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Survival in changing environments –
Modeling the impact of climate change and
land use on raptors in arid savanna

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Survival in changing environments -
Modeling the impact of climate change and land use
on raptors in arid savanna

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aus Bleicherode an der Hainleite

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Immortal Birds

I could tell you a story, a legend of immortal birds that fly high above the peaks of the Himalaya. They spend their whole lives suspended in the air, released from gravity. They need no food and make love in the open air, never once setting foot on the earth below.

The only moment of danger in their divine lives is at the very beginning. Without a nest, the mother bird climbs high into the air to lay her egg. As the egg falls the sun warms it and wakes the sleeping chick inside. If the mother has flown high enough the chick has time to break the falling shell, feel the wind in its young feathers, spread its wings and begin its lifelong flight.

*Sometimes the young bird is not so lucky. Perhaps the mother bird has not flown high enough, **or the clouds have covered the sun that day**, the fall is too fast, gravity too strong. The unborn chick remains in its chalky prison, unawakened by the sun, as it is sucked down to shatter on the surface of the earth.*

If it survives, the young bird emerges, dazed, from the shards of broken shell. Broken winged, it lies on the ground, having missed its chance to fly. It gathers itself, resigned to the feeling of its own weight against the earth and slowly tries to teach itself to walk.

Most succeed. They find a life as vertical beings, running around on the surface of the earth. Some of the grounded birds talk later in their lives of the importance of keeping an erect posture. But often they are haunted by the feeling that something is missing. In a hidden corner of their minds the suspicion lingers that once other possibilities had been open to them.

Text from Peter Sloterdijk.

Introductory reading in the play "FALLEN", dance performance
by Jess Curtis/Gravity & fabrikCompanie,
Potsdam, Germany and San Francisco, California, U.S.A.



Juvenile Tawny Eagle (*Aquila rapax*) shortly after becoming independent from the adults. In the background the trunk (left) and on the sandy soil the pods of *Acacia erioloba*.

Kgalagadi Transfrontier Park, November 1999.

This thesis aims to investigate the general impacts of environmental changes, and more specifically on the tawny eagle population in the southern Kalahari. Consequently, the results presented here cover a range of approaches, from the analysis of field data (chapter three) to particular modeling scenarios for the tawny eagle (chapters two and four) and the use of simple but general models in population biology (chapters five and six). As the single chapters focus on specific aims, each one showing an autonomous contribution into ecological research, they are composed as autonomous readable papers. Thus, each of the chapters represents a thematic unit, in which methods and the state of research are highlighted more explicitly yielding some short but inevitable repetitions of previous chapters. Slightly modified versions of every single chapter (two to six) of this thesis are submitted or previewed for submission to scientific journals in cooperation with co-authors. Co-authors include my thesis advisor Prof. Florian Jeltsch and ecologist Dr. W. Richard J. Dean who provided his experience derived from field studies on raptors for the model development. All co-authors have been partner to discussion of the results and their presentation. Nonetheless, all findings presented here resulted from work that has been done independently by the author of this thesis.

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TABLE OF CONTENTS

ABSTRACT	1
1 INTRODUCTION	3
1.1 General introduction	3
1.2 Subject of the study, aims and methods.....	3
1.3 Structure of this thesis.....	5
2 CLIMATE CHANGE DRIVEN MODIFICATIONS IN PRECIPITATION AFFECT POPULATION PERSISTENCE OF RAPTORS IN ARID SAVANNA	7
2.1 Abstract.....	7
2.2 Introduction.....	7
2.3 Subject of the study, study area and methods.....	9
2.3.1 Subject of the study	9
2.3.2 Study area	10
2.3.3 Model description	10
2.3.4 Individual-oriented model	11
2.3.5 Stochasticity	11
2.3.6 Output parameters	13
2.3.7 Sensitivity analysis	14
2.3.8 Simulation experiments	16
2.3.9 Auto-correlation analyses	18
2.4 Sensitivity analysis: Results and Discussion	18
2.4.1 Demographic parameters	18
2.4.2 Environmental parameters	20
2.5 Results of simulation experiments	22
2.6 Discussion	26
2.6.1 Model selection	26
2.6.2 Tawny Eagle population persistence under climate change	27
2.6.3 Periodically fluctuating precipitation	28
2.6.4 Extinction theory	29
2.6.5 Escaping in space?	29
2.6.6 Studying the impact of climate change on population dynamics	30
2.6.7 Conclusion	31
2.7 Link to the proceeding chapter.....	31

3	THE BREEDING SUCCESS OF ARID AREA RAPTORS IN RELATION TO PRECIPITATION	33
3.1	Abstract	33
3.2	Introduction	33
3.3	The theoretical approach.....	34
3.4	Application on available field data	36
3.5	Conclusion.....	38
3.6	Link to the proceeding chapter	38
4	STRUCTURAL DIVERSITY IN ARID SAVANNA IMPACTS THE PERSISTENCE OF RAPTORS	39
4.1	Abstract	39
4.2	Introduction	39
4.3	Subject of the study, study area and methods	41
4.3.1	Subject of the study	41
4.3.2	Study area	42
4.3.3	Model description	42
4.3.4	Scenarios of non-random tree distribution	46
4.3.5	Output parameters of the model	46
4.4	Results and sensitivity of the model.....	47
4.4.1	Model sensitivity: number of attempts to find a territory	47
4.4.2	Limitation of potential nesting trees (PNT)	48
4.4.3	Effects on persistence time	49
4.4.4	Scenarios of non-random tree distribution	49
4.4.5	Model sensitivity to various distribution modes	54
4.4.6	Critical tree densities for various distribution scenarios	55
4.5	Discussion	56
4.5.1	Spatial mechanisms influencing the survival of tawny eagles	56
4.5.2	Critical tree densities for survival of tawny eagles	58
4.5.3	Natural tree distribution and tawny eagles	59
4.5.4	Current land use practice, structural diversity and tawny eagles	59
4.5.5	The potential impact of structural diversity on species survival	60
4.5.6	Conclusions	61
4.6	Link to the proceeding chapter	61
5	EXTINCTION RISK IN PERIODICALLY FLUCTUATING ENVIRONMENTS	63
5.1	Abstract	63
5.2	Introduction	63
5.3	Methods	64
5.3.1	Model description	64
5.3.2	Scenarios of environmental noise	65
5.3.3	Noise color analyses	67
5.4	Results.....	67
5.4.1	Standardized Persistence Time (T_s)	67
5.4.2	Auto-correlation	67
5.4.3	Floaters per Time Step	68

5.5	Discussion	70
5.5.1	<i>General results for periodically fluctuating environments</i>	70
5.5.2	<i>Auto-correlation in periodically fluctuating environments</i>	71
5.5.3	<i>Density regulation in periodically fluctuating environments</i>	71
5.5.4	<i>Conclusion: the importance of monotonic trends in the environment</i>	73
5.6	Link to the proceeding chapter.....	74
6	STUDYING THE EFFECTS OF COLORED NOISE: AN ALTERNATIVE METHOD OF GENERATING TIME SERIES WITH GIVEN COLOR AND VARIANCE	75
6.1	Abstract.....	75
6.2	Introduction.....	75
6.3	Scaling to expected variance	76
6.3.1	<i>Scaling to expected asymptotic variance</i>	76
6.3.2	<i>Scaling to expected variance over a certain time scale T</i>	76
6.3.3	<i>Scaling to asymptotic variance versus scaling to a certain time scale T</i>	77
6.3.4	<i>Applicability of Equation (6.2) and (6.3)</i>	77
6.4	Scaling to the actual variance	78
6.5	Impact on the calculated extinction risk.....	82
6.6	Discussion	84
6.6.1	<i>Impacts on extinction risk</i>	84
6.6.2	<i>Applicability of rescaling to the actual variance</i>	84
6.6.3	<i>Further descriptive attributes of time series</i>	85
6.6.4	<i>Conclusion</i>	86
7	SUMMARY	87
7.1	Summarizing discussion and future perspectives	87
7.2	Final conclusion.....	89
	DEUTSCHE ZUSAMMENFASSUNG	91
	ACKNOWLEDGEMENTS	93
	REFERENCES	95
	APPENDIX	105

TABLE OF FIGURES AND TABLES

Figure 2.1: Simplified AQUQUA flow chart.....	12
Table 2.1: Model parameter	15
Figure 2.2: Coincidence of precipitation and extinction events	21
Figure 2.3: Variability in T_m	22
Figure 2.4: Impacts of mean, CV and auto-correlation in precipitation.....	24
Figure 2.5: Impact of varying survival rates	25
Figure 2.6: Periodically fluctuating precipitation.....	26
Table 3.1: Breeding success, precipitation and territory size in arid area raptors.....	35
Figure 3.1: Relating breeding success to territory size and precipitation	37
Figure 4.1: Simplified flow chart of the spatial model version.....	44
Figure 4.2: Definition of neighboring cells	45
Figure 4.3: Model sensitivity to number of attempts to find a territory	47
Figure 4.4: Potential nesting trees depend on tree density.....	49
Figure 4.5: Limitation of T_s by tree density.....	50
Figure 4.6: Analyzing patterns of varying tree distribution	52
Figure 4.7: PNT for varying tree distribution.....	55
Figure 4.8: Impact of tree distribution on T_s	57
Figure 5.1: Patterns of periodicity.....	66
Figure 5.2: Impacts of period length and pattern on T_s	69
Figure 5.3: Impacts of auto-correlation and pattern on T_s	69
Figure 5.4: Periodic pattern, extinction risk and density regulation	72
Figure 6.1: Variability in average variances for samples of time series fragments	80
Figure 6.2: Deviation of variances of particular time series fragments	81
Figure 6.3: Impacts of the rescaling variance technique on extinction risk.....	83
Figure A1: Mean and variability of standard deviation in auto-correlated time series.....	105

Abstract

The assessment of persistence time and extinction risk of populations has become a focus in recent research in ecology and nature conservation. Accordingly, in this thesis I developed a stochastic, individual-oriented model of the population dynamics of an arid area raptor, namely the tawny eagle (*Aquila rapax*) in the southern Kalahari arid savanna. I performed an extensive sensitivity analysis and found the model to be suitable to study the impacts of modified environments on the persistence of the tawny eagle population. I simulated various modifications in precipitation patterns (yielding prey availability) to the tawny eagle model population and found considerable influences on persistence time. Scenarios of climate change, in particular which were projected to be the most likely, led to dramatic increases in extinction risk. Even if average precipitation remains unaffected but variation among years increases I found the extinction risk to be severely augmented. Moreover, in this context this thesis presents a new way of relating breeding success of arid area raptors to annual precipitation that explicitly considers territory sizes. Furthermore, in a spatial model version, I found tree density and the pattern of tree distribution to also impact tawny eagle population persistence. Consequently, land use practices such as cattle farming and wood cutting that change these characteristics of the vegetation structure may potentially limit tawny eagle persistence and should be taken into account for nature conservation efforts. The impact of structural diversity on species diversity and the linkage between these two aspects of biodiversity are emphasized. However, the results of the model also led to new insights in theoretical population biology. I could show that our current knowledge of extinction risk in temporally stochastic environments does not hold for periodically fluctuating environments. Specifically, fluctuating environments with short periods lengths decrease the extinction risk over random environments - although other descriptive attributes of the time series remain constant. Furthermore, I present an alternative and broadly applicable method allowing the generation of time series that have strong auto-correlation with given variance. Applying this method and calculating the extinction risk in strongly auto-correlated environments led to results that deviate from what is known.

On one hand, the results of this thesis document the implications for the conservation of tawny eagles and other raptors in arid savanna. In a more general context, these results offer future directions to guide ecological studies by considering climate change impacts on local populations and emphasizing the importance of structural diversity. On the other hand, my results contribute novel and exciting knowledge to the theory of population dynamics and extinction risk. New insights into both fields of ecological research found in this thesis will increase our understanding of population survival in changing environments.

1 Introduction

1.1 GENERAL INTRODUCTION

Our world is characterized by changing environments. Due to the activities of a highly technically developed human population environmental modification is no longer restricted to short term, local effects but instead occurs on all temporal and spatial scales (e.g. IPCC 2001a,b, van Jaarsveld et Chown 2001, O'Neill et al. 2001, see also Kirschbaum 1995, Joel et al. 2001, DeLucia et al. 2001, Hannah et al. 2002 and references therein). Consequently, society faces new and fundamental challenges in the fields of ecological science and nature conservation, as well as in politics and environmentally friendly engineering and in the interplay between them.

Arid ecosystems are especially sensitive to and currently threatened by human activities, in particular savanna, for example the Kalahari in southern Africa (e.g. Rutherford 1999, van Jaarsveld et Chown 2001). On one hand, in a rather applied part this thesis focuses on the impacts of human induced changes in the Kalahari arid savanna on the raptor species, the tawny eagle (*Aquila rapax* Temminck). On the other hand, in a more general context, this thesis investigates general population dynamics phenomena arising from the tawny eagle case study. Accordingly, this thesis is designed to contribute new ecological knowledge for tackling the problems emerging in a world of environmental change.

1.2 SUBJECT OF THE STUDY, AIMS AND METHODS

One subject of this thesis is changing environments in the Kalahari arid savanna. The Kalahari is situated in southern Africa and spans Botswana, western Zimbabwe and the northwest Republic of South Africa. Typically, the rainfall is erratic limiting vegetation growth. Arid savannas are open woodlands with scattered large trees, interspersed with grassland and a rather poorly developed shrub layer (Scholes et Walker 1993, Low et Rebelo 1998). In this thesis I explore two human driven modifications that may affect the arid savanna ecosystem: (1) global climate change and (2) the effects of farming.

Global climate change is an infamous phenomenon referring to expected and already partially observed changes in surface temperature and precipitation patterns due to the ongoing emission of greenhouse gases such as CO₂ (IPCC 2001b). While on a global scale an increase in precipitation is expected, climate change studies predict reduced precipitation for southern Africa (e.g. IPCC 2001b). This may have severe impacts on the already climatically erratic Kalahari region. Farming in the Kalahari is generally cattle farming, but recently game farming and wood cutting have emerged. High stocking rates in cattle farming, as well as wood cutting practices, change the vegetation structure in the Kalahari arid savanna (Trollope et Tainton 1986, Tietema et al. 1991, Tainton et Walker 1992, Jeltsch et al. 1996, 1997a, 1998, 2000, Milton et al. 2001, BIOTA AFRICA Project 2002). In this thesis I investigate the impact of both guises of environmental change, i.e. farming and climate change, on the tawny eagle population in the southern Kalahari.

The tawny eagle is a large bird of prey occurring in the arid areas of southern and eastern Africa. Along with the bateleur (*Teratopius ecaudatus*) and the martial eagle (*Polemaetus bellicosus*), the tawny eagle is one of the characteristic raptors of the Kalahari arid savanna. Tawny eagles are long-lived animals (longevity 16 years) and usually raise one nestling per pair per year. The birds build their nests and perch in large solitary trees that are

1 Introduction

characteristic to the Kalahari (Milton et Dean 1995, Dean et al. 1999). The tawny eagle feeds mainly on small mammals and game birds but also on reptiles, amphibians and insects. The Afrikaans name “Roofarend” (“robber eagle”) refers to occasionally observed attacks on other hunting raptors with the intent of stealing their prey. In years of low precipitation when food shortage arises, adult birds may also feed on carrion. However, the nestlings require living prey and cannot survive on carrion alone. Tawny eagles are well adapted to both, vegetation structure and climatic rainfall conditions in the Kalahari arid savanna, thus, they may be potentially threatened when these conditions change. (Brown et Amadon 1968, Steyn 1973, Smeenk 1974, Brown et al. 1982, Steyn 1983, Brown 1984, Herholdt et de Villiers 1991, Liversidge 1994, Herholdt 1995, Herholdt et al. 1996, Herremans et Herremans-Tonnoeyr 2000).

Conducting field experiments in order to study the behavior of the southern Kalahari tawny eagle population under modified precipitation pattern or vegetation structure would be a monumental - and most likely impossible – goal regarding the required space, time and expense. Tawny eagles live on far too large temporal and spatial scales to design reasonable and feasible field experiments. Whenever it is not possible to extensively study a system in nature, computer models can provide a powerful alternative by replacing field experiments with computer simulated experiments (e.g. Trenberth 1997, Grimm 1999). Computer based modeling approaches investigate the long term effects of phenomena which have been observed on short time scales in the field (e.g. Jeltsch et al. 1997a, Stelter et al. 1997, Grimm 1999, Weber et al. 2000). Consequently, in this study I developed a model of the population dynamics of tawny eagles in order to assess their extinction risk in modified environments in the Kalahari arid savanna. Moreover, models provide the opportunity to generalize processes occurring in similar guises in various ecological systems. Modeling approaches can reduce these processes to their basic characteristics and hence enable us to study general ecological phenomena (chapters five and six).

General ecological phenomena are the second focus of this thesis contributing new knowledge to theoretical population biology. Initially, theoretical studies found and described general phenomena of population dynamics and more recently, they have focused on the impacts of environmental variation on the extinction risk of biotic populations (e.g. Lotka 1925, Volterra 1926, May 1973, Roughgarden 1975, May et Oster 1976, Ripa et Lundberg 1996, Johst et Wissel 1997, Lloyd et May 1999). Variation in the environment may be considered over space and/or time (e.g. Ripa et Lundberg 1996, Heino 1998, Lundberg et al. 2000, Bjornstad 2001). Temporal variation in the environment over time is described by a time series that explicitly gives the value of an environmental parameter at each time point. Various attributes of these environmental time series, such as mean (describing quality but not variation), variance and first order auto-correlation were found to impact the extinction risk of a population experiencing this time series (e.g. May 1973, Ripa et Lundberg 1996). Other attributes, such as auto-correlation of higher orders or the frequency distribution of values within the time series, are poorly studied (but see Cuddington et Yodzis 1999). In this thesis and while using the model I developed for tawny eagle population dynamics, I approach these issues in theoretical population biology. In particular, I will show that extinction risk in periodically fluctuating environments cannot be explained with existing knowledge in theoretical population biology. In addition, I introduce an alternative method for generating auto-correlated time series with given variance that influences the results for the calculation of the corresponding extinction risk.

1.3 STRUCTURE OF THIS THESIS

The proceeding (second) chapter is the most extensive chapter of this thesis presenting and discussing the model developed and used. In chapter two, I explore the impacts of modified precipitation patterns on the tawny eagle population in the southern Kalahari and I derive implications of climate change. In the third chapter I present a new idea for comparing the breeding success of large raptors in arid areas with precipitation. The fourth chapter presents a spatial version of the model investigating the threats to tawny eagles of a changing vegetation structure due to human land use. The subsequent two chapters (five and six) contribute new knowledge to theoretical population biology: while the fifth chapter points out further attributes of time series of environmental noise impacting population's extinction risk, the sixth chapter describes a new method of implementing auto-correlation in environmental noise. The final chapter seven summarizes the results of this thesis and discusses future perspectives. Additionally a German "Zusammenfassung" is given. Please note also the explanation concerning the composition of this thesis on the page prior to the table of contents.

2 Climate change driven modifications in precipitation affect population persistence of raptors in arid savanna¹

2.1 ABSTRACT

Arid savannas are regarded as one of the ecosystems most likely to be affected by climate change. In these dry conditions, even top predators like raptors are affected by water availability and precipitation. However, only a few research initiatives have addressed the question of how climate change will affect population dynamics and the extinction risk of particular species in arid ecosystems. Here, I use an individual-oriented modeling approach to conduct experiments on the population dynamics of long-lived raptors. I investigate the potential impact of precipitation variation caused by climate change on raptors in arid savanna using the tawny eagle (*Aquila rapax*) in the southern Kalahari as a case study.

I simulated various modifications of precipitation scenarios expected during climate change, such as lowered annual precipitation mean, increased inter-annual variation and increased auto-correlation in precipitation. Each modification had a high impact on the extinction risk of tawny eagles, with reduced population persistence in most cases. Both decreased mean annual precipitation and increased inter-annual variation caused dramatic decreases in population persistence. Increased auto-correlation in precipitation led to only slightly accelerated extinction of the simulated populations. Finally, I found both increased and decreased population persistence for various patterns of periodically fluctuating precipitation. My results suggest that the impacts on raptor population dynamics and survival caused by climate change in arid savannas will be great. I emphasize that even if, under climate change, the mean annual precipitation remains constant but the inter-annual variation increases, the persistence of raptor populations in arid savannas will decrease considerably. This suggests a new dimension of climate change driven impacts on population persistence and consequently on species diversity and biodiversity. However, more investigations on particular species and/or species groups are needed to increase our understanding of how climate change will impact population dynamics and how this will influence biodiversity.

2.2 INTRODUCTION

Raptors play an important role in ecosystems as they are at the top of food webs, have a direct effect on prey communities, cover wide home-range areas and changes in their population structure may indicate environmental changes (Dean et Milton 1988, Rodriguez-Estrella et al. 1998, Herremans et Herremans-Tonnoeyr 2000). Southern African ornithologists have been studying long-lived raptors for about 100 years. These studies have focused on morphological characteristics, behavior, nest site features, breeding performance, effects of persecution by farmers and migration (e.g. Moreau 1945, Steyn 1965, Brown et Cade 1972, Hornby 1974, Kemp 1978, Osborne 1982a, Brown 1984, Brown 1991, Clark 1992, Herholdt et al. 1996). However, little is known about how breeding success and population dynamics interact with environmental fluctuation. In southern African arid savanna, precipitation is often the most important environmental factor for species performance (e.g. Wiegand et Jeltsch 2000) and also impacts vegetation structure (Jeltsch et al. 1997a,b) as it determines primary production, which is the basis of the food web. Several studies have argued that breeding success may be correlated with current precipitation amounts even for top predators. However, only Hustler

¹ A shortened and slightly modified version of this chapter will be published as:
Wichmann MC, Jeltsch F, Dean WRJ, Moloney KA, Wissel C (in press). Implications of Climate Change for the persistence of raptors in arid savanna. *Oikos* 102.

and Howells (1990) have been able to collect sufficient data to show that higher rainfall is correlated with higher breeding success of raptors in southern Africa. (Note, that similar results have been found for the golden eagle in Israel by Bahat et Mendelssohn 1996).

A number of recent studies have investigated the influence of weather fluctuations, especially rainfall, on various demographic parameters for a range of different animal species. They have found that rainfall patterns can affect abundance (birds: Bridges et al. 2001), survival rates (Australian passerines: McCleery et al. 1998), egg laying date (UK breeding birds: Crick et Sparks 1999), clutch size and breeding success (arid zone birds: Hustler et Howells 1990, Bahat et Mendelssohn 1996, Lloyd 1999), growth rates (moose calves: Ball 2001), fitness and reproductive activity (rodents: Madens et Shine 2001), as well as behavior (wolves: Post et al. 1999). However, all of these studies are based on data observed under prevailing precipitation patterns and do not explicitly consider the effects of long-term climate change.

The phenomenon called “climate change” generally refers to future impacts of anthropogenic factors on the global climate and is caused by the ongoing emission of greenhouse gases (GHG) such as CO₂ (e.g. IPCC 2001b, O'Neill et al. 2001). On a global scale, a rise in surface temperature, along with secondary effects such as melting of glaciers, sea level rise or changes in precipitation pattern are expected, but on a regional scale these effects can be very different (IPCC 2001a,b). Changing precipitation patterns are probably the most important secondary effect of GHG accumulation, since they are one of the key determinants of structure and species composition in ecological systems. Under climate change, precipitation is projected to increase on a global scale, but will decrease in some regions (IPCC 2001a). Whereas most studies have focused on the effects of changes in average values, Katz et Brown (1992) emphasized the importance of changes in the variability and frequency of extreme events. For example, Matyasovszky et al. (1993) found increasing variability in precipitation when they simulated climate change for a dry continental climate. This implies that we have to take into account not only mean values but also (inter-annual) variation and the frequency of extreme events, as well as regional specifics, when studying the effects of climate change on ecosystems and particular species.

Unfortunately, only little progress has been made in investigating the explicit effects of climate change on specific animal populations, although the importance of climate change for the survival of populations and species has been recognized since one of the first meetings concerned about the “Consequences of the Greenhouse Effect for Biological Diversity” in 1988 (Roberts 1988). In their recent opinion paper Hannah et al. (2002) complain about the “present static conservation paradigm” and emphasize the need to integrate knowledge on climate change into efforts of conserving species and biodiversity. A first step going into this direction is done by Rutherford et al. (1999) when concerning about southern African floristic composition in preserved areas when climate changes as projected. Moss et al. (2001) implicate climate change, i.e., a progressively delayed spring warming over the past 25 years, as a factor causing a decline of Scottish capercaillie (*Tetrao urogallus*). Post et al. (1999) also demonstrate a correlation between weather dependent vegetation growth, herbivore density and behavior of wolves (*Canis lupus*), which contributes to an understanding of the links between climate change and ecosystem function. Coulson et al. 2001 found populations of soay sheep (*Ovis aries*) of varying age and sex structure to react differently on changing climatic conditions. Janzen et Morjan (2001) and Morjan (2002) have shown that increased local temperatures induced by climate change can modify the sex ratios of turtles in the Mississippi river valley. Hughes (2000) is arguing that the consequences of global warming are already apparent (see also references therein). However, beside these studies, there are no more examples known to the author that directly examine the effects of climate change on

animal population dynamics. This might be due to the same factors impacting studies on long-lived species: constraints of time and money limiting the ability to conduct investigations over a sufficiently long time period.

Whenever it is not possible to extensively study a system in nature, computer models can provide a powerful alternative by replacing field experiments with computer simulation experiments (e.g. Trenberth 1997, Grimm 1999). The models used in these experiments are based on field data and can be used to increase our knowledge by systematically investigating the implications of field data. When modeling dynamics of populations of conservation interest, the focus is often on extinction risk and population persistence (Burgman et al. 1993). A useful metric in this context is the Mean Time to Extinction as it provides a currency for comparing population persistence among different populations or climate scenarios. The Mean Time to Extinction (T_m) is the time span that populations simulated in the model survive on average. The term “Mean Time to Extinction” might be misleading as it implies the population really goes extinct, which does not have to be the case for the population in nature. However, high T_m values indicate high population persistence and low extinction risk due to favorable conditions, whereas low T_m values indicate low population persistence, high extinction risk and unfavorable conditions. T_m enables to compare population persistence under different conditions – such as various precipitation scenarios - and to estimate the relative impact of different conditions on population persistence (Wissel et al. 1994, Stelter et al. 1997).

In this study, I investigate the effects of modifications in precipitation patterns on population persistence of a long-lived raptor. I develop a model of the population dynamics of the tawny eagle (*Aquila rapax* Temminck) in the southern Kalahari dry-savanna using the data collected by Hustler et Howells (1990). With this model, I conducted experiments simulating climate change driven modifications in southern African precipitation patterns according to the current knowledge of how climate change will occur. The quality and quantity of changes in population persistence produced by these modified environmental conditions are the focus of this study. I use T_m as a currency to compare my experimental results. The intention of this study is not to provide an exact extinction probability for the southern Kalahari tawny eagle population. The aim, instead, is to estimate the qualitative and quantitative impact of climate change driven modifications in precipitation on the population persistence of tawny eagles. I address the following three questions: (1) will the tawny eagle population be affected by climate change driven modifications in precipitation scenarios? And if it is, 2) what is the qualitative and quantitative impact of the various modifications in precipitation pattern that are assumed under climate change (such as changes in annual mean value, inter-annual variation and frequency of extreme events)? And finally 3) when summarizing these effects, should we - according to current knowledge on climate change - expect an increase or a decrease in population persistence of tawny eagles and other raptors in the Kalahari dry-savanna?

2.3 SUBJECT OF THE STUDY, STUDY AREA AND METHODS

2.3.1 Subject of the study

The tawny eagle (*Aquila rapax* Temminck), sometimes considered a race of the steppe eagle (*Aquila nipalensis* Hodgson) (Clark 1992) occurs in the arid to mesic savannas of Africa, including the Sahara Desert, Mediterranean North Africa and Arabia. Tawny eagles are common in southern African savanna, with densities ranging from about one pair/150 km² in Kalahari arid savanna, to a density of about one pair/40 km² in mesic savanna in the Kruger

National Park, South Africa (Kemp et al. 2001). The tawny eagle feeds on a wide range of food items and has been appropriately described by Steyn (1983) as "... a scavenger, a pirate and a rapacious killer...".

Tawny eagle pairs usually lay two eggs in May or June and mostly the female incubates the eggs for about six weeks. Due to infertility or sibling aggression in most cases only one chick is reared over a fledging period of 12 weeks, followed by a post-fledging period of about six weeks during which the adults feed the juvenile before becoming independent at about 18 weeks (Brown et al. 1982). Many studies have investigated breeding performance but due to low individual numbers of tawny eagles the sample size is often small (Steyn 1980a, Brown 1991, Herholdt et al. 1996, but see Hustler and Howells 1986). About 75% of all juveniles die before they reach maturity in their third to fourth year (Newton 1979, Steyn 1983), but thereafter have an average life expectancy of 16 years (Brown et al. 1982). The breeding success of tawny eagles is positively correlated with annual rainfall via primary production and prey population dynamics (Hustler et Howells 1989, 1990).

2.3.2 Study area

My model focuses on the population dynamics of tawny eagles in the arid savannas of southern Africa, which includes western Zimbabwe and the southern Kalahari. All arid savannas are open woodlands with scattered large trees, interspersed with grassland and a rather poorly developed shrub layer. Rainfall is generally erratic, with high coefficients of variation, over the region in which arid savanna occurs, and varies from about 200 mm mean annual rainfall in the southwest to >500 mm in the east and north. "Arid savanna" encompasses a number of vegetation sub-types differentiated by species composition, dominant tree species, tree spacing and average vegetation height, as well as soil types and underlying geology but does never shade off into pure wood- or grassland (Scholes et Walker 1993, Low et Rebelo 1996, Jeltsch et al. 2000). The default parameter set for the model refers to the area of the "Kgalagadi Transfrontier Park" which is situated in the arid savanna at the northwestern tip of the Republic of South Africa and southeastern Botswana.

2.3.3 Model description

I developed an individual-oriented, stochastic simulation model of tawny eagle population dynamics, named AQUQUA (*Aquila* needs *aqua*; expressing the dependence on precipitation, compare below). This model is based on the population dynamics of the tawny eagle in the arid savanna of the southern Kalahari. Parameters of the model are adjusted to results of field studies on the biology and life history of this species (Steyn 1973, Hustler et Howells 1986, Herholdt et al. 1996), on similar species (Brown et Cade 1972, Harris et al. 1994, Weimerskirch et al. 1987) and on general findings (Newton 1979). For an overview of all model parameters see Table 1.

The model was written in C++ and simulations were conducted on a common personal computer.

Figure 2.1 shows the AQUQUA flow chart and table 1 gives values and references for the model parameters. AQUQUA is simulating tawny eagle population dynamics in yearly time steps. During each simulation year the main processes like mating, breeding, reproduction (i.e. successfully breeding), aging and mortality are modeled for each individual. The model is initialized with 180 individuals of tawny eagles, a number that is supported by a carrying capacity of 50 territories according to observations in the southern Kalahari (Herholdt et al. 1996). The age distribution of the initial population equals the stable age structure given by survival and fecundity rates. During the mating process unmated mature eagles are paired.

This continues as long as individuals of the opposite sex remain single. Only paired individuals take part in the breeding process. Here, with a probability according to the percentage of breeding pairs out of all pairs found in the field, for every single pair a decision is made whether they start to breed or not. The pairs that start to breed, limited by the available number of territories, take part in the reproduction process. Here, with a probability according to the precipitation amount of the current year, for every single pair a decision is made whether breeding is successful or not. Successful breeding pairs have a probability of 0.01 to produce two offspring instead of only one, whereas unsuccessful breeding pairs produce no offspring at all. Juveniles are added to the population with an age of zero years and with undetermined sex. During the aging and mortality process age is incremented by one year for all individuals. Individuals at the end of their third year have a 50 percent chance to reach maturity, and all others reach maturity at the end of the fourth year. Once maturity is reached the sex of the individual is determined with an equal chance of 50 percent for being male or female. If an individual exceeds the maximum age it dies. For all other individuals age specific survival rates apply as a probability to reach the next year and a decision on survival is again made individually. (Note that adult survival rates also apply to mature individuals of three years.) Thereafter all marks related to the breeding status are removed and all pairs have equal chance to breed the following year. If a mated eagle dies the remaining spouse is marked as unmated. The time is incremented by one and the new year starts again with the mating process (Fig.2.1).

2.3.4 Individual-oriented model

AQUIQUA is an individual-oriented model in the sense of Uchmanski et Grimm (1996). Thus, the model tracks every single virtual tawny eagle from the moment it is hatched until it dies. At any given time the model knows the exact age of any individual, the number of fledglings it has produced up to now, its mate, its current breeding status, as well as the chance to survive the current year. All relevant events during an individual's life are recorded by the model. However, individuals do not differ in their behavior, i.e. when facing the same conditions one individual is as likely to breed or to die as the other.

2.3.5 Stochasticity

AQUIQUA is a stochastic model. Stochasticity is regarded as an important factor influencing modeling results (Shaffer 1981, Lande 1993). AQUIQUA includes demographic, as well as environmental stochasticity.

Demographic stochasticity

Demographic stochasticity is the variation of demographic parameters (e.g. survival), around the population average (e.g. survival rate). Thus, demographic stochasticity in the model is realized by interpreting rates (i.e. the average of the population or of a fraction of the population) as probabilities, i.e. for each individual the model is "rolling the dice". A new random number is drawn for every individual decision from a uniform distribution in the interval [0;1) and is compared with the rate (e.g. survival rate). If the random number is smaller than the rate the individual performs the process (e.g. surviving the current year), if not it does not (e.g. it dies).

