# Linking landscape structure to population dynamics

## The role of movement in a structured population of the arboreal gecko *Gehyra variegata*

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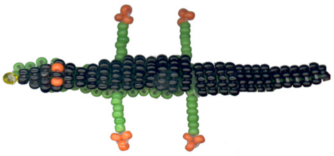

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# Preface

The thesis is divided into six chapters. Each chapter is intended to be submitted independently to journals for publication. Therefore these chapters are written in the style of a particular journal and it is unavoidable that some parts are repeated in the different chapters. At the beginning of the thesis a summary is given, which outlines the central questions and summarizes the contents and results of each chapter. A review paper (chapter VI) completes the thesis.

# Summary

"*To an ecologist, the beauty of landscapes lies not only in their reality, but in the challenge of understanding how their complex spatial structure affects ecological patterns and processes. This is the focus of the science of landscape ecology*" (Wiens 1995). The citation of Wiens outlines the motivation behind this thesis. It poses the question, how landscape spatial structure is linked with ecological processes.

The most important factor that mediates the effects of spatial structure to ecological processes is movement (May & Southwood 1990, Wiens et al. 1993, Wiens 1995). Very different ecological processes and concepts are based on movement, such as population genetics, territorial behavior, home ranges, population dynamics or metapopulation dynamics. Movement adds or subtracts individuals to a population (Turchin 1998), provides important genetic variability, is necessary to let individuals fulfil their daily needs (Ims 1995) (foraging, finding suitable resting places etc.), and let individuals find a mating partner or new habitat patches.

The most common view of spatially-structured populations is that animals live in a binary landscape consisting of suitable patches of habitat surrounded by a hostile matrix (Gilpin & Hanski 1991). Populations living in such a landscape, are interconnected to a varying degree (Wiegand et al. 1999) by movement of individuals. Often it is assumed that movement in the hostile matrix results in an increased mortality risk (Fahrig 1998). Mortality during migration (movement) is the most obvious cost of migration (Comins et al. 1980, Olivieri and Gouyon 1997, Hanski et al. 2000), but it is very hard to measure empirically (Ims & Yoccoz 1997, Fahrig 1998, but see Van Vuren & Armitage 1994).

In order to understand the effects of landscape structure on population processes, the individuals' specific response to the landscape structure (movement behavior) has to be taken into account. Hence, tools for linking individual with population processes are needed.

One of the most prominent approaches to solve this problem is to use landscape indices that measure an important feature of landscape and try to correlate the index to measurements of ecological processes (i.e. density, distribution, survival of a species) (Tischendorf 2001). Many different landscape indices have been proposed and checked for their usefulness to predict ecological processes (e.g. Gardner et al. 1987, Turner 1989, Cullinan & Thomas 1992, McGarigal & McComb 1995, Riitters et al. 1995, Schumaker 1996, Cain et al. 1997, reviewed by Gustafson 1998, Hargis et al. 1998, Jaeger 2000a, Tischendorf 2001). Despite the efforts which have been spent on finding useful landscape indices, many different indices do exist,

which sometimes correlate nicely with an ecological process, but fail under different circumstances (i.e. a different species or a different landscape configuration). For example the amount of suitable habitat in a landscape is a good predictor for the occurrence of some bird species, but fails for other species of birds in the same area (Vos & Verboom 2001). The index developed in this thesis is species oriented, i.e. it measures the landscape through the eyes of a species (Grimm et al. 1996, Wiegand et al. 1999, Frank & Wissel 2002). It is very flexible and can be applied to other species using different movement rules and different risks of mortality, when moving through the landscape. This is possible because it is a functional index that can predict an important aspect of population dynamics of animal species, namely the chance to meet a conspecific in a landscape.

To summarize, the thesis presents a way, how to link habitat structure to an important population process. This is a prerequisite to understand and predict population dynamics in heterogeneous landscapes, which is very needed in the preservation of endangered species in fragmented landscapes.

The thesis demonstrates the advantage of a close connection between field study and modeling. Ideally the connection between field work and modeling is a feedback loop (Wissel, pers. comm.). Field data and knowledge about processes are used to create a model, which reflects the known processes and parameters. The model helps to focus on the relevant parameters and produces predictions. The predictions can be tested in further field experiments and the results of the experiments can be used to refine the model, which produces better predictions and allows to ask and answer more detailed questions.

## *The system "Gehyra variegata"*

If a relatively new field of science is entered, it is a reasonable approach to start with a case study (Wissel, pers. comm.). During the case study the first insights are gained and this allows to widen the view on the scientific field step by step, until more general conclusions can be drawn. In this thesis, a dataset of the arboreal gecko *Gehyra variegata* serves as a reference case for studying movement. The first part of the thesis (chapters I, II and III) is mainly based on field work. It deals with the problem how to measure and describe movement of an arboreal gecko.

For several reasons *G. variegata* is an ideal system to study. The population dynamics of this species has been well studied under an intensive capture-mark-recapture regime and the locations of individuals has been recorded and are known for up to 14 years (Henle 1990a, Gruber & Henle, unpubl.). The activities of this arboreal species are strongly linked to trees

(Bustard 1968, Henle 1990a), hence an easy distinction between habitat (tree) and matrix (between trees) can be made and movement is very easily recorded. The very good knowledge of the biology and the excellent field data form the basis for this thesis and allows to ask questions, which could not be answered otherwise.

The second part of the thesis presents a more general view and results in a landscape index that is capable of describing the effects of movement for a variety of species in a patchy landscape. The analysis of the field data provided the basis for the second part of the thesis (chapters IV and V), which used an individual-based simulation model to study the effects of movement on the mating success of a female gecko. The last chapter is a review on the different techniques of modeling movement and the concepts to link it to ecological processes.

So far, no common methodology for measuring movement does exist (Turchin 1998). Hence, the first difficulty is to define a way for measuring and describing movement, which is the theme of the first three chapters. (chapters I, II and III).

## *Chapter I*

An automatic activity monitoring system was developed to study activity of geckos. The system recorded activity of geckos using passive integrated transponder (PIT) technology. The task of the system was to record movement of individual geckos when they leave or return to their tree. Therefore, ten units of an automatic monitoring system, which detects geckos when they pass a PIT reading coil, were placed at the basis of the trunk of trees. Chapter I describes the suitability of the automatic activity monitoring system and reports results on the activity of the geckos. Activity was related to temperature and time of day. So far, researchers reported a unimodal distribution of activity for nocturnal geckos during the night (Bustard 1967a, Pianka & Pianka 1976, Henle 1990a, How & Kitchener 1983, Sarre 1995, Walker et al. 1991). With the aid of the automatic system a second peak of activity at sunrise was found. Such a peak fits well the hypothesis that geckos have to actively thermoregulate during the day.

## *Chapter II*

The ability of geckos to orientate between trees was studied by translocation experiments. Geckos were captured, marked with fluorescent powder, and translocated to neighbouring trees. The tracking of the animals showed their ability to return to their tree of capture. Another way to test the orientation ability of animals is studying their movement and trying to connect the observed movement to structural components of the habitat. Movement data of a long-term mark-recapture study were analyzed and related to the configuration of trees. Different movement rules were compared with the moved distances that were observed in the field data. The data from the capture-mark-recapture experiment gave evidence that geckos do orientate visually. The movement rule: "move to one of the 3 next neighbouring trees that can be seen" fitted best observed movement data.

## *Chapter III*

The focus of chapter III was to test the hypothesis, whether movement in a structured population is dangerous and results in higher mortality, hence the effect of movement on survival. An approach is presented, which uses capture-mark-recapture data to determine the effect of individual movement on survival in a structured population. Because capture-mark-recapture data are widely available for a range of animal species, it should be possible to extent its application to other species. The approach was applied to the data of *Gehyra variegata*. The study revealed a negative effect of movement on survival. Hence animals that moved more often between trees, had a lower survival rate. Interestingly, the mean movement rate for males (0.23) was significantly higher than for females (0.14), which should lead to a biased sex ratio towards females in the population. However, males had a higher basic survival rate than females and the combination of both effects resulted in a similar survival rate between sexes.

The findings are in accordance with the predictions of the theory of the evolution of mating systems. In species in which females contribute more to the offspring, the male reproductive success is determined by the numbers of mates and the female reproductive success is determined by the resources (Trivers 1972). The most important resource for this arboreal gecko species are trees (Bustard 1968). Trees provide resting places, food and protect from predators. Females have only one option, to find suitable trees and stay there once settled, hence that's the females' way to optimize resources. For males there are two options. Either stay at a suitable tree with a female or try to increase the numbers of mates by looking for other females at other trees. Hence, it can pay for males to move between trees, despite a higher risk of dying. Once a methodology to describe movement is developed and the effect of movement on survival is known, it is possible to link these processes.

### *Chapter IV*

In Chapter IV an individual-based simulation model is presented. The model is based on the same parameters and processes that were determined by the field study. The output variable of the model was the reproductive success of a female gecko during a mating season. In combination with optimality theory unknown values of movement parameters were determined (the number of days geckos need to move until the highest reproductive success is achieved) and the robustness of the movement strategy of the geckos were tested in different habitat configurations. The model predicted the same movement strategy as found in the field. The exhibited movement strategy was optimal in very different landscape configurations. The ecological implications of the movement strategy are discussed.

### *Chapter V*

In the previous chapters of the thesis the movement parameters necessary to describe an important determinant of dynamics in structured populations were identified, namely the reproductive success of a female gecko. Chapter V presents an approach that derives the same quantity as the individual-based model with mathematical techniques. If these parameters are determined for other species, the approach can be extended to other species by analyzing their movement behavior. The reproductive success in a structured population is an important determinant of population dynamics and is used as a landscape quality index, hence for different landscape configurations the reproductive success of a species can be calculated. Additionally, the relative contribution to the mating success of each patch in a landscape can be calculated. The index was tested with the dataset of the arboreal gecko ( *Gehyra variegata*). It successfully improved the prediction of the number of animals caught at a specific tree.

### *Chapter VI*

The main goal of the last chapter is a review of the different approaches that have been suggested to link movement with ecological processes. Each approach is based on a different concept of movement and is often coupled with a specific modeling technique. Most movement concepts are linked with a certain response variable of an ecological process.

I identified five different approaches (landscape index, diffusion models, percolation theory, transition probability models and individual-based models,). The advantages and disadvantages of these approaches for linking movement with ecological processes are discussed and the results of the previous chapters are placed in this context.

# Chapter I

## Measuring circadian activity of free-living arboreal geckos with an automatic monitoring system using passive integrated transponder (PIT) technology

### *Introduction*

Activity of ectotherms is closely related to ambient temperature (Huey & Kingsolver 1989). Ectotherms generally have limited physiological scope for regulating body temperature (Stevenson 1985), but many species can maintain relatively high and constant body temperatures, despite considerable variation in their thermal environment, by using behavioral mechanisms, e.g. varying activity time, shuttling between sun and shade and adjusting posture (Huey 1982). For nocturnal ectotherms, such as most members of the family Gekkonidae, there are additional constraints. At night there are limited possibilities for ectotherms to thermoregulate (because there is no natural heat source available) and geckos are usually active with body temperatures 10-35 °C lower than those of similar diurnal lizards (Cowler and Bogert 1944, Huey et al. 1989).

Since velocity of physiological processes, like digestion, decreases exponentially with temperature below the thermal optimum (Autumn & De Nardo 1995), there is a need to compensate the lower temperatures during nocturnal activity and reach higher body temperatures for speeding up physiological processes. Surprisingly, geckos' physiology is not optimized to perform best at low temperatures. Thermal optima for a variety of performance variables are high (approximately 35 °C or higher) in both nocturnal and diurnal lizards (Huey et al. 1982, Autumn & Full 1994, Autumn et al. 1994, 1997). Since nocturnal geckos are not optimized to perform optimal at lower temperatures than diurnal species, other behavioral adaptations must exist that let geckos increase their body temperatures for physiological processes such as digestion.

So far activity patterns of nocturnal reptiles have been less well studied than those of diurnal species (Kearney & Predavec 2000). The reason for this is that it is much easier and less tedious to observe an animal during the day than during night. Many researchers report a bimodal activity distribution of diurnal species in hot weather and a unimodal distribution in cooler weather (e.g. Pianka 1973 , Huey et al. 1977). Activity pattern is less clear for nocturnal species. For 12 nocturnal species of Australian geckos Pianka & Pianka (1976) found a unimodal activity distribution having its peak shortly after sunset, ceasing quickly and finishing before midnight (see also Bustard 1967a, b, Henle 1990a, How & Kitchener 1983, How et al. 1986, Kitchener et al. 1988, Walker et al. 1991). Pianka & Pianka (1976) pointed out that their data may be biased due to a heavier sampling effort earlier in the evening. Bustard (1967a, b) and Henle (pers. comm.) mentioned that in nights with overall high temperatures activity of Australian geckos lasted well beyond midnight. Most of these findings were based on direct human observations and not many observers tried to catch geckos throughout the whole night, because of the high effort involved.

To study the activity distribution of a secretive, nocturnal gecko, a method for automatically recording the activity is required to avoid bias due to biased activities of observers. I developed such a system using passive integrated transponder (PIT) technology. The new system was tested by studying a population of a nocturnal gecko (*Gehyra variegata*) living on eucalypt trees. The task of the system was to record movement of individual geckos when they are active leaving their trees or returning to them. Therefore ten units of an automatic monitoring system, which detects geckos when they pass a PIT reading coil, were placed at the basis of the trunk of ten randomly chosen trees (Fig. 1). Since the diurnal resting places were always on the tree above the reading coil, every movement of a gecko leaving or returning to its tree was recorded. As the position in relation to the coil of a captured gecko was known, it was possible to determine whether a gecko returned or left its tree. With this

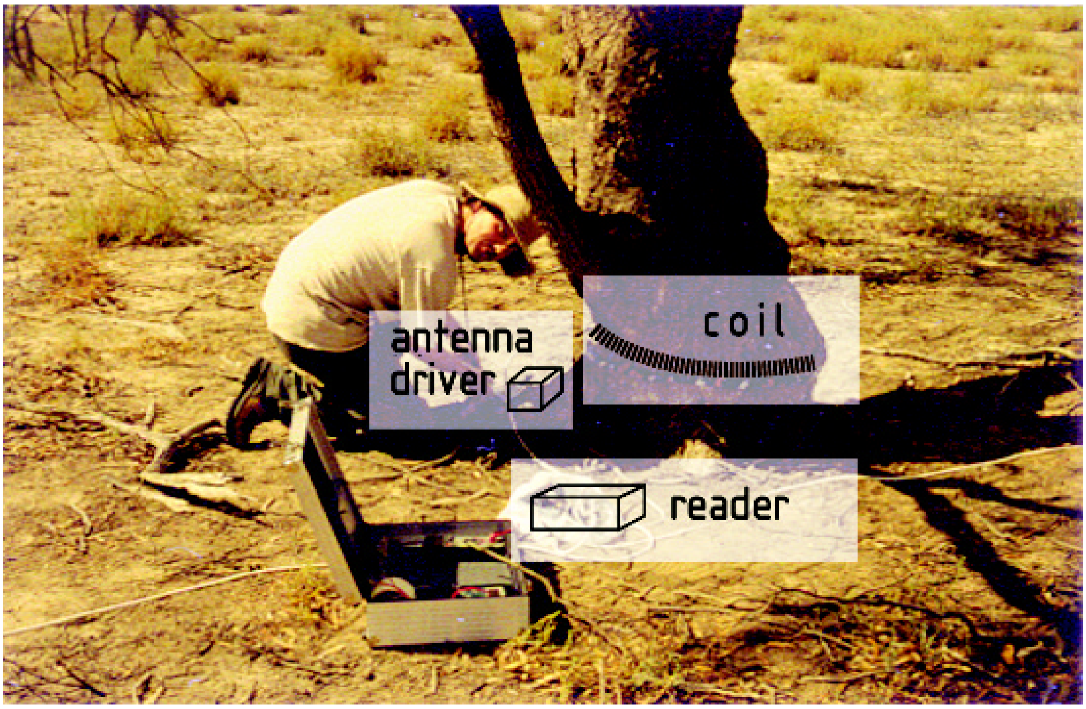

*Fig. 1 Components of the automatic movement monitoring system.*

system the movements of geckos during nights could be observed without any disturbance by an observer. This movement served as an index for activity, because whenever an animal was recorded, it had moved from its resting place to another place or returned to its resting place.

## *Methods*

### Model species *Gehyra variegata*

From former studies some of the daily activity pattern of the arboreal gecko *Gehyra variegata* is known. Bustard (1968) suggests that after digestion ceased (due to dropping air temperatures) from about midnight until 7 or 8 am, nocturnal geckos become active again, shortly after sunrise, to increase the metabolic rate by increasing body temperature. He described that *Gehyra variegata* thermoregulates during the day by movements to warmer places inside their hiding places.

At favourable conditions (windy, warm temperatures and abundant food) *Gehyra variegata* seems to leave their trees and hunt on the ground (Henle pers. comm.). There is an emerging view that geckos are active hunters (Werner et al. 1997a,b). The hypothesis is that hunting on the ground has several advantages. The food is more abundant on the ground than at the branches of the trees and some of the most favourable food is found here (members of orthopteran species, Bustard 1968, Gruber direct observations). Secondly, on ground a predator can hunt in a two-dimensional way, which increases the hunting area and the hunting success. On the contrary, a gecko hunting on a “one-dimensional” branch, has much more difficulties to get its prey. Additionally there are more geckos hunting on the ground, if it is a windy night (Henle, Gruber pers. observ.). At windy nights the numbers of flying insects around the leaves of the tree are much lower and they are probably also harder to catch due to movements of the twigs in the wind. Another reason for a gecko to leave its tree is to defend its territory against conspecifics. (Bustard 1967a, Henle 1990a).

### Study area

The study was carried out in two consecutive years from 19.02.-15.03. in 2000 and from 18.02.-09.03. in 2001 in Kinchega National Park (32°28’ S, 142°20’ E) in western New South Wales, Australia. Kinchega is located at the eastern border of the arid zone. The study site contained 41 black box trees (*Eucalyptus largiflorens*) in a plot of approximately 150x100 m of riverine woodland (Fig. 2). The climate is characterized by a highly variable and patchy rainfall, hot summer and mild winters (Robertson et al., 1987). For a detailed description of the study site see Henle (1990a) and for the climate of the area Caughley (1987).

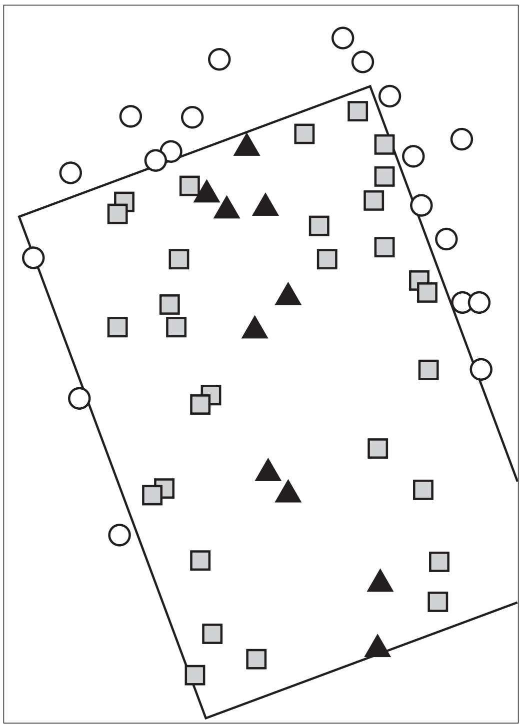

*Fig. 2 Configuration of the 41 trees at the study site in Kinchega National Park. The rectangle frames the 41 trees inside the study site (drawn as boxes and triangles), that were searched for geckos. Trees plotted as triangles were equipped with an automatic activity recording system. Trees outside the study area are marked as circles.*

Air temperature was measured hourly by an automatic weather station, located 500 m away from the study site. Substrate temperature was recorded at 20 minute intervals with an automatic datalogger, which was placed in a hollow trunk of a tree. Due to failure of the data logger, the substrate temperatures were only recorded in Summer 2000 (see Fig. 7). Body temperature of captured geckos was not measured, as body temperature is almost identical to substrate temperature, when geckos are captured at night (Kitchener et al. 1988, Henle 1990a) Sampling of geckos was started approximately 30 minutes after sunset. Each tree of the habitat was examined for at least three minutes for active geckos by spotlighting. Geckos were caught by hand and treated by a standard handling procedure consisting of sex and age determination (if possible), measuring snout vent length, and weighting (accuracy ±0.01 g). Each gecko was marked by toe clipping and with an inconspicuous color using permanent marker pens. Geckos, which were captured at trees equipped with the automatic activity recording system, were tagged with an PIT tag (see below).

### Automatic activity monitoring system using passive integrated transponder (PIT) technology

Ten of the 41 trees were equipped with an automatic activity monitoring system (Fig. 2). The system consists of three components: the reading unit, the information carrying device (PIT tag) and the data storing unit. The reading unit itself consists of the reader (LID 4100 Mini Reader, Euro ID) an antenna driver (EUR 3110, Euro ID), and a PIT reading coil. Except of the reading coil all components are standard components and no modification was necessary. Every reading coil was fitted individually to each tree. For this purpose a wire (0.75 $mm^2$ diameter) was wound around a tree and fixed to the trunk using hot-glue. The installation of the reading coil is quite a delicate task, because the coil has to emit an electromagnetic field of a specific frequency (125 kHz). Attainment of the required frequency was achieved by measuring repeatedly the frequency while winding the wire around the trunk up or down.

To record every activity of a tagged animal, it is important to accomplish a reading distance, which is greater than the height of a tagged animal. Reading distance is a function of the strength of the reader´s electromagnetic field, orientation and velocity of a passing animal (Boarman et al. 1998). The strength of the electromagnetic field increases with the number of coils, and this number depends on the perimeter of the tree trunk, hence the bigger the diameter of the tree trunk, the lower is the detection distance. The detection distance of the reading unit was checked regularly during the study.

For the information carrying device a standard PIT tag (ID 100, Euro ID) was used. The tag was attached to the back of a gecko (Fig. 3) by a very small amount of super glue (Cyanoacrylate). Other glues were tested in a pilot study, but none lasted longer than super glue. The size of each tag is about 2.1 mm in diameter and about 11.5 mm in length, which is the size of a rice corn. The mass is 0.1 g which is 2-3 % of the mass of an adult gecko (3.5-4.5 g). Passive integrated transponder (PIT) tags use radio frequency identification technology (Ames 1990). The tag derives its power and timing signal from the reader´s field. When activated by a gecko passing the coil, and hence the electromagnetic field of the reader, the PIT tag emits its unique identification number by modulating the electromagnetic field. The reader detects and decodes the modulation of the field and sends the code together with time and date to a datalogger. Every morning the data of each tree of the previous night were downloaded to a computer. The recording system was switched off at about 11:00 (EST) and switched on again at about 17:00 (EST), because it was not sure how the technique will resist the very high temperatures during midday.

In total 29 animals were studied using 40 PIT tags, because some animals were tagged more than once (Tab. 1). The sex ratio was different in both studies but when combined about the same number of males (14) and females (12) were tagged; the remaining three subadults could not yet be sexed. For the rest of the analysis the data of both years were combined.

*Tab. 1 Number of animals tagged and PIT tags used.*

| year | animals tagged 1 x | animals tagged 2 x | animals tagged 3 x | animals tagged 4 x | used pit tags | males | females | sub adults | tagged anmimals |
|---|---|---|---|---|---|---|---|---|---|
| | 9 | 4 | 2 | 0 | 23 | 10 | 4 | 3 | 17 |
| | 9 | 2 | 0 | 1 | 17 | 4 | 8 | 0 | 12 |
| | 18 | 6 | 2 | 1 | 40 | 14 | 12 | 3 | 29 |

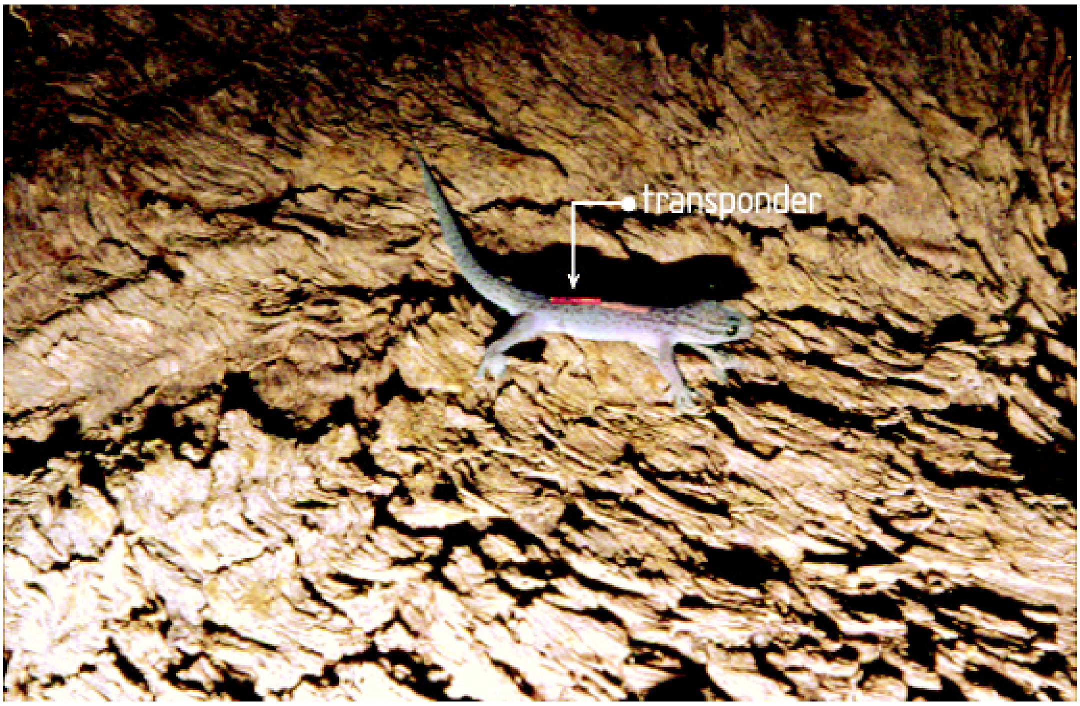

*Fig. 3 Gecko tagged with a transponder.*

## *Results*

### Durability of PIT tags

I scored the minimum durability of tag attachment. The minimal durability is the time a tag stayed attached on an animal, as confirmed either by the automatic system or by an observation of the animal with the tag still on its back. A high variation in the durability of tags was observed (Fig. 4). This was expected since geckos regularly renew their skin. Some tags lasted probably much longer, but were not recorded. Out of 40 tags attached 15 tags were never recorded and were lost almost immediately. Seven tags (at seven different animals) lasted for more than a week, and 18 between a day and a week.

