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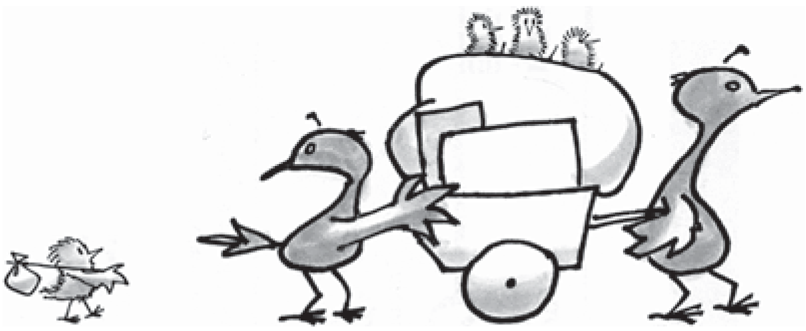
Andrés López-Sepulcre

The Evolutionary Ecology of Space Use and its Conservation Consequences



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To my grandfather Roque and to Bibiana,
who will never know how much they have taught me

To my sister Ana, my father Andrés
and to my mother 'que me parió'

ABSTRACT

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Yhteenveto: Elintilan käytön ja reviirikäyttäytymisen evoluutioekologia luonnonsuojelullisine seuraamuksineen
Diss.

Dispersal, habitat selection and territoriality are important determinants of the fitness of individuals and are therefore expected to be subject to natural selection. Since the fitness of individuals is no less than a measure of the demography of their offspring, these behaviours also have a key role in shaping the dynamics of populations. As population sizes change in time and space, they affect the selective pressures on different space-use strategies. Consequently, new individual strategies will evolve, and these will determine new population sizes. This dissertation is dedicated to the study of this feedback between demography and the evolution of space-use behaviours; and to its consequences for conservation. The incorporation of a dynamic link between demography and evolution in models of territorial behaviour helps understand the evolutionary stability of territorial systems as well as predict the modes of population regulation they will follow. One important theoretical result is that the outcome of natural selection on territorial behaviour does not maximize population performance. This has important conservation consequences. Indeed, territorial conflict has a significant negative impact in the recovery of an endangered bird species, the Seychelles Magpie Robin (*Copsychus sechellarum*). More interestingly, when territories differ in food availability, higher competition for the better territories strongly decreases their productivity. In homogeneous habitats, this effect is weaker and the population is more productive, suggesting new management approaches. Incorporating costs of dispersal to these same principles of individual-based evolutionary ecology have the potential to predict the spacing of individuals on a larger scale, and understand species reactions to global change.

Keywords: Behaviour-based models; conservation biology; dispersal; eco-evolutionary feedback; habitat selection; population regulation; Seychelles Magpie Robin; sociality; species recovery; territorial conflict

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on five original articles, which are referred to in the text by their Roman numerals. I have contributed significantly to planning, data collection, modeling and analyses, as well as writing of all articles.

I. Kokko, H., López-Sepulcre, A., & Morrell, L.J. 2006. From hawks and doves to self-consistent games of territorial behavior. *American Naturalist*, 167: 901-912.

II. López-Sepulcre, A. & Kokko, H. 2005. Territorial defense, territory size and population regulation. *American Naturalist*, 166: 317-329.

III. López-Sepulcre, A., Norris, K. & Kokko, H. Competition for territories delays the recovery of a critically endangered species (unpublished manuscript)

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V. Kokko, H. & López-Sepulcre, A. 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science*, 313: 789-791.

CONTENTS

1 INTRODUCTION: A HISTORICAL JUSTIFICATION

'The beauty of doing research on vulnerability is that it abolishes the distinction between pure and applied science, and is therefore more satisfying than is either alone"

Michael E. Soulé, Viable Populations for Conservation, 1987

1.1 Demography, evolution and conservation science

The origin of evolutionary theory (Darwin 1859; Wallace 1858) was strongly influenced by the advances in the science of demography brought by Thomas Malthus five decades before (Malthus 1798). The potential of populations to grow exponentially is confronted with the limited nature of resources, setting the scene for natural selection to favour those individuals who compete best, and their descendants. The relationship between demographic and evolutionary processes goes even deeper. As population densities vary, so do the selection pressures acting upon the traits involved in reproduction and survival; and as these traits evolve, they determine new densities. The modern evolutionary synthesis brought the first attempts to model the population consequences of evolution (Fisher 1930; Haldane 1932; Wright 1938) and by the time evolutionary ecology became a well-established science the idea of density-dependent selection had advanced substantially (Anderson and Arnold 1983; Asmussen 1983; Charlesworth 1971; Roughgarden 1971).

As our understanding of the origins of biological diversity increased, so did our concern to preserve it and, coincidentally, our ability to destroy it. By the 1970's, ecologists, biogeographers and evolutionary biologists started pooling their knowledge to the service of nature conservation. The science of conservation biology was born, and the first integrative treaty on the matter was soon published (Soulé and Wilcox 1980). Population geneticists brought evolutionary biology into the new science, expressing concerns about genetic variability, inbreeding depression and the ability of populations to adapt when they reach small numbers (Frankel 1974). Today, conservation genetics is a unique example of evolutionary principles being considered in the everyday management of endangered populations (e.g. Frankham et al. 2002). In contrast, considerations on the dynamical feedback between individual adaptations and demography described in the previous paragraph remain a pure academic exercise, rarely put in a conservation context. Recent refinements of the theoretical tools dealing with such feedbacks and their application to empirical systems have the potential to change this situation (Ferrière et al. 2004).

