

# Animal Space Use, Second Edition



# Animal Space Use, Second Edition:

*Memory Effects, Scaling  
Complexity and Biophysical  
Model Coherence*

By

Arild O. Gautestad

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# TABLE OF CONTENTS

Preface .....	x
0. Introduction: the broad picture .....	1
0.1 Complex space use from memory utilization.....	1
0.2 Spatially explicit patch selection in behavioural ecology .....	9
0.3 Optimal foraging in stochastic movement models.....	10
0.4 From individual space use to population kinetics .....	13
0.5 Reflection of individual space use at coarse scales.....	15
0.6 Challenging the mean field assumption .....	16
0.7 From mean field to multi-scaled dynamics .....	18
0.8 The statistical-mechanical approach .....	20
0.9 The next step .....	23
1. A large mystery in a little detail .....	25
1.1 The first glimpse .....	25
1.2 Pinpointing a feasible reason for ignorance: KDE.....	35
1.3 Leaving the comfort zone: confronting memory effects.....	38
1.4 The basics of studying individual space use .....	42
1.5 The home-range ghost.....	45
1.6 The next step .....	49
2. Basics of movement physics: the standard models.....	51
2.1 Transitions from deterministic to stochastic movement.....	51
2.2 From mechanistic to statistical-mechanical modelling .....	57
2.3 Behavioural ecology at the statistical-mechanical level.....	61
2.4 Markov compliance and the characteristic scale.....	64
2.5 Markov from another angle: the principle of superposition.....	66
2.6 Linearization of non-linear mechanistic interactions .....	68
2.6.1 Spatial coarse-graining .....	68
2.6.2 Temporal coarse-graining.....	76
2.7 The cross-scale homogenization assumption .....	77
2.8 From non-equilibrium to equilibrium .....	81
2.9 The next step .....	87

3. Approaching memory .....	89
3.1 Preparing to exterminate the home-range ghost.....	89
3.2 Spatial memory from a mechanistic premise .....	90
3.3 Coarse-graining the mechanistic memory model.....	95
3.4 Statistical-mechanical simulation of MemRW .....	98
3.4.1 Model simplifications and simulation methods.....	98
3.4.2 Simulation results.....	100
3.4.3 Conclusion.....	103
3.5 The next step .....	106
4. Movement physics beyond Markov compliance .....	106
4.1 System complexity.....	106
4.2 The memory aspect and resilience to model details.....	109
4.3 Site fidelity under continuous time random walk (CTRW) .....	110
4.4 The next step .....	114
5. Parallel processing: the concept.....	115
5.1 A heuristic introduction to multi-scaled random walk.....	115
5.2 Initial descriptions of the parallel-processing conjecture.....	119
5.3 Parallel processing in later publications.....	124
5.4 Why invoke the parallel-processing conjecture? .....	132
5.5 The next step .....	135
6. Modelling parallel processing.....	136
6.1 Inter-level model coherence and ergodicity .....	136
6.2 Population kinetics: premises for the classical approach .....	137
6.3 Classic population kinetics.....	143
6.4 Population kinetics under the parallel processing premise .....	145
6.4.1 Structure of scale-free space use .....	145
6.4.2 Distribution of space use over a scale range.....	146
6.4.3 Emergence of a scale-free population dispersion .....	150
6.4.4 Mathematical formalism of parallel processing .....	152
6.4.5 Parallel-processing properties .....	154
6.4.6 Dispersion of kinetic energy over a scale range .....	158
6.4.7 Redefining statistical mechanics .....	160
6.5 Statistical properties of a parallel-processing system.....	163
6.5.1 Scale-specific versus scale-free spatial variance .....	163
6.5.2 South state hospitality .....	167
6.5.3 The Z-paradox .....	169
6.5.4 The density dilution issue of classical models.....	173
6.6 The next step .....	176

7. Parallel processing at the individual level .....	177
7.1 Testing inter-level model coherence .....	177
7.2 Simulating multi-scaled random walk (MRW).....	180
7.2.1 The non-mechanistic premise for spatio-temporal memory .	180
7.2.2 The step-generating algorithm: scale-free movement .....	181
7.2.3 Adding site fidelity to a scale-free movement path .....	183
7.2.4 Simulating space use: the generic MRW model.....	184
7.2.5 The characteristic scale and the home-range ghost paradox .	186
7.2.6 Fractal dimension of the spatial dispersion of fixes .....	188
7.2.7 Site fidelity and habitat selection .....	192
7.3 Model extensions .....	193
7.3.1 Strength of site fidelity .....	193
7.3.2 Constraining memory .....	193
7.4 The Lagrangian aspect of MRW .....	194
7.4.1 Step distribution functions.....	194
7.4.2 The distribution hump from site fidelity under MRW.....	197
7.4.3 Lagrangian and Eulerian system aspects .....	200
7.4.4 Truncation and mean free path .....	201
7.5 Distinguishing MRW from composite Brownian motion .....	202
7.5.1 What is composite Brownian motion?.....	202
7.5.2 Applying the parallel shift method to verify scale-free movement .....	203
7.5.3 Simulating multi-level composite Brownian motion.....	205
7.5.4 Simulating scale-free processes.....	207
7.5.5 Simulation results of scale-specific versus scale-free processes.....	208
7.6 Testing for parallel processing: red deer GPS fixes .....	213
7.7 Parallel shift and the statistical-mechanical approach.....	216
7.8 Effect from area constraint on model parameters .....	219
7.9 Density distribution of fixes.....	225
7.10 The next step .....	229
8. Movement classes at the statistical-mechanical level.....	230
8.1 Testing protocols for movement class compliance .....	230
8.2 The scaling cube .....	234
8.3 Parallel processing: planning for the future .....	242
8.4 Summary of individual-level test protocols .....	243
8.5 Path analysis and cross-scale complexity .....	244
8.6 The next step .....	246