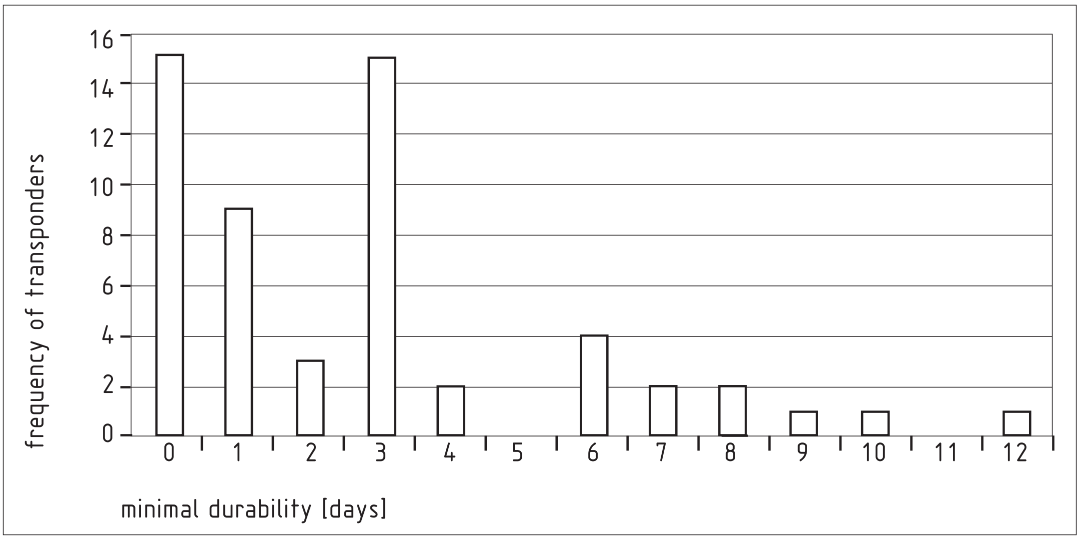

*Fig. 4 Minimal durability of PIT tags (n=17) attached on geckos in Summer 2001.*

### Reading distance

The reading distances of coils at ten different trees were measured (Fig. 5). The detection distance varied between 1.5-2.8 cm and was well above the height of an gecko tagged with a PIT tag (1.0 cm). The system was tested by passing a PIT tag by hand faster than the known maximum aerobic speed of nocturnal geckos (0.24-0.33 km $h^{-1}$) (Autumn 1999). To test the system further, newly tagged geckos were placed close to the coil. Every gecko who passed the coil was recorded by the system. Some of the trunks had crevices and were hollow so that the gecko could pass the coil at the inside. This causes no problem for the system, because the strength of the magnetic field is much stronger inside than outside of the coil, and is able to penetrate organic materials. Here, the reading distance was much higher: about 30 cm, so that every gecko which entered the tree via a hollow trunk could be detected.

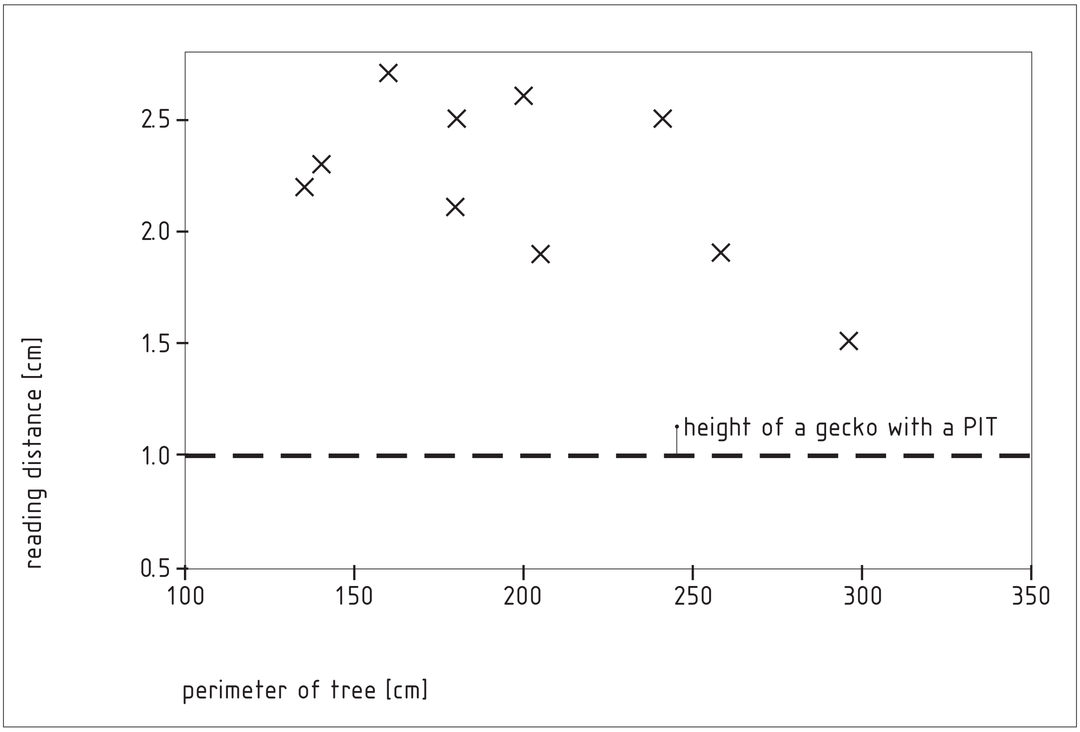

*Fig. 5 Reading distance [cm] of PIT tags at different perimeters of tree trunks.*

### Ambient temperature and activity

The substrate temperature ranged from 19.4 to 40.9 °C during the day to 15.7 to 32.9 °C during the night. Temperature reached its maximum at about 16:00 (EST) and continuously dropped until the minimum at about 5:00 am in the early morning was reached. A rather steep rise in substrate temperature occurred at sunrise (about 6:00 am).

The system recorded 178 movements of geckos (139 in summer 2000 and 39 in summer 2001) moving up and down the trees. The reason for the low number of records in summer 2001 were the smaller number of observing days and the lower temperatures. The overall picture of activity is the same for both years and therefore the results were combined. Geckos started to be active around sunset, which was at about 19:30 (EST) (Fig. 6). The activity decreased until midnight, but some animals were active throughout the whole night. Just before sunrise at about 6:00 am (EST) there was a second peak in activity.

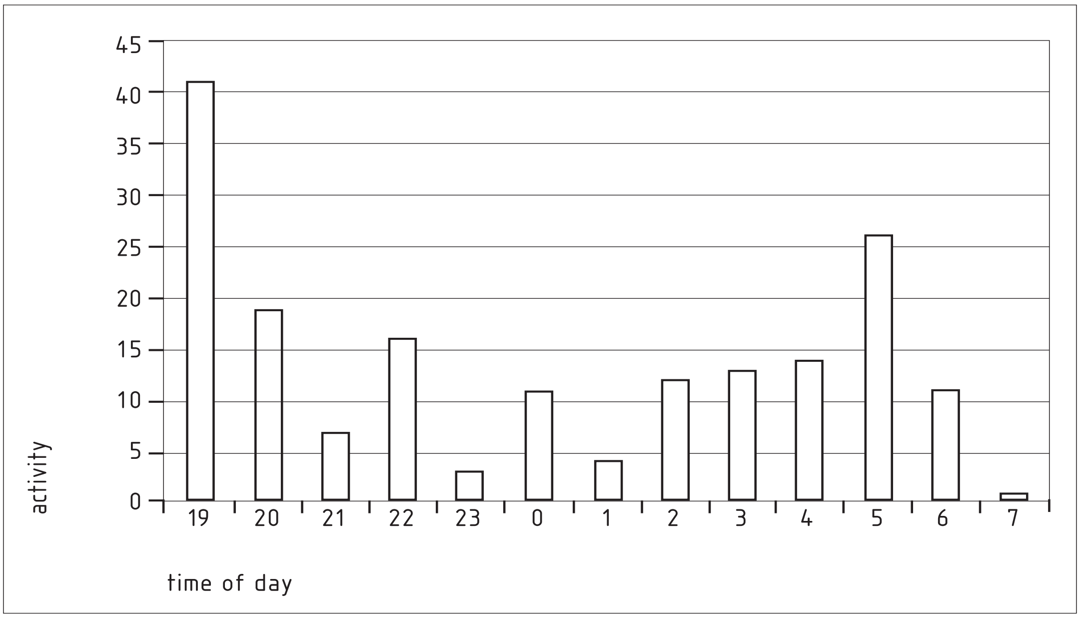

*Fig. 6 Activity of geckos in relation to the time of day in both years.*

For summer 2000 activity can be related to substrate temperature (Fig. 7). At sunset a net number of geckos left their tree. Some returned before midnight, the rest during the early morning. At sunrise (indicated by the time, when the temperature starts to rise) there is a second activity peak, when geckos started to leave their trees again until activity ceases after 7:00 (EST).

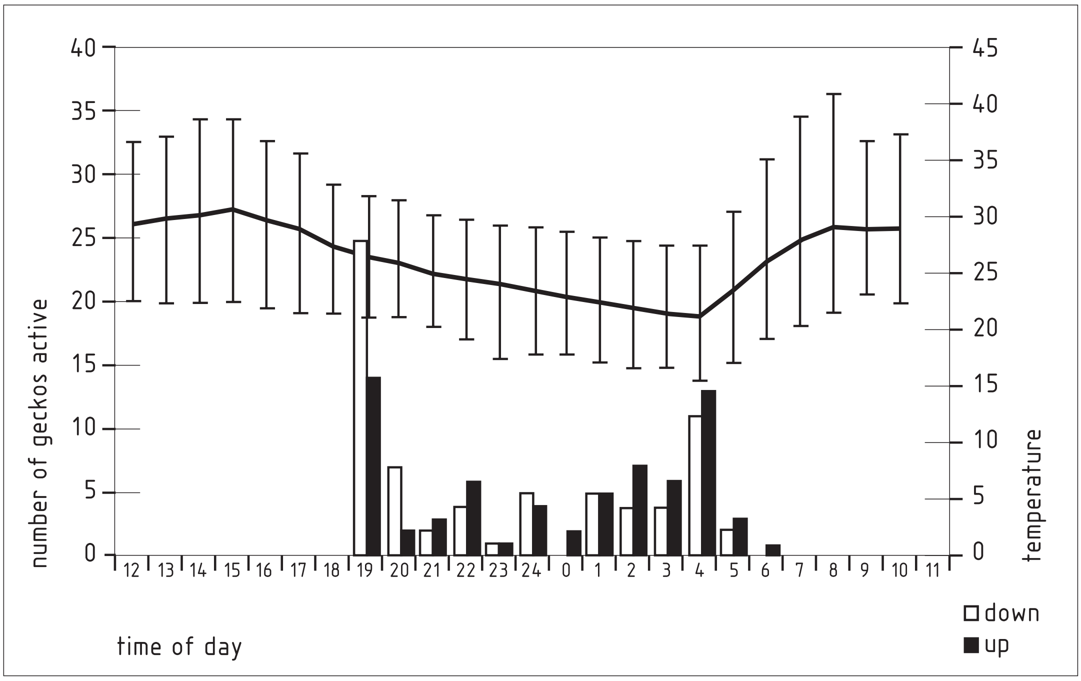

*Fig. 7 Temperature (mean, daily maxima and minima of the study period in a hollow tree trunk) and activity of geckos (movements up and down of trees) in summer 2000 in relation to time of the day.*

## *Discussion*

### The automatic movement monitoring system

The new system worked very reliably and had no malfunction. Unfortunately, a main problem is the high number of tag losses. Examining the distribution of the minimal durability, there are some tags which are lost almost immediately, possible because tags, have not been attached properly. After three days the losses distributed uniformly. This kind of distribution is expected when the sloughing of the animals is randomly in respect to gluing PIT tags on them. However, on seven animals the mark of the permanent color pen was still visible when recaptured, but the PIT tag was lost. Hence these animals lost their tag without complete sloughing. Nevertheless, from animals marked with the water resistant color pen, it is known that this occasionally can limit the ability of animals to slough at the marked parts of the body. So it seems possible for some individuals to partly renew their skin under the PIT tag without loosing the skin at other parts of their body. The best results were achieved by using only a very small amount of glue and letting the glue dry at least ten seconds. Then the PIT tag was pressed firmly on the back of the animal, holding the tag and the animal still for about 20 seconds. If another method could be found (e.g. using a rucksack made of latex) and this problem could be solved, a continuous recording of activity over a long period of time would be possible. Injection of tags under the skin was rejected, because of the small size of the animals. PIT tags had been injected in even smaller sized newts (*Triturus carnifex* and *T. alpestris*) without reporting a harmful effect (Fasola et al. 1993). However other studies reported from 1-40% death of individuals in studies on different species of reptiles (*Sistrurus miliarus:* Jemison et al. 1995, *Triturus alpestris:* Faber 1997) and amphibians (*Xenpous laevis:* Mrozek et al. 1995) (for a review see Henle et al. 1997).

The detection distance of the reading coil was higher than the height of a gecko with a PIT tag and was adequate to detect every movement across the coil. No gecko equipped with a PIT tag was found at another tree without recording. This was further confirmed by animals observed during inspections at the vicinity of the reading coil and their regular registration on the the datalogger the following day. Due to the limited range of the magnetic field only animals at fixed locations can be observed, which is reflected by the ecological systems studied so far with the help of PIT technology [e.g. birds at their nesting sites (Freitag et al. 2001), desert tortoise moving through culverts under roads (Boarman 1998), swarms of fishes at fishways (Castro-Santos et al. 1996), and a tree living gecko (this study)). A new invention in this study were the "self-made" coils, which generate the electromagnetic field for the PIT tag. The field must have a specific frequency and it is necessary to fix each loop of the coil precisely for a long period of time. This was done by using hot glue which proofed to resist the harsh climate for over a month. A long-term test for determining the durability of the reading coil is under way.

This study demonstrates the advantage of the new developed system. The activity of small and cryptic animals can be observed under natural conditions without disturbance. Moreover the animals can be observed during a long period of time and new findings like a second peak of activity at sunrise were obtained, which had been overlooked so far. There are several opportunities to further improve the presented system. In this study the data were recorded via a datalogger, but it is possible to directly connect a computer to the system. So a field ecologist could notice when geckos are active and try to observe activity directly for collecting additional behavioral data. Another possibility would be to connect the system to the Internet and download the data from there. This would be a very cost effective way (because not much human labour is involved) of obtaining long-term activity data of animals in remote areas.

### Activity

It is known that nocturnal lizards may actively thermoregulate during the day (Bustard 1967a, Huey et al. 1989, Kearney & Predavec 2000), because nocturnality imposes a thermal handicap which constrains performance to suboptimal levels (Autumn 1994). There are several findings which support this hypothesis. It was long known that geckos prefer higher temperatures when held in a thermal gradient in a laboratory (Licht et al. 1966, Pianka & Pianka (1976), Huey (1982), Arad et al. (1989). Comparing the growth of a gecko (*Eublepharis macularius*) in different temperature regimes, Autumn & DeNardo (1995) showed an increased growth rate by geckos raised at higher temperatures. In a telemetry study of Autumn (1995) the nocturnal lizard *Teratoscincus przewalskii* showed a body temperature cycle very similar to diurnal lizards, which is high during day and low during night.

Nevertheless, many researchers reported an unimodal distribution of activity for nocturnal geckos during the night (Bustard 1967a, Pianka & Pianka 1976, Henle 1990a, How & Kitchener 1983, Sarre 1995, Walker et al. 1991), and activity during the day was rarely reported (but see Bustard 1967a). This study shows a second peak of activity at sunrise. Such a peak fits well the hypothesis that geckos have to actively thermoregulate during the day. Activity peaks just before sunrise were also observed by Cooper (1985) in the Banded Gecko (*Coleonyx variegatus*), held in an outdoor facility.

The lack of similar field observations can be explained with the activity patterns of researchers that rarely extend across the whole night. I suggest the following activity regime for *Gehyra variegata,* which should be similar in other arboreal nocturnal gecko species in semiarid climate. Activity is at its peak shortly after sunset and decreases as temperature drops down. In hot nights when temperature remains high, the activity takes place longer and may extend until sunrise. At sunrise a second peak in activity occurs, because geckos try to increase their body temperature, which is best done in direct sunlight. To achieve this they leave their hiding places and try to get as much sunlight as possible. They move down to the basis of the trunks where more direct sunlight is available, because there is no shadow, cast by twigs at higher levels of the trees. After they have increased their body temperatures to an optimal level for digestion they rest during the day in their hiding places, maintaining high temperatures. This allows geckos to immediately respond to disturbance during the day, in contrast to diurnal reptile species that require a longer response time, in their nocturnal retreats (Henle, pers. comm.). Thus, suitable diurnal retreat sites may have important consequences for the distribution and abundance of nocturnal species of geckos (Kearney & Predavec 2000).

# Chapter II

## Orientation and movement in a structured population of the arboreal gecko (*Gehyra variegata*)

### *Introduction*

Understanding how organisms move through landscapes is important for predicting the effects of landscape structure on population dynamics and distribution of organisms (Johnson et. al 1992, Wiens et al. 1993, With & Crist 1995, 1996, Ims 1995, Turchin 1998). There are various components of movement behavior, which influence the movement of animals via a given landscape (Goodwin et al. 1999). An important aspect of movement behavior is the ability to orient, to detect familiar and suitable habitat. Despite this importance our knowledge about the perceptual ability in vertebrates is limited (Zollner & Lima 1997, 1999), especially lizards.

Successful homing after translocation has been reported for some species of lizards: *Sceloporus undulatus* (Noble 1934, Hein & Whitaker 1997), *Sceloporus orcutti* (Mayhew 1963), *Sceloporus graciosus* (Guyer 1978), *Sceloporus jarrovi* (Ellis-Quinn & Simon (1989), *Uta stansburiana* (Spoecker 1967), *Takydromus tachydromoides* (Ishihara 1969), *Dipsosaurus dorsalis* (Krekorian 1977), *Phrynosoma douglassi, Tiliqua rugosa* (Freake 1998, 1999), *Podarcis sicula* (Birukow et al. 1963, Verbeck 1972) and *Lacerta viridis* (Fischer & Burikow 1960, Peters 1970). To my knowledge no report on homing behavior of geckos exists in the literature. Different mechanisms for successful homing have been proposed for a number of different taxa [compass orientation, geotaxis, use of sensorial (visual, magnetical, and olfactorial) cues, and use of e-vector direction of polarised light] but were rarely demonstrated for reptiles (compass orientation: Fischer & Burikow 1962, Burikow et al. 1963, Newcomer et al. 1974, Murphy 1981; use of visual cues: Weintraub 1970, Krekorian 1977; use of olfactorial cues: Peters 1970; and use of e-vector direction of polarised light: Adler & Philips 1985, Chelazzi 1992, Freake 1999.

The daily activity of the nocturnal and arboreal gecko *Gehyra variegata* suggests that they have a highly developed ability to orientate in the area close to their home range. *Gehyra variegata* is strongly territorial (Bustard 1968, Henle 1990a, Sarre et al. 1996). During the activity period at night the geckos often leave their trees and hunt for insects around the base of trees. At the end of their hunting activity they return back to their tree to hide during the day (Henle 1990a, Gruber pers. observation, chapter I). Some individuals have been recaptured on the same trees for many years (Henle, pers. comm.). For this kind of behavior it is necessary to have a good orientation and knowledge of the habitat surrounding the territory.

From studies of the vision of geckos, it is known that they are well adapted to orientate in darkness (Loew et a. 1996, Röll 2000). Moreover, they have highly moveable eyes for binocular vision (Röll 2001). This enables them to estimate distances by the use of asymmetry of the images on the two retinae of the eyes (Crescitelli 1977).

Homing ability has been studied with direct and indirect approaches. Translocation experiments allow a direct study of homing ability. As this kind of approach is a controlled experiment, it is easy to control covariates believed to be important. For example if temperature is meant to be important for homing success, animals can be translocated under a controlled temperature regime. However, for some animals this approach is not possible, because it is too difficult to translocate them. Also translocation of animals may result in an increased stress due to handling and animals under stress might respond differently compared with undisturbed individuals (Goodwin et al. 1999)

An indirect way of testing the orientation ability of animals is the study of their movement in relation to structural components of the habitat. This approach is limited due to the fact that many covariates are not controlled and results are just based on circumstantial evidence (i.e. an animal that seems to orientate visually to a tree can just move because of conspecific attraction or any other reason). Its advantage is that there is no need to transfer animals and therefore the movement behavior is less likely to be influenced by the study.

The goal of this study was an analysis of the homing ability of the nocturnal arboreal gecko *G. variegata*, combining the advantages of the direct and indirect approach. The direct approach (translocation of animals) demonstrated the ability to orientate and to home. Based on the observation that geckos are able to home successfully, hypotheses about the underlying movement rules were created and tested with the second approach (studying movement in relation to structural components of the habitat). The hypotheses were tested by comparing the fit of different movement rules with real movement. These comparisons gave evidence for the importance of vision in orientation of geckos.

## *Methods*

The study was conducted at Kinchega National Park (32°28’ S, 142°20’ E) in western New South Wales, Australia, from 22nd of February till 23rd of March 2000. Kinchega is located at the eastern border of the arid zone. The study site contained 41 black box trees (*Eucalyptus largiflorens*) in a plot of approximately 150x100 m of riverine woodland. The climate is characterized by a highly variable and patchy rainfall, hot summer and mild winters (Robertson et al., 1987). For a detailed description of the study site see Henle (1990a) and for the climate of the area Caughley (1987).

### Short-term homing behavior

Short-term homing behavior was tested experimentally by translocating adult animals to neighbouring trees and tracking the animals using fluorescent powder technique (Fellers & Drost 1989). The distance to the next neighbouring tree varied between 10-30 m; the original tree was still visible after translocation. As it was known from previous studies (Sarre et al. 1996, cf. chapter III) that there are two types of individuals, floaters and territorial individuals, a control group was released at the tree of capture. Floaters are individuals who possess no territory and drift between trees. Territorial individuals stay at a certain tree for many years. Hence, if floaters are translocated, it is not expected that they return to the tree of initial capture, but territorial holders are expected to.

Animals were captured at the beginning of their activity immediately after sunset. The captured animals were marked with fluorescent pigment of different colors (Radiant colors, R-105 series, red, orange, pink, green, chartreuse, and blue) to allow their tracking and randomly allocated to the treatment or the control group. The animals were tracked with a portable UV-Light (6 W, 365 nm) during the next night. It was necessary to run the light under a powerful 12 V lantern battery to get enough light for tracking. Unlike in other tracking studies with fluorescent pigments, it was not possible to track all animals longer than one night and therefore only data from the night after capture were used in the analysis. After initial trials pigment blue was omitted from the study, because it was too difficult to track. The best colors for tracking were orange and green.

### Long-term movement behavior

For studying the intra-population movement and to deduce the underlying movement rules the data of a long-term capture-mark-recapture study were used (Henle 1990a, Gruber & Henle, unpubl.). The configuration of 41 trees in the habitat was mapped by measuring distances between trees and using triangulation techniques to obtain cartesian coordinates of the trees in the study area.

Each time an individual was captured the location (tree) was recorded. When an animal was captured at a different location, the euclidean distance was calculated. As geckos are almost exclusively caught at trees, it is obvious that the moved distances must somehow reflect the distances that are determined by the configuration of all trees in the habitat.

To link movement with the structural configuration of the habitat, I calculated the distribution of distances assuming different movement rules. This was done by calculating the distances between all pairs of trees in the habitat. The movement rules restricted the possible movements between trees. For example, one of the movement rules assumed that a gecko leaving a tree would choose one of the four next neighbouring trees (nn4, see Fig. 8). The distances of the allowed movements were recorded and histograms of the frequencies of distances for each movement rule were plotted (Fig. 9, Fig. 10). As it was supposed that vision was of primary importance for orientation of geckos, some movement rules took realistic visional rules into account, e.g. a gecko that decided to move to the four next neighbouring trees, would choose one of the four trees that are visible from its location and not hidden by other trees, although these trees may be further away than other trees (nn4 visible, Fig. 8). These two basic movement rules were varied in the number of trees that were taken into account (nn2 to nn6, nn2 visible to nn6 visible).

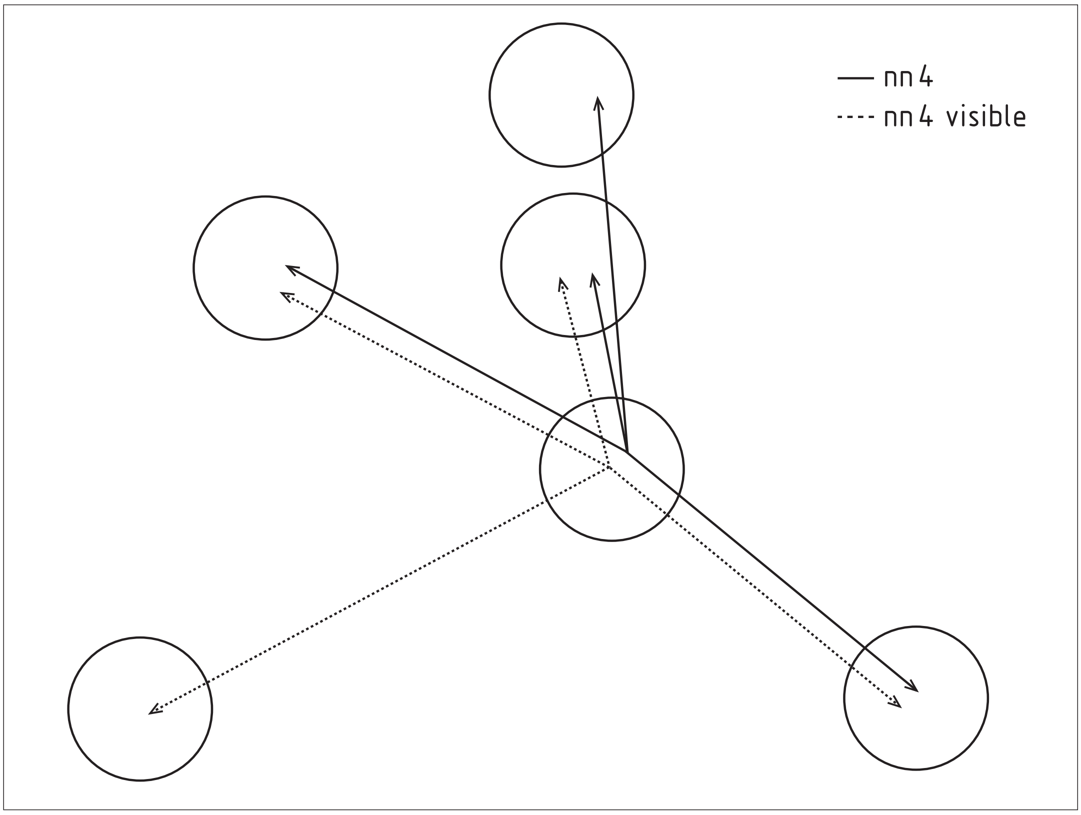

*Fig. 8 Example of two different movement rules.* nn4*: geckos move to one of the four next neighbouring trees;* nn4 visible*: geckos moves to one of the four next neigh-boring trees that can be seen from the origin.*

For each movement rule the distribution of distances was calculated and compared with the distribution of moved distances. The difference of these distributions were tested and ordered for all movement rules by their $\chi^2$ value.