1. 2 From adaptive behaviour to population dynamics

The importance of a behaviour-based understanding of population processes has been long acknowledged. For example, Ricker's classical formulation of density-dependent population dynamics, resulted from considering intraspecific cannibalism (Ricker 1954), and can be equally derived from a range of behavioural mechanisms (e.g. Brännström and Sumpter 2005; Geritz and Kisdi 2004). Even earlier, Warden C. Allee described how the underperformance of social behavour at low population sizes would further decrease their growth (Allee 1931). However, these approaches, as well as most subsequent studies of the effects of dispersal, mating systems or strategies of resource competition on demography, lacked an evolutionary reasoning behind the occurrence of the considered behaviours. Behavioural ecology, the search for Niko Tinbergen's 'ultimate' or adaptive mechanisms driving animal behaviour (Tinbergen 1963), can provide such reasoning and increase the predictive power of population biology.

One of the important lessons drawn from viewing individual behaviour as an adaptation is that natural selection does not necessarily favour traits that maximize population performance. The reason is that selection results from changes in the relative fitness of individuals (or genomes) with respect to the others, rather than to the average or absolute population fitness (Williams 1966; Wright 1969). This reasoning gained predictive power with Willam Hamilton (1967) and John Maynard Smith's (1979; 1982) application of the economic models of game theory (Nash 1950; von Neumann and Morgenstern 1944) to behavioural ecology. In these models, individual behaviours evolve in response to the frequency of the different behavioural strategies in the population until an evolutionary stable strategy (ESS) is fixed that no other can outperform. Again, these models often predict selfish evolution (i.e. individual-level selection) to fix behaviours that are suboptimal in absolute terms. Already J. B. S. Haldane (1932) and, even earlier, Charles Darwin himself (1859; 1871) flirted with the idea that natural selection may favour traits that eventually turn out to be harmful to individuals and populations. Furthermore, when the density-dependent nature of evolution is incorporated into game-theoretical models of frequency-dependent selection, individual adaptation can even be predicted to drive populations extinct (Matsuda and Abrams 1994; Parvinen 2005; Rankin and López-Sepulcre 2005).

Although the disparity between individual and group performance has been at the heart of virtually every study of social evolution and animal conflict (Frank 1998; Hamilton 1964; Wilson 1975), it is largely disregarded by population ecologists. From a conservation angle the conceptual twist is that, as opposed to conservation genetics, social evolution raises concern over populations that are adapting, rather than failing to do so. But a behavioural approach to conservation can bring much more than such a concern. Behaviour-based models have been proposed as a robust tool to predict population responses to new environments (Norris 2004; Sutherland 1996; Sutherland 2006; Sutherland and Norris 2002). In essence, these are based on an understanding of two processes: how the environment determines the behavioural adaptations of individuals, and how that behaviour affects population demography. Examples of their application to empirical systems have considered behaviours ranging from territoriality (Liley and Sutherland in press; Ridley et al. 2004) and foraging (Caldow et al. 2004; West et al. 2003) to social behaviour (Ridley et al. 2003; Stephens et al. 2002). Despite being shown to outperform commonly used phenomenological models (Stephens *et al.* 2002), they are yet to be fully incorporated into the conservation routine. There lies the challenge.

1.3 Conservation theory or evolutionary practice?

Biodiversity is being degraded at alarming rates (Millennium Ecosystem Assessment 2005). Confronted with this emergency situation, some have argued that highbrowed academic science is little more than useless to conservation practice (Whitten et al. 2001), giving the image that ecologists, somehow, face a choice between being intellectually satisfied or proving useful. However, I couldn't agree more with Michael Soulé's opening quote. I particularly believe that the interface between behavioural ecology and population biology ranks, to the relief of the passionate biologist, among the neatest examples of a necessary integration between theoretically sound reasoning and applied conservation aspects. In this thesis, I have dedicated myself to the study of space use behaviour in animals, revisiting the evolutionary logic behind competition for space as well as evaluating its conservation implications. I have intended to order the chapters in a way that provides a natural flow from the highly theoretical evolutionary questions to the more empirically driven and applied ones. By the end, I hope to have blurred the distinction between the two ends of the continuum.

2 THESIS OUTLINE: CONFLICTS OVER SPACE USE

The feedback between individual behaviour and demography forms the conceptual backbone of this thesis. In particular, my co-authors and I have investigated the results of such feedback for the case of territorial and dispersal behaviours, both theoretically and empirically. The thesis starts with a reinterpretation of the origins and nature of territorial behaviour, by incorporating demography into game theoretical models (chapter I). Keeping these feedbacks in mind, we examine the consequences of optimal territorial behaviour to population regulation, contributing to a mechanistic understanding of the link between division of space among animals and population limitation (chapter II). The following two chapters bring these theoretical considerations down to earth and apply them to the case of an endangered bird species, the Seychelles Magpie Robin (III & IV). In these chapters, we estimate the negative consequences of territorial conflict from real data and derive management advice to minimize those effects. Finally, the thesis ends with some considerations on how the same principles of individual-based ecology can be applied to the spacing of individuals on a larger scale, providing a novel framework for the understanding of species reactions to global anthropogenic change (chapter V).