9. Is parallel processing applicable to invertebrates?.....	247
9.1 Classifying path integration in insect movement .....	247
9.2 Exploring complex population kinetics in sycamore aphids .....	248
9.3 Sycamore aphid data .....	252
9.4 Hypotheses for local dispersion of aphids .....	255
9.4.1 Outline for the study.....	255
9.4.2 Method 1: the density distribution.....	256
9.4.3 Method 2: the variance-mean relationship .....	257
9.4.4 Method 3: testing for dominance of movement rate.....	257
9.5 Results.....	258
9.5.1 Local correlation of abundance .....	258
9.5.2 The density distribution.....	260
9.5.3 The variance-mean relationship .....	261
9.5.4 Testing for dominance of movement rate .....	264
9.6 Summary and concluding remarks.....	265
9.7 The next step.....	266
10. Intrinsic complexity: 1/f noise and the scaling paradox .....	267
10.1 Population availability over space and time.....	267
10.2 Chaos and self-organized criticality.....	270
10.3 Linking alternative descriptors of complexity .....	273
10.4 The power spectrum.....	274
10.4.1 Fourier transforms and reddened spectra.....	274
10.4.2 Flicker noise .....	276
10.4.3 Invoking a grain/window conjecture to quantify complex spectra.....	280
10.4.4 Complexity may require an extra Cartesian coordinate....	284
10.4.5 Linking 1/f noise to the variance-mean relationship .....	286
10.4.6 Variability of intrinsic and extrinsic origin .....	288
10.5 Red noise of extrinsic origin .....	289
10.5.1 Local causality means a serial process .....	289
10.5.2 A serial process has a characteristic response rate .....	290
10.5.3 Flicker noise, ergodicity, and environmental stochasticity .....	294
10.6 Flicker noise in a time series: coffee leaf miner.....	295
10.7 The next step.....	297

11. Implications and applications .....	299
11.1 What does multi-scaled movement really mean?.....	299
11.2 Two variants of the standard model.....	300
11.3 Standard model variants: implications for applications? .....	305
11.4 Markovian, multi-scaled movement: the evidence?.....	306
11.5 Scrutinizing empirical support for mode-switching.....	307
11.6 Implications for theoretical ecology.....	315
11.7 Implications for applied ecology.....	316
12. Concluding remarks.....	323
Appendix A. Influence from fix sampling interval.....	328
A.1 Scale-specific movement process: from CorrBM to BM.....	329
A.2 Scale-free movement path: Lévy walk.....	330
A.3 Scale-free movement with site fidelity: MRW.....	332
References .....	333
Subject Index .....	350

## PREFACE

A preface normally presents a brief background for a book's content. The present outline is more extensive. Given the theoretical challenge with respect to making sense of animal space use in a realistic and coherent manner, I have chosen to enlarge this section in two directions. First, some basic memory- and scale-related concepts are described. Second, some main points from each chapter are outlined and given some introductory comments. Hopefully, these enlargements of the preface will provide a valuable theoretical preparation to the main body of the book. It should in fact be read as an introduction to the introduction.

Animal space use may be conceptualized and modelled at two levels, individual and population. At the individual level movement, ecology is a field in rapid theoretical progress (Nathan *et al.* 2008, Smouse *et al.* 2010, Viswanathan *et al.* 2011, Lewis *et al.* 2013, Humphries and Sims 2014, Méndez *et al.* 2014). Population ecological theory has also matured; with emphasis on spatially explicit model designs, age-structured dynamics, and multi-species interactions (Hiebeler 1997, Keeling 1999, Turchin 2003, Hanski and Gaggiotti 2004, Ranta *et al.* 2006). However, the main theme for the present book is not ecological inference, but rather a critical evaluation of the biophysical framework implicitly assumed when making ecological inference. “Biophysical” does in this context specify a meso-scale observational level of movement and space use.

For example, when studying individual space use, this level is reflected in a sample of GPS fixes where behavioural modes and movement-influencing events are hidden at finer temporal resolutions than the sampled path. The temporal scale interval from the fine-resolved movement path to the sampled path (leading to a set of relocation dots on the map, rather than a continuous line) is referred to as “the hidden layer” in this book. At the population level the hidden layer is best reflected by the spatial resolution of the study. This resolution determines local population density; number of individuals per spatial unit at this resolution; and at a chosen temporal resolution (a day, week, or year, depending on context). Again, the actual biological events and interactions like individual searching, feeding, courting, resting, and a myriad of other

aspects are spatially and temporally fine-grained processes being executed by the population's constituents at micro-scale below the resolution for the study; i.e., below the hidden layer.

Whether we consider local density of GPS fixes from a given individual as accumulated over a sampling period or local population density representing a snapshot of individuals' whereabouts, we have changed focus away from direct observation of biological processes at micro-scales. Instead we perform indirect observation of these processes at a coarser resolution; the biophysical system representation. The hidden layer, which has both a temporal, a spatial, and a scale range dimension, is a core concept under the extended framework for analysis of animal space use to be presented in this book. Observe that I define scale range as an independent aspect of time and space. I define this dimension as a scale range, not a specific scale. This dimension reflects the depth of the hidden layer. In process terms the deeper the layer the clearer the difference between the fine-grained biological scales and the coarse-grained biophysical scales.

Such system coarse-graining is common in ecological research both at the individual and the population level, but the transition from a biological to a biophysical system abstraction is only rarely explicitly acknowledged. This is unfortunate, for three main reasons. First, the biophysical approach opens the door towards a huge theoretical framework, "statistical mechanics," which few biologists are trained in or even consider relevant. Second, statistical mechanics in its present state is—in my view—unfortunately not sufficiently extensive to cover the kind of biophysics generally applicable to animal space use. Third, this discrepancy has led to implicit application in ecological theory of principles from classical statistical mechanics—as a consequence of invoking the hidden layer for system modelling—despite the intrinsic issue that the current framework is based on assumptions that are frequently violated by animal space use behaviour. This book circulates among these three aspects and in particular the third one. Hence, proposals for extensions of the traditional biophysical framework percolate the chapters, for the sake of—hopefully—stepping towards a more realistic biophysical representation of animal space use.

Scrutinizing the foundation of ecological models based on the hidden layer is not a walk in the park. It implies that movement ecology's standard toolbox (containing model designs and statistical protocols, see Box 1 towards the end of the preface) is rattled with respect to applicability of

very general assumptions (Box 2). A critical evaluation of the foundation of individual movement models by necessity percolates to the population level, where I put a corresponding set of core assumptions under scrutiny. At respective levels—individual space use behaviour and population dynamics—the specific assumptions I refer to are in fact so deeply buried under layers of historic consensus that they are rarely explicitly mentioned in ecological analyses that depend on their support (Gautestad and Mysterud 2005, Gautestad 2011, 2013b). For some, this consensus may simply reflect “case solved”; others are not so confident. Here are examples of opposing views:

*It seems to me to be beyond doubt that population ecology has a mature theory.*

Turchin (2003), p. 392

*It is time to acknowledge the need for a scathing indictment of the poor practices that have accumulated in species distribution modelling over the decades.*

O'Connor (2002), p. 33

Does the book's focus on modelling theory and accompanying assumptions make it peripheral to a general audience of animal ecologists? Definitely not! Ecology regards the branch of biology that deals with the relations of organisms to one another and to their physical surroundings. What regards animal space use and population dynamics, the basic level of ecological inference regards exploration of (a) why intensity of habitat use is stronger in some places than other places (and/or other times), (b) how this insight may produce predictions about space use intensity at other locations, and (c) what kind of statistical consistency may be expected when changing observational scale (spatial or temporal resolution; changing the depth of the hidden layer). From this broad perspective the present book drills to the core of animal ecology by proposing both revisions and enlargements of the generally applied biophysical space-use framework, which currently provides conceptual and predictive models for ecological inference.