2 Climate change affects population persistence of raptors in arid savanna

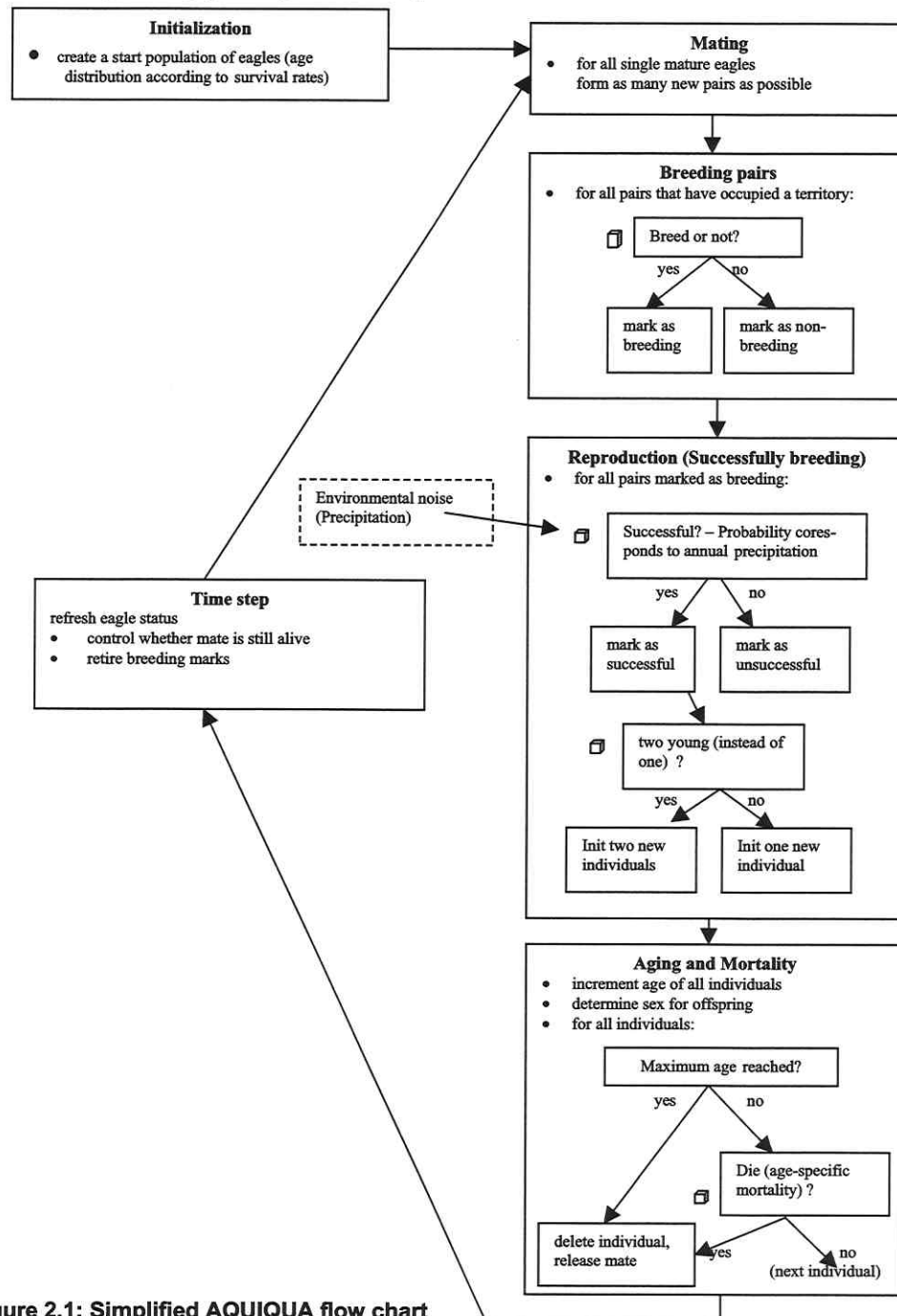


Figure 2.1: Simplified AQUQUA flow chart

The dice (🎲) marks processes where the result is determined by a constant probability and an individual random number. Note, that breeding success is impacted by precipitation. For more detailed description see text.

Environmental stochasticity: Rain and breeding success

However, recent investigations emphasized the importance of environmental stochasticity (i.e. environmental noise) and its fluctuations (Ripa et Lundberg 1996, Halley 1996, Johst et Wissel 1997, Cuddington et Yodzis 1999). Lande (1993) considers environmental noise as posing an even greater extinction risk than the demographic noise. Environmental noise is included in the model by using various precipitation scenarios.

A southern African rain model by Zucchini et al. (1992) was used to produce more than 60,000 different statistically realistic rain scenarios for the southern Kalahari. This model is based on Southern African rain records during the past century and does not consider any climatic change. Rain scenarios differed in data stochastically but were constant in descriptive features like mean annual precipitation, inter-annual variation and auto-correlation. I systematically modified these features for my experiments as described later in this section.

Environmental noise was realized in the model by including a precipitation-breeding success-relationship found by Hustler et Howells (1990) providing a link from environmental noise to population dynamics. However, territory size, i.e. the distance between territories *ind*, must be taken into account when comparing data for areas of different *average* annual precipitation (chapter three). This leads to the promotion of the breeding success-precipitation-relationship (Hustler et Howells 1990) to a breeding success-territory size-precipitation-relationship in chapter three. I explored the amount of rain per territory and year *RD* (given in m³) yielding the breeding success in this year *BS* (averaged over all the pairs that breed) for a given inter-nest distance *ind*. (For detailed instructions on transferring territory size and rain amounts into *RD* see chapter three.) Using the data from Hustler et Howells (1990), including additional data from other studies (Steyn 1973, 1980, Herholdt et al. 1996) and with linear regression I obtain:

$$BS = 1,999 * 10^{-4} * \frac{RD}{ind} + 3.23 * 10^{-2} \quad [\text{Equation 2.1}]$$

where π is approximately 3.1416 and the average inter-nest distance *ind* remained constant at 17,600 m (Herholdt et al. 1996). Note, while the breeding success *rate BS* is subject of environmental stochasticity (impacted by precipitation) the *individual* breeding success underlies demographic stochasticity fluctuating around *BS*. I did not include any time delay for the impact of precipitation on breeding success, as there is no indication for it and a time delay should not change my results but only shift them. The within year time delay of a few month is redundant as the time step in the model is one year.

2.3.6 Output parameters

Mean Time to Extinction (T_m)

I chose the *Mean Time to Extinction* (T_m) (Wissel et al. 1994) as an output metric since it quantifies population persistence and extinction risk. As already mentioned in the introduction, T_m is the average time span that simulated populations survived. I define the term “ T_m computation” as the process of calculating T_m . During one T_m computation I conducted 5,000 “replicate runs”, i.e. simulation runs with the same parameter set. However, among replicate runs demographic and environmental stochasticity was allowed what caused variations in extinction times. The average extinction time of replicate runs yields T_m . I methodologically follow Stelter et al. (1997) to avoid “infinite” population runs by populations that do not become extinct.

Probability of a Sparse Population

When discussing results of the model I will focus on T_m (see above). However, in addition I measured the relative time that a population persisted below a threshold of 30% of its carrying capacity, i.e. when less than 30% of the available territories were occupied. This parameter contains further information about population stability, i.e. whether populations take the full advantage of habitat's carrying capacity and fluctuate around it or whether population dynamics are too weak to do so. I will refer to this parameter as the probability for reaching the state of a *sparse population*.

2.3.7 Sensitivity analysis

Demographic parameters

Sensitivity analysis of demographic parameters was conducted according to Burgman et al. (1993). Based on field data I created a default parameter set for the AQUIQUA model (see Table 1). Then, I modified each parameter in succession while keeping all other parameters constant. Thus, sensitivity of each parameter was investigated separately and T_m was plotted as a function of each parameter.

Furthermore the sensitivity SI of each parameter is calculated by

$$SI = \frac{\Delta T_m / T_m}{\Delta P / P} \quad [\text{Equation 2.2}]$$

where SI is the sensitivity of the parameter P , T_m is the corresponding Mean Time to Extinction and ΔT_m and ΔP are the differences to the default. I modified the parameter by 10% of its default value and compare the resulting T_m with those of the default parameter set. The sensitivity for each demographic parameter is given in Table 1. The higher the absolute value of SI the higher is the sensitivity of this parameter. Unsigned values are positive and suggest a direct relationship between the parameter and T_m , whereas values with negative signs (e.g. age of maturation) correspond to an inverse relationship, i.e. increasing the parameter value results in a decreased T_m .

Furthermore the quality of the parameter default is given in Table 1. There are good data based on extensive field studies with large sample sizes (+), few data and/or data from related taxa (-/+) or expert's estimations without data (-).

Environmental parameters

Mode of including environmental variation

The amount of annual precipitation is a very important environmental parameter for tawny eagles in the Kalahari arid savanna (see environmental noise: rain and breeding success) and was included in the AQUIQUA model. Environmental parameters have to be taken into account if they affect demographic parameters, as in this case precipitation affects primary production, population dynamics of prey species and finally tawny eagle's breeding success (Hustler et Howells 1990). When investigating model's sensitivity to the precipitation pattern, I performed two different tests. More than 60,000 rain scenarios were used that differed stochastically in data values but data were drawn from the same distribution with respect to mean, inter-annual variation and auto-correlation. Note, that I will refer to the terms "replicate runs" and " T_m computation" as defined under Output parameters.

Table 2.1: Model parameter

Parameters of the AQUQUA model are listed with their value for the default parameter set and the corresponding references. Furthermore the sensitivity of the model to every parameter (SI) is given: high absolute values indicate high sensitivity and low absolute values indicate low sensitivity. Positive values represent positive correlation between parameter and T_m and negative values stay for a negative correlation. Parameter quality is given according to the underlying data basis in three categories (+, -/+, -). See text on sensitivity analysis for further description.

Parameter	Value	SI	Quality	References
Maximum age (years)	55	0.35	-/+	Newton (1979)
Juvenile survival rate (survival to maturation)	0.3		-/+	Newton (1979)
- 1st year survival (fraction per year)	0.4	9.24		Newton (1979)
- 2nd year survival (fraction per year)	0.8	9.16		Newton (1979)
- 3rd year survival (fraction per year)	0.9375	9.04		Newton (1979)
Adult survival rate (fraction per year)	0.945	157.43	-/+	Compare: Brown et Cade (1972), Newton (1979)
Decreased survival during senescence (per year)	0.015	-10.00	-	Compare: Newton et Rothery (1997), Weimerskirch (1992), Harris et al. (1994)
Age of senescence (years)	24	7.93	-	Brown et Amadon (1968)
Age of maturation (years)	3.5	-294.30	+	Steyn (1973)
Sex ratio at maturation (portion females)	0.5	7.02	+	Newton (1979)
Clutches with two fledged young (portion of all clutches)	0.01	0.19	+	Steyn (1973), Hustler et Howells (1986)
Breeding pairs (fraction of pairs that breed)	0.72	9.50	+	Hustler et Howells (1986); Herholdt et al. (1996)
Number of territories	50	2.55	-/+	Herholdt et al. (1996)
Number of individuals at simulation start	180	0	-/+	Herholdt et al. (1996)
Breeding success varies annually with rain	(Eq.2.1)		+	Compare: Hustler et Howells (1990), see text

In a first experiment, the rainfall scenario was identical for all replicate runs within the same T_m computation, but rain scenarios differed among T_m computations. I repeated T_m -computations 100 times for each of the eleven different rain scenarios. This experiment reveals whether rain scenarios that differ stochastically produce significantly different extinction times for simulated tawny eagle populations. In case that the model is sensitive to stochastic variation in precipitation pattern I would expect significant differences in T_m among various T_m computations for different rain scenarios, but no significant differences among T_m computations for the same rain scenario.

In a second experiment, rainfall scenarios differed among replicate runs of the same T_m computation, i.e. they were chosen randomly out of a whole set of rain scenarios for each of the replicate runs. I provided the same set of stochastic different rain scenarios and repeated the T_m -computations 100 times for each of the eleven sets of rain scenarios. I conducted this

experiment to eliminate stochastic variation in data for rain pattern and thus, I expect no significant differences among T_m for various T_m -computations, not for the same set of rain scenarios nor among different sets.

Correlation between environment and extinction events

I intended to focus closer on the environmental conditions that lead to extinction events. Hence, I searched for a correlation between the explicit time series of precipitation data and the resulting pattern of extinction events over time. I performed 5,000 repeats simulating population dynamics using the same parameter set *and* the same environmental conditions, i.e., every population experienced the same time series of precipitation. Demographic noise, however, was different and lead to differences in extinction times among simulation repeats. The resulting distribution of extinction events over time characterizes the particular rain scenario used during these simulation repeats. Extinction events over time will be given as portion of the still living populations referring to the probability to go extinct during the current time step. Since the corresponding precipitation data show high variation among successive years I calculated a moving average of annual precipitation over the past y years, where y was varied from 20 to 300.

Current variability in precipitation

My next issue in sensitivity analysis was to investigate possible impacts on the predicted T_m due to limited knowledge on the actual future rain scenario. Although attributes describing the rain scenarios remained constant this includes a variability that might lead to differences in T_m . Hence, again I kept rain scenarios constant during the simulation repeats of one T_m computation obtaining T_m values that are characteristic for particular rain scenarios. Rain scenarios differed among T_m -computations but descriptive attributes (mean, variance) remained constant. This enables me to estimate the variability in T_m due to rain scenarios and possibly resulting effects on the explicit value for T_m .

2.3.8 Simulation experiments

My aim is to investigate projected effects of climate change on the southern Kalahari tawny eagle population. As precipitation is the most important environmental parameter in arid areas, climate change driven modifications in precipitation pattern might cause severe effects in dry-savanna. In contrast to most of the African continent, studies of climate change project a decline of precipitation by 10% by the year 2050 for southern Africa, including the Kalahari dry-savanna (IPCC 2001a). Some studies suggest that the inter-annual variation in precipitation amounts might increase, especially in arid areas. However, there are no quantitative local projections for southern Africa available that refer to inter-annual variation in precipitation. Furthermore, a shift in frequency distribution and duration of extreme events like especially dry or wet years must be considered. Here, trends towards increasing auto-correlation in data of climate related factors are expected as a global perspective (Matyasvsky et al. 1993, Katz et Brown 1994, Hennessy et al. 1997, Wigley et al. 1998, Karl et Knight 1998, Schulze 2000, IPCC 2001b, van Jaarsveld et Chown 2001, O'Neill et al. 2001, Schiermeier 2001).

For simulating these modifications in precipitation pattern within the model I modified Zucchini's rain scenarios in different ways as described in the following. I tested for modifications in all three features describing the precipitation pattern as mentioned above. I always tested for both, modifications as projected and in the opposite direction.

a) Annual mean

Effects of decreased mean annual precipitation amounts were simulated. Here, I decreased all data within a rain scenario by a constant value resulting in a decreased annual precipitation mean, while auto-correlation remained constant. Inter-annual variation (CV) changed only slightly but was nevertheless readjusted according to the method described in the next paragraph. In the same way I tested for increased precipitation amounts.

b) Inter-annual variation (CV)

The inter-annual variation of precipitation amounts (Coefficient of Variation = CV) was changed by modifying the distance of each data point of the rain scenario to the precipitation mean. The distance was multiplied by a constant value k over the whole rain scenario and data values were changed accordingly. When k was smaller than 1.0, the resulting data were closer to the long-term mean, and consequently the inter-annual variation decreased. When k was larger than 1.0, distances to the long term mean increased, data were scattered in a wider range around the mean, and inter-annual variation increased. Thus CV was changed but precipitation mean, as well as the auto-correlation, remained constant.

c) Auto-correlation (noise color)

Assuming that years of similar precipitation amounts tend to occur successively over time I increased (and decreased, respectively) temporal auto-correlation in precipitation data. Auto-correlation (AC) refers to the similarity among temporal successive rain data. The term “noise color” also describes AC and is used equivalently referring to the analogy in frequency distribution of blue, white and red light. A positive AC (“red noise”) refers to time spans of rather wet respectively dry conditions, whereas a negative AC (“blue noise”) expresses that a wet year is very likely followed by a dry year and vice versa. AC is close to zero (“white noise”) when the value of the successive data point is not or only very uncertainly predictable.

I used a first order auto-regressive process to change auto-correlation of Zucchini’s rain scenarios:

$$P_{t+1} = P_0 + \Phi_{t+1} \quad [\text{Equation 2.3}]$$

where P_t is the precipitation at time point t , P_0 equals the long term precipitation average and

$$\Phi_{t+1} = \alpha * \Phi_t + \beta * \varepsilon_{t+1} \quad [\text{Equation 2.4}]$$

where α is the auto-correlation on a scale from -1.0 to 1.0 , ε is a random number drawn from a normal distribution with unit variance and zero mean, β is a constant factor determining the amplitude of the fluctuation and thus yielding the CV or inter-annual variation in precipitation. Φ_0 equals zero. (Compare also Eq.6.1 and associated description). Note, that variance has to be rescaled when generating auto-correlation (“dyeing”, Heino et al. 2000) but here, a new alternative method of rescaling is used which is presented in detail in chapter six.

First, I produced an auto-correlated rain scenario completely independent of Zucchini’s original scenario. Second, I re-arranged all values in Zucchini’s rain scenario according to the order of values in the auto-correlated scenario. Thus I allowed a variance of 2% assuring to find a suiting value in Zucchini’s scenario. I did not change data values compared to the original rain scenario but re-arranged them in time. Consequently, the long term mean and CV of the various rain scenarios remained constant, whereas auto-correlation varied from -0.9 to $+0.9$.

d) Periodically fluctuating rain scenarios

As an additional scenario I assumed that precipitation might fluctuate periodically over time. Once again, I re-arranged data over time and created environments fluctuating periodically in three different patterns (Fig.2.6c-e).

First, I subdivided the whole time scale of rain scenarios in periods of equal length. Within each period I retained data values but re-arranged them as a saw tooth pattern, i.e. lowest value at beginning and end of the period, highest in the middle (i – Fig.2.6c) and descending, i.e. highest value at the beginning of a period, lowest at the end (ii – Fig.2.6d). Second, I used the descending pattern and divided periods further into two parts, where the first part contained data above time series mean and the second part contained data below time series mean. Data within both parts were averaged and replaced by their mean value. As the averaging process affects the CV I hereafter modified the CV back to the original value using the same process as described above under b). To this third scenario I refer as “cog-pattern” (iii – Fig.2.6e).

For all three patterns of periodically fluctuating environment the lengths of periods were varied between 1 (equals no modification) and 400. The long term mean and CV remained constant compared to the original time series. AC however, is naturally affected by data re-arrangement and was close to zero at period lengths 1, slightly negative at period length 2 and then strongly increasing with increasing period length getting close to a maximum of AC=1.0. AC for the cog-pattern was higher than AC for the descending pattern but it was lower than AC for the saw tooth pattern.

2.3.9 Auto-correlation analyses

For some of my simulation experiments I modified the temporal auto-correlation in rain patterns directly (2.3.8c) or as a side effect (2.3.8d). An auto-correlation analysis was performed for the corresponding precipitation scenarios. To calculate auto-correlation r_k of the order k (i.e. distance between data points) I used the formula (Chatfield 1984)

$$r_k = \frac{c_k}{c_0} \quad [\text{Equation 2.5}]$$

where c_0 is given by c_k for $k=0$ and

$$c_k = \frac{1}{N} \sum_{t=1}^{N-k} (x_t - \bar{x})(x_{t+k} - \bar{x}) \quad [\text{Equation 2.6}]$$

and N is the total number of data in the precipitation scenario, x_t is the particular data value at position t , and \bar{x} is the average. (Compare chapter five, Eq.5.1 and Eq.5.2.)

2.4 SENSITIVITY ANALYSIS: RESULTS AND DISCUSSION

I conducted a series of sensitivity analyses to estimate the vulnerability of the model to uncertainties in parameter values and thus, to estimate the capabilities of the model.

2.4.1 Demographic parameters

As expected, I found the model to be mostly sensitive to changes in demographic parameters concerning survival and reproduction (Table 1). First, I tested parameters impacting the reproductive life span and thus, the potential for recruitment. The model was highly sensitive to parameters for adult survival rate, as well as age of maturation and senescence parameters.

Although maximum age also affects the reproductive life span I found its impact on recruitment rate to be very low, as more than 99% of all individuals die before reaching the maximum age. As a consequence, the model was insensitive to changes in maximum age.

Second, I tested the sensitivity to parameters that determine the proportion of individuals taking part in reproduction. Again, as expected, I found high sensitivities to juvenile survival rates, to the fraction of breeding pairs out of all pairs, as well as to the sex ratio. Here, the sensitivity of sex ratio might be somewhat surprising. However, as the tawny eagle is considered to be monogamous, any slight change of the sex ratio results in fewer possible breeding pairs and in lower reproduction, as long as the population has not reached carrying capacity.

Third, I tested model sensitivity to a parameter for the fraction of clutches with two offspring out of all clutches. This is a parameter that directly impacts recruitment, and the model should be highly sensitive to this parameter. Nevertheless, I found only a low sensitivity to this parameter, as two offspring from one tawny eagle's nest are very rare and the parameter default value was only 0.01. I investigated model's sensitivity to a parameter variation of only 10% (see above and table 1) and thus the absolute change in the value of this parameter is effectively very low, i.e. only 0.001. Hence, the parameter value lies out of the sensible range. If a tawny eagle raised two offspring much more often (for example, half of all clutches, i.e. 0.50) the model would be more sensitive to a 10% modification of this parameter (i.e. an effective modification of 0.05). However, this would be unrealistic as even in a highly productive floodplain, only 0.13 clutches produced two offspring (Osborne 1982a).

Fourth, I investigated the model's sensitivity to the carrying capacity. As expected, I found high sensitivity to the number of available territories since this parameter yields the carrying capacity of the density dependent population. The model was not sensitive to the number of individuals at simulation start since T_m does not consider initial conditions (Wissel et al. 1994).

I was then looking for parameter quality, i.e. the quality of default values of parameters according to the underlying data basis, in combination with sensitivity. Two combinations, good parameter quality but high sensitivity, and bad parameter quality but low sensitivity, avoid biasing model results (Burgman et al. 1993). As a third combination, Table 1 shows parameters with high sensitivity but only intermediate parameter quality, in particular the juvenile, adult and senescent survival rate. These parameters may cause a bias in the quantitative results of the model. Nevertheless, I have confidence in my model for the three following reasons: First, the default values for adult survival and senescence produce an average adult life expectancy of 17 years that is similar to that observed in the field (16 yr., Brown et al. 1982). Second, the lack in parameter quality of survival rates is due to data observed in other species that nevertheless are ecologically very similar (e.g. Bateleur *Teratopius ecaudatus* Brown et Cade 1972, for ecological similarity see Smeenk 1974). Furthermore, other parameter values are set according to the most current information based on data from the tawny eagles and similar species and on the expertise of ornithologists. And finally, my aim is not – and could not be – to give a precise estimate of time to extinction or percent probability of extinction, but to compare the resulting extinction risks under various conditions and estimate their relative impact (see introduction). Assuming that the bias introduced through the use of uncertain parameter values is constant across scenarios this does not affect the comparative results. Consequently, I claim that the model's utilities for my goals remain unaffected by parameter quality and sensitivity.

2.4.2 Environmental parameters

Mode of including environmental variation

After performing the sensitivity analysis for demographic parameters I then examined the model's sensitivity to environmental parameters, i.e., in this case the sensitivity to the rainfall scenario. Note that again I will refer to the terms "replicate runs" and " T_m computation" as defined under Methods/Output parameters. All the rain scenarios used during this sensitivity analysis differed stochastically in data values but data were drawn from the same distribution with respect to mean, inter-annual variation and auto-correlation. In a first experiment, the rainfall scenario was identical for all replicate runs within the same T_m computation (but differed among T_m computations). In a second experiment, rainfall scenarios differed among replicate runs of the same T_m computation, i.e. they were chosen randomly for each of the replicate runs.

I found high sensitivity of the model to the rainfall scenario when keeping it constant for all replicate runs within the same T_m computation. Extinction times of replicate runs within the same T_m computation were often similar. However, resulting T_m values among various T_m computations - using different rainfall scenarios - differed significantly ($p=0.05$, $n=11$, Bonferroni multiple range test). These results indicate that model results depend on the specifics of the rainfall scenario. Consequently, under these conditions, model results, i.e. T_m , depend in fact on the rainfall scenario used.

In contrast I found low model sensitivity when rainfall scenarios were chosen randomly for each of the replicate runs. Here, extinction times of replicate runs within the same T_m computation differed widely. However, resulting T_m values among various T_m computations showed no significant differences ($p=0.05$, $n=11$, Bonferroni multiple range test). By varying the rainfall scenario for replicate runs within the same T_m computation, I was able to average out the stochastic variabilities among rainfall scenarios. Here, model results, i.e. T_m , are not biased by the choice of the rainfall scenario.

This implies that providing randomly differing rainfall scenarios for each replicate run of the same T_m computation avoided any bias that would be introduced by using a particular rainfall scenario. For my simulation experiments, consequently, rainfall scenarios for replicate runs were not constant but were chosen randomly from a mixture of rain scenarios that differed in data stochastically but were constant in descriptive features like mean annual precipitation, inter-annual variation and auto-correlation.

Correlation between environment and extinction events

I then focused on a relationship between the past precipitation and current extinction events. I found the best correlation between annual precipitation and the amount of current extinction events when using the moving average over the past 200 years. In Fig.2.2 the probability to extinct in a particular time interval is shown for the populations that survived up to this time. Furthermore, the moving average of annual precipitation over the past 200 years is plotted. Note, that in Fig.2.2 precipitation values were signed negatively in order to visualize the negative correlation between extinction events and precipitation.

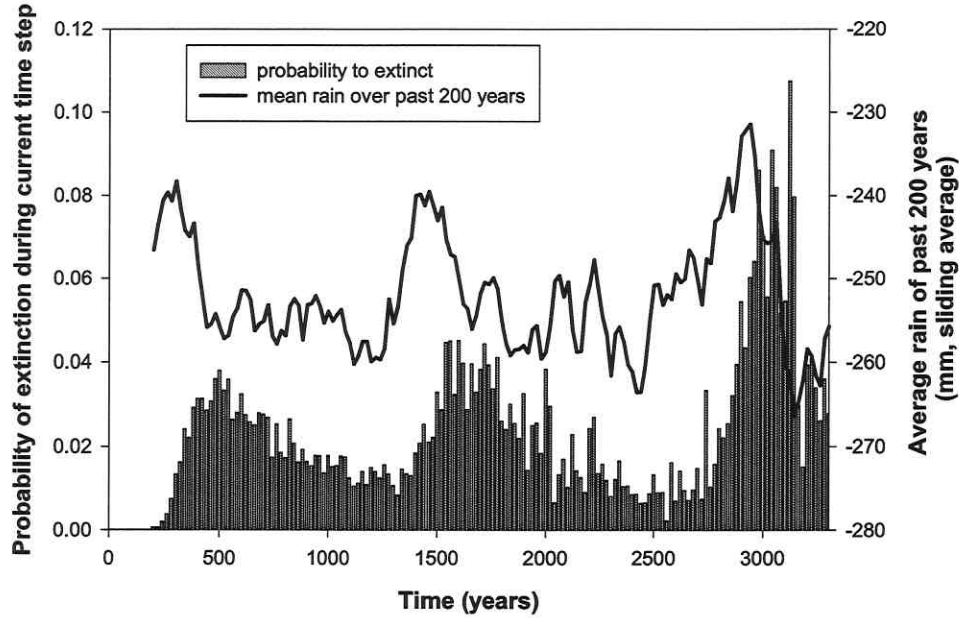


Figure 2.2: Coincidence of precipitation and extinction events

Periods of low 200-year mean rainfall are followed by population extinction very often, whereas extinction events rarely follow periods of high mean rain. Time series of rain were the same for all populations and all populations started at the same time point within this time series. Time is given on bottom axis. The bar plot shows distribution of extinction events for 5,000 population runs under exactly the same rain data as the probability to extinct during current time interval (width: 20 time steps) when survived up to now (left axis). The line plot shows mean value of rainfall for the past 200 years as sliding average (right axis). Note that rain values are signed negative, so the line plot is inverted (axis on the right).

Fig.2.2 visualizes that extinction probability is correlated with mean annual precipitation of the past 200 years. Whereas periods of low rainfall are followed by high probabilities of population extinction, high rainfall is followed by a decrease of population extinction. (Note inversion of right axis in Fig.2.2.) Quantifying the time delay between rainfall and the following response in extinction risk I found the correlation with the highest R^2 for a time delay of 160 years (equals to 10 generations). Then extinction probability ep can be calculated from the average annual rainfall over the past 200 years ar_{200} as follows:

$$ep = 1.7 * 10^3 ar_{200} + 0.4491 \quad (r^2 = 0.45) \quad [\text{Equation 2.7}]$$

according linear regression.

This relationship approaches the causes behind the variation in extinction for the various rain scenarios: Only a sufficiently low average in amounts of rain over a time horizon of 200 years can lead to an increase in extinction risk.

Similar but slightly less evident results were produced when calculating the moving average of annual precipitation for the past 150 or 220 years. However, considerable lower time spans (100 or 50 years) showed a much more noisy curve and higher time spans (300 years) showed more smooth curves but the correlation lost on evidence. The rather large time scale of 200 years gives respect to the fact that only a high accumulation of bad conditions can cause an

extinction event. Several successive generation of tawny eagles have to suffer these bad conditions before the population is pushed down to extinction.

Current variability in precipitation

As a part of the sensitivity analysis I investigated the effects of current variability in rain scenarios on the predicted T_m . I compare the T_m resulting from particular rain scenarios with the default T_m resulting from a mixture of rain scenarios used during the same T_m computation. When investigating current variation in precipitation that are realistic even without further climatic changes I found that most resulting values of T_m lie in a range between 50% and 130% of the default value (Fig.2.3). This causes a considerable variation of estimated extinction times in dependence of the real future rain scenario without considering further climatic changes. However, it still gives me a good estimation on the scale of the expected T_m and – with values from 400 to 1,000 years – suggesting rather stable population persistence. The rather high variability of T_m in Fig.2.3 (standard deviation = 0.36) detects the impact of the actual, future rain scenario on population persistence. As a result of the sensitivity analysis I emphasize the sensitivity of tawny eagle's population dynamics and persistence to precipitation in arid areas. The results of the sensitivity analysis also show that my aim could not be to exactly quantify the presumable high persistence time (T_m) of tawny eagles. My work, however, enables me to estimate the impacts of possible changes in the environment on T_m .

As precipitation directly biases mostly primary production this indirect impact on a top predator species like the tawny eagle seems surprising. However, an other top predator response on weather fluctuation is reported by Post et al. 1999 for wolves (*Canis lupus*) on Isle Royale, U.S.A.

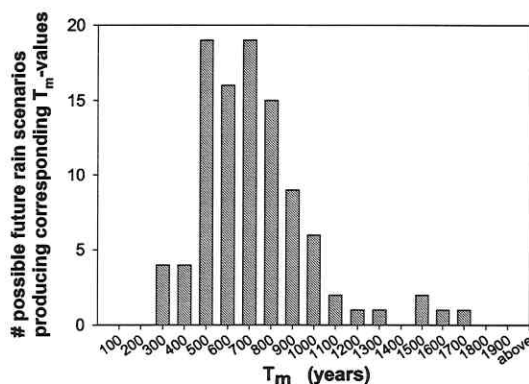


Figure 2.3: Variability in T_m

Expected T_m (mean time to extinction) strongly depends on the specific, actual future rain scenario. The number of rain scenarios (left axis) producing the correlating T_m (bottom axis) is shown. Here, the same rain scenarios were used during the simulation repeats for the same T_m computation what reveals the variability of T_m due to variation in precipitation. 100 randomly chosen rain scenarios were tested.

2.5 RESULTS OF SIMULATION EXPERIMENTS

With the default parameter set (see table 1) and a set of original precipitation scenarios produced by the rain generator (Zucchini et al. 1992) I obtained a T_m of 735 years. However, I standardized all following values for T_m to this default value, as my aim is to compare T_m under different (environmental) conditions.

a) Modified annual mean

I modified the rainfall scenarios for the model simulations by lowering mean annual precipitation, since this is projected to occur for southern Africa. Decreasing the mean annual precipitation resulted in a lower T_m (Fig.2.4a). This is not surprising since lower precipitation lessens primary production, and thus, conditions deteriorate for the tawny eagle's breeding performance. Remarkably, the model results are extremely sensitive to mean precipitation, with a decrease of 2% (-5 mm) in mean annual precipitation cutting T_m in half, a 4% decrease (-10 mm) reduces T_m by two thirds and a 10% decrease (-25mm) forces the T_m down by nine tenths, which approaches the life span of only a few generations. In contrast, an increase of mean precipitation by 2% (+5mm) doubles the value of T_m and larger changes increase T_m far above our time horizon.

b) Modified inter-annual variation (CV)

In a second set of experiments, I examined the effects of changes in inter-annual variation (CV) in precipitation, another factor that is projected to be impacted by climate change. I found that T_m for tawny eagles was very sensitive to modifications of CV, with an increase in CV lowering T_m (Fig.2.4b). Increasing the default CV of 0.325 by 10% (to 0.357) results in a T_m decreased by one third, and a severe increase in CV by 50% (to 0.487) reduces T_m by three quarters. On the other hand, decreasing CV by 20% (to 0.260) doubles T_m . Although the model is very sensitive to the CV, it does not have the extreme sensitivity seen in changing the mean annual precipitation.

c) Modified auto-correlation (noise color)

Climate change studies assume an increase in the auto-correlation of rainfall amounts, i.e. similar precipitation for successive years. I found that increasing auto-correlation of rainfall data leads to a decrease in T_m and a decrease in auto-correlation results in increased T_m (Fig.2.4c). However, the impact of AC on T_m appears to be much lower than the impact of the mean or CV. Even under severe decreases in AC, T_m increased only by a factor of 1.4 and it decreased by a factor of 0.4 when AC was severely increased. The curve shows a linear relationship over a wide range of intermediate values for AC, but tends to reach an asymptote at extreme AC values close to 1.0 and -1.0.

