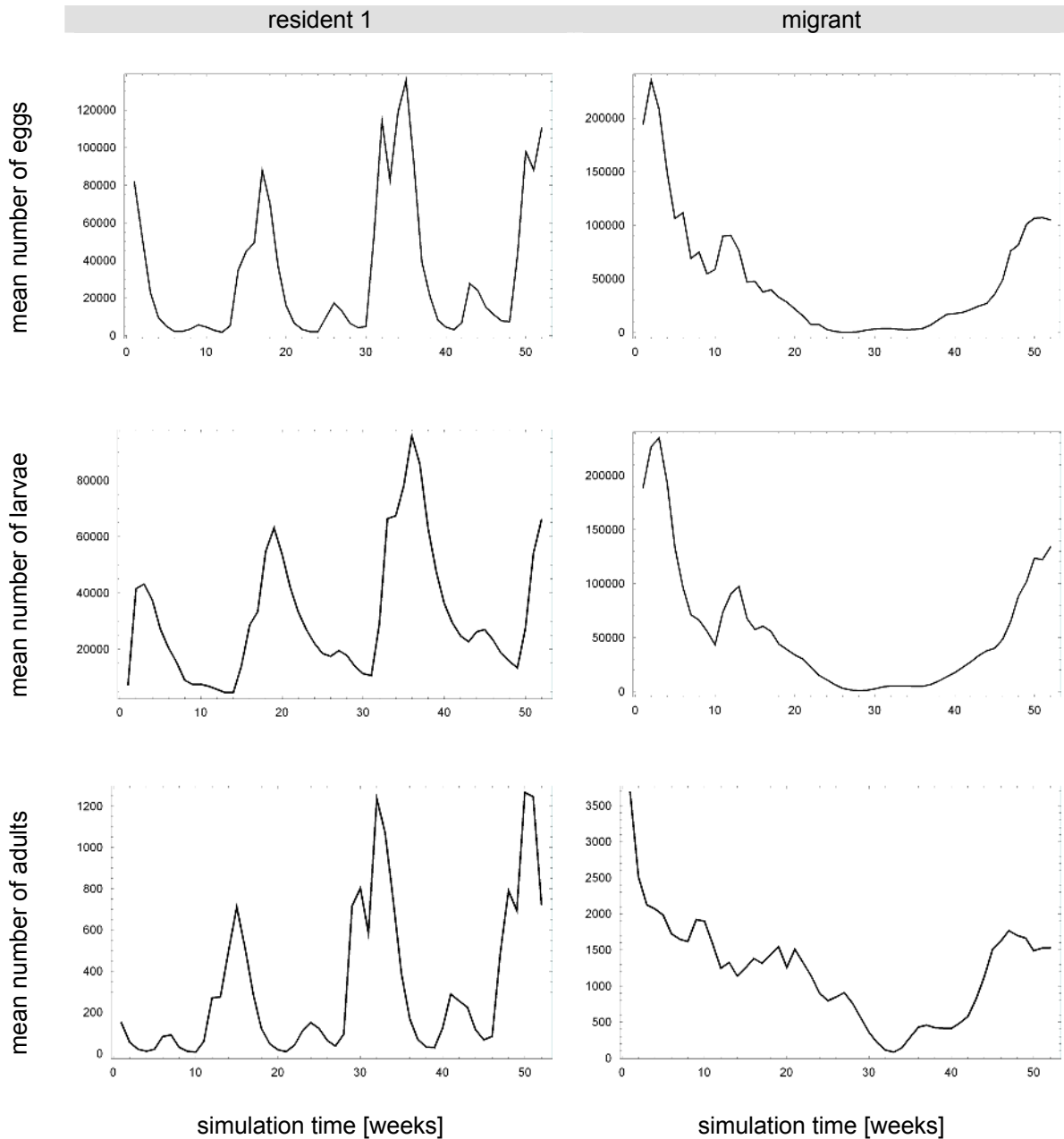
Figure 4.31: Mean numbers of individuals in the different stages during the simulation. Scenario: Tsaobis_R1_M_s.

Scenario R2_M_s

In the "von Bach" region this scenario resulted in a concentration of the resident 2 in the area around the S. von Bach dam in the northeast corner of the section throughout the year (Figure 4.32). In the rainy season situation there were cells downstream of the Swakop River course occupied by this species but only in low densities compared to the S. von Bach dam. The migrant again dispersed over the whole landscape section but with lower densities in the northeast corner. In the rainy season, the population densities of the resident 2 were in the same dimension as those of the migrant. The "Tsaobis" section showed a similar pattern in the spatial distribution (Figure 4.33). In the rainy season situation the migrant reached higher

densities in the northern part of the landscape section and lower densities in the southern part, whereas resident 2 with habitat preferences towards the presence of rivers as guidelines focused in the southern part of the cellular automaton where the river bed of the Swakop River was located. The densities of the migrant were higher than those of the resident 2.

a)

b)
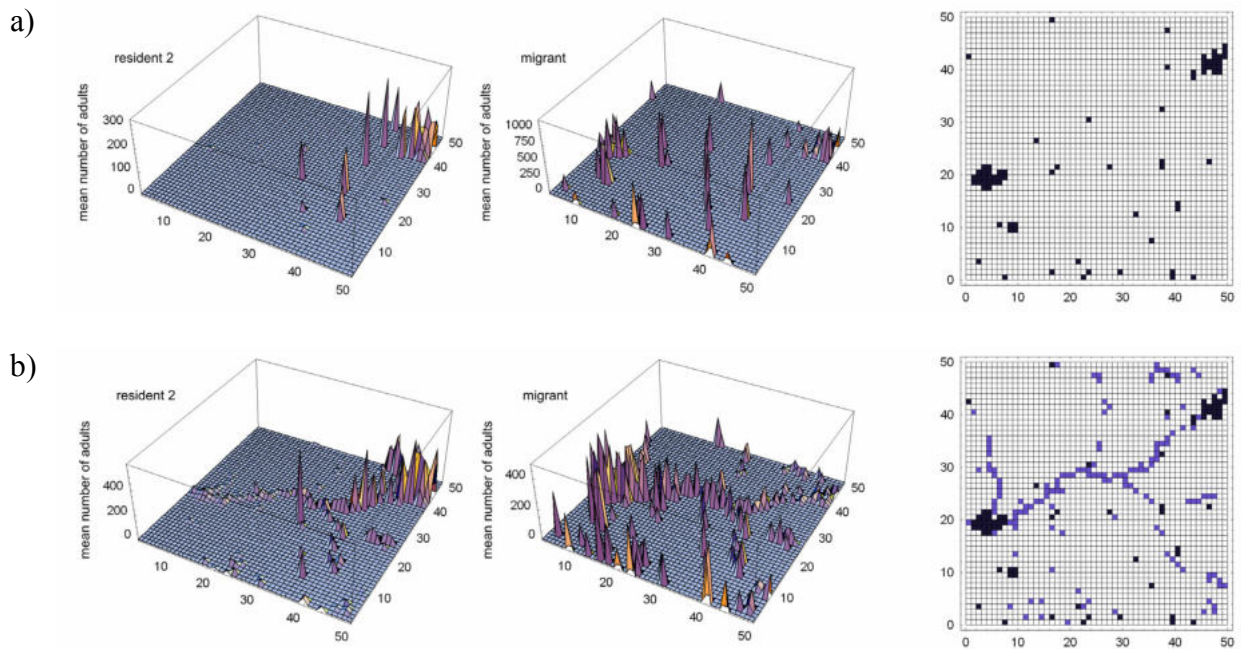
Figure 4.32: Results for the von Bach_R2_M_s simulation. a) climax of dry season b) climax of rainy season (end of simulation).