Any ecologist with field experience will agree that animal space use is more challenging than appears in textbooks. From a trivial perspective this may be because of insufficient data or too simplistic models. Even larger samples of GPS relocations, improved GIS data, and more fine-grained population monitoring should then suffice to resolve the challenges at hand. The model might also gain from additional terms to cover the system in more detail. Such a quest for improved system details may also need to be supplemented by considering the given model foundation at a



deeper theoretical level. I advocate that an explicit application of the biophysics of space use that is most relevant for the given system should determine the most realistic set of models for ecological inference. In this book I present eight such conditions, called biophysical universality classes, for animal movement and space use. In statistical mechanics, universality is the observation that there are properties for a large class of systems that are independent of the dynamical details of the system. Unfortunately, at present only one of these classes provides the foundation for most of ecological theory, and two others are only now slowly making a broader entry. The other five classes are probably totally unfamiliar to you. In my view, the broadly applied class of movement is stretched to the extent that the model assumptions become unrealistic for many scenarios. Old challenges and even paradoxes that haunt the present arena may thus find better solutions in the extended system containing a broader range of universality classes. Hopefully you will agree after reading the following chapter that the eight classes present great opportunities for a more diversified arena for realistic model representation of animal space use both at the individual and the population level.

In a concrete example of the potential shortcoming of the dominating class (yes, I will define it in more detail shortly), consider space-use intensity. What is space-use intensity? According to the dominating system class, it may be represented by local variability of *density*, either the spatial dispersion of GPS relocations (individual level) or the dispersion of individuals themselves (population level). However, an individual or a population may express higher space-use intensity in some parts of available space even when the habitat characteristics seem similar to less utilized areas. There may be many reasons for this apparently paradoxical pattern, but in this book I'm focusing on some intrinsic drivers. In particular, by diversifying between eight biophysical universality classes for movement and space use, I bring you into the arena of process complexity. Complexity is qualitatively different from complicatedness (for example, for adding more terms to a model). Basically, space-use complexity may boil down to explicitly considering the "scaring" properties (from a system modeller's perspective) of site fidelity and philopatric behaviour on the individual level and intra-specific population cohesion from conspecific attraction at the population level. In other words, it regards the behavioural tendency to constrain space use despite living in an open environment.

The common denominator of complexity seems to be influence from temporal and spatial memory influence on space use. Why are memory effects so scaring from a theoretical point of view? Because the structuring

force that emerges from this important biological capacity involves positive (self-reinforcing) feedback loops, which is mathematically difficult to handle and formulate in models under the dominant biophysical universality class. The “balance of nature” idea, which basically rests on negative rather than positive feedback loops, becomes further undermined in the context of animal space use, lending support to critics of this dogma (Andrewartha and Birch 1954, Nicholson 1954, Pimm 1991, den Boer and Reddingius 1996) but from another and perhaps surprising theoretical angle. Consideration of spatial memory effects as an important intrinsic driver for space-use complexity opens for a new direction of system conceptualization and process modelling. In other words, a wider range of biophysical universality classes is needed to make complexity less scaring and, in fact, both theoretically and *empirically* fascinating! The broader system offers great opportunities for ecological inference.

A system abstraction is represented by models, whether these regard equations for static relationships (like statistical correlations) or dynamical simulation algorithms. If some core assumptions for the actual model are violated by the dynamics of a specific individual or population it is meant to represent, one may easily run into a dead end: even more data will not produce substantially improved results. On the contrary, it is common in animal space-use research to find that more data tend to blur results that emerged from shorter series. From such frustrating experience one should be open-minded to explore alternative paths—a wider range of universality classes. If such an extended toolbox provides theory for better compliance with the actual organism at the given place and time, one should retest the actual hypothesis under more context-realistic assumptions. One may then expect improved clarity with respect to ecological inference from a given data set. Consequently, the study of the relations of organisms to one another and to their physical surroundings has two main directions for improvement: extended data and extended theoretical foundation with respect to universality classes. Acknowledging this trivial duality will bring animal ecology closer to hard science, like we envy physicists who achieved this level of theoretical maturity a long time ago.

This book presents a general process approach (Box 3) towards understanding and modelling individual movement and population dynamics, in quite cotton-less wrapping in some sections, I must admit (a benefit that presents itself from writing a book rather than a journal paper). The reason to drill to the core of the biophysical aspect of animal ecology is a pile of quite generally verified empirical patterns which seem to defy classical system representations. Despite a growing menagerie of sophisticated

statistical analyses under what I will define as the classical toolbox compartment (under the dominating universality class), interpretation and dynamic modelling of some of these aspects seem to ignite both confusion and controversies, in particular in movement ecology, where studies involving additional universality classes are now emerging (Benhamou 2007, 2008, Reynolds 2008, Edwards *et al.* 2012, Gautestad 2012, Humphries *et al.* 2012, Sims and Humphries 2012, Boyer and Solis-Salas 2014). The distance to consensus still seems to lie well beyond the horizon. In fact, while the horizon for some looked close a few years ago, others may—from the ongoing theoretical discussions in movement ecology—advocate that a general agreement on the sticking issues is sliding further away owing to the multitude of complex aspects that continue to expand (Fagan and Calabrese 2014, Fleming *et al.* 2014). In this book I explore whether an explicit definition and exploration of eight universality classes—in tandem with an explicit consideration of the hidden layer—may contribute to resolving some paradoxes. Exciting times, indeed!

I'm confident that the present book provides food for thought, whether you are a theoretician, an empiricist in a field of applied ecology, or somewhere in between. I suspect that if you are working in wildlife management but are also keeping an eye on developments in theoretical ecology, you may get the largest upshot. Personal experience with the study objects may already have led you towards a similarly critical attitude with respect to some aspects of mainstream theoretical models. Perhaps you will be surprised by some of the statistical model assumptions under present scrutiny, and you may even immediately agree on the critique and/or ideas for an extended model framework that is outlined. Alternatively, you may find the ideas provocative but sufficiently interesting to pilot test some of them on your own data. Whether you find empirical support for the alternative system or not, your results will be important for further clarification of the proposed directions. In order to determine success or failure, the present ideas and directions do of course require the same process of scientific scrutiny from peers as I'm performing here on the standard model designs. This book thus provides a combination of paradigm critique, presentation of alternative approaches, and respective outlines for how these extensions may be tested empirically.