Results for modifications in mean, CV and auto-correlation of precipitation might be biased by the length of individual life spans, i.e. if individuals are able to survive time spans of unfavorable rainfall data. Thus, I modified the average life span by changing adult survival rates and again I tested for impacts of changing mean, CV and auto-correlation in the rainfall pattern. My results showed that, of course, populations on average lived longer when survival rates were higher. However, I found higher impact of auto-correlation for higher survival rates, i.e. longer individual life spans, when standardizing data to zero auto-correlation (Fig.2.5). This indicates higher sensitivity to auto-correlation for populations that have higher population persistence per se. On the other hand, I found almost no impact of changing auto-correlation on T_m for very low survival rates. Furthermore, for the lowest survival rates supporting the population for only few generations, the quality of the relationship seemed to be reversed. Here, T_m increased slightly with increasing auto-correlation. In contrast to AC the impact of mean and CV of annual precipitation on T_m changed only slightly when using various adult survival rates.

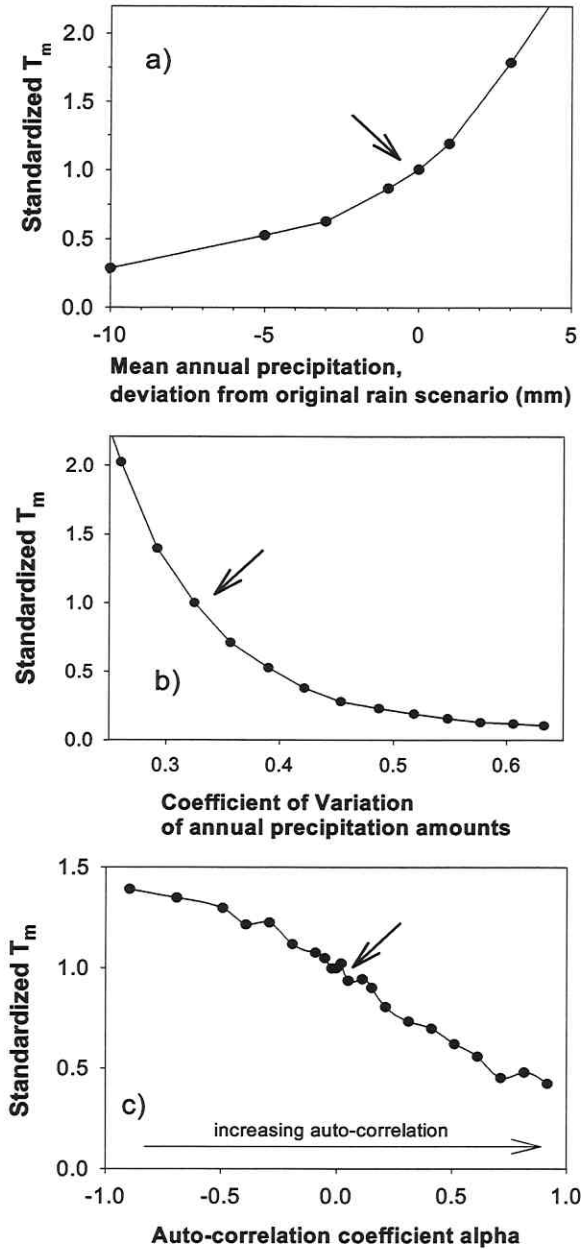


Figure 2.4: Impacts of mean, CV and auto-correlation in precipitation

Mean Time to Extinction (T_m) for tawny eagles (left axis) depends on various features of the corresponding rain scenario (bottom axis). While keeping two out of three features of the original rain scenario constant, I modified the third (increasing and decreasing, respectively):

a) mean annual precipitation (original: 250 mm);

b) inter-annual variation in precipitation (i.e. Coefficient of Variation, original: 0.325);

c) auto-correlation of rain data (i.e. noise color, original: 0.0, i.e. white noise).

The term "standardized T_m " refers to the fact that all T_m were standardized to the T_m resulting from the original rain scenario. Arrows indicate the original rain scenario.

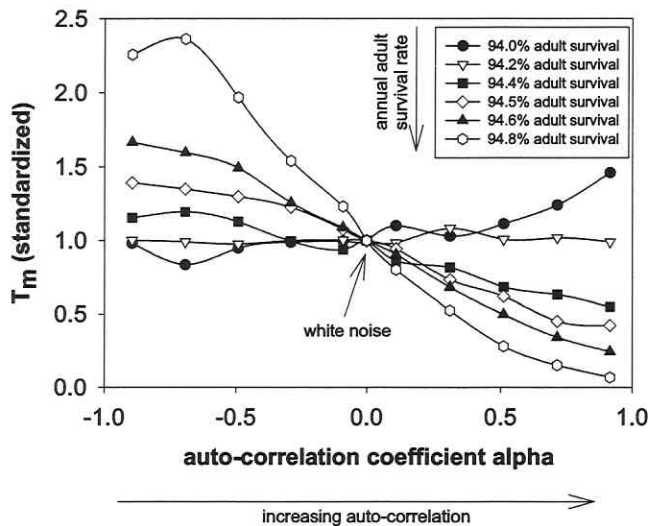


Figure 2.5: Impact of varying survival rates

The standardized T_m - auto-correlation relationship from Fig.2.4c for various annual adult survival rates. Note that T_m is standardized according to T_m for white noise, i.e. differently among curves. Also note that the slope of the curve varies when modifying adult survival. As in Fig.4c mean annual precipitation, as well as inter-annual variation (CV) were kept constant while auto-correlation was modified.

d) Periodically fluctuating rain scenarios

In a final experiment I produced three different patterns of periodicity in the rainfall scenario. For each general pattern I varied the period length of the fluctuations. There was a general decrease in T_m with increasing period length for all three scenarios. However, at very small period lengths there was a slight but significant increase in T_m , again in all three scenarios (Fig.2.6a).

When comparing different scenarios of data re-arrangement, the “cog-pattern” scenario (iii - Fig.2.6e) resulted in highest T_m (Fig.2.6a). The “descending” scenario (ii - Fig.2.6d), with constantly decreasing precipitation within one period and then suddenly much higher precipitation when entering the beginning of the next period, produced far lower T_m , especially for short period lengths. However, these extinction times were still higher than those of the “saw tooth” pattern (i - Fig.2.6c) where data are highest in the middle of a period and decrease towards both ends.

In analyzing the differences among the three patterns I measured the probability of populations falling below a threshold of 30% of their carrying capacity, i.e. the state of sparse population as defined earlier. This contains information on how stable populations were, i.e. whether they took the full advantage of habitat’s carrying capacity and fluctuate around it or whether population dynamics were too weak to do so. Here, the cog-pattern scenario (iii) exhibited the lowest probability of sparse population, suggesting stable populations that persist close to carrying capacity (Fig.2.6b). At small and intermediate period lengths for the descending (ii) and saw tooth (i) scenarios the populations had a higher probability of sparse population, i.e., falling under the threshold. With long period lengths the descending and cog-pattern scenarios showed similar values.

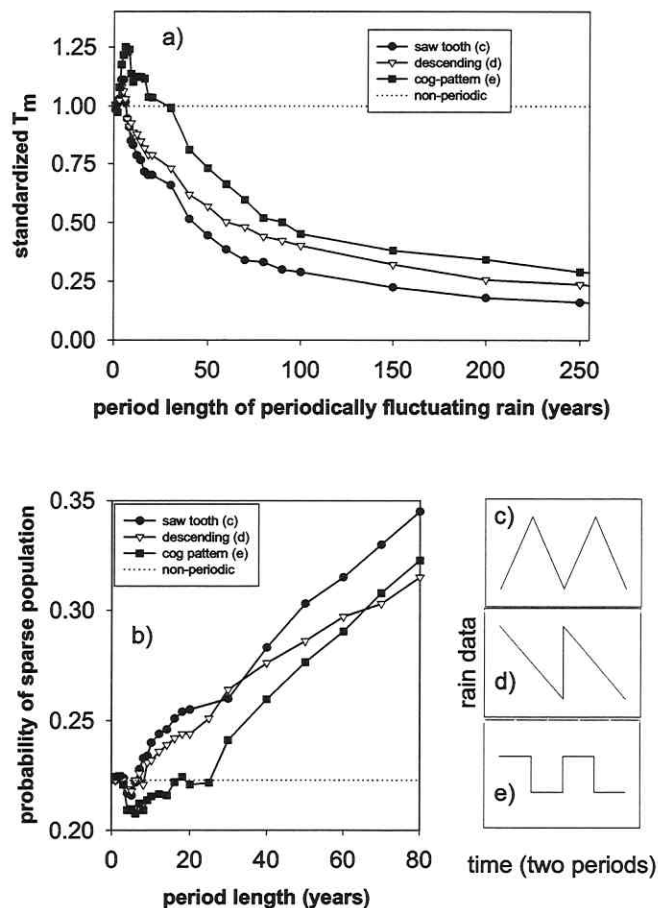


Figure 2.6: Periodically fluctuating precipitation

Results for three different patterns of periodically fluctuating precipitation amounts.

a) T_m (left axis, standardized, cf. Fig.2.4) depends on period length (bottom axis) of fluctuating precipitation and varies for different patterns of periodical fluctuation.

b) Probability of populations to fall below a threshold of 30% of the carrying capacity (left axis) depends on the period length (bottom axis) and on the pattern of periodically fluctuating precipitation.

c-e) Scheme for different patterns of periodically fluctuating precipitation: saw-tooth pattern (c), descending (d), cog-pattern (e).

2.6 DISCUSSION

In this study, I investigated the influence of climate change driven modifications in precipitation on population persistence of raptors in arid savanna. Here, the tawny eagle in the southern Kalahari is regarded as a case study. I conducted model experiments simulating various precipitation patterns according to current knowledge of how climate change will occur. I found that changes in various aspects of precipitation pattern will have intermediate and high impacts on population persistence. According to projections of future climate change rather unfavorable conditions for tawny eagles and a decreased probability of population persistence have to be expected.

2.6.1 Model selection

It is certainly not possible to study tawny eagle population dynamics under predefined precipitation patterns in nature. Instead I used an individual-oriented, stochastic computer model to simulate climate change and tawny eagle population dynamics. As demanded by Uchmanski et Grimm (1996) my approach takes resource dynamics explicitly into account,

which makes this an appropriate and powerful tool for the aims of this study. Using an extensive sensitivity analysis (Burgman et al. 1993) I examined the capabilities of the model (Table 1) and found them suitable according to the aim of my study. I analyzed how patterns of environmental variation, i.e. variation in rainfall, impacted the extinction pattern of tawny eagles (Fig.2.2). I tested two different ways of including rainfall pattern in the model and, according to the aim of this study, I chose the one that allows investigating features of rainfall pattern systematically. (See also section sensitivity analysis for further discussion).

2.6.2 Tawny Eagle population persistence under climate change

Studies of climate change suggest modifications in several features of precipitation patterns, such as mean, inter-annual variation (CV) and auto-correlation (IPCC 2001b, see also Katz et Brown 1992, Matyasvsky et al. 1993, Hennessy et al. 1997). In this study I investigated explicitly the impact of the mentioned features of precipitation patterns on tawny eagle's population persistence and found the long-term mean precipitation to have the highest impact on T_m .

My results indicate a severe decrease in population persistence with only slightly decreasing mean annual precipitation but increasing population persistence with increasing mean (Fig.2.4a). For climate change in southern Africa, a decrease in mean precipitation by 10% is expected by the year 2050 (IPCC 2001a). For this scenario my results suggest a dramatically increased extinction risk, i.e. a T_m decreased by nine tenths, for the tawny eagle population. The quantity of this result might be biased in two ways. First, a few, extremely long-lived individuals might arbitrarily extend population persistence as long-lived individuals have higher impact on shorter extinction times. Quasi extinction, i.e. the cessation of reproduction, might however occur even earlier. Second, the population might be buffered by a high initial number of individuals, i.e. far above carrying capacity, as carrying capacity declines when environmental conditions become less favorable. T_m is independent of initial conditions but only gives the time that populations persist once carrying capacity is reached (Wissel et al. 1994, Stelter et al. 1997). Indeed, an increase in population persistence was measured when taking the initial population into account. Both of the biases discussed here have minor quantitative effects and do not impact the projection of a dramatically increased extinction risk for tawny eagles due to climate change.

Although the model appears to be less sensitive to the inter-annual variation (CV) than to the annual mean, changes in CV of precipitation still cause severe effects in T_m and the extinction risk of tawny eagles. Here, population persistence decreases with increasing inter-annual variation but increases with decreasing inter-annual variation (Fig.2.4b). An increased inter-annual variation is characterized by more and/or stronger – favorable and unfavorable - extreme events. However, due to limits placed on the population by the carrying capacity, extremely favorable events have a limited positive impact on the population, whereas extreme unfavorable events have a full negative impact and can easily bring the population close to extinction. Climate change driven modifications in inter-annual variation are emphasized by several authors (e.g. Katz et Brown 1992, Hennessy et al. 1997, Karl et Knight 1998) and suggest that variation will increase (e.g. Matyasvsky et al. 1993). Thus, my results again imply lower populations persistence for tawny eagles under climate change. To my knowledge, climate change studies cannot yet quantify changes in inter-annual variation in local precipitation. However, my study suggests a very sensitive response by tawny eagle population dynamics to any change in the variability of the precipitation variation among years.

Under climate change, the probability for occurrence of extended dry and wet periods will most likely change, which is equivalent with increased auto-correlation (Katz et Brown 1992,

1994). Figure 2.4c shows increased population persistence for negative auto-correlation (i.e., when dry and wet years alternate) but decreased population persistence for positive auto-correlation (i.e., when similar conditions occur in successive years). Both the projection and the recent observation of heavy rain events and severe droughts (Hennessy et al. 1997, Karl et Knight 1998) intuitively may imply similar precipitation in successive years, i.e. positive auto-correlation. However, the underlying investigations refer rather to CV than auto-correlation. Thus, up to now there is only little indication in which direction auto-correlation will develop under climate change, and both, positive and negative impact on population persistence, seem to be possible. However, for intermediate modifications in auto-correlation my results indicate rather moderate impacts on tawny eagle population persistence. Thus, effects of a modified auto-correlation on population persistence might be masked by the negative but highly sensitive effects of decreased mean values and/or increased CV.

I also tested various values of adult survivorship when investigating the impact of precipitation mean, CV and AC on T_m , since the model is highly sensitive to the rates of adult survival (Table 1). Modifications in individual life spans due to changed survivorship might influence the ability of the population to survive periods of unfavorable conditions under positively auto-correlated precipitation. As expected I found differences in absolute T_m -values for varying adult survivorships due to the sensitivity of the model to this parameter. Though, more interesting is the question of differences in the relative, i.e. standardized, T_m values. Indeed, in Fig.2.5 the slope of the T_m - AC relationship varies when modifying the value of adult survivorship. Although my results indicate an intermediate quantitative bias of the adult survivorship on the impact of AC on T_m this observation does not change the resulting implications. Fig.2.5 also shows an extreme case of very low adult survivorship where the impact of AC on T_m seems to reverse (solid dots in Fig.2.5). This scenario, however, is very unlikely as here, absolute T_m values are very low and populations persist for only few generations what is inconsistent with field observations. I found only slight differences in the slopes of T_m when investigating the impact of mean annual precipitation and inter-annual variation for various values of adult survivorship. This is due to the fact that - in contrast to AC - the mean and inter-annual variation do not refer to temporal scales.

2.6.3 Periodically fluctuating precipitation

Closely related to increased auto-correlation, where periods of dry conditions alternate with periods of wet conditions, is the idea of precipitation amounts fluctuating periodically over time (e.g. Kot et Schaffer 1984, Li 1992). For periodically fluctuating environments, auto-correlation is positive but in addition monotonic trends occur, i.e. data increase or decrease steadily over short time intervals. My results indicate that depending on the period length, T_m were very different (Fig.2.6a). In general, populations on average died earlier with increasing period length due to the increasing accumulation of years with low precipitation at one (descending - Fig.2.6d) or both (saw-tooth and cog-pattern - Fig.2.6c,e) ends of the period. These accumulations of unfavorable data lead to extended periods where reproduction is low, individual numbers decrease steadily and populations stay far below carrying capacity (Fig. 2.6b), resulting in stochastic extinction and decreased population persistence for tawny eagles.

For short period lengths I found increased population persistence (Fig.2.6a). Here, auto-correlation is low or even negative, and both favorable and unfavorable environments occur periodically, alternating within short time intervals (i.e. frequently and regularly but not successively), and precipitation tends to be evenly distributed over time. Consequently, small period lengths systematically avoid long, unfavorable phases during which the population could be destabilized and would be prone to higher extinction risk. On the other hand, regularly and frequently occurring favorable data support population persistence close to carrying capacity (Fig.2.6b). Thus, small scale periodicity in the environment leads to weaker

fluctuations in the tawny eagle population. In other words, a set of given precipitation data is optimally arranged over time when fluctuating in small period lengths to favor population persistence.

I observed differences in T_m for different patterns of periodically fluctuating environment, even when auto-correlation was constant (Fig.2.6a). These results reveal the special case of periodically fluctuating environments as compared to simple auto-correlation under non-fluctuating conditions. Differences in T_m correspond to differences in probability of a sparse population, i.e. - as defined - when population falls below a threshold of 30% of the carrying capacity (Fig.2.6b). For the cog-pattern treatment (iii - Fig.2.6e) the probability of sparse population is low as individuals face constantly favorable precipitation over half of the period time and thus, they take the full advantage of the carrying capacity, and establishing a population that is able to survive the second half of the period facing unfavorable precipitation. This yields higher T_m for the cog-pattern. For the descending and saw tooth patterns (Fig.2.6c,d) data are less evenly distributed over time and thus the populations are more prone to stochastic variation and unfavorable phases might last longer, resulting in lower T_m .

2.6.4 Extinction theory

The parameters of the precipitation scenarios investigated during this study are general features of time series and environmental noise. Their influence on extinction risk of populations was investigated earlier in extinction theory (Roughgarden 1975, Ripa et Lundberg 1996, Johst et Wissel 1997, Kaitala et al. 1997, Cuddington et Yodzis 1999) and my results show qualitative consistence with this theoretical framework. Nevertheless, for any particular species and situation specific models are needed to give specific answers. Laakso et al. (2001) emphasized the importance of explicitly considering the biological process that filters the environmental noise, i.e. the transformation of environmental variation into biological variation, as done in this study by transforming precipitation into breeding success. The case of periodical fluctuating environments has not yet been investigated in extinction theory and I cannot evaluate these results. Instead I address this question in a following, more theoretical study (chapter five).

2.6.5 Escaping in space?

In this study I used a non-spatial simulation model and thus, spatial differences in the precipitation pattern were not taken into account. However, raptors might be able to avoid unfavorable precipitation patterns by escaping in space, i.e. migrating to areas with temporally more favorable conditions. Indeed, migration of raptors to highly productive areas has been observed (Brooke et Steyn 1972, Jensen 1972, Liversidge 1994). This observation was made on both short and long term scales, i.e. raptors briefly gathered in areas that had extremely high prey density in one year, as well as an increasing accumulation of birds in areas that have experienced above average prey density over several years. However, this applies only for non-breeding individuals since territory establishment and breeding performance do not allow migration during the breeding season. Two points speak against higher breeding success due to accumulation in highly productive areas. First, choosing a territory in an area with above average productivity seems to be difficult as territories are established before the breeding season and the prey density is not known in advance. Second, raptors defend breeding territories against individuals of the same and other raptor species (Newton 1979, Steyn 1983) which would be almost impossible under high raptor densities and consequently would not allow breeding. Thus, breeding success is not likely to increase when taking spatial pattern into account.

Furthermore, avoiding unfavorable rain conditions by escaping in space may be hampered by a general problem, i.e. that the borders of conservation areas are fixed (Rutherford et al. 1999, Hannah et al. 2002). Conservation areas are commonly established where favorable conditions for endangered species and communities are found. However, when conditions change, i.e. turning unfavorable within or turning more favorable outside reserves, species might more or less easily migrate. But once established reserve borders are hard to move. Consequently, a modification in environmental conditions such as changing precipitation pattern is likely to face us with the problem to have conservation areas at the wrong place as pointed out by the authors mentioned above. The situation may turn even more severe when human impact has established modified conditions outside the park, as it is the case in the southern Kalahari. Here, vegetation structure is modified due to area-wide land use and overgrazing by cattle (Jeltsch et al. 1996) showing higher tree density but lower tree heights than within the park area. Thus, animals such as tawny eagles leaving the Kgalagadi Transfrontier Park when following more favorable climatic conditions will nevertheless face modified habitats (compare chapter four).

2.6.6 Studying the impact of climate change on population dynamics

Most studies on the effects of climate change concern only on global scales. However, Hannah et al. (2002) call for modeling of climate change effects on regional scales since “global models have inadequate resolution for conservation planning”. My study goes into this direction as regional characteristics are explicitly accounted. The regionally projected effect of decreased precipitation in South Africa stands opposite to the globally projected increase and, of course, the impacts on the local savanna ecosystem differ for both scenarios. Thus, the present study gives an example that information on climate change is needed on regional levels.

Studies that address the question how life will be impacted in a world of climate change may differ in the scale of the biological system that they investigate, (e.g. particular populations, species, species groups, communities or whole ecosystems). Moreover, these studies can be separated according to their approach into at least four groups. First, there are observational studies in the field assuming that climate change is already taken place and we can currently observe the effects on plant communities and animal populations (e.g. Clark 1990, Balling et al. 1992, Moss et al. 2001). Second, there are field and greenhouse studies that simulate the projected climate change effects, (e.g. elevated CO₂ concentrations) on single species and communities of plants or soil microbes (e.g. Kirschbaum 1995, Hu et al. 2001, Joel et al. 2001, DeLucia et al. 2001) but not on animal populations, which is probably due to limited constraints for experimental design. Third, results in extinction theory (Roughgarden 1975, Ripa et Lundberg 1996, Johst et Wissel 1997, Cuddington et Yodzis 1999) contribute knowledge on population persistence in changing environments but their application to different situations and species has to be investigated in particular. Fourth, there are modeling studies simulating the effects of climate change on biological systems often focusing on plant communities and vegetation structure (e.g. Jeltsch et al. 1996) but rarely investigating specific plant and animal populations (but see Reuter et Breckling 1999, Coulson et al. 2001, Morjan 2002). My study fits into this last category and thus it increases our understanding of how climate change affects biological systems at the scale of populations and how this might impact species diversity and finally biodiversity. However, to form an understanding of life in a world of climate change all the approaches mentioned above are needed investigating the problem on different levels of biological systems. The results point in different directions as they suggest increased productivity on one hand, but decreased population persistence on the other. But most of them agree that life will be considerably impacted by the effects of climate change.

2.6.7 Conclusion

My study implies a new dimension for the impact of climate change on biodiversity exceeding the worst expectations. Up to now studies that investigated climate change effects on biotic populations focused on changes in mean values of environmental parameters (McDonald et Brown 1992, Post et al. 1999, Hughes 2000, Moss et al. 2001). However, my results underline that not only mean values but also slight modifications in inter-annual variation of environmental parameters will have dramatic consequences for population persistence (Fig.2.4b). In other words, even when climate change does not result in modified mean values of environmental parameters, changes in variation among time units (e.g. years) might severely impact population dynamics, composition of biological communities and finally biodiversity. Furthermore, even when mean and variation remain constant, auto-correlation and monotonic trends in temporal succession of data can be important and may impact population persistence.

The results of this study suggest a great impact of the future rain scenario on population persistence of raptors in southern African arid savanna. Although investigations were conducted on the tawny eagle, similar mechanisms for other large raptors (e.g. bateleur, martial eagle) suggest that my results maintain for these species. We can expect high sensitivity of raptors to modifications in the precipitation pattern. As my results indicate, most of the projected climate change driven modifications in precipitation will lead to a decrease in the population persistence of raptors in arid savanna. I suggest that more studies are needed that explicitly investigate climate change effects on particular populations in order to form our picture of population persistence and biodiversity in a world of climate change.

2.7 LINK TO THE PROCEEDING CHAPTER

In this chapter (two), I introduced and tested a model of tawny eagle population dynamics in the Kalahari arid savanna. I used this model to explore the impacts of varying precipitation patterns on tawny eagle population persistence. Therefore, I used a promotion of a breeding success-precipitation-relationship that has been observed in the field (Hustler et Howells 1990). However, this breeding success-precipitation-relationship changes between different study areas. In the next chapter (three), I will present a method that allows to establish a breeding success-territory size-precipitation-relationship on a non-local scale. I will test this new method with the available data sets.

3 The breeding success of arid area raptors in relation to precipitation²

3.1 ABSTRACT

The breeding success of raptors in arid areas is suggested to be higher in years of high annual precipitation. However, this relationship seems to vary within in a species but among different regions. In this contribution I present a new idea to tackle the breeding success-precipitation-relationship in raptors on non-local scales. Here, in a theoretical approach, I derive the importance of taking territory sizes into account. Thereafter, I show that these theoretical considerations are consistent with the available data sets. However, more field data are needed to further evaluate this approach. Hence, this contribution may stimulate future field studies on breeding success of raptors, their comparison with existing literature and implications for nature conservation.

3.2 INTRODUCTION

Birds are often very popular in society since they are easy to observe, aesthetically pleasing and engage in interesting behavior. They are also useful indicators of disturbances associated with droughts and land use changes, and are thus frequently priorities for conservation efforts (Rodriguez-Estrella et al. 1998, Herremans et Herremans-Tonnoeyr 2000). Studies of birds for conservation are usually at the population level, and their population performance can be limited in various ways. Newton suggests limitation by food supply or “some supposed index of food” (Newton 1998: p.171) among other factors to control the survival and/or the reproduction in birds. This might be especially valid for raptors that depend on prey availability and prey population dynamics including cyclic rhythms (Newton 1979, 1980, 1998, Steyn 1980a, b, c, Osborne 1982a,b, Hustler et Howells 1986, 1987, 1989, 1990, Steenhof et Kocher 1988, Village 1989, Watson 1990, Brown 1991, Herholdt et al. 1996; Bahat et Mendelssohn 1996, Herholdt and Kemp 1997, Gerstell and Bednarz 1999; predators beyond birds: e.g. Post et al. 1999).

In arid areas, the base of the food web, i.e. primary production, is controlled by water availability and thus, precipitation is the most important environmental factor yielding food supply. In particular, in the climatically erratic areas in which southern African raptors dwell means that, although on the top of the food web, raptors might be affected by variations in annual precipitation amounts (Hustler et Howells 1990, Herholdt 1996, monthly variation: Watson 1991). While adult birds remain unaffected and can survive by feeding on carrion, youngsters, especially nestlings, need high quality food, i.e. live prey, in order to grow, to develop and to finally fledge successfully (e.g. Newton 1979, 1998). Previous studies have tested for breeding success-precipitation correlations. However, in southern Africa, only Hustler et Howells (1990) could collect a sufficient sample size to show this correlation. In Israelian deserts, Bahat et Mendelssohn (1996) found a breeding success-precipitation-relationship for the golden eagle (*Aquila chrysaetos*). However, studies on raptors always searched for “year to year” (i.e. temporal) changes but not for “place to place” (i.e. spatial) changes in precipitation (compare Newton 1998: p. 147). (But note that Hustler et Howells 1989 considered spatial variation in soil composition.) Consequently, in this chapter I will

² A slightly modified version of this chapter was submitted to the forum section of a journal with conservation focus:

Wichmann MC, Dean WRJ, Jeltsch F: Breeding success of raptors in arid areas: What makes the difference?

3 Breeding success of arid area raptors in relation to precipitation

focus on comparing the breeding success of arid area raptors with precipitation over time *and* space.

3.3 THE THEORETICAL APPROACH

In this study I assume that food supply for raptors in arid areas is limited by precipitation (Hustler et Howells 1990, Bahat et Mendelsohn 1996) and that precipitation is a “supposed index of food” (Newton 1998). When exploring the dependence of breeding success on precipitation we then have to measure the *total* amount of water (provided by precipitation and yielding the amount of food) that pairs of raptors have available to rear their young. Here, it becomes evident that precipitation should not be given as a water column of a certain height but as volume per territory and hence, that territory size should be included in a breeding success-precipitation-relationship. In the following I will distinguish between (1) the common measure of “water column precipitation” given in mm (or meters) and (2) “volume precipitation per territory” given in m³. Regarding territories as circular areas with a diameter *ind*, leads to the following equation:

$$RD = p * \frac{\pi * ind^2}{4} \quad [\text{Equation 3.1}]$$

where *RD* is the total amount of volume precipitation per territory per year given in m³, *p* gives water column precipitation in meters (!), *ind* is the inter-nest distance in meters and π is approximately 3.1416. Note that the right hand term in Eq.(3.1), i.e. $\pi/4 \text{ ind}^2$, gives the idealized area of the territory in m². Eq.(3.1) enables me to consider data from different regions with different territory sizes and different amounts in water column precipitation. This gives respect to the fact that for constant amounts of water column precipitation larger territories receive more volume precipitation than smaller territories, and vice versa.

When precipitation is an index of food supply then raptors in one area, which own larger territories but experience a smaller water column of rain, should have the same amount of food available as raptors in other areas owning smaller territories but experiencing higher water columns of rain. This leads to the conclusion that low precipitation amounts (i.e. water column) yielding low prey density can be balanced out by large territories.

However, larger territories might be less efficient, i.e. more “expensive”, since prey is harder to find and raptors have longer ways to go. Hence, the power balance in larger territories is less favorable than in smaller territories even when volume precipitation and food supply remain constant. Consequently, territory size, i.e. the inter-nest distance *ind*, impacts the breeding success-precipitation-relationship in two ways: (1) large territories may increase the breeding success due to more prey in large areas (cf. Eq.3.1), and (2) hunting in large territories is at higher costs and may decrease successful predation, available food and breeding success. Therefore, in order to draw conclusions about the effects of volume precipitation per territory and year (*RD*) on breeding success (*BS*) I have to take inter-nest distance (*ind*) into account. Most pragmatic, I simply divide *RD* by *ind*. These considerations lead to transferring the variable *RD* from Eq.(3.1) into the index of breeding success *BS* using a linear relationship:

$$BS = a * \frac{RD}{ind} + b \quad [\text{Equation 3.2}]$$

where *a* and *b* are the parameters to specify the linear relationship. For a given sample of data sets from various single studies on the same raptor species one can derive the parameters *a*

and b in Eq.(3.2) by linear regression (Fig.3.1 and chapter 3.4). Also note that here, a and b are assumed to be constant over different regions.

While the parameter RD is very suggestive, by giving the volume of water per territory, RD/ind is somewhat harder to grasp. However, according to Eq.(3.2) the term RD/ind is used as a metric of territory quality, which is linearly correlated with breeding success BS . Eq.(3.2) in combination with the results derived from the data base (Tab.3.1, Fig.3.1) suggests that the total amount of water available RD has to be standardized to territory diameter ind , i.e. the distances that birds have to cover to reach food sources.

Criticizing the presented approach one might argue that raptors may adapt territory sizes according to the available water column precipitation. However, territories are hard to defend and they are established at the beginning of the breeding season when this year food supply cannot yet be known. Thus, I can assume that territories are established with a size according to *average* water column precipitation and based on the experiences of the *last couple of years*. This implies that territory sizes are adapted at a much slower rate than precipitation varies.

Table 3.1: Breeding success, precipitation and territory size in arid area raptors

Parameters related to the breeding success of raptors are given: ind indicates the distances between nests, i.e. territory size; $rain$ gives the average water column precipitation per year during the study period. Accordingly, RD gives the volume precipitation per year and territory in million m^3 . Finally, the rate of successful breeding (BS) and RD standardized to territory diameter are given yielding the plots in Fig.3.1. All available data sets of a sufficient sample size are shown for **a) tawny eagle**; **b) martial eagle**; **c) bateleur** and corresponding references are given. Note that e.g. Steyn (1980b) was not included since only one pair was observed over several years.

reference	ind (km)	rain (mm)	RD (mio m^3)	BS	RD/ind (m^2)
a) Tawny Eagle					
Herholdt et al. 1996	17.6	221	53.77	0.63	3054.88
Hustler et Howells 1986,1989,1990	5.9	828	22.64	0.80	3836.83
Hustler et Howells 1986,1989,1990	5.9	603	16.49	0.60	2794.21
Steyn 1973, 1980a	7.0	687	26.44	0.83	3776.98
Brown1991	15.3	350	64.35	0.74	4205.81
Osborne 1982a	4.8	698	12.63	0.76	2631.40
b) Martial Eagle					
Herholdt et Kemp 1997	24.1	221	100.40	0.72	4174.43
Hustler et Howells 1987,1989,1990	5.9	828	22.64	0.75	3836.83
Hustler et Howells 1987,1989,1990	5.9	603	16.49	0.62	2794.21
Brown1991	25.8	350	182.98	0.83	7092.15
c) Bateleur					
Herholdt et al. 1996	13.5	221	31.63	0.61	2343.24
Steyn1980c	14.5	687	113.44	0.77	7823.74
Watson 1990	5.1	400	8.17	0.57	1602.21
Osborne 1982b	5.5	698	16.58	0.75	3015.14

3.4 APPLICATION ON AVAILABLE FIELD DATA

In a next step I test the theoretical considerations described above on the available data sets. For raptors occurring in southern African arid areas I found data set of sufficient sample size for three species (Table 3.1a-c): the tawny eagle (*Aquila rapax* Temminck), the bateleur (*Terathopius ecaudatus* Daudin) and the martial eagle (*Polemaetus bellicosus*). All these are characteristic raptors of the Kalahari and beyond that they occur in various regions of the African continent (e.g. Smeenk 1974, Steyn 1983). All data sets found for each of the three species are included in Table 3.1 and plotted in Figure 3.1a-c applying linear regression. Note that Hustler et Howells (1990) deliver two data sets at a time for the tawny eagle, as well as for the martial eagle, i.e. one for high and one for low precipitation (water column).