2.1 Why are animals territorial? (I)

Evolutionary game theory is perhaps the theoretical framework that has contributed most to the view of natural selection as an individual-level process and the realization that behaviour evolves in a ways that diverge from the common good. One of its very first applications in the field dealt with the evolution of animal contests with what came to be called the Hawk-Dove game (Maynard Smith and Price 1973). Despite the fitness payoffs being highest to all participants when resources are shared and contests avoided (i.e. individuals play 'Dove'), such a state is not stable, since any deviant that invests in fighting (i.e. plays 'Hawk') will easily gain the highest success. So animals fight.

But many animals also defend territories that are to a large extent respected by other individuals in the population. Why is territoriality stable? The classical game theoretical explanation is that there exists a third strategy, namely the 'Bourgeois' strategy or 'respect for ownership' (i.e. fight if you're the owner but retreat if not), which beats both 'Hawks' and 'Doves' (Maynard Smith and Parker 1976). But the argument is close to circular. For an asymmetry in behaviour between owners and intruders to hold, there must be an asymmetry in the payoff matrix, and this is not the case in the original formulation of the problem. Therefore, an equally successful strategy would be the inverse: intruders challenge and owners always retreat. Since this is clearly not what happens in nature, we need a better explanation.

While classical game theory models have the virtue of considering frequency-dependent selection, their weakness lies in their lack of density-dependence. Recently, theoretical ecologists have proposed the integration of both density and frequency-dependence into models of behaviour in what has been called 'self-consistent' game theory (Houston and McNamara 2006; Houston et al. 2005), 'ecogenetic' models (Eshel and Sansone 1995) or models with eco-evolutionary feedback (Le Galliard et al. 2005). In our re-analysis of owner-intruder conflicts over territories, the incorporation of demography creates a payoff asymmetry in favour of owners defending their territories aggressively and intruders respecting, at least partially, this ownership (chapter I; Kokko et al. 2006). In summary as amount of intruder aggression in the population increases and mortality rises accordingly, it becomes more advantageous to fight less and wait for breeding vacancies available when territory owners die. Incorporating differences in fighting ability among individuals expectedly strengthens this pattern. The model, however rarely predicts complete respect for ownership by non-territorial floaters: challenges still occur shortening the breeders' tenure. The following three chapters (II, III & IV) consider the consequences of such challenges.

2.2 Territoriality, conflict and the regulation of populations (II)

The acknowledgement of territoriality as a driver of population regulation has a long history that can be traced back as far as eighteenth century naturalist Gilbert White (1789). Over a century later, C. B. Moffat clearly exposed these ideas: as density increases, a higher proportion of individuals remain without territories. As these do not reproduce, the *per capita* productivity decreases (Moffat 1903). This idea was retaken and refined several times throughout the century (e.g. Brown 1969a; Brown 1969b; e.g. Howard 1920; Kluyver and Tinbergen 1953) and it still has a big influence on population biology (e.g. Hunt 1998; Kokko et al. 2004; Penteriani et al. 2005).

The problem with this model is that it considers territories as fixed pre-existing entities that are to be filled by individuals as their number increase (e.g. Kokko and Sutherland 1998). In most cases, however, territory sizes are flexible and respond to population feedback (Both and Visser 2000; Heg et al. 2000; Keeley 2000; e.g. Stamps and Krishnan 1995). As populations increase, so do the costs of defending bigger areas, since there will be more floaters to challenge territory owners. Chapter II (López-Sepulcre and Kokko 2005) incorporates these two components — the dynamic nature of territory boundaries and the feedback between defense strategies and demography via the negative effects of non-breeders on breeders — into a model of territoriality-driven population regulation. The novelty lies in the fact that population regulation is derived from first optimality principles of individual costs and benefits, rather than merely resulting from *a priori* assumed strategies. This way, the model can predict two modes of regulation by territoriality found in nature: (i) flexible territory sizes that decrease as populations grow, reducing equally all individuals' performance or (ii) fixed territory sizes that preclude some individuals from breeding as populations increase. Interestingly, these two modes of population regulation are comparable to Fretwell and Lucas' classical models of animal distributions: the ideal free and ideal despotic distributions, respectively (Fretwell and Lucas 1970).

One of the most important results of this exercise is that the outcome of interactions among adapting individuals does not maximize population performance. Furthermore, strong negative effects of non-breeding individuals on breeder fitness can further reduce the carrying capacity of the environment (López-Sepulcre and Kokko 2005).

2.3 From theory to practice and back: the case of the Seychelles Magpie Robin (III, IV)

So far, chapters I and II have developed a formal derivation of two important consequences of eco-evolutionary feedbacks in the context of territoriality. The first is that non breeding individuals are expected to respect the ownership of territories only partially, and are therefore expected to affect breeder performance by challenging their ownership (chapter I; Kokko et al. 2006). The second is that this negative effect of selfish competition for territories can decrease the carrying capacity of the environment (chapter II; López-Sepulcre and Kokko 2005). But how important are these processes in natural populations? Are they something that can become of concern for conservation biologists? And more importantly, if this is so, can something be done about it?