a)

b)
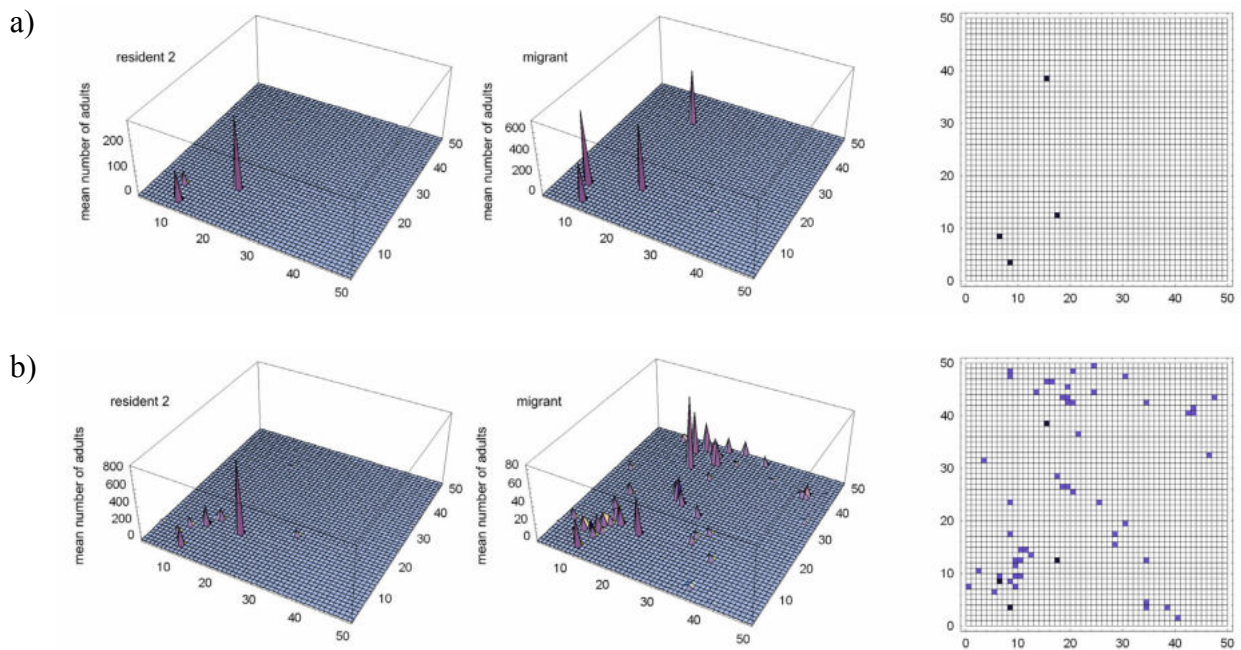
Figure 4.33: Results for the Tsaobis_R2_M_s simulation. a) climax of dry season b) climax of rainy season (end of simulation).

As for the R1_M_s scenario the fertility reduction of the migrant in the dry season led to a clear decrease in the average population density while the resident 2 without a seasonal phenology was able to develop throughout the simulation time (Figures 4.34 and Figure 4.35). In the "von Bach" section both species reached metapopulation densities more than 10 times higher than in the "Tsaobis" section. In the "Tsaobis" section the resident 2 seemed to have a slight increase in metapopulation density while the migrant's densities were lower at the end of the simulation year than at the beginning. The trend of a metapopulation increase for the resident 2 was not observed in the "von Bach" section, while the population density curve of the migrant had a similar shape as the one of the "Tsaobis" section.
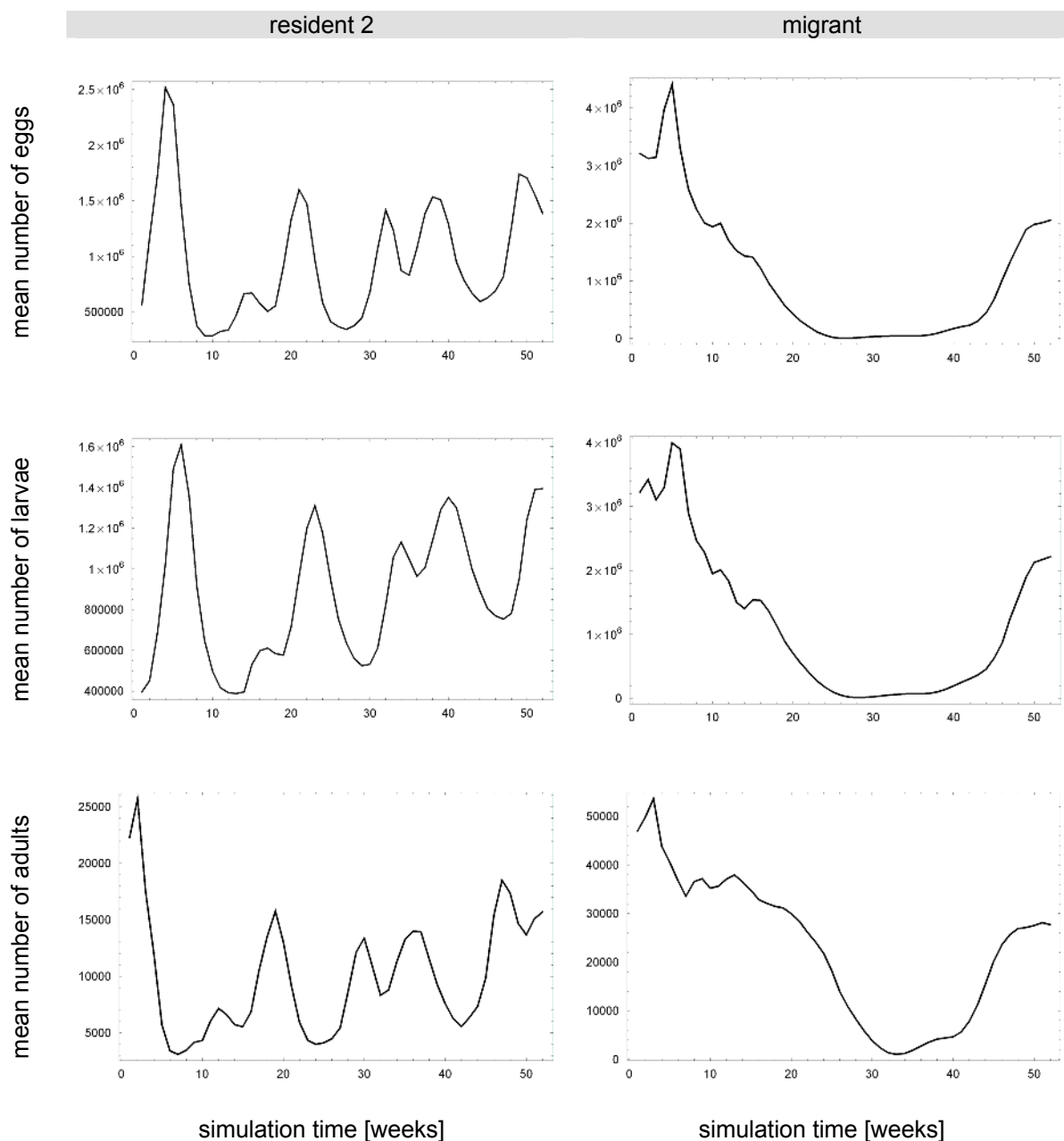
Figure 4.34: Mean numbers of individuals in the different stages during the simulation. Scenario: von Bach_R2_M_s.
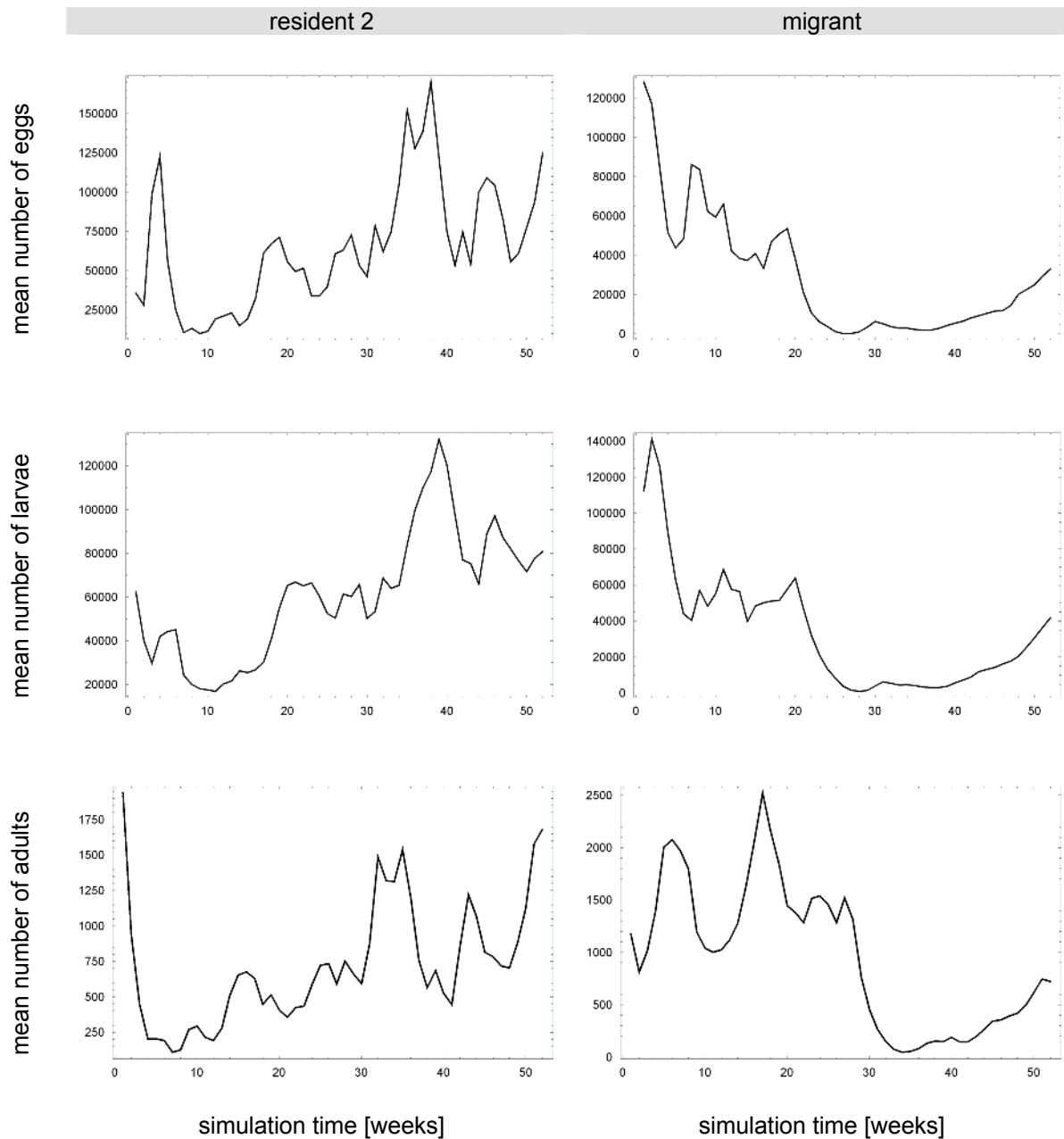
Figure 4.35: Mean numbers of individuals in the different stages during the simulation. Scenario: Tsaobis_R2_M_s.