For the tawny eagle I included six data sets providing six points in Fig. 3.1a showing an obvious trend of increasing breeding success with increasing precipitation per territory. Linear regression yields a rather low $r^2=0.31$ ($a=8.078 \cdot 10^{-5}$ and $b=0.4533$). On closer inspection two outliers are apparent. On one hand, the data collected by Osborne (1982a) in a floodplain, suggest considerably reduced limitation in primary production, and thus, high breeding success despite low territory sizes and intermediate water column precipitation (O82a in Fig.3.1a). On the other hand, data collected by Brown (1991) from a declining population show low breeding success, albeit at high inter-nest distances and low to medium water column precipitation (B91 in Fig.3.1a). Removing these two points yields a much better fit of linear regression ($r^2=0.97$; $a=2.204 \cdot 10^{-4}$; $b=-2.68 \cdot 10^{-2}$).

For the martial eagle four data sets were included and the fit of the linear regression was quite good ($r^2=0.83$; $a=4.295 \cdot 10^{-5}$; $b=0.5378$). Here, removing the data from a declining population (Brown 1991, B91 in Fig. 3.1b) did not affect the fit of the linear regression ($r^2=0.80$; $a=8.481 \cdot 10^{-5}$; $b=0.3912$).

For the bateleur once again four data sets were found to be sufficiently large. Data from Table 3.1c give a satisfying fit for a linear regression ($r^2=0.59$; $a=2.736 \cdot 10^{-5}$; $b=0.5739$). Data by Osborne (1980b) were collected in the same floodplain in southern Zambia as for the tawny eagle (O82b). Assuming a bias by water availability beyond precipitation and removing this data point the linear regression fit was much better ($r^2=0.99$; $a=3.104 \cdot 10^{-5}$; $b=0.5282$).

I am aware that samples of four to six data points as I used them here are not ideal for statistical calculations and linear regression. They are, however all the data available since sufficient sample sizes are hard to collect for raptors living on large temporal and spatial scales. Therefore the available data sets can be used to improve our knowledge but future studies using my approach should further evaluate it with new field data. The method presented here allows the comparison of breeding success of raptors in different region with precipitation for the very first time. This should be seen as the main result of this chapter. Future studies providing new field data or developing other approaches to address the aim of this method may use this study as a basis.

Although there would be good reasons to exclude data from declining populations (yielding reduced competition and high inter-nest distances, Brown 1991) and populations experiencing additional food supply (floodplain, Osborne 1982a,b) I initially retained these data in order not to decrease the already low number of data points. However, when removing these data (as done for chapter two, Eq.2.1) the fits of linear regression were considerably elevated for the tawny eagle, as well for the bateleur.

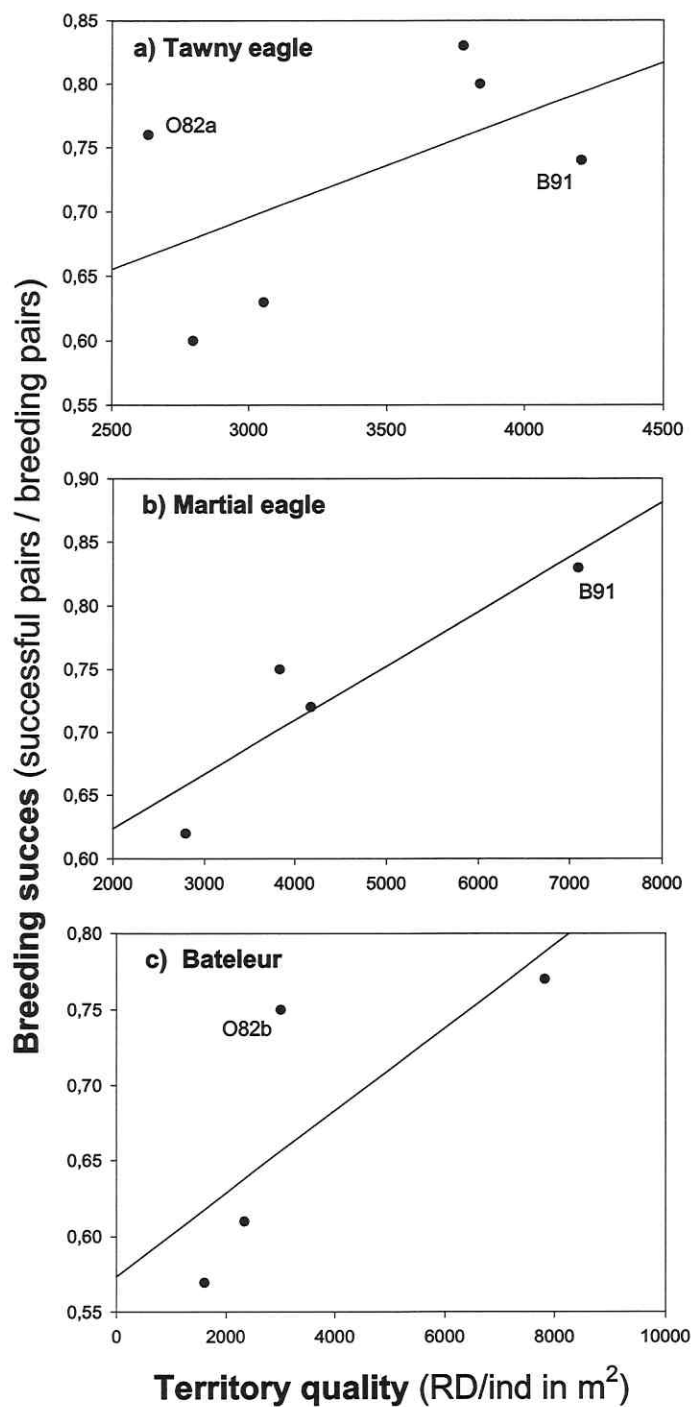


Figure 3.1: Relating breeding success to territory size and precipitation

For the available data sets the breeding success *BS* (left axis) is plotted versus territory quality *RD/ind* (bottom axis, compare text below Eq.3.2). In application of Eq.(3.2) linear regression is performed for all available data points (see text for results). O82a, O82b and B91 mark possible outliers as discussed in text. Data are shown for

- a) tawny eagle;
- b) martial eagle;
- c) bateleur.

3.5 CONCLUSION

The approach presented in this study is the first that allows a comparison of the breeding success of raptors with precipitation for both, “year to year” and “place to place” changes (see Newton 1998). In contrast to earlier studies, here, territory size is explicitly considered. Thus, breeding success-precipitation-relationships as found by Hustler et Howells (1990) and Bahat et Mendelssohn (1996) can be promoted to a breeding success-*territory size*-precipitation-relationship. This new approach reveals that in areas of different average precipitation (water columns) raptors hold territories of different sizes. The impact of temporal fluctuations in *annual* precipitation on breeding success can be compared for different areas (varying in precipitation average) when territory size is explicitly taken into account.

Studying the effects of temporal variation in precipitation on arid area raptors is especially important when considering projections for climate change. Global climate change is expected to modify precipitation patterns leading to impacts on the extinction risk of raptors in arid areas (compare chapter two). However, beyond climate change this approach may also help to tackle recent issues in nature conservation in arid areas all over the world. Thus, the insights from this study are not restricted to southern Africa (this study) or Israel (Bahat et Mendelssohn 1996). An extensive literature search and/or further field studies might reveal similar relationships for other erratic regions of the world such as central Asia (e.g. steppe eagle: Savinetsky et Shilova 1996) or central America and Mexico (e.g. Bednarz 1988, Bednarz et Ligon 1988, Rodriguez-Estrella et al. 1998, Rivera-Rodriguez et Rodriguez-Estrella 1998). Future field studies on arid area raptors should explicitly relate breeding success to annual precipitation amounts and compare the results on non-local scales by taking territory sizes explicitly into account.

3.6 LINK TO THE PROCEEDING CHAPTER

In this chapter (three) I presented a new way of relating the breeding success of raptors in arid areas to annual precipitation amounts. In contrast to earlier studies, I emphasize that territory size must be included in a breeding success-precipitation-relationship and that precipitation should be given as volume per territory, not as water column in mm as is more usual. This consideration is closely related to chapter two where the impact of varying precipitation patterns on tawny eagle persistence was investigated. In chapter two of this thesis I introduced a model of the population dynamics of the tawny eagle in the southern Kalahari arid savanna and performed an extensive sensitivity analysis. However, in chapter two the model did not explicitly consider spatial aspects (although it did implicitly by a limited number of territories, compare chapter 2.6.5). Now, in the following chapter (four), two spatial scales are explicitly included in the model. First, on a smaller scale I will consider the given vegetation structure yielding nesting sites and hunting area for tawny eagles. Second, a larger scale takes into account intra-specific competition for territories.

4 Structural diversity in arid savanna impacts the persistence of raptors³

4.1 ABSTRACT

Various guises of land use modify the environment. This includes various aspects of biodiversity, such as vegetation structure, geomorphologic structure, biomass amounts, bio-chemical composition and species composition. In this chapter I focus on spatio-structural diversity as an often-underestimated aspect of biodiversity. Using a case study, I investigate the impacts of recent land use practices, such as cattle farming and wood cutting, in the southern Kalahari arid savanna on the persistence of a large raptor, the tawny eagle (*Aquila rapax*). I use an existing model of the population dynamics of tawny eagles to simulate likely land use driven changes in the vegetation structure to model populations. I investigate scenarios of varying tree density, as well as various tree distribution patterns. The results of this study show that (1) very high, as well as very low tree densities can limit tawny eagle persistence, and (2) that deviations from a random tree distribution (i.e. clumped or evenly distributed) can shift these limiting tree densities. Reduced persistence of tawny eagles was found for critical tree densities below 0.036 and above 5.5 trees per ha, but model populations remained unaffected for intermediate tree densities. Thus, wood cutting can reach the lower threshold only by (almost) complete clearing. However, specific targeting of large trees for cutting may reduce tawny eagle persistence beyond tree densities. Overgrazing favors woody plants and this may lead to upper thresholds being exceeded. However, if clumping is related to increased tree densities (as indicated) my results suggest an upward shift of both thresholds and no, or at least reduced, impact on tawny eagle persistence due to overgrazing.

On one hand, this study reveals that there is a potential impact of land use and modified vegetation structure on population persistence, in particular on the tawny eagle in the Kalahari. However, more detailed studies are required to quantify and specify the impacts of land use on vegetation structure in order to clarify the risk to tawny eagles and other species. On the other hand, in general, my results emphasize the importance of structural diversity. Structural diversity can influence population persistence and consequently species diversity, providing a link between these two aspects of biodiversity.

4.2 INTRODUCTION

During the past decade “biodiversity” evolved to a frequently used term in ecological science and nature conservation. Especially in conservation politics, where decision makers have to be convinced to support the protection of natural resources, biodiversity is used to emphasize the value of natural areas. The simplest and most frequently used measurement of biodiversity is species richness, i.e. the number of species in an arbitrarily defined geographical area (e.g. Houston 1994). However, furthermore biological diversity is more than species diversity and “includes diversity within species, between species and of ecosystems” (UNESCO 1992, article 2). Beside species diversity in a broader sense including taxic, genetic or phylogenetic measures on various levels the term biodiversity also applies to diversity in molecular, in functional and in spatio-structural scope (Harper et Hawksworth 1994, Begon et al. 1996).

³ A revised version of this chapter is previewed for submission to a journal with focus in applied ecology: Wichmann MC, Jeltsch F, Dean WRJ, Wissel C: Structural diversity in arid savanna impacts the persistence of raptors.

4 Structural diversity in arid savanna impacts the persistence of raptors

In particular, structural diversity might be underestimated in the biodiversity debate. Although diversity in structure is indirectly taken into account by a number of authors, e.g. when investigating on the impacts of diversity in leaf-structure or in soil types on species diversity (Rosenzweig 1995), the term “structural diversity” is rarely used and seldom claimed as an autonomous aspect of biodiversity (but see Jeltsch 2002). However, recent studies in forest management focused on “structural diversity” referring to diversity in spatial structures (e.g. Ferris et Pritchard 2000, Herles 2000). According to other authors the term structural diversity also includes diversity in functional structures like food webs (Jeltsch et al. 2001, Jeltsch 2002). Both, spatial (e.g. trees) and functional (e.g. food webs) structures form the medium to perform processes (e.g. settling, nesting, feeding) which essentially sustain the life cycle of biotic organisms and hence, their population survival. In the consequence structural diversity might yield species diversity.

An ecosystem with an easily describable but characteristic vegetation structure, i.e. structural diversity in space, is the arid savanna. Typically, arid savannas are open woodlands with scattered large trees, interspersed with grassland and a rather poorly developed shrub layer (Scholes et Walker 1993). In arid savanna large trees provide foci points of species diversity since here, animals gather in the shade beneath the tree or in the crown which provides perch, hide and food. This phenomenon leads to the accumulation of nutrients and seeds under large trees. Milton et Dean (1995) and Dean et al. (1999) conclude that large, solitary standing trees play a keystone role in maintaining the processes characteristic to arid savanna and that any possible changes in tree distribution and vegetation structure might essentially disturb the natural dynamics.

Currently, two kinds of human activities are observed that might potentially impact the vegetation structure in southern African arid savanna. These are (1) overgrazing by cattle farming and (2) wood cutting. Overstocking with cattle decreases the grass layer leading to reduced competition between grass and saplings of woody species. Hence, woody individuals are favored, which however, remain small (“bushy”) due to arising intra wood competition (Tainton et Walker 1992, Jeltsch et al. 1996, 1997a, 1999, 2000, Weber et al. 1998, 2000). Additionally, a reduced grass layer yields reduced fuel and lower fire frequency. Thus, the control of tree growth by fire is reduced and thus the favor of woody vegetation is even amplified (Trollope et Tainton 1986, Scholes et Walker 1993, Jeltsch et al. 2000). The second practice, i.e. woodcutting, refers to the combat of bush thickening by farmers using mechanical clearing or herbicides. Furthermore, harvested wood is sold as fire wood or charcoal (Tietema et al. 1991, Anderson et Anderson 2001, Milton et al. 2001, BIOTA AFRICA Project 2002). Whereas overgrazing is a long known phenomenon with its impacts on vegetation structure already very evident in some areas, fire woodcutting for commercial reasons appears to be a newer practice that emerged recently. While the secondary effects of cattle farming are well studied in quality and quantity only few studies focus on the impact of firewood harvesting on vegetation structure (e.g. Milton et al. 2001).

As plants and animals living in arid savanna are adapted to the characteristic vegetation structure any change in this structure may potentially impact the performance, dynamics and survival of populations. Thus, reduction in the rate of grass matrix going along with shrub encroachment might lead to food shortages for grazers on one hand and might favor browsers on the other. A decrease in number and density of large trees reduces the foci points for animals to gather, for seed and nutrient accumulation and also reduces the nesting possibilities for some bird species attached to large trees like the sociable weaver (*Philetarius socius*) or the tawny eagle (*Aquila rapax* Temminck) (Milton et Dean 1995, Dean et al. 1999). The tawny eagle prefers tall, solitary standing trees for nesting but at the same time it needs open

space for hunting interspersed with only few trees for perching (Steyn 1973, Smeenk 1974, Brown et al. 1982, Herholdt et al. 1996). Hence, I hypothesize human induced changes in arid savanna vegetation structure may impact the population performance of tawny eagles.

Studying the impact of a modified vegetation structure on tawny eagles in field experiments would be a monumental goal concerning the required space, time and money. However, computer based modeling approaches can provide a powerful alternative investigating the long term effects of phenomena observed on short time scales in the field (e.g. Stelter et al. 1997, Jeltsch et al. 1997a, Grimm 1999, Weber et al. 2000). Here, the Mean Time to Extinction (T_m), gives the time span that simulated populations in the model survive on average. Calculating the “Mean Time to Extinction” does not mean that populations truly face extinction. Instead, high T_m values indicate high population persistence due to favorable conditions, whereas low T_m values indicate unfavorable conditions. Hence, T_m provides a currency which enables me to compare different conditions – such as various tree densities and distribution patterns - and to estimate their relative impact on population persistence (Wissel et al. 1994, Stelter et al. 1997).

Here, I use a tawny eagle population in an arid savanna ecosystem to perform a case study on how changes in structural diversity might impact the performance and survival of species. I use an existing model of tawny eagle population dynamics (chapter two) in combination with a spatially explicit approach to simulate the consequences of expected modifications in vegetation structure. I will use standardized T_m -values as a currency to compare the results of my simulation experiments and to estimate the qualitative and quantitative impact of man induced modifications in arid savanna vegetation structure on the population persistence of tawny eagles. The following two aims are addressed to this work: (1) in a general context, I intend to perform a case study on possible impacts of structural diversity on the performance and survival of populations, and (2) in particular, I will give an estimation on the impact of man induced changes in arid savanna vegetation structure on population persistence of a large raptor, i.e. the tawny eagle.

4.3 SUBJECT OF THE STUDY, STUDY AREA AND METHODS

4.3.1 Subject of the study

The tawny eagle (*Aquila rapax* Temminck), sometimes considered a race of the steppe eagle (*Aquila nipalensis* Hodgson) (Clark 1992) occurs in the arid to mesic savannas of Africa, including the Sahara Desert, Mediterranean North Africa and Arabia. Tawny eagles are common in the savannas of southern Africa, with densities ranging from about one pair/40 km² in mesic savanna in the Kruger National Park, South Africa to densities of about one pair/150 km² (Kemp et al. 2001) or even one pair/250 km² in the Kalahari arid savanna (cf. Herholdt 1995). The tawny eagle feeds on a wide range of food items and has been appropriately described by Steyn (1983) as "... a scavenger, a pirate and a rapacious killer...".

Tawny eagle pairs usually lay two eggs in May or June and mostly the female incubates the eggs for about six weeks. Due to infertility or sibling aggression in most cases only one chick is reared over a fledging period of 12 weeks, followed by a post-fledging period of about six weeks during which the adults feed the juvenile before becoming independent at about 18 weeks (Brown et al. 1982). Many studies have investigated breeding performance but due to low individual numbers of tawny eagles the sample size is often small (Brown 1991, Herholdt et al. 1996, but see Hustler et Howells 1986). About 75% of all juveniles die before they reach maturity in their third to fourth year (Newton 1979, Steyn 1983), but thereafter have an average life expectancy of 16 years (Brown et al. 1982). The breeding success of tawny eagles

is positively correlated with annual rainfall via primary production and prey population dynamics (Hustler et Howells 1989, 1990).

4.3.2 Study area

My model focuses on the population dynamics of tawny eagles in the Kalahari, an arid savanna in southern Africa including Botswana, western Zimbabwe and northwestern Republic of South Africa. Like most arid savannas, the Kalahari forms open woodland with an extended grass matrix. (Compare also introduction for further information on arid savanna.) Rainfall is generally erratic, with high coefficients of variation, over the region in which arid savanna occurs, and varies from about 200 mm mean annual rainfall in the southwest to >500 mm in the east and north of the Kalahari savanna. Arid savanna encompasses a number of sub-types differentiated by the dominant tree species, tree spacing and average vegetation height, as well as soil types and underlying geology but does never shade off into pure wood- or grassland (Scholes et Walker 1993, Low et Rebelo 1996, Jeltsch et al. 2000). The default parameter set for my model refers to the area of the “Kgalagadi Transfrontier Park” which is situated in the arid savanna at the northwestern tip of the Republic of South Africa and southeastern Botswana (compare chapter two).

As pointed out in introduction the vegetation structure in southern Kalahari arid savanna is currently modified by cattle farming and wood cutting. When cattle farming in arid savanna exceeds a threshold in stocking rates this initializes changes in vegetation structure (Jeltsch et al. 1997a). Exceeding this threshold is dangerous as it is both, hardly reversible and hardly to detect in the field since the effects only show up after 20 years and later. Vegetation structure will then develop towards more woody vegetation cover and less solitary, but smaller trees and in extreme cases the vegetation structure might change severely and the grass matrix might be significantly reduced (Jeltsch et al. 1996, 1997a, 2000). While overgrazing is followed by an increase in woody density, in contrast, one can assume that woodcutting reduces the woody density. Moreover, woodcutting directly impacts the vegetation structure and the effects appear much faster than those of overgrazing. Furthermore, fire wood harvesting might specifically target on large trees, i.e. the keystone structures of savanna vegetation. Hence, this practice may quickly lead to even more dramatic effects than overgrazing and this process has to be critically observed and evaluated in order to preserve the characteristic savanna vegetation structure (Milton et al. 2001, BIOTA AFRICA Project 2002).

In this study I focus on the impact of modifications in vegetation structure as they can be caused by human influence (described above) on the persistence time of the tawny eagle population. I here simulate various tree densities to model populations of the tawny eagle in order to study the impacts of modified tree densities. Moreover, I investigate the effect of various modes of tree distribution (hyperdispersion, clumping) that beyond tree density might change under human impacts.

4.3.3 Model description

I use the simulation model AQUIQUA to investigate the dynamics of the tawny eagle population in the southern Kalahari (chapter two). The model is based on empirical finding on the biology and life history of tawny eagles in southern Africa (Steyn 1973, Hustler et Howells 1986, Herholdt et al. 1996), on similar species (Brown et Cade 1972, Harris et al. 1994, Weimerskirch et al. 1987) and on general findings (Newton 1979). AQUIQUA is an individual-oriented model in the sense of Uchmanski et Grimm (1996). AQUIQUA includes demographic, as well as (at first temporal) environmental stochasticity (Burgman et al. 1993,

Lande 1993) the latter given by food availability determined by yearly rain amounts (compare Hustler et Howells 1990). Fig.4.1 shows the flow chart of the model. More detailed information including sensitivity analysis is given in chapter two. The model was written in C++ and simulations were conducted on a common personal computer.

In order to study the effects of a changing vegetation structure on tawny eagle populations I introduce spatial aspects into the AQUICUA model, i.e. I add environmental stochasticity in space. The spatial component of the model determines the available breeding territories, i.e. the carrying capacity, for the tawny eagle population. Spatial effects are included on two different scales. First, on the smaller scale of 5 to 150 meters, the vegetation structure yields potentially available nesting trees (PNT) regarding tree vicinity and tree height (cf. Herholdt 1995, Herholdt et al. 1996). Second, on the larger scale of 5 to 20 km, the territorial behavior of tawny eagles decides about the establishment of a breeding site, i.e. whether PNT in a certain area can be indeed used for nesting when considering intraspecific effects. On both scales dynamic boundary conditions are realized.

Vegetation structure (small spatial scale)

My intention is to investigate the effects of a spatially explicit tree distribution on tawny eagle population dynamics. Therefore, I generate a grid of discrete cells of $5 * 5 \text{ m}^2$ in size where each cell can contain no trees (matrix), one tree or several trees (according to Jeltsch et al. 1996). The grid size is $1,000 * 1,000$ cells representing an area of 25 km^2 . This can be regarded as the minimum territory size for tawny eagles in the southern Kalahari (Herholdt et al. 1996). Note, that in the model the tree distribution is constant over time, i.e. I do not consider the characteristics of temporal dynamics of trees as establishing, growing and dying.

In a first step I randomly distribute trees on the grid according to a varying tree density (1 to 20,000 trees per 25 km^2). Second, I analyze the generated tree distribution according to the characteristics of tawny eagle nesting trees found by Herholdt (1995).

If *all* of the following conditions are fulfilled I claim a tree as a Potential Nesting Tree (PNT):

- Solitary tree? (*Only one tree in current cell?*)
- Minimum distance to the closest three trees is 5 m (*No trees in first order neighborhood?* - cf. Fig.4.2)
- At least one tree in a 150 m (30 cells) neighborhood?
- Not more than 23 trees in a 150 m (30 cells) neighborhood?

I perform 1,000 simulations for each tree density. First, I calculate the average number of PNT in order to study model behavior. Second, the percentage of simulation runs (i.e. grids = areas of minimum territory size) containing at least one PNT is given. The latter yields P_{VS} , i.e. the probability to find a PNT according to (two dimensional) spatial aspects of vegetation structure:

$$P_{VS} = \frac{terr_{PNT}}{terr_{all}} \quad [\text{Equation 4.1}]$$

where $terr_{PNT}$ gives the number of grids (potential territories) containing at least one PNT and $terr_{all}$ is the number of simulation repeats (=1,000, i.e. all potential territories).

4 Structural diversity in arid savanna impacts the persistence of raptors

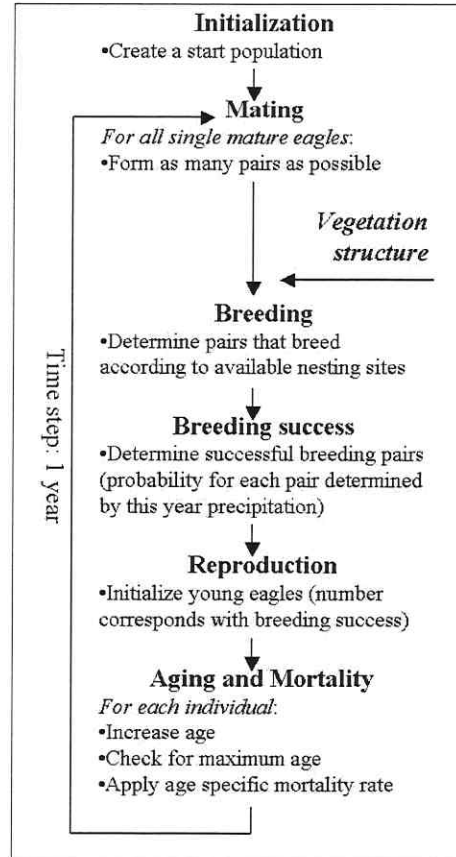


Figure 4.1: Simplified flow chart of the spatial model version.

Note, that the number of breeding pairs is impacted by vegetation structure yielding carrying capacity. For more detailed description see text and chapter two.

Thereafter, I take into account P_{VH} , i.e. the probability that a tree is high enough for nesting. Only about 10% of all trees reach 6 m in height (Steenkamp 2000, BIOTA AFRICA Project 2002) what was observed as the minimum height for tawny eagle nesting trees in the southern Kalahari (Herholdt et al. 1996). This yields $P_{VH} = 0.1$. Thus, P_{VS} is reduced to P_V , i.e. the probability to find a nesting tree according to constraints of spatial distribution *and* tree height.

$$P_V = P_{VS} * P_{VH} \quad [\text{Equation 4.2}]$$

In the following, I then use P_V in combination with results from the large-scale simulation to calculate the total probability P_C to choose a nesting site.

Interaction of tawny eagle breeding pairs (territoriality: large spatial scale)

In order to include the spatial effects of territorial behavior of tawny eagles I use the size of the small-scale grid (i.e. potential territories) as the cell size in a larger scale grid. Thus, with a cell size of $5 * 5 \text{ km}^2$ I generate a grid of $22 * 22$ cells representing an area $110 * 110 = 12,100 \text{ km}^2$. In the model this yields approximately 50 territories for tawny eagles as it is given by field data for the size of the simulated area (compare Herholdt et al. 1996), see also section on model sensitivity). Within the simulated area all potential breeding pairs seek for a breeding site (Fig.4.1). Every year anew the probability P_T to choose a nesting site according to territorial behavior is determined by the rules below according to field observations (Herholdt et al. 1996: inter-nest distances range from 6 to 32 km, longer distances are preferred). Under the premise of “first come, first served” for each pair of eagles the following procedure is simulated. The vicinity of a randomly chosen cell is scanned for other tawny eagle pairs. Starting with $P_T = 1.0$, for *every pair* found in the vicinity (i.e. 24 neighboring cells, i.e. 3rd order neighborhood, Fig.4.2) P_T is modified as follows:

- $P_T = P_T * 0$ if there is a pair nesting in this cell or in 1st order neighborhood
- $P_T = P_T * 0.3$ if there is a pair nesting in 2nd order neighborhood
- $P_T = P_T * 0.6$ if there is a pair nesting in 3rd order neighborhood

For a cell $[x_i y_j]$ with the given coordinates i, j I define neighborhood as follows (cf. Fig.4.2):

1st order: $[x_{i-1} y_j], [x_{i+1} y_j], [x_i y_{j-1}], [x_i y_{j+1}]$
 2nd order: $[x_{i-2} y_{j-1}], [x_{i-1} y_{j-1}], [x_{i+1} y_{j-1}], [x_{i+2} y_{j-1}], [x_{i-2} y_j], [x_{i-1} y_j], [x_{i+1} y_j], [x_{i+2} y_j], [x_{i-2} y_{j+1}], [x_{i-1} y_{j+1}], [x_{i+1} y_{j+1}], [x_{i+2} y_{j+1}]$
 3rd order: $[x_{i-3} y_{j-1}], [x_{i-2} y_{j-1}], [x_{i-1} y_{j-1}], [x_{i+1} y_{j-1}], [x_{i+2} y_{j-1}], [x_{i-3} y_j], [x_{i-2} y_j], [x_{i-1} y_j], [x_{i+1} y_j], [x_{i+2} y_j], [x_{i-3} y_{j+1}], [x_{i-2} y_{j+1}], [x_{i-1} y_{j+1}], [x_{i+1} y_{j+1}], [x_{i+2} y_{j+1}]$

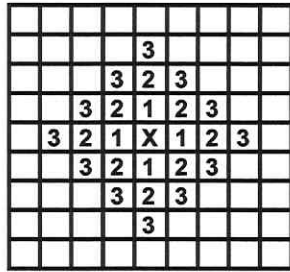


Figure 4.2: Definition of neighboring cells

Visualization of the definition of neighboring cells as given in text and applied for model rules. The cell considered for breeding is marked with 'X'. The numbers '1', '2' and '3' indicate that this cell belongs to the 1st, 2nd and 3rd order neighborhood, respectively.

Final decision on breeding site

The final probability P_C to chose a nesting site according to vegetation structure (nesting tree vicinity and height) and territorial behavior is

$$P_C = P_V * P_T \quad [\text{Equation 4.3}]$$

If the final P_C is smaller than a random number drawn from a uniform distribution in the range $(0, 1]$ the pair breeds at the chosen site. Otherwise a new cell is picked and tested again.

However, the model finally sets $P_C = 0.0$ if attempts to find a nesting site have reached a limit reflecting the limited time (March to April) and features that tawny eagles have available to establish breeding sites. The model allows tawny eagle pairs up to 15 attempts to find a nesting site since this reproduced breeding densities observed in the southern Kalahari (compare section on model sensitivity). Nesting sites are chosen for one year and all pairs seek anew for nesting sites every year on the whole grid (cf. Herholdt et al. 1996).

Note, that $P_C < 1.0$ additionally reduces the percentage of pairs that breed out of all pairs (i.e. 0.72 in the non-spatial model; compare chapter two, table 2.1). When applying P_C to the percentage of breeding pairs, the underlying assumption is that this parameter does not implicitly cover a limitation of breeding pairs by vegetation structure or territorial behavior.

4.3.4 Scenarios of non-random tree distribution

At first, I investigated scenarios of varying tree density assuming a random distribution of trees (see above). However, vegetation structure does not only refer to tree density but mode of tree distribution might also deviate from random (Menaut et al. 1990, Jeltsch et al. 1996). Hence, in order to investigate the effects of various scenarios of tree distribution on the tawny eagle population, I generated patterns of non-random tree distribution and conducted 100 simulation repeats for every pattern and density.

For two clumped scenarios 33% (66%, respectively) of all trees were distributed in aggregations. Here, centers were set with randomly chosen coordinates and each cell within the distance of 10 cells was assigned a probability to harbor a tree, decreasing from the center to the edge in accordance to Fibonacci numbers as percent values. This was continued until the fraction of trees, which were to be distributed in clumps, is reached (33% and 66% of all trees, respectively). Accordingly, for two further scenarios 33% and 66%, respectively, of all trees were evenly distributed yielding hyperdispersed distribution. Here, according to their number, I calculated the optimal distance between trees to spread them evenly over the whole grid. For any of the four scenarios the remaining trees (64% and 34%, respectively) were distributed randomly. In addition to the default random scenario this yields four distinct scenarios differing in degree and mode of tree aggregation.

(Note: due to discrete numbers of trees and discrete cells in the model inaccuracies in the real percentage of evenly (respectively clumped) distributed trees and distances between trees may occur. Thus, rounding errors may appear: first, in tree numbers for low tree densities (e.g. 66% of 55 trees equals 36.3 trees and is rounded to 36 trees = 65.5%). Second, high tree densities yield small and inaccurate distances between evenly distributed trees.)

Finally, in order to quantify the differences in distribution mode I calculated spatial autocorrelation for all five aggregation scenarios at various tree densities. Here, I used cross-correlation technique yielding a correlogram (e.g. Rossi et al. 1992).

4.3.5 Output parameters of the model

In the model I measure the *Mean Time to Extinction* (T_m) of the tawny eagle population, which is the average time span that simulated populations survive model runs (Wissel et al. 1994, Stelter et al. 1997). I performed 5,000 simulation repeats allowing demographic and environmental stochasticity what caused variations in extinction times despite a constant parameter set. I methodologically follow Stelter et al. (1997) to avoid “infinite” population runs by populations that do not become extinct. However, as I am not specifically interested in giving an absolute extinction risk but rather in comparing results for various given vegetation structures (environments), I will convert all the results to a *Standardized Persistence Time* (T_s). T_s is given as the ratio of the corresponding T_m divided by the default T_m obtained using a vegetation structure with no limitation in nesting trees.