In order to answer these questions, in chapters III and IV we travel to the Seychelles islands, in the Western Indian ocean, to study the case of a rare bird that has been uniquely monitored for the past nearly two decades: the Seychelles Magpie Robin, *Copsychus sechellarum* (Newton 1865; Figure 1). Once widespread throughout the archipelago (Newton 1867; Vesey-Fitzgerald 1940), the species was driven down to just 12 individuals in 1965, all confined to the island of Fregate (Penny 1968). In 1989 a recovery program was designed and progressively implemented to boost population numbers (Norris and McCulloch 2003). The population now exists on four islands (Fregate, Cousin, Cousine and Aride) and, at the time of writing, has reached 178 individuals.

FIGURE 1 A Seychelles Magpie Robin *Copsychus sechellarum*, (left) and two of the studied islands, where the species occurs: Cousin (top right) and Cousine (bottom right). [photographs: Andrés López-Sepulcre]

Seychelles magpie robins live in social groups that defend territories and consist of a breeding dominant pair and a number of non breeding subordinates, from zero to eight, that compete for dominance positions with established breeders (Komdeur 1996; Watson et al. 1992). Since 1988, when 23 individuals remained, the entire world population has been individually marked and monitored. This data, consisting of a monthly record of every individual's location, social and breeding status, provides a unique opportunity to study the interplay between individual behaviour and demography.

Armed with this wealth of data and some solid theoretical reasoning, my co-authors and I found the following results. Chapter III shows that subordinate individuals compete aggressively for dominance positions and increase the probabilities of dominants having their positions taken over. These takeovers reduce territory productivity by delaying the production of two consecutive chicks. Moreover, an individual based simulation fully parameterized with field data shows that the effect of this competition for territories has an important effect on demography. The decrease in productivity brought about by territorial conflict is responsible for an estimated average delay in the upgrading of the species from "Critically Endangered" to "Endangered" by over 30% since the implementation of the recovery plan. The effect of individual conflict is indeed profound, even for a population that has been intensively and successfully managed.

Chapter IV digs further into the details of the competitive process until a way to reduce its negative effects is proposed. The key lies in the differences in quality among territories. The struggle for dominance is strongest for the best territories, and they are the ones who suffer most from the consequences of breeding delays caused by territorial conflict. Moreover, for an equal amount of resources, heterogeneity in their distribution decreases population productivity. Habitat quality heterogeneity is something that can indeed be managed for this species by, for example, careful planning of habitat restoration or supplementary feeding of the poorest habitats. Thus a potentially important management tool – mitigation of territorial conflict through habitat management – logically follows from the deepest theoretical considerations of social evolution.

The analysis of the Seychelles Magpie Robin data has taught us more than lessons from evolutionary ecology to conservation. Chapter IV is an example where monitoring data from conservation can, in return, bring new insights into theoretical questions. The results break the long established distinction between ideal free and ideal despotic distributions (Fretwell and Lucas 1970), by acknowledging the motivation of non-breeders (or breeders in poor territories) to compete for higher quality territories. Although the initial settling patterns of this territorial species follow a typically despotic order of settlement from higher to lower quality (Njoroge 2002), unequal competition for territories ends up diluting the differences in reproductive output between territories of different qualities in a fashion that recalls the ideal free distribution (Chapter IV). This contrasts with the classical result that territorial species occupying heterogeneous habitats are regulated by variation in the reproductive performance of individuals (Carrete et al. 2006a; Ferrer and Donázar 1996; Krüger and Lindström 2001; Rodenhouse et al. 1997; Sergio and Newton 2003). In species where strong conflict is expected the situation may look quite different. Indeed, in an initially site-dependent regulated population of bearded vultures, *Gypaetus barbatus*, artificial increases in territorial conflict brought by supplementary feeding have been found to reduce population performance in a way that resembles our results (Carrete et al. 2006b).

2.4 Dispersal and species responses to global change: the bigger picture (V)

I hope to have illustrated, using the case of territorial conflict, how a mechanistic understanding of behaviour can provide useful, and sometimes counterintuitive, insights into the management of populations. The scale of our studies was quite local and we could safely ignore the costs of individual movement. What happens if we consider wider scales? Dispersal can prove highly costly at the level of the individual, yet it also opens the possibility of colonizing empty habitat free of competition (Bowler and Benton 2005). The study of the evolutionary mechanisms and tradeoffs that underlie dispersal behaviour is thriving with exciting results and new insights brought together by the integration of molecular, behavioural, ecological and evolutionary approaches (chapter V; Kokko and López-Sepulcre 2006). In the meanwhile, biodiversity is in crisis. Humans are currently acting as enormous modifiers of the selective pressures behind dispersal, causing contractions and expansions in species ranges through habitat fragmentation, climate change and the transport of invasive species.

Our aim in this chapter is to encourage the study of species distributions, the very phenomenon to sparkle Darwin and Wallace's idea of evolution by natural selection, through an integration of its offspring sciences. If successful, such a research program would not only bring hopes for our ability to reduce species loss, but also provide an ultimate test of evolutionary reasoning itself.