Discussion

For the R1_R2_s scenario, both resident species have the same life-cycle parameters (cf. Chapter 3) but differ in their dispersal abilities and their habitat preferences. Resident 1 (represented by *C. erythraea*) is defined to be a better disperser based on the population genetic analysis than resident 2 (represented by *P. genei*). The synchronized development of both species leaded to the suppression of resident 2 in the spatial context as the better disperser may get a temporal advantage when occupying a new habitat. For the

metapopulation in the landscape sectors the consequences of this temporal advantage were depicted in Figure 4.26 and Figure 4.27. Due to the increase of the density of resident 1 with a simultaneous decrease of the densities of resident 2 the latter species had an increased risk of a competitive exclusion in the whole landscape section. Overall, the "Tsaobis" region, located in the Nama Karoo biome, reached much lower densities in both species than the "von Bach" region in the tree and shrub savannah. This can be explained by the general lower number of habitats in the more arid region and consequently a lower pool of habitats, which are necessary for emigration and re-settlement.

In contrast to the scenario R1_R2_s, the scenarios R1_M_s and R2_M_s show that coexistence of two different species groups is possible. This corroborates with Amarasekare & Nisbet (2001), who state that the inferior competitor (in this case the residential species) can be rescued from extinction if colonisation in patches, which the superior competitor (in this case the migrant) cannot colonize, is possible. The life cycles of the groups migrant and resident are different from each other. Habitat specialisation of the resident 1 in scenario R1_M_s led to a preference for well-vegetated habitats, which the migrant rather avoided based upon the non-significant HSM model (Chapter 2). This led to the consequence that resident 1 was able develop source populations in these permanent habitats while the migrant was able to use nearly all habitats at lower densities.

Permanent habitats with high vegetation diversity additionally act as a kind of reservoir as well as a refuge for this species due to the implemented habitat choice algorithm. If no habitat with a better quality is present in the determined dispersal distance, the adults remain in their cell of origin. The well-vegetated outlets of the dams have these properties, so an accumulation of resident 1 was the result.

The R1_M_s simulation also showed the difference between the biomes in which the cellular automata are located. Due to higher variability of the habitats in the more arid region the initial population of the migrant was much higher than that of resident 1 whereas in the region around the S. von Bach dam the initial population of the migrant had about the same dimension than that of the resident 1. This was observed throughout the simulation. The analysis of the persistence of temporary waters (Table 4.2 and Figure 4.16) underlined this finding. These results can be interpreted as a better adaptation of the migrant in fragmented landscapes.

The average numbers of individuals of resident 1 in the "von Bach" region displayed a trend of a population growth while this trend was much smaller in the "Tsaobis" region. This can be

explained by the total number of habitats and the ratio between permanent to ephemeral habitats. In a region with a higher proportion of perennial habitats, a species with preferences towards habitats with longer duration, which is also reflected in the aquatic vegetation diversity, may have competitive advantages against the habitat unspecific migrant. The more arid landscapes provide not enough suitable habitats for the resident to get this advantage.

In the scenario R2_M_s the residential species 2 seemed to get a relative advantage reflected by the average metapopulation density in the more arid region located in the Nama Karoo. The population density exceeded the density of the migrant while this effect has not been recorded in the "von Bach" region. The reason for this advantage in the Nama Karoo biome may be due to the fertility reduction of the migrant, which aggravates the settlement for the migrant in a region with only few habitats present when these habitats are already occupied by another species. The difference to the R1_M_s scenario with an advantage for resident 1 in the tree and shrub savannah can be explained by the different habitat preferences. Resident 1 prefers higher vegetation complexity, which is mainly present at perennial habitats. These habitats are more frequent in the "von Bach" section, leading to the advantage of resident 1. For resident 2 the preferences are towards cells defined as "rivers as guidelines". These cells can be found in the southern part of the "Tsaobis" scenario. A more or less constant population in these habitats leads to the observed advantage in contrast to the migrant with the reduction of the population in the dry season.

4.3.5.2 Validation of the results of the standard scenario

A crucial point in the interpretation of spatially explicit population models is the validation of the models as only in few cases data for the validation exist (Higgins et al. 2001; Macdonald & Johnson 2001). As some of the monitoring sites were included in the area covered by the cellular automata (Figure 4.1), these sites were analysed regarding the abundances of the representatives of the modelled ecological groups throughout the year. However, only the wetland below the S. von Bach dam was visited often enough to get an impression of the incidences of the modelled species. This is a permanent habitat with high aquatic vegetation diversity.
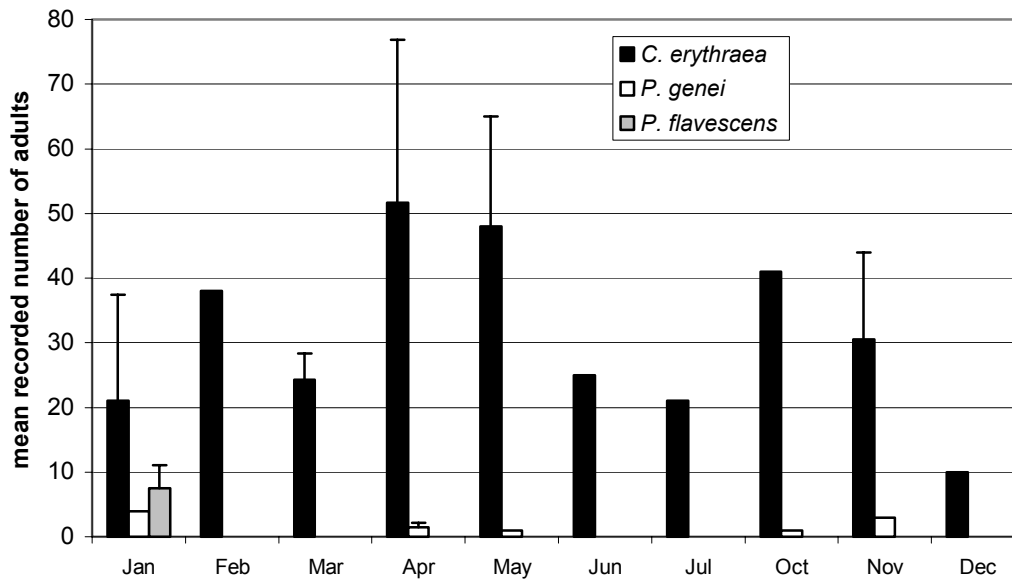
Figure 4.36: Mean number of adults + SD recorded at the wetland below the S. von Bach dam. Only months with data being available are displayed.

C. erythraea, which is the representative of group 2 (resident 1), reached the highest densities throughout the year (Figure 4.36). The only records for *P. flavescens* (migrant, group 1) were in January, directly before the onset of the rainy season. *P. genei* (resident 2, group 3) was not present at this habitat in every month of the survey and when a presence was recorded, the densities are about 10 times lower than those for *C. erythraea*. Generally, adults of *P. genei* are not always present at the water site, although they may be present in the surrounding of the habitat. Therefore the densities of this species are surely underestimated. It is likely that it is present the whole year like *C. erythraea* though in lower density (Suhling, pers. comm.).