To further evaluate whether geckos orient visually, the number of movements to a tree that can be seen from the origin, was compared to the number of movements to a hidden tree. The proportions of visible to hidden trees of the 3 next neighbouring trees for each tree in the habitat was calculated using basic geometric laws. For each tree in the habitat the 3 next neighbouring trees were determined. A computer program determined the number of trees covered by other trees, and the number of trees not covered by other trees assuming an average crown width of 5 m. (the average crown width was determined by measuring the crown width of each tree using standardized photographs of each tree).

## *Results*

### Short-term homing behavior

50 Geckos were captured and marked with fluorescent powder. 25 were released at the same tree and 25 were released at the next neighbouring tree (at least ten m away). Of 25 animals released at the tree of capture, 23 were found on the same tree the following night (Tab. 2). Of 25 translocated geckos 14 stayed at the tree of release and 11 returned to the tree, where they were initially captured. Significantly less of the translocated animals stayed at the tree of release (exact-Fisher-test, doublesided $p = 0.0083$). All translocated animals that moved away (11) returned to the tree of capture. Two of 25 animals, which were not translocated, left the tree. One gecko moved to a fence and the track of the other animal was lost 25 m away from the tree.

*Tab. 2 Number of translocated and control animals, which stayed/moved away from the tree of release.*

| | not translocated | translocated | sum |
|---|---|---|---|
| stayed | 23 | 14 | 37 |
| moved | 2 | 11 | 13 |
| sum | 25 | 25 | 50 |

### Long-term movement behavior

The distances moved as revealed by the capture-recapture study were plotted against the distances between trees, under different movement rules (Fig. 9, Fig. 10). The strategies to move randomly to 2..6 next neighbouring trees, (nn2..nn6), regardless of their visibility are shown in Figure 9. For these movement rules, the best fit was obtained for nn4. This was the only movement rule not based on vision that is not significantly different from the distribution of moved distances (Tab. 3). The nn5 and nn6 movement rules show worse fit, especially for distances higher than 30 metres. Movement rules that took vision into account exhibited a considerably better fit than the purely random movement rules. This indicates that geckos use visual cues, when they move between trees. The best fit was observed for random movement to one of the three next neighbouring trees not hidden by other trees. Interestingly there was a step in the distribution of moved distances between 8 to 12 metres. The same step was exhibited by movement rules, which take vision into account (Fig. 10).

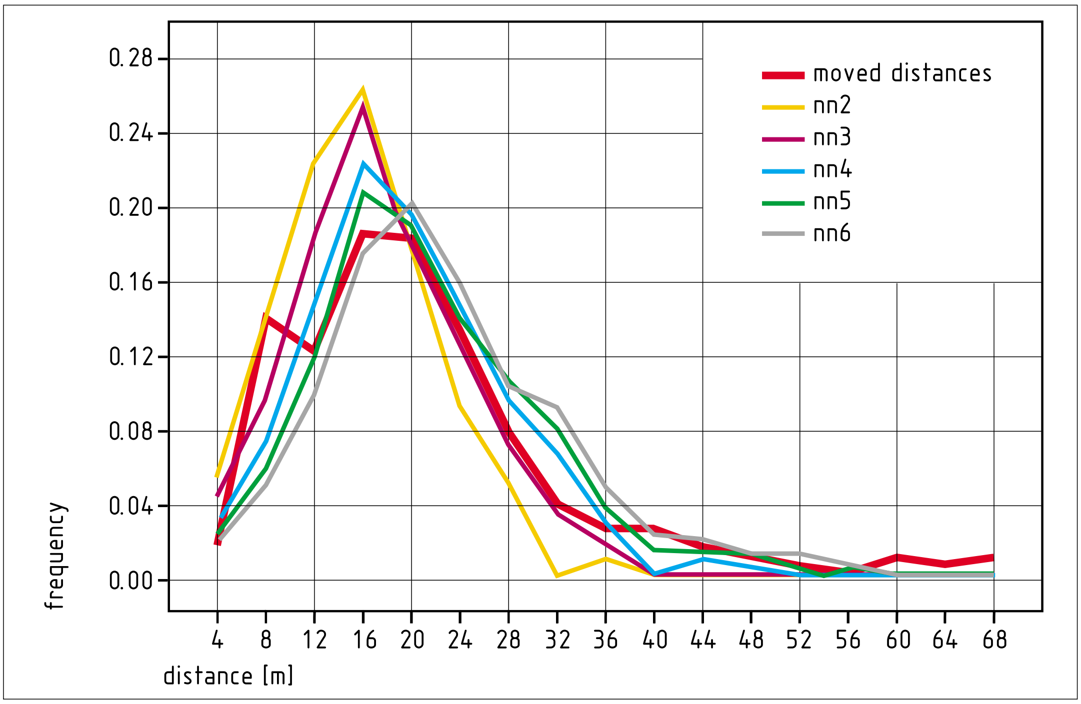

*Fig. 9 Frequency of distances for moved distances and for different movement rules (nnx indicates that a gecko chooses one of the x next neighbouring trees when it decides to move.)*

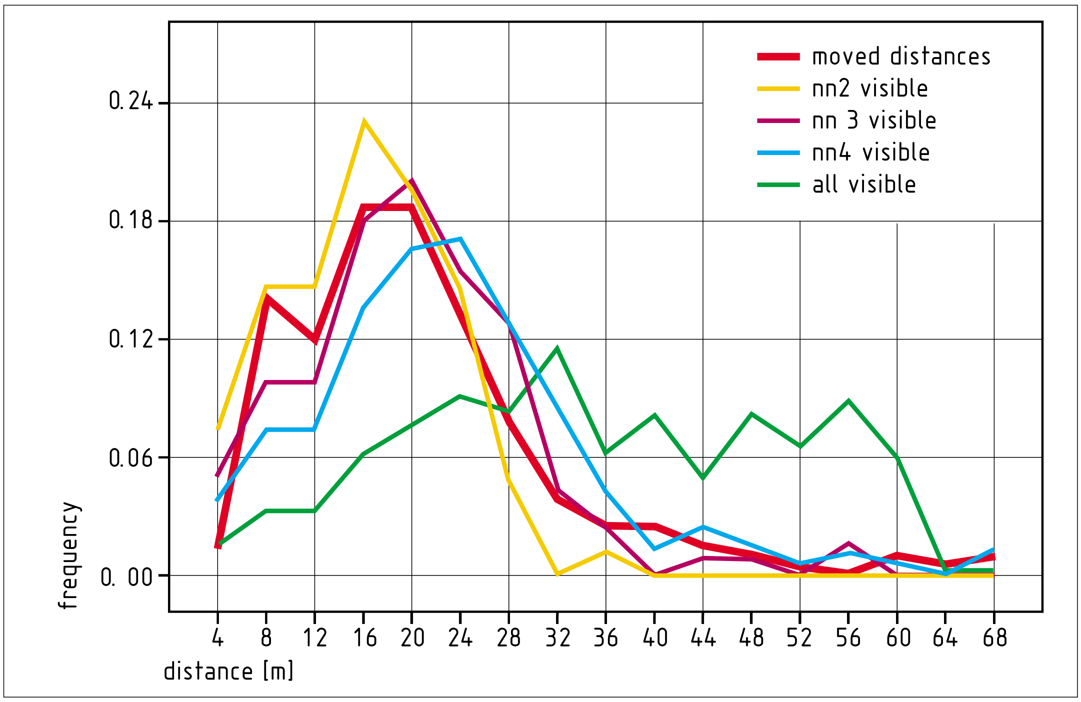

*Fig. 10 Frequency of distances for moved distances and for different movement rules (e.g. nnx visible indicates that a gecko chooses one of the x next neighbouring trees that are not hidden by other trees.)*

*Tab. 3 Results of $\chi$2-tests between the frequencies of moved distances and the frequency of distances for different movement rules. Note that the degree of freedom is the same for every test, as the pooling was the same for all movement rules.*

| movement rule | $\chi^2$ | dg | p |
|---|---|---|---|
| nn3 visible | 14.950 | 16 | 0.528 |
| nn4 visible | 16.579 | 16 | 0.413 |
| nn2 visible | 18.289 | 16 | 0.307 |
| nn4 | 24.803 | 16 | 0.073 |
| nn2 | 31.451 | 16 | 0.012 |
| nn3 | 37.432 | 16 | 0.002 |
| nn5 | 38.663 | 16 | 0.001 |
| nn6 | 55.738 | 16 | 0.000 |
| all visible | 281.826 | 16 | 0.000 |

To study the effect of tree visibility on movement, movements were grouped into two types. The first group contained all movements of individuals that moved to a tree, which can be seen from the tree of departure. The second group contained all movements of individuals to hidden trees. Of a total of 206 movements analyzed, 83.5% fall into the first group and 16.5% into the second group. From the configuration of trees the proportions of visible to hidden trees was calculated using basic geometric laws. There were significantly more movements to trees that are visible before departure (Test on differences of proportions $z=-2.24$, $p=0.032$) than would be expected, if movement is based purely on the habitat configuration. Since the movements are based on capture-recapture events, which are likely to include gaps in the movement history, the real number of animals that move to hidden trees is probably even lower.

*Tab. 4 Proportion of movements to visible/hidden trees compared with proportion of visible/hidden trees in the habitat patch.*

|  | visible | hidden |
|---|---|---|
| trees in habitat | 70.30% | 29.60% |
| movements to | 83.50% | 16.50% |

## *Discussion*

Empirical information on “landscape level” behavioral phenomena is an important missing link in the study of animal ecology (Stamps et al. 1987, Wiens et al. 1993, Lima & Zollner 1996). Animal ecologists have identified animal movement as a particularly important determinant of the dynamics and spatial distribution of populations in heterogeneous landscapes (Turner 1989, Turchin 1998).

During the translocation experiment geckos showed the ability and a high tendency to return to their initial tree. All animals (n=11) that were translocated and moved away from the tree of release returned to their home tree (Tab. 2). The tracks of movement were almost straight back to the tree of capture. Due to the short duration of the tracking study animals that did not return in the next night were not tracked and it is likely that the tendency to return was even higher. Nonetheless, 14 translocated animals remained on the tree of release at least for one night. This could have been due to the fact that they were floaters, which show less tendency to return. However, only two of 25 animals moved away from the tree, if they were not translocated, indicating a low number of floaters. In any case the random allocation of individuals to treatment and control group preclude floaters as an explanation between the treatment and control group. Since individuals were randomly allocated, the motivation to move after capture and marking was much higher in the translocated individuals than in the non-translocated individuals. Another explanation is that those animals that did not return were translocated to trees, where no other gecko was present. In such a case they would not have been driven away by territory owners and either may have stayed on the tree or returned only after the end of the experiment. Most translocation experiments do not take into account individual variability in the motivation to return (e.g. Ellis-Quinn 1989, Zollner & Lima 1997, 1999), but it has been shown that the individual status of an animal (sex, age, territory holder) is important (Rodda 1984, Sinsch 1992, Freake 1998).

Movement is a key process for population dynamics in a structured population (Ims 1995, Lima & Zollner 1996, Turchin 1998) to maintain a connection between individuals of the population. Moreover, if the density in patches is low (about one adult male and one adult female gecko per tree (cf. chapter III)), there is a high need for movement to achieve a high reproductive success for the population and to avoid Allee effects (Allee 1931, Wiegand et al. 2001). It has been shown that the predation risk is high, when moving on the ground between trees (chapter III). Therefore, it is an advantage for an individual to be able to orientate to the next tree as quickly as possible, making the predation risk as low as possible.

Among the possible mechanisms for visual homing behavior of *Gehyra variegata* are compass orientation, geotaxis, use of sensorial cues, and use of the e-vector of polarised light.

As most geckos, *Gehyra variegata* is nocturnal, and therefore, use of e-vector direction of polarised light is not possible. No slope exists in the habitat of study, hence no gravitational cues do exist. Compass orientation is exhibited and found by animals that live close to a shoreline or a similar linear landscape feature (Ferguson 1967, Newcomer et al. 1974, De Rosa & Taylor 1982). No such feature does exist in the habitat, hence this kind of orientation mechanism is not possible. Regarding other sensorial cues, vision and olfactorial cues are most likely. It is not possible to discriminate between these two senses in this study, but there is strong indirect evidence for vision as the orientation system. A peak of activity of geckos occurs immediately after sunrise (chapter I), which indicates that vision seems to be important for orientation. In a study on vertebrates Zollner & Lima (1999) demonstrated the importance of different levels of light for orientation of white-footed mice (*Peromyscus leucopus*).

The data from the capture-mark-recapture experiment gave evidence that geckos do orientate visually. The movement rule: “move to one of the three next neighbouring trees that are not hidden” fitted best. The only purely random movement rule that caused no significant difference in the distribution of distances, was the 4nn rule. This is reasonable due to the fact that the 3nn visible rule shifts the distances of trees to higher values than the 3nn rule, resulting in a distribution similar to the 4nn rule. The runs of the curves of the visible rules have a step between 8-12 m, very similar to the distribution of distances moved. Due to geometric reasons this is expected, as the “shadow-effect” of a tree that hides another tree is greater the closer the tree is. Importantly, this step is absent in all movement rules that do not take vision into account, indicating a qualitative, albeit not statistically significant, difference.

Additionally, geckos moved significantly more often than expected from habitat geometry to trees that were visible from their initial trees, which indicates the importance of vision for orientation of geckos. There seems to be a visual range limiting the distances moved. Almost no moves occurred beyond 40 m and movement rules taking more than four trees into account fitted badly; this is especially the case for the movement rule: “move to any tree, which is not hidden”, showing by far the worst fit. However, the short distances individuals cover during movement may also be attributed to a higher risk of mortality (cf. chapter III) instead to a limitation in the range of vision. The indirect approach of observed movement data cannot discriminate among these two mutually not exclusive hypotheses.

Zollner & Lima (1999) showed the importance of different levels of light on orientation of white-footed mice. Recent advances in robotic technology have shown that it is possible for robots to show homing behavior with a minimal set of visual information (Basri et al. 1999).

A robot equipped with a camera is able to return to its home just by comparing the image of its home location with the images during its search.

To conclude, this study demonstrated the ability of geckos to orient and to show successful homing behavior. Moreover, the comparison of different movement rules with the observed movement behavior provide well evidence that vision is important for orientation of nocturnal geckos. Since the movement behavior could be related to habitat structure, movement behavior can be used to link population processes to landscape structures (cf. Lima & Zollner 1996, chapter IV). This is a prerequisite to understand and predict population dynamics in heterogeneous landscapes, which is absolutely vital for the preservation of endangered species in fragmented landscapes.

# Chapter III

## To stay or to go? The effect of movement on survival in a structured population of the arboreal gecko (*Gehyra variegata*)

### *Introduction*

In recent years it has become increasingly clear that movement is a key process in landscape ecology. Turchin (1998) states "The understanding of how an animal is affected by moving through a given landscape is a basic need for an adequate description of population dynamics in heterogeneous landscapes". The statement is based on the observation that fragmentation of habitat (hence alteration of habitat structure) can have significant effects on population dynamics (Fahrig 1998, Andrén 1994).

The most common view of spatially-structured populations and metapopulations is that animals live in a binary landscape, consisting of suitable patches of habitat surrounded by a hostile matrix (Gilpin & Hanski 1991). Subpopulations that live in such a landscape are interconnected to a varying degree (Wiegand et al. 1999) by movement of individuals. The more individuls are unable to move through the matrix, the more they will be restricted to isolated patches. Animals in such isolated patches are at greater risk of extinction because of stochastic events (Fahrig & Merriam 1994).

Understanding the factors influencing the survival and the spatio-temporal distribution of a population can be helpful for rebuilding threatened populations (Newman 1998). For example, population viability analysis (PVA) is used to predict the fate of populations of threatened species (e.g., Soulé 1987, Shaffer 1990, Possingham et al. 1997). Even if extensive background information for the modeled species is available, accurate predictions are difficult (Wiens 1996, Lindenmayer et al. 2000). Lindenmayer et al. (2000) tested the predictive power of a PVA by comparing it with the known fate of three different species and concluded that valuable predictions could only be made, when dispersal and movement rates are known. Therefore, approaches which allow to assess movement rates and the effect of movement on survival rates are necessary.

Hence, for modeling adequately the dynamics of spatially structured populations, estimates of survival and movement rates are needed (Conroy et al. 1996). Often it is assumed that movement in the hostile matrix results in an increased mortality risk (Fahrig 1998). Mortality during migration (movement) is the most obvious cost of migration (Comins et al. 1980, Olivieri and Gouyon 1997, Hanski et al. 2000). However, this is very hard to measure empirically (Ims & Yoccoz 1997, Fahrig 1998, but see Van Vuren & Armitage 1994).

The focus of this study was to develop an approach to test the hypothesis that movement in a structured population results in higher mortality and apply it to a population of the arboreal gecko *Gehyra variegata*. As capture-mark-recapture data are widely available for a range of animal species, it should be possible to extend its application to other species.

### Biology of *Gehyra variegata*

Four intensive studies on the ecology of the arboreal gecko *Gehyra variegata* exist (Bustard 1968, 1969, Henle 1990a, Kitchener et al. 1988, Sarre 1998). All show that this gecko species is long-lived, with delayed maturity, reduced fecundity and low clutch size. These K-selected life-history traits are attributed to an arboreal life style and are found in other arboreal reptile species as well (Dunham et al. 1988, Henle 1990a). The underlying hypothesis is that an arboreal live style reduces the risk of predation, because it reduces the number of potential predators and therefore favours species with K-selected life-history traits (Dunham et al. 1988). In line with this hypothesis is that terrestrial species of geckos have a much higher individual mortality compared to arboreal species (Dunham 1988, Henle 1990a, b, 1991). One way to test this hypothesis on the species level is to compare the survival rates of individuals that tend to stay at their trees with the survival rates of individuals that move more often between trees.

*Gehyra variegata* is strongly territorial. Both males and females defend their home trees against intruders. Usually one adult pair lives on a tree (Sarre et. al 1996). In addition to territorial adults there are individuals that seem to have no territory and drift between trees (Henle, unpubl. observ.). These animals are referred to as floaters. Floaters should have a higher risk of predation and hence lower yearly survival rates. If one sex is more likely to have floating individuals, then the yearly survival rate of this sex should be lower and the sex ratio should be skewed, if not compensated by other factors. This can be checked by comparing the sex ratio. The arboreal lifestyle of *Gehyra variegata* is an optimal system to study, because the habitat patches (trees) and matrix (area surrounding trees) are easily determined, and movement can be defined as movement between trees.

In this paper I first estimated the population size of a population of the arboreal gecko *Gehyra variegata* in the study area. Second, I determined how often geckos moved between trees and looked for sex specific differences in movement rates. Third, I compared the yearly survival rates for males and females and related them to movement. I validated my findings with an individual-based simulation model, which resembles the capture-mark-recapture study.

## *Methods*

### Study Site

The study was carried out in Kinchega National Park (32°28′ S, 142°20′ E) in western New South Wales, Australia, from February 1994 until March 2001. Kinchega is located at the eastern border of the arid zone. The climate is characterized by a highly variable and patchy rainfall, hot summer, and mild winters (Robertson et al. 1987). The study site contained 60 black box trees (*Eucalyptus largiflorens*) in a plot of approximately 150x100 m of riverine woodland. For a detailed description of the study site see Henle (1990a) and for the climate of the area Caughley (1987). Every year at the end of February, except 1995, for 9-21 days a population of the arboreal gecko *Gehyra variegata* was studied by mark-recapture (Tab. 6). Population estimates are based on geckos living on 41 trees located in the centre of the study side and surrounded by a circle of 19 trees (Fig. 16). The 19 outer trees were also investigated during the study to detect individuals, which left the study site. Geckos were captured by hand and marked with a permanent ink for short-term and by toe-clipping for long-term identification. As it is not possible to determine sex before the geckos reach maturity (at 2-3 years of age), only adults were included in the analysis.

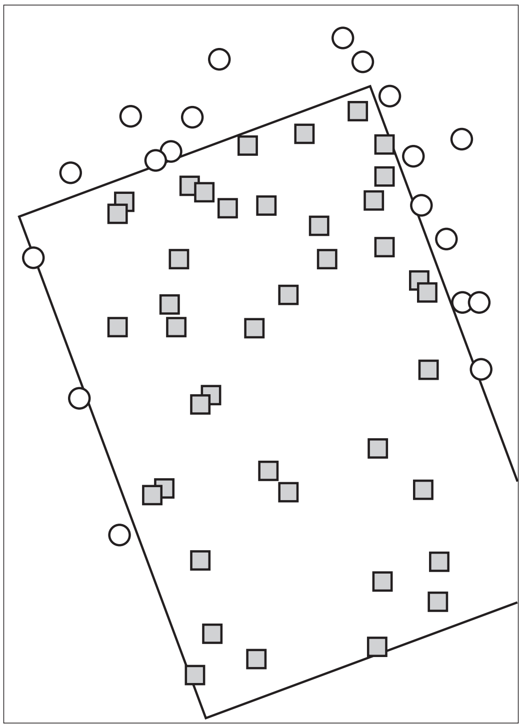

*Fig. 11 Study site with 41 inner (boxes) and 19 outer trees (circles).*

### Population size, movement rates, and survival rates

The study used the robust design of Pollock (1982) and Henle (1988). There are seven primary periods (years) which include 9-21 secondary periods (days). This approach assumes a closed population during a short-term period (several days) and an open population during a long-term period (one year). Population size was estimated using program CAPTURE (Otis et al. 1978). Program CAPTURE allows to relax the often unrealistic assumption of equal capture probability during the whole study period (Model $M_o$). Otis et al. (1978) distinguished between three different sources of variability in capture probability. The possible sources of variability are individual heterogeneity (Model $M_h$), behavioral response to capture (Model $M_b$) or temporal variation (Model $M_t$). CAPTURE provides estimators for numbers of animals for all possible combination of these sources of variability (except for Model $M_{thb}$).

Survival estimates were calculated with MARK (White & Burnham 1999). This computer package allows to fit different Cormack-Jolly-Seber (CJS) models to capture-mark-recapture data and to determine the most appropriate model. The notation of Lebreton et al. (1992) is used for model specification. The bootstrap approach for goodness-of-fit tests (Lebreton et al. 1992) was used to investigate the fit of models. Model selection was based on the corrected Akaike Information Criterion (QAICc), an adjustment for the AIC due to small sample sizes (Anderson et al. 1994, Buckland et al. 1997). QAICc weights were applied to assess the relative probability of each model being correct.

The effects of sex and the frequency of movement between trees (in other words the degree of territorial behavior) by modeling them as individual covariate on yearly survival rates were assessed. The individual covariate for the amount of movement (*mp*) was calculated from the individual capture histories. An animal recaptured between years gets +30 points if it was on the same tree and -1 point if it was on a different tree. An animal recaptured during a trapping session on the same tree get +1 point and -3 points if it was recaptured on a different tree (Tab. 5). Therefore, an animal changing the trees very often (i.e. moves a lot) will receive a negative score of *mp,* and an animal that tends to stay on the same tree will get a positive score. The difference of +30 for an animal that stays on the same tree between a year and just -3 for an animal that changes trees between days accounts for the higher numbers of capture occasions (about 10) available to assess between year changes and the different time lags.

*Tab. 5 Calculation of the individual covariate movement points (mp).*

| mp | | between | |
|---|---|---|---|
| | | day | year |
| captured at | same tree | +1 | +30 |
| | another tree | -3 | -1 |

### Virtual biologist simulation model

To further validate the conclusions from the analyses of the field data, a virtual biologist approach was chosen (Grimm et al. 1999) by implementing an individual-based, spatially-explicit movement model. In this virtual biologist approach two models are combined. The first model simulates the movement pattern and survival of a gecko population, based on the field data obtained (for a detailed description see chapter IV). To model movement of geckos in a given configuration it is necessary to answer the following questions:

How often do males/females move between trees? (sex specific movement rates)? How dangerous is it to move between trees (distance dependent mortality) What kind of movement rules do individuals follow? The sex specific movement rate for adult males and females was calculated as the ratio of the number of recaptures when an animal was located at the same tree to when it was located at a different tree. The magnitude of distance dependent mortality was calculated by comparing the survival rates of floaters and territorial animals. For describing movement I chose the following rule: A gecko deciding to move will choose randomly one of the three next trees if they are not hidden by other trees (for explanation, cf. chapter II).

The second model simulates a capture-mark-recapture study of a virtual biologist. This model mimics a biologist, that is capturing geckos. The simulated capture-recapture regime (i.e. 7 years and 12 capture days per year) was designed to resemble the field study as closely as possible. The modeled recapture data were analyzed in the same way as the field data. The idea behind this approach is to test whether the assumed movement rules and capture models can reproduce the results of the field study. If this is the case, then this is strong evidence that the underlying processes (in particular the assumed movement rules and the scoring of movement) and their interactions are sufficiently understood. Furthermore, it is a test whether it is possible to detect sex-specific survival rates and the estimated effect of movement rates on survival under the given capture regime.

## *Results*

### Population size

Between 29-48 animals were captured in each study period, which means between 60% to 86% of the estimated population was captured (Tab. 6). Estimated numbers were very similar between years. The selection procedure of CAPTURE chose $M_o$ for 1994 and 1996, for all other years $M_h$ or $M_{th}$ showed the best fit. On average 55 geckos were estimated in the habitat which equals about one pair of geckos on each suitable tree. The sex ratio was 1:1.