3 CONCLUSION: A PERSONAL VIEW

This thesis integrates different aspects of behavioural ecology, evolutionary biology and population ecology into a common framework in order to understand the regulation of populations via individual strategies of competition for space. The lessons I have learned radiate in different directions.

On an evolutionary and behavioural side, considering eco-evolutionary feedbacks has clarified the origins and nature of territoriality, by providing an adaptive explanation for the partial respect for ownership frequently observed in nature (chapter I). On the ecological side, one of the main results is an improved mechanistic understanding behind observed patterns of population growth and limitation, gained by explicitly considering the feedback between demography and conflicts for territories (chapters II, III & IV). From these results we have derived lessons (e.g. conflict reduction through habitat management) for the conservation of the Seychelles magpie robin or other social and territorial species. The lessons have in turn fed back to the theory and refined it, by uncovering a continuum between ideal free and despotic distributions (chapter IV). All these results, to my eye, illustrate a fruitful dynamic interaction between evolution and ecology, and between theoretical and applied questions.

These lessons open new questions and directions of research. On the theoretical side, for example, chapter IV calls for a formalization of the ideal free-despotic continuum into a unifying model of ideal distributions. With respect to the empirical work, I am curious to see the unfolding of conflict as Seychelles magpie robin densities continue to increase. If detrimental conflict for the best territories has lead to a situation where all territories have equated their realized value in an ideal free manner, should we expect no further asymmetries in conflict at higher densities? How relevant would then habitat heterogeneity become to population regulation at more advanced stages? Ultimately, such mechanistic understanding should be put to test by constructing case-specific models of individual-based demography, deriving predictions and testing them, for example, with new population reintroductions (Sarrazin and Barbault 1996).

The Seychelles magpie robin case study demonstrates the value of individual-based monitoring for population ecology and conservation biology. This is of particular importance when populations are small and an individual-level understanding of the population patterns brings mechanistic reasoning and robustness to inevitably weak statistical results due to low sample sizes at the population level. This is particularly feasible for small populations confined to islands, like our study system.

Biodiversity is suffering a decline of a magnitude unprecedented in human history (Millennium Ecosystem Assessment 2005). With its loss, humanity is losing invaluable ecosystem services (Carpenter and Folke 2006; Myers 1996) and biologists, the very source of their science. Some have proposed it is our moral obligation to put aside so-called pure science and spend our time being useful to applied conservation (Whitten et al. 2001). Does such radical dichotomy actually exist? Scientists have always realized that not only there is no such tradeoff between pure and applied science, but that their mutual cooperation is essential. The science of biodiversity should be no exception (Ferrière et al. 2004; Norris 2004; Sutherland et al. 2004).

Examples of evolutionary theory being directly applied to conservation are still rare (but see Clout et al. 2002). I hope that the case study I present with my thesis contributes in some measure to narrow the distance between theoretical evolutionary biology and applied conservation. After all, if evolutionary reasoning has helped us understand the fascinating diversity of nature, it seems only logical that it should help us preserve it, too.

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When I look back at these four years of work, and think of all the people that have made this thesis possible, I feel humbled and almost ashamed that only my name appears in the cover. But most of all, I feel privileged to have fully experienced the most beautiful side of science: cooperation. It has not only brought me better work, but also wonderful friends. The last four years have no doubt been the most beautiful, challenging and intense of my life, both professionally and personally. It is impossible to make justice and express, in such limited space, all my gratitude to all those who have made them so. But here goes my attempt.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Elintilan käytön ja reviirikäyttäytymisen evoluutioekologia luonnonsuojelullisine seuraamuksineen

Yksilöt, populaatiot ja ekosysteemit ovat muokkautuneet nykyasuunsa evoluutioprosessin tuloksina. Evoluutio ei kuitenkaan toimi tyhjiössä, vaan lajin ekologia ja ympäristötekijät ohjaavat evoluution suuntaa ja muokkaavat näin yksilöiden sopeumia. Ekologian ja evoluutioteorian välisen yhteyden voidaankin väittää olevan niin perustavanlaatuinen, että vain yhteen näistä kahdesta sisartieteestä keskittyvä tutkimus ei voi antaa tutkimuskohteesta täydellistä kuvaa. Väite on erityisen keskeinen tutkittaessa populaatioiden dynamiikkaa. Yksilöiden kelpoisuus (*fitness*) on suure, jonka määrää jälkeläistuotannon demografia. Tämän vuoksi populaatiodynamiikka, ekologian alan demografinen termi, riippuu suoraan populaation yksilöiden kelpoisuudesta, joka puolestaan on evoluutiobiologinen käsite. Yksilön kelpoisuuteen taasen usein vaikuttaa lajikumppaneiden populaatiotiheys. Tyypillisesti tietyt yksilöt kärsivät lisääntyneestä tiheydestä toisia herkemmin, mikä avaa ovet luonnonvalinnan toimintamahdollisuuksille. Tätä ekologisen demografian ja evoluutiobiologian molemminpuolista riippuvuutta kuvaa käsite ”ekologis-evolutiivinen vuorovaikutussilmukka”. Silmukassa yksilöiden geneettisesti ohjatut käyttäytymis- tai elinkiertopiirteet heijastuvat populaation dynamiikkaan (vaikuttaen esimerkiksi tasapainotilan tiheyteen tai dynamiikan vakauteen). Populaation dynamiikan muuttuminen puolestaan suosii tiettyjä genotyyppejä toisten kustannuksella tai vaihtoehtoisesti suosii tietyntyyppistä ilmiasun joustavuutta (plastisuutta).