As an additional output parameter I give the ratio of floaters, i.e. pairs that did not find a territory (Hunt 1998), as percentage of the carrying capacity (occupied territories).

4.4 RESULTS AND SENSITIVITY OF THE MODEL

4.4.1 Model sensitivity: number of attempts to find a territory

My model rules allow tawny eagles to attempt various territories for establishing a breeding site. The number of the allowed repeats to attempt territory establishment is limited due to limited features and time that tawny eagles have available. This number of repeats, however, might impact model results and thus I tested the model sensitivity to it (Fig.4.3).

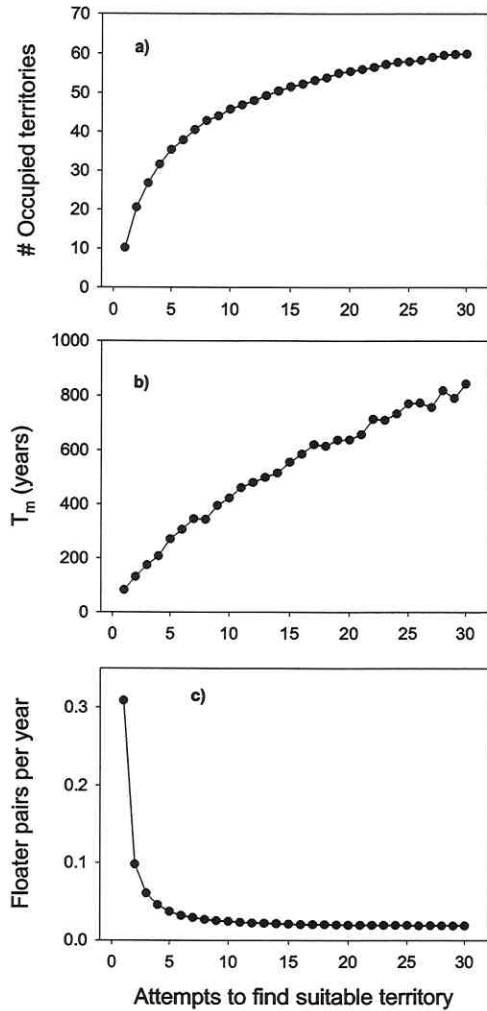


Figure 4.3: Model sensitivity to number of attempts to find a territory

Sensitivity of various model output values (left axis) to the number of repeated attempts to find a territory (bottom axis):

a) average number of occupied territories per year for an established population (measured over years 100 to 150 after population start);

b) persistence time T_m ;

c) pairs of floaters (as percentage of carrying capacity).

Note that here probability to find a suitable nesting tree within a territory is $P_V = 1.0$ in order to investigate large scale effects independent of small scale. Mean of 100 repeated T_m calculations is shown.

The mean number of occupied territories raises with increasing number of attempts according to a non-linear function (Fig.4.3a). On one hand these results indicate that, obviously, the number of attempts to find a territory increases the really occupied territories. On the other hand for a high rate of territory occupancy the number of attempts shows a lower impact. This

4 Structural diversity in arid savanna impacts the persistence of raptors

is due to the fact that for high densities of tawny eagles it is becoming harder and harder to find a spare territory – even with high effort, i.e. a high number of attempts (Fig.4.3a).

The persistence time T_m increases almost linearly with increasing number of attempts (Fig.4.3b). This suggests that tawny eagle persistence time increases when the birds are able to search through larger areas for a suitable breeding site. Even when the number of territories increases slower with a large number of attempts to establish a breeding site (Fig.4.3a) the persistence time is still increasing considerably (Fig.4.3b). This gives respect to the fact that persistence time is known to increase strongly with increasing carrying capacity (except for strong environmental noise; compare Burgman et al. 1993, for tawny eagles see chapter two).

The number of floater pairs given as percentage of the occupied territories decreases exponentially with increasing number of attempts to establish a breeding site (Fig.4.3c). When tawny eagles have more attempts available they consequently have a higher chance to find a territory and the number of floaters decreases. The increase in this chance is reduced (correspondingly the slope in Fig.4.3c is less steep) for a higher number of attempts when spare territories become very rare (compare Fig.4.3a).

As discussed above, the number of attempts to find a nesting tree impacts the results of the model (Fig.4.3). The limited features and time that tawny eagles have available for territory establishment would be hard to quantify in the field and one could argue that uncertainties about this parameter may bias model results. However, setting the number of attempts to find a nesting tree to be 15 reproduces field observations. Thus, assuming no limitation by vegetation structure (i.e. $P_v=1.0$), 15 attempts result in an average of 50 occupied territories for an established population as it is estimated from field data for the simulated area size (Fig.4.3a, Herholdt 1995, Herholdt et al. 1996) and as it is also assumed for the non-spatial model version (compare chapter two). Moreover, 15 attempts also results in a persistence time (T_m) in the range of the default parameter set of the non-spatial model version (Fig.4.3b, cf. chapter two). For these reasons I have confidence into the value of the parameter discussed here and I can claim to have put the best available knowledge into my model.

4.4.2 Limitation of Potential Nesting Trees (PNT)

In a first step, I analyzed the small-scale part of the model where vegetation structure yields available nesting trees. Here, I found the number of PNT to vary unimodal with increasing tree density (Fig.4.4, small enclosed plot). I am, however, not interested in the total number of nesting trees since only one nesting tree per territory is needed. Hence, in the large plot of Fig.4.3a shaded patterned areas indicate critical values where PNT falls below the threshold of one nesting tree per territory. I found that tree densities below 65 and above 15,300 trees per 25 km² ($=0.026$ and 6.12 trees per ha, respectively) lead to limitation in nesting trees for tawny eagles (Fig.4.4).

However, when not using the average number of PNT but the percentage of territories containing at least one PNT (applying Eq.4.1 and 4.2) this leads to slightly different results (Fig.4.5a). Applying Eq.(4.1) gives respect to the fact that only one pair is nesting within 25 km² and that territories with two or more nesting trees are of the same value as territories containing only one nesting tree. With this methodology I found the range where tree density does not limit nesting trees to be slightly smaller (Fig.4.5a) when compared to the use of average PNT (above, Fig.4.4). $P_v < 1.0$ indicates limitation of nesting trees and is reached for tree densities below 85 trees /25 km² and above 14,300 trees /25 km² ($=0.034$ and 5.72 trees / ha, respectively).

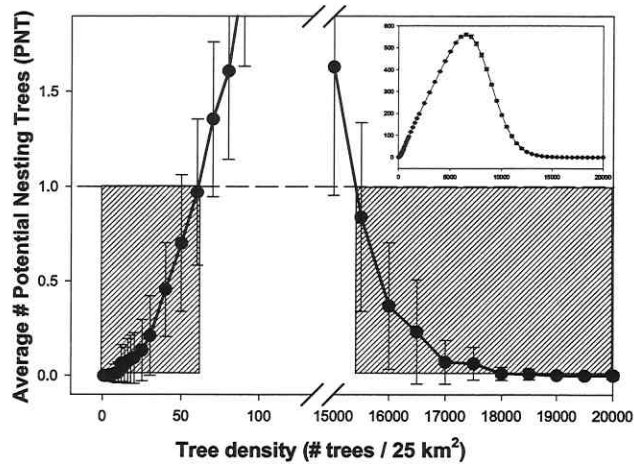


Figure 4.4: Potential nesting trees depend on tree density

Number of potential nesting trees (PNT, left axis) versus tree density (bottom axis) according to constraints of nesting tree vicinity and height (random tree distribution). Note the break in bottom axis. Average of 1,000 simulation repeats is shown and standard deviation is given by error bars. Dashed line indicates the critical PNT value, accordingly shaded areas indicate critical tree densities. Enclosed small plot shows same data with non-broken bottom axis.

4.4.3 Effects on persistence time

In a second step, I investigated how limitation in nesting trees affects the persistence time of tawny eagles (Fig.4.5b). When nesting trees are unlimited ($P_V=1.0$, cf. Fig.4.3b: 15 attempts) the model results in a persistence time T_m of 550 years yielding $T_S=1.0$. With decreasing P_V (probability to find a nesting tree) the standardized persistence time T_S decreases to 0.51 for $P_V = 0.4$ and down to 0.0 when no nesting trees are available ($P_V = 0.0$). Surprisingly, I found the slope of the T_S - P_V -relationship to be steeper when P_V falls below 0.4 (Fig.4.5b).

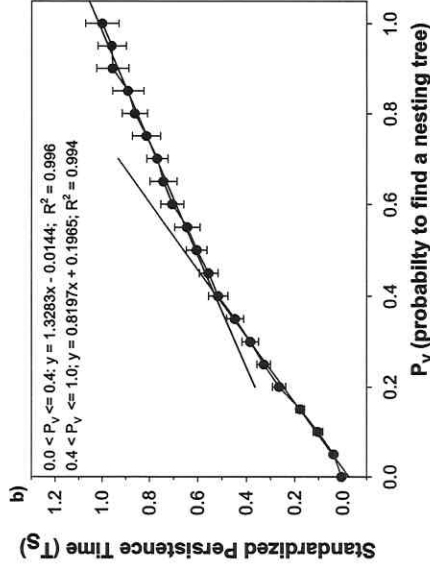
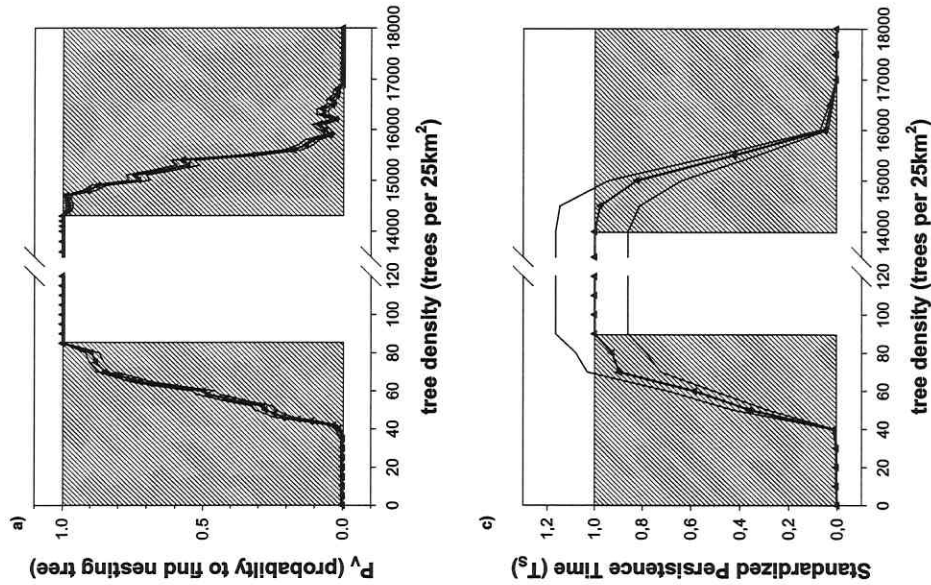
In a third step I combined small and large-scale results and found the persistence time T_S to vary unimodal with increasing tree density (Fig.4.5c). While for a broad range of tree densities T_S remained unaffected T_S was reduced for low (< 90 trees /25km²) and high ($>14,000$ trees /25km²) tree densities. These results indicate that tawny eagle persistence can be considerably impacted by tree density (Fig.4.5c).

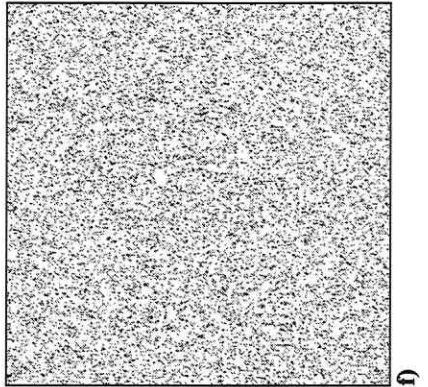
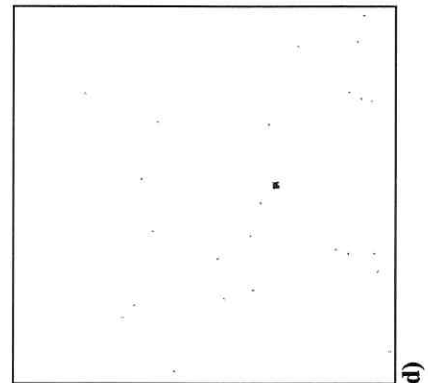
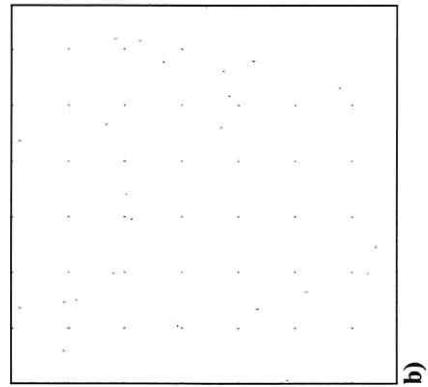
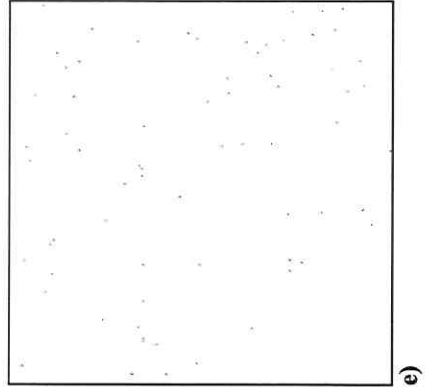
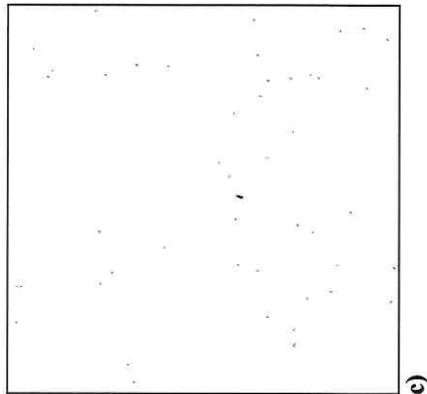
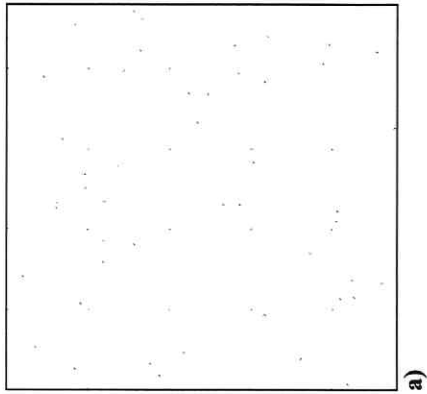
4.4.4 Scenarios of non-random tree distribution

Four non-random patterns of tree distribution were generated. Fig.4.6.1 gives examples of realizations of these patterns and the random pattern visualizing the tree distribution for two tree densities, which were found to be critical for tawny eagle persistence (cf. Fig.4.5c, Fig.4.8). Fig.4.6.1c and 4.6.1d emphasize that for aggregated patterns low tree densities result in only few tree clumps on one hand yielding large areas without any tree on the other. This changes for high tree densities in clumped patterns (Fig.4.6.1i, j). Fig.4.6.1h visualizes the limitation of open space that tawny eagles need for hunting when tree distribution is hyperdispersed.

Figure 4.5: Limitation of T_s by tree density

Model results for random tree distribution: **a)** Small scale results: Probability to find a nesting tree (P_V , left axis) versus tree density (bottom axis). Triangles show the results for 1,000 simulation repeats and hairlines give the 99% confidence interval. Shaded areas show critical tree densities, i.e. where P_V is limited by vegetation structure. **b)** Large scale results: Limitation of tawny eagle persistence time T_s (left axis) versus probability to find a nesting tree within 25 km² (P_V , bottom axis). The median for 100 repeats of calculating T_s (each of them based on 5,000 simulation repeats) is shown and error bars give the deviation from median. Regression is shown for $P_V < 0.4$ and $P_V > 0.4$, separately. **c)** Combining small and large scale results: Limitation of tawny eagle persistence time T_s (left axis) versus tree density (bottom axis) for a random distribution. The median is shown for 100 T_s computations (5,000 simulation repeats each) and thin lines indicate the interval within which 95% of the calculated T_s laid. Shaded areas show critical tree densities, i.e. where persistence time T_s is limited by vegetation structure. Note break in bottom axis of a) and c).





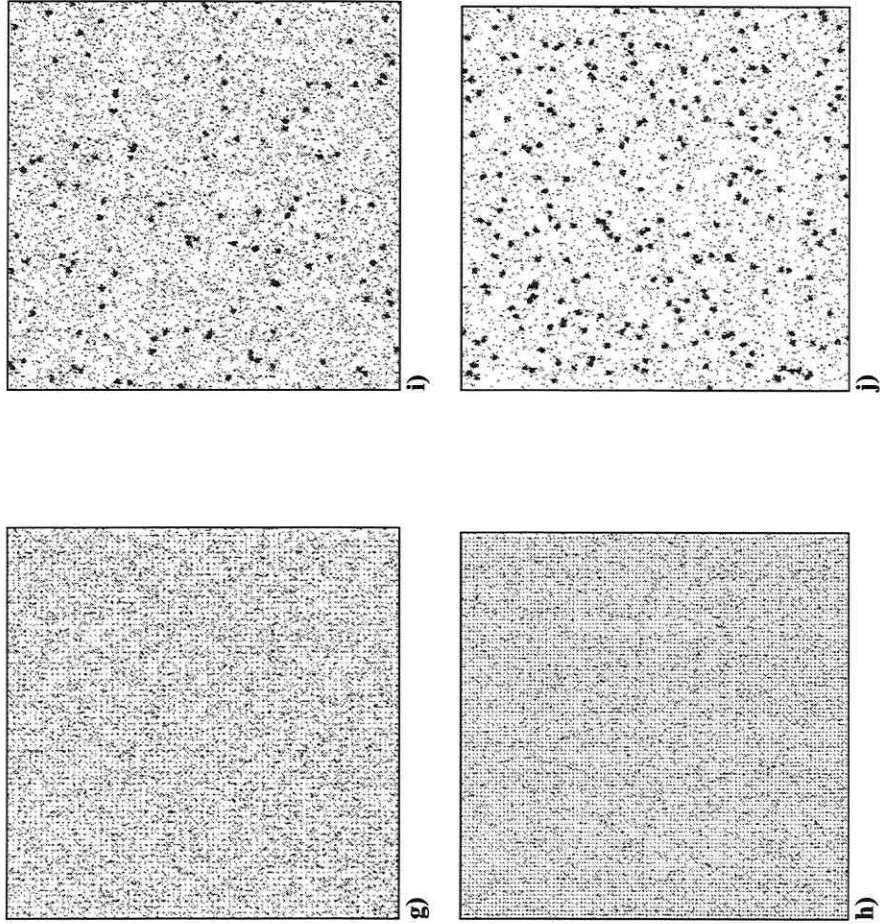


Figure 4.6: Analyzing patterns of varying tree distribution

(This page, previous page, following page.)
Description of vegetation pattern for the five
modes of tree distribution. Single simulation
realizations are exemplarily shown for one
lower and one upper critical tree density
derived from Fig.4.5c.

Fig.4.6.1 Visualization of vegetation patterns
(This page and previous page):

- a,g) 33% hyperdispersed;
- b,h) 66% hyperdispersed;
- c,i) 33% clumped;
- d,j) 66% clumped;
- e,f) random distribution.

Tree densities:

- a-e) 70 trees per 25km^2 ;
- f-j) 15,000 trees per 25km^2 .

Dark points indicate trees (enlarged by factor
five to improve contrast), bright symbolize
points matrix.

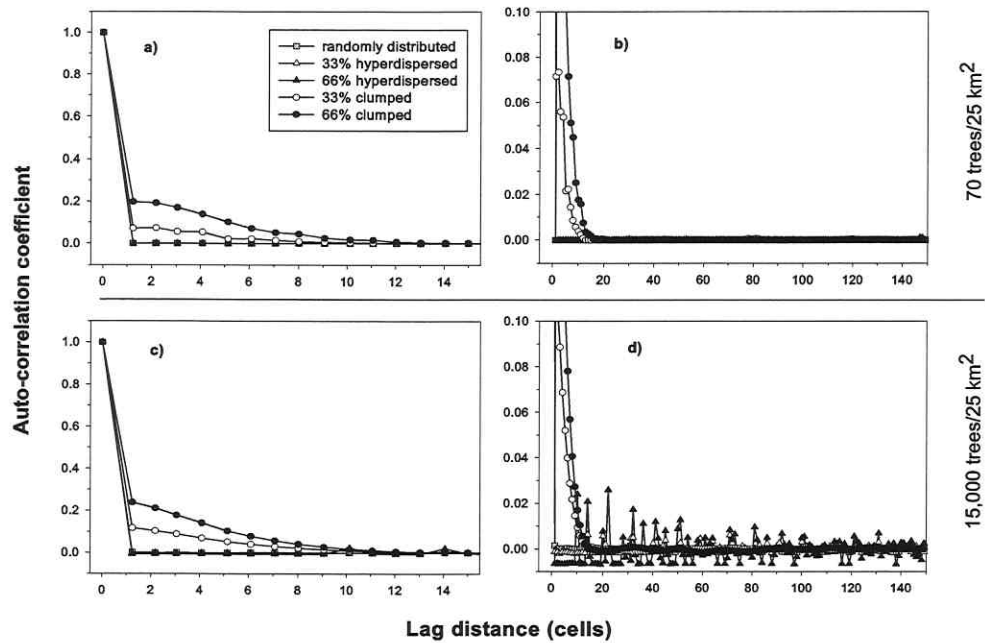


Fig.4.6.2 Correlogram for the various modes of tree distribution for 70 trees/25km² (a,b) and 15,000 trees/25km² (c,d), respectively. Lag distance is given as cell length (1 unit = 5 meter). Plots are shown for two different scales on both axes: for small lag distances yielding high auto-correlation (a,c) and for large lag distances yielding moderate auto-correlation (b,d). Symbol shape indicates distribution mode: hyperdispersed (triangles), clumped (circles), random (squares). Symbol color gives the percentage of trees distributed according to the given mode (remaining trees are distributed randomly): 33% (white), 66% (black), and 100% random (gray). Both clumped patterns clearly show positive auto-correlation at smaller lag distances (a,c) while the runs for hyperdispersed patterns are very similar to random patterns showing modest (d) or no (b) auto-correlation.

Fig.4.6.2 gives the spatial auto-correlation for the patterns shown in Fig.4.6.1. Both clumped patterns resulted in considerable (positive) auto-correlation at smaller lag distances (<10) for the two investigated tree densities (Fig.4.6.1a,c, also b,d). No auto-correlation could be detected at higher lag distances for clumped patterns. The hyperdispersed patterns show a much more modest effect. For the 66% hyperdispersed pattern for high tree densities auto-correlation can be recognized only on a high-resolution scale (Fig.4.6.1d). When assuming a very low fraction of randomly distributed trees yielding a high fraction of hyperdispersed trees (e.g. a 95% hyperdispersed pattern) this resulted in more considerable values for auto-correlation (not shown). However, I appraise those scenarios to be very artificially and did not include them in the study. The hyperdispersed patterns investigated here show slightly negative auto-correlation for most lag distances (i.e., evenly distribution, Fig.4.6.2d) but slightly positive auto-correlations for few certain lag distances yielding the well-defined distances between evenly distributed trees (e.g. Fig.4.6.2d: lag distances 14, 22, 131, the reader may also guess this from Fig.4.6.2b: lag distance 144). The random pattern, as

expected, shows no auto-correlation at all. However, of course all patterns showed auto-correlation values of 1.0 for lag distance 1 expressing that there are no differences when comparing the value of one grid cell with itself.

4.4.5 Model sensitivity to various distribution modes

In Fig.4.7 the number of PNT is plotted versus tree densities for all five scenarios of tree distribution (according to Fig.4.4). Although PNT are only limited below one (compare above) the whole range of PNT is shown in order to discuss the sensitivity of the model to the distribution mode of trees. Like the randomly distributed pattern, also all non-random patterns show unimodal curves.

In Fig.4.7 the 33% hyperdispersed pattern shows no recognizable deviation from the random pattern. The summit of the curve is reached for about 6,000 trees per 25 km² yielding 585 PNT. This suggests that 33% hyperdispersed trees are too few to show an effect (compare below). The 66 % hyperdispersed pattern, at first, follows the same increase as the random and the 33% hyperdispersed pattern indicating that tree density is limiting PNT in all three patterns (Fig.4.7). In contrast to the other patterns, the 66 % hyperdispersed pattern then continues increasing and the summit is reached for about 8,000 trees per 25 km² yielding about 680 PNT. This suggests that in this range of tree density hyperdispersion lays favorable foundations and the remaining trees added in random distribution have a good chance to provide PNT. Thereafter, however, the curve decreases rapidly suggesting that now hyperdispersion leads to a decrease of available PNT. This is due to the fact that the distance of evenly distributed trees now exceeded a threshold, i.e. 8,200 trees per 25 km². Now, evenly distributed trees are too dense and the remaining (i.e. randomly distributed) trees have very low chances to become a PNT. The curve drops down from PNT=680 to PNT=110 but thereafter continues decreasing moderately. The critical range of less than one PNT is reached with 13,000 trees per 25 km², i.e. for little lower tree densities than for the other distribution patterns. While 33 % hyperdispersion seems to be too low to show a recognizable effect 66 % hyperdispersion considerably impacts the PNT-tree density-relationship (Fig.4.7).

For 33 % clumped trees the curve increases with a smaller slope compared to the random pattern showing a lower summit at higher tree densities (9,000 trees per 25 km² and 435 PNT). Accordingly, also the decline is delayed and the upper critical density occurs at 21,000 trees per 25 km², i.e. at much higher densities as for the random pattern. These effects are even amplified for the 66% clumped pattern showing the summit at 14,000 /25km² trees with about 230 PNT (Fig.4.7) and the upper critical tree density at 34,000 trees /25km² (compare also Fig.4.8d). Clumping of trees harbors two effects: first, the trees in clumps grow too tight to act as PNT. In contrast, second, the remaining, i.e. randomly distributed, trees have a high chance to provide PNT. At first, both effects counteract. However, when clumps (!) increase in numbers the density among (!) clumps also increases, and now randomly distributed trees have lower chances to become a PNT. Then the two effects cooperate and cause the observed decline in PNT numbers (Fig.4.7).

In summary, I claim that the model is sensitive to the distribution mode of trees. While moderate hyperdispersion shows hardly any influence, strong hyperdispersion causes a threshold in tree density yielding a decline in PNT. In contrast to hyperdispersion, the aggregation of trees leads to an attenuation of maximum PNT corresponding with a shift towards higher tree densities.

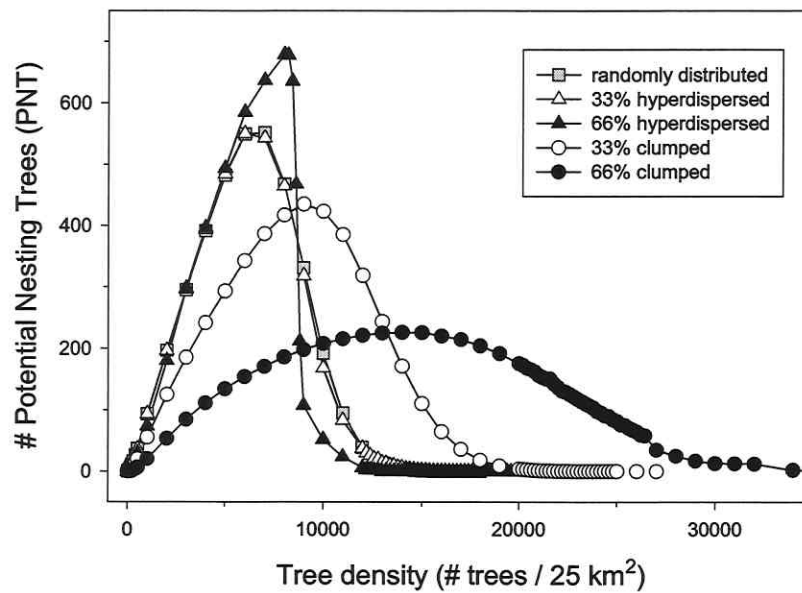


Figure 4.7: PNT for varying tree distribution

Small scale results for various tree distribution modes: number of PNT (left axis) versus tree density (bottom axis). Medians of 100 simulation repeats are shown. Symbol shape indicates distribution mode: hyperdispersed (triangles), clumped (circles), random (squares). Symbol color gives the percentage of trees distributed to the given mode (remaining trees are distributed randomly): 33% (white), 66% (black), and 100% random (gray).

4.4.6 Critical tree densities for various distribution scenarios

I then finally investigated the impact of tree distribution pattern on tawny eagle persistence, using P_V instead of PNT as pointed out earlier in this section and also treated in the discussion section. Fig.4.8 shows the lower and upper ranges of critical tree densities, i.e. where persistence time T_S for tawny eagles is reduced. For both hyperdispersed patterns I found no deviation from the random pattern in the ranges of lower and upper critical tree density (i.e., between 0 and 100 trees /25km², and between 14,000 and 16,000 /25km² trees, respectively, Fig.4.8a,b).

In contrast, for the clumped pattern, the response of P_V to tree density is delayed, i.e., here P_V reacts slower to increasing tree density. For clumped patterns lower critical tree densities cover a range between 0 and 150 trees /25km² (33% clumped), and between 0 and 300 trees /25km² (66% clumped), respectively (Fig.4.8c). Upper critical tree densities are between 20,000 and 24,000 trees /25km² for the 33% clumped pattern and between 34,000 and 40,000 trees /25km² for the 66% clumped pattern, i.e. much higher than for the random pattern. Thus, the 66% clumped pattern shows the most severe effect among scenarios of non-random distribution.

4.5 DISCUSSION

In this study I investigated the impacts of structural diversity in space on the persistence of the tawny eagle population in the southern Kalahari arid savanna. I found that structural diversity can limit the persistence of tawny eagles for very low or very high tree densities. Moreover, the persistence time of tawny eagles also depends on the pattern of tree distribution (clumped, random, hyperdispersed). In the following these effects are discussed in detail. Considering the current land use practice, I carefully conclude what the results of this study might suggest for the Kalahari tawny eagle population in future. Finally, I discuss potential impacts of structural diversity on population persistence and species diversity.

4.5.1 Spatial mechanisms influencing the survival of tawny eagles

Small spatial scale (vegetation structure)

With increasing tree density I found a unimodal trend for the average number of potential nesting trees (PNT, Fig.4.4), as well as for the probability to find a suitable nesting tree within an area of 25 km² (P_V , Fig.4.5a) and for all investigated patterns of tree distribution mode (Fig.4.7). From these results I conclude that first, tree density impacts the availability of nesting trees and second, that tree density can be too low *or* too high, i.e. that only intermediate tree densities sufficiently yield nesting trees for tawny eagles. This suggests that both, factors increasing tree density, as well as factors decreasing tree density may limit the available nesting trees.

When using the probability P_V I found slightly larger critical ranges of tree density (Fig.4.5a) as compared to the usage of the average number of PNT (Fig.4.4). I here emphasize the preference of P_V , since this parameter gives respect to the evident fact that only one nesting tree per territory is needed (Eq.4.1). This also points out, that the threshold in tree density for 66% hyperdispersion yielding a sudden decrease in PNT (Fig.4.7) is biologically redundant, since the probability to find a nesting tree P_V remains 1.0 and thus the threshold does not limit breeding sites.

I critically revised the rules and the field database for the model on the small spatial scale. One could criticize that the field data by Herholdt et al. (1996) that were used to develop the model rules are based on extensive field observations but lack of experiments. An experimental study on the characteristics of nesting trees for raptors would however need an extremely monumental - probably impossible - effort and I here suggest using the available data set. A second point of criticism considering my model could be the lack of temporal dynamics in tree distribution. As long as tree density and distribution pattern remain more or less constant temporal dynamics will not impact tawny eagle persistence. However, when these parameter changes over time, the same population will face different environments at different time points what might influence the resulting persistence time. For this reason, I intend to investigate these effects in a further study using records of temporal tree dynamics under various scenarios of human impact produced by a model of Kalahari vegetation dynamics (Jeltsch et al. 1996, 1997a, 1998). As a third point of criticism, the model is accounting tree height only implicitly but not in direct combination with spatial rules (Eq.4.2). Again, I here used the best available data set. Also note, that model rules on small spatial scale take tree height and surrounding vegetation into account but that further parameters (e.g. geomorphologic structures) might play a role bearing the potential to further reduce PNT and P_V .