*Tab. 6 Capture-recapture periods with number of captured animals, estimated population size, capture probability and capture probability per day.*

| year | days of capture | captured animals | | | selected model | estimated animals | 95% confident interval | capture proba-bility | capture proba-bility per day |
|---|---|---|---|---|---|---|---|---|---|
| | | males | females | sum | | | | | |
| 1994 | 9 | 18 | 22 | 40 | $M_o$ | 50 | 45-63 | 0.800 | 0.164 |
| 1996 | 9 | 13 | 16 | 29 | $M_o$ | 39 | 33-56 | 0.744 | 0.140 |
| 1997 | 9 | 17 | 16 | 33 | $M_h$ | 68 | 50-108 | 0.485 | 0.071 |
| 1998 | 10 | 19 | 20 | 39 | $M_h$ | 56 | 44-84 | 0.696 | 0.112 |
| 1999 | 16 | 24 | 23 | 47 | $M_h$ | 60 | 53-76 | 0.783 | 0.091 |
| 2000 | 11 | 22 | 20 | 42 | $M_{th}$ | 50 | 39-59 | 0.840 | 0.153 |
| 2001 | 21 | 26 | 22 | 48 | $M_{th}$ | 60 | 55-67 | 0.800 | 0.074 |
| mean | 12 | 20 | 20 | 40 | | 55 | | 0.736 | 0.115 |

### Sex-specific movement rates

All recapture events of all animals were recorded and mapped (Fig. 12). All movements between two recapture events are represented by a straight line between the trees. Some groups of trees are almost completely isolated from the rest of the population, and on some trees no geckos were found.Within years, males always moved more often than females, though it differed from year to year (Fig. 13). The mean daily movement rate for males (0.23) is significantly higher than for females (0.14) (paired t-test, $t=6.34$, $df = 6$, $p < 0.001$).

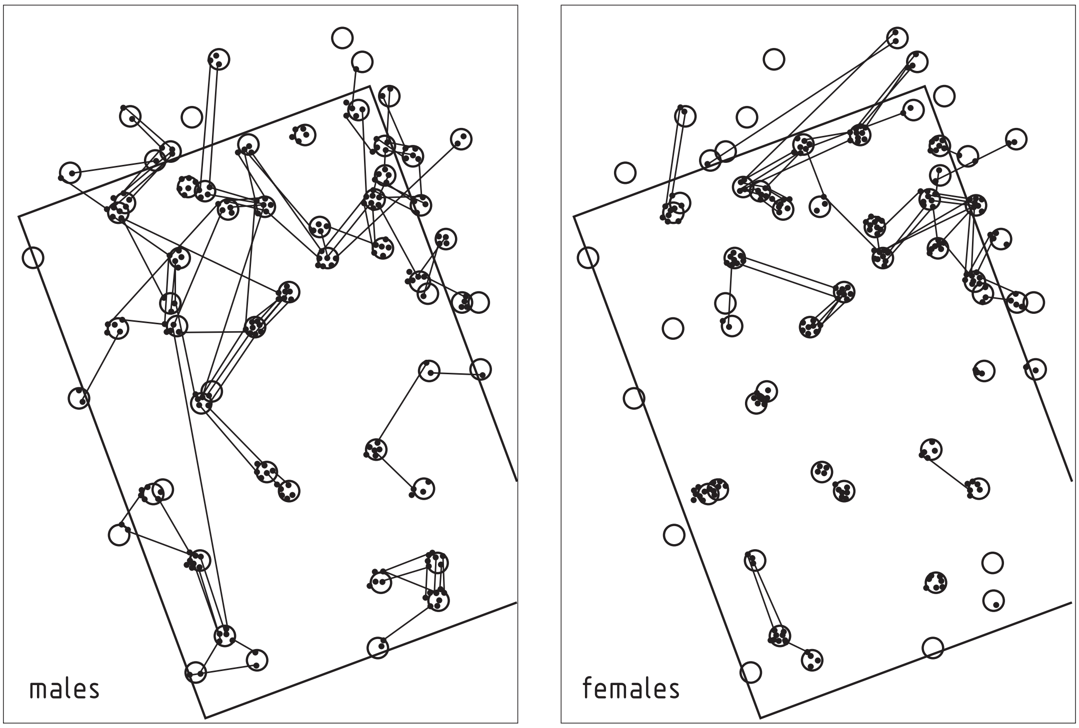

*Fig. 12 Recorded movements of males and females during all study periods.*

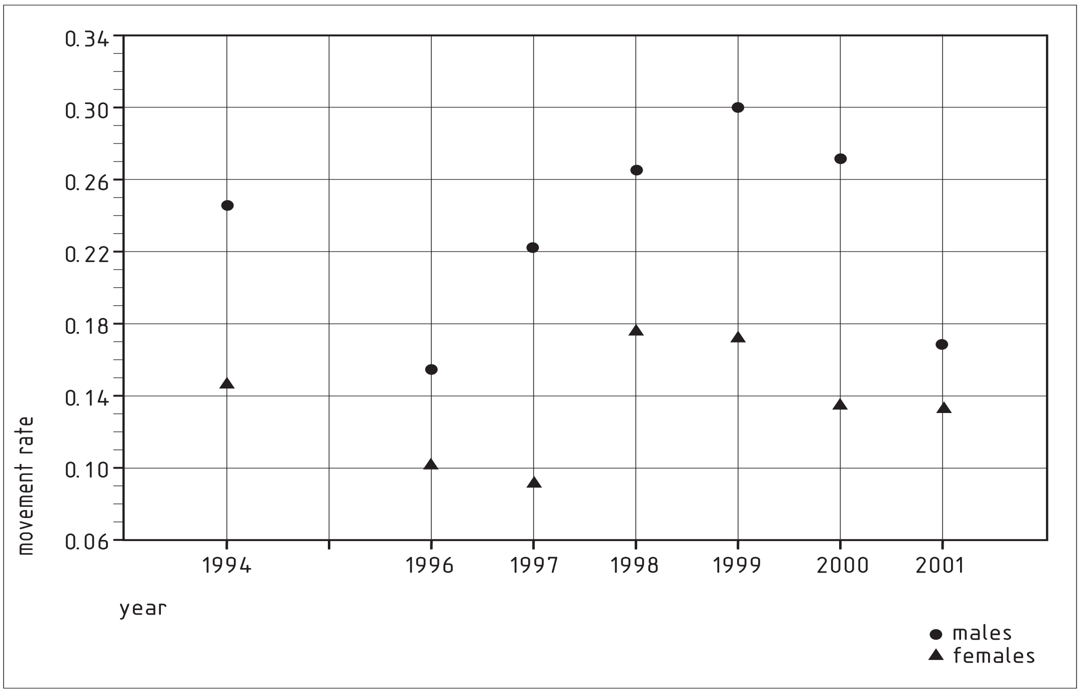

*Fig. 13 Daily movement rates of males (circles) and females (triangles) during the study periods.*

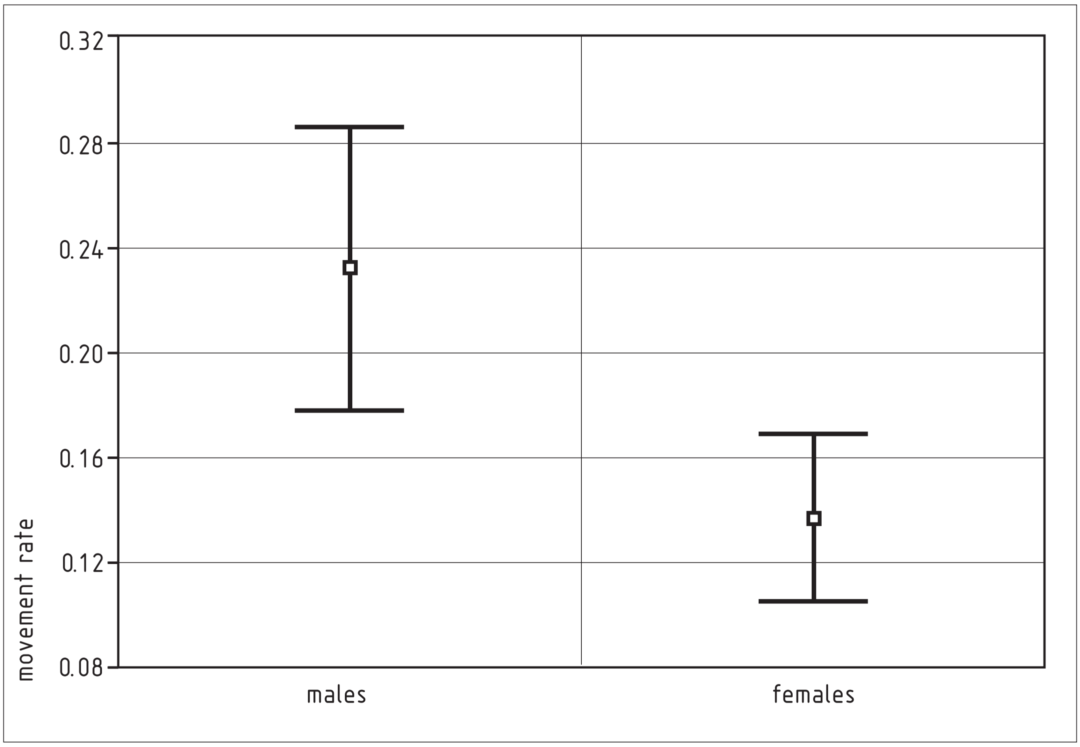

*Fig. 14 Mean daily movement rates and standard deviation of males and females.*

### Sex-specific survival rates

The initial goodness-of-fit tests in RELEASE suggested no violation of the basic CJS assumptions for both sexes (every marked animal present in population at time (i) has the same probability of recapture ($p_i$), every marked animal in the population has the same probability of survival from time (i) to (i+1), test2+test3 of RELEASE for males $\chi^2=3.77$, df=13, p=0.993, for females $\chi^2=5.33$, df=13, p=0.967). The bootstrap test (Lebreton et al. 1992) showed no lack of fitness for the most general CJS-model [phi(sex*t), p(sex*t)] and the variance inflation factor $\hat{c}=1.34$. In real data a $\hat{c}$ smaller than four indicates no overdispersion and because of the low $\hat{c}$ it is assumed that the CJS-model adequately fits the data (Burnham & Anderson (1998). For model selection the adjusted $QAIC_c$ was used. The most general CJS-model would have been phi(sex*t, *mp*) p(sex*t, *mp*) but there is no procedure available to apply a goodness-of-fit test to a CJS-model with an individual covariate.

*Tab. 7 Results of model selection based on QAICc for field data of Gehyra variegata.*

**field data**

| hypotheses tested | | | | | |
|---|---|---|---|---|---|
| factors affecting survival (ϕ) | factors affecting capture probability (p) | parameter | $QAIC_c$ | $\Delta QAIC_c$ | $QAIC_c$ weight |
| ϕ(sex+mp) | p(.) | 4 | 287.456 | 0.000 | 0.899 |
| ϕ(.+mp) | p(.) | 3 | 291.840 | 4.380 | 0.100 |
| ϕ(t+mp) | p(.) | 8 | 301.586 | 14.130 | 0.001 |
| ϕ(.) | p(.) | 2 | 318.937 | 31.480 | 0.000 |
| ϕ(sex) | p(.) | 3 | 320.636 | 33.180 | 0.000 |
| ϕ(.) | p(t) | 7 | 325.974 | 38.490 | 0.000 |
| ϕ(sex) | p(t) | 8 | 327.743 | 40.290 | 0.000 |
| ϕ(t) | p(.) | 7 | 327.796 | 40.340 | 0.000 |
| ϕ(t) | p(t) | 11 | 333.419 | 45.960 | 0.000 |
| ϕ(sex*t) | p(.) | 13 | 338.945 | 51.490 | 0.000 |
| ϕ(sex*t) | p(t) | 17 | 345.028 | 57.570 | 0.000 |
| ϕ(sex*t) | p(sex*t) | 22 | 355.741 | 68.280 | 0.000 |

There was no difference in catchability for males and females, hence these models were not considered. The most parsimonious model with the lowest QAICc was the model with constant recapture rate p(.) and different yearly survival rates for males and females plus the individual covariate *mp* (Tab. 7). Additionally, all models that included *mp* as an individual covariate performed better than any other model tested. Using the model with the lowest QAICc *mp* ranged from -21 to 124 for males and -17 to 191 for females (Fig. 15), and therefore the individual survival rate ranged from 0.47 to 0.99 for males and from 0.28 to 0.99 for females (Fig. 14). The individual covariate *mp* has quite a strong effect on survival (Fig. 16) and the estimated survival rate (at mean *mp*) for males (0.73) was higher than for females (0.59, Tab. 7). Males have a higher basic survival rate than females, but as the average *mp* for males is higher than for females the realized difference in mortality becomes smaller.

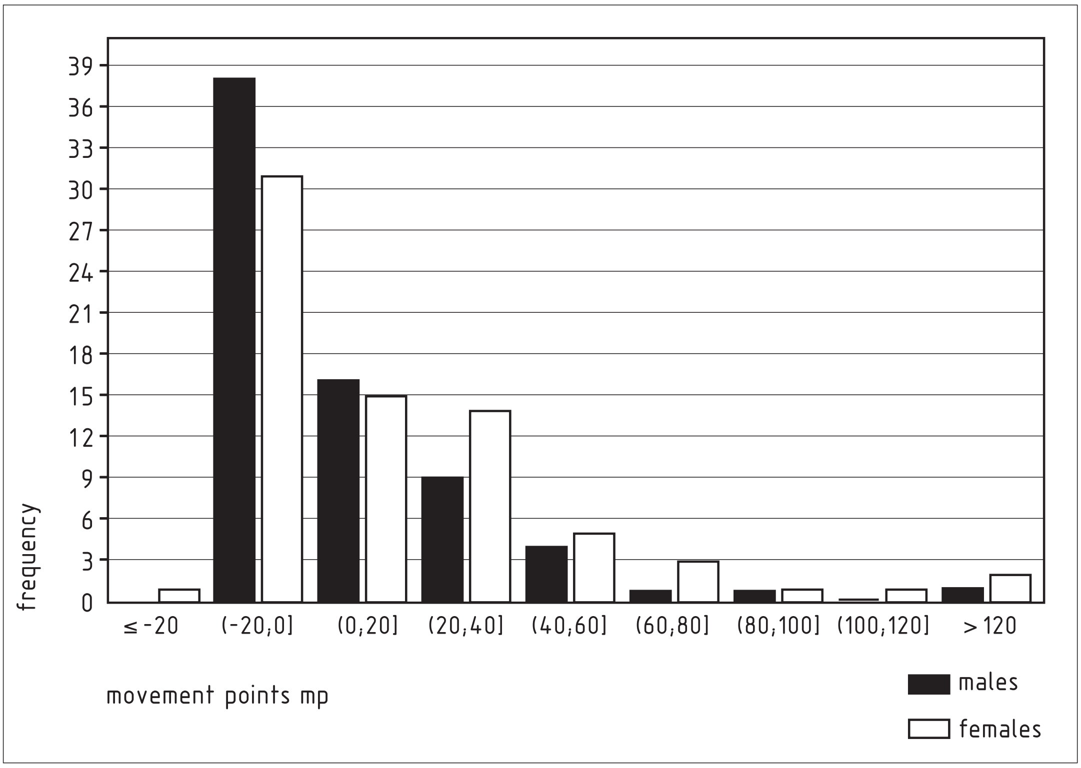

*Fig. 15 Distribution of movement points mp for males and females.*

*Tab. 8 Estimated survival rates for males and females for mean mp and estimated capture probability. b1 and b2 are the not transformed parameters, estimated by mark. To get the survival rates, a logit transformation has to be performed (cf. Figure 16).*

| | estimated parameter | | survival estimate | standard error | 95% confidence interval | |
|---|---|---|---|---|---|---|
| | b1 | b2 | | | lower | upper |
| $\phi$ (male) | 1.192 | 1.162 | 0.730 | 0.049 | 0.633 | 0.809 |
| $\phi$ (female) | 0.235 | 1.162 | 0.592 | 0.065 | 0.464 | 0.720 |
| p(.) | 1.184 | | 0.766 | 0.047 | 0.663 | 0.845 |

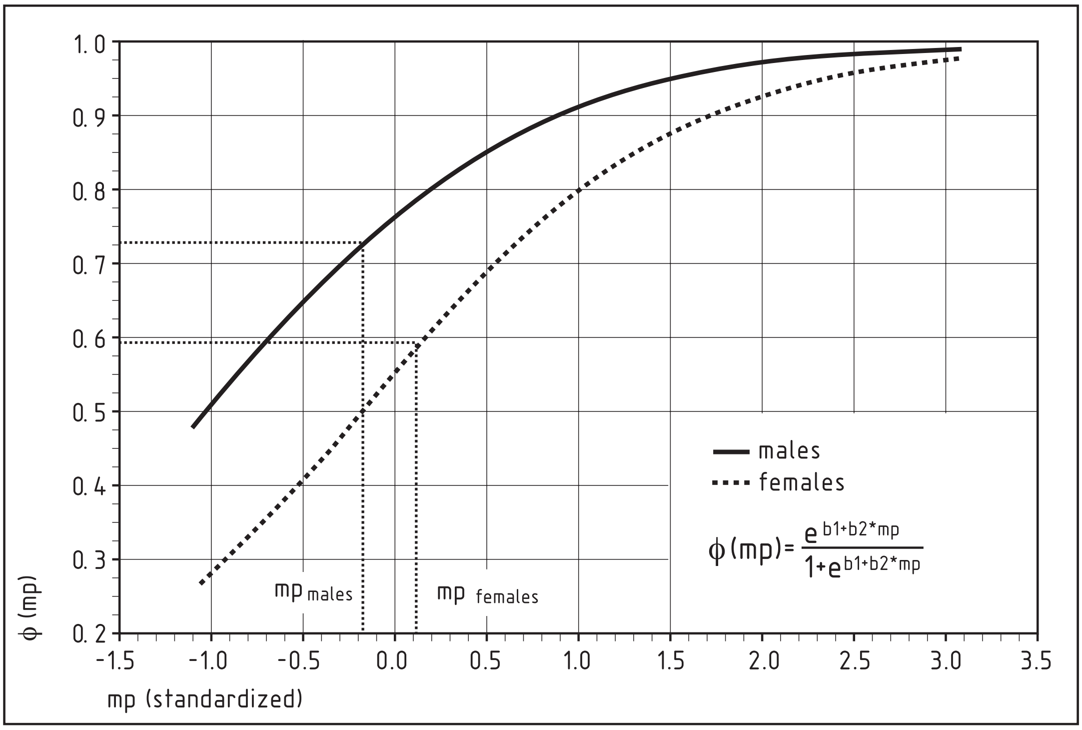

*Fig. 16 Relationship between movement points mp and survival rate for males and females. Survival estimates for males and females for standardized mean mp are shown. The formula describes the logit transformation to estimate the survival rates from the not transformed parameters b1 and b2.*

### Virtual biologist simulation model

To initialize the simulation model, the mean population size of geckos (n=54) and the mean estimated recapture probability per day (p=0.115) were taken (Tab. 6). To resemble the real study as closely as possible, the same number of primary (7) and secondary periods (12) as in the field were used. In the simulated data no overdispersion was found and therefore the $AIC_c$ was used instead of $QAIC_C$ ( $\hat{c}=1$). Fifty runs were performed and analyzed in MARK. Table 9 shows the results from one of this runs. In 45 of 50 runs the same model as in the field data (ϕ(sex+*mp*)p(.)) was the most appropriate model. In five runs ϕ(.+*mp*) p(.) was the model with the lowest $AIC_c$. As expected the $AIC_c$ of the simulated data is lower than the $AIC_c$ of the field data, because there is less heterogeneity in the simulated data, as the capture rate was held constant and the basic survival rate (without mortality due to movement) was exactly the same for all animals.

The estimates of the simulated data were close to the estimates of the real data and also standard errors were about the same [$\phi$(males+*mp*)= 0.66 – 0.73 for the field data –, standard error =0.056, 95% confidence interval 0.54-0.76, $\phi$(females+*mp*)=0.58 – 0.59 for the field data –, standard error = 0.064, 95% confidence interval = 0.44-0.68].

*Tab. 9 Results of model selection based on AICc for simulated capture-mark-recapture data*

**simulated data**

| hypotheses tested | | | | | |
|---|---|---|---|---|---|
| factors affecting survival ($\phi$) | factors affecting capture probability (p) | parameter | AIC$_c$ | $\Delta$AIC$_c$ | AIC$_c$ weight |
| $\phi$(sex+mp) | p(.) | 4 | 229.907 | 0.000 | 0.561 |
| $\phi$(.+mp) | p(.) | 3 | 230.700 | 0.790 | 0.378 |
| $\phi$(t+mp) | p(.) | 8 | 236.197 | 6.290 | 0.024 |
| $\phi$(.) | p(.) | 2 | 236.652 | 6.740 | 0.019 |
| $\phi$(.) | p(t) | 7 | 238.574 | 8.670 | 0.007 |
| $\phi$(sex) | p(.) | 3 | 238.626 | 8.720 | 0.007 |
| $\phi$(sex) | p(t) | 8 | 240.705 | 10.800 | 0.003 |
| $\phi$(t) | p(.) | 7 | 244.592 | 14.690 | 0.000 |
| $\phi$(t) | p(t) | 11 | 245.163 | 15.260 | 0.000 |
| $\phi$(sex*t) | p(.) | 13 | 256.867 | 26.960 | 0.000 |
| $\phi$(sex*t) | p(t) | 17 | 258.157 | 28.250 | 0.000 |
| $\phi$(sex*t) | p(sex*t) | 22 | 269.200 | 39.290 | 0.000 |

## *Discussion*

### Population size

The high capture effort allowed good estimates for population size. Pollock et al. (1990) propose to be careful, when using the selection procedure implemented in CAPTURE. They suggest to use biological information to reduce the numbers of considered models. Model $M_h$ takes individual capture probabilities into account, which makes sense biologically, because some individuals were easier to catch, since their hiding places were close to the ground or because of trees with less holes for hiding. This kind of variation is probably always present. Model $M_t$ allows for variation in time. This is a likely source of variation in some years, because activity of geckos is strongly dependent on ambient temperatures (How & Kitchener 1993, Autumn et al. 1994, Kearney & Predavec 2000) and high variations in ambient temperatures occurred. The effect of temperature variation is expected to be stronger in years, where longer sampling efforts were undertaken, which is likely to be the reason why Model $M_{th}$ is favoured in these years (2000,2001). The selection of $M_o$ in 1994 and 1996 is probably an effect of the smaller catching effort in these years (9 days), which results in choosing simpler models (Otis et al. 1978). However, the estimates for $M_h$ in these years were similar. Model $M_b$ accounts for trap response and could not be detected in any year. As geckos were recaptured by sighting, variation caused by trap response is unlikely to occur.

The population size was very constant among years. Even the flooding of the whole area that occurred between December 1999 and January 2000 had no effect on population size. On average 55 geckos were caught on 41 trees. Not all trees provided adequate habitat for geckos. Some trees are quite young and offered no suitable shelter and four trees fell down within the study period. On this kind of trees, geckos were caught only rarely. Furthermore the crowns of some trees standing close to each other overlapped and were possibly perceived as one tree by geckos. On average there seemed to live about one pair of gecko per suitable tree. Very rarely more than two geckos were caught on the same tree.

### Sex-specific survival rates

The capture effort during the study was high resulting in a high pooled capture probability for a complete study period (Tab. 6). Except for 1997 it was always higher than 0.7. The recommendation of Pollock et al. (1990) that for populations sizes smaller than hundred individuals recapture probability should be higher than 0.3 to get reasonable estimates was very well met. The advantage of the robust design is clearly demonstrated. Though the estimates of population size indicate heterogeneity (model $M_{th}$) in capture probabilities, there was no heterogeneity found in the pooled capture probabilities and hence CJS-models with constant recapture probability p(.) were chosen. This further reduced the number of estimated parameters and enhanced the precision of survival estimates. It was possible to detect differences in sex-specific survival rates by the capture-mark-recapture study and by the simulated data. This is strong evidence that the extent of the study was sufficient.

The sex ratio of males to females was very close to 1:1 as found by Henle (1990a). Bustard (1968) found a different sex rate of one male and three females, which Henle (1990a) attributed to a sampling bias. When movement dependent mortality is included, survival rates should be the same between sexes, due to the even sex ratio. In accordance to that, the 95 % confidence intervals do overlap (Tab. 7) and the estimated survival rates is 0.73 for males and 0.59 for females, which is quite similar. Using model $\phi$(sex)p(.) for estimating survival rates, they become even more similar (0.72 for males and 0.68 for females)

### Movement and survival

As mentioned above, the commonly used assumption that movement is associated with a higher mortality risk has rarely been demonstrated empirically (Fahrig 1998). The most straight forward approach for estimating the effect of movement on survival would have been to use the Arnason-Schwarz multistrata CJS-model (Arnason 1972, for examples see Coffman et al. 2001, Hestbeck 1995, Hestbeck et al. 1991, Schwarz & Ganter 1995). The Arnason-Schwarz model adds another parameter $\Psi_{ij}$ to the standard CJS-model to include the probability to move from patch *i* to patch *j* (transition probability). As Schwarz & Seber (1999) noted it is sometimes impossible to implement this approach, because the data are too sparse and/or the resulting models would be too complex (too many parameter have to be estimated, which results in poor precision of estimates). This is especially true if there is a high number of patches. In my study there are 41 patches (trees) and this would add $41^2 = 1681$) parameters to the "basic" CJS-models (if time dependency were considered the number would even be higher by an order of magnitude). To overcome this problem, I used CJS-models with an individual covariate which reflects the amount of movement of an individual animal. The idea of using individual covariates was discussed by Skalski et al. (1993) and used by Kingsolver & Smith (1995) for addressing other ecological problems. The approach can be used for every capture-mark-recapture study, where the location of captured animals is recorded. Its advantage is that there is just one additional parameter to estimate, which lets address this kind of questions and test hypothesis with field data. A necessary assumption is that the effect of movement on survival is constant during the study, because with available models it is not possible to update values of a time-varying covariate in a mark-recapture analysis (Skalski et al. 1993).

One problem arises if a covariate is based on the individual capture history (cf. Skalski et al. 1993). It is possible that the value of movement points *mp* depends on the number of recaptures, and are accurately known only for individuals that are captured. However, the capture probability for an animal was high (see Tab. 6), the bias should be low. This was further confirmed by the good fit of the simulation model. Furthermore, no correlation between movement points and numbers of recaptures was found. The individual covariate *mp* can be thought of as an index of the movement frequency of an individual.