These data corroborate the results of the spatially explicit models under current climatic conditions. Resident 1 reached high densities throughout the year, confirming the assumption that the permanent wetlands serve as a refuge. In the models comparing resident 2 with resident 1, the former reached only low densities induced by competitive exclusion, which is reflected by the low population densities in the wetland below S. von Bach dam. Finally, the number of migrants was higher than those of the resident 2 but lower than those of resident 1.

In the model the migrant was present throughout the year while in the survey it has been recorded only in one month. This may be caused by the implicit modelling of the migratory behaviour via the reduction of the fertility rates. Implementation of an explicit migration procedure may lead to other results. However, the model seems to yield reasonable results concerning the proportions of adult dragonflies from the respective modelled groups. More

data for a "real" validation of the model would be helpful to see if the model produces realistic result also in other habitats.

The absolute values of adult individuals in the spatial model exceeded the numbers of recorded adults in this habitat. This can be explained by another scale in the model with a cell size of 1 km² in contrast to an area of the real locality of about 1600 m². Another reason is the abstract and coarse differentiation of habitats regarding the capacity of the unspecific prey, which is connected with the density of dragonflies in the habitat (Chapter 3).

4.3.5.3   Climate change scenarios

The climate change scenarios are analysed by a comparison between two scenarios of the same landscape under different climatic boundary conditions. This analysis focuses on the larval stage as this stage is influenced by the variability of the temporary habitats as well as by interactions between the species. A selection of some of the modelled variations is chosen to illustrate the behaviour of the spatially explicit model in reaction to the changing landscape dynamics.

Comparison between R1_M_s and R1_M_cc, "von Bach"

The results of the simulations with the standard and the climate change scenario for resident 1 and the migrant showed that the form of the curves in both simulations was similar (Figure 4.37 and Figure 4.38). Differences existed in the numbers of larvae per cell, which were lower throughout the simulation year in the climate change scenario for both species. Another effect, which can be stated at least for resident 1, is that the curve of the standard scenario appeared to be a little more smoothened compared to the climate change scenario.
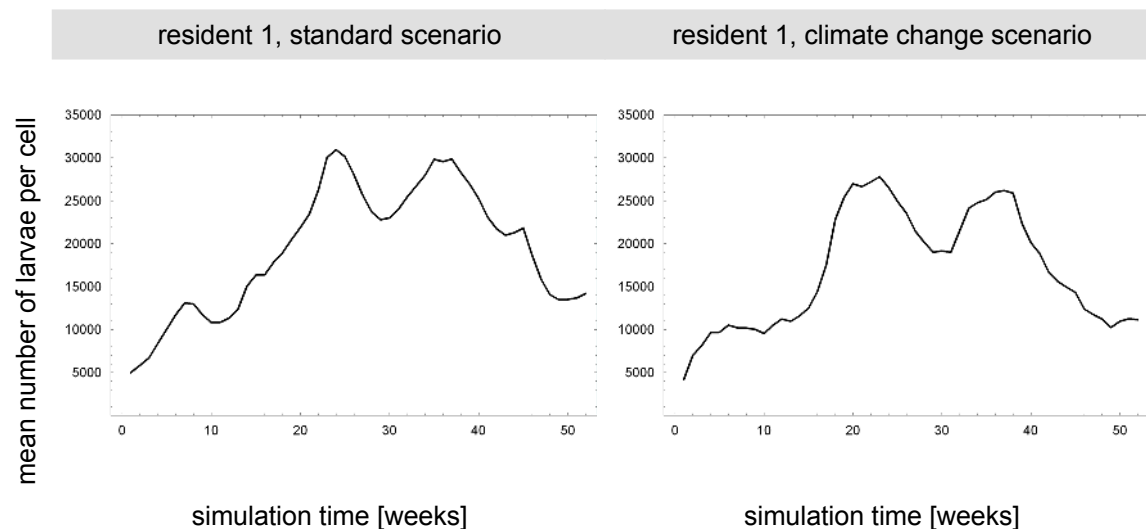
Figure 4.37: Comparison between the standard and the climate change scenario for the resident 1 in competition with the migrant, landscape section: "von Bach". Displayed are mean larval numbers per cell.
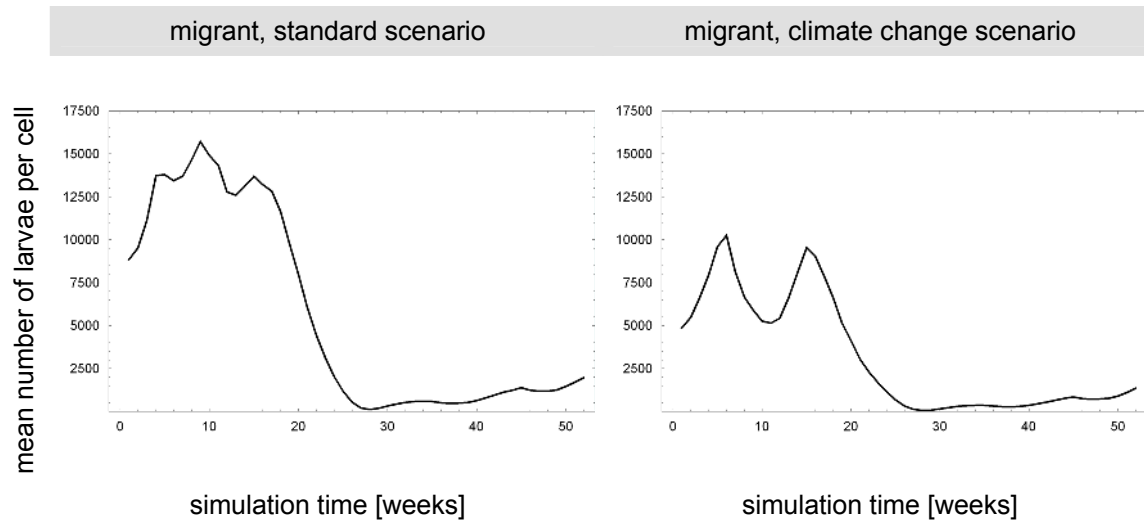
Figure 4.38: Comparison between the standard and the climate change scenario for the migrant in competition
with the resident 1, landscape section: "von Bach". Displayed are mean larval numbers per cell.

Comparison between R2_M_s and R2_M_cc, "Tsaobis"

The climate change scenario for resident 2 and the migrant in the "Tsaobis" section resulted in
a much lower density per cell for resident 2 throughout the simulation year associated with
another character of the curve (Figure 4.39). The densities of the migrant in the climate
change scenario were only about half of the densities of the standard scenario but with similar
temporal dynamics (Figure 4.40).
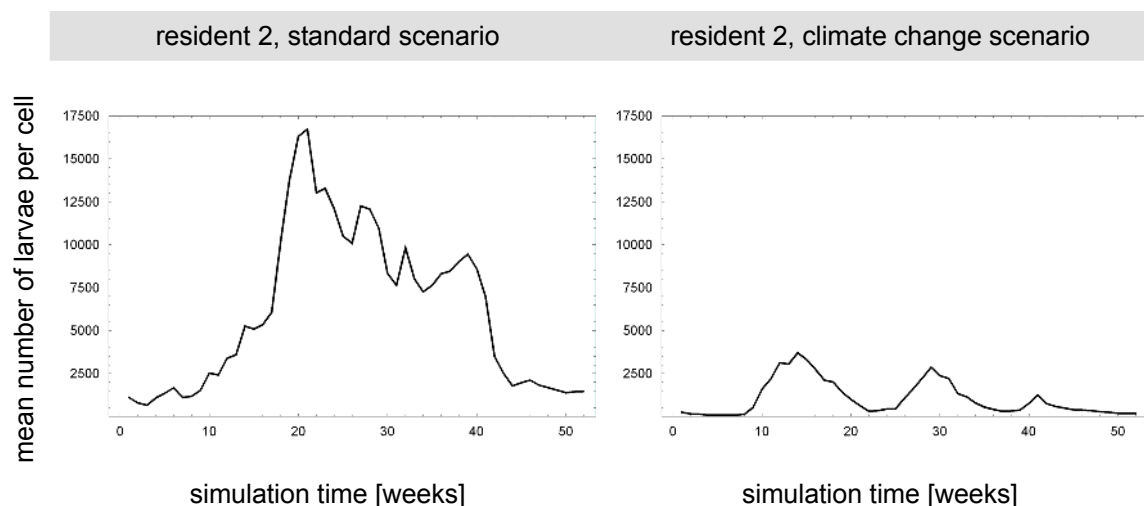
Figure 4.39: Comparison between the standard and the climate change scenario for the resident 2 in competition
with the migrant, landscape section: "Tsaobis". Displayed are mean larval numbers per cell
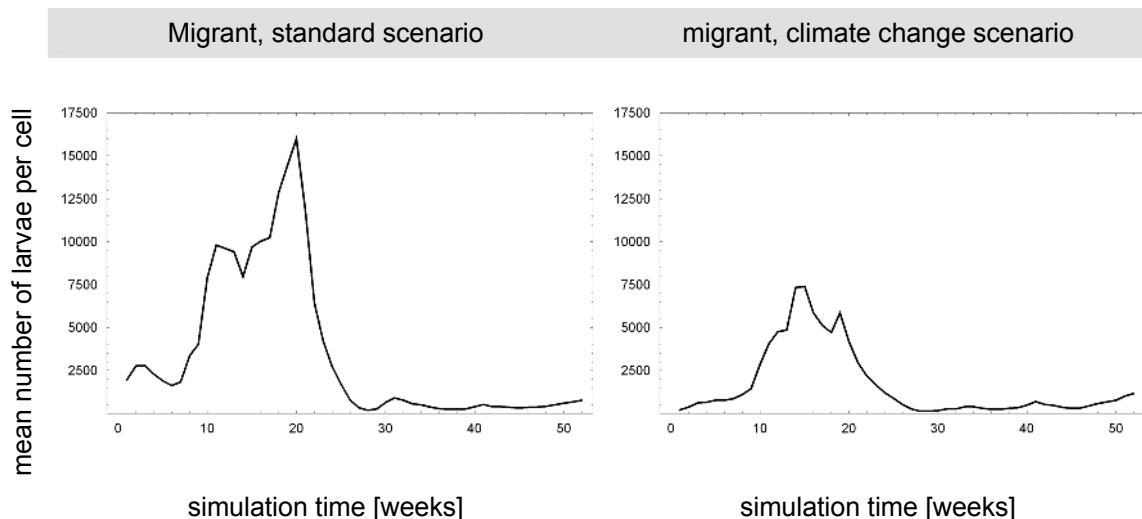
Figure 4.40: Comparison between the standard and the climate change scenario for the migrant in competition with resident 2 (Figure 4.39), landscape section: "Tsaobis". Displayed are mean larval numbers per cell