Many of the nagging issues in focus here are not new. Here are some quotes from twenty- to thirty-year-old publications:

*... when they are nectar-feeding, the flight patterns of butterflies cannot be simply described as correlated random walks. We do not know what complications might be involved in nectar-feeding that violate the simplifying assumptions ...*

Kareiva and Shigesada (1983)

*It has proven extremely difficult to model how animals interact with the habitat dynamics through processes such as habitat selection, foraging site choice, and juvenile dispersal. The basic problem is that animals interact with the habitat at several spatial and temporal scales, using behavioral cues and experience (memory maps) in complex and poorly understood ways.*

Walters (1992)

*... real-life movement distributions may have complex forms that are not amenable to explanations using simple models.*

Porter and Dooley (1993)

*Exactly how the translation from individual movements to population distribution and interactions should be accomplished is one of the most vexing problems confronting a metapopulation-landscape synthesis.*

Wiens (1997)

Where do these old challenges stand today? The complexity revealed by analysis of individual space-use data—lately mainly based on GPS-based relocation series—may be summarized by two properties; on one hand the quite broad verification of multi-scaled movement (Viswanathan *et al.* 2011, Humphries *et al.* 2012, Sims and Humphries 2012), and on the other hand a general recognition that individual memory map utilization by vertebrates and perhaps some branches of invertebrates is the rule rather than the exception (Frank 1964, Morris 1981, Collett *et al.* 1986, Garber 1989, Rodriguez *et al.* 1994, Bailey 1995, Ostfeld and Manson 1996, Sherry 1996, Mendl *et al.* 1997, Beekman and Ratnieks 2000, Burt de Perera 2004, Boyer *et al.* 2006, Merkle and Wehner 2009, Wolf *et al.* 2009, Levett and Walls 2011, Pokorny *et al.* 2014). Both aspects, memory and scaling, may turn out to represent two sides of the same coin, as will be explained later in this book. The concepts of single-scaled, multi-scaled, scale-free, and memory-influenced movement are defined in Box 4. In fact, this scaling/memory duality hypothesis is, to my knowledge, brand-new and is presented here in explicit detail for the first time.

To account for the observed process complexity from scaling and memory, various directions of research have emerged. The dominating approach in movement ecology is to apply mechanistic model designs with increased

level of mathematical and computational sophistication (van Moorter *et al.* 2009, Song *et al.* 2010, Giuggioli and Bartumeus 2011, Moorcroft 2012, Reynolds 2012, Spencer 2012, Fronhofer *et al.* 2013, Lewis *et al.* 2013, Nabe-Nielsen *et al.* 2013, Benhamou 2014, Humphries and Sims 2014, Méndez *et al.* 2014, Merkle *et al.* 2014). These approaches are generally constructed under the umbrella of classic model assumptions, referred to as the standard group of universality classes in the biophysical framework. They have contributed not only to greatly improved model realism by explicitly considering memory and scaling effects, but they have also led to a broader realisation of the system complexity—and theoretical challenges—at hand. Consequently, an extremely dynamic melting pot for biologists, physicists, and statisticians has now emerged.

However, this dynamic field of research is still for the most part contained within the walls of the theoretical pool provided by classical biophysics. In this book I explore an alternative direction to “stretching the string” under mechanistic modelling principles when approaching the complexity of memory effects. I describe concepts and models where I invoke elements from an extended framework, based on *non*-mechanistic system assumptions for some of the universality classes. In this respect, the term “non-mechanistic” in the context of system dynamics is theoretically challenging (and provocative!) and explicitly elaborated on here for the first time: I argue for the need to distinguish between two types of dynamics: mechanistic and non-mechanistic. Non-mechanistic dynamics? Strange, indeed! However—as will be described in this book—a potentially problem-solving concept with respect to animal space use. Non-mechanistic dynamics require—according to the arguments and accompanying support—model formulations based on statistical-mechanical principles (Box 5), which in this system representation (and opposed to classical statistical mechanics) explicitly rests on premises of scale-free and memory-dependent space use.

The term “statistical-mechanical” may sound strange and perhaps even outright scary from a biologist’s perspective, invoking concepts from thermodynamics like mathematical- and probability-theoretical heavy concepts. However, rest assured that the present book is relaxingly simple in this respect. I apply some core principles from statistical mechanics to design the extended theoretical framework, but the equations are in the present context very simple. The challenge is primarily at the conceptual and cognitive level: how to imagine the difference between the mechanistic and the non-mechanistic modelling approach, how to define and formulate the difference between micro- and meso-scale process

properties in this respect, and so on. This is where the hidden layer, already referred to, becomes a key concept.

I argue that observationally coarse-graining the process under scrutiny and thus invoking the hidden layer may provide a necessary operation to make sense of some central parts of a complex system's dynamic and statistical properties, in particular with respect to its emergent properties (to be defined in other chapters). In other words, where spatial memory and scaling are involved, the hidden layer approach (and thus a statistical-mechanical system representation) may be necessary for improved predictive power of ecological models of animal space use. The following chapters basically regard exploration of this obviously controversial working hypothesis from many angles, both from the individual and the population level of system abstraction. With this biophysical foundation one should be better equipped to perform studies involving ecological inference.

While mechanistic model designs regard micro-scale behaviour like detailed movement rules and local rates of change at fine temporal resolutions, a statistical-mechanical description describes the system states and dynamics at meso- and macro-scale resolutions (coarse-graining; see Box 4 and Box 5). In a nutshell, the distinction between the stretching-the-string approach (enhanced mechanistic modelling) and the alternative path outlined here regards the toolbox-extension referred to above, where the traditional compartment embeds the mechanistic framework and its complementary classical statistical-mechanical representation. The other compartment carries the novel label “non-mechanistic,” and contains the (extended) statistical-mechanical system representation only. This implies that—at least at this stage—I have not been able to formulate a logically and mathematically coherent dynamic representation of micro-scale non-mechanistic animal space use that fills the role of mechanistic models *below* the hidden layer in the classical framework. My present working hypothesis is that it does not exist. In other words, non-mechanistic dynamics may actually *require* conceptualization as a meso-scale (statistical-mechanical) process, as will be described from many angles in this book.