Tässä väitöskirjassa tutkitaan esimerkkejä ekologis-evolutiivisista vuorovaikutussilmukoista yksilöiden ominaisuuksien ja populaatiotason ilmiöiden välillä. Reviiri- sekä dispersaalikäyttäytyminen muodostavat väitöskirjan keskeisimmät tutkimuskohteet. Näiden kahden ominaisuuden tutkimuksella on yleisempääkin merkitystä evoluutiobiologiassa ja ekologiassa valottaessaan vaikutussilmukan käsitettä sekä tutkimusmetodeja.

Ensimmäinen osatyö osoittaa, että kun demografiset prosessit otetaan huomioon evolutiivisessa peliteoriassa, reviirikäyttäytymisen alkuperä joudutaan tulkitsemaan uudelleen. Koska demografiset prosessit kohtelevat reviirien omistajia ja reviireille tunkeutujia eri tavoin, populaatioissa voi kehittyä sääntö, jonka mukaan omistusoikeutta kunnioitetaan, vaikka omistajat eivät olisikaan muita vahvempia yksilöitä.

Vuorovaikutussilmukka osoittautuu tärkeäksi myös toisessa osatyössä, jossa tutkitaan optimaalisen reviiripuolustuksen yhteyttä populaatioiden säätelyyn. Tämä malli valottaa eläinten elintilan käytön ja populaatioiden säätelyn mekaanista yhteyttä. Yksinkertaisilla ja klassisilla ekologisilla oletuksilla saadaan aikaan kaksi hyvin erityyppistä säätelymekanismia, joista kumpaakin havaitaan luonnossa: populaatioiden kasvua rajoittaa joko reviirien pinta-alan pieneneminen tai vaihtoehtoisesti pesimättömien yksilöiden lukumäärän kasvu.

Kahden ensimmäisen osatyön perusteella voidaan päätellä, että luonnonvalinta voi suosia populaatiotasolle haitallisia käyttäytymismalleja. Kahdessa seuraavassa osatyössä tätä teoreettista ennustetta sovelletaan todelliseen luonnonsuojelulliseen ongelmaan, uhanalaisen seychellienharakkarastaan (*Copsychus sechellarum*) populaatiobiologiaan. Näissä osatöissä käytetään luonnonpopulaatioista saatua aineistoa määrittämään reviirikiistelyn aiheuttamia populaatiotason haittoja. Aineistosta johdetaan myös ohjeita populaatioiden tehokkaampaa suojelua varten. Reviirikiistoilla todetaan olevan merkittävä harakkarastaspopulaatioiden kasvua hidastava vaikutus. Tätäkin tärkeämmäksi havainnoksi osoittautuu, että reviirien tarjotessa toisistaan poikkeavan määrän ravintoa, parhaille reviireille kohdistuu niin paljon kiistoja, että niiden jälkeläistuotanto putoaa huonoimpien reviirien tasolle. Tämä kiistojen vaikutus heikkenee tasalaatuisemmissa ympäristöissä, mikä puolestaan antaa mahdollisuuden lievittää kiistojen negatiivisia vaikutuksia harakkarastaspopulaatioissa tasaamalla paikallisia eroja ravinnon saatavuudessa.

Viimeisessä osatyössä laajennetaan perspektiiviä, ja luodaan katsaus yksilöihin kohdistuviin valintapaineisiin ennustettaessa yksilöiden paikallisuutta ja muuttoliikkeitä. Tässä katsauksessa luotujen puitteiden avulla voidaan pyrkiä ennustamaan ihmisen aiheuttamien ympäristömuutosten vaikutuksia lajien levinneisyyteen.

Väitöskirjan teoreettisten sekä empiiristen osatöiden muodostama kokonaisuus osoittaa, että ekologis-demografisten ja evolutiivisten prosessien välisellä vuorovaikutussilmukalla on muutakin kuin teoreettista mielenkiintoa: sillä voi olla tärkeä sanoma myös luonnonsuojelubiologiassa.

REFERENCES

Allee, W. C. 1931, Animal aggregations. A study in general sociology, University of Chicago Press.

Anderson, W. W., and J. Arnold. 1983. Density-regulated selection with genotypic interactions. American Naturalist 121:649-655.

Asmussen, M. A. 1983. Density-dependent selection incorporating intraspecific competition. II. A diploid model. Genetics 103:335-350.

Both, C., and M. E. Visser. 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. Journal of Animal Ecology 69:1021-1030.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205-225.

Brännström, A., and D. J. T. Sumpter. 2005. The role of competition and clustering in population dynamics. Proceedings of the Royal Society B: Biological Sciences 272:2065-2072.

Brown, J. L. 1969a. Buffer effect and productivity in tit populations. American Naturalist 103:347-354.