The amount of points given for movements were varied in reasonable limits (+10..+40 for a recapture on the same tree between years and -2..-8 for a recapture on another tree between days) and did not change the results. Another measurement for moving would have been the distance in meters an individual covers between recapture events. An analysis of this kind of data showed no significant results in real and simulated data (not presented). The reason is probably that the distances travelled depend more on the configuration of trees than on the movement frequencies. Geckos that have covered a large distance once would be classified as floaters in contrast to geckos that move very often short distances, just because they are lucky and live in a group of trees that are close to each other.

The assumption of Wiegand et al. (2002) that there are floating individuals, which do not occupy a territory, could be confirmed. Moreover these floaters are mainly males. Comparing the sex-specific survival rates females have a lower basic survival rate but this is compensated by the lower movement rate. The lower basic survival rate of females possibly can be attributed to higher costs of reproduction, a relationship observed in many ectotherm species (Roff 1992, Madson & Shine 1993, 2000, Luiselli et al. 1996, Sutherland 1996).

Predation risk most likely account for the additional mortality, when moving on the ground (Henle 1990a, b, 1991). In line with this hypothesis is the much lower yearly survival rate of syntopic, terrestrial geckos of the same size is (0.33, <0.20, and 0.28) for the three terrestrial gecko species *Diplodactylus damaeus*, *Diplodactylus tesselatus* and *Heteronotia binoei*: Henle 1990b). Other live-history traits also show that terrestrial geckos are more r-selected species with higher clutch sizes, higher growth rates and younger age at maturity. In conclusion, the predation pressure for ground living species is much higher (Henle 1990a, b) and leads to fast growing species with a high turnover rate.

Sutherland (1996) and Kokko & Sutherland (1998) developed a model for predicting the number of floaters in a population. The model predicts that the number of floaters should increase, if the survival rate of breeding individuals increases. The reasoning behind the model is that floaters should not queue (hence wait until a territory becomes empty) when survival probability is low, because the queuing individual is relatively less likely to be alive when the territory owner dies (Southerland 1998). This is in accordance with this study, when looking at males and females separately. Females have a lower survival probability and therefore the number of floaters is lower.

From the theory of mating systems it is known that the distribution of females determines the distribution of males. Females themselves are distributed by resources (Davies 1991). This is expected on theoretical reasons. In species in which females contribute more to the offspring, male reproductive success is determined by the number of mates and the female reproductive success is determined by the resources (Trivers 1972). The most important resource for this arboreal gecko species are trees (Bustard 1968). Trees provide resting places, food, and protect from predators. Females have only one option, they will try to find suitable trees and stay there once settled, hence that's the females' way to optimize resources. For males there are two options. Either stay at a suitable tree with a female or try to increase the numbers of mates by looking for other females at other trees. Hence, it can pay for males to move between trees, in spite of a higher risk of dying. It is planned to study this further by applying genetic techniques of parental analysis. This could prove that there are two equivalent strategies available for males.

## Conclusion

Temporal change in population density is the result of births, death, and movement (immigration and emigration) (Turchin 1998). It is easier to study birth and death processes than to study movement of organisms. This difficulty resulted in an "avoidance behavior" by ecologists (Southwood 1972, Crist et al. 1992). As noted above, it is necessary in many ecological fields to know the effect of movement on population dynamics. Using an individual covariate in CJS-model allowed to estimate the effect of movement on survival. As much less parameters have to be estimated, the precision and the likelihood to detect trends in data is much higher. Another way of reducing parameters was proposed by Hanski et al. (2000). They also used capture-mark-recapture data, but did not use CJS for estimation of parameters. Instead they created their own biologically justified model with a low number of parameters to be estimated. The drawback of this approach is that for every species new models (and probably different, because of different traits of species) have to be created and furthermore no standard model selection tool (like AIC) is available (see Burnham & Anderson 1998). The approach presented here is in accordance to the existing and well established framework of CJS-models. A rich literature and many computer programs support analysis (e.g. Anderson et al. 1994, White & Burnham 1999). The approach can be used in every capture-mark-recapture study, where individual movement rates can be summarized in an individual attribute, which expresses the amount of movement of individuals.

As movement is the glue, which links individuals in structured populations and subpopulations in metapopulations (dispersal), it is a basic need to study its effect on survival (Turchin 1998). This knowledge (the effect of movement on survival) is very needed for modeling population dynamics and assessing the vulnerability of an endangered species to fragmentation.

# Chapter IV

## Optimal movement of an arboreal gecko in a spatially structured population

### *Introduction*

#### Movement and population dynamics

To implement sustainable land use, it is necessary to understand the interplay of spatial structure and ecological processes. Animal ecologists have identified animal movement as a particular important factor of the dynamics and spatial distribution of species (Fahrig 1988, Kareiva 1990, Hansson 1991, Turchin 1991, Pulliam et al. 1992, Wiens et al. 1993, Dunning et al. 1995) or as Turchin (1998) put it: “Movement is the glue that connects local population dynamics in space”.

Though movement as a linking factor is regarded as important and a vast number of studies on animal movement on the one hand (e.g. Merriam & Lanoue 1990, Crist et al. 1992, Hobbs 1992, Johnson et al. 1992, Ims et al. 1993, Zollner & Lima 1997, Andreassen et al. 1998a, b) and dynamics of population on the other hand [reviewed by Capuccino & Price (1995)] were undertaken, no common framework for modeling animal movement and linking it with population dynamics has been developed so far. Lima & Zollner (1996) are explicitly arguing for a unification of the study of animal behavior, population dynamics, and landscape ecology. One of the major problems is that these two different approaches address two very different scales and it is not easy to link these scales (Turchin 1991, 1996, Lima & Zollner 1996).

Animal behavior operates on the individual level and population dynamics on the landscape level. To capture all details on the individual level, very complex models of behavior are needed. For example, a model of animal movement on the most detailed level in a given landscape would have to include the sensory abilities of an animal to perceive the landscape, the effect of sensory cues to the animal`s internal states, and the effect of the internal states, on an animal`s behavior. Moreover, movement decisions of an individual animal depend on other individuals of the same and other species. Up to now, it has not been possible to include even a fraction of these functions and parameters in models of animal behavior. Not enough knowledge and data of species exist, and even if they existed, the accuracy of the input data probably would be much too poor and hence the uncertainty of the output data would be much too high to be useful, let alone to make valuable predictions on the population dynamics of the species under study. Moreover, the complexity of such models would inhibit an understanding of the effects of movement on population dynamics.

To reduce the number of parameters, many models of population dynamics use a "behavior minimalism" (e.g. random walks), which is clearly simplified, but the hope is that they include all main known and unknown factors affecting movement (Turchin 1991). This is often necessary if landscape-level ecological models are to retain a reasonable degree of tractability (Lima & Zollner 1996, but see Wiegand et al. 1999 as an exception). The drawback of this approach is that there is a growing knowledge from studies that individual behavior effects population dynamics (Grimm et al. 1996, Uchmanski et al. 1999) and that individuals do not follow a random walk. Hence the results of such models are not likely to be very useful for application in real landscapes. A major challenge of behavioral ecologists will be to develop a more complex "behavioral minimalism", which still captures the important determinants of movement behavior but is still tractable (Lima & Zollner 1996). Remains the difficulty to decide, what factors and level of detail should be included in a movement model.

A solution to this dilemma is to have a more complex (more realistic), but not overburdened model of movement behavior, which produces parameters (such as the effect of movement on reproductive success) that can be directly linked to population dynamics and included routinely in field studies and models of population dynamics (Fig. 17). These parameters are output parameters of the movement models and input parameters of models of population dynamics therefore, I will refer to them as "interface parameters".

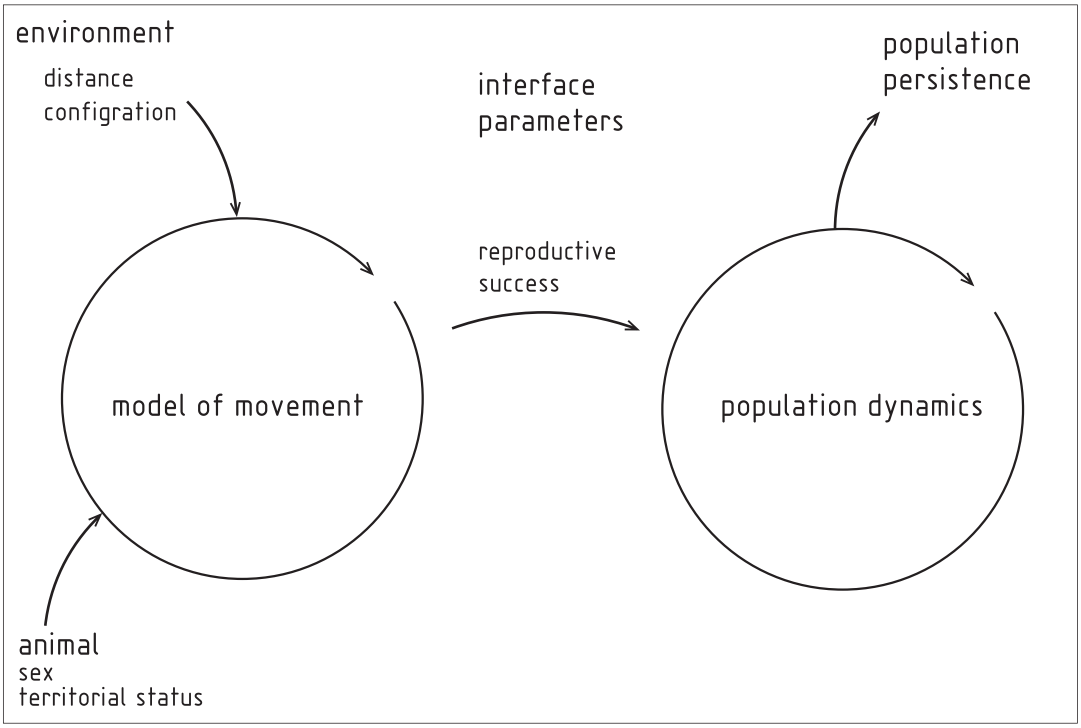

*Fig. 17 Modeling concept for the movement model, which includes individual movement behavior and produces the interface parameter (reproductive success), which is an input parameter for models of population dynamics.*

### Optimality models

Often it is difficult to determine values of parameters of movement models. In the first stage of this study optimality theory is used to estimate these values.

Optimality theory has often been used to understand and predict a variety of types of animal behaviors (e.g foraging, mating, parental care, diet composition). There has been a long discussion in the literature about the usefulness of optimality theory (Maynard-Smith 1978, Pyke 1984, Pierce & Ollason 1987, Stearns & Schmid-Hempel 1987, Orzack & Sober 1994, Steen 1999, Sih & Christensen 2001). The diverging arguments were mainly settled by a review of Parker & Maynard Smith (1990). They proposed a protocol how to build and analyze optimality models. In this paper I will follow this protocol when applying optimality theory to movement of a species of the arboreal gecko *Gehyra variegata*.

An individual-based model, which allowed to study the effect of different movement strategies was implemented. To be able to compare these strategies with the aid of optmality theory, a variable must be defined, which should be maximised. This variable should be somehow related to Darwinian fitness (Parker & Maynard Smith 1990). In the past many different surrogates or components of fitness have been used (Stearns 1992). Unfortunately, many of the variables that are often used in optimality models (such as foraging strategy, diet composition) do not show a clear relationship to fitness components (for a review see Stephens and Krebs 1986, Pierce & Ollason 1987). I used yearly reproductive success of female geckos as a surrogate of fitness, since this parameter frequently is a comparably good measure of fitness (Parker & Maynard Smith 1990). The resulting quantity of optimality models (reproductive success) can easily be incorporated in models of population dynamics (Fig. 17) and can serve as a linkage between movement behavior and population dynamics.

### The study system "*Gehyra variegata*"

For several reasons *G. variegata* is an ideal species to model. The activities of this arboreal species are strongly linked to trees (Bustard 1968, Henle 1990a), hence an easy distinction between habitat (tree) and matrix (between trees) can be made. Next to smaller activities at the basis of the trunk of trees, movement is almost completely determined by the configuration of trees. The geckos have a good knowledge of the habitat surrounding their tree and navigate very directional between trees (chapter II). Therefore, if geckos were captured in two following sessions at different trees, the travelled distance could be calculated by simply measuring the distance between trees. The population dynamics of this species has been well studied under an intensive capture-mark-recapture regime and the location of individuals has been recorded and are known for up to 14 years. It has been demonstrated that movement between trees results in a higher risk of mortality probably due to higher predation pressure on the ground (Henle 1991, chapter III). The additional mortality risk should influence the frequency of movement of individual geckos. The reasoning behind this is that an individual that does not move at all has a higher life expectancy than an individual that moves very often. However, an individual that does not move at all, has the risk of not finding a mating partner during the mating season. Therefore, it is also a benefit to move in terms of a higher reproductive success. The optimum movement strategy should lie somewhere between the strategies "do not move at all" and "move around all the time", and should depend on the density of the population, the number of available days to find a mating partner, the ability to navigate between trees, and the distances between trees.

In this study I will demonstrate how optimality theory can be used to estimate unknown values of parameters of the movement process. In the second stage, I will use these values to study the robustness of the movement strategy in relation to the reproductive success of the geckos in different landscape configurations. Additionally, the ecological plausibility and consequences of the gecko´s movement strategy are discussed.

## *The simulation model*

The aim of the model is to predict the rate of fertilized females when accounting for mortality caused by movement in different habitat configurations. As individual behavior, density of geckos, the number of days available, and the configuration of habitat was assumed to be important, an individual-based, spatially explicit approach was implemented, which allows to track the fate of individuals of different sex in different configurations of landscapes. The output of the model is the rate of reproductive success of a female gecko after a mating season. It is calculated by multiplying the rate of fertilized females (which includes the chance to die during movement) by two, because adult female geckos produce two eggs per year (Henle 1990a).

### Overall structure

At the beginning of a simulation run a certain number of geckos (*n_gecko*) with an even sex ratio were placed randomly at a number of trees (*n_tree*) in a given habitat configuration. For a specified number of days (*n_days*) the geckos were allowed to move between trees. Each day a gecko stayed or moved to another tree. The probability to move to another tree differed for males (*m_move_p*) and for females (*f_move_p*). When a gecko decided to move to another tree, the movement rule parameter (*nn*) determined how many of the next neighbouring trees that are visible are taken into account. It was found that there is an additional risk of mortality, when geckos move between trees (chapter III), hence a distance dependent movement mortality (*mm*) was included. If a male and a female were on the same tree at the end of a day (or when they were initially placed on the same tree) the female was marked as fertilized, i.e. each meeting of individuals of opposite sex resulted in a successful mating. For a given dataset 5000 runs were performed and the mean number of fertilized females was used for analysis.

### Habitat

The real habitat, where the study of *Gehyra variegata* was undertaken, consisted of a configuration of 41 trees (Fig. 18) in a rectangular area of approximately 150 x 100 m. The configuration of trees of the real habitat was measured to the nearest meter. Using the algorithm of Adler & Nürnberger (1994) seven different landscape configurations were generated. The algorithm creates landscapes differing in the degree of clumpedness by shifting trees from an initial landscape configuration. The real landscape was used as the initial landscape configuration. Adler & Nürnberger (1994) used the variance of a crowding index to evaluate the degree of clumpedness. The variance of this parameter ranged from 0 (for the equal distances habitat) to 30 for the extremely clumped habitat. The crowding index of the real habitat has a value of 6.123 and was closer to the equal distances habitat than to the not extremely clumped habitat. For the simulated configurations a grid of the extent of 150 x 100 cells and the grain size of 1 m was created, hence the area of the habitat, and the overall density of trees were the same for the real habitat and the simulated configurations.

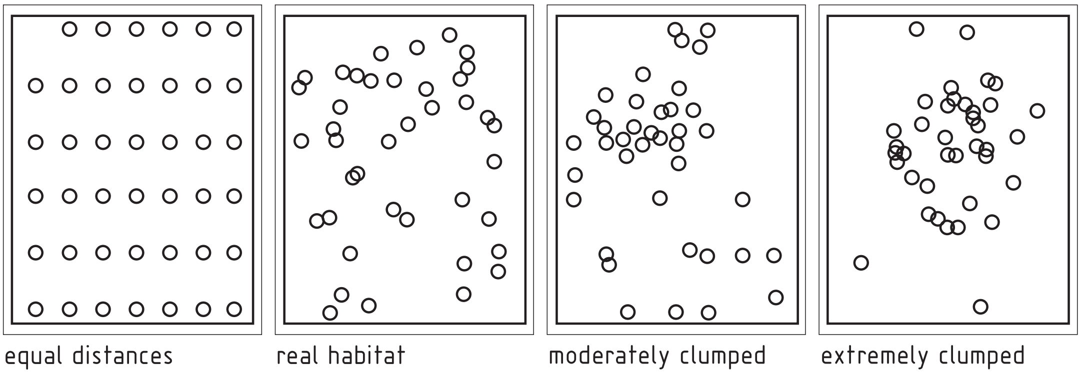

*Fig. 18 Examples of different habitat configurations with increasing clumpedness. Ranging from no clumping to extremely clumped habitat)*

### Movement

Movement of individuals is divided in three successive phases, the emigration, the dispersal, and the immigration phase. The emigration phase includes the decision of an individual to leave its current tree. The sex dependent probability of a gecko to move to another tree was estimated by mark-recapture (*m_move_p* for males and *f_move_p* for females). Each day a random number for each gecko was drawn and, if the number was lower than the sex dependent probability to move, the animal moved to another tree and entered the dispersal phase.

In the dispersal phase the animal decides to which tree it wants to move. From field studies it was known that geckos are able to orientate directly to neighbouring trees (chapter II). The parameter *nn* determined the number of next neighbouring trees that are taken into account, when an animal moved to another tree. This was implemented by drawing a random number to decide to which tree the animal will move. Depending on the movement rule parameter *nn*, the animal took one of the *nn* next neighbouring trees, with the same probability for every tree.

During the dispersal phase, the animal actually moved to another tree. From field studies, it is known that there is a higher risk of mortality, when moving on the ground (chapter III). The probability to die was assumed to be constant for each moved meter, hence the probability to die during a move between two trees ($q$) was calculated via the formula:

$$q = 1 - (1 - mm)^{distance},$$

where $mm$ is the probability to die per meter, and $distance$ is the distance between the trees in meters. A random number was drawn and if the number was smaller than $q$, the animal died during movement.

If an animal moved successfully to another tree, it entered the final immigration phase. In the immigration phase, it was checked whether another animal of the opposite sex was on that tree. If a mating partner was found, females were recorded as mated and stayed at the tree, but males were allowed to move to other trees the following days.

### Number of days

The mating season of *Gehyra variegata* starts in October and lasts probably until the beginning of December (Henle 1990a). As the precise number of days animals move to find a mating partner is not known, it was varied between 1 to 60 days.

### Number of geckos

The number of geckos and hence density of the population was varied between 10 to 80 individuals. The real numbers of geckos found during the seven years of study were between 35 and 60 $\bar{x}$ (=50) individuals. As the sex ratio was constant and very close to 1:1, it was not changed in the simulations (Henle 1990a, Gruber & Henle unpubl. data).

### Additional parameter values

Parameter values and configurations used in the simulation are summarized in Table 10. Bold values are extracted from field data (see chapter II and III). There were 41 trees in the population under study. Male geckos moved with a probability of 0.23, and female geckos with a probability of 0.14 per day to another tree (chapter III). The movement rule was that geckos move to one of the three next neighbouring tree, which are visible best explained the observed movement data (chapter II). From the mean travelled distances of all individuals and the mean effect of movement on survival, the probability to die per travelled meter on the ground ($mm$=0.002) was calculated.

*Tab. 10 Overview on the parameters and values used during simulations. The bold values were estimated from a capture-mark-recapture dataset of Gehyra variegata.*

| parameter | parameter description | value |
|---|---|---|
| habitat | | |
| n_tree | number of trees in the habitat | **41** |
| configuration | clumpedness of habitat | equal distances ...<br>... **real** ...<br>... clumped |
| movement | | |
| m_move_p | probability of a male gecko to move to another tree | **0.23** |
| f_move_p | probability of a female gecko to move to another tree | **0.14** |
| nn | movement rule (number of next neighbouring trees that are taken into account | 1 ... 3 ... 7 |
| mm | movement mortality (probability to die per meter moved) | **0.002** |
| others | | |
| n_day | number of days, the geckos were allowed to move | 1 ... 60 |
| n_gecko | number of geckos | 10 ... **50** ... 80 |
| runs | number of runs used in a simulation | 5000 |

## *Results*

### Modeling stages

The number of days geckos move per season (*n_days*) was not known, and the number of trees that are taken into account (*nn*), when moving to another tree was only determined by statistical methods. In the first stage of the study I will show the suitability of optimality theory to find these values. In the second stage the robustness of the movement strategy derived from optimality theory are explored in different habitat configurations.

### First stage

The reproductive success was studied for a varying number of days at different densities of geckos (Fig. 19). An optimum of reproductive success exists at an intermediate number of days. The optimum is shifted to higher numbers of days at lower densities. If animals do not move at all (*n_days*=0) the reproductive success is higher at higher densities, because most of the female geckos live together with a mating partner on a tree initially. Therefore, it does not pay to move around for a long time, because it is unlikely to find another mating partner. At low densities maximum reproductive success is much lower than at high densities. At the average observed densities in the study site (50 adult geckos) the number of days necessary to achieve an optimal reproductive success is about 18 days.

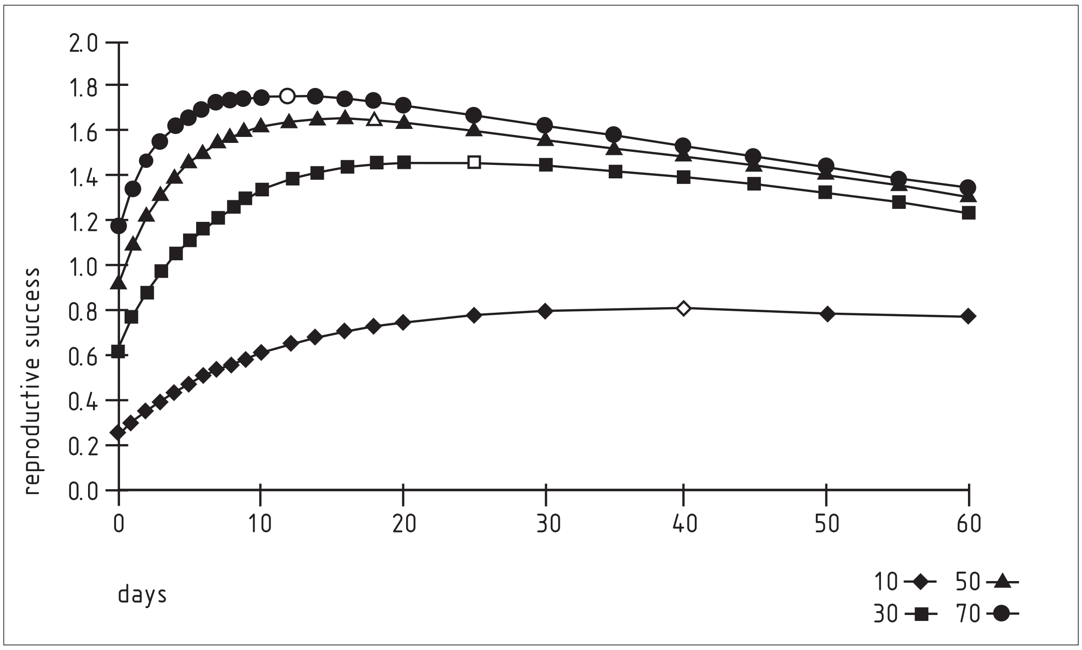

*Fig. 19 Reproductive success per female gecko in the real habitat as a function of the numbers of days geckos are allowed to move for different numbers of geckos using the movement rule (nn3). An optimum exists where the reproductive success is maximised. The optimum is shifted to lower values, when the numbers of geckos is increased.*

When holding the number of days constant (*n_days* = 18) and varying the numbers of trees that can be chosen (*nn*) when moving to another tree, reproductive success reaches an optimum at intermediate *nn* values (Fig. 20). At low densities the optimum is shifted to lower values of *nn*. This can be explained by the reasoning that at higher densities it does not pay to move far, because most females have already found a mating partner. However at low densities there are some females, where no partner is close by and therefore higher *nn* values do increase the reproductive success. The reproductive success is less sensitive to increasing *nn* than increasing the numbers of days of movement. Though the optimum is less pronounced, there is an additional reason, why the optimum indicates an optimal value for the geckos´ movement strategy. A movement strategy using a higher *nn* value results in longer movement distances and therefore, in higher mortality risks and higher energy expenses. Hence a strategy using a higher *nn* rule without increasing the reproductive success is clearly inferior to a strategy that uses a lower *nn* rule and achieve a higher reproductive success (even if it is only slightly higher). A lower *nn* rule (left from the optimum) results in a decline in reproductive success and is therefore also inferior to the optimal value of *nn*; moreover the decrease left from the optimum is comparable steep at realistic densities.

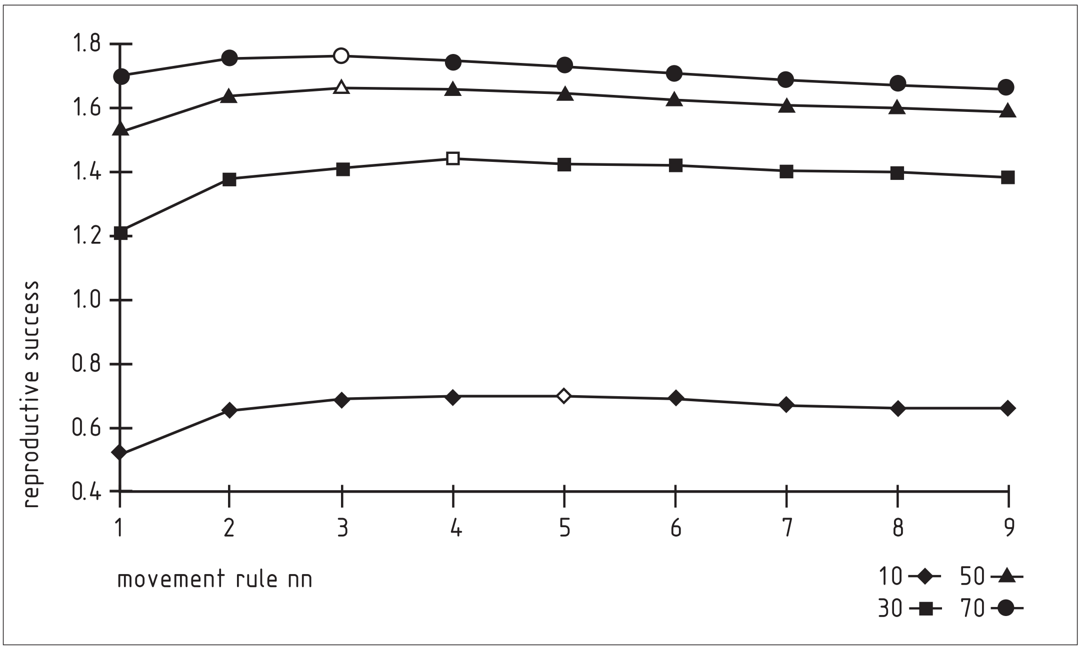

*Fig. 20 Reproductive success per female gecko in the real habitat for different movement rules and densities, when allowed to move a constant numbers of days (n_days = 18). The optimal movement rule depends on density, i.e. the higher the density the lower is the movement rule which results in an optimal reproductive success. At the observed average density of the study site of about 50 geckos the optimal movement rule is nn3.*

### Second stage

In the second stage of simulations the values of parameters found in the field study and by the optimality approach are used to explore the robustness of the movement strategy that was optimal in the real landscape to changes in habitat configurations.