“Non-mechanistic” does not—in this context—represent “static.” Non-mechanistic and mechanistic models represent different subsets of universality classes for dynamic processes. As you will learn in various chapters of the book, mechanistic models will appear as the limiting case where non-mechanistic dynamics are squeezed towards a mechanistic

system, conceptually similar to a non-linear equation tuned towards a linear one. Thus, non-linearity is the general case, while linearity represents the exception (albeit more frequently applied, owing to simpler mathematics). These concepts will become clearer over the following chapters. The goal for both toolbox compartments—mechanistic and non-mechanistic—is of course improved theoretical coherence between movement theory and real data, for the sake of improved protocols for ecological studies involving both animal movement and population dynamics. However, owing to a broadened toolbox for system representations and ecological analyses, new pathways for analysis of complex systems become available. An additional string to stretch becomes available.

I describe how the alternative model premises may be conceptually and mathematically formulated to allow the respective hypotheses to be statistically tested against the traditional model premises at a very basic level of system design. In other words, does the contrarian set of ideas and hypotheses presented here make sense? Do they provide advantages when confronted with real data and applied in ecological studies? Some of the proposed tests are summaries of already published methods; others are described here for the first time. A potential for actual applications of these ideas and model constructions in follow-up ecological research is outlined. I also highlight some consequences of ignoring a closer scrutiny of the actual premises in contemporary theory on movement and population ecology. In particular, a statistical and/or dynamic modelling framework that depends on compliance with a memory-less process—while the actual dynamics do not comply with this premise—will both inflate the error term in the analyses, leave it open for misinterpretation, and even create paradoxical results.

All these aspects are exemplified in many contexts throughout the book. For example, in the last chapter; *11 Implications and applications*, I argue that the empirically verified knowledge that animals are able to relate and respond to environmental conditions over a range of spatio-temporal scales (the concept of multi-scaled movement) seems to have become theoretically derailed. The mechanistic class of individual-based models and accompanying mathematical formulations that dominate this field depend on the study object actually ignoring its memory capacity to execute goals at several spatio-temporal scales in parallel—perhaps the strongest source of information-sorting the animal has when relating to its environment beyond its current perceptual field!

Attacking the memory and scaling aspects from the present book's perspective is a formidable theoretical and perceptual challenge, despite relatively simple mathematical and statistical-mechanical formulations at this stage. This volume is only a toe-dipping into what may emerge as a deep and wide ocean for future research—or conversely, the approaches may in due course turn out to be a futile attempt to penetrate the complex issues at hand. One should always seek to balance optimism and confidence with a self-critical attitude. However, given the fact that I finally dare to synthesize the extended individual/population level theory into a book format reflects that a certain level of confidence has been reached. Each chapter could indeed be the theme for separate books. I hope that the collection of ideas, concepts, mathematical formulations, simulations, and empirical tests should at this stage appear sufficiently mature and empirically supported by pilot tests to be of interest for a broad audience. However, be warned that some of the elements of the proposed framework extensions are still highly speculative, and others are at this stage only supported by a limited range of empirical pilot tests. Thus, in these sections I'm rattling a wasp nest with limited protective gear.

The presentations should not be considered reviews of the respective aspects; the topics are too diverse and wide in scope to allow for this. As a background for the evolution of general movement models towards improved realism, the recent review by Smouse *et al.* (2010) is a good choice, since it covers—in an introductory manner—both the memory and the scaling challenges. Additionally, as an introduction to the physical aspects of scale-free movement, I recommend the review by Zaburdaev *et al.* (2014).

The multi-scale space use aspect of animal ecology is of particular importance in the present context. The recent critics of basic models in this field have been raised by and large in two disparate theoretical environments. On one hand a growing group of scientists are studying the property of scale-free movement (Box 4), which recently has been empirically verified in large GPS data sets from a broad range of species (Sims *et al.* 2008, Humphries *et al.* 2010, Humphries *et al.* 2012, Sims *et al.* 2012). On the other hand, a consensus is now emerging where it is acknowledged that spatial memory effect on movement and habitat choice has received insufficient attention by ecologists (Frank 1964, Börger *et al.* 2008, van Moorter *et al.* 2009, Levett and Walls 2011, Nabe-Nielsen *et al.* 2013, Pokorny *et al.* 2014). The first group generally ignores aspects related to spatial memory (site fidelity from cognitive map utilization). The other group generally ignores the scale-free aspect of movement. An



integrative approach is thus clearly needed, as already indicated in Box 5. Such an integrative approach would fit nicely into classic ecological concepts like top-down and bottom-up space-use strategies [for a recent overview and model formulation, see Vergara *et al.* (2015)].

To summarize, in the present book I support the view that the classical toolbox for models in the respective fields of scale-free movement and memory-utilizing space use may be insufficient to mimic many animals' behaviour (Gautestad and Mysterud 2005, 2010b, Song *et al.* 2010, Boyer *et al.* 2012). Consequently, one should—from this premise—build an extended theory brick by brick, starting by defining testable hypotheses related to universal or generic system descriptions. In this book I advocate that even a redesign of the biophysical frame of reference may be needed to understand systems showing intrinsic process complexity from the combined effects from scaling and memory. This regards what I called non-mechanistic system dynamics above, which—without this redesign and framework extension—will present itself as a contradiction in terms! By defining eight universality classes of animal space use and their respective transitions, this statistical-mechanical foundation hopefully provides a constructive starting point for deeper theoretical spin-offs. The ultimate goal is—from my personal background—a more coherent modelling toolbox for ecological inference both at the individual and the population level of analysis. However, by challenging the mechanistic paradigm in the context of modelling memory-influenced space use—and additionally proposing an alternative kind of dynamical framework for this condition—I'm definitely rattling the wasp nest.

In Chapter 0, *Introduction: the broad picture*, I elaborate on the general themes raised above, with weight on the individual/population duality from the perspective of complex system dynamics. The chapters following this introduction will then start out with a detailed practical illustration of studies on individual space use and the underlying system assumptions, continuing in the direction of stronger reference to population level dynamics in general and between the two levels in particular.

Chapter 1, *Large mystery in a little detail*, gives a brief overview of how the individual-level topics of this book got their initial kick-start with respect to biophysics of space use. As in all research, locking in on a new direction often starts with a frustration. In the present case it was the contradiction that observed space use by some animals on one hand seemed to be spatially stationary while on the other hand expanded non-trivially with observation intensity (sample of spatial relocations,  $N$ ).