Discussion

The results of the climate change scenarios showed that the density and the species composition of the Odonata in the area of investigation may undergo significant changes. The general trend of the simulations with the climate change scenario was a decline in metapopulation density. There are several reasons for this response, which sum up to the observed effects. The increasing variability of the habitats modelled in the climate change scenarios may lead to the decrease in metapopulation density. The number of cells that have the needed duration for completion of larval development are reduced (Table 4.2) and therefore the number of offspring is lower.

Regarding the larval stage, which is not able to move away from a desiccating habitat, the increase of variability additionally leads to a population decrease as the model assumes that all larvae will die if a habitat runs out of water. This may be the reason for the more smoothed character of the curve in Figure 4.37 in the standard scenario. Fluctuations in the number of larvae per cell may be a consequence of local extinctions of the larvae. Not only the persistence of the ephemeral habitats but also the number of temporary and permanent cells in the climate change scenario is reduced compared to the standard scenario. This may also lead to a lower metapopulation density as fewer cells that may serve as a source habitat are being present in the landscape sections.

One important process that determines metapopulation structures is the local extinction of species. The classical metapopulation approach assumes a quasi-equilibrium between colonization and extinction. In an approach describing variable landscapes the dynamic

distribution of the habitats will have a high influence on the metapopulation dynamics. The change of the status of the habitat, which is mainly a destruction of the habitat or at least a disturbance in habitat continuity, disables colonization after a local extinction (Thomas & Hanski 2004).

The peak of the residential species during the dry season in the standard scenario can be explained by a crowding effect induced by progressing fragmentation of the landscape (Debinski & Holdt 2000). However, this effect cannot be seen in the scenario Tsaobis_R2_M_cc. Habitat fragmentation in the Nama Karoo under climate change may explain this result. Resident 2 with poor dispersal abilities was not able to reach the rare suitable permanent habitats with the consequence of dying adults in the dry season and an absence of the crowding effect.

Overall, the standard scenarios show some important mechanisms regarding the spatial population structure in the modelled regions. The metacommunity consisting of two residential species with same life-history parameters but different dispersal abilities and habitat requirements leads to a trend of competitive exclusion of the species with the lower dispersal ability due to the synchronized life cycle. Both other species combinations (R1_M_s and R2_M_s) allow the species to coexist together. The effect of the landscape dynamics and consequently the habitat characteristics result in different patterns in the single metapopulation dynamics. The residential species 1 with better dispersal and habitat preferences for aquatic vegetation benefits from the landscape with higher number of permanent habitats while the residential species 2 with lower dispersal abilities benefits from the situation provided by the landscape in the Nama Karoo. The comparison with real data as far as available from the survey shows that at least the proportions of the densities of the dragonflies are well reproduced by the model.

The climate change scenarios show a decrease in the local population densities as well as in the metapopulation density. The metapopulation concept which is realised in the model – connection of local populations through dispersal into a metapopulation – enables the modelled species to survive the aggravation of the landscape concerning the decrease in the number and duration of reproduction habitats (Levin 2000). Even resident 2 with the lowest dispersal ability can buffer local extinctions of a subpopulation, although the general shape of the population density per cell (Figure 4.39) already shows that the oscillations between high and low abundances increase significantly in the climate change scenario.

The theoretical scenarios have emphasized the importance of the landscape structure by habitat connectivity especially for the habitat specialist regarding vegetation structure (resident 1) and the poor disperser (resident 2). The resident 1 is highly dependent on the permanent habitat with high vegetation diversity, which appears to attract the adult dragonflies and serves as refuge as well as a source for further colonization. The resident 2 is limited by its dispersal ability and therefore isolation of this species is possible due to missing stepping stone habitats in an acceptable distance.

A consequence of the modelling results for biodiversity assessment and conservation management is that the metapopulation approach is able to buffer local extinctions due to desiccation. However, habitat specialisation and low dispersal ability, as it can be observed in the residential species, may be followed by isolation of the species in a suited habitat (Watts et al. 2004). Therefore specialised species are more susceptible to extinctions – either of the local population or the metapopulation, especially under the premise of increasing influence of climate change (Svensson et al. 2005). The habitats, which are inhabited by these species, deserve special attention in concepts for conservation management.

5 Summary and conclusions

I have developed a model system, which allows the modelling of the responses of the three major ecological groups of dragonflies in arid Namibia under current and future climatic conditions. The habitat models that were introduced in Chapter 2 served to distinguish the three groups regarding their ecological preferences. Especially the use of the habitat web was valuable for the evaluation of the relative habitat preferences. Additionally it allowed estimating the different preferences of the species regarding the landscape layers, which were included in the landscape model (Chapter 4.2).

The population dynamic model, which refined the extended Leslie matrix approach for age and size structured populations via the introduction of inter- and intraspecific interactions, showed the importance of the colonisation sequence of the dragonflies at the habitat. The model indicated that local extinctions due to size differences of larval stages are possible between the two species types "migrant" and "resident". The chosen mathematical approach did reproduce the pattern of multivoltinism, which is typical for tropical centred dragonflies, very well (Chapter 3).

The construction of the landscape and especially its inherent dynamic was another crucial aspect of this work. The use of satellite images for the derivation of the ecological relevant landscape parameters combined with indispensable expert knowledge about the processes and characteristics of the landscape sectors facilitated to change the model's scale (Chapter 4.2.2). The larger scale led to new insights for the explanation of occurring spatial distribution patterns of the dragonflies. The dynamic change of the landscape showed that in more arid regions the residential species with longer duration of their larval stages were impeded by the smaller number of habitats and a higher level of habitat variability in terms of continuity (Chapter 4.2.3). The combination of landscape dynamics with the dispersal abilities of the modelled species made the impact of landscape fragmentation in the more arid regions apparent (Chapter 4.3.3).

Theoretical scenarios were used to get first results of the model's performance in an explicit spatial context. These scenarios showed the general importance of habitat structures preferred by the residents as a refuge and source habitat, but also as an obstacle for dispersal and consequently the colonisation of habitats in larger distance. The migrant, defined as a habitat generalist, was able to establish at least small subpopulations in the most distant habitats (Chapter 4.3.4).

The results of the scenarios based on the real landscape sections in the Swakop River catchment were compared with the survey data from the wetland below the S. von Bach dam. This validation showed that the results of the spatially explicit model reproduced the patterns observed in reality very well (Chapter 4.3.5.2). The coexistence of two residential species in a community seems to be difficult to realise as the results have shown competitive exclusion of the weaker disperser (Chapter 4.3.5.1). Therefore species with equal life-history parameters are supposed to use other mechanisms to coexist in the same habitat. One possible factor, which may promote coexistence despite of the same life-cycle or competitive advantage of one species, may be resource partitioning in the freshwater habitat.