Brown, J. L. 1969b. Territorial behavior and population regulation in birds: a review and re-evaluation. Wilson Bulletin 81:293-329.

Caldow, R. W. G., H. A. Beadman, S. McGrorty, R. A. Stillman, J. D. Goss-Custard, S. E. A. L. V. d. Durell, A. D. West et al. 2004. A behavior-based modelling approach to reducing shorebird-shellfish conflicts. Ecological Applications 14:1411-1427.

Carpenter, S. R., and C. Folke. 2006. Ecology for transformation. Trends in Ecology & Evolution 21:309.

Carrete, M., J. A. Sánchez-Zapata, J. L. Tella, J. M. Gil-Sánchez, and M. Moleón. 2006a. Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. Oikos 112:680-690.

Carrete, M., J. A. Donázar, and A. Margalida. 2006b. Density-dependent productivity depression in Pyrenean bearded vultures: implications for conservation plans. Ecological Applications 16:1674-1682.

Charlesworth, B. 1971. Selection in density dependent populations. Ecology 52:469-474.

Clout, M. N., G. P. Elliott, and B. C. Robertson. 2002. Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. Biological Conservation 107:13-18.

Darwin, C. 1859, On the origin of species by means of natural selection. London, J. Murray.

Darwin, C. 1871, The descent of man, and selection in relation to sex. London, J. Murray.

Eshel, I., and E. Sansone. 1995. Owner-intruder conflict, Grafen effect and self-assessment: the Bourgeois principle re-examined. Journal of Theoretical Biology 177:341-356.

Ferrer, M., and J. A. Donázar. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. Ecology 77:69-74.

Ferrière, R., U. Dieckmann, and D. Couvet. 2004. Evolutionary conservation biology, Cambridge University Press.

Fisher, R. A. 1930, The genetical theory of natural selection, Oxford University Press.

Frank, S. A. 1998, Foundations of social evolution: Monographs in Behavior and Ecology, Princeton University Press.

Frankel, O. H. 1974. Genetic conservation; our evolutionary responsibility. Genetics 78:53-65.

Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002, Introduction to conservation genetics, Cambridge University Press.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Geritz, S. A. H., and E. Kisdi. 2004. On the mechanistic underpinning of discrete-time population models with complex dynamics. Journal of Theoretical Biology 228:261-269.

Haldane, J. B. S. 1932, The causes of evolution. London, Harper and Brothers.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. Journal of Theoretical Biology 7:1-52.

Hamilton, W. D. 1967. Extraordinary sex ratios. Science 156:477-488.

Heg, D., B. J. Ens, H. P. Van der Jeugd, and L. W. Bruinzeel. 2000. Local dominance and territorial settlement of nonbreeding oystercatchers. Behaviour 137:473-530.

Houston, A., and J. McNamara. 2006. John Maynard Smith and the importance of consistency in evolutionary game theory. Biology and Philosophy 20:933.

Houston, A. I., T. Szekely, and J. M. McNamara. 2005. Conflict between parents over care. Trends in Ecology & Evolution 20:33-38.

Howard, H. E. 1920, Territory in bird life. New York, Dutton & Co.

Hunt, W. G. 1998. Raptor floaters at Moffat's equilibrium. Oikos 82:191-197.

Keeley, E. R. 2000. An experimental analysis of territory size in juvenile steelhead trout. Animal Behaviour 59:477-490.

Kluyver, H. N., and L. Tinbergen. 1953. Territory and the regulation of density in titmice. Archives Neerlandaises de Zooologie 10:265-289.

Kokko, H., M. P. Harris, and S. Wanless. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. Journal of Animal Ecology 73:367-376.

Kokko, H., and A. López-Sepulcre. 2006. From individual dispersal to species ranges: perspectives for a changing world. Science 313:789-791.

Kokko, H., A. López-Sepulcre, and L. J. Morrell. 2006. From hawks and doves to self-consistent games of territorial behavior. American Naturalist 167:901-912.

Kokko, H., and W. J. Sutherland. 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. American Naturalist 152:354-366.

Komdeur, J. 1996. Breeding of the Seychelles magpie robin *Copsychus sechellarum* and implications for its conservation. Ibis 138:485-498.

Krüger, O., and J. Lindström. 2001. Habitat heterogeneity affects population growth in goshawk *Accipiter gentilis*. Journal of Animal Ecology 70:173-181.

Le Galliard, J. F., R. Ferriere, and U. Dieckmann. 2005. Adaptive evolution of social traits: origin, trajectories, and correlations of altruism and mobility. American Naturalist 165:206-224.

Liley, D., and W. J. Sutherland. in press. Predicting the population consequences of human disturbance for ringed plover *Charadrius hiaticula* population size: a game theory aproach. Ibis.

López-Sepulcre, A., and H. Kokko. 2005. Territorial defense, territory size and population regulation. American Naturalist 166:317-329.

Malthus, T. R. 1798, An essay on the principle of population. London, UK, J. Johnson.

Matsuda, H., and P. A. Abrams. 1994. Runaway evolution to self-extinction under asymmetrical competition. Evolution 48:1764-1772.

Maynard Smith, J. 1979. Game theory and the evolution of behaviour. Proceedings of the Royal Society of London Series B 205:475-488.