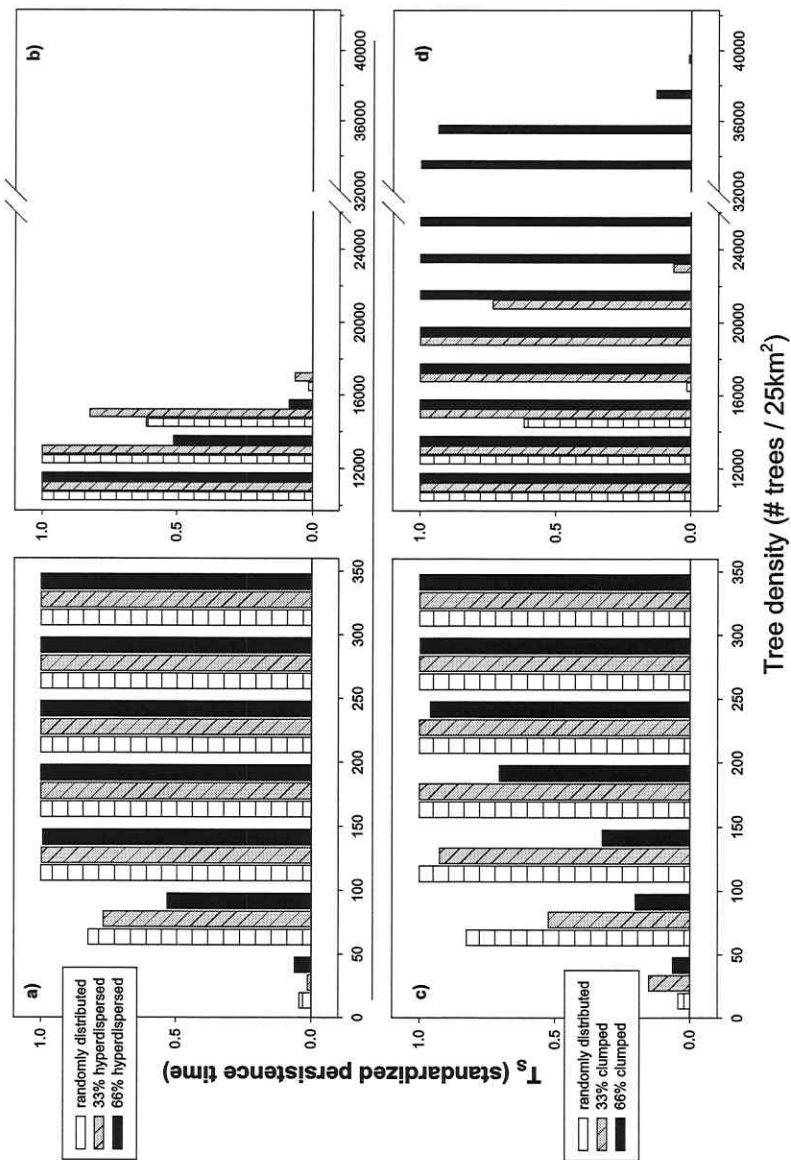


Figure 4.8: Impact of tree distribution on T_s

Persistence time of tawny eagles T_s (left axis) versus tree density (bottom axis). Critical ranges (i.e. $T_s < 1.0$) are shown for low (a, c) and high (b, d) tree densities. Hyperdispersed pattern (a, b) and clumped pattern (c, d) are compared with random distribution. Bar color and pattern gives the percentage of trees distributed to the given mode: 33% (gray, diagonal), 66% (black, no pattern), and completely random (white, horizontal). The average T_s is given for ranges of tree densities separated by lag 50 (a, c; low densities) and by lag 2,000 (b, d; high densities). Note the break in bottom axis for high tree densities (b, d).

Large spatial scale (territoriality)

The persistence time of tawny eagles T_S is reduced when available nesting trees are limited ($P_V < 1.0$, Fig.4.5b). These results emphasize the need of nesting trees that are essential for territory establishment and successful breeding. As a consequence of limitation in nesting trees, breeding sites are limited the carrying capacity (i.e., the number of territories) is reduced yielding lower persistence times.

My results indicate linear increases concerning the T_S - P_V -relationship (Fig.4.5b) but I found a reduced slope when P_V exceeds approximately 0.4. This is surprising since there is no evident explanation for this change. However, instead of two linear relationships (Fig.4.5b) also a sigmoid curve might fit the regression. One possible explanation might be that when the environment (i.e. vegetation structure) turns more favorable the population becomes denser, competition increases and density regulation is limiting the population more severe (rules on large spatial scale). This yields a slower increase of persistence time with increasing probability to find a nesting tree P_V .

4.5.2 Critical tree densities for survival of tawny eagles

For the persistence of tawny eagles I found one lower and one upper critical tree density were T_S is reduced when compared to intermediate ranges of tree density (Fig.4.5c). As already shown the reduction in T_S is due to a limitation in nesting trees (Fig.4.5b) that in turn results from a modified tree density (Fig.4.5a). These results suggest that vegetation structure, i.e. structural diversity in space, can indeed limit the persistence time of tawny eagles and other raptors in arid areas.

When considering various patterns of tree distribution, for hyperdispersed patterns I found no deviations in critical tree densities when compared to complete random patterns (Fig.4.8a,b). This coincides with the results found with spatial auto-correlation analysis: no (lower critical densities, Fig.4.6.2 a,b) or only slight (higher critical densities, Fig.4.6.2 c,d) deviations when comparing hyperdispersed and random patterns. Auto-correlation analysis of hyperdispersed patterns (Fig.4.6.2) suggests indeed that evenly distributing 66% of all trees produces only moderate hyperdispersion. One could argue that I should additionally investigate scenarios with a higher fraction of hyperdispersed trees and, indeed, I considered scenarios of 95% and 100% hyperdispersed trees. However, such scenarios of (nearly) complete hyperdispersion of the available trees seem fairly unrealistic to me and thus, those are not included into this study.

Nevertheless, my results indicate that the investigated hyperdispersed patterns are unlikely to produce a tree distribution too sparse for model rules, i.e. they resulted in at least one tree in a 150 meters neighborhood (compare rules on small spatial scale). This is due to the fact that every randomly distributed tree potentially can break off the hyperdispersed pattern providing the one PNT that is needed within a territory. This maintains $T_S=1.0$ avoiding an upward shift of the lower critical tree densities for the 33 and 66% hyperdispersed patterns. When the amount of randomly distributed trees approaches 0, i.e. 100% hyperdispersion, indeed, the model indicated an upward shift of the lower critical tree density (not shown). These considerations clarify that tawny eagle persistence T_S for hyperdispersed pattern is controlled rather by the presence (and the “right placement”) of randomly distributed trees than by hyperdispersion itself.

In contrast to hyperdispersed patterns, for the 33% clumped pattern, I found the lower critical density to be slightly higher and the upper critical densities to be considerably higher when compared to random patterns. This effect is even amplified for the 66% clumped pattern

(Fig.4.8c,d). These results coincide with increasing auto-correlation coefficients for increasing amounts of clumped trees (Fig.4.6.2a,c). For constant tree densities clumping results in clumped trees on one hand but patches without trees on the other. The latter is (locally) providing more space and consequently the limitation of tawny eagles persistence due to dense standing trees is shifted towards higher tree densities.

4.5.3 Natural tree distribution and tawny eagles

The natural tree density in the southern Kalahari is about 2 trees/ha (5,000 trees/25km², e.g. (Bothma et al. 1992, Jeltsch et al. 1996, 1997a). For tawny eagles persistence the lower critical range of tree density as found in this study (0.06 - 0.12 tree/ha = 150 - 300 trees/25km²) lies far below this value while the upper critical range (5.6 - 13.6 trees/ha = 14,000 - 34,000 trees/25km²) lies considerably above. The conclusion is that tree spacing in the southern Kalahari fits well to the demands of the tawny eagle what is supported by observation of this species in the area for a long time (Steyn 1983, Liversidge 1994, Herholdt et al. 1996, Herremans et Herremans-Tonnoeyr 2000). In other savanna regions, where tree density is higher (e.g. Kimberley region), trees tend to be clumped (field data: Schurr 2001, model results: Jeltsch et al. 1998, 1999) and the critical range is shifted upwards (Fig.4.8). Thus, there is no disagreement of my results with observations of tawny eagles in areas of higher tree density (Osborne 1982a, Steyn 1983, Tarboton et Allan 1984). Human impacts in the area, however, modify the vegetation structure and thus ranges of critical tree densities might be reached in present or future as discussed in the following.

4.5.4 Current land use practice, structural diversity and tawny eagles

As pointed out by earlier studies past and current land use practices like cattle farming and wood cutting considerably impact arid savanna vegetation structure in the Kalahari (compare introduction and section on "study area", (Tietema et al. 1991, Tainton et Walker 1992, Jeltsch et al. 1996, 1997a, 1999, 2000, Weber et al. 1998, 2000, Anderson et Anderson 2001, Milton et al. 2001, BIOTA AFRICA Project 2002). In this study I found, both, processes decreasing tree density (e.g. woodcutting), as well as processes increasing tree density (e.g. overgrazing) can control population persistence of tawny eagles (Fig.4.5c, Fig.4.8). Combining these results, I conclude that the mentioned land use practices may potentially affect tawny eagle persistence in the southern Kalahari. The more interesting question now is, whether the modifications caused by land use also show the quantity to lead to noticeable changes in tawny eagle persistence.

Effects of overgrazing

Heavy grazing leads to dramatic increase in woody vegetation on longer time scales (e.g. Tainton et Walker 1992). The results of a modeling study by et al. (1997a) gives quantitative implications for the increases in woody density - including shrubs - under increased grazing pressure. However, the term "woody density" (Jeltsch et al. 1997a) should not be confused with tree density (Herholdt et al. 1996, this study) and thus I cannot derive a quantitative estimation. An essential issue for solving the problem seems to be a distinct morphological separation between trees and shrubs. Defining trees as individuals of *Acacia* species being older than 10 years the model by Jeltsch et al. (1997a, 1998) found an increase from 2 to 10 trees per ha (5,000 to 25,000 trees/25km², respectively) over 500 years for a scenario of heavy grazing (F.Jeltsch, unpublished data). For randomly distributed patterns this exceeds the upper critical tree density (gray bars in Fig.4.5c, Fig.4.8b,d) suggesting a limitation of tawny eagle persistence T_s by vegetation structure. This implication, however, changes when taking into account that an increase in tree density coincides with clumping (see above: Jeltsch et al.

4 Structural diversity in arid savanna impacts the persistence of raptors

1997a, 1998, Schurr 2001). When assuming a 33% clumped pattern for elevated tree densities due to overgrazing (25,000 trees/km²) my results suggest extinction of tawny eagles as for the random pattern (white bars Fig.4.8d). In contrast, for a 66% clumped pattern I could conclude no limitation of T_s by the effects of cattle grazing on vegetation structure (Fig.4.8d, black bars) as long as sufficient randomly distributed trees are available. These uncertain implications seem somewhat unsatisfying and I therefore plan to investigate the effects of overgrazing on tawny eagle persistence by linking a model of vegetation dynamics (Jeltsch et al. 1997a, 1998) and the model of tawny eagle population dynamics (this study).

Effects of woodcutting

In contrast to overgrazing, woodcutting is reducing the tree density (Tietema et al. 1991, Anderson et Anderson 2001, Milton et al. 2001, BIOTA AFRICA Project 2002) driving it towards the lower critical tree density (Fig.4.5c, Fig.4.8a,c). While the initial intention of wood clearing was to increase grazing potential and the wood was solely collected for domestic use, recently, the commercial sale of firewood emerged (Milton et al. 2001). The first intention targets on open space resulting in complete clearing but maybe omitting solitary, large trees. In contrast, the latter intention targets on high wood biomass that might result in a preference for removing large trees. Also note, that if woodcutting is not continued it is followed by re-growth of “bushy” trees. Under these conditions of specific but different treatment of large trees, i.e. potential nesting trees, obviously, tree density is not a proper measurement anymore and it seems not reasonable to give a quantitative estimation using the present results. Instead, as already claimed for the effects of overgrazing, here, the use of an spatially explicit output of a vegetation model including tree age and height (Jeltsch et al. 1997a) as an input parameter into this model of tawny eagle population dynamics is previewed. This may lead to deeper insights and may give quantitative answers to the question discussed here.

Combining results for overgrazing and woodcutting:

Although the effects of overgrazing and woodcutting may balance out the woody biomass, both practices favor bushy growth forms and potentially reduce the number of large, solitary trees. Thus, they reduce the available nesting trees for tawny eagles (compare Fig.4.5a), i.e. the key stone structures of the whole ecosystem (Milton et Dean 1995) leading to an increase in the extinction risk of tawny eagles (Fig.4.5b). For this reason, in my opinion the impacts of overgrazing and woodcutting on tawny eagles persistence cannot balance out when applying both practices at the same time. This implies that nature conservation should focus on controlling both of the discussed land use practices.

4.5.5 The potential impact of structural diversity on species survival

How does structural diversity change among the scenarios of tree density and distribution mode? This is not an easy question to answer since a currency for structural diversity is hard to define. Unlike structural diversity, studies on species diversity developed convenient and simple measurements, e.g. the number of species per area (e.g. Houston 1994, Rosenzweig 1995). For structural diversity, first, one has to define the structures that contribute to this type of diversity on certain scales, i.e. trees in the case of this study. However, the number of structures per area does not provide a satisfying measurement for structural diversity as shown by my investigations for various tree distribution modes (Fig.4.8). I suggest, that finding a measurement for spatial structural diversity should be the focus of a further study.

Starting a broader literature search I found earlier studies that stress the importance of spatio-structural characteristics on the performance of raptors and other species. For example,

Herremans et Herremans-Tonnnoeyr (2000) claim the “poor status of raptors on unprotected land” to be a consequence of the “widespread depletion of biomass and biodiversity following structural changes in vegetation” in Botswana. Thiollay (2001) found “habitat modification due to rapidly increasing human pressure to explain most changes” for raptor populations in northern Cameroon. The long term breeding success of Red-tailed Hawks (*Buteo jamaicensis*) was primarily correlated with the density and dispersion of perches in north-central Oregon, U.S.A (Janes 1984). Immature imperial eagles (*Aquila adalberti*) preferred to establish territories on sites with pasture or cultivated farmland covered by scattered oaks but avoided irrigated fields and paved roads (Ferrer et Harte 1997). Also beyond raptors other studies found a dependence on trees as structural elements (e.g. skinks: Cooper et Whiting 2000, birds in general: Dean et al. 1999) or the preference of certain habitats (e.g. wallabies: Fisher 2000, birds: Rotenberry et Wiens 1980).

These are only few examples where studies found an influence of elements of structural diversity without, however, using this term. Nevertheless, the present study is in accordance with these earlier studies. The present study explicitly reveals that structural diversity in space has the potential to impact the population persistence and survival of a certain species, the tawny eagle in the southern Kalahari. Moreover, for other raptor species in the Kalahari similar observations on breeding habitats were made (e.g. martial eagle (*Polemaetus bellicosus*) and bateleur (*Terathopius ecaudatus*), (Brown et al. 1982, Herholdt et Kemp 1997, Herholdt 1995) as those used in this study for the tawny eagle. This leads to the conclusion that beyond the tawny eagle structural diversity can also impact the persistence of other raptor species in arid savanna.

4.5.6 Conclusions

In this chapter I presented a case study on the influence of structural diversity on the persistence of the tawny eagle in the southern Kalahari arid savanna and I found a considerable impact on population's extinction risk. First, combining the results of this study with earlier studies leads to the implication that structural diversity impacts species diversity, i.e. a linkage between two forms of biodiversity. Moreover, beyond single species, this can lead to a general understanding of the functional impacts of spatio-structural characteristics on population persistence and species diversity. Accordingly, I call for conducting similar studies on species of other guilds and in other ecosystems. Second, this study contributes to the growing evidence that structural diversity is underestimated in the biodiversity debate. I suggest that the focus of research in biodiversity should move from species diversity towards structural and functional diversity.

4.6 LINK TO THE PROCEEDING CHAPTER

In this chapter (four), I presented a spatial version of the AQUQUA model. I investigated the impacts of a varying vegetation structure referring to tree density and tree distribution pattern. Aspects of territorial behavior were also studied. In combination with chapter two, which investigates the impact of precipitation patterns, this chapter (four) presents one main focus of this thesis, i.e. the impacts of changed environmental conditions on the persistence time of the tawny eagle population in the Kalahari. Moreover, chapter three suggests a new way to tackle the breeding success-precipitation relationship in raptors. Thus, the first three chapters (two, three and four) form the applied part of this thesis, studying the population dynamics in a particular case, i.e. raptors in the Kalahari arid savanna. Moreover, the AQUQUA model produced novel results within a general context of population biology generating a second focus of this thesis. In the following two chapters I approach general phenomena in theoretical

4 Structural diversity in arid savanna impacts the persistence of raptors

population biology. In particular, in the next chapter (five) I use the AQUQUA model to illustrate that, in periodically fluctuating environments, the extinction risk changes considerably from what is currently known. These results will contribute new insights to our general knowledge of population dynamics and extinction risk.

5 Extinction risk in periodically fluctuating environments⁴

5.1 ABSTRACT

Periodically fluctuating environments occur in various ways in nature but have, however, not yet been studied in detail in the context of the color of environmental noise and extinction risk of populations. I use a stochastic model to simulate population dynamics with compensatory density regulation under four different patterns of periodically fluctuating environments. I found that extinction risk changed dramatically from what was known if the underlying environmental stochasticity driving population dynamics is periodically correlated rather than randomly correlated. Fluctuating environments with a very short period are found to decrease extinction risk over "white noise" fluctuations because a species is never in a bad environment for too long. Conversely, long periods increase extinction risk because species accumulate too much time in a bad environment. Moreover, I found the mean, variance, frequency distribution and especially the extensively studied noise color not to be sufficient for predicting extinction risk in periodically fluctuating environments. Rather, additional attributes of environmental noise have to be considered. Furthermore, the guise of monotonic trends within time series of environmental data (e.g. after 'disturbance' events), in combination with density regulation, may also affect extinction risk. My study exemplifies that the investigation of periodically fluctuating environments lead to new insights into the interaction between environmental variation, population dynamics and the resultant extinction risk.

5.2 INTRODUCTION

Environmental variation in its various guises is very important in determining population dynamics and the extinction risk of populations (Lande 1993, Foley 1994, Ripa et Lundberg 1996, Johst et Wissel 1997, Petchey 2000). Attributes of environmental conditions include the mean of time series data, the variance (i.e., magnitude of variation) and the noise color. Noise color refers to the temporal correlation in time-series data and is expressed either as the degree of (first-order) auto-correlation for auto-regressive noise (e.g. Foley 1994, Ripa et Lundberg 1996, Johst et Wissel 1997) or as the spectral exponent β for $1/f^\beta$ noise (Halley et Kunin 1999). Early investigations used white noise, which assumes temporally non-correlated environmental fluctuations, to characterize environmental variation (Lande 1993 and references therein). However, several studies have revealed that the environmental noise found in nature is not always white but often reddened, implying positive temporal correlation in the environmental fluctuations (Steele 1985, Pimm et Redfearn 1988).

A number of recent studies have focused on the impact of noise color on population dynamics and extinction risk, and complex relationships have been found between noise color, underlying dynamics and extinction risk (Ripa et Lundberg 1996, Johst et Wissel 1997, Petchey et al. 1997, Kaitala et al. 1997a,b, Heino 1998, Halley et Kunin 1999, Cuddington et Yodzis 1999, Ripa et Heino 1999, Ripa et Lundberg 2000). Modifications of noise color have also been seen in response to biological filter processes (Laakso et al. 2001). All these studies emphasized the importance of considering noise color, and thus auto-correlation, in investigations on population dynamics and extinction risk. Such auto-correlation also arises in periodically fluctuating environments.

⁴ This chapter was accepted for publication in *Ecological Modelling* as:
Wichmann MC, Johst K, Moloney KA, Wissel C, Jeltsch F: Extinction risk in periodically fluctuating environments.

5 Extinction risk in periodically fluctuating environments

Periodically fluctuating environments appear naturally in all seasonal parameters (Kot et Schaffer 1984, Li 1992), such as temperature, precipitation or the amount of vegetation cover. We can assume that although the population dynamics of species is well adapted to seasonal variation, it might not be adapted to non-seasonal variation. Examples of non-seasonal periodic variation include (1) the removal of vegetation by large, migrating herbivores and subsequent recovery (buffalos in prairie systems or elephants in savanna, Caughley 1976), (2) the absence of winter flooding in Central Europe every few years (Brandenburg Department of Waterways [Wasserstraßenamt Brandenburg], unpublished data), (3) alternating decades with low and high precipitation in southern Africa (Tyson 1987), (4) cyclic and vertical currencies in water that transport algae in regions of high and low light availability (i.e. close to vs. far below surface, Huisman 1999), and (5) school terms (periods of school attendance preceded and followed by holidays – cog-pattern) in relation to the outbreak of measles (Grenfell et al. 2001). These examples show the importance of investigating periodic fluctuations as a particular case of environmental noise.

Note that periodically fluctuating environments might instead be referred to as non-random “forcing” rather than (more or less) random “noise”. However, periodically fluctuating environments in this study underlie random influences since they are generated by re-ordering data of real time series. Thus, like “colored noise”, periodically fluctuating environments consist of temporally correlated random numbers. Though, the question of nomenclature seems to be a minor issue and I here keep using the term “environmental noise”.

In this study I assume that environmental variation is periodic since, to my knowledge, periodically fluctuating environments have not yet been studied in detail in connection with noise color and extinction risk. I present a case study to show that in periodically fluctuating environments, attributes of environmental variation other than noise color and magnitude may affect the extinction risk of populations. Thus, my example reveals that the current theoretical knowledge cannot explain extinction risk in periodically fluctuating environments.

5.3 METHODS

5.3.1 Model description

For my investigations I used an existing simulation model named AQUQUA. This model was developed to investigate the impact of climate change on extinction risk of *Aquila rapax* Temminck (tawny eagle) in southern Africa. AQUQUA includes annual precipitation as temporally explicit environmental noise. I assume that average mortality is constant, but that breeding success, i.e. the average birth rate, is impacted by precipitation yielding a positive linear relationship between the amount of rainfall and the number of juveniles leaving the nest. (For more examples see Post et al. 1999, Moss et al. 2001.) The upward bound (carrying capacity) for population density is set by a constant number of available breeding territories (contest competition). In the absence of environmental (and demographic) noise, density regulation causes the population to reach equilibrium, i.e. the carrying capacity. AQUQUA is an individual-oriented model and keeps track all processes such as birth, aging, reproduction and mortality separately for each individual within the population (Uchmanski et Grimm 1996). This allows me to include demographic noise (i.e. stochasticity) on an individual level for any of the demographic processes. For further description of the model see chapter two.

In the model I measure the *Mean Time to Extinction* (T_m), which is the average time span that simulated populations survive model runs (Wissel et al. 1994, Stelter et al. 1997). As I am not specifically interested in giving an absolute extinction risk but rather in comparing results in periodically and non-periodically environments, I will convert all the results to a *Standardized*

Persistence Time (T_s). T_s is given as the ratio of the corresponding T_m divided by the default T_m obtained using non-periodic white noise. Furthermore, I also measured the intensity of density regulation as the average number of *floaters* (cf. Hunt 1998) occurring per time step yielding the breeding pairs that did not own a territory and, consequently, could not reproduce. This parameter is given as percentage of the carrying capacity. In my model the carrying capacity limits the number of territories and consequently the number of individuals that can reproduce. Thus, the percentage of floater pairs indicates how severe the carrying capacity prevents further growth of the population what I here call the intensity of density regulation.

Although I use AQUQUA to perform a case study examining how population dynamics behaves under periodically fluctuating environments, my results might be of general validity, at least for populations with fluctuating birth rates and contest competition.

5.3.2 Scenarios of environmental noise

A southern African rain model by Zucchini et al. (1992) based on records over the past century was used to produce statistically realistic scenarios of environmental variation in precipitation. The Zucchini model generates non-auto-correlated data and is used to study the impact of white noise on extinction risk. Modifying these data, I then generated non-periodic scenarios of various noise color and investigated their impact on extinction risk according to Ripa et Lundberg (1996). In order to rescale variances in the generated time series of auto-correlation (Heino et al. 2000) an alternative and newly developed method was applied that is presented and discussed in detail in chapter six.

In addition to the non-periodic scenarios of various noise colors I generated four distinct patterns of periodically fluctuating environments (Fig.5.1). For this purpose, data generated by the Zucchini model were re-arranged in four different ways keeping the mean value and variance constant. I subdivided the entire time series of a rainfall scenario into periods of constant length. Within each period I retained the data values but re-arranged their temporal order. For each of the four patterns of periodically fluctuating environments I varied the lengths of periods, ranging from 1 to 400. In detail for any of the four patterns I investigated scenarios of period lengths of 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 14, 16, 18, 20, 25, 30, 40, 50, 60, 70, 80, 90, 100, 120, 140, 150, 160, 180, 200, 250, 300, 350 and 400. The schematic view of the four periodic patterns given in Fig.5.1 is an idealistic view. I modified scenarios in a way that they followed these idealistic patterns as close as possible. However, due to variation in data the resulting real pattern were always slightly different and also periods in the same scenario were not exactly constant.

I generated a *saw-tooth pattern* including continuous increases and decreases (Fig.5.1a) and a *descending pattern* of continuous decreases but sudden increases (Fig.5.1b). The *ascending pattern* is opposite to the descending pattern with continuous increases but sudden decreases (Fig.5.1c). I created the *cog-pattern* with sudden increases and decreases (Fig.5.1d) by first producing the descending pattern as described above. Second, I divided periods further into two parts, the first part containing data above the time series mean but the second part containing data below the time series mean. Data within both parts were averaged and replaced by their mean values and thus, in contrast to the other patterns, the cog-pattern differs in data values. As the variance was affected when generating the cog-pattern, I again modified data, keeping all attributes constant but adapting the variance to its original value.

Comparing the four periodic patterns, the mean and variance were kept constant but auto-correlation varied among patterns and period lengths. In addition, the cog-pattern differed from the other three in the frequency distribution of values. As the saw-tooth, the descending

5 Extinction risk in periodically fluctuating environments

and the ascending pattern all contained the same data (albeit in different order), data values showed the same frequency distribution that is close to a bell-shape and given by the Zucchini model. Although the cog-pattern has the same mean and variance as the other three patterns, the frequency distribution of time series data is different, i.e. two-peaked. However, I do not know the impact of deviations in the frequency distribution of the cog-pattern since this attribute of time series is not yet investigated in the context of extinction risk. Thus, I can only keep in mind that the cog-pattern is special and one should be careful when comparing it to the other three patterns.

In order to quantify the extinction risk under a given set of parameters I calculated T_S from the results of 5,000 simulation repeats. Simulations were conducted under the same demographic and environmental parameters but stochasticity was included. Demographic stochasticity is realized by random numbers that are compared with a fixed rate (parameter). Environmental stochasticity is based on the fact that time series differ in single data values even when descriptive attributes (including period length) are constant.

Note, that for each simulation repeat I randomly chose the starting point within the first period of the corresponding environmental time series. This practice avoids any bias by favorable or unfavorable conditions at simulation start. I use the term *favorable conditions* to mean environments temporarily resulting in high birth rates and increasing individual numbers. In contrast, *unfavorable conditions* produce temporarily low birth rates and decreasing population size.

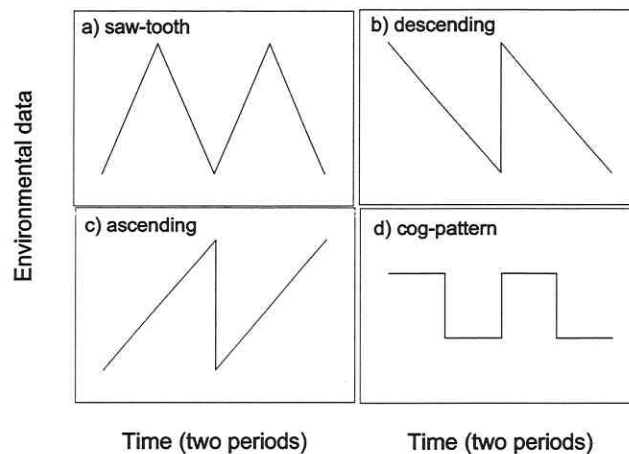


Figure 5.1: Patterns of periodicity

Schematic view of the four patterns of periodically fluctuating environments used in the simulation experiments. The temporal order of data in time series produced by the Zucchini model (Zucchini 1992) was re-arranged in accordance to the patterns shown in this figure. See text for further description.

5.3.3 Noise color analyses

To classify and compare the different patterns of periodically fluctuating environments I measured noise color as the auto-regressive noise of the order k , where k is the temporal distance between data points. The auto-correlation AC_k is calculated using the formula (e.g. Chatfield 1984)

$$AC_k = \frac{c_k}{c_0} \quad [\text{Equation 5.1}]$$

where

$$c_k = \frac{1}{N} \sum_{t=1}^{N-k} (x_t - \bar{x})(x_{t+k} - \bar{x}) \quad [\text{Equation 5.2}]$$

and c_0 is given by c_k for $k=0$. N is the total number of data in the rain scenario, x_t is the particular data value at time t and \bar{x} is the average. I calculated auto-correlation versus k , varying from 1 to 350 for every period length and any pattern. Thus I am able to compare both the first order auto-correlation (AC_1 , $k=1$) and the complete auto-correlation function ($k=[1..350]$) of environmental noise for the scenarios of periodic environment. Since I consider periodic auto-correlation functions, they cannot be equivalently described by $1/f^b$ noise (Halley et Kunin 1999, Cuddington et Yodzis 1999).

5.4 RESULTS

5.4.1 Standardized Persistence Time (T_s)

Using the default set of white environmental noise I obtained a T_m of 735 time steps (i.e., 735 years in the case of tawny eagles). Thus, I consider the model population not to be threatened by extinction in the near future. However, the quantitative and qualitative estimation of extinction risk might change if modifications in the environment lead to deviations in persistence time. Following my definition, T_s for white noise equals 1.0.

Fig.5.2 shows the influence of periodically fluctuating environments on T_s . For all four periodically fluctuating patterns I found a general trend of decreasing persistence times with increasing period length. At very short period lengths, however, there was a slight but definite increase in T_s over period lengths from 1 to 5, again for all four patterns (Spearman rank order correlation; saw-tooth pattern: $r_s = 0.98$, ascending and descending pattern: $r_s=0.8$, cog-pattern: $r_s= 0.9$). Note that for any pattern of periodically fluctuating environment a period length of 1 equals white noise and consequently T_s is 1.0.

When comparing different patterns of periodically fluctuating environment, the saw-tooth pattern always produced T_s values below the other patterns (Fig.5.2). When comparing the descending and ascending pattern, I obtained equal results for period lengths up to 50 time steps. Surprisingly, (albeit dynamic starting conditions compare methods), I found definite longer persistence times for the descending pattern compared to the ascending pattern when period lengths were longer than 50 time steps (Fig.5.4a). The cog-pattern showed the highest T_s values for period lengths up to 140, but dropped below the descending pattern for longer period lengths (Fig.5.2).

5.4.2 Auto-correlation

A general trend for the dependence of first order auto-correlation (AC_1) on period lengths was found for all four scenarios (no figure). In accordance with the properties of white noise I

found an AC_1 coefficient of 0.00 for a period length of 1. For period length 2 AC_1 was slightly negative. Then, for period lengths larger than 2 AC_1 increased steadily and soon approached 1.00. The saw-tooth pattern showed higher AC_1 at the same period length than all the other patterns. AC_1 was intermediate for the cog-pattern but was smallest for the descending and ascending pattern. There was no difference in AC_1 for the descending and ascending pattern throughout the whole range of period lengths.

In addition to AC_1 I compared the auto-correlation functions for all the scenarios of different period lengths. I found an exponentially decreasing auto-correlation function for the non-periodic scenario and various periodic auto-correlation functions for the four periodic patterns. The shape of the auto-correlation functions varied among the various patterns but was identical for the ascending and descending patterns. Consequently, in contrast to the other periodic patterns the ascending and descending patterns were identical not only in their mean value, amplitude, frequency distribution and AC_1 but also in their auto-correlation function.

As the relationship between noise color, especially AC_1 , and persistence time is widely studied, in Fig.5.3 persistence times from Fig.5.2 are plotted versus AC_1 . Additionally, a curve describing auto-correlated but non-periodic noise is plotted by way of comparison showing decreasing T_s with increasing AC_1 . Surprisingly, however, T_s of all four patterns of periodically fluctuating environments clearly differed from those of the non-periodic pattern despite the same AC_1 . Here, for a broad range of AC_1 values the corresponding T_s were higher for the periodic pattern than for the non-periodic pattern.

Moreover, results clearly differed among various patterns of periodically fluctuating environment. The cog-pattern shows the greatest difference from the non-periodic scenario, whereas the saw-tooth pattern shows an intermediate difference. The plots for the ascending and descending pattern are very similar, differing only for auto-correlation coefficients larger than 0.8, corresponding to period lengths above 50. Compared to the other fluctuating patterns, both the ascending and descending scenarios are closer to the non-periodic scenario (Fig.5.3).

5.4.3 Floaters per Time Step

Fig.5.4a emphasizes the differences in T_s between the ascending and the descending pattern when period lengths exceed 50 time steps (cf. also Fig.5.2). Fig.5.4b tracks the reasons for these differences in T_s , measuring the intensity of density regulation as the average ratio of floaters. For shorter period lengths up to 50 time steps Fig.5.4b indicates similar intensity in the action of density regulation for the saw-tooth, the descending and the ascending scenario. For period lengths above 50 time steps, however, when using the descending pattern, density regulation acted considerably less intensely compared to the descending pattern and saw-tooth pattern (Fig.5.4b). Over the whole range of period lengths density regulation acted most intensely for the cog-pattern.

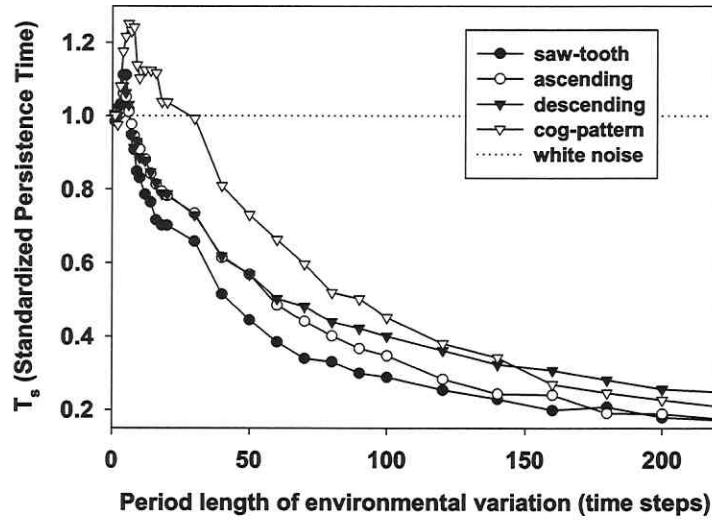


Figure 5.2: Impacts of period length and pattern on T_s

Period length of a periodically fluctuating environment (bottom axis) affects the standardized persistence time of a population T_s (left axis). This figure shows different patterns of periodically fluctuating environment, as well as non-periodic environment with no auto-correlation (white noise). For white noise an average model run lasted 735 time steps ($T_s=1.0$) and life expectancy was 16 time steps.