Observed space use not only expanded non-asymptotically and thus violated expectation, but in accordance to a power law and with a power exponent that was consistent between data sets from various species. In Chapter 1, I provide a walk-through of the stepwise developments towards a solution of the paradox after raising and falsifying the most obvious explanations based on classical system assumptions.

It should take more than twenty years before an explicit adjustment for sample size effect according to the “home range ghost” formula (presented in Chapter 1) is applied by others as a premise for ecological analysis of relocation data (Morellet *et al.* 2013, Campos *et al.* 2014). Finally, other researchers in the field of complex movement are also beginning to publish what seems to support home-range ghost-compliant space-use patterns, with accompanying model proposals that resemble some of the ideas summarized and extended in this book (Song *et al.* 2010, Boyer *et al.* 2012, Boyer and Solis-Salas 2014, Fleming *et al.* 2014).

More explicitly, in a recent paper Merkle *et al.* (2014) tested a set of contemporary hypotheses on memory-influenced movement in free-ranging bison, *Bison bison*, and found support for a central premise of the present theory (the MRW model) in the summer ranges of bison movement. Multi-scaled random walk (MRW) is our approach towards statistical-mechanical simulation of the combination of scale-free and memory-influenced space use. Returns of bison to familiar patches were quite independent of physical distance to these patches and time since last visit, implying that even relatively distant resource experiences were appreciated despite energy costs to reach these locations. Hence, spatial memory utilization seemed to be an important component of this species' optimal foraging strategy and connection to familiar sites-influenced movement. In another study, foraging by Japanese Black cows *Bos taurus*, the animals discriminated preferred patches from others before they visited the patches to eat (Hirata *et al.* 2014), in compliance with previous findings (Gross *et al.* 1995) but with more explicit revelation of patch utilization as a two-step process; choice of where to move and decision when to leave. In other words, they utilized spatial memory to return non-randomly to previously rewarding patches. These results also showed that time since last visit was subordinate, given that the actual patches had been sufficiently rewarding in the past.

I find the results by Merkle *et al.* and Hirata *et al.* both encouraging and inspirational since they lend support to a basic premise of the generic MRW model (ignorance of time and distance with respect to return targets,

but both properties may be adjusted slider-like), in addition to supporting memory map utilization. However, it remains to be seen if these aspects of grazing behaviour are generally applicable beyond ungulate species. Theoretical developments that resemble the MRW approach are now also taking place from a mathematical angle; with recent papers from Boyer et al. (Boyer and Romo-Cruz 2014, Boyer and Solis-Salas 2014) as prime examples.

In Chapter 1, I suggest a feasible reason—backed up by recent third party research—why the home-range ghost paradox (Gaustestad and Mysterud 1995) still has not been more generally recognized among wildlife ecologists, more than twenty years since its presentation and subsequent empirical support. The most widely acknowledged method to demarcate space use from a set of relocations—the Kernel Density Estimate (KDE) (Worton 1989)—has an Achilles’ heel, as verified by relatively recent simulations and application of KDE on real data. KDE produces isopleths; contour lines representing expected equal-sized intensity of space use given the actual sample of relocations (fixes),  $N$ . If the dynamics behind the pattern do not comply with standard statistical assumptions, the demarcated area from KDE will overcompensate for the effect from change in  $N$  (Belant and Follmann 2002, Barg *et al.* 2005, Fieberg 2007, Fieberg and Börger 2012, Schuler *et al.* 2014). In other words, the home-range ghost paradox from non-asymptotic space-use demarcation with increasing  $N$  (based on a non-parametric protocol for area demarcations) may be camouflaged by violation of a specific statistical assumption under the KDE protocol. Crucially, this hypothesis is supported by applying simple, non-parametric demarcation methods described in Chapter 1.

In Chapter 2, *Basics of movement physics: the standard models*, I turn more explicitly towards the biophysics of animal movement. This is important background for what follows. Starting with very basic principles and illustrations (and a few simple equations), I describe the current paradigm for movement dynamics and the transitions between (a) deterministic-mechanistic models, (b) stochastic-mechanistic models, and (c) a mixture of the two as representation of animal space use. In particular, I describe how the common denominator—the mechanistic approach—depends on a shared assumption with respect to the dynamics: Markov compliance. In statistical-mechanical terms a Markovian process reflects a system close to local equilibrium. An animal makes a move based on a superposition of local movement-influencing factors at that point in time. These factors embed both environmental influence (for example, attraction and repulsion) and internal state (for example, hungry

or frightened). At successive moments previous factors are already reflected in the animal's current location, and new influences are leading to new moves. In absence of further change in these conditions the animal is expected either to stay put or to unidirectionally continue to move forward with a constant speed.

In simple systems, like a bouncing billiard ball, a deterministic-mechanistic model reflects the actual process well; principles from differential and integral calculus may be applied to describe it realistically. In other systems like a moving individual where motion is influenced by a myriad of factors from one point in time to the next, the deterministic-mechanistic approach is typically replaced by a stochastic-mechanistic model. Creating a large equation with many terms for the respective influences (in order to keep the model deterministic-mechanistic) will in this case be counterproductive. The archetypical stochastic-mechanistic function is a Brownian motion model. Movement satisfying a Brownian motion process leads to classical (so-called Fickian) diffusion at the population level and, consequently, provides the necessary support for application of classical calculus to model the dynamics of both individual space use and population dispersion. Again—as for the deterministic system description—a stochastic-mechanistic model may provide realism and thus high predictive power, given that the Markov premise is satisfied.

Markov compliance is a very convenient assumption both from a modeller's perspective and with respect to statistical analysis of empirical data. Accepting the Markov premise *a priori* allows for application of a mature and broad toolbox of classical and contemporary mathematics and statistical methods. This approach rests on the theory of standard statistical mechanics. Fine-grained Markov-based theory, represented by mechanistic models and “standard” statistics, provides the backbone of movement ecology in particular and idealization of animal space use in general both at the individual and the population level.

What if Markov is not satisfied? The answer seems simple, but difficult to digest: remove differential and integral calculus from population dynamical theory, and little remains. Remove Brownian motion (and variants like correlated random walk with or without environmental bias) from movement ecology and little is left there as well. These broad theoretical foundations rest on the Markov assumption as satisfied for the underlying process. Consequently, the core question raised in this book is this: may a Markovian biophysical framework be extended to account for spatial memory and multi-scaled dynamics in a realistic manner? There are

currently many theoreticians in the Yes camp, where sophisticated mechanistic models are now flourishing. This book—on the other hand—represents the (non-crowded) No camp, where a conditional “No” is raised as a testable working hypothesis by scrutinizing the statistical-mechanical premises on which the Yes camp depend. The No answer is conditional, since I advocate that a distinction between mechanistic and non-mechanistic dynamics is needed. There are obviously a large number of systems and a range of observational scales where the Markovian framework not only suffices but is the correct choice. However, in my view there are also a large number of systems for which the Markovian framework should be considered unrealistic. Thus, the answer Yes should not be accepted *a priori*, but should be verified empirically as a realistic premise for the system in question.