Furthermore, the habitat preferences, which were confirmed by the HSM, were also reflected by the spatial patterns produced by the model. Regarding aspects of conservation biology, the model clearly indicated the importance of permanent and well vegetated habitats for the residential species with certain habitat preferences. In the model, these habitats were represented by the outlets of the dams but also permanent springs may provide the required properties and should therefore be regarded as valuable for conservation.

The application of climate change scenarios based on IPCC forecasts showed that the mean metapopulation densities in the investigated landscape sections will potentially decrease. Fragmentation of the landscape regarding the presence of freshwater habitats will increase and affect especially the species with poorer dispersal abilities. However, the survival of this species was possible despite of the aggravation of the habitats. Nevertheless, the theoretical scenarios have shown that extreme fragmentation may lead to isolation of a species, which enhances the risk of a complete extinction of a metapopulation (Chapter 4.3.5.3).

More empirical data concerning the construction of the landscape and its dynamic are just as desirable as more information on the parameters which drive the local population dynamics. Both would lead to an improved model whose accuracy would increase regarding the predictions of changes in the water balance. Another factor promoting the model's accuracy would be the linkage between the cellular automata to model the far distance dispersal. This would certainly improve the results especially for the migrant species. A refinement of the scale of the cellular automaton on the locality level would also add accuracy. To minimise the proximate extension of calculation time this should only be done in regions with high water densities, where a multitude of single but linked freshwaters exist.