Maynard Smith, J. 1982, Evolution and the theory of games, Cambridge University Press.

Maynard Smith, J., and G. A. Parker. 1976. The logic of asymmetric contests. Animal Behaviour 24:159-175.

Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. Nature 246:15-18.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: Biodiversity synthesis. Washington DC, World Resources Institute.

Moffat, C. B. 1903. The spring rivalry of birds: some views on the limit to multiplication. Irish Naturalist 12:152-166.

Myers, N. 1996. Environmental services of biodiversity. PNAS 93:2764-2769.

Nash, J. F. 1950. Equilibrium points in n-person games. Proceedings of the National Academy of Sciences of the USA 36:48-49.

Newton, A. 1865. On an apparently undescribed bird from the Seychelles islands. Ibis 2:337.

Newton, E. 1867. On the land birds of the Seychelles archipelago. Ibis 3:335-360.

Njoroge, P. 2002. The Seychelles magpie robin *Copsychus sechellarum*: territory quality, demography and conservation of a threatened species. PhD. Thesis thesis, University of Reading.

Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. Journal of Applied Ecology 41:413-426.

Norris, K., and N. McCulloch. 2003. Demographic models and the management of endangered species: a case study of the critically endangered Seychelles magpie robin. Journal of Applied Ecology 40:890-899.

Parvinen, K. 2005. Evolutionary suicide. Acta Biotheoretica 53:241.

Penny, M. 1968. Endemic birds of the Seychelles. Oryx 9:267-175.

Penteriani, V., F. Otalora, and M. Ferrer. 2005. Floater survival affects population persistence. The role of prey availability and environmental stochasticity. Oikos 108:523-534.

Rankin, D. J., and A. López-Sepulcre. 2005. Can adaptation lead to extinction? Oikos 111:616-619.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada 11:559-623.

Ridley, J., J. Komdeur, and W. J. Sutherland. 2003. Population regulation in group-living birds: predictive models of the Seychelles warbler. Journal of Animal Ecology 72:588-598.

Ridley, J., J. Komdeur, and W. J. Sutherland. 2004. Incorporating territory compression into population models. Oikos 105:101-108.

Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. Ecology 78:2025-2042.

Roughgarden, J. 1971. Density-dependent natural selection. Ecology 52:453-468.

Sarrazin, F., and R. Barbault. 1996. Reintroductions: challenges and lessons for basic ecology. Trends in Ecology & Evolution 11:474-478.

Sergio, F., and I. Newton. 2003. Occupancy as a measure of territory quality. Journal of Animal Ecology 72:857-865.

Soulé, M. E., and B. A. Wilcox. 1980. Conservation biology: an evolutionary-ecological perspective. Sunderland, Massachusetts, Sinauer Associates.

Stamps, J. A., and V. V. Krishnan. 1995. Territory acquisition in lizards. III. Competing for space. Animal Behaviour 49:679-693.

Stephens, P. A., F. Frey-Roos, W. Arnold, and W. J. Sutherland. 2002. Model complexity and population predictions. The alpine marmot as a case study. Journal of Animal Ecology 71:343-361.

Sutherland, W. J. 1996, From individual behaviour to population ecology, Oxford University Press.

Sutherland, W. J. 2006. Predicting the ecological consequences of environmental change: a review of the methods. Journal of Applied Ecology 43:599-616.

Sutherland, W. J., and K. Norris. 2002. Behavioural models of population growth rates: implications for conservation and prediction. Philosophical Transactions of the Royal Society of London Series B 357:1273-1284.

Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. Trends in Ecology & Evolution 19:305-308.

Tinbergen, N. 1963. On the aims and methods of ethology. Zeitschrift für Tierpsychologie 20:410-433.

Vesey-Fitzgerald, D. 1940. The birds of the Seychelles. 1. The endemic birds. Ibis 14:482-489.

von Neumann, J., and O. Morgenstern. 1944, Theory of games and economic behavior, Princeton University Press.

Wallace, A. R. 1858. On the tendency of varieties to depart indefinitely from the original type. Journal of the Proceedings of the Linnean Society (Zoology) 3:53-62.

Watson, J., C. Warman, D. Todd, and V. Laboudallon. 1992. The Seychelles magpie robin *Copsychus sechellarum*: ecology and conservation of an endangered species. Biological Conservation 61:93-106.

West, A. D., J. D. Goss-Custard, S. McGrorty, R. A. Stillman, S. Durell, B. Stewart, P. Walker et al. 2003. The Burry shellfishery and oystercatchers: using a behaviour-based model to advise on shellfishery management policy. Marine Ecology-Progress Series 248:279-292.

White, G. 1789, The natural history of Selborne. London, Benjamin White.

Whitten, T., D. Holmes, and K. MacKinnon. 2001. Conservation biology: a displacement behavior for academia? Conservation Biology 15:1-3.

Williams, G. C. 1966, Adaptation and natural selection, Princeton University Press.

Wilson, E. O. 1975, Sociobiology: the new synthesis. Cambridge, Massachussetts, Harvard University Press.

Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science 97:430-431.

Wright, S. 1969, Evolution and the genetics of populations. Vol 2. The theory of gene frequencies., University of Chicago Press.