Alternatives to the Markovian methods in general terms are the theme of Chapter 3, *Approaching memory*, and Chapter 4, *Movement physics beyond Markov compliance*. Here the Markov assumption in the classical biophysics of animal movement is scrutinized theoretically. As already mentioned, the rapid growth of the field of movement ecology has been sparked by two main directions of research; on one hand a recognition of scale-free movement and on the other hand a more sophisticated modelling of spatial memory influence. Designing dynamic models where memory-influenced space use (site fidelity) is explicitly considered are now popping up and growing in sophistication (Gautestad and Mysterud 2010b, Song *et al.* 2010, Boyer *et al.* 2012, Gautestad and Mysterud 2013, Nabe-Nielsen *et al.* 2013).

Interesting models have begun also to invoke non-Markovian mathematics in this respect: continuous time random walk (CTRW) to mimic scale-free movement and biased random walk to mimic scale-specific but memory-influenced movement (van Moorter *et al.* 2009, Bartumeus *et al.* 2010, Giuggioli and Bartumeus 2011, Spencer 2012, Nabe-Nielsen *et al.* 2013). Implementation of temporal (but not spatially explicit) memory effects on movement by applying the CTRW approach (Giuggioli *et al.* 2006, Bartumeus *et al.* 2010) may seem to contradict my claim above that a mechanistic model by necessity has to be Markov compliant. However, I argue in Chapters 3 and 4 that the respective model classes are—in a *statistical-mechanical* frame of reference—in fact Markov compliant. The apparent contradiction is resolved by considering that the mathematics of scale-free movement may be non-Markov (current behaviour is influenced by the past in a slowly decaying manner), while the statistical-mechanical

application of this class of mathematics implies a Markovian interpretation. This aspect will also be elaborated on later in the book.

Similarly, mechanistic models describing spatially explicit memory-influenced movement—resulting in site fidelity under some parameter range—also describe a slowly decaying influence from past experiences on present movement behaviour, in the form of a potential drift towards locations that were visited in the past (Börger *et al.* 2008, Dalziel *et al.* 2008, van Moorter *et al.* 2009, Song *et al.* 2010, Spencer 2012, Fronhofer *et al.* 2013, Nabe-Nielsen *et al.* 2013, Boyer and Solis-Salas 2014). While this may sound non-Markovian, it is not. Biophysically, the memory influence is implemented as a “field” force. This field regards the directional bias towards historically visited locations, owing to utilization of spatial memory. At every point along a movement path, the direction, directional persistence, and movement speed are determined by a resultant vector where the influence from the memory field represents one of many components of movement. The memory-invoked vector field implies that the next displacement is recalculated on a moment-to-moment basis.

In summary, I advocate the need to make a distinction between models where (a) the memory influence is processed in a sequential and immediate manner and thus leading to micro-scale local/temporal equilibrium in statistical-mechanical terms at the model's time resolution (increments), and (b) memory influence where such micro-scale equilibrium cannot be expected. The first variant regards mechanistic and thus Markov-compliant modelling while the latter regards the extended toolbox proposal; non-Markovian and non-mechanistic system dynamics represented by parallel processing.

In Chapter 5, *Parallel processing: the concept*, I confront the third direction of contemporary space-use models at the individual level: integration of scale-free movement (direction 1) and spatial memory-influenced movement (direction 2). Applying a statistical-mechanical approach, the concept of parallel processing—as opposed to Markov-compliant processing—is outlined. Parallel processing regards system dynamics, but in a non-mechanistic sense. I suggest that a statistical-mechanical representation is not only an option but a necessity to model this kind of process. This direction of memory implementation is—according to the parallel-processing postulate—incompatible with mechanistic principles in biophysical terms. In a stepwise manner the concept of parallel processing has matured from a loosely defined graphical illustration in our publications in the 1990s to more

mathematically and biophysically formulated models over the last ten years or so. In the present description additional elements of the parallel-processing framework are introduced.

I show how the application of the parallel-processing postulate has resulted in theory and space-use simulations that seem to resolve specific paradoxes. Under this conjecture the actual system properties appear paradoxical only from the perspective of classical premises. Crucially, statistical expectations from parallel processing are now in the onset of being supported by larger and better empirical datasets, where the falsified null hypothesis is based on Markovian statistics (Gautestad *et al.* 2013, Gautestad and Mysterud 2013).

Chapter 6, *Modelling parallel processing*, transforms for the first time the concept of non-mechanistic space-use dynamics at the individual level to the framework of statistical mechanics at the population level. Several new aspects and specifications are introduced. For example, the principle of ergodicity and inter-level system coherence between individual movement and population dynamics is here outlined in more detail. I propose in a biophysical (statistical-mechanical) context how kinetic energy of scale-free space use should be expected to be distributed in a self-organized manner over a scale range. Also for the first time, I describe a population-level simulation model of parallel processing, the “Zoomer model”. The model allows for “fine-tuning” of the dynamics along the continuum from a scale-specific and Markovian-compliant (mechanistic) kind of population kinetics to a non-mechanistic and parallel processing-compliant kind of process. By this approach the alternative framework not only connects individual and population dynamics in a coherent manner; it also presents a transition between apparently disparate system classes by connecting non-mechanistic dynamics to its mechanistic counterpart.

Interesting statistical properties of population dispersion emerge from the simulations of the Zoomer model, which brings up what may appear to be a potential solution to an old and still unsolved controversy in ecology: Taylor’s power law (Taylor 1961, 1986). This empirically derived law has over the years been subject to a large number of attempts to explain it, but a consensus has still not been obtained (Kendal and Jørgensen 2011). Taylor’s power law is one of the most widely tested empirical patterns in ecology and is the subject of an estimated thousand papers (Eisler *et al.* 2008)! It describes how variance ( $V$ ) of population abundance ( $M$ ) in a time series or over a spatial transect tends to comply empirically with  $V(M)=aM^b$ , with  $b \gg 1$  (often close to 2). However, one aspect of this law

has by and large been ignored: the V(M) pattern unexpectedly emerges also when abundance is measured at different spatial resolutions within a given extent (Taylor 1986). Larger spatial units (grain size) give larger M on average, and the scaling law with  $b \approx 2$  even in spatially non-auto-correlated data appears even more paradoxical in the context of this property. I call this the Z-paradox, and propose (with support from simulations) that a parallel-processing kind of population kinetics may contribute to solve it. Will it succeed under closer scrutiny and when confronted with real data? Time will show, but in a later chapter I provide a pilot test.