The model approach, which was presented in this work, allows making predictions of the spatial patterns of dragonfly communities in the arid regions of Namibia. A change in the life-history parameters of the species may allow modelling of other species or communities, respectively. Furthermore, the implementation of other ecologically relevant properties of the landscape is possible if the information for the construction of the landscape layer exists. Hence, other dragonfly communities can be modelled with little effort. The presented model system can be used as a tool for the assessment of biodiversity of Odonata and may help to identify and emphasise valuable regions for freshwater conservation management.

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1. Landscape layers "aquatic vegetation diversity" and "rivers as guidelines" used in the theoretical scenarios.
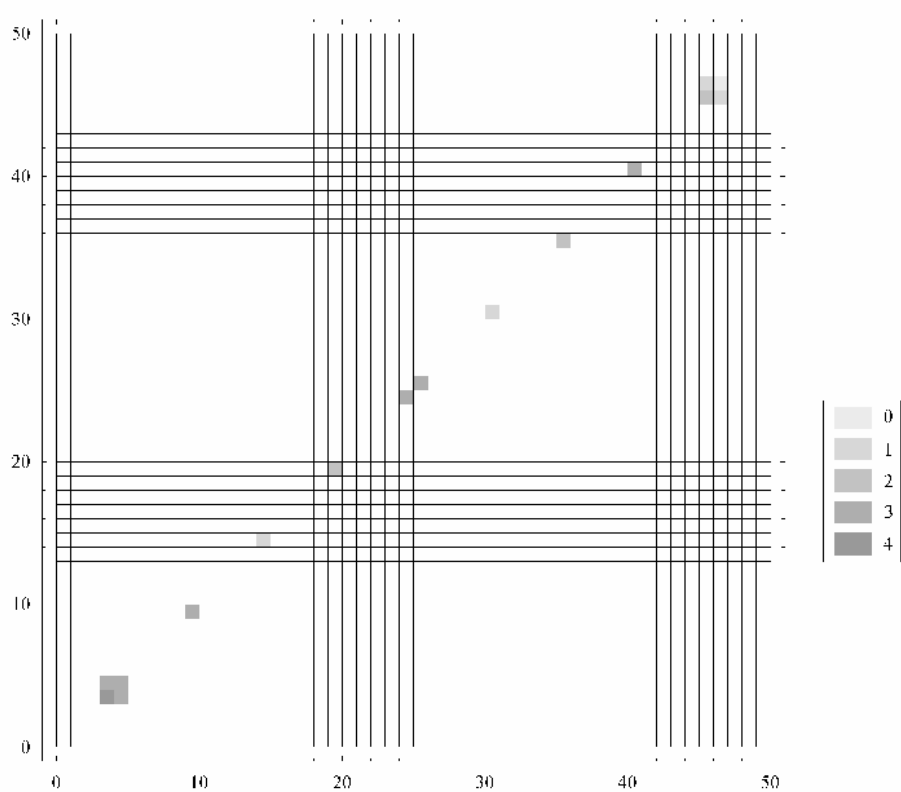
Figure A.1: Aquatic vegetation diversity for the theoretical scenarios T2 and T4. Numbers on the axis represent the internal program addresses of the cells. Different grey shades represent values for aquatic vegetation diversity.
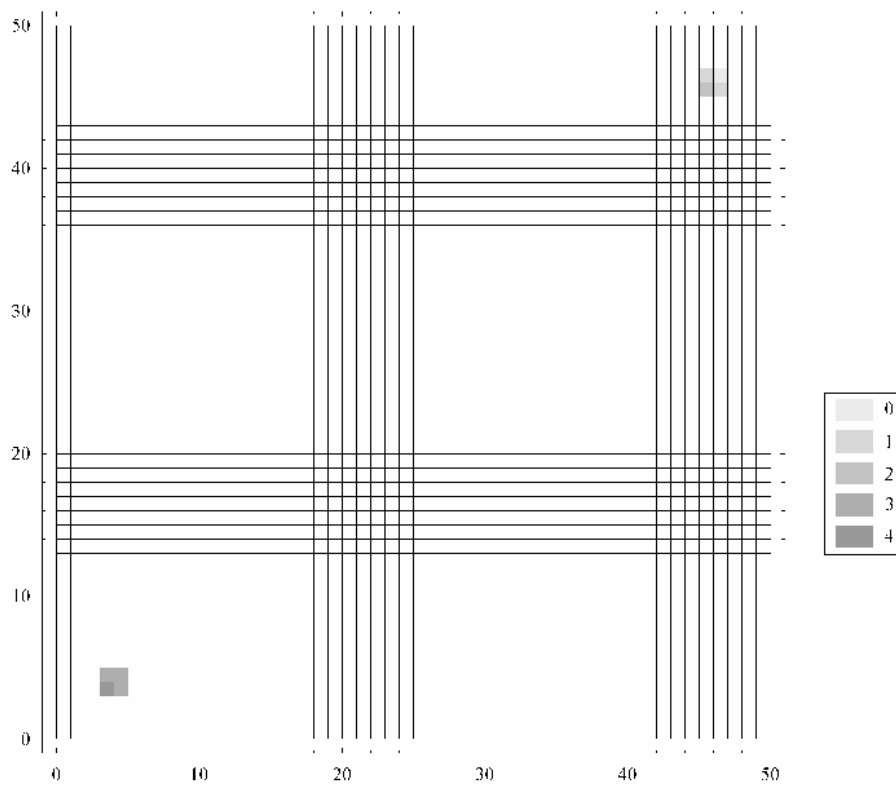
Figure A.2: Aquatic vegetation diversity for the theoretical scenario T1. Numbers on the axis represent the internal program addresses of the cells. Different grey shades represent values for aquatic vegetation diversity.
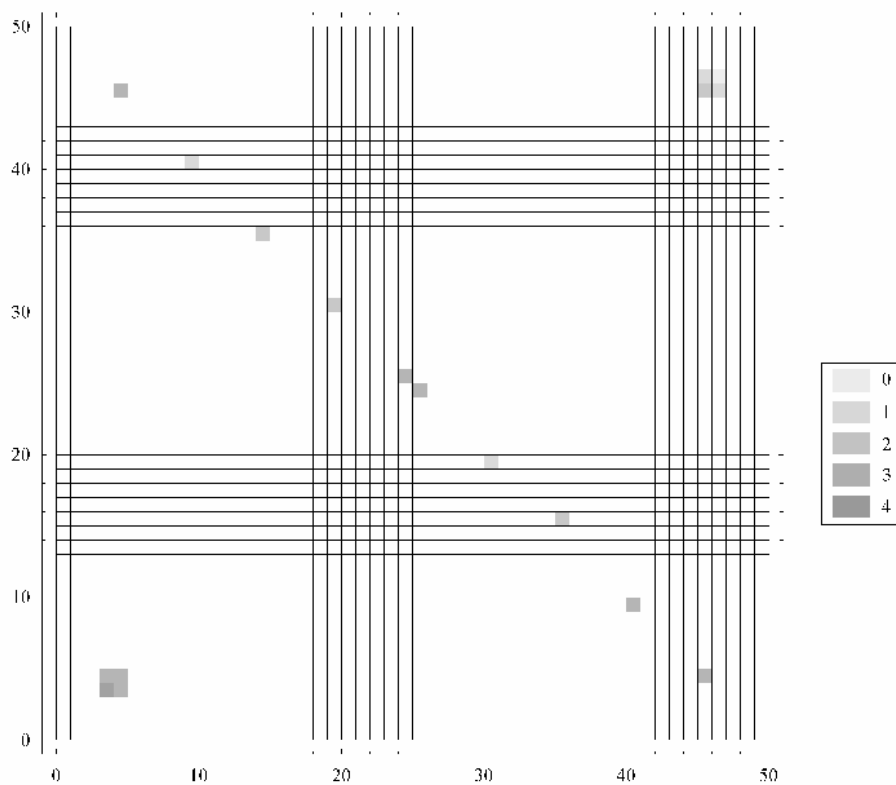
Figure A.3: Aquatic vegetation diversity for the theoretical scenario T3. Numbers on the axis represent the internal program addresses of the cells. Different grey shades represent values for aquatic vegetation diversity.
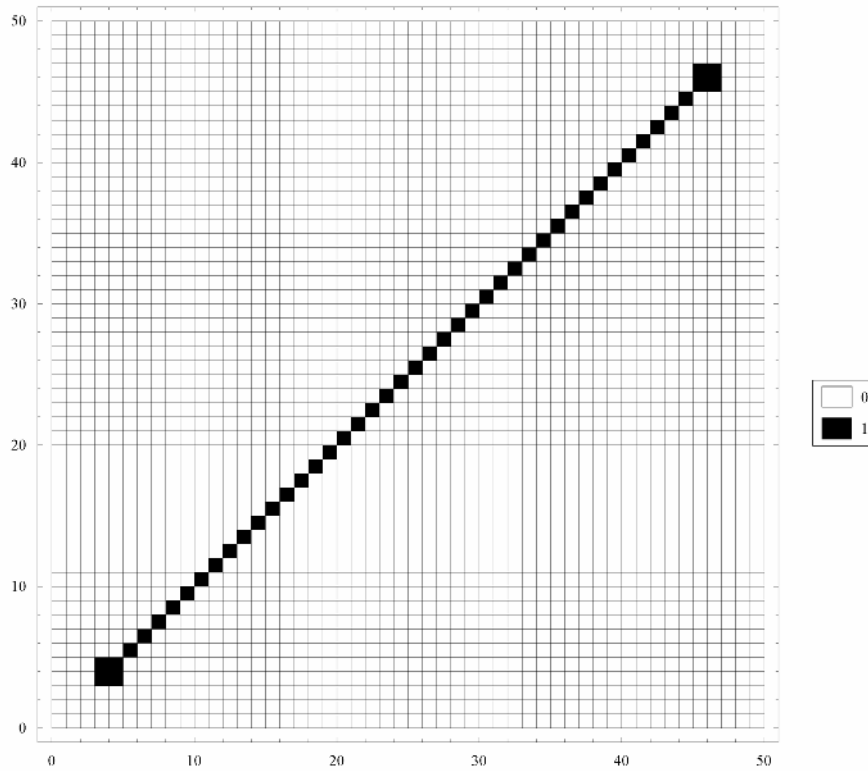
Figure A.4: Rivers as guidelines for the theoretical scenarios T1, T2 and T4. Numbers on the axis represent the internal program addresses of the cells. Black cells were defined as containing linear structures representing the riverbed.
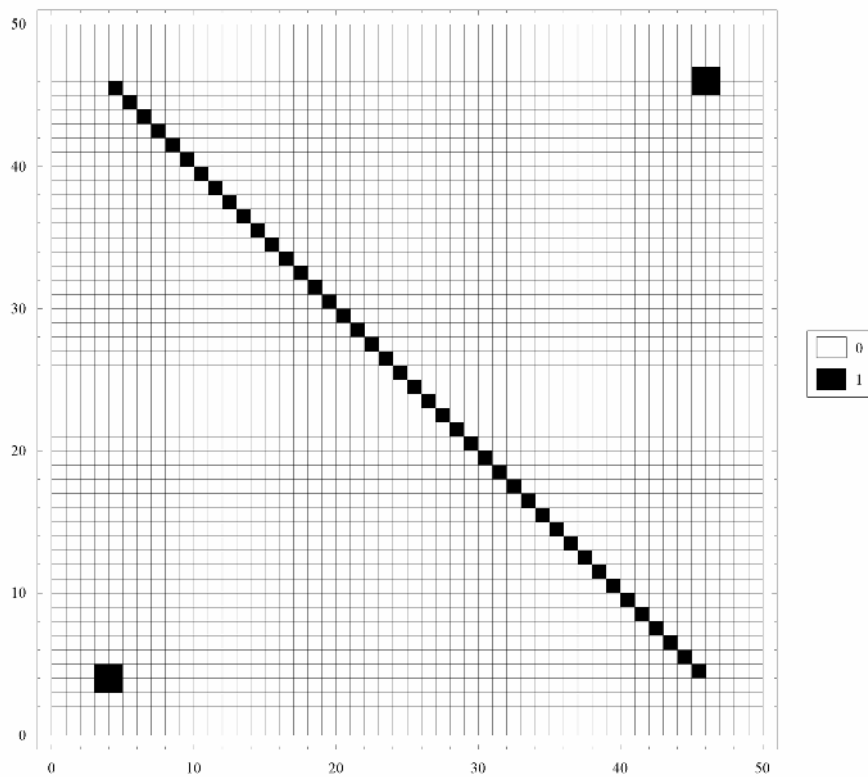
Figure A.5: Rivers as guidelines for the theoretical scenario T3. Numbers on the axis represent the internal program addresses of the cells. Black cells were defined as containing linear structures representing the riverbed.