The effect of tree configuration on reproductive success is shown in Fig. 21. In contrast to previous simulations, which varied number of movement days and the movement rule, no optimum at intermediate values of clumpedness is found. For all movement rules can be stated, the more clumped the configuration of trees the higher is the reproductive success. This can be explained by the fact that at more clumped configurations, the distances between trees are smaller and hence the risk to die when moving is lower. The most extreme case would be all trees at the same place (hence the distances between trees is zero) and no mortality would be found. Surprisingly, the configuration of equal distances performed worst. The differences between higher clumped configurations were rather small compared to the differences to the equal distances scenario.

Independent of tree configuration, the more neighbouring trees were taken into account in the movement rule, the higher was the reproductive success until a value of *nn*3-4 was reached (Fig. 22). If more neighbouring trees were taken into account, the reproductive success declined. A high *nn* rule increased the risk to die, because greater distances during movement were covered, and therefore these movement strategies were less successful. On the contrary, if the strategy with only one next neighbouring tree was taken, the reproductive success was much lower. Here, many animals did not find a mating partner, especially when the habitat is less clumped.

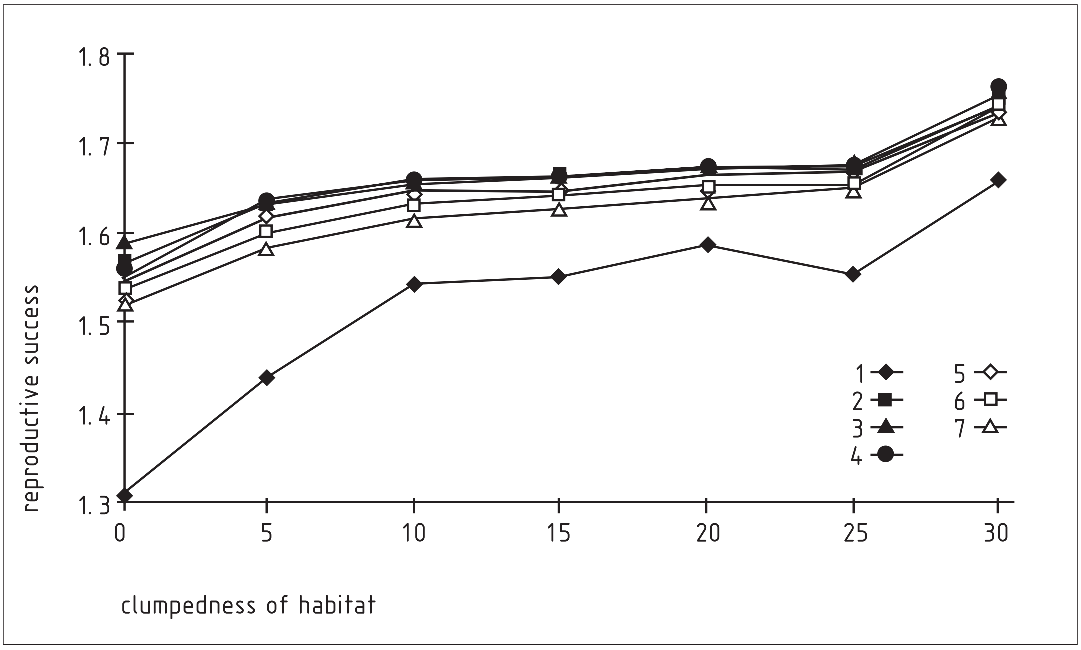

*Fig. 21 Reproductive success per female gecko for different clumpedness of habitats and movement rules (nn1...7, n_days = 18). The more clumped the habitat, the higher is the reproductive success.*

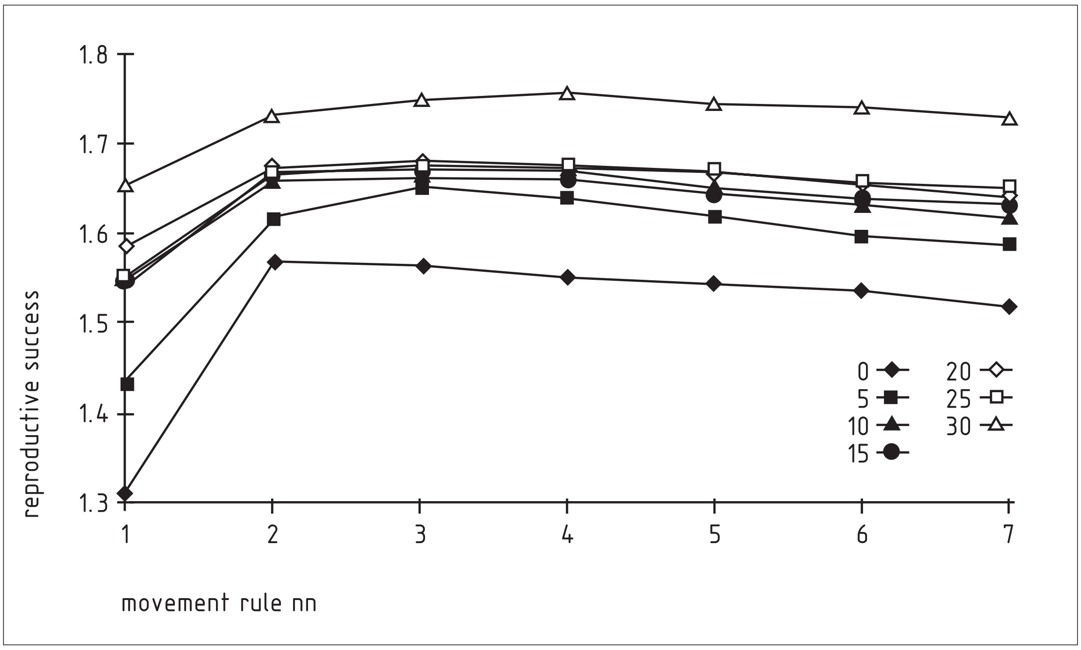

*Fig. 22 Reproductive success per female gecko for different movement rules and clumpedness of habitat*
*(n_days = 18).*

## *Discussion*

### Optimality-based parameter estimation

Often it is difficult and/or very labour intensive to estimate values of certain parameters by field studies. This is especially true for parameters of movement, which is per se a difficult phenomenon to observe (Turchin 1998). The presented approach can be used to estimate the values of such parameters. An individual-based model was implemented to reflect the rules and parameters found in the field realistically. For this kind of task individual-based models are superior to state variable models, as they usually make more realistic assumptions (Grimm 1999). Hence, parameter of the models can easily be interpreted in an ecological context. The output parameter of the model was the reproductive success of a female gecko. This parameter can be interpreted by optimality theory. A prediction of optimality theory is that the reproductive success is maximized. Using this criteria, the values of parameters (*n_days, nn*) could be estimated and compared to results of field studies. Thus, the movement strategy of geckos could be further determined.

The approach follows the idea of Dunning et al. (1995). He proposed that, when field data on dispersal are lacking, optimality theory could help identify realistic dispersal strategies in spatially explicit population models. So far many studies exist that have modeled movement without knowing how to link it to important processes of population dynamics. In some models the arrival of an individual in a patch was used to indicate successful movement [e.g. Ruckelshaus et al. (1997), Tischendorf (1997), Zollner & Lima (1999)]. Without further assumptions (about establishment and reproduction) arrival alone cannot be used to predict population dynamics (Turchin 1998, South 1999b). The optimality approach helps to focus on the factors affected by movement that are relevant for population dynamics and an adequate component of individual fitness (Parker & Maynard-Smith 1990).

Ecological interpretation of the movement strategy Optimality theory allows to interpret the movement strategy in an ecological context. The model predicted that, at realistic densities, about 18 days of movement are necessary to achieve an optimal reproductive success. It is known that the number of days geckos can search for a mating partner is limited. After emerging from hibernation, which occurs in the study area in September, mating can take place from October until early December. Direct observations of mating in November have been made. Females lay one egg each in two clutches and hatching takes place from January to March. Small juveniles have a higher mortality than larger ones (Henle 1990a) and thus hatching later in the year would dispose juveniles to higher risks, because they may not have time to produce enough energy reserves for hibernation. The number of days needed for an optimal reproductive success depends strongly on density. At low densities the reproductive success remains very low, even if geckos are allowed to search for a long time. This is caused by additional mortality due to additional movement. Hence at low densities reproductive success is restricted, thus showing an Allee effect (Allee 1931, Stephens et al. 1999). In conclusion, at low densities the number of days necessary to achieve a high reproductive success may not be available.

### Movement rules and configuration of trees

At realistic densities the optimal movement strategy predicted by the model (nn3) fits the value found in the field (chapter II). The nn3 strategy is also optimal in most types of habitat configurations (Fig. 22). Only if the configuration is extremely clumped or regular, other strategies perform better. In the extremely clumped configuration nn4 is the optimal strategy. In such a habitat the average distances between trees become smaller and therefore a higher number in next neighbouring trees does not increase much the distances moved. The connectivity between trees is higher (more connections between trees exist), hence the number of isolated trees that are poorly connected to others is lower.

Interestingly, the same movement strategy (using the 3-4 next neighbouring patches) has been found to be optimal in a study on foraging strategies of hummingbirds moving between inflorescences (Pyke 1981) and also by Gross et al. (1995) for bighorn sheep feeding on plants. Therefore, the rule has great potential to successfully describe the movement of other species as well. Additionally, the movement strategy of nn3-4 seems to be robust and optimal to variations of configurations of trees that occur in nature. The movement strategy found confirms with predictions of optimality theory. The movement of geckos results in maximizing the reproductive success, which is consists of a high mating success and a low risk to die due to movement.

Remains the question: Why does the regular habitat configuration perform so badly? Even if the degree of clumpedness is just a little bit increased, the reproductive success is much higher. The reason for this effect is that in a regular landscape all trees have the same importance, i.e. each tree has the same number of connections to and away from itself. In contrast, in a clumped configuration trees have different importances, i.e. some have a higher number of connections to itself than away from it (cf. Fig. 26,chapter V). At these trees the same kind of effect occurs as in the “hilltopping” that some species of butterflies use to find a mating partner (Ehrlich 1988, Tennent 1995). At these trees geckos tend to concentrate, because they are more likely to end on these trees than on less important trees. At low densities this can have a very pronounced effect and helps to lower the Allee effect, because the remaining geckos will concentrate on these trees, resulting in a higher local density. An additional bonus is that in clumped regions the distances between trees are lower, resulting in an even lower mortality due to movement. When population size is increasing again, the concentration is less pronounced (simply because more individuals will move to less important trees by chance) and also less important trees will be colonized. Gruber (chapter V) developed a habitat model in which the importance of trees was included as a significant factor for the prediction of the number of geckos captured on a tree.

The results lead to an important recommendation for conservation management. If habitat patches are constructed or can somehow be arranged and movement between patches is associated with costs, then an irregular configuration of patches is more favourable than a regular configuration. Interestingly, a clumped configuration is also supported by models operating on the metapopulation level. These models predict a higher dispersal success in clumped configurations of habitat (Adler & Nürnberger 1994, Fahrig & Paloheimo 1988). This parallel suggest that the same optimality principles apply to movement strategies for metapopulations and single structured populations, if costs are associated with dispersal.

### Sex dependent movement rate

In studies of movement behavior and activity of lizards it has been found that males are less territorial and move further distances than females [*Scelporus jarrovi* (Ruby 1978), *Gehyra variegata*, *G. nana* (Moritz 1987), *Tiliqua rugusa* (Freake 1998), *Crocodylus johnstoni* (Tucker 1998) *Oligosoma grande* (Eifler & Eifler 1999)] but see Read (1999) for exceptions: *Diplodactylus stenodactylus*, *D. conspicillatus*, *Rynchoedura ornata*. Recapture studies of the gecko species analyzed in this study and of a similar species (*Oedura reticulata*) found a biased movement frequency towards males as well (Henle 1990a, Sarre 1995, Höhn (unpubl. data), Wiegand et al. 2002). This kind of behavior is expected, because males are less valuable than females in a sexually reproducing species. If a male gecko dies when looking for a mating partner another male gecko can replace this individual and mate with females. In a very extreme case, a single male gecko could fertilize all females and the growth rate would be the same for the population as in the presence of many males. Of course this does not hold if there would be a population consisting of only males and a single female.

The bias in movement frequency towards males can also be explained with the theory of evolution of mating systems. In mating systems with no parental care the distribution of females depends primarily on resources, whereas the distribution of males depends primarily on the distribution of females (Krebs & Davies 1998). The most valuable resource for female *Gehyra variegata* are trees, because they offer shelter and food supply. If females are the one that select trees, then males will have to move and search for females, because male reproductive success relies on access to females.

Though field data and model predictions agree very well, there are some limitations in the approach presented here. All animals used the same movement strategy, hence optimization was frequency independent. If only pure strategies for individuals are allowed one could find an evolutionary stable state which is not necessarily an evolutionary stable strategy (ESS), because individuals using mixed strategies may perform better (Orzack & Sober 1994). In this case, the use of an ESS would be a better approach (Parker & Maynard-Smith 1990).

An ESS approach could result in two different movement strategies for males and only one movement strategy for females. Males may have two options to increase their reproductive success. Either they stay at one tree, have a low risk to die, and mate with one female per year, increasing their longevity or they move around and look for additional mating partners. This increases their yearly reproductive success, but decreases their average life expectancy. Females are unlikely to have two different strategies. They cannot increase their yearly reproductive success by moving around, so the only possibility for them is to decrease the risk of mortality by staying at the same tree. In a further model we will test these hypothesis with an ESS approach that allows different inherited strategies and will compare the model predictions with the results of genetic studies on parentship that are underway.

# Chapter V

## A functional landscape index to predict the mating success in a structured population

### *Introduction*

Finding the missing link between landscape pattern and population processes is crucial for understanding and predicting the future of populations of animals in space and time (Turner 1989, Turner et al. 1989a, Johnson et al. 1992, Wiens et al. 1993, Wiegand et al. 1999). One of the most important processes that is affected by landscape and affects population dynamics is movement. To put it in other words, movement is the glue that determines the distribution of populations in space and time (Turchin 1998). In order to fully understand the effects of landscape structure on population processes, the individuals' specific response to the landscape structure (e.g. movement behavior) has to be taken into account. Hence, tools for linking individual behavior with population processes are needed.

In contrast to this, one of the most prominent approaches to solve this problem is to use landscape indices that measure an important feature of landscape and try to correlate the index to measurements of ecological processes (i.e. density, distribution, survival of a species) (Tischendorf 2001). A huge number of different landscape indices has been proposed in the past. The problem of these indices is that they are calculated without resting on the underlying movement processes (Vos & Verboom 2001), though some of them have been used successfully to predict ecological processes. Hence no further insight into the effects of landscape on population dynamics is gained by using these indices. A recent advance has been proposed by Vos & Verboom (2001). They used ecologically scaled landscape indices, which incorporate the different scales at which species operate. Previously, landscape indices were solely based on the configuration of the landscape, which resulted in the same value, no matter how different species are ecologically. This is clearly not appropriate and has been a major limitation for the usefulness of landscape indices so far. Some authors have proposed to invent landscape indices, which are based on traits of animal species. This is a promising approach and has been used successfully by Wiegand et al. (1999) to predict the population dynamics of brown bears in different simulated landscape configurations.

I present an individual-based, spatially explicit model that allows the individual probability of meeting a partner (and therefore the rate of fertilized females) to be assessed and analyzed in terms of the consequences of both, different landscape structures and different (sex-specific) movement rules. A similar approach was taken by Jaeger (2000a), who proposed a coherence index C that calculates the chance of two individuals to meet each other, but based on the number and size of patches in an area. Here, the index calculates the probability of two individuals to meet each other using several movement rules. Therefore, it is more flexible, as different movement rules can be used for different species.

Finally, I will show that a landscape quality index $\lambda$ "reproductive success" can be derived that contains the whole essence of the presented simulation model and provides a tool for analyzing a given landscape through the eyes of the considered species. This index depends only on the landscape structure and on the movement rules. It can be calculated directly without having to resort to the underlying individual-based model itself.

The index calculates the probability to meet a partner by summing up the probability to meet a partner at each habitat patch of the landscape. Due to the habitat configuration some patches have a relatively high probability that two individuals will meet. These patches will contribute more to the overall sum to meet a partner than some more isolated patches. In other words, the relative importance of a single patch $k$, $\gamma_k$, in terms of providing a meeting place can be assigned. The presented model-based approach was tested and validated in a case study, using a long-term data set of a population of an arboreal gecko (*Gehyra variegata*) in Australia.

## *Individual-based model derivation of the landscape index*

The same individual-based simulation model as in chapter IV was used, hence I will describe the model here very briefly. A certain number of geckos were placed in a configuration of trees, and the geckos moved according to the movement rules a certain number of days. The aim of the model was to count the number of meetings that occur on each tree. Every meeting of two animals of the opposite sex was counted as a mating event, and I will refer to this quantity as the landscape quality index (or simply landscape index) $\lambda$.

The simple structure of the model allows calculation of the chance to meet a partner at each tree directly with mathematical methods, without the need to refer to the individual-based simulation model.

## *Mathematical derivation*

Here, I will explain the derivation in words, which is easier to follow for the mathematically unskilled readers. The full mathematical derivation and an example of the index can be found in the appendix.

Think of a configuration of *N* patches (trees), on which two animals of different sex are placed randomly. The probability $\lambda(0)$ that both individuals are placed on the same tree at time 0 can be calculated by:

$$\lambda(0)=\frac{1}{N}\times\frac{1}{N}\times N=\frac{1}{N} \tag{1}$$

At the next time step they move with a certain probability $p_{move}^{male,female}$ (which can depend on the sex) to another tree. When moving to another tree they have to choose one of the next neighbouring trees, depending on the movement rules. There exists a probability to die $p_{die}(distance)$, if they move to another tree (depending on the distance between trees). If they do not die, they have a certain probability to end at the same tree. This probability depends on the position where they have been before and to which tree they move, the number of trees *N,* and on the connectivity between trees, which depends on the movement rules.

The probability for a female to move from tree *i* to tree *k* is:

$$w_{i\Rightarrow k}^{f}=p_{move}^{f(i,k)}\times\ (1-p_{die})^{distance(i,k)} \tag{2}$$

The probability for a male to move from tree *j* to tree *k* is:

$$w_{j\Rightarrow k}^{m}=p_{move}^{m(j,k)}\times\ (1-p_{die})^{distance(j,k)} \tag{3}$$

The probability that they met at time step 1 at a tree can be calculated as:

$$\lambda(1)=\sum_{k}^{N}\sum_{i}^{N}\sum_{j(j\neq i)}^{N}w_{i\Rightarrow k}^{f}\times w_{j\Rightarrow k}^{m} \tag{4}$$

This is the sum of the probabilities to end at the same tree over all possible movements, but excluding the case, when two animal have been at the same tree before time step 1.

Mathematically spoken, the only thing one has to do is to track the probabilities of the two animals to be on the same tree at a certain time step and add up these probabilities. Additionally, if the two animals have met at a tree, they do not move anymore and do not contribute to the meeting probability in future time steps.

For each following time step the calculation has to be repeated until the desired time $n$ is reached. This is then called the mating index $\lambda(n)$, expressing the rate of fertilized females in a given configuration of patches after $n$ time steps.

The whole simulation model can be viewed as a Markov-process. The Markov-process can be calculated via matrix calculations and this mathematical technique is used in the appendix. At the beginning one has to calculate the probability that two animals are on a specific tree for each tree. The probabilities are the entries of a starting vector, which is multiplied by the transition matrix. The entries of the transition matrix are determined by the distances between trees, the probabilities to move to another tree, the probability to die during a move, and the movement rules. It contains the whole structural configuration of the patches, the movement probability, and the movement mortality. After multiplication, the resulting vector shows the probabilities of the two animals to be on two specific trees. To find the probability that two animals met on any tree, one has to add the probabilities that the two animals met for each single tree. Another way to use the resulting vector is to take the probability that two animals met at a certain tree. The sum of these probabilities equals the probability to meet in a given landscape configuration or the rate of fertilized females. If the ratio of the probability to meet at a certain tree to the probability to meet at any tree is calculated, one can determine the relative contribution of each tree to the whole probability to meet. This is a direct measurement for the structural importance of each tree, $\gamma_k$.

The index can be extended to more than two animals and used to calculate the rate of fertilized females in a population. If $m$ males and $f$ females are in a population, then the rate of fertilized females at time step $n$ can be calculated by

$$\lambda_{m,f}(n) = 1 - [1 - \lambda_{m=1,f=1}(n)]^m \tag{5}$$

The formula is based on the assumption that there are no interactions between animals of the same sex. Each additional male increases the chances of a female to find a mating partner, but additional females do not change the average rate of fertilized females, because each additional female has the same chance to find a mating partner as the first female.

## *Comparison of the two derivations*

Figure 23 shows a comparison of the two derivations of the landscape index $\lambda$, and demonstrates the equivalency of the two approaches. The very small differences between the two derivations reflect the mathematical differences of the two approaches. The individual-based model is a stochastic simulation model that delivers different results for the same parameter set in each run of a simulation. The mathematical derivation of the landscape index results in a fixed value for each parameter set.

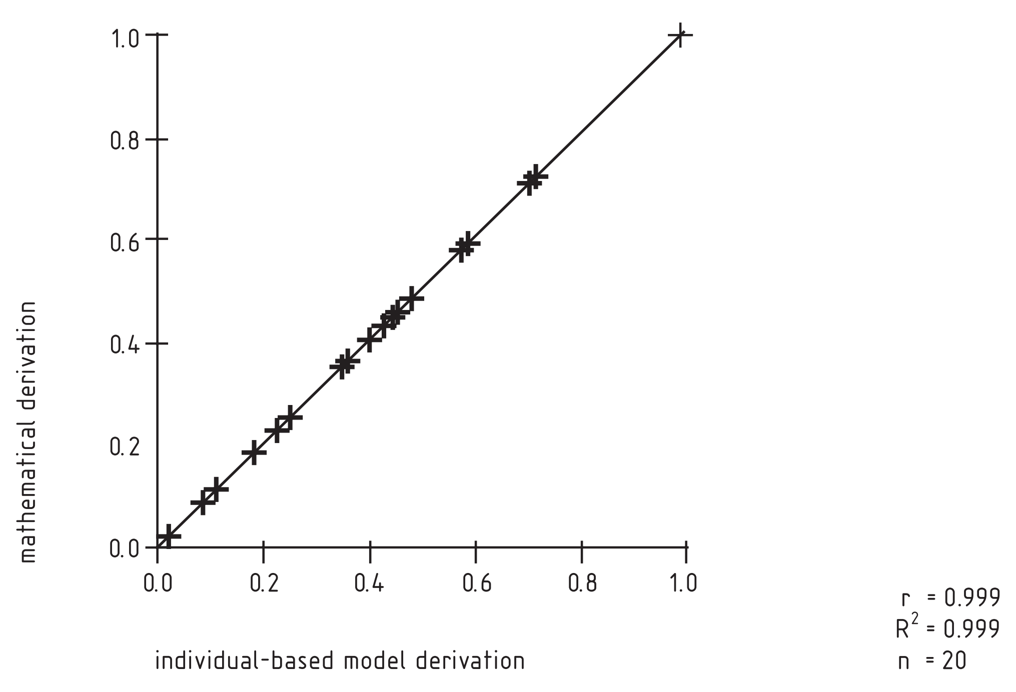

*Fig. 23 Correlation between the two different derivations of the landscape index $\lambda$ for 20 randomly chosen parameter sets.*

## *Case study*

To test the suitability of the landscape index to explain the distribution of geckos across trees, its predictive power was analyzed using a habitat model. A multiple regression analysis with the number of different geckos caught at each tree during the entire study as dependent variable was performed. I included size of a tree and the number of hiding places as independent variables, since these parameters have been found to be important determinants of the number of geckos caught per tree (Henle 1990a). As an additional independent variable I calculated the index of **relative importance of each tree, $\gamma_k$** (see Appendix for derivation).

The relative importance of each tree, $\gamma_k$ was calculated via the landscape index using the movement rules determined by earlier capture-mark-recapture studies (see chapter II and III, ). The idea of the index $\gamma_k$ is that each tree contributes a amount to the overall rate of fertilized females in a structured population (i.e. at some trees individuals meet very often, at other more isolated trees very rarely). This amount depends on the movement rules and the position of the tree in relation to other trees of the habitat.

The **size of trees** was determined photographically (Fig. 25). Each of the 41 trees of the habitat was photographed twice from the same distance from two different angles (north and east). A transparent paper was placed over the photos and the shape of each tree was outlined with a pen. The transparent paper was scanned into the computer and the shape of trees was filled by aid of imaging software. The program FRAGSTATS (Mc Garigal & Marks 1995) was used to calculate the size of the trees by counting the number of pixels necessary to fill the shape of trees. The configuration of trees was determined using triangulation techniques. From the original 41 cases (trees) in the habitat only 37 were finally used for the multiple regression. Twice two trees were recorded as one tree, because they were very close to each other and had highly overlapping crowns. Two other trees died shortly after the beginning of the study and these trees were deleted from the analysis. On these trees, no leaves were left, hence, these trees probably do not supply enough food for supporting a gecko and are very rarely visited by geckos.