In Chapter 7, *Parallel processing at the individual level*, I show that individual-level statistics for V(M) when generated from the parallel processing-compliant MRW model is coherent with population-level statistics for the same aspect in output from the Zoomer model. The MRW model is also specified in more detail than in previous publications, with weight on clarifying some aspects that have led to common misinterpretations. Chapter 7 also summarizes various methods—called protocols—to test for compliance with MRW, using respective standard models in respective fields as null hypotheses. The methods now span many statistical aspects of space use, like the distribution of step lengths of a path that is sampled at regular intervals (the Lagrangian aspect), the extent of space use as a function of sample size of fixes (the Eulerian aspect, also containing home-range ghost paradox), the fractal dimension of fix dispersion, and so on. In all respects, MRW is now a testable hypothesis, and I summarize already published empirical support for the model.

Chapter 8, *Movement classes at the statistical-mechanical level*, focuses on one main topic: a conceptual model I call the scaling cube, which is presented here for the first time. In a statistical-mechanical frame of reference, I show how a three-dimensional system (the cube) may diversify between Markov-compliant types of movement (represented by the x- and y-dimension) and parallel processing-compliant space-use dynamics (the z-dimension). The x-axis regards degree of spatial memory utilization, the y-axis regards degree of compliance with scale-free movement in the time dimension, and the z-axis represents hierarchical scaling. The latter expresses the degree of parallel-processing compliance by linking past experiences to execution of future goals. In contrast, a Markovian-based memory model only implements past experience as a term in the model for current movement decision in a stepwise manner (the memory field vector, as explained above). It does not allow embedment



of parallel execution of future goals at different temporal resolutions. For example, an animal may decide to move towards a given target even if the direction deviates from a parallel goal to reach another target in a different direction within a wider time frame, and thus higher in the temporal hierarchy of parallel goals. Under the Markov premise only one goal may be executed at any point in time, but this goal may contain influence from past experiences. This goal is embedded in the resultant vector for the directional bias under Markovian memory execution; see above. Consequently, in the scaling cube spatial memory is represented by two qualitatively different processes: with and without hierarchical execution of goals. This aspect thus requires an independent axis, orthogonal on the Markov floor of degree of scaling and degree of memory implementation. A cube has eight corners tentatively representing eight universality classes of movement. In Chapter 8, various methods to distinguish individual space use under the respective eight movement classes that are embedded in the scaling cube are summarized.

Chapter 9, *Is parallel processing applicable to invertebrates?*, returns focus to the population level. In 1990, I sampled a local population of sycamore aphids, *Drepanosiphum platanoides*, at the campus of University of Oslo. The purpose was to test compliance with the parallel-processing concept, and how it might cast new light on Taylor's power law and scale-free (fractal-compliant) population kinetics. Owing to the challenge of the home-range ghost paradox that received the focus over the following years, the aphid material had to be put on the shelf for a later day. This day has hereby finally arrived twenty-five years later. Chapter 9 provides a synthesis of novel theoretical aspects—as outlined in the previous chapters—and what appear to be matching empirical patterns in the spatial dispersion of the aphid population. In particular, the analysis shows coherence between how the home-range ghost paradox was resolved at the individual level and how the Z-paradox gets its proposed solution at the population level. Thus, the Z-paradox may represent the population-level analogue to the individual-level home-range ghost! Both concepts turn up as respective levels' expressions of parallel processing, and the aphid data apparently support compliance with this memory-extended kind of statistical mechanics. This is obviously a speculative and controversial statement, since it implies a quite advanced memory capacity of these tiny insects with respect to spatial reorientation and non-random path crossing. I'm looking forward to learning whether others may find less contrarian (read: Markov-compliant and mechanistic) biophysical explanations for the results. With respect to the variance-mean relationship, the aphid population shows scaling compliance with Taylor's power law,

and the empirical pattern is thus encouragingly similar also to the simulated data from the Zoomer model.

In Chapter 10, *Intrinsic complexity: 1/f noise and the scaling paradox*, I turn towards yet another nagging issue of statistical mechanics, 1/f noise (also called flicker noise, fractal noise, and pink noise). An alternative way of demonstrating the increase of  $V$  over spatial or temporal scales in a series is to decompose population variability into cycles using techniques like Fast Fourier Transforms (FFT) and then study how the power (squared magnitude of amplitudes) of those cycles varies with their frequency. The frequency equals the inverse of cycle length, and the power spectrum is an expression for cycle-specific variance. A larger frequency means a smaller cycle length. Cycle length is proportional with the lag in the series, which is the time interval or space distance between successive measurements we use for calculating the power. In the spectra this analysis produces, the longer cycles typically have the greatest power (larger squared amplitude).

The theoretical issue in this respect regards systems which show power increasing inversely proportional with frequency;  $P \approx 1/f^\eta$  with  $\eta \approx 1$ . This statistical pattern is problematic when trying to explain the underlying process, since it apparently does not comply with classical Markovian-compliant statistical mechanics ( $\eta \approx 2$  for Brownian motion and  $\eta \approx 0$  for white noise; the latter satisfies increments of Brownian motion). On one hand I show in Chapter 10 how simulated space use from the population-level—the Zoomer model—seem to confirm a 1/f noise pattern. On the other hand I verify 1/f noise also empirically. Both the sycamore aphid population and a multi-year time series of leaf miners, *Leucoptera meyricki* (Bigger and Tapley), apparently comply with 1/f fluctuations. Again the parallel-processing extended kind of statistical mechanics allows for a potential solution of a paradox, in this case the issue of 1/f noise. Again I hope for the emergence of presentations and discussions of alternative model proposals that may show similar statistical coherence between simulation output and real data, both with respect to variability at a specific scale (a time series or a spatial transect) and with respect to variability over a range of scales.

In Chapter 10, I show how the Z-paradox in  $V(M)$  and the 1/f paradox are inter-related. Thus, apparently for the first time, Taylor's power law is studied in the context of 1/f noise. The coherence between inter-scale  $V(M)$  analysis and output from power spectrograms at the population level and a similarly coherent  $V(M)$  and power pattern at the individual level