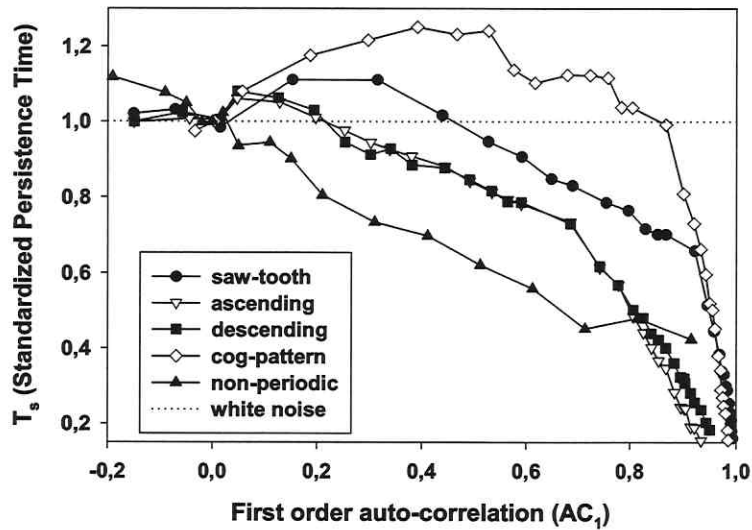


Figure 5.3: Impacts of auto-correlation and pattern on T_s

Persistence Time of population T_s (left axis) depends on first order auto-correlation of environmental noise (bottom axis). However, this relationship differs among various patterns of periodically fluctuating and non-periodically fluctuating environments.

5.5 DISCUSSION

Periodically fluctuating environment in the context of extinction risk of populations is an important case of environmental variation. Here I performed a case study showing that periodically fluctuating environments lead to particular and unexpected impacts on the extinction risk of populations. Complementary to other authors in theoretical population biology who mainly studied the impact of the color of environmental noise on extinction risk (e.g. Ripa et Lundberg 1996, Johst et Wissel 1997, Petchey et al. 1997), I found differences in extinction risk even when noise color (and other attributes) remained constant, but the pattern of periodicity was changed. Below I discuss these aspects in detail.

5.5.1 General results for periodically fluctuating environments

My results presented in Fig.5.2 show that persistence time in periodically fluctuating environments depends on both the periodic length and the pattern of periodicity. In periodically fluctuating environments favorable as well as unfavorable conditions (see methods for definition) are temporally accumulated. In accordance with positive auto-correlation this causes two counteracting effects on extinction risk: on one hand the successive accumulation of favorable conditions has the tendency to raise persistence time (i.e. decrease extinction risk); on the other the accumulation of unfavorable conditions has the tendency to lower persistence time (i.e. increase extinction risk, Petchey et al. 1997). When period length (and consequently auto-correlation) is increased, both effects are intensified. Populations go extinct during sufficiently long time spans of unfavorable conditions, and afterwards, of course, they cannot profit anymore from favorable conditions. Thus, when focusing on the resulting extinction risk, unfavorable effects are expected to superimpose favorable effects for longer period lengths. This leads to shorter persistence times with long period lengths, as is clearly shown by my investigations (Fig.5.2). Here, theory also coincides with the empirical findings of Huisman (1999) on light-limited phytoplankton. Higher mixing depths, i.e. longer periods in periodically fluctuating light, led to decreases in population performance of algae.

For very short period lengths, however, surprisingly I found a slight increase in persistence times (Fig.5.2). This effect can be explained as follows: (1) Short period lengths mean the time spans of unfavorable conditions are not long enough to drive populations to extinction and this explains why persistence times do not decrease. (2) In addition, in periodically fluctuating environments, unfavorable conditions resulting in weak populations are deterministically followed by favorable conditions increasing population size (alternation) similar to negatively auto-correlated environments (Petchey et al. 1997). Consequently, these populations are less prone to extinction and show higher persistence times compared to both non-periodic environments and environments fluctuating in long periods.

The results presented in this study might be regarded as consistent with the findings of Stelter et al. (1997). In a model investigation, these authors found the survival of a meta-population of the grasshopper *Bryodemus tuberculata* to be higher for regularly occurring floods than for randomly occurring floods of the same average frequency. This can be seen in analogy to higher persistence times for periodic environments compared to randomly fluctuating environments found in this study.

The cog-pattern underlines my results discussed in the previous paragraph since it shows an amplification of the effect in question. In the introduction I give examples where environments switch between (approximately) binary states. For these two reasons, albeit uncertainties in comparing the cog-pattern to the remaining patterns (see methods), I decided to include the cog-pattern into this study.

5.5.2 Auto-correlation in periodically fluctuating environments

First-order auto-correlation (AC_1) of the environment is considered to highly impact the extinction risk of populations (Ripa and Lundberg, 1996). Therefore, in Fig.5.3 I turn from the period length to AC_1 in order to find the reason for differences among the various periodicity patterns. Fig.5.3 also allows periodically fluctuating environments with non-periodically auto-correlated noise to be compared on the basis of the same first-order auto-correlation. Decreased persistence times for long period lengths (Fig.5.2) correspond to increased auto-correlation coefficients (Fig.5.3) in accordance with earlier investigations of compensatory population dynamics (Ripa et Lundberg 1996, Johst et Wissel 1997, Petchey et al. 1997). Negative auto-correlation corresponding to period lengths 2 and 3 increased persistence times (cf. Ripa et Lundberg 1996, Petchey et al. 1997). However, persistence times were highest at period lengths 4 and 5, where auto-correlation was slightly positive. This suggests that a moderate auto-correlation generated by periodicity can be advantageous for the persistence of populations in contrast to the same auto-correlation in non-periodic environments (Fig.5.3).

There are two more attributes of environmental noise, which may explain different persistence times among different periodicity patterns: (1) the frequency distribution of time series data and (2) the auto-correlation function (i.e. auto-correlation of higher order). The frequency distributions of the cog-pattern differs from the constant frequency distribution of all other patterns shown in Fig.5.3 and this might at least partly explain different persistence times for the cog-pattern. Furthermore, I found auto-correlation functions to differ among most patterns what also could be the reason for differences in persistence times in Fig.5.3. These considerations in combination with my results show that in a periodically fluctuating environment (despite constant mean and variance), AC_1 is of reduced value when estimating the extinction risk (cf. also Cuddington et Yodzis 1999). Therefore, it is important to know whether noise is colored, i.e. temporally correlated, due to periodicity or not.

5.5.3 Density regulation in periodically fluctuating environments

I found that auto-correlation functions as well as frequency distribution were completely identical for the ascending and descending pattern. Consequently, neither the auto-correlation function nor any other known attribute of environmental variation can explain differences in persistence times between these patterns (for $AC_1 > 0.8$ in Fig.5.3, for period lengths > 50 in Fig.5.4a). The key to this problem is the density regulation. As the data values are the same for the ascending and descending patterns, the “quantitative power” is constant. However, once the population has reached its carrying capacity it cannot grow any further. Favorable environmental conditions occurring in this state do not result in increased population growth but are “wasted”. My results indicate that carrying capacity suppressed pairs from breeding (floaters) – and thus stopped population growth – far more often for the ascending than for the descending pattern (Fig.5.4b). For the ascending pattern most favorable conditions follow other favorable conditions and the population might have already reached carrying capacity. By contrast, for the descending pattern the most favorable conditions follow the worst conditions when populations are likely to be far below carrying capacity. This ultimately leads to differences in persistence times for larger period lengths (Fig.5.4a).

5 Extinction risk in periodically fluctuating environments

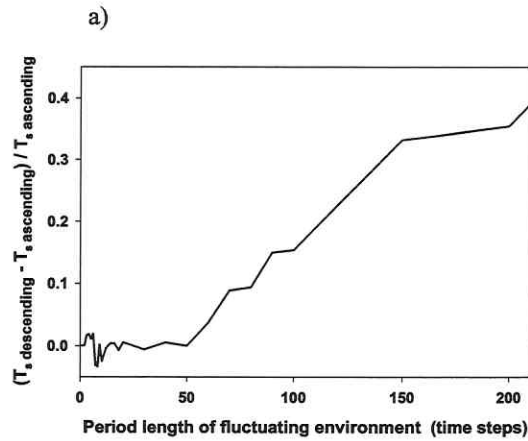
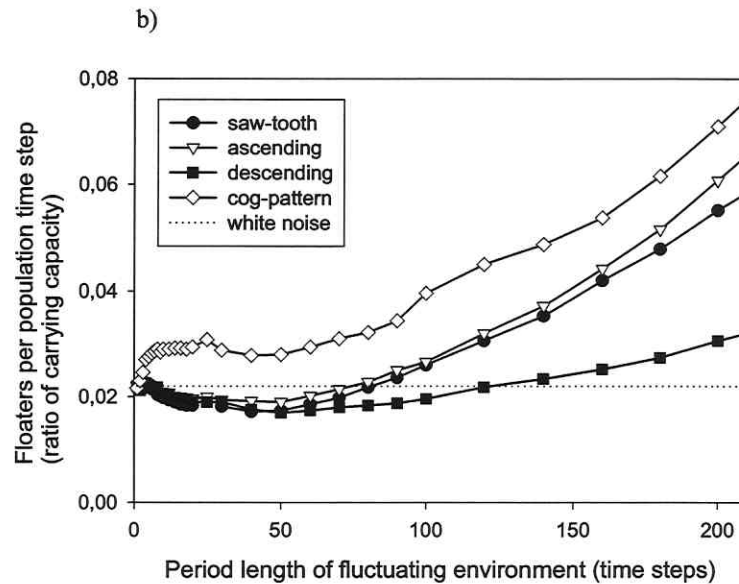


Figure 5.4: Periodic pattern, extinction risk and density regulation

a) Difference of extinction times between the descending and the ascending pattern standardized to the ascending scenario is shown at the left axis. As in Fig.5.2 the period length is shown at the left axis.

b) Period length of periodically fluctuating environment (left axis) affects amount of floaters per time step. The average numbers of floaters per time step are given as ratio of carrying capacity (left axis), showing how intense density regulation is working. See text for further explanation on bottom axis parameter. Standard deviation did not exceed symbol size.



From the above considerations, I learn that the accumulation of favorable conditions might decrease the persistence time of populations as shown for the ascending pattern (Fig.5.4a). Thus, for positive auto-correlation, I have to claim that decreased persistence time is due to the accumulation of both unfavorable and favorable data. (The latter fact is greatly corresponding with the results found by Petchey et al. 1997 for compensatory population dynamics.) In short period lengths the accumulation of favorable conditions is lower and consequently density regulation acts less intensely compared to long period lengths (Fig.5.4b). For short period lengths density regulation is also less intense compared to non-periodic environment due to alternating favorable and unfavorable conditions (see general

results, Fig.5.4b). This, as a third point, additionally explains the increased persistence times for short period lengths stated earlier.

Note that in my model environmental conditions impact the growth rate (via breeding success). If environmental noise affects the carrying capacity (e.g. Ripa et Lundberg 1996), the interaction between density regulation and environment might be different and might affect the results.

5.5.4 Conclusion: the importance of monotonic trends in the environment

Periodically fluctuating environments are characterized by monotonic trends. Whereas auto-correlation only provides information about the similarity in values between adjacent (and surrounding) points, periodicity provides additional information on whether the next point will be of lower or higher value. Monotonic trends, especially as exhibited by the ascending and descending pattern, are characteristic of regularly “disturbed” environments (“disturbance” in the sense of the absolute definition in White et Jentsch 2001). Consequently, my results should be considered when studying disturbances as they might also lead to new insights in this field of research.

Recent research directed towards spatially explicit systems, i.e. spatial variability in the environment has been added to temporal variability (e.g. White et al. 1996, Heino 1998, Lundberg et al. 2000, Bjornstad 2001). My study reveals novel insights on the effects of temporal variability and thus, I here emphasize not to underestimate temporal variability.

The unexpected effects found in periodically fluctuating environments are (1) differences in persistence times for environments of constant descriptive attributes and (2) the increased persistence times for short period lengths. Summarizing my considerations, monotonic trends in combination with density regulation can explain both these unexpected effects.

Many studies have focused on non-periodic environments where the effects of auto-correlation on persistence times can be solely related to the parameter ‘noise color’ (e.g. Ripa et Lundberg 1996, Johst et Wissel 1997, Petchey et al. 1997, Heino 1998). The different results I found for various periodic patterns, however, stress the importance of other parameters for estimating persistence times in periodically fluctuating environments. In particular, this includes (1) the poorly studied impact of frequency distribution of time series data and (2) the whole auto-correlation function. The latter supports findings by Cuddington et Yodzis (1999), who found that $1/f^\beta$ noise models make considerably different predictions for persistence compared to auto-regressive noise models.

Several authors have already stressed that the impact of environmental stochasticity on persistence can depend on the type of density regulation (undercompensatory versus overcompensatory density regulation; Petchey et al. 1997, 2000, Cuddington et Yodzis 1999, see also Kaitala et al. 1997a, b). My results indicate yet another finding: different forms of periodicity can interact differently with the same type of density regulation and can cause differences in persistence times, especially at larger period lengths.

My results clearly show that attributes of environmental noise known from earlier studies (Ripa et Lundberg 1996, Petchey et al. 1997, Johst et Wissel 1997, Kaitala et al. 1997a, b, Heino 1998, Cuddington et Yodzis 1999, Lundberg et al. 2000) are insufficient to describe environmental variation. The occurrence of monotonic trends within environmental time series in combination with the density regulation of populations is an essential element in determining extinction risk.

5.6 LINK TO THE PROCEEDING CHAPTER

In this chapter (five), I revealed that extinction risk in periodically fluctuating environments behaves differently than expected from existing knowledge. One of the new insights presented in this chapter (five) is that - even when other descriptive attributes of an environmental time series remain constant - first order auto-correlation cannot predict the extinction risk in periodically fluctuating environments. However, beyond periodically fluctuating environments, the impact of auto-correlation in time series of environmental noise on a population's extinction risk has become one main focus in general research in population biology. When studying this impact we obviously have to generate auto-correlated time series for our experiments. However, currently known processes generating auto-correlation always entail changes in variance. Hence, variance has to be rescaled in order to compare time series of varying auto-correlation under constant conditions and a rescaling technique is commonly used (compare Heino et al. 2000). In the next chapter (six) of this thesis, I reveal disadvantages of this recently applied rescaling technique. Due to these disadvantages I have been using an alternative and newly developed method of rescaling the variance in this chapter (five), as well as in chapter two. This method, which overcomes the shortcomings of the earlier technique, is presented in more detail in the proceeding chapter six.

6 Studying the effects of colored noise: an alternative method of generating time series with given color and variance^{5,6}

6.1 ABSTRACT

The impact of temporally correlated fluctuating environments (colored noise) on the extinction risk of populations has become a main focus in theoretical population ecology. When generating temporally correlated time series, however, the variance has to be rescaled in order to avoid variance-driven biases when comparing the extinction risk for white and colored noise. I tested a frequently used method for rescaling the variance. While the method worked perfectly for modest auto-correlation, I found high variability in the resulting variances of different time series for strong auto-correlation. I therefore present an alternative method that always delivers the target variance, even in the case of strong temporal correlation. Concerning the resulting extinction risk I found differences between both methods. Furthermore, my very intuitive method can be applied to every way of generating colored noise, which is an additional advantage compared to earlier methods. I recommend the method introduced here be used when the target of interest is the effect of noise color on extinction risk not obscured by any variance effects.

6.2 INTRODUCTION

Research into theoretical population ecology has focused on factors impacting populations' performance and hence their extinction risk. On one hand these factors include all the parameters characteristic of the system (e.g. birth rate, mortality, intra-specific competition, carrying capacity) yielding the population's growth rate and competition mode. On the other hand these factors are subject to variations in time – often called noise – occurring as demographic noise (intrinsic to the population) and environmental noise (extrinsic to the population). While demographic noise is regarded as random, environmental noise is known to be often auto-correlated to various degrees (Steele 1985, Pimm et Redfearn 1988, Lande 1993, Halley 1996).

There are at least four descriptive attributes of environmental time series affecting corresponding population dynamics: (1) the mean, (2) variance, (3) the frequency distribution of values and (4) noise color, i.e. temporal auto-correlation. The effects of the first two attributes, the mean and variance, have been studied extensively during the past (e.g. Goel et Richter-Dyn 1974, Roughgarden 1975, Tuljapurkar 1989, Lande 1993, Foley 1994, Wissel et al. 1994). The third attribute – frequency distribution – remains insufficiently studied and has not been primarily addressed by any publications. Recent research has focused on the fourth attribute, i.e. the color of environmental noise, and complex relationships have been found between noise color, underlying population dynamics and extinction risk by several authors (Roughgarden 1975, Ripa et Lundberg 1996, Johst et Wissel 1997, Petchey et al. 1997, Kaitala et al. 1997a, Kaitala et al. 1997b, Heino 1998, Halley et Kunin 1999, Cuddington et Yodzis 1999, Ripa et Heino 1999, Ripa et Lundberg 2000). All these studies emphasized the

⁵ An extended and considerably revised version of this chapter was submitted to a journal with focus in general and theoretical ecology as:

Wichmann MC, Johst K, Schwager M, Blasius B, Jelsch F: Studying the effects of coloured noise: an alternative method of generating time series with given colour and variance.

⁶ Note, the submitted manuscript includes Fig. A1 shown in appendix.

importance of considering noise color and thus the temporal auto-correlation of environmental fluctuations in studies of population dynamics and extinction risk.

When investigating the effects of noise color on extinction risk, the original white noise was dyed, i.e. I modified the temporal correlation of environmental fluctuations in order to study the resulting effects on population dynamics. For this purpose a first-order auto-regressive process (AR₁) was often used (alternatively cf. Cuddington et Yodzis 1999):

$$\Phi_{t+1} = \alpha * \Phi_t + \beta * \varepsilon_{t+1} \quad [\text{Equation 6.1}]$$

where Φ_t is the temporally correlated fluctuating quantity, α is the auto-correlation on a scale from -1.0 to 1.0 , ε_t is a random number drawn from a normal distribution with unit variance and zero mean, β^2 is the variance and Φ_0 is arbitrarily set to zero. In order to remove a possible bias by starting at the mean value ($\Phi_0=0$) an initial transient of the first 1,000 steps is omitted (for the impact of initial conditions compare Heino et al. 2000). The time series of an environmental parameter (e.g. the carrying capacity K) then results from $K_t = K_0 + \Phi_t$ with K_0 being the desired average. (Compare also chapter two, Eq.2.3 and Eq.2.4.)

When modifying the color of time series according to Eq.(6.1), however, a problem arises: changing the degree of auto-correlation (color) always entails a change in variance σ^2 of Φ (i.e. $\sigma^2 > \beta^2$, cf. Roughgarden 1975, Heino et al. 2000, this study Figs.6.1a-i - dashed lines). Thus, one faces the problem that “the effects of change in color will be masked by the effects of [changing] variance” (Heino et al. 2000: p. 178). Hence, a common technique is to scale β depending on the auto-correlation coefficient α (e.g. Chatfield 1984) such that the red noise of different α and white noise can be compared on the basis of the same variance. Here I present some new ideas for tackling this problem. I propose alternatives to the current practice of generating dyed time series in order to avoid variance-induced biases when calculating the extinction risk of populations in colored environments.

6.3 SCALING TO EXPECTED VARIANCE

6.3.1 Scaling to expected asymptotic variance

Many authors (Roughgarden 1975, Foley 1994, Ripa et Lundberg 1996, Petchey et al. 1997, Cuddington et Yodzis 1999 and others) used a factor that scales the colored noise to the desired *asymptotic* variance σ_∞^2 depending on the auto-correlation coefficient α .

$$\beta \equiv \beta(\alpha) = \sigma_\infty \sqrt{1 - \alpha^2} \quad [\text{Equation 6.2}]$$

In particular, Heino et al. (2000) call for scaling to the expected asymptotic variance when long-term properties of noise are likely to be important for extinction risk. Note that Eq.(6.2) corrects the variance as it is *expected* to result from the AR₁ process (Eq.6.1).

6.3.2 Scaling to expected variance over a certain time scale T

When studying Eq.(6.2), Heino et al. (2000) pointed out that in short colored time series of length T , the variance σ_T^2 of Φ may deviate from the desired asymptotic variance σ_∞^2 (dotted lines in Fig.6.1). The dash/double-dot lines in Fig.6.1 show that this deviation grows with increasing α for a given T (compare for instance Figs.6.1a and b or Figs.6.1e and f) and decreases with increasing T (compare for example Figs.6.1a and c or Figs.6.1b and d). One problem common to all colored time series is that the longer the time series, the greater the variance. Heino et al. (2000) discussed this problem intensively, and suggested that the proper length of the time series be chosen when rescaling the variance. These authors call for scaling

to the expected variance of the time interval T over which the extinction risk is to be assessed as shown in the following.

In order to tackle the problem of decreased variance in short samples of colored noise, Heino et al. (2000) suggest *varying the scaling factor* depending on the sample size T and the time horizon of the considered extinction risk. Starting an AR_1 process from its mean value, they suggest the following scaling:

$$\beta \equiv \beta(\alpha, T) = \sigma_T \sqrt{\frac{(1 - \alpha^2)(T - 1)}{T - \frac{2 + 2\alpha + \alpha^2 - \alpha^{2T}}{1 - \alpha^2} + \frac{(1 - \alpha^T)(1 + 2\alpha - \alpha^T)}{T(1 - \alpha)^2}}} \quad [\text{Equation 6.3}]$$

σ_T^2 is now the target variance of the first T values of Φ_t . Note that Eq.(6.3) approaches Eq.(6.2) for large T .

6.3.3 Scaling to asymptotic variance versus scaling to a certain time scale T

A snag of Eq.(6.3) (and also Eq.(6.4), see below) is that the final time of the simulated population dynamics has to be fixed. This is only partly a problem when investigating the extinction risk $P_0(T)$ at a certain time T , where some populations might not experience the entire time series when going extinct before reaching T . However, the snag of fixed simulation time should be particularly kept in mind when focusing on the Mean Time to Extinction where the function $P_0(t)$ is needed (e.g. Wissel et al. 1994, Johst et Wissel 1997, Stelter et al. 1997, compare chapter two of this thesis). An additional snag of scaling to short time scales T is that the mean value might change during the AR_1 -process due to the fact that positive autocorrelation supports similar values and may not balance out the mean in short series. This point is, however, not investigated here but may be the subject of a further study.

Note that the first alternative, i.e. scaling to the asymptotic variance (Eq.6.2) does not hold for $1/f^\beta$ noise. For $1/f^\beta$ noise the variance at each frequency scales according to a power law leading to the fact that $1/f^\beta$ noise does not have finite variance when time approaches infinity (Halley 1996, Heino et al. 2000). Therefore, the second alternative (Eq.6.3) is always required. Scaling to asymptotic variance (Eq.6.2), however, becomes more important when applying a common practice of implementing environmental variation in studies on the extinction risk of populations. Here, I produce a long time series (say 100 times as long as needed for one simulation) and pick the starting point within this time series randomly assuring different environments among simulation repeats. (This practice also removes any bias by starting the AR_1 -process at its mean; compare description below Eq.6.1.) Nevertheless, the first alternative breaks always down for $T \ll \infty$.

6.3.4 Applicability of Equation (6.2) and (6.3)

General considerations

Heino et al. (2000) extensively discuss Eq.(6.2) pointing out a problem for short time series samples T . These authors solve this - and only this - problem by providing Eq.(6.3). However, I here claim at least two more problems of Eq.(6.2) (and also Eq.6.3) that are not discussed by Heino et al. (2000). First, Eq.(6.2) and Eq.(6.3) are attached to the AR_1 -process and consequently, they are restricted to this process and cannot be applied to other processes of noise generation. Second, Eq.(6.2) and Eq.(6.3) both rescale to the expected variance but do not consider variability in the actual variance. The latter point is explained in more detail in the following paragraph. Thereafter, I will present an alternative method of rescaling the variances of colored noise tackling all three problems pointed out here, i.e. (1) dealing with

the problem of short sample lengths T discussed by Heino et al. (2000), as well as (2) overcoming the restriction to the AR_1 -process and, (3) taking variability in the actual variance into account.

Applicability of scaling to the expected variance

In my simulations I explore the variability of variances for different auto-correlation. I found considerable deviations of the actual from the expected variance for high auto-correlation. [Please note Fig.A1 p.105.] In particular, I found that depending on the underlying random number series, the variances produced by Eq.(6.2) to be reduced (Figs.6.1a,b,f,h) *or* elevated (Figs.6.1d,i). Thus, in some simulation runs Eq.(6.2) might produce a seemingly asymptotic variance that may considerably deviate from white noise variance (Fig.6.1f). I also used Eq.(6.3) to generate colored noise for small sample lengths. Considering single simulation runs Fig.6.2 shows that, despite scaling adapted to T , the variance σ_T^2 of the colored time series (dash/double dot line) could be greatly reduced compared to the desired variance (dotted line) or compared to the original time series (solid line), especially for large α .

Heino et al. (2000) claimed the coincidence of short samples *and* large α to be essential for the occurrence of reduced variance. Considering individual simulation realizations, my results revealed that very large α alone can lead to deviations in variance compared to white noise (double-dot/dashed line in Fig.6.1b,d,f,h,i). What are the reasons for this observation? Eq.(6.2) and Eq.(6.3) both rescale the time series according to the *expected variance*. In fact, however, for large α the *actual variance* of a particular time series might considerably deviate from the expected variance depending on the underlying random number series (cf. un-scaled variances – dashed line – in Figs.6.1d and h). Tiny deviations in the sample of random numbers apparently only become important when α is large, albeit even for long time scales (Figs.6.1d,g,h). Hence, deviations of actual from expected variance are due to the type and initialization of the random number generator (Figs.6.1d vs. 1h) and cannot be removed by scaling to the expected variance, even when using Eq.(6.3). As a result, using Eq.(6.2) and (6.3), the extinction risk calculated for strong auto-correlation might nevertheless be influenced by biases in the variance.

For strong auto-correlation my results imply that on one hand long time series of 3,000 or 10,000 time steps are not long enough to sufficiently filter random deviations (Fig.6.1). On the other hand, calculating the extinction risk of populations on this scale often exceeds the reasonable time horizon. Accordingly, I conclude that rescaling to infinity might be less rational than rescaling to the appropriate time horizon of extinction risk (compare also Heino et al. 2000). When comparing white and red noise on the basis of the same variance one has to remove random deviations in variances as I suggest here. In the following I present an alternative method of rescaling variances, i.e. rescaling according to the *actual variance*. I further discuss the applicability of scaling to the expected variance when comparing both methods in the final section of this chapter.

6.4 SCALING TO THE ACTUAL VARIANCE

Below I present a simple method of scaling according to the actual variance in order to generate colored time series of a given variance even for large auto-correlation (α). In contrast to the current practice of coupling the AR_1 process of Eq.(6.1) with rescaling β to the expected variance (Eq.6.2 and 6.3), I here suggest first running the AR_1 process without any rescaling and then simply readapting the variance to the original value afterwards.

A very easy and intuitive way of determining the rescaling factor yielding the target variance is to measure the difference in variances of the non-rescaled auto-correlated time series and the original white noise. This yields the scaling factor c that might be regarded as equivalent to the term square root of $(1-\alpha^2)$ in Eq.(6.2) and (6.3), but is named differently as, in contrast to β , it will be applied separately from the generating AR_1 -process. For $c < 1.0$ the variance decreases; for $c > 1.0$ it increases and c can be easily calculated from:

$$c \equiv c(\alpha, T) = \frac{\sigma_{T_WN}}{\sigma_{T_RN}} \quad [\text{Equation 6.4}]$$

where σ_{T_WN} is the standard deviation for the sample size T for the original time series of white noise and σ_{T_RN} is the standard deviation for un-scaled red noise. When T approaches ∞ one can assume

$$c \equiv c(\alpha) = \frac{\sigma_{\infty_WN}}{\sigma_{\infty_RN}} \quad [\text{Equation 6.5}]$$

Then σ_{T_WN} turns into σ_{∞_WN} , i.e. the desired target standard deviation and σ_{T_RN} turns into σ_{∞_RN} , i.e. is the standard deviation of the auto-correlated time series without any rescaling. Note, that for scaling to infinity the variability in variances disappears and Eq.(6.5) approaches Eq.(6.2). Moreover, σ_{∞} is unknown as it approaches zero and thus, Eq.(6.5) remains a theoretical option. Hence, in general Eq.(6.4) applies.

Post AR_1 -process – rescaling can easily be done by multiplying the distance of each data point from the time series mean by the rescaling factor c and changing data values accordingly:

$$K_t^* = K_0 + c * (K_t - \bar{K}) \quad [\text{Equation 6.6}]$$

where K_t refers to the time series after applying the AR_1 -process (Eq.6.1), \bar{K} is the actual average of this time series while K_0 is the target average (compare AR_1 -process). Finally, K_t^* gives the value for the new, rescaled time series.

Note, that in contrast to earlier methods (Eq.6.2 and 6.3), Eq.(6.4) is not attached to the AR_1 -process but can be applied to any colored time series regardless of the way of noise generation.

When scaling to “infinity”, i.e. very long environmental time series, my method results in variances very close to that desired of white noise (Fig.6.1). Here under moderate conditions it can reproduce the results of Eq.(6.2) (Fig.6.1c,e) whereas in other cases (in particular when α is large) it leads to variances much more similar to white noise than those produced by Eq.(6.2) (Fig.6.1a,b,d,f,g,h). When variances are scaled depending on T , Eq.(6.4) produces a time series with variances equal to those of the actual time series of white noise (Fig.6.2).

6 An alternative method of generating time series with given color and variance

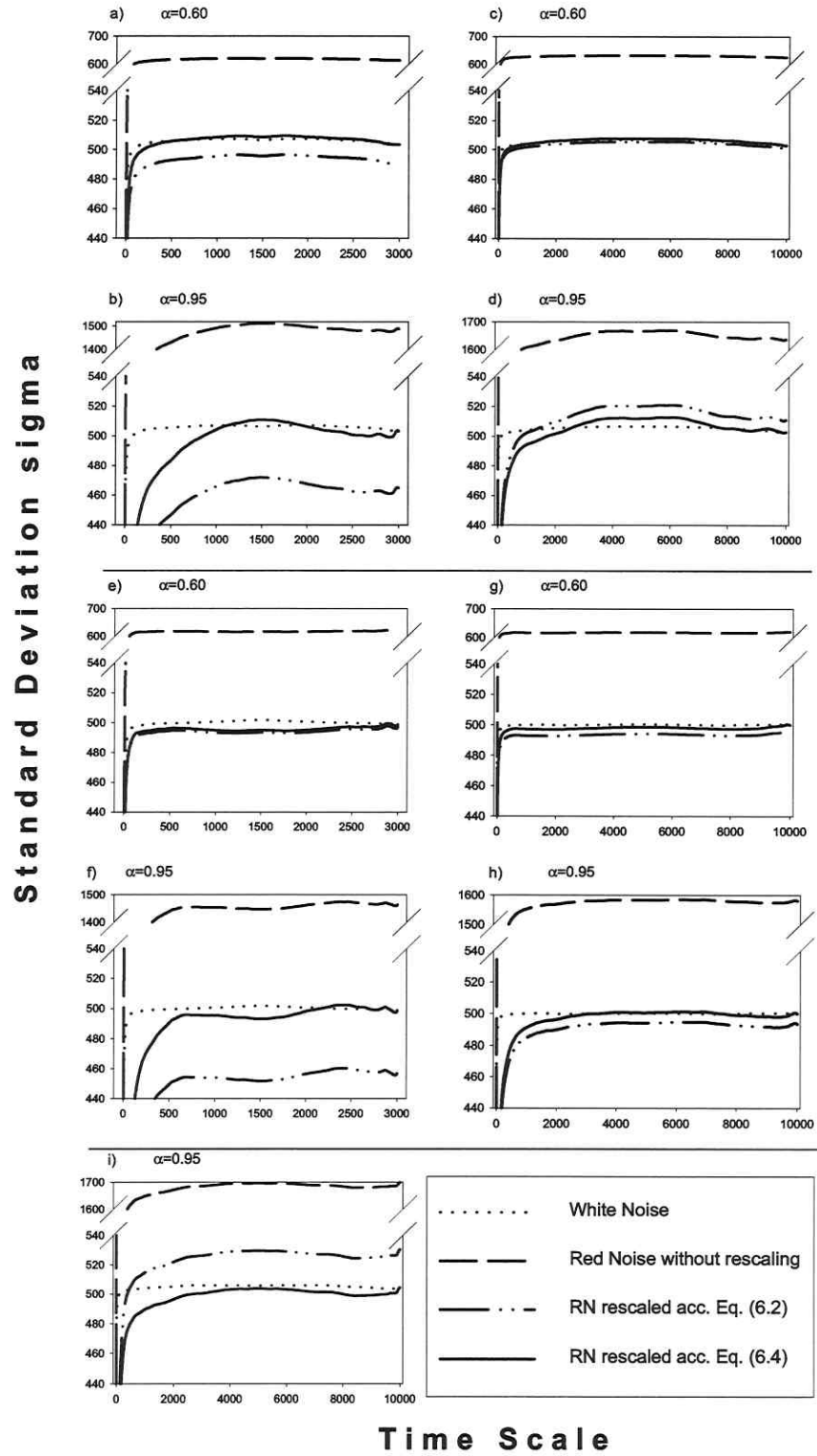
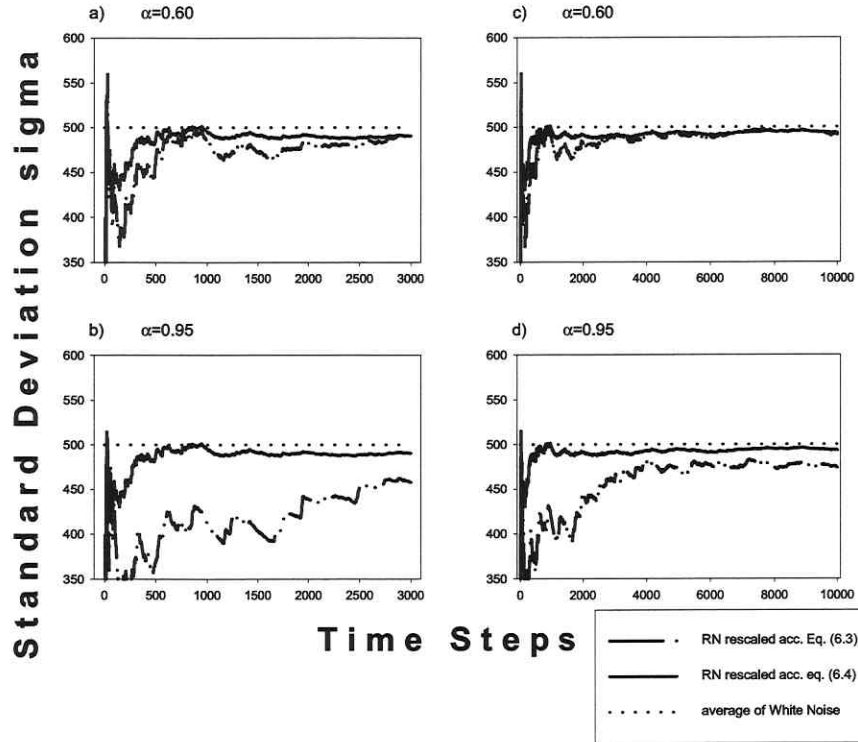


Figure 6.1: Variability in average variances for samples of time series fragments

(Previous page 80.) Standard deviation σ (left axis) of time series created by various techniques versus the length of time series fragments (bottom axis). I take a time series of constant length ($T_{\text{total}}=3,000$ and $10,000$). In order to calculate σ I average over *all samples of fragments* of smaller lengths T (bottom axis shows *time scale*). Accordingly, the number of samples is $T_{\text{total}}-T+1$ and on right plots σ is averaged over a larger number of samples when compared to the same time scale value on left plots. The underlying assumption is to use time series fragments drawn randomly from a long time series to perform repeats in the simulation of extinction risk (by contrast see Fig.6.2). The standard deviation σ of colored noise is shown without scaling (dashed line), scaling according to Eq.(6.2) (dash/double-dot line) and scaling according to Eq.(6.4) (solid line). The desired σ (e.g. for white noise) is given as a reference (dotted line). Plots are shown for two different random number initializations (a–d and e–h) and for two different time series lengths ($T_{\text{total}}=3,000$: a, b, e, f and $T_{\text{total}}=10,000$: c, d, g, h). The auto-correlation parameter is $\alpha = 0.60$ (a, c, e, g) and $\alpha = 0.95$ (b, d, f, h). Additionally, a third random number initialization (i) is shown for $\alpha = 0.95$ and $10,000$ time steps. Note, that here rescaling according Eq.(6.2) produces variances larger than white noise variance.