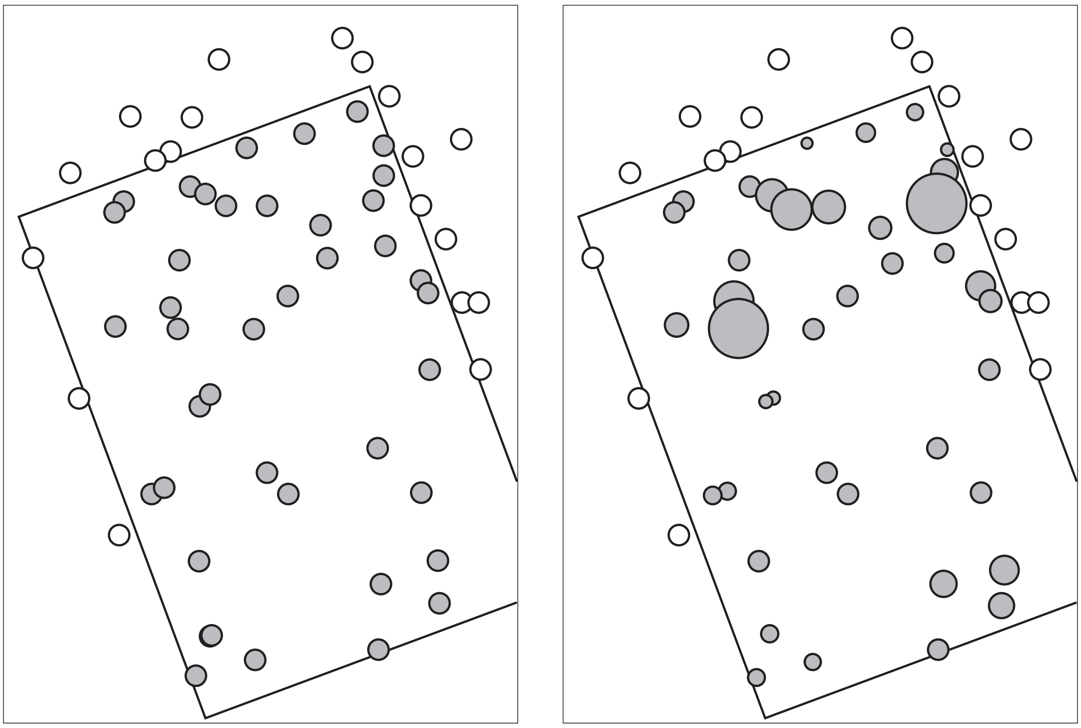

*Fig. 24 Configuration of trees in the study area. Both figures show the configuration of the trees (circles) in the habitat. The different size of trees in the right diagram is proportional to the calculated relative importance of each tree,* $\gamma_k$ *in the habitat.*

On each tree **hiding places** were recorded by counting hollow stems and openings that are big enough to support geckos.

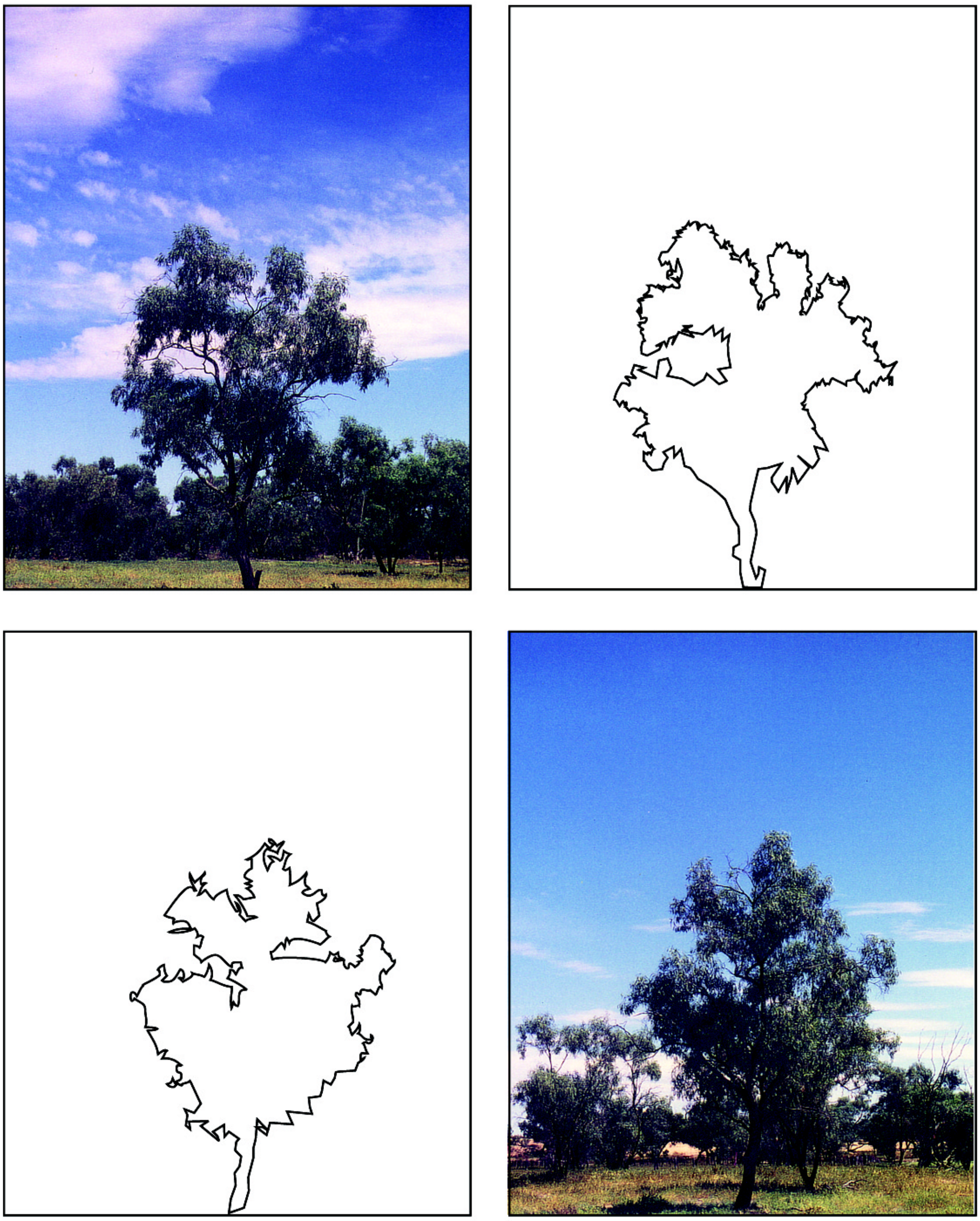

*Fig. 25 To determine tree size, trees were photographed from two different angles. Photos were scanned and shapes of trees were filled by aid of image editing software. FRAGSTATS determined the size of each tree by counting the pixels needed to fill the shape.*

## *Results*

The two sizes of each tree determined from two angles were highly correlated ($r=0.90$, $R^2=0.84$, $\alpha<0.0001$) and rather similar, hence the mean of both sizes was taken as a size index.

A standard multiple regression was performed between number of geckos caught (*caught*) as the dependent variable, and tree size (*size*), tree importance $\gamma_k$, (*importance*), and number of hiding places (*hiding*) as independent variables. Prior to the analysis, confirmation with the assumptions of multivariate analysis was tested for the variables using the protocol of Tabachnik & Fidell (2001). None of the variables showed strong deviation from a normal distribution when checked for skewness and kurtosis,so no transformation was necessary. No outliers among the cases were found using $\alpha<0.001$ as significance criterion for the Mahalanobis distance. Variables were also checked visually for homoscedasticity and linearity. Table 11 displays the correlations between all variables, the unstandardized regression coefficients, $B$, and constants, the standardized regression coefficients $\beta$, the semipartial correlations $sr^2$ and $R^2$, and adjusted $R^2$. The regression coefficient $r$ was significantly different from zero, $F_{3;37}=13.31$, $\alpha<0.0001$.

The correlation between the independent variables was weak and all of them contributed significantly to the prediction of the numbers of animal caught at each tree. The semipartial correlations for *hiding*, *size* and *importance* were $sr^2=0.540$, $sr^2=0.394$ and $sr^2=0.246$ respectively. Altogether, 54% (51% adjusted) of the variability in the dependent variable *caught* was predicted by knowing scores on these three independent variables.

*Tab. 11 Correlations among variables and results of standard multiple regression analysis of habitat factors on number of animals caught on trees*

| variable | caught | hiding | size | importance | B | β | sr² |
|---|---|---|---|---|---|---|---|
| hiding | 0.596 | | | | 1.534*** | 0.545 | 0.540 |
| size | 0.392 | 0.050 | | | 0.001*** | 0.399 | 0.394 |
| importance | 0.264 | 0.123 | -0.135 | | 1799.82* | 0.250 | 0.246 |
| constant | | | | | 3.247 n. s. | | |
| mean | 15.000 | 2.946 | 3201.721 | 0.002 | $R^2 = 0.547$<br>adjusted $R^2 = 0.506$<br>$r = 0.734$***<br>$\alpha < 0.0001$ | | |
| standard deviation | 6.218 | 2.210 | 1792.989 | 0.001 | | | |

## *Discussion*

### Suitability of the landscape index

Many different landscape indices have been proposed and checked for their usefulness to predict ecological processes (e.g. Gardner et al. 1987, Turner 1989, Cullinan & Thomas 1992, McGarigal & McComb 1995, Riitters et al. 1995, Schumaker 1996, Cain et al. 1997, reviewed by Gustafson 1998, Hargis et al. 1998, Jaeger 2000a, Tischendorf 2001). Despite the efforts which have been spent on finding useful landscape indices, many indices do exist, which sometimes correlate nicely with an ecological process, but fail under different circumstances (i.e. a different species or a different landscape configuration). The reason for this is that most landscape indices are lacking any explicit relationship to ecological processes (Vos & Verboom 2001).

To be useful as a predictor a landscape index must meet the suitability criteria suggested by Jaeger (2000a). The landscape index $\lambda$, derived in this paper is based on the same idea as the coherence index C of Jaeger (2000a), and most of his criteria apply (intuitive interpretation, mathematical simplicity, detection of structural differences). Additionally, an index should be topological sensitive (Jaeger 2000b), which means, it should be sensitive to changes in landscape configurations.

Landscape indices have to predict reliably an important ecological process of a species. This can only be achieved if the index is species specific, i.e. if it measures the landscape through the eyes of a species (Grimm et al. 1996, Frank & Wissel 2002). Interestingly, most of the studies that reported an excellent fit of a landscape measurement with an ecological process are examples of human mediated processes (e.g. development of land use O'Neill et al. 1988, Pan et al. 1999). Here the human eye is ideal to look at the landscape, because the focus is the human species and, moreover, an idea about the underlying processes exists and helps to use the appropriate landscape measurements. For example O'Neill et al. (1988) found a close correlation between decreasing fractal dimension and increasing agricultural or urban disturbance in a landscape. As fractal dimension measures the edge to area ratio, it is appropriate for measuring additional agricultural activities, as these activities result in bigger fields and less smaller patches.

Landscape indices that are suitable for predicting important ecological processes have been found also for other animal species. Wiegand et al. (1999) could express the population dynamics of brown bears and Vos et al. (2001) predicted metapopulation survival of bird species with a landscape index. The drawback of the approaches oriented at single species and problems, is that many different indices for different ecological processes and different species have to be developed and no general results can be drawn from these approaches.

The advantage of the approach developed in this paper is its suitability as a framework for a variety of species and habitats. The index proposed here is very flexible and can be applied to other species using different movement rules and different risks of mortality, when moving through the landscape. This is possible because it is a functional index that can predict an important aspect of the population dynamics of animal species, namely the chance to meet a conspecific in a landscape (compare Jaeger 2000b). Notwithstanding, the direct linkage to population dynamics require that an additional assumption is met (every meeting leads to a successful mating).

For some species the most critical resource is to find a mating partner as in the system presented here, for other species it is to find a nesting place or to find places to forage on. Hence a systematics of appropriate landscape indices is needed, which captures different important aspects of different species and allows the prediction of the effect of an altered landscape on the species. The framework developed here is suitable for the development of such landscape indices.

### Validation of the landscape index

The index was applied to a dataset of an arboreal gecko and successfully improved the prediction of the numbers of animals caught at a specific tree. In a multiple regression analysis Henle (1990a) showed that the size of trees and the number of hiding places are important factors. In his study, the distance to the next neighbouring tree failed to correlate with the number of geckos occurring at a tree. In contrast to this, the movement rule nn3 (moving to one of the 3 next neighbouring trees that are visible) used to calculate the index was successful in predicting the number of geckos. Hence, it stresses the importance that simple measurements of configurations (simple landscape indices) can be inappropriate to explain ecological processes.

Another interesting feature of the index is its time dependency [as the effect of landscape configuration on ecological processes clearly has a temporal dimension (see appendix)]. The longer animals are allowed to move in a landscape, the less fragmented the landscape will be from the view of the species (if mortality is not too high). It is well known that, given enough time, mammals are capable to cover unexpected great distances (Szacki 1999), hence the longer the available time span, the less important will be the effect of landscape configuration (Fahrig 1998).

The time dependency is also important, when species with different mortality and longevity are compared. For individuals of a long-living species, it is very likely that the same landscape will be less fragmented than for a short-living species (Harrison & Fahrig 1995). In other words, the effect of landscape pattern on population dynamics has a spatial and a temporal dimension, and both dimensions need to be taken into account for predictions of ecological processes (Harrrison & Fahrig 1995, Turchin 1998).

The presented landscape index can be calculated in two different ways. Either using a spatially explicit, individual-based simulation model or by using matrix calculations. As the simulation model is driven by easily explained movement rules and can be visualized during simulation, it is easy to understand for mathematically unskilled people. The mathematical version is preferable for the calculation of the index in practise, as it is easier to implement and can be used by persons who are just interested in the results and not in the full understanding of the technical details of the approach (e.g. for management tasks).

## *Appendix*

The landscape index is calculated via matrix multiplication of a vector $\vec{p}$, expressing the probability of two animals to be on two specific trees (patches) and the transition matrix $\tilde{A}$, expressing the transition probabilities of two animals to move to other trees within one time step. In each time step, the probabilities of the animals being on the same tree are summed up for all trees. This sum, defined as the mating index $\lambda$, is a direct measurement of the meeting probability of two animals of the opposite sex in a given configuration of patches and, if the assumption that each encounter leads to a successful mating is true, a measurement for the rate of fertilized females. Additionally, the probability that two animals meet at a certain tree $k$, $\gamma_k$, can be calculated for each tree in the habitat. This probability is a measurement of the relative importance of a tree compared to all other trees in the habitat.

When two animals are placed with equal probability on N trees, then there are $N^2$ possible states. This determines the $N^2$-dimensional starting vector $\vec{p}$. Each entry ( $tree_{1..N/1..N}$ ) in the vector represents a state of the two animals on two trees. Note that the equal distribution is just an arbitrary assumption and can be replaced by other distributions, if other information on the initial distribution of animals is available:

$$\vec{p}=\begin{pmatrix} tree_{1/1} \\ tree_{1/2} \\ \dots \\ tree_{N/N} \end{pmatrix}=\begin{pmatrix} \frac{1}{N^2} \\ \frac{1}{N^2} \\ \dots \\ \frac{1}{N^2} \end{pmatrix} \qquad \text{(A1)}$$

The transition matrix $\tilde{A}$ describes the possible movements in terms of transition probabilities to all other states. The quadratic transition matrix $\tilde{A}$ consists of $N^2$ rows and columns, i.e. if there are *41* patches it results in a matrix of $41^2=1641$ elements. With modern computers, this should not cause any problems, except if the number of patches is several orders of magnitude higher.

Each entry of the matrix represents a transition probability of two animals siting on two trees and moving to two other trees (which may be the same or not).

$$\tilde{A}=\begin{bmatrix} m_{\substack{1\Rightarrow 1\\1\Rightarrow 1}} & m_{\substack{1\Rightarrow 1\\2\Rightarrow 1}} & m_{\substack{1\Rightarrow 1\\3\Rightarrow 1}} & m_{\substack{1\Rightarrow 1\\4\Rightarrow 1}} & .. & m_{\substack{N\Rightarrow 1\\N\Rightarrow 1}} \\ m_{\substack{1\Rightarrow 1\\1\Rightarrow 2}} & m_{\substack{1\Rightarrow 1\\2\Rightarrow 2}} & m_{\substack{1\Rightarrow 1\\3\Rightarrow 2}} & m_{\substack{1\Rightarrow 1\\4\Rightarrow 2}} & .. & m_{\substack{N\Rightarrow 1\\N\Rightarrow 2}} \\ m_{\substack{1\Rightarrow 1\\1\Rightarrow 3}} & m_{\substack{1\Rightarrow 1\\2\Rightarrow 3}} & m_{\substack{1\Rightarrow 1\\3\Rightarrow 3}} & m_{\substack{1\Rightarrow 1\\4\Rightarrow 3}} & .. & m_{\substack{N\Rightarrow 1\\N\Rightarrow 2}} \\ m_{\substack{1\Rightarrow 1\\1\Rightarrow 4}} & m_{\substack{1\Rightarrow 1\\2\Rightarrow 4}} & m_{\substack{1\Rightarrow 1\\3\Rightarrow 4}} & m_{\substack{1\Rightarrow 1\\4\Rightarrow 4}} & .. & m_{\substack{N\Rightarrow 1\\N\Rightarrow 2}} \\ .. & .. & .. & .. & .. & .. \\ m_{\substack{1\Rightarrow N\\1\Rightarrow N}} & m_{\substack{1\Rightarrow N\\2\Rightarrow N}} & m_{\substack{1\Rightarrow N\\3\Rightarrow N}} & m_{\substack{1\Rightarrow N\\4\Rightarrow N}} & .. & m_{\substack{N\Rightarrow N\\N\Rightarrow N}} \end{bmatrix} \tag{A2}$$

with

$$m_{\substack{i\Rightarrow k\\j\Rightarrow l}}= w^{f}_{i\Rightarrow k}\times w^{m}_{j\Rightarrow l}= p^{f\,(i,k)}_{move}\times (1-p_{die})^{distance(i,k)}\times p^{m\,(j,l)}_{move}\times (1-p_{die})^{distance(j,l)}$$

A(3)

The transition probability $m_{\substack{i\Rightarrow k\\j\Rightarrow l}}$ is the product of the probability of a female moving from tree *i* to tree *k*, $w^{f}_{i\Rightarrow k}$, times the probability of a male moving from tree *j* to tree *l*, $w^{m}_{j\Rightarrow l}$.

$p^{f\,(i,k)}_{move,}\, p^{m\,(j,l)}_{move}$, are the probabilities that a male *m* respectively female *f* moves to another tree and are calculated by

$$p^{f\,(i,k)}_{move}=(1-p^{f}_{stay})/nn,\; p^{m\,(j,l)}_{move}=(1-p^{m}_{stay})/nn, \tag{A4}$$

if a connection between trees *i*, *k* (*j*, *l*) exists, otherwise $p^{f\,(i.k)}_{move}$ and $p^{m\,(j,l)}_{move}$ are set to zero. $p_{die}$ is the probability to die per moved distance and *distance(i,k)* is the euclidean distance between tree *i* and tree *k* in meters. In this study, $p_{die}$ was assumed to be independent of the sex of the animal moved, but it is possible to include sex dependent mortality rates during movement.

Since animals meeting on a certain tree usually remain together, it is important not to count them again in future time steps. Therefore, all transitions of two animals being on the same tree to any other trees $m_{\substack{i\Rightarrow k\\i\Rightarrow l}}$ are set to zero.

*nn* is the number of next neighbouring trees that may be selected when an animal moves and depends on the movement rules. It is possible to use any other movement rule, if they can be expressed in terms of probability to move from one patch to another. For example in most metapopulation approaches, movements depend solely on distances between patches, hence movement is not limited to a few patches and it is possible to move to every patch in the habitat. If there is additional information that some patches are acting as corridors, this can also be incorporated. Also asymmetric movement rules can be included, which can be useful in studies on source and sink patches.

To calculate the meeting probability $\lambda(1)$ at time step 1, one has to multiply $\tilde{A}$ x $\vec{p}$ and sum up the probabilities of each entry of the resulting vector that expresses a meeting at a certain tree $k$:

$$\lambda(1)=\sum \tilde{A}\times\vec{p} \tag{A5}$$

The final probability to have met until time step $n$ is obtained by $n$ iterative multiplications of the resulting vector $\vec{p}_i$ ($i=1..n$) with the transition matrix.

$$\lambda(n)=\sum_{i=0}^{N}\lambda(i) \tag{A6}$$

with $\lambda(0)=\frac{1}{N}\times\frac{1}{N}\times N=\frac{1}{N}$, which is the probability of being on the same tree at time step 0.

The extension to more than two animals can be used to calculate the rate of fertilized females in a population. If $m$ males and $f$ females are in a population, then the rate of fertilized females at time step $n$, $\lambda_{m,f}(n)$, can be calculated by:

$$\lambda_{m,f}(n)=1-[1-\lambda(n)]^{m}, \tag{A7}$$

which is one minus the probability of a single female not to meet a single male ( $1-\lambda(n)$ ) to the power of $m$. Additional females do not change the rate of fertilized females as it is the same for all females. An implicit assumption is that no interactions between animals of the same sex occur.

The relative contribution of a single tree *k* to the meeting probability can be calculated for each tree by adding the entries of $\vec{p}_i$ resulting in a meeting at a specific tree in each time step separately and divide it by $\lambda(\boldsymbol{n})$ :

$$\gamma_k(\boldsymbol{n}) = \frac{\lambda_k(\boldsymbol{n})}{\lambda(\boldsymbol{n})} \tag{A8}$$

## *Example*

To illustrate the approach a simple example will be presented. Figure 26 shows the habitat configuration of the four trees and Table 12 the values of parameters used.

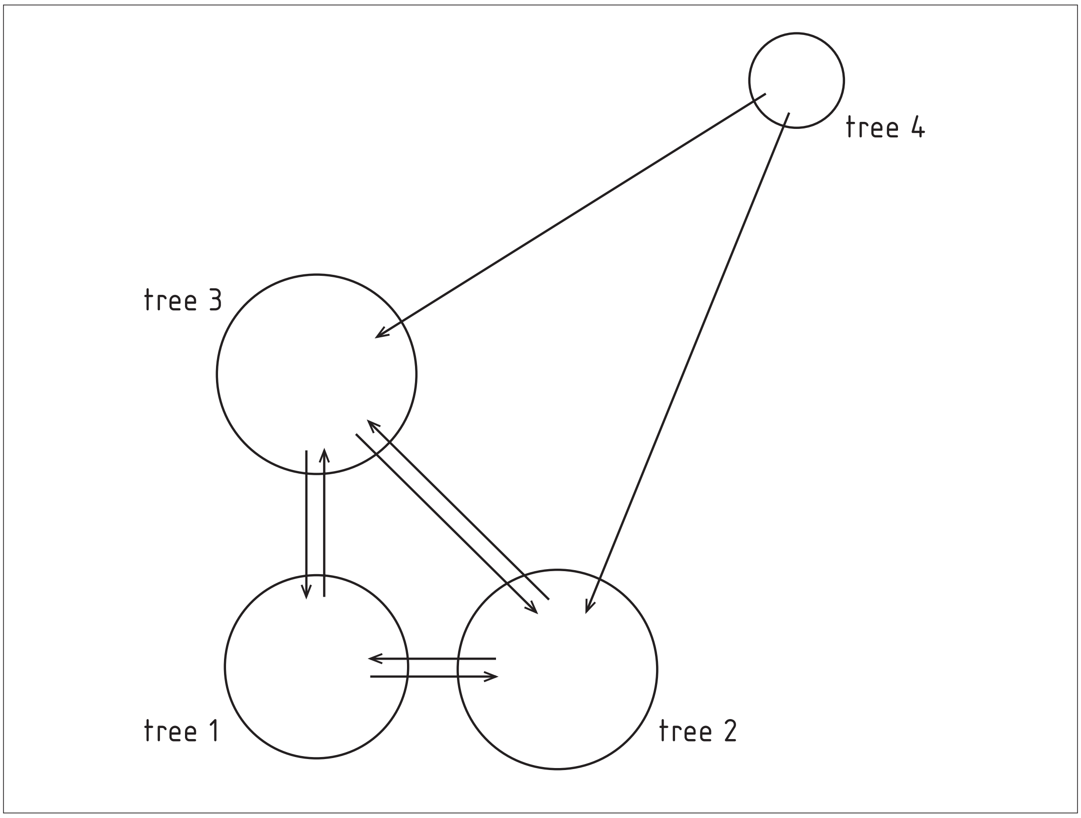

*Fig. 26 Configuration of example habitat and relative importance of trees,* $\gamma_{k,}$ *with movement rule: 2nn (go to one of the 2 next neighbouring trees). The size of circles represents the the relative importance of each tree. Tree 4 has lowest importance, because it is never the next neighbour of other trees. Tree 2 and tree 3 have the highest value of relative importance, i.e. they are the next neighbours of all other trees.*

*Tab. 12 Value of the parameter used in the example.*

| variable | description of the variable | value |
|---|---|---|
| $N$ | number of patches | 4 |
| $p^{f}_{stay}$ | probability to move for females | 0.8 |
| $p^{m}_{stay}$ | probability to move for males | 0.6 |
| $p_{die}$ | probability to die per distance unit | 0.01 |
| $nn$ | number of next neighboring trees, when an animal decides to move | 2 |

The starting vector $\vec{p}$ is of dimension $N^2=16$ .

$$\vec{p}=\begin{pmatrix} tree_{1/1} \\ tree_{1/2} \\ \dots \\ tree_{N/N} \end{pmatrix}=\begin{pmatrix} \frac{1}{16} \\ \frac{1}{16} \\ \dots \\ \frac{1}{16} \end{pmatrix}$$

To calculate the entries of the transition matrix, first the movement probabilites have to be determined (equation A4):

$$p^{f\,(i,k)}_{move}=(1-p^{f}_{stay})/nn=0.1\ ,$$

$$p^{m\,(j,l)}_{move}=(1-p^{m}_{stay})/nn=0.2\ ,$$

and the transition probability for each possible combination using equation A3:

$$m_{\substack{i\Rightarrow k\\ j\Rightarrow l}}=\ w^{f}_{i\Rightarrow k}\times\ w^{m}_{j\Rightarrow l}=\ p^{f\,(i,k)}_{move}\times\ (1-p_{die})^{distance\,(i,k)}\times\ p^{m\,(j,l)}_{move}\times\ (1-p_{die})^{distance\,(j,l)}\ .$$

Suppose, there is a male on tree3 and a female on tree2 and the distance between tree1 and tree2 (tree3) is ten units. Then the transition probability is:

$$m_{\substack{2\Rightarrow 1\\ 3\Rightarrow 1}} = 0.2 \times (1-0.01)^{10} \times 0.1 \times (1-0.01)^{10} = 0.0164$$

As shown in Fig. 26 there is no connection between tree1 and tree4, hence all transition probabilities containing these transitions (e.g. ) $m_{\substack{2\Rightarrow 3\\ 1\Rightarrow 4}}$ are set to zero. The full matrix is shown below (compare equation A2).

$$\tilde{A} = \begin{vmatrix}
0.000 & 0.054 & 0.054 & 0.000 & 0.145 & 0.000 & 0.016 & 0.000 & 0.145 & 0.016 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 \\
0.000 & 0.480 & 0.052 & 0.048 & 0.016 & 0.000 & 0.016 & 0.014 & 0.016 & 0.145 & 0.000 & 0.014 & 0.000 & 0.000 & 0.000 & 0.000 \\
0.000 & 0.052 & 0.480 & 0.048 & 0.016 & 0.000 & 0.145 & 0.014 & 0.016 & 0.016 & 0.000 & 0.014 & 0.000 & 0.000 & 0.000 & 0.000 \\
0.000 & 0.000 & 0.000 & 0.480 & 0.000 & 0.000 & 0.000 & 0.145 & 0.000 & 0.000 & 0.000 & 0.145 & 0.000 & 0.000 & 0.000 & 0.000 \\
0.000 & 0.016 & 0.016 & 0.000 & 0.480 & 0.000 & 0.054 & 0.000 & 0.139 & 0.016 & 0.000 & 0.000 & 0.128 & 0.014 & 0.014 & 0.000 \\
0.000 & 0.145 & 0.016 & 0.014 & 0.054 & 0.000 & 0.052 & 0.048 & 0.016 & 0.139 & 0.000 & 0.014 & 0.014 & 0.128 & 0.014 & 0.000 \\
0.000 & 0.016 & 0.145 & 0.014 & 0.054 & 0.000 & 0.480 & 0.048 & 0.016 & 0.015 & 0.000 & 0.014 & 0.014 & 0.014 & 0.128 & 0.000 \\
0.000 & 0.000 & 0.000 & 0.145 & 0.000 & 0.000 & 0.000 & 0.480 & 0.000 & 0.000 & 0.000 & 0.139 & 0.000 & 0.000 & 0.000 & 0.000 \\
0.000 & 0.016 & 0.016 & 0.000 & 0.139 & 0.000 & 0.016 & 0.000 & 0.480 & 0.054 & 0.000 & 0.000 & 0.128 & 0.014 & 0.014 & 0.000 \\
0.000 & 0.145 & 0.016 & 0.014 & 0.016 & 0.000 & 0.015 & 0.014 & 0.054 & 0.480 & 0.000 & 0.048 & 0.014 & 0.128 & 0.014 & 0.000 \\
0.000 & 0.016 & 0.145 & 0.014 & 0.016 & 0.000 & 0.139 & 0.014 & 0.054 & 0.052 & 0.000 & 0.048 & 0.014 & 0.014 & 0.128 & 0.000 \\
0.000 & 0.000 & 0.000 & 0.145 & 0.000 & 0.000 & 0.000 & 0.139 & 0.000 & 0.000 & 0.000 & 0.480 & 0.000 & 0.000 & 0.000 & 0.000 \\
0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.480 & 0.054 & 0.054 & 0.000 \\
0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.054 & 0.480 & 0.052 & 0.000 \\
0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.054 & 0.052 & 0.480 & 0.000 \\
0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000 & 0.000
\end{vmatrix}$$

The resulting vector of the multiplication gives the probabilities of all possible combinations of the two animals on all trees. The sum of the probabilities of all possibilities, where the two animals met on the same tree, gives the overall chance that they met. For further time steps, the multiplication with the transition matrix and the resulting vector has to be repeated. At each time step the sum of the meeting probabilities has to be recorded, which is the mating index $\lambda(n)$. Figure 27 shows $\lambda(n)$ and the relative importance of all trees, $\gamma_k(n)$, for the first 50 time steps. $\lambda$ increases with time $n$ until a saturation is reached. If there would be no mortality when moving, $\lambda$ would reach one and all females would be able to find a mating partner, given enough time. The relative importance of each tree also reaches asymptotic values. At time 0 all trees have the same relative importance due to the initial equally likely distribution of the two animals. With increasing time steps the relative importance of tree3 decreases, because at this tree no further meeting can take place. While tree3 is declining in importance, the other trees become more important over time.

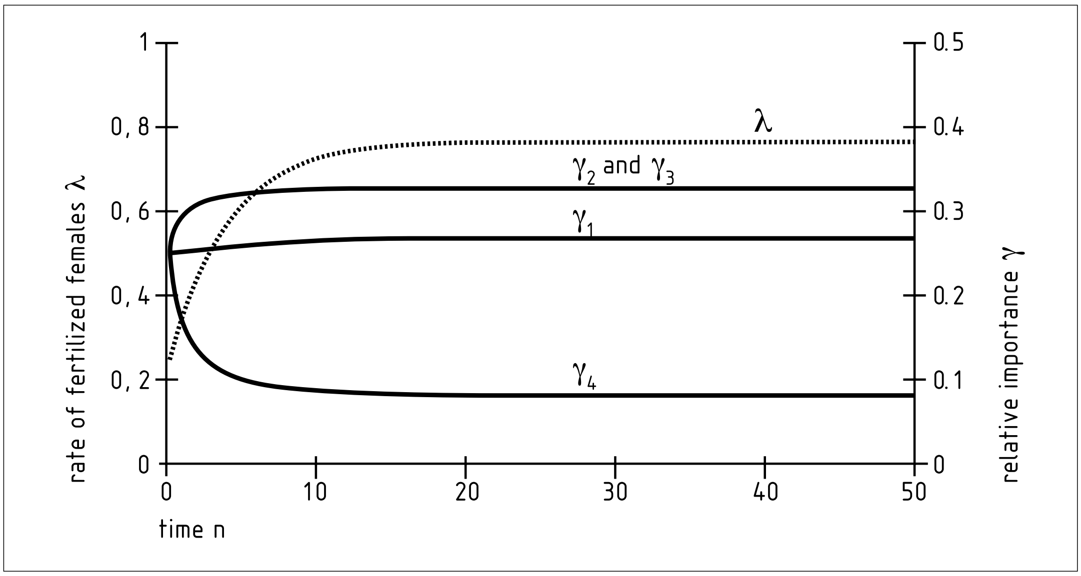

*Fig. 27 Relationship between the rate of fertilized females* $\lambda$*, relative importance of trees,* $\gamma_k$*, and time. Note that tree2 and tree3 have the same relative importance, due to the symmetric structure of the habitat.*

# Chapter VI

## Linking landscape structure to population dynamics – a review

### Introduction

"*To an ecologist, the beauty of landscapes lies not only in their reality, but in the challenge of understanding how their complex spatial structure affects ecological patterns and processes. This is the focus of the science of landscape ecology*" (Wiens 1995).

One of the most intriguing problem of landscape ecology is, how to link spatial patterns with ecological processes. The underlying premise is that the landscape structure affects ecological processes differently, if the landscape structure were altered (Wiens 1995).

The main goal of this paper is a review about the different modeling approaches of movement that have been applied for finding the linkage between landscape structure and population dynamics. The issue has been addressed theoretically by many different authors in the literature (Turner 1989, Dunnings et al. 1992, Vos 1993, Wiens et al. 1993, reviewed by Hanson et al. 1995, Gustafson 1996, 1998, With et al. 1997) but the "Elements of relevant theory on the subject are distributed over several approaches, favored by scientists with very different backgrounds; from behavioral ecology, through population ecology to mathematics and computer modeling." (Ims 1995). The intention of the review is to give an overview about the different modeling approaches and to discuss the strengths and weaknesses of each approach. Also, a vast number of empirical studies to link animal movement to population dynamics have been undertaken (fragmentation experiments: Davies & Margules 1998; creating artificial landscapes: Crist et al. 1992, Wiens et al. 1997; corridor experiments: Andreassen & Ims 1998, Ims & Andreassen 1999, Bowne 1999). A review would be well beyond the limits of this work, hence in this review I will not refer to them.

To begin I will define some important terms used in this review.

#### Landscape structure

Landscape structure is the spatial distribution of important resources in the landscape for a particular species. These resources can be trees, which provide food and shelter for arboreal species such as some geckos, or animals, such as antilopes, for a hunting lion, or inflorescences of flowers for a nectar feeding hummingbird. If the distribution of these resources occurs on a local scale, many studies use the term habitat structure. In many studies these resources are distributed on a much broader scale as patches of habitat that are suitable for the species under study in a structured population or a metapopulation (Gilpin & Hanski 1991). For simplicity of writing I will use the term landscape structure for both scales (habitat and landscape), but explicitly refer to the scale where relevant.

### Movement

The most important factor that mediates the effect of spatial structure to ecological processes is movement (May & Southwood 1990, Wiens et al. 1993, Wiens 1995). Ecologist have realized that movement is a critical but little understood process affecting population dynamics. (Turchin 1998). In this review I will use the most general definition of movement formulated by Turchin (1998): Movement is the process by which individual organisms are displaced in space over time. Movement adds or subtracts individuals to a population (Turchin 1998), provides important genetic variability, is necessary to let individuals fulfil their daily needs (Ims 1995) (foraging, finding suitable resting places etc.), let individuals find a mating partner and new habitat patches. For example, many animals forage and mate at different places an do cover enormous distances (e.g. migrating birds and whales). Individual movement is also necessary to disperse in a heterogeneous landscape.

Very different ecological processes are based on movement. Such well known processes and concepts like population genetics, territorial behavior, home ranges, population dynamics, metapopulation dynamics are closely linked to individual movement that is caused by landscape patterns. The effect of individual movement can take place on very different spatial and temporal scales and hence very different theories are applied to each specific level. For this review I identified three different scales: population genetics (movement of genes), population dynamics (movement of individuals), metapopulation dynamics (movement of populations). Notwithstanding, the phenomena are all based on individual movement. When predicting dynamics of genes and dynamics of populations, it is necessary to be able to predict movement of individuals. Individual movement is the fastest movement on the spatial and temporal scale, and often particularly difficult to measure. Moreover, so fare no commonly accepted framework for measuring individual movement exists (Turchin 1998).

### Movement rules

Movement is a complex process and is believed to rest on many different decisions that are based on rules. Each decision can be itself the outcome of a complex interplay of the internal state of an animal, the surrounding habitat and other animals and plants. There are many different ways to model this complex process. The following description of the movement process breaks it down into three different phases and is capable to cover most of the ways movement can be modeled, however other ways are possible.

To describe movement of individuals, it can be divided in three successive phases, the emigration, the dispersal and the immigration phase. All phases can include several decision rules that describe the decisions of an animal.

The emigration phase includes the decision of an individual to leave its current location. At the beginning of the dispersal phase the animal decides, to which location it wants to move. During the dispersal phase, the animal actually move to its new location. Often a higher mortality or a loss of energy is associated with movement, hence the animal can die during the dispersal phase. If an animal moved successfully to another location, it enters the final immigration phase. In the immigration phase decisions about the effect of movement are made. The effect depends on the status of the new location. For example, whether an animal that enters an empty patch, will colonize it or not. If the patch is not empty the animal can fight with a territory holder or mating can take place. Another possibility is an interaction wit h a prey or a predator.

Depending on the complexity of movement, the rules of each phase range from rather simple stochastic movement rules to very complex decision movement rules. In some models the organism move at every time step of the model (e.g. Schumaker 1996, Fahrig 1997, Ruckelshaus et al. 1997, With & King 1999, Baum & Grant 2001), hence they do move to another location independent of other factors. Many models that deal with dispersal as a response variable do use this kind of mechanism. Another way is to use a probability that represents the chance that an animal decides to move to another location; the probability can be sex dependent (Gruber, this work). Many models use a variation of the next neighbour rule in their model to mimic the decision, where to an animal wants to move. If a model is based on a grid, an animal takes one of the 4 (8) next neighbouring cells. The probability to move to one of the next neighbouring cells can depend on the quality of the surrounding habitat (Tischendorf 1997, Wiegand et al. 1999), on the density of animals in the patch (South 1999a) or can be purely stochastic (Fahrig 1998). More sophisticated movement rules are based on the internal state of an organism (Dreyfus-Leon 1999, Dagorn 2000), the surrounding habitat (Fahrig 1998) or both (Wiegand et al. 1999), Railsback et al. 1999, Ahearn et al. 2001). Here animals have a kind of memory incorporated, which summarizes the previous history of the individual and has an effect on its decision. Some models that mimic optimal foraging of animals move to locations were the expected energy intake is maximised. (Railsback et al 1999, Johst et al. 2001). To simulate the searching behavior of fishermen Dreyfus-Leon (1997) used neuronal networks to mimic the fishermens decisions to stay or to move to new fishing sites.

The above mentioned movement rules are just examples. Actually there is almost no limitation in the way movement can be described by movement rules and a vast number of different movement rules has been used in the literature. This can cause problems, as it is difficult to compare studies that used different movement rules.

### Linking landscape structure and population dynamics

Most studies do not try to connect landscape structure with the whole complex processes of population dynamics directly. Instead different measurements of response are used, either surrogate parameters of population dynamics like genetic variability and persistence (extinction): (Wiegand et al. 1996, 2002) or demographic parameters like distribution of individuals: Angel (1993), South (1999a), Langlois (2001); natality: Ahearn et al. (2001), mortality, reproductive success (combines natality and mortality): Gruber this work; dispersal (combines emigration and immigration): Schumaker (1996), With & King (1999), Tischendorf (2001). These studies try to link the response measurement with spatial structure, hence additional assumptions are needed to link it to population dynamics. A model, for example, predicting the dispersal distances of individuals, cannot be linked to population dynamics without considering additional informations or assumptions (e.g. one needs to assume that each individual reaching a new patch, will colonize the patch).

Most often the use of a specific response variable is strongly associated with a certain modeling technique (i.e. distribution of species with diffusion models, metapopulation dynamics with probability transition models). Nevertheless, some studies link landscapes structure with (meta)populations dynamics (Wiegand et al. 1999, Hanski et al. 2000, Petit et al. 2001, Frank & Wissel 2002, Wahlberg et al. 2002).

Tab. 13 gives an overview of the different modeling approaches, the main response variables predicted and a short characterization about the concept of movement associated with a specific approach.

*Tab. 13 Different approaches to link landscape structure to population dynamics*

| approach | response variable | concept of movement |
|---|---|---|
| landscape index | distribution, persistence, dispersal | movement process is generally not taken into account |
| diffusion models | distribution of dispersal distances over time | movement as a (correlated) random walk |
| percolation theory | connectivity | movement through a landscape (2 types of patches) |
| transition probability models | metapopulationdynamics, reproductive success | movement modeled as a probability to reach patch b from patch a, movement rules |
| individual-based movement models | all possible measurements of response | movement is a step by step process, movement rules are necesarry, movement rules |

### *Landscape indices*

Landscape indices try to correlate a measurement of landscape structure with a response variable of population dynamics (e.g. dispersal success) (Tischendorf 2001). Many different landscape indices have been proposed by various authors (Forman & Godron 1986, O'Neill et al. 1988, Turner 1989, Riitters et al. 1995, Hargis et al. 1998, Jaeger 2000a). Landscape indices have the advantage of being easy to calculate and can be applied easily to a given landscape structure by using GIS computer packages. Landscape indices have been used to predict a variety of response variables of population dynamics (dispersal success: Gustafson & Gardner 1996, Schumaker 1996, Tischendorf 2001; abundance: McGarigal & McComb 1995, Hamazaki 1996; distribution: With & Crist 1995, With et al. 1997; mating success: Gruber, this work; metapopulation viability: Vos et al. 2001; population dynamics: Wiegand et. al 1999; and survival probability: Fahrig 1997, 1998). Most of these studies have shown a good statistical relationship between landscape indices and the response variables.

However, investigations on the usefulness of landscape indices have shown that many of them provide redundant information (O'Neill et al. 1988, Riitters et al. 1995, Hargis et al. 1998). Interestingly studies (O'Neill et al. 1988, Pan et al. 1999) of human population dynamics could successfully predict ecological processes (e.g. development of human land use). As it is not difficult to look on the landscape in a human way and the ecological processes of human population dynamics are quite well understood, it is not surprising that landscape indices work quite well in predicting ecological processes of humans. For example O'Neill et al. (1988) found a close correlation between decreasing fractal dimension and increasing agricultural or urban disturbance in a landscape.

The problem is that a good correlation of a landscape index cannot easily be transferred to another species or landscapes. As landscape indices do not give insights on the underlying processes (e.g. movement) as Vos et. al (2001) stated: "Their weakness is the lack of any explicit relationship to ecological processes". The landscape index proposed by Gruber (this work) is somewhat different, as it is explicitly based on the movement process. It can be applied to other species using different movement rules and different risks of mortality, when moving through the landscape. Another way of applying landscape indices to different species is to scale indices ecologically (Vos et. al 2001).

These kind of approaches show a promising perspective, because they try to describe the landscape through the eye of a species (Grimm et al. 1996, Wiegand et al. 1999, Frank & Wissel 2002), hence they offer the possibility to estimate the effect of landscape structure for different species.

## Diffusion (random walk) models

Diffusion models have a long tradition in ecology (Okubo 1980. Turchin 1991, 1998 for a review) and are closely related to random walk models. Mathematical diffusion models have been used to predict the spread of organisms in space (Ims 1995). Diffusion models have their origin from physics, in which movements of particles (animals) are assumed to be random. In the simplest random walk model, movement is a step by step process, where the length and the direction of each step is drawn from a uniform distribution. If the direction of the next step is independent of the previous step, then random walk is the same as a diffusion of an animal through a featureless landscape. If the selected direction of the next step depends on the direction of the previous step, the movement is called a correlated random walk. The response variable of many diffusion models of animal movement is the expected squared net displacement and can be calculated via partial differential equations. Often ecologists are interested in calculating the mean displacement distances over time for species by analyzing movement paths of animals. Several authors have tried to give approximations to calculate this quantity (Kareiva 1983, Bovet & Benhamou 1988, Turchin 1991, Johnson et al. 1992, Byers 2001). Recently there have been theoretical advances that allow to predict the net squared displacement in heterogeneous landscapes using a correlated random walk (Turchin 1998). Byers (2001) gives a correction factor from simulation models that allows to calculate the mean displacement distance from the less meaningful mean squared displacement distance in a heterogeneous landscape.

For mathematical tractability movement rules have to be rather simple. Animals have no knowledge of the landscape and immediate surrounding. Not surprisingly, all empirical studies that report a good fit with these models are studies of "hard-wired" arthropods (e.g. Cain 1991, Turchin 1991, Levin 1992, Crist et al. 1992), which are not considered to possess higher cognitive abilities (Lima & Zollner 1996). In accordance to this, Bergman et al. (2000) showed the inappropriateness to predict the dispersal distances of caribous (*Rangifer tarandus*) using a correlated random walk approach. Some authors justify the approach of random walks, as it does not necessarily mean that animals move randomly with respect to landscapes, but movement can only be interpreted as random, because the underlying cues are not known (Turchin 1991). Another use of the diffusion approach is that it can serve as a null model to compare real movement patterns of individuals (Ims 1995, Turchin 1998). Lima & Zollner (1996) argue that it is the challenging task of ecologists to develop more sophisticated, but still tractable movement rules to model more sophisticated animals such as vertebrates. A strength of the approach is that it can easily link individual movement patterns to population dynamics. This is easily done, because the diffusion model approach is written in the same mathematical language (partial differential equation) as differential equation models of population dynamics. Hence an interaction term can express the spatial structure-movement relationship (Ims 1995).

### *Percolation theory*

Percolation is another theoretical framework from physics that was originally developed to describe movement of liquids through solid lattice networks (Orbach 1986). Percolation theory has been termed "a somewhat esotheric way of modeling corridor effects in landscapes" (Wiens 1995). It was originally used to serve as a neutral model of animal movement through a heterogeneous landscape (McIntyre & Wiens 1999). The landscape consists of two types of patches in a lattice landscape. One type of patch is permeable (i.e. habitat), whereas the other is impermeable (matrix). Percolation theory has been used to predict the probability of an animal (or disturbance event) to move across a landscape, consisting of a given proportion p of habitat (Turner et al. 1989b, Wiens et al. 1997, With & King 1997, McIntyre & Wiens 1999). An interesting prediction of this rather theoretical approach is that there is a threshold quantity, changing the characteristic of the landscape from being fragmented (i.e. the animal cannot cross the grid from one side to the other) to being connected. If the proportion of habitat is higher than a critical value, then it is likely that the animal can traverse the landscape. Of course the value of the threshold is dependent on the movement rules (i.e. if animals are allowed to cross from two cells of habitat that are just connected by a common corner or not). A rather stringent assumption of the approach is that animals are not allowed to spread into matrix cells; this limits its application to a small number of species. The measurement of response of percolation models, is the chance of an individual to traverse a given landscape structure. The link of this quantity to population dynamics is not straightforward, because additional assumptions are necessary.

As for diffusion models all applications of this theory have been made to movements of insects (tenebrionid beetles). In contrast to the predictions of percolation theory, McIntyre & Wiens (1999) found that the connectivity of a experimental landscape for beetles did depend more on the amount of habitat, than on the degree of connectivity of the habitat cells. A promising extension of the approach could be to allow more types of habitat with different permeabilities.

The so far discussed approaches do not include sophisticated types of movement defined by movement rules. This distinguishes the previous approaches from the following ones.

### *Transition probability models*

Transition probability models (cf. Turner 1989) are of intermediate complexity between landscape indices and individual-based movement models. In transition probability models movement is modeled as a product of two probabilities. The probability for an individual to move to a certain patch is the product of the probability to leave a patch times the probability to reach a certain patch. The probability to leave a patch can depend on the size of the patch. Often there is a constant mortality per meter of distance assumed (Gruber, this work, Hanski et al. 2000, Wahlberg et al. 2002). This results in negative exponential function for the probability to reach a patch with increasing distance. In transition probability models only the effective movement of reaching another patch in a structured population is modeled. This movement is an important quantity that directly affects population dynamics and also other quantities such as genetic variation among subpopulations.

Probability transition models have been mainly used to predict dispersal success of animals (mainly butterflies) (Hanski et al. 2000, Petit et al. 2001, Wahlberg et al. 2002). Furthermore Frank & Wissel (2002) showed a way, how to calculate the mean life time of metapopulations in heterogeneous landscapes. South (1999b) used a transition probability model to study the role of dispersal in a structured population. The response variable of Gruber (this work) was the chance to meet a mating partner in a structured population (mating success). An advantage is that empirical data from capture-mark-recapture studies, which are available for many species can be used to validate this kind of models (cf. Skalski et al. 1993, Gruber this work). As these quantities are easily linked to (meta)population dynamics, transition probability models proved to be very successful and have been validated by empirical data.

Often models of this kind are still tractable with mathematical techniques (e.g. matrices) and the outcome of the whole process (the effect of landscape structure on a certain response variable/process) can be expressed in a single value: a landscape index. In contrast to the landscape indices mentioned above, the landscape indices derived from probability transition models, are based on the underlying movement process (Hanski et al.2000, Petit et al. 2001, Frank & Wissel 2002, Wahlberg et al. 2002, Gruber this work).

The limitation of the approach is that the movement rules are still rather simple for mathematical tractability. For example the internal state of an animal or external effects, such as the presence of a predator, which can be important, are difficult to incorporate in this kind of models.

Transition probability models have proved to be successful in systems, in which successfully reaching a patch immediately effects population dynamics. This is true for models of metapopulation dynamics and models of finding a mating partner in a structured landscape. For other types of systems, where the effect of reaching a patch is not directly linked with population dynamics (e.g. models on foraging), the approach may not be applicable.

### *Individual-based simulation models of movement (IBSMM)*

Individual-based simulation models of movement (IBSMM) are the most direct approach to model movement for linking landscape structure to population dynamics. The idea is that all the details that are important are incorporated in the model and movement is simulated as a step by step process often influenced by internal (e.g. territory holder, energy state) and/or external variables (e.g. habitat type). IBSMM can be linked to very different ecological processes, hence virtually all measurements of response can be studied. This flexibility is reflected in the variety of models that exists in the literature. Movement rules range from very simple stochastic processes to sophisticated rules that include memory and learning. Movement rules can depend on the patch an animal is located or on the patch the animal intends to move (e.g. Wiegand et al. 1998, , With & King 1999, Baum & Grant 2001). Some model base the decision when to move and where to move to on very advanced models of neuronal networks (Dreyfus-Leon 1999) or on predictions of optimality theory (Railsback et al. 1999, Johst et al. 2001).

As movement is modeled as a step by step process, the time step of the movement model has to be of the same dimension as one movement step. This can cause problems, when the interest is in a long-term response variable (such as time to extinction), but techniques exists to overcome this problem (Fahse et al. 1998, Wiegand et al. 1998)

The strength of this kind of models, they are fairly simple to explain to other people and can be intuitively understood by other people. Another strength is as many parameters are used to model movement, more realistic assumption can be incorporated for specific case studies. On the other side, the more complex a model is, the more difficult it is to analyze and to come to general conclusions (Grimm et al. 1999). Therefore, generalisations are difficult to be drawn, since the processes that lead to certain results cannot be followed, if models are to complex. Many of these individual-based models fail to promote general understanding in science, as they are of purely descriptive use.

### *Conclusions*

The aim of this review was to give an overview about the existing approaches to link landscape structure with population dynamics. Movement of animals is the most important process mediating landscape structure and population dynamics, and hence all but one approach (landscape indices) do explicitly deal with movement. As movement is a very complex process, it is obvious that the problem can be tackled from two sides. Either using a top-down or a bottom-up approach. On the side of bottom-up approaches are individual-based movement models and transition probability models. On the side of top down approaches are percolation theory, diffusion models and landscape indices. Each approach has its strengths and its weaknesses reflected by its position on the bottom-up and top down continuum. The more bottom-up an approach, the more flexible it can incorporate the movement process. However, so far not enough empirical data on a range of animals do exist, to use the potential of the bottom-up approaches. Additionally the flexibility leads to the difficulty to find generalisations from these approaches. The top-down approaches are less flexible and generalisation are much easier gained by them. Unfortunately, they often include restrictive and not realistic assumptions. This limits them to rather simple cases of movements (e.g. insects).

Recently, models of intermediate complexity (transition probability models) led to promising results and in my opinion, as technology to study movement is rapidly advancing and more empirical data about movement are collected, models of this type will be the ones, which will be most successful in advancing this field of landscape ecology.

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