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2. Landscape layers "aquatic vegetation diversity" and "presence of open water" used for the climate change simulations in the modelled landscape sectors. The layer "rivers as guidelines" did not change between the simulations under current climatic conditions and climate change as the riverbed has been identified regardless of the climatic conditions.
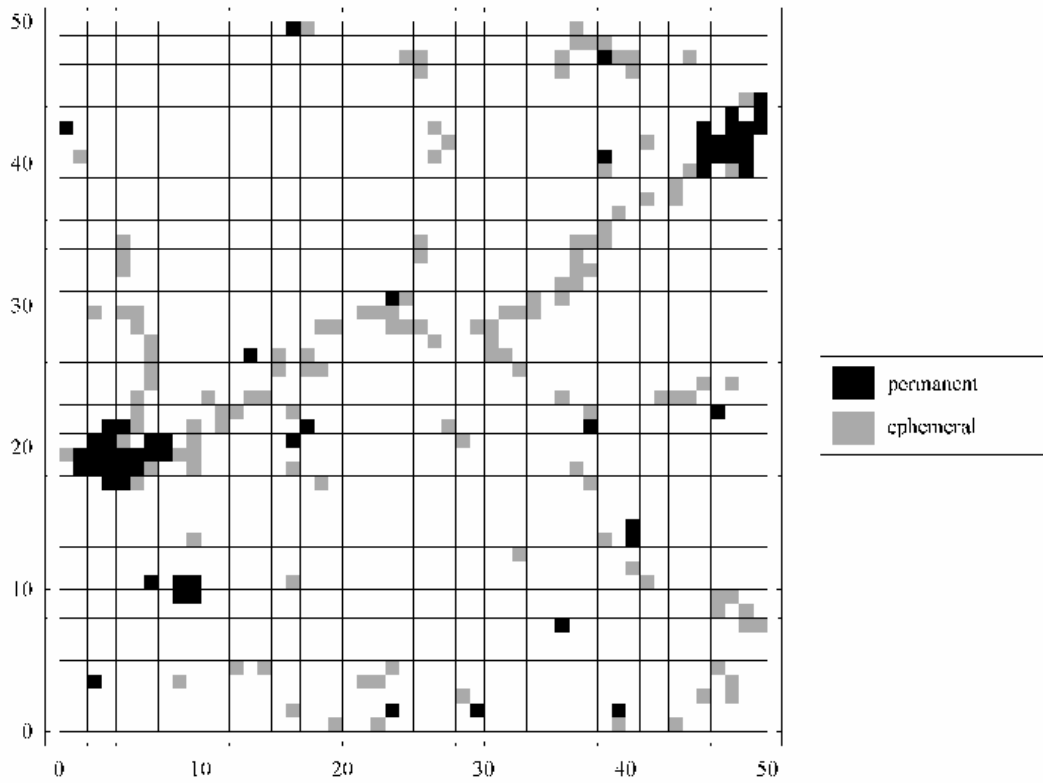
Figure A.6: Landscape layer "presence of open water" for the "von Bach" section under climate change conditions. Depicted is the climax of the rainy season. Black cells: permanent waters, grey cells: temporary waters.
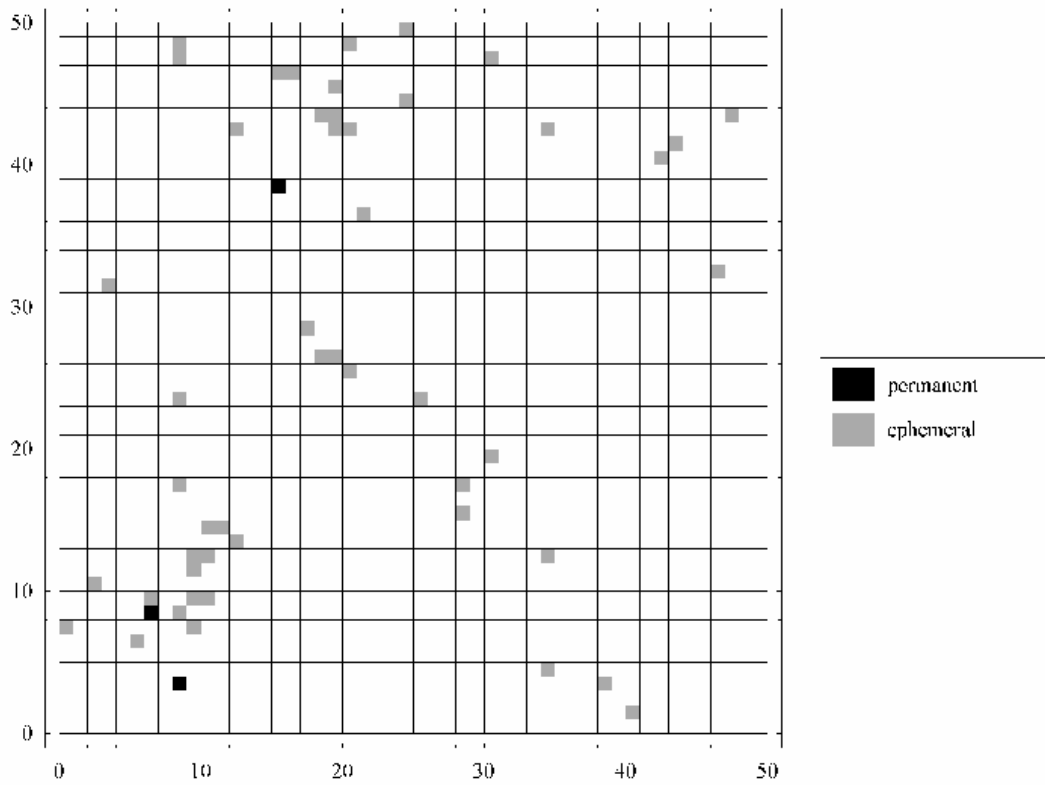
Figure A.7: Landscape layer "presence of open water" for the "Tsaobis" section under climate change conditions. Depicted is the climax of the rainy season. Black cells: permanent waters, grey cells: temporary waters.
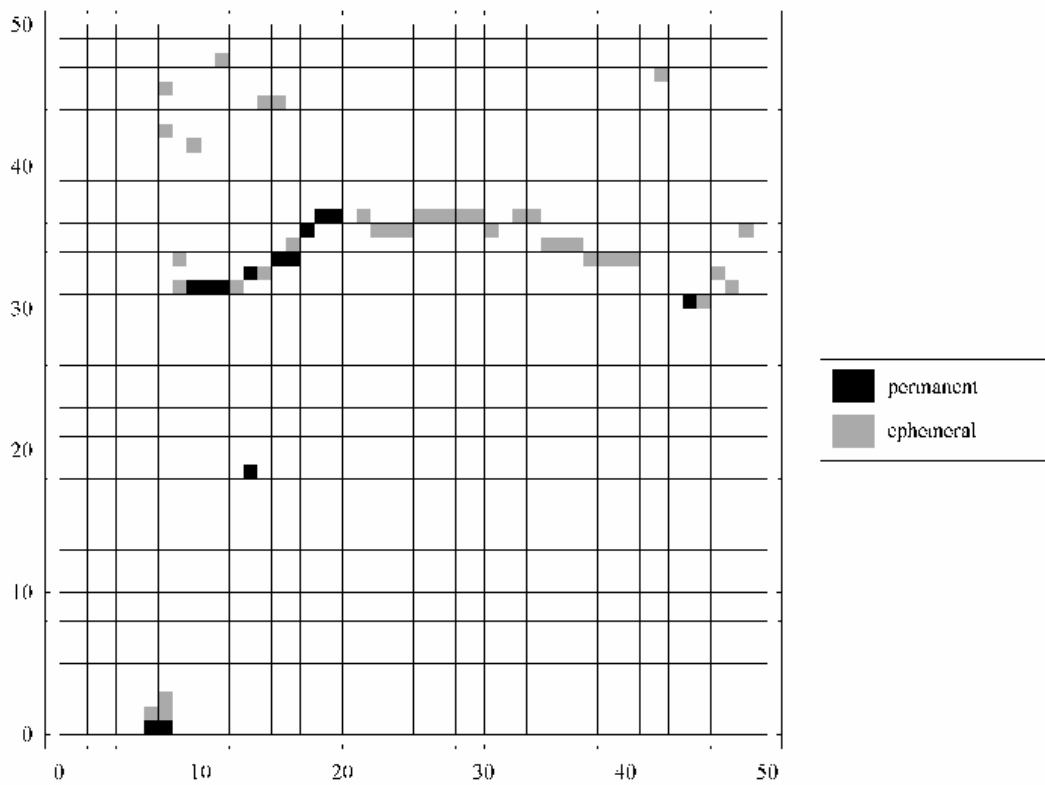
Figure A.8: Landscape layer "presence of open water" for the "Swakopmund" section under climate change conditions. Depicted is the climax of the rainy season. Black cells: permanent waters, grey cells: temporary waters.
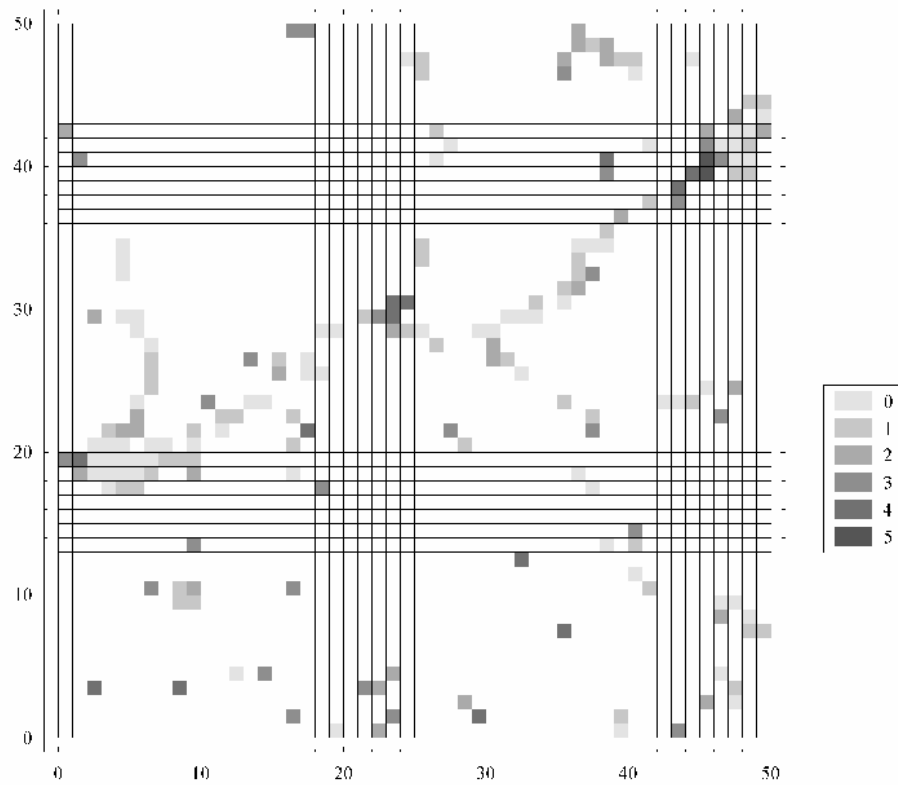
Figure A.9: Landscape layer "aquatic vegetation diversity" for the "von Bach" section under climate change conditions. Numbers on the axis represent the internal program addresses of the cells. Different grey shades represent values for aquatic vegetation diversity.

Figure A.10:Landscape layer "aquatic vegetation diversity" for the "Tsaobis" section under climate change
          conditions. Numbers on the axis represent the internal program addresses of the cells. Different grey
          shades represent values for aquatic vegetation diversity.

Figure A.11:Landscape layer "aquatic vegetation diversity" for the "Swakopmund" section under climate change
          conditions. Numbers on the axis represent the internal program addresses of the cells. Different grey
          shades represent values for aquatic vegetation diversity.

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