**Figure 6.2: Deviation of variances of particular time series fragments**

(This page.) Standard deviation σ (left axis) of time series created by various techniques versus the length of a particular time series (bottom axis). Note that in contrast to Fig.6.1, σ is calculated from just *one particular time series fragment* (from time step 1 to time step left axis value) yielding the fluctuations in the plot (bottom axis gives *time steps*). Therefore, left and right plots show identical values but the left plot gives a smaller scale on bottom axis. The standard deviations of colored noise are shown for scaling according to Eq.(6.3) (dash/double dot line) and scaling according to Eq.(6.4) (solid line), the latter yielding exactly the same curve as desired (e.g. white noise (T)). Additionally, the asymptotic variance of white noise is given as a further reference (dotted line). Like in Fig.6.1, two different maximum lengths of the time series ($3,000$: a, b and $10,000$: c, d) and two degrees of auto-correlation ($\alpha = 0.60$: a, c, and $\alpha = 0.95$: b, d) are shown while random number initialization remains constant. Also note Fig.A1 in appendix.

6.5 IMPACT ON THE CALCULATED EXTINCTION RISK

I have investigated different methods of rescaling the variance of dyed time series of environmental noise in the main part of this study. Finally, I am now interested in the relevance for the calculated extinction risk, i.e. whether differences in variance rescaling lead to differences in expected extinction risk. Therefore, I use a well-known model of population dynamics, the Maynard-Smith model (Maynard Smith et Slatkin 1973, May et Oster 1976, Bellows 1981):

$$N_{t+1} = N_t * \frac{R}{1 + (R-1) * \left(\frac{N_t}{K_t}\right)^b} \quad [\text{Equation 6.7}]$$

where N gives the population size at time steps t and $t+1$, respectively. R is the growth rate, K_t is the carrying capacity at time step t (see environmental noise) and b is a competition parameter controlling the dynamic behavior of the model (for the latter also compare Petchey et al. 1997). I chose this model since it was found to be particularly flexible, broadly applicable and well capable to describe a wide range of data (Bellows 1981).

In accordance to Heino et al. (2000) I studied the extinction risk for short time scales (50 time steps) and longer time scales (1,000 time steps). For my simulations I chose a parameter set of an average $K=100$, maximum $R=4.5$ and $b=1.0$. Demographic noise was included by letting N_{t+1} be an integer number Z_t drawn from a Poisson distribution with the deterministic expectation for N_{t+1} as its mean, i.e. $N_{t+1} = Z_t(N_{t+1})$ (compare Petchey et al. 1997). Environmental noise was generated according to Eq.(6.1) and the appending description. The auto-correlation coefficient α was varied in steps of 0.05 between 0.00 and 0.95 but $\alpha=0.99$ was additionally studied. Standard deviation σ was also varied ($\sigma=25; 30; 35; 40; 45$) yielding the factor β in Eq.(6.1). The variance (σ^2) was then rescaled according to Eq.(6.2) and Eq.(6.4) when generating time series for 1,000 population time steps (Fig.6.3a-c) but according to Eq.(6.3) and Eq.(6.4) for 50 time steps (Fig.6.3d-e). The finite time series of environmental noise had an additive effect on the mean carrying capacity K as presented in the introduction. In the case of $K_t < 0$ I set $K_t = 0$ in order to avoid artificially negative values for carrying capacity. Hence, the rules of this model are the same as for earlier investigations but I use the Maynard Smith model instead of the Ricker equation (compare Heino et al. 2000, see also Ripa et Lundberg 1996, Petchey et al. 1997, Cuddington et Yodzis 1999). Here, however, I use the alternative scaling practice presented in this chapter.

Fig.6.3 shows the calculated extinction risks for the two discussed methods of rescaling the variance and the differences between them based on 10,000 simulation repeats. For long time scales ($T=1,000$ time steps) I found elevated extinction risks for high auto-correlation when applying Eq.(6.4) (Fig.6.3b) compared to the application of Eq.(6.2) (Fig.6.3a, for difference see Fig.6.3c). For short time scales ($T=50$ time steps), again my results show different extinction risks for different rescaling methods (Fig.6.3f). Here, for higher autocorrelation ($\alpha > 0.5$) I found considerable lower extinction risks when applying Eq.(6.4) (Fig.6.3e) compared to Eq.(6.3) (Fig.6.3d). As expected, I found higher extinction risks for higher variances.

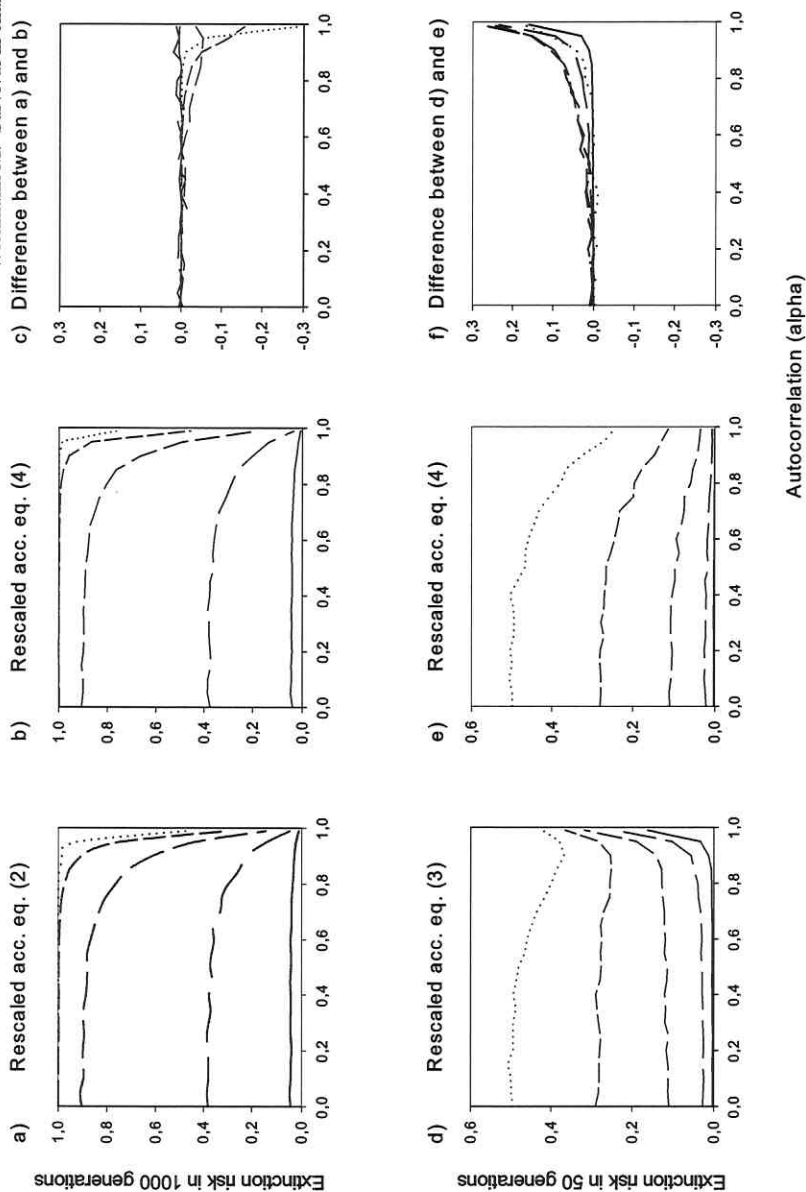


Figure 6.3: Impacts of the rescaling variance technique on extinction risk

The extinction risk (left axis) is plotted versus auto-correlation coefficient α (bottom axis). Extinction risks were assessed on two different time scales: after 1,000 time steps (a-c) and after 50 time steps (d-f). Two methods of rescaling the variance in dyed time series of colored noise are compared: the commonly used method discussed by Heino et al. 2000 (a, d) and the method introduced in this study (b, e). Additionally, the absolute difference between the resulting extinction risks of both methods (a-b and d-e, respectively) is shown (c, f). Various line styles represent varying standard deviation from $\sigma=25$ (solid line) to $\sigma=45$ (dotted line).

6.6 DISCUSSION

In this study I tested a frequently used method of adapting the variance in colored time series (cf. Heino et al. 2000 and references therein). I investigated the variances on the scale of individual simulation runs. While variances behaved as expected for modest auto-correlation, I found high variability among simulation repeats in resulting variances for strong auto-correlation. I then presented an alternative method for transmitting the low variability in variances from white noise to colored noise. This method avoids variance-driven biases even for strong auto-correlation when investigating the impact of colored noise on the extinction risk of populations. I finally compared both methods considering the resulting extinction risk and found remarkable differences.

6.6.1 Impacts on extinction risk

As a first point I state that my calculation of extinction risk reproduced the results of an earlier study when using the earlier method (Eq.6.2 and Eq.6.3, respectively; Fig.6.3a and Fig.6.3d, compare with figures in Heino et al. 2000: Fig.4c and 3b, respectively). This underlines that different results are due to different rescaling techniques but not to the usage of deviating models of population dynamics. But is there an impact of the different rescaling methods on the extinction risk? And, if so, what is the quality and quantity of this impact? When evaluating the method presented in this paper these are important questions that I discuss in the following.

Fig.6.3c and f show that both methods produce consistent results for small and intermediate auto-correlation but different results for high auto-correlation. This is in accordance with what is implied by my results for comparing variances of different rescaling methods (Figs.6.1, 6.2). I conclude that, concerning the resulting extinction risks, (1) the choice of the rescaling method does not matter for moderate autocorrelation but (2) this choice obviously matters for high auto-correlation (Fig.6.3c,f).

The method presented here, reduces the “variability in variances” (and thus, the variance itself) when compared to the earlier method and consequently, applying this method I would expect lower extinction risks (compare e.g. Roughgarden 1975, Ripa et Lundberg 1996). Surprisingly, for different time scales I found contraire deviations in extinction risks (compare Fig.6.3c and f), i.e. my method unexpectedly produced higher extinction risks for 1,000 time steps but the expected lower extinction risks for only 50 time steps. In this study I focus on presenting and discussing the applicability of an alternative rescaling method but currently I cannot explain the results for 1,000 time steps. However, my results suggest that applying different rescaling methods drives the extinction risk in opposite directions on different time scales.

6.6.2 Applicability of rescaling to the actual variance

In both cases, i.e. scaling to asymptotic variance (Eq.6.5) and scaling to a certain time scale T (Eq.6.4), my method reproduces white noise variance more reliably than the method currently used (Heino et al. 2000 and references therein). It meets the initial aim by providing a way of generating colored noise not only for slight and moderate but also for large auto-correlation with a given variance.

The main characteristic of the method presented here (Eq.6.4 and 6.5) is the high accuracy in rescaling the variance even for individual simulation runs of large α as shown in Figs.6.1 and 6.2. The extra technical effort due to the separation of the generation of the colored time series from the rescaling process and measuring the actual variances could be seen as a

disadvantage. However, this effort remains small, especially since the work can easily be done on a personal computer running simple spreadsheet software. Thus, in my opinion it does not outweigh the advantages of the method discussed below.

In this study, the here newly presented method of variance rescaling was applied to colored noise generated by an AR_1 -process. However, in contrast to existing methods (Eq.6.2), this new method of variance rescaling is not attached nor specifically designed for a particular noise generating process but it is applied *after* noise generation. Consequently, this method can be applied to *any* way of generating noise including $1/f^b$ -noise (compare e.g. Cuddington et Yodzis 1999). Moreover, this method can even be applied to colored time series where the underlying process of noise generation remains completely unknown.

Another advantage of this method is its straightforward practicality. It is very intuitive to measure a deviation in variance and to correct it accordingly what makes my method easy to grasp. This contribution is also designed to stimulate the search for solutions that are simple but workable rather than mathematically elegant. I suggest that the newly presented method should be preferred for the technical advantages pointed out in this paragraph and below.

However, from a statistical point of view, post AR_1 rescaling might bear a shortcoming. The rescaling process is different for different time series and thus one could argue that the process from where the time series arise is not constant. A closely related point of criticism would be that these deviations of actual from expected variance are subject to stochasticity and thus they should not be removed. Here, the essential but completely open question is whether this stochasticity is characteristic to the AR_1 process or whether it also occurs for auto-correlation in nature. If the first case is valid this supports my method, the latter case would speak against its application in population biology. However, on the current state of knowledge and heading for the aim to investigate the effects of auto-correlation while keeping the variance constant, I here recommend rescaling according to the actual rather than the expected variance of the corresponding time series.

From yet another point of view one might argue that using the actual instead of the expected variance of the time series, as I do here, is subject of a particular assumption, i.e. the assumption of a more predictable future. Then, evidently, this assumption leads to different results than the assumption of existing methods for rescaled variances (Figs.6.1, 6.2), as well as for the resulting extinction risk (Fig.6.3). Thus, one might discuss what the more reliable assumption is. In this context I claim again that when systematically studying and modifying one parameter (e.g. auto-correlation) other conditions (e.g. variance) should be kept constant. Rescaling according to the actual variance, as I suggest, copies the variances of the original time series (of “white noise”) and thus it explicitly gives respect to stochastic variability in variances as found in white noise (compare Fig.6.2). Consequently, I prefer the method presented here. In my opinion scaling to the expected variance is not always reliable but instead, the actual variance should be taken into account for rescaling (Eq.6.4 and 6.5, see Fig.6.1). Hence, the method presented here can be regarded as a simple, consistent way of tackling the problems discussed by Heino et al. (2000) and those additionally revealed by my investigations. I have already successfully used this method in chapters two and five.

6.6.3 Further descriptive attributes of time series

I am aware that the problems claimed for the variance of time series also hold for auto-correlation, i.e. the auto-correlation coefficient α may randomly deviate from the expected value for short sample sizes and/or strong variances. I found that random number generators in combination with Eq. (6.1) might not deliver the expected α on short time scales. However, taking a step back, I recollect that the aim is not to produce time series with exactly given α

but to compare the effects of white and colored noise on the basis of the same variance. I therefore emphasize that these deviations in α are rather minor and do not matter: One may simply calculate and refer to the actual α . However, in addition, those problems may also concern the time series average, i.e. for strong autocorrelation also the mean value might deviate from the expectance and this might cause more severe problems. However, in this study, accordingly to variances, I preferred the actual to the expected mean value (Eq.6.6) what might additionally affect the differences I found for extinction risks (Fig.6.3).

Moreover, one should also bear in mind that mean, variance, auto-correlation and further “attributes” of time series do always generalize and yield imperfect descriptions of the time series. Thus, even the sum of all known descriptive attributes can never completely describe a time series, but for complete description every time series point must be given explicitly. Consequently, one may always find differences in extinction risk resulting from different time series of constant descriptive features.

6.6.4 Conclusion

This manuscript contributes to the growing evidence that dealing with time series is a tricky business posing several problems in population ecology and the assessment of extinction risk. Heino et al. (2000) claimed differences in the impact of noise color on extinction risk among various studies (e.g. higher extinction risk due to colored noise: Mode and Jacobsen 1987, Foley 1994, Johst et Wissel 1997, Roughgarden 1975, Wichmann et al. in press, but lower extinction risk under colored noise: Roughgarden 1975, Ripa et Lundberg 1996) and suggest the reason to be differences of the scaling practices of the variance of the colored time series. Other authors stress the importance of density regulation on the results, i.e. whether there is undercompensatory or overcompensatory density dependence (Petchey et al. 1997, Cuddington et Yodzis 1999, Petchey 2000). It should also be borne in mind that the impact of colored noise on extinction risk depends not only on the noise color itself but also on its relation to the time scale of population growth (growth rate) of the species considered (Johst et Wissel 1997). Furthermore, the results may significantly differ when $1/f^\beta$ noises are used instead of an AR_1 process to generate the dyed time series (Cuddington et Yodzis 1999).

The suggestions for scaling the colored time series made here can help to deal with the problems discussed above. In particular, I present a very simple and consistent procedure to generate time series with given color and variance even for strong temporal auto-correlation. Compared to earlier studies, this method harbors at least two advantages: (1) the variability in variances is reduced, and (2) this method is not restricted to the AR_1 -process but can be applied independently of the way of noise generation. While the latter point favors the general applicability of this method the first point enables me to compare the extinction risk $P_0(T)$ and the persistence time T_m of populations experiencing different colors of environmental noise on the basis of the same variance. Accordingly, I have shown that omitting – maybe unintended – stochasticity in variances alters the calculated extinction risk. The method proposed here may help increase our understanding of the impact of colored environmental noise on extinction risk.

7 Summary

7.1 SUMMARIZING DISCUSSION AND FUTURE PERSPECTIVES

In this thesis I used a modeling approach investigating the survival of a biotic population under different environmental conditions. In particular, I developed a model of the population dynamics of the tawny eagle in the southern Kalahari. I considered changes in precipitation patterns, which may be caused by climate change, as well as modifications in vegetation structure, which can follow land use. Moreover, the results led to new insights into existing knowledge of population dynamics, i.e. the model produced novel effects that are valid beyond the tawny eagle. Thus, I revealed unexpected effects for environments that fluctuate periodically. Furthermore, I presented an alternative technique for studying auto-correlated environments generating results that partly differ from those of earlier techniques. While the individual results are discussed within single chapters, in the following, a summarizing discussion is given that links the main results of this thesis and points out future perspectives.

Arid area ecosystems are regarded as being particularly sensitive to environmental changes (e.g. Wiegand et al. 2000) and raptors are especially vulnerable to modification in the environment (e.g. Dean et al. 1988, Rodriguez-Estrella et al. 1998, Herremans et al. 2000). In this thesis I could illustrate the sensitivity of the tawny eagle population in the Kalahari arid savanna to modifications (1) in precipitation pattern and (2) in vegetation structure. These two environmental characteristics are subject to human driven modifications by global climate change and land use (e.g. IPCC 2001b, Jeltsch et al. 2000). The results of this thesis indicate high impacts of these human activities on the persistence of the tawny eagle population (Fig.2.4, Fig.4.8). This has at least two implications: first, global climate change and land use must be taken into account in nature conservation efforts, in particular for raptors in the Kalahari arid savanna and most probably also for other species in other ecosystems. The latter is implied by earlier studies (compare chapters 2.6.6 and 4.5.5) and should be further verified. In this context, the considerations in chapter three of this thesis are also important, presenting a new approach for a breeding success-precipitation relationship in raptors (Fig.3.1). As a second implication, the results of this thesis underline the impacts of human activities that are not always evident due to considerably delayed responses (e.g. climate change, IPCC 2001b; but also land use, Jeltsch 1997a and chapter 4.3.2).

When regarding altered precipitation patterns, the results of chapter two coincide with earlier studies, which also indicate effects of climatic conditions (e.g. McCleery et al. 1998, Crick et al. 1999, Bridges et al. 2001, Madens et al. 2001) or explicit climate change (e.g. Post et al. 1999, Moss et al. 2000) on species performance. Beyond that, this thesis revealed a particularly important finding: even if annual mean precipitation remains unaffected population persistence can be dramatically reduced by increased variation in precipitation among years (Fig.2.4b). This implies that even optimistic projections of climate change may have dramatic effects on the population persistence of single species and on biodiversity. However, climate change may cause further effects beyond precipitation patterns that are not taken into account in this study. Unknown buffer mechanisms might exist and could blur my results. These and similar issues might be the subject of future studies.

The explicit investigation of local climate change effects on particular populations – as performed in chapter two of this thesis – is regarded an urgent aim in nature conservation as

stated by Hannah et al. (2002). These authors claim the “static conservation paradigm”, i.e. that projections for environmental change remain unaccounted for the establishment of conservation areas in fixed borders. In this context, the results of chapter four on the impacts of vegetation structure are important: outside conservation areas a modified vegetation structure (e.g. driven by land use) reduces species survival (Fig.4.5, Fig.4.8) and thus it strengthens the attachment of a species to the conservation area (see chapters 2.6.5 and 4.5.4). Here I follow Hannah et al. (2002) in calling for similar studies on other systems in order to enable us to take climate change effects into account in conservation and management efforts.

Considering environments modified by land use, on one hand the implications of chapter four coincide with earlier studies that found spatio-structural characteristics to be important for species performance (for references see chapter 4.5.5). On the other hand, here, I explicitly refer to structural diversity as one aspect of biodiversity that remains underestimated (chapter 4.1). However, existing data on the impacts of land use on Kalahari vegetation structure are not sufficient to quantify this impact on tawny eagles. Further studies may use field methods, remote sensing techniques and modeling (compare Biota Africa Project 2002) to quantify the impacts of land use on vegetation structure in order to draw conclusions on the actual risk to tawny eagles and other species of land use.

In chapter two, periodically fluctuating annual precipitation was investigated as one less likely scenario of climate change. However, my exploration of extinction risk in periodically fluctuating environments led to novel results for general population biology. Several earlier studies explored the extinction risk in relation to environmental stochasticity (“noise”) and found the estimation of the persistence time to be constant when the describing attributes of the underlying environmental time series remained also constant (e.g. May 1973, Ripa et Lundberg 1996, Kaitala et al. 1997a). In chapter five of this thesis I show that extinction risk in periodically fluctuating environments may differ from randomly fluctuating environments - even for constant attributes (Fig.5.3). This, on one hand, may lead to the generation of additional attributes describing environmental time series, e.g. monotone trends (chapter 5.5.4). On the other hand, when changing one attribute in simulation experiments chapter six focuses on keeping the remaining attributes of the time series constant (Fig.6.1, Fig.6.2).

However, taking a step back, other, more fundamental questions arise: Can “describing attributes” fully describe an environmental time series and allow conclusions on the resulting extinction risk? Or do we have to know the complete time series when drawing conclusion on extinction risk? How reasonable, i.e. artificial versus natural, is it to change one attribute by keeping the others constant (chapter 6.6.3)? Moreover, how “random” are time series of auto-correlated or periodically fluctuating environments (chapter 5.1)? When considering the single values, which we do not know explicitly, they are random. Time series are, however, not random when referring to the run of the time series curve that we know, at least to a certain extent, for these cases. Accordingly, what or where is the difference between environmental “noise” and environmental “forcing”? These questions must be borne in mind when investigating extinction risk in stochastic environments and may form the premise for future studies.

7.2 FINAL CONCLUSION

This thesis provides an assessment of the extinction risk in the case of the tawny eagle in the southern Kalahari for two of the most severe environmental changes: land use and altered precipitation due to climate change. The presented results suggest unexpected and severe effects of global climate change and land use practices on raptors and imply similar results for other species. Furthermore, this thesis contributes new knowledge to theoretical population dynamics that may help to explain recently observed sudden increases or crashes in populations potentially due to human impacts. Consequently, this thesis contributes to our scientific understanding of population dynamics in modified environments. This will help us to tackle the challenges that arise from environments that change on local and global scales and will contribute to biodiversity conservation efforts.

Deutsche Zusammenfassung

Ein Schwerpunkt der aktuellen Forschung in Ökologie und Naturschutz ist die Abschätzung der Persistenzzeit - also die zu erwartende Zeit, die eine Population im System überlebt - und damit des Aussterberisikos von Populationen. Daran anknüpfend wurde in dieser Arbeit ein stochastisches, individuenbasiertes Modell entwickelt, das die Populationsdynamik einer in ariden Gebieten vorkommenden Greifvogelart abbildet. Dieses Modell bezieht sich auf den Raubadler (*Aquila rapax*) in der Kalahari-Trockensavanne. Im Ergebnis einer umfangreichen Sensitivitätsanalyse wurde das Modell für geeignet befunden, die Einflüsse von Umweltveränderungen auf die Persistenz der Raubadlerpopulation zu untersuchen.

Es wurden verschiedene Veränderungen in der Niederschlagsverteilung über die Zeit simuliert, die die Beuteverfügbarkeit für den Raubadler beeinflussen. Diese Ergebnisse zeigen einen deutlichen Einfluss des Niederschlagsszenarios auf die Raubadler-Persistenz an. Ein dramatischer Anstieg des Aussterberisikos wurde beobachtet, wenn die von verschiedenen Klimastudien für das südliche Afrika prognostizierte Regenszenarien simuliert wurden. Selbst wenn die mittlere Niederschlagsmenge unverändert bleibt, aber die Variation zwischen den Jahren erhöht wird, erhöht sich das Aussterberisiko beträchtlich.

Im Zusammenhang mit der Reaktion von Greifvogelpopulationen auf die zeitliche Verteilung von Niederschlägen wird in dieser Dissertationsschrift ein neuer Ansatz vorgestellt. Dabei wird die Beziehung zwischen Niederschlag und Bruterfolg für Greifvögel in ariden Gebieten untersucht und die Bedeutung der Territoriengröße für den überregionalen Vergleich betont.

Unter Nutzung einer räumlichen Variante des Raubadler-Modells wurde ein Einfluss von Baumdichte und Verteilungsmuster der Bäume auf die Persistenz des Raubadlers festgestellt. Daraus wird die Schlussfolgerung gezogen, dass Formen der Landnutzung, die diese Charakteristika der Vegetation beeinträchtigen, eine potentielle Gefahr für den Raubadler darstellen. Das trifft in besonderem Maße für eine Überbeweidung mit Fleischrindern und den Holzeinschlag zu. Der Einfluss dieser Landnutzungsformen sollte daher bei der Konzeption von Naturschutzmaßnahmen berücksichtigt werden. Hier wird auch die Bedeutung der *Strukturellen Diversität*, ihr Einfluss auf die Artendiversität sowie die Verbindung zwischen diesen beiden Erscheinungsformen der Biodiversität hervorgehoben.

Diese Dissertationsschrift liefert jedoch auch Ergebnisse, die weit über den Raubadler hinaus für die allgemeine Theorie in der Populationsdynamik bedeutend sind. So konnte gezeigt werden, dass Aussterbeereignisse in über die Zeit *periodisch fluktuierender* Umwelt nicht mit dem aktuellen Wissen über Extinktion in stochastischer Umwelt erklärbar sind. Obwohl die Eigenschaften, die die Zeitreihe beschreiben, gleich sind, wurde für in kurzen Perioden fluktuierende Umweltparameter ein niedrigeres Aussterberisiko festgestellt als für zufällige Fluktuation dieses Umweltparameters.

Weiterhin stellt die vorliegende Arbeit einen alternativen und in großer Breite anwendbaren Ansatz vor, der die Erstellung von stark auto-korrelierten Zeitreihen für gewünschte Varianzen erlaubt. Die Anwendung dieser neuen Methode führt zu neuen Ergebnissen für die Aussterbezeit in stark auto-korrelierter Umwelt, die von den Ergebnissen früherer Arbeiten abweichen.

Auf der einen Seite geben die Ergebnisse dieser Arbeit Hinweise für konkrete Aufgaben im Naturschutz, d.h. den Schutz des Raubadlers und anderer Greifvögel in der Trockensavanne. Auch in einem allgemeinen Kontext zeigen die hier vorgestellten Ergebnisse mögliche

Zusammenfassung

Richtungen für künftige Forschungsansätze auf diesem Gebiet auf: Den Einfluss des globalen Klimawandels auf lokale Populationen und die Bedeutungen der Strukturellen Diversität. Auf der anderen Seite liefert diese Arbeit neuartiges Wissen für die generelle Untersuchung von Populationsdynamik und Aussterberisiken. Neue Erkenntnisse in beiden Gebieten der ökologischen Forschung, wie sie in dieser Arbeit gefunden wurden, verbessern unser Verständnis für das Überleben von Population in einer veränderten Umwelt.

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Appendix

Note, Figure A1 is not part of the original thesis. It is, however, included in the submitted manuscript based on chapter 6 (see page 75). This figure was added here for a better understanding of the issue of rescaling to the actual variance (chapter 6).

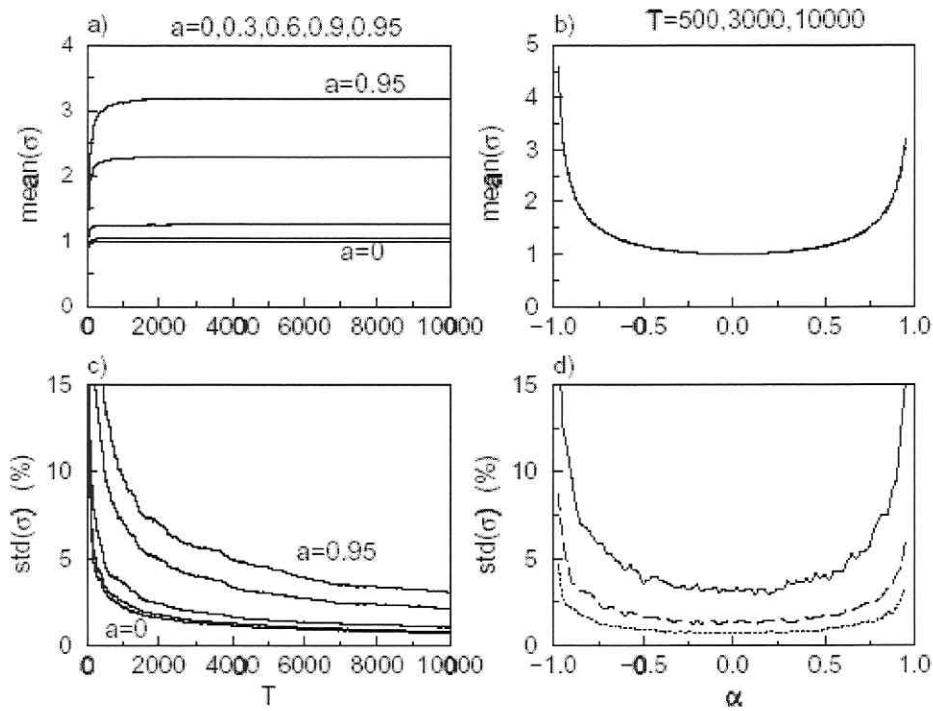


Figure A1: Mean and variability of standard deviation in auto-correlated time series.

Mean, as well as variability of the standard deviation of colored time series from AR_1 process (Eq.6.1) depend on sample length T and autocorrelation parameter α . A set of 200 time series has been generated. No re-scaling technique was applied. For each series the average standard deviation, $\text{mean}(\sigma)$, is shown depending on time series length T (a) and auto-correlation parameter α (b). Moreover, the variability of the standard deviation, $\text{std}(\sigma)$, among repeated simulation is shown (c,d). Note, that there is a high variability in variances for large auto-correlation parameters (d) which also maintains when applying Eq.(6.2) or Eq.(6.3) but is eliminated by Eq.(